EXPLORING GXEXM SYNERGIES IN WORLD-WIDE WHEAT PRODUCTION AND THE OPPORTUNITIES FOR INTERNATIONAL COLLABORATION

EDITED BY: Brian L. Beres, Jerry Lee Hatfield, Henning Kage and James Robert Hunt

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EXPLORING GXEXM SYNERGIES IN WORLD-WIDE WHEAT PRODUCTION AND THE OPPORTUNITIES FOR INTERNATIONAL COLLABORATION

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Toward a Better Understanding of Genotype × Environment × Management Interactions—A Global Wheat Initiative Agronomic Research Strategy

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The Wheat Initiative (WI) and the WI Expert Working Group (EWG) for Agronomy (www.wheatinitiative.org) were formed with a collective goal to "coordinate global wheat research efforts to increase wheat production, quality, and sustainability to advance food security and safety under changing climate conditions." The Agronomy EWG is responsive to the WI's research need, "A knowledge exchange strategy to ensure uptake of innovations on farm and to update scientists on changing field realities." The Agronomy EWG aims to consolidate global expertise for agronomy with a focus on wheat production systems. The overarching approach is to develop and adopt a systems-agronomy framework relevant to any wheat production system. It first establishes the scale of current yield gaps, identifies defensible benchmarks, and takes a holistic approach to understand and overcome exploitable yield gaps to complement genetic increases in potential yield. New opportunities to increase productivity will be sought by exploiting future Genotype × Environment × Management synergies in different wheat systems. To identify research gaps and opportunities for collaboration among different wheat producing regions, the EWG compiled a comprehensive database of currently funded wheat agronomy research (n = 782) in

countries representing a large proportion of the wheat grown in the world. The yield gap analysis and research database positions the EWG to influence priorities for wheat agronomy research in member countries that would facilitate collaborations, minimize duplication, and maximize the global impact on wheat production systems. This paper outlines a vision for a global WI agronomic research strategy and discusses activities to date. The focus of the WI-EWG is to transform the agronomic research approach in wheat cropping systems, which will be applicable to other crop species.

Keywords: wheat, Wheat Initiative, agronomy, Expert Working Group, Genotype × Environment × Management

INTRODUCTION

Genetic improvements in yield continue in the world's staple crops (Li et al., 2018), but to realize the potential of these improvements in farmer's fields to meet global demands will require improved agronomic practices (Fischer and Connor, 2018). The yield gap between potential and farm yields for major crops is substantial. For example, farm yields in rice, wheat, and maize are just 80% of potential yields under irrigated conditions, and 50% or less under rainfed conditions (Lobell et al., 2009). Potential yield is defined here as the yield of the best adapted cultivar with current best practice agronomic management ensuring the absence of manageable abiotic and biotic stresses (Fischer, 2015). Potential yields are constrained in many climates by water limitations, but additional constraints are within the capacity of farmers to mitigate. Economic yield is the yield attained by farmers given the prevailing weather, but inputs and practices are applied at the economic optimum (maximizing margin), which may not necessarily coincide with the levels that produce a maximum yield. This remains at approximately 75–85% of potential yield or water limited potential yield (Zhang et al., 2019). The difference between economic yield and farm yield is the exploitable yield gap. Recent research also suggests that the yield gap for the crop sequence is even larger than for individual crops due to inefficiencies in the system as a whole (Hochman et al., 2014). Comprehensive efforts to improve food security must couple genetic increases in potential yield with agronomic approaches to reduce exploitable yield gaps in all major cropping systems. Global intervention to improve agronomy can also increase the resilience of agriculture and agriculture-based livelihoods by increasing and stabilizing the returns to producers and ensuring the capacity of these systems to provide ecosystem services (Food and Agriculture Organization of the United Nations, 2016). Agronomic approaches to achieve these ends can fall under the concept of Agroecology: *The discipline that provides the basic ecological principles for how to study, design, and manage agroecosystems that are both productive and natural resource conserving, and that are culturally sensitive, socially just, and economically viable* (Altieri and Nicholls, 1995).

Wheat is second to rice as a source of calories in developing countries and first as a source of protein (Braun et al., 2010). It is grown on more land area than any other crop. Wheat currently provides 20% of the daily protein and of food calories for 4.5 billion people (Shewry and Hey, 2015). Although estimates of the demand for food by 2050 vary (Hunter et al., 2017), the challenge to increase production by 30–50% is still a major endeavor requiring a global response. Many studies indicate that a warming climate has a general negative effect on yield of staple crops like wheat (Porter et al., 2014). Under projected temperature increases of 2°C above late 20th century levels for the period 2030–2049, models predict wheat yield reductions up to 25% in many areas without modifications of existing cropping practices. However, in some regions, increases in average yield are anticipated due to extended growing seasons and elevated CO_2. Global temperature increases of approximately 4°C or more would lead to further declines in wheat yield, which when combined with projections of increasing food demand, poses a large risk to regional and global food security.

Wheat production is challenged not only by changes in climate and the extreme growing conditions that could accompany predictions for climate change, but also by changing disease and insect pressures (Figueroa et al., 2018) and management (Zhang et al., 2019). Wheat breeding programs, both public and private, have and will continue to develop new varieties with higher yield potential in the current production conditions and improved resistance to current economic disease and pest problems. While breeding resistance to pest and disease problems is generally thought of as the most cost effective and sustainable approach to combat economic losses, shifts in climate and the resulting changes to weather patterns, cropping system responses, and pest and pathogen populations indicate that breeding targets and goals are likely to shift faster and more frequently than ever before. An integrated deployment of genetics and management options becomes essential in situations where breeders cannot provide genetic solutions in a timely manner or where the frequency of pest and disease outbreaks are too infrequent and variable to allow breeders to incorporate genetic resistance effectively. Furthermore, breeders and government agencies that conduct variety performance evaluations in many of the world's wheat growing regions test new wheat varieties under relatively constant and often conservative management regimes. The rationale for this approach is quite simple; application of management inputs masks differences in responses to biotic and abiotic stressors among varieties. This means that wheat variety performance evaluations in many regions do not actually measure the attainable yield, but rather the actual yield. This approach potentially biases results in favor of more disease or pest resistant varieties rather than those

with the highest genetic yield potential. While logical and defendable, it is a poor reflection of the genetic potential of individual varieties when a cost-effective management input, such a single application of a fungicide, can drastically change the performance and thus ranking of the variety. In many regions, this means that agronomists or producers themselves are left to develop management practices *ad hoc* to exploit the available genotype × management interactions.

Many of the challenges of increasing climate variability, increasing world population, and its resultant impact on food demand and global food security can be addressed by improvements in wheat genetics and agronomy; however, this requires a globally concerted R&D effort. The problem is that these efforts are often fragmented across the globe, conducted in silos, and often lack cross-disciplinary approaches. The recognition of these challenges and issues gave rise to the Wheat Initiative (WI) in 2010[1]. The WI presently has 17 countries as members, two international research centers (International Wheat and Maize Center and International Center for Agricultural Research in Dry Areas), and a number of private sector corporations largely interested in the genetic improvement of wheat (Wheat Initiative, 2020b). There are four themes for research priorities in the WI's Strategic Research Agenda and two cross-cutting themes that relate to enabling technologies and knowledge sharing and education. Themes 1 and 2 encompass aspects of breeding new wheat cultivars that have increased yield and increased resistance to biotic and abiotic stressors. Theme 3 addresses *protecting the environment and improving the sustainability of wheat production systems.* Theme 4 relates mainly to ensuring the quality and safety of wheat.

Ten Expert Working Groups (EWGs) were established within the WI focused on technical issues, predominantly genetic improvement and crop protection, but also including wheat germplasm conservation, phenotyping, nitrogen use efficiency, and wheat quality (Wheat Initiative, 2020a). In 2016, the WI established a new EWG in Agronomy[2], recognizing that crop management is an essential complement to genetic improvement in order to achieve the potential economic yields of new and improved wheat cultivars in farmer's fields. The Agronomy EWG contributes primarily to Theme 3, but also ensures that varieties developed under Themes 1 and 2 approach their potential yield in the hands of farmers. The EWG views itself as a discovery group linking research priorities and research inventories from each country to help improve the efficiency of the global agronomic research efforts in wheat, and to establish synergies among the various agronomy networks around the world. In this policy paper, we describe the vision, aims, and ongoing efforts of the Agronomy EWG within the WI since its establishment in 2016. The EWG acknowledges that certain challenges require an international approach to make significant progress via new collaborative partnerships, more efficient use of research funds, and effective networks to share and communicate new knowledge to farmers who grow wheat in both developed and developing countries. The WI welcomes new members and the EWGs are open for interested parties to join.

[1]www.wheatinitiative.org

[2]https://www.wheatinitiative.org/wheat-agronomy

VISION FOR AN AGRONOMIC RESEARCH STRATEGY WITHIN THE WI

The Agronomy EWG will be guided by the principles inherent to sustainable intensification (SI) as called for by the FAO (Hunter et al., 2017) to meet projected increases in demand for food with projected increases in global population. The definition of SI varies, but the Agronomy EWG defines SI as increased agricultural production without adverse environmental impact and without the conversion of additional non-agricultural lands (Hunter et al., 2017). This necessitates increasing farm yields on existing crops lands. While breeders develop new wheat varieties with higher potential yield and resistance to abiotic and biotic stresses, agronomists must design and help implement cropping systems that allow the potential to be realized. These wheat cropping systems must also maintain or improve soil, water, and air quality, and ensure profitability and economic security for farmers. Crucially, those countries that import large quantities of wheat but with potential to increase their domestic wheat production (e.g., countries in Africa, Middle East, and SE Asia) will require agronomists working closely with farmers to develop strategies to adapt new technologies to local conditions more effectively than in the past. By 2030, the Agronomy EWG seeks to promote a framework to improve the effectiveness of global agronomic efforts in wheat-based systems to enhance farm profitability, increase environmental resilience, and ensure an adequate supply of food and feed for the value-added and processing industries.

To accomplish this vision, the focus will be on four priorities with specific actions and outcomes:

Priority 1—Development of Sustainable Wheat Cropping Systems

Wheat production occurs within a range of different systems worldwide that span the intensive irrigated rice-wheat systems of the Indo-Gangetic Plain, subsidized high input and high yielding systems of northern Europe and China, to the semi-arid broad-acre systems of Australia and North America. Despite the differences in specific details of these systems, most share common challenges including lack of crop diversity, rundown in soil fertility, decreasing terms of trade for growers, increasing risk from climate change, increasing public scrutiny over environmental concerns of soil degradation, N leaching, and chemical usage. Significant research into farming systems innovations such as better integration of legumes and oilseeds, no-till and controlled traffic systems, dual-purpose cropping systems, opportunity cropping to replace summer fallow, and integrated pest, disease and weed management strategies are in progress in many regions of the world. This multi-year systems research provides the broader agronomic framework into which novel wheat genotypes and agronomy must be integrated, and also provide the only way in which to monitor the longer term ecosystem impacts of wheat farming systems such as soil

degradation, off-site impacts, and greenhouse gas emissions to inform investigations. As specific new technologies emerge in wheat agronomy (e.g., new autonomous digitally enabled machinery, novel soil microbial amendments, or fertilizer formulations), it will be important to understand how this technology interacts with different systems of production and various growing environments to ensure most effective impact on wheat production systems. The impact of new practices and innovations will be, in part, measured by influences on yield gaps wherever adopted. Yield gaps vary widely depending on country, weather conditions, and soil types; and closing the exploitable gap would add significantly to world wheat production without expansion of current agricultural land. To be useful as a learning and measurement tool, yield gap data need to be developed using a standardized approach that is replicable in different growing regions and accounts for the biophysical limits for production as imposed by weather conditions. Yield gap analysis based on using FAO yield data for wheat collected over time allows the rate of progress in wheat yield to be measured in different countries (Hatfield and Beres, 2019). The ability to calculate yield gaps at a resolution close to the farm level may be possible through the Global Yield Gap Atlas (GYGA) project[3], which provides a worldview and country differences of actual yields of wheat relative to potential yield and adjusted for weather. The GYGA project also estimates yield gaps at small zones with similar soils and weather, which has utility not only at the local or farm level, but can be upscaled to regional and country levels to contribute to the development of policies and prioritization of research and development funds; and finally to help develop principles for regional cropping system maximizing wheat productivity.

It is recognized that wheat varieties are developed to be adapted to specific growing regions, but wheat production system development is likely to share commonality across growing regions. Partnership in these situations, resulting in large internationally coordinated projects, is a powerful tool to understand the impact and best use of these technologies. The challenge is to have enough understanding of the diverse elements that impact wheat production in order that the best combination of sustainable practices can be employed profitably, so that farmers have the incentive to continue to innovate. The EWG would initially select one or more of the following actions as a pilot to build international partnerships. Workshops held in conjunction with other agronomy scientific conferences would be the primary method to gain active participation and encourage more members from areas currently underrepresented (e.g., Asia, Africa, South America) to join the EWG. Some of the potential collaborative areas are large disciplines that would require further discussion to identify projects with international significance.

Actions

- Perform a meta-analysis of research on global wheat production systems.
- Establish wheat yield gaps for all important wheat-producing regions and understand the socio-economic factors that influence yield gap closure.
- Develop diverse wheat cropping systems for improved water and nutrient use efficiency to stabilize and enhance crop production through appropriate choice of crops and agronomic practices in different agro-ecological regions.
- Develop sustainable pest (insects, diseases, weeds) management systems that maintain or build biodiversity.
- Develop cropping systems that reduce greenhouse gases through increased sequestration of CO_2 and reduced NO emissions.

Anticipated Outcomes

- Greater use of legumes (pulses, forages, and cover crops) in wheat crop sequences to reduce reliance on synthetic fertilizers and biocides.
- Increased water and nutrient use efficiency of wheat cropping systems to meet crop demands and reduce damage to the surrounding environment (air, water, soil).
- Reduced greenhouse gas emissions for wheat production systems.

Priority 2—Improved Management of Wheat Biotic and Abiotic Threats to Sustainable Production

Several agronomy-related issues are common across current wheat systems including the alignment of crop life cycle to changing seasonal patterns; biocide resistance in weeds, fungal pathogens, and insect pests; increasing yields while reducing biocide use due to product withdrawals or social acceptance; provision of sufficient N to achieve potential yields while minimizing environmental damage; new production and product quality possibilities afforded by hybrid, perennial, and gene-edited cultivars of wheat. These themes of research all require linkages between groups (including EWGs) that address single-component issues (e.g., nutrient use efficiency) for effective impact. The Agronomy EWG uses a holistic approach to improve wheat production systems by focusing on the integration of relevant discipline-specific expertise (Hunt et al., 2019). The approach acknowledges the need to capture effective synergies between innovations emerging from discipline-specific research in order to have the greatest impact on production, socio-economic, and ecological outcomes.

Actions

- Conduct studies on better aligning crop life cycles, including new wheat varieties with changing seasonal patterns.
- Identify specific management practices for new wheat cultivars to ensure consistent supply and enhanced quality to meet market and consumer needs for feed, food, nutrition, fiber, and other industrial uses.
- Evaluate in-crop non-chemical forms of weed, disease, and insect control to mitigate biocide resistance.
- Develop integrated management systems that allow for lowered use of biocides.

[3]http://www.yieldgap.org

- Development of N management strategies and evaluation of novel products to improve NUE.

Anticipated Outcomes

- Scoping studies on possible management interactions with perennial, hybrid, and gene-edited cultivars.
- Improved pest and weed management to reduce the risk of pest outbreaks and employ integrated methods for managing pests.
- Reduction of the carbon footprint in the wheat phase of cropping systems.
- Improved management practices for new wheat cultivars that realize the genetic improvement in potential yield and quality.

Priority 3—Tools to Support Improved Management Systems for Wheat

Historically, concomitant advancements in breeding and agronomy translated into yield improvements for wheat at the farm level, though the individual contribution of each varied by region (Bell et al., 1995; Nalley et al., 2008; Lollato et al., 2020). Technologies developed to support efforts related to plant breeding more consistently resulted in deployment of tools when compared to agronomy, perhaps because the end user of the tool is the breeder rather than the producer. Fischer and Connor (2018) provide many examples of such technologies, including molecular markers resulting in genomic selection (e.g., Bernardo, 2016), the development of high throughput phenotyping tools (e.g., Araus and Cairns, 2014; Reynolds et al., 2020), and the use of dynamic crop simulation models to inform breeding programs of traits of interest (Chenu et al., 2009; Sciarresi et al., 2019). Despite the potential for improved agronomy through deployment of tools to improve in-season management decisions by producers, these have been scarce.

A few successful examples of tools impacting agronomic on-farm decisions can be cited. The EPIPRE is one of the first interactive decision support systems that incorporated mesoscale weather data and in-field observations to guide producers when to apply fungicides to control foliar pathogens in winter wheat (Zadoks, 1981). A decade later the epidemiological underpinnings of EPIPRE were adapted to the HRSW production of Minnesota and North Dakota[4]. This led to the Fusarium Head Blight Prediction Center that is available to wheat producers across 22 states in the United States[5]. Another example is, Yield Prophet®, an internet service that uses a dynamic crop simulation model to inform Australian growers about seasonal yield prospects and potential effects of management practices on yield and profit so that in-season management adjustments were data-driven (Hochman et al., 2009). Tools have also been developed to improve nitrogen management for winter wheat and other crops using remote sensing technologies in the Great Plains region of the United States. These efforts started by estimating the crop's yield potential using canopy reflectance (Raun et al., 2001), followed by the development of a commercial GreenSeeker™ sensor (Solie et al., 2002), the development of response indices (Mullen et al., 2003), including soil- and seasonal-specific conditions on the crop's yield potential (Raun et al., 2008). A more recent example includes Canopeo (Patrignani and Ochsner, 2015), an easy-to-use smartphone tool that quantifies fractional green canopy cover and can improve the management of irrigation (Libardi et al., 2019) and wheat grazing in dual-purpose systems (Butchee and Edwards, 2013). While these are successful examples, deployment on-farm is often challenging due to a perception by farm managers or their advisors that adopting new technologies is either too costly or operationally prohibitive (Hochman et al., 2009). Involving growers or other users into the process in a participatory way from the outset would help to overcome issues around on-farm adoption.

The combination of the wealth of agronomic research, the availability of tools to deliver interactive decision support systems, and the nearly ubiquitous access to cellular data networks globally, means that the potential to develop and deploy decision support systems is grossly underutilized. For instance, research papers have exploited the variation in productive capacity for wheat across a field and integrated it with growing season assessments of crop growth for improved nitrogen management (e.g., Schwalbert et al., 2019). Likewise, weed and disease monitoring with remote sensing is an emerging area of crop management (e.g., Franke and Menz, 2007; Cruppe et al., 2017; Pott et al., 2019). Farmers have variable rate seed and fertilizer equipment and often access local weather stations. They also have access to unmanned aerial vehicles (UAVs) that can be used to remotely sense crop growth, the onset of disease and pest stresses, and patterns of water or nutrient stress (Malveaux et al., 2014), though this technology is still at the early stages and opinions on its potential for full integration into on-farm use vary (Freeman and Freeland, 2015). Likewise, no-cost satellite imagery is available to individual producers to help them understand the crop's yield potential and adjust on-farm decisions accordingly (e.g., Schwalbert et al., 2018, 2020). Precision agriculture has advanced rapidly over the last 20 years (Chlingaryan et al., 2018); however, having more ground-truthing studies is needed to better understand the potential and ROI of proprietary tools around "what works where."

Actions

- Evaluate the efficacy of precision agriculture and large data analysis to improve wheat productivity and sustainability.
- Capitalize on the yield gap assessment as a learning and measurement tool for yield enhancement of wheat.
- Evaluate the ability of images and vegetation indices derived from satellites or ground-based tools to forecast wheat yield mid-season to improve on-farm decisions (e.g., nitrogen management).

[4]https://www.ag.ndsu.edu/cropdisease/small-grain-disease-forecasting-model-homepage

[5]http://wheatscab.psu.edu

Anticipated Outcomes

- Increase nutrient use efficiency and reduced environmental impact of over fertilization.
- Improve reliability of the wheat supply through improved yield stability on a regional basis.
- Deployment of new tools to help improve decisions that can contribute to closing the exploitable yield gap.

Priority 4—Improved Knowledge Mobilization and Sharing

Success improving agronomic practices to enhance wheat productivity and sustainability depends upon designing these practices for compatibility with current technology, cultures, and other regional conditions. Producers face a plethora of risks of which agronomic risks are but one. Consequently, producers often choose risk avoidance strategies even when a scientific body of evidence indicates that particular practices are needed. Success will require farmer consultations and input at the on-set of research projects, rather than after the research is completed. This typically will entail transdisciplinary engagement with farmers and educators in formulating these approaches (Eigenbrode et al., 2018). Using participatory on-farm research networks such as the University of Nebraska On Farm Research Network[6], or grower groups such as in Australia's national water-use efficiency Initiative (Kirkegaard et al., 2014), allows not only for validation of small plot research but also identifies early-adopters of new technologies or management tactics who, in turn, can serve as multipliers locally once results have shown to be positive. It will also require effective communication for dissemination to ensure correct implementation and documentation of adoption. A key element to successful adoption is for researchers to recognize and be sensitive to local or regional socio-economic barriers to adoption.

Actions

- Strengthen capacity for knowledge sharing through increased membership in the Agronomy EWG (both international and in-country EWGs).
- Assess and implement effective methods of knowledge sharing that are regionally sensitive.
- Adapt a methodology to assess changes in the sustainability of wheat production systems.
- Explore the 'G × E × M' × 'S' (social aspect).
- Synthesize papers from the GxExM special journal issue into an educational format for use in Continuing Education Credits/Continuing Education Units (CEC/CEU) activities and examinations.
- Develop a metric to determine the degree of exploitable wheat yield gap closure to determine technology sharing success.

Anticipated Outcomes

- Increased global linkages and knowledge sharing among producers, agronomists, innovators, scientists, producer organizations, private companies, and governments.
- To better understand how effective knowledge mobilization and sharing systems can be adapted to meet regional needs in a digital world.

[6]https://cropwatch.unl.edu/on-farm-research

IMMEDIATE GOALS OF THE AGRONOMY EWG OF THE WI

Goal 1: Develop Agronomic Research Priorities That More Broadly Reflect International Requirements for Collaboration

We have taken the first, essential steps toward the development of agronomic research priorities. These included joint meetings of agronomists from different member countries to share information about current projects, and an ongoing effort to establish a database or research inventory of agronomy projects. Beyond the projects led by the agronomists participating in the meetings, we also asked for the participating agronomists to contact colleagues and funding bodies nearby their geography to compile information specifically on wheat that were either funded at the time of data collection (i.e., 2017–18), had recently been terminated, or had received confirmation of future funding. We collected information from 782 research projects originating from Australia (15% of total projects in the database), Canada (30%), China (10%), Spain (1%), United States (42%), and CIMMYT (2%) (**Table 1**). While 106 projects did not report start or end dates, the start date of the remaining projects ranged from 1999 to 2020; with termination dates ranging from 2015 to 2022. Average project duration (weighted by the number of projects in each duration category) was 4.2 years, ranging from 1 to 20 years (**Figure 1**). About 30% of the projects were funded for periods of 3 years or less, and the majority (c.a., 67%) of the projects were funded for a period of 4–6 years. The pilot database in its present form is a starting point and will be added to the Wheat Vivo database of the WI and potentially expanded with the inclusion of other key countries that produce wheat (e.g., Argentina, Uruguay, Black Sea Region) and developing countries that might wish to expand wheat production (e.g., North Africa, Sub Sahara, and South Africa). The pilot database has been used by the EWG to analyze ongoing work with collaborative opportunities and perhaps more importantly where there are gaps in knowledge that require a broad approach. While there has been no discussion within the EWG, the database could be further developed into a centralized repository for agronomic data particularly if the EWG is successful in launching internationally coordinated studies to address common research priorities. Data driven agricultural innovation [Genetics, Environment, Management, Socioeconomics (GEMS)], an international effort led by the University of Minnesota (GEMS, 2020) integrates special and temporally distributed genomic, environmental, management, and socio-economic data into a single platform. The interpretation of big data will require a much more diverse expertise than agronomy alone, but offers solutions to real world challenges.

TABLE 1 | Number of research projects currently funded by Wheat Initiative (WI) Strategic Research Agenda theme and country (or institution).

	Country or institution						
WI strategic research agenda theme	**Australia**	**Canada**	**China**	**CIMMYT**	**Spain**	**USA**	**Total**
Increase wheat yield potential	6	72	30	4	1	75	188
Controlling wheat diseases and pests	1	43	9	2	–	84	139
Improving wheat tolerance to abiotic stress	2	3	–	1	1	15	22
Nutrient use efficiency	2	10	16	1	4	25	58
Agronomy and crop management	52	72	23	3	1	80	231
Ensure the supply of high quality, safe wheat products	1	24	2	–	–	26	53
Enabling technologies and shared resources	–	10	–	–	–	4	14
Knowledge exchange and education	19	4	–	–	–	18	41
Other	36	–	–	–	–	–	36
Total	119	238	80	11	7	327	782

The "Other" category included projects that were either transdisciplinary (e.g., interaction between fertility management and weed control), that focused on non-growing season management (e.g., fallow, stubble, or break-crops), or that involved crop modeling and weather-related crop stresses.

This information is particularly important as longer term funding allows for better sampling of environments, development of probabilistic response curves to given management practices, and for a more representative measurement of sustainability indicators. While single-year funded projects might not allow for development of these indicators and many times consisted of industry-sponsored research protocols; single-year projects can also be extremely relevant in cases where a rapid outcome from agriculture research is needed in response to emerging or unanticipated threats. The EWG will work to grow that database and update it regularly, which will be particularly important as the Agronomy EWG expands its membership.

Initial analysis of the wheat agronomy research inventory showed there is a considerable body of work underway in general agronomy and crop management (30% of the projects in the database), followed by increasing wheat yield potential (24%), and controlling wheat diseases and pests (18%) (**Table 1**). Other notable projects focused on nutrient use efficiency (7%), ensuring the supply of high quality and safe wheat products (7%), and improving wheat tolerance to abiotic stresses (3%). Only around 5% of the projects were either transdisciplinary, focused on non-growing season management, or involved crop modeling and weather-related crop stresses, and were grouped in the "Other" category. Projects focused on knowledge exchange and education (5%), and enabling technologies and shared resources (2%) completed the reported activities. Much of this work produces regionally specific results with few projects linked to national or international collaborations. However, even though the impacts of the work are often regional and specific to the area in which each project is conducted, many of the constraints they address are universal or at least experienced in some other production systems around the world. While the specifics of agronomy may be context dependent, the principles and approaches of transformational agronomic research can be universal (Hunt et al., 2019). The EWG will work to improve global collaborations addressing common constraints or opportunities and promoting the principles of transformational agronomy. The EWG could play an important role in establishing a central repository for agronomy protocols similar to that put in place by CSIRO in Australia (Nictora and McIntosh, 2011) that would support more standardized procedures as has been evident [e.g., Global Yield Gap Atlas (2020)], and in sharing SI approaches through collaboration and partnerships.

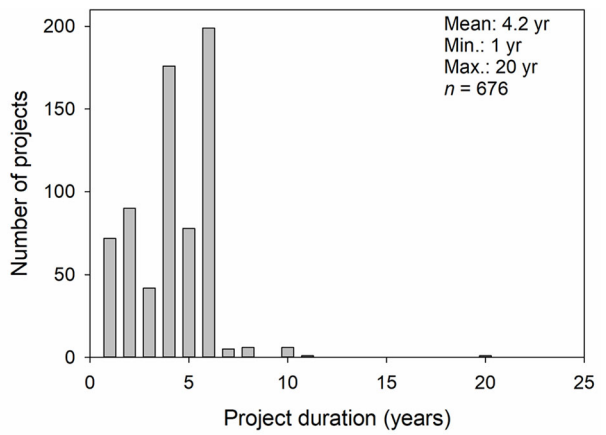

FIGURE 1 | Number of projects in each project duration category for 676 funded wheat agronomy research projects in Australia, Canada, China, Spain, United States, and CIMMYT. A total of 106 projects did not report start or termination dates so project duration was not calculated.

The draft agronomic research strategy developed by the EWG has research priority areas that have been formulated to address the overall need to increase production but balanced to protect the environment. The approach is intended to bring together research, knowledge sharing, and funding capacity to focus on a common vision of SI and outcomes to move the industry forward. An integrated crop management strategy is suggested as the priorities for research, technology sharing, and capacity building are shared while respecting the specific mandates of all contributors. The strategy encompasses

crops, soils, environment, climate change, production, and economics. The central assumption is that wheat is not grown in isolation but in systems that include other field crops, the crop/animal interface and the socio-economic context of different production environments. The strategy integrates systems research to: (1) enhance sustainability, both economic and environmental; (2) find more effective methods for long-term crop production, which support and preserve soil, water, air and economic viability of agriculture; (3) enhance economic return through a more efficient conversion of inputs, natural or manmade, to economic product; capturing and holding more components of the system (e.g., carbon credits, biodiversity) and to reduce movement of nutrients beyond the agricultural system (environmental risk); and (4) implement systematic approaches to manage disease, weeds, and insects that are significant threats to crops and the crop/livestock interface that impact value-chains.

Goal 2: Assessment System for Wheat Sustainability (e.g., an Index); Global Assessment of Wheat Production Systems for Sustainability

A successful global network of sustainable wheat agronomic research will require a common framework of metrics to enable comparative work and sharing of findings, and as a basis to assess the global success of its efforts to reduce yield gaps. The goal would not be to develop a new sustainability index but to understand the work that has been done in many countries and adopting a common approach to measuring sustainability and how SI can be achieved. Adoption of common understanding of definitions and metrics for SI will enable coordinated efforts and serve to amplify the potential impact of the technological advances in wheat production supported by the other EWGs within the WI. A workshop with full participation of the EWG is needed to develop the working definitions for the sustainability of wheat production systems to meet the criteria of SI.

Goal 3: Country-Specific EWGs for Agronomy Established; Ideas for International Collaborations Developed

To maximize effectiveness, the Agronomy EWG needs nodes for implementation at the country level that bring in key players such as producer groups or associations, private industry, and others such as federal and provincial governments. Thus, performance and success of the Agronomy EWG will also be measurable in terms of level of involvement of key players and development of influential partnerships. The number and types of collaborative partnerships to address the challenges identified by the Wheat Initiative will be key performance indicators. The representational structure that has developed within the Agronomy EWG with members from different regions and countries can be extended to maximize involvement. Agronomy EWG members chosen for their strong credentials, achievements, and influence in wheat agronomy in their countries and regions is needed.

WHEAT INITIATIVE AGRONOMISTS COMMUNITY IN THE AMERICAN SOCIETY OF AGRONOMY

In 2017, the Agronomy EWG applied to the American Society of Agronomy to consider the formation of a WI Agronomists Community within its Global Section. The main aim of this Community was to consolidate global expertise for agronomy with a focus on wheat production systems. The approach developed and adopted a "systems agronomy framework" relevant to any wheat production system in the world. Such an approach first establishes the scale of current yield gaps identifying physiologically defensible benchmarks, and then takes a holistic approach to understand and overcome exploitable yield gaps. Finally, new opportunities to increase current and potential yield would be sought by capturing future G × E × M synergies identified in different systems. It will be important to have Agronomy EWG in participating countries to feed into the WI as this will allow flexibility for each distinct country and their funding systems.

Supporting aims include:

- Establish a protocol for sharing member country's approaches and priorities to integrated research, outreach, and policy to improve climate resilience of cereal systems in wheat producing regions worldwide.
- Support interdisciplinary collaboration around wheat production systems through symposia, special publications, and coordinated efforts to link member country funding.
- Expand the scope of the WI to ensure research on wheat is effectively implemented to produce actionable efforts and changes in wheat sustainability, profitability and livelihoods of those dependent on wheat production systems worldwide.

The aim of this Community and the Agronomy EWG is to bring together experts from a broad range of disciplines (vs. a silo approach) who would all contribute to the enhancement of the wheat phase as part of a systems agronomy approach that will meet the global challenges facing wheat growers and end-users today and well into the future. Thus, we encourage members from all supporting disciplines, industry colleagues, policy-makers, and funding stakeholders to join this Community and the WI's Agronomy EWG.

APPLICABILITY OF THE FRAMEWORK FOR OTHER CROPS

Although the Agronomy EWG within the WI is focused on wheat and wheat-centered systems, its vision and framework as described above is applicable to many other crops grown on a global scale. Advances in genetics and crop breeding can only be realized when deployed in agronomic production

systems suited to the natural and social resources of a region and in systems designed with resilience to local biotic and abiotic stresses. We are not aware of initiatives of similar scope for other staple or key nutritional crops. We hope the Agronomy WI will serve as a model and thereby serve more broadly to enhance food security and agricultural sustainability worldwide.

AUTHOR CONTRIBUTIONS

BB prepared the original manuscript with input, revisions, and editorial contributions provided by all co-authors. JK, JRH, SE, DL, RL, JW, and SS provided significant contributions in the subsequent revision.

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Yield Gaps in Wheat: Path to Enhancing Productivity

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Wheat production is required to supply food for the world's population, and increases in production will be necessary to feed the expanding population. Estimates show that production must increase by 1 billion metric tons to meet this demand. One method to meet future demand is to increase wheat yields by reducing the gap between actual and potential yields. Potential yields represent an optimum set of conditions, and a more realistic metric would be to compare actual yields with attainable yields, where these yields represent years in the record where there is no obvious limitation. This study was conducted to evaluate the yield trends, attainable yields, and yield gaps for the 10 largest wheat producing countries in the world and more localized yield statistics at the state or county level. These data were assembled from available government sources. Attainable yield was determined using an upper quantile analysis to define the upper frontier of yields over the period of record and yield gaps calculated as the difference between attainable yield and actual yield for each year and expressed as a percentage of the attainable yield. In all countries, attainable yield increase over time was larger than the yield trend indicating the technological advances in genetics and agronomic practices were increasing attainable yield. Yield gaps have not shown a decrease over time and reflect that weather during the growing season remains the primary limitation to production. Yield gap closure will require that local producers adopt practices that increase their climate resilience in wheat production systems.

Keywords: yield, wheat production, yield gap, weather, gap analyses

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INTRODUCTION

Productivity of agricultural commodities throughout the world must increase in order to supply the food needs of the expanding population. Alexandros and Bruinsma (2012) estimated that by 2050, an additional 1 billion metric tons per year of cereals would be needed to meet the demand, which would require an increase in production from 2.1 to 3.0 billion metric tons. This requires that we either increase yield of crops through closing the yield gap between the potential and actual yields or by increasing the potential yield of crops. Evans and Fischer (1999) introduced the concept of potential yield in crops and the value of considering potential yield in evaluating progress of crop management programs. Most would argue that decreasing the yield gap is more achievable than increasing the potential yield. If we assume that the potential yield can be described as

$$Y_p = Cx\ St\ x\ \varepsilon_i\ x\ \varepsilon_c\ x\ \varepsilon_p \quad (1)$$

where Y_p is the potential yield, St is the incident solar radiation, C is the fraction of photosynthetically active radiation in total solar radiation, ε_i the interception efficiency, ε_c the conversion efficiency of solar radiation into photosynthetic products, and ε_p the efficiency of the conversion of stored carbon into harvestable products. Long et al. (2006) conducted an in-depth analysis on these terms and concluded that ε_i and ε_p are near the theoretical maximum for agronomic crops while there is improvement in ε_c possible and potentially increase Y_p by 50%. This relationship was first described by Monteith (1977) to evaluate the efficiency of light capture by crops and understanding how light is efficiently captured by agronomic crops will pay dividends in increasing crop productivity. We can describe the yield gap as

$$Y_g = Y_p - Y_a w \quad (2)$$

where Y_g is the yield gap and Y_a the actual yield. There have been several studies on the yield gap for a variety of crops that has led to the development of a global yield gap atlas (www.yieldgap.org) based on the application of the use of Y_p and Y_a as described by van Ittersum et al. (2013). Guilpart et al. (2017) provide a methodology for estimating Y_g at the cropping system level. The approach has demonstrated the utility of being able to quantify yield gaps for different crops and climates.

In their analysis of yield gaps for a variety of crops, Fischer et al. (2014) provided an in-depth assessment of the trends in yields for different crops in their megaclimatic regions and proposed that Y_p would represent yields with no limitations of water or nutrients of the best-adapted varieties. Evans and Fischer (1999) proposed this definition to provide a standard for comparison among experiments. Fischer et al. (2014) defined farm yield (Y_{af}) as the crop yield reported at the field, district, regional, or national average, and attainable yield (Y_{at}) is the yield achieved under economically optimal practices with minimal limitations due to the weather during the growing season. Fischer et al. (2014) proposed yield gaps (Y_g) should be expressed as a percentage of Y_{at} because this metric would have more impact in evaluating the limitations to production rather than Y_p.

In their analysis of wheat (*Triticum aestivum* L.) yields and Y_g, Fischer et al. (2014) found that increasing Y_p is an important factor in increasing Y_a and that increases in Y_a are a result of improved agronomic practices and would require implementation of multiple practices. They proposed that increases in Y_p are associated with increased grain number, harvest index, grain weight, and total dry matter. Yield gaps in wheat are closing slowly because of the adoption of agronomic practices that enhance Y_a (Fischer et al., 2014). Yield gaps have been the focus of several studies on a range of agronomic crops. Lobell et al. (2009) evaluated Y_g and found in irrigated wheat, rice (*Oryza sativa* L.), and maize (*Zea mays* L.) that yields were near 80% of the Y_p, and that weather was the major constraint on productivity variation during the growing season. Nuemann et al. (2010) evaluated yield gaps of global grain production and suggested that closing the yield gap would require a detailed understanding of the specific limitations for each region. Mueller et al. (2012) found nutrient and water management were key to closing the yield gap because yield variability was affected by fertilizer use, irrigation, and climate. This conclusion was also supported by Sinclair and Rufty (2012) where they observed crop yield increases were more closely associated with nitrogen and water than plant genetics. Ray et al. (2015) observed that climate variation explained one-third of the global crop yield variability and in some areas of the world over 60% of the yield variability could be attributed to climate variation. Grassini et al. (2013) cautioned that historical yield trends needed to be evaluated to determine their trends and potential plateaus. They reported that wheat yields since 1960 in northern Europe, e.g., France, the Netherlands, and United Kingdom, had plateaued while increases were still evident in Australia, China, and India. In developing countries, George (2014) argued that crop yields have not increased in proportion to the advances in agronomic practices and there is much potential in productivity to be realized with adoption of improved practices.

Using yield gap analysis based on Y_{at} from country-level data in the Midwestern US, Hatfield et al. (2017) showed that Y_g on maize and soybean (*Gylcine max* L. Merr.) was related to July maximum temperatures, August minimum temperatures, and July–August total precipitation. Each of these climatic variables has a direct relationship to the physiological efficiency of these crops. However, in Great Plains wheat production, Hatfield and Dold (2018) found that Y_g was closely related to precipitation during the grain-filling stage and that temperatures were not a consistent limiting factor because wheat in these areas was not exposed to temperatures above the upper range for development. Analysis of the factors causing yield gaps can provide a valuable tool for assessing the limitations to productivity and improved management strategies to increase Y_{af}. The objective of this study is to evaluate the yield gaps in the major wheat growing regions of the world using readily available data and to determine the limitations to productivity using yield gap analysis. The study serves as the foundation to develop strategies to decrease the yield gap for the major yield producing areas.

METHODOLOGY

Data on wheat yields were collected from various sources to represent a range of scales. The primary data source was Food and Agriculture Organization Statistics (FAOSTAT) (www.fao.org/faostat accessed 3-June-2019) for the 10 highest-producing countries in the world. These countries are shown in **Table 1** with the area harvested and production for 2017. Data from 1961 through 2017 were extracted for the area harvested, yield, and total production. For the United States, state-level data were extracted for the top three wheat producing states, Kansas, North Dakota, and Washington, from the National Agricultural Statistics Service (nass.usda.gov, accessed June 3, 2019) for the period from 1950 through 2018. A more in-depth analysis was conducted for the top three producing counties in Kansas, Mitchell, Saline, and Sumner, with the data extracted from the NASS site for the period from 1950 through 2007. The area harvested and total production for these states and counties are shown in **Table 2**.

TABLE 1 | Area of wheat production and annual production in 2017 and the average yield gap from 1960 to 2017 for the top 10 wheat producing countries.

Country	Area harvested in 2017 (ha)	Production in 2017 (metric tons)	Yield gap (1960–2017) and confidence limit
China	24,510,393	134,000,000	0.12 (0.01)
India	30,600,000	98,510,000	0.04 (0.005)
United States	15,210,680	47,370,880	0.12 (0.01
Russia Federation	27,517,354	85,863,132	0.21 (0.02)
France	5,464,689	36,924,938	0.15 (0.007)
Canada	9,035,993	31,818,744	0.24 (0.009)
Germany	3,202,600	24,481,600	0.00 (0.0009)
Australia	12,191,153	22,274,514	0.24 (0.01)
Pakistan	8,972,000	26,674,000	0.08 (0.007)
Turkey	7,662,273	21,500,000	0.12 (0.009)

Data extracted from FAOSTAT (www.fao.org/faostat).

TABLE 2 | Area harvested and total production in 2018 for the three top producing states in the United States and the average yield gap from 1950 through 2018 and the area harvested and total production for the top three producing counties in Kansas and the average yield gap from 1950 through 2007.

State	County	Area harvested in 2018 (ha)	Production in 2018 (metric tons)	Yield gap (1950–2018)
Kansas		3,116,021		0.22 (0.03)
	Mitchell	82,069	187,653	0.36 (0.05)
	Saline	61,794	62,336	0.25 (0.04)
	Sumner	161,467	184,600	0.29 (0.05)
North Dakota		3,130,185	10,020,199	0.24 (0.03)
Washington		8,933,855	4,277,552	0.17 (0.02)

Data extracted from the National Agricultural Statistics Service (www.nass.usda.gov). Standard errors are shown in parentheses.

Analysis of the data was conducted across all yield records with the same approach. The process used quantile regression at the 95th percentile (PROC QUANTREG in SAS, SAS for Windows v 9.3, SAS Institute, Cary, NC). This procedure was followed to find the attainable yield (Y_{at}) for all of the observed yield data for a country, state, or county. Use of this approach to obtain boundary lines was described by Webb (1972) and Cade and Noon (2003). This method was used by Egli and Hatfield (2014a, 2014b) and uses a statistical method to select the years at the upper frontier of the record across the observed period of record to determine Y_{at} for different counties in the Midwest. These Y_{at} yields are assumed to represent the years in which weather was not a limitation to production. The yield gap is calculated as

$$Y_g = \left(Y_{at} - Y_a\right) / Y_{at} \tag{3}$$

where Y_{at} is the attainable yield obtained from the quantile statistical analysis. Equation 3 provides the fraction yield gap. For each year, Y_{at} and Y_g are computed and an average of the Y_g computed across the total record. Data are presented to show the yield trend and Y_{at} and the temporal trend of Y_g for the 10 countries with the largest production since 1960. To obtain the yield trend line in the Y_a values, we used linear regression through the observed data with (PROC REG from SAS).

RESULTS AND DISCUSSION

Yield Trends and Attainable Yield

In this analysis, we focused on two metrics from the yield record, the Y_{at} and Y_a values. The assumption made was that the slope of the Y_{at} line would represent the technology increase for a given country, while the slope of Y_a would represent the ability of the country-level yields to increase given the combination of technology and weather within the growing season.

Wheat yields in all countries have shown a continual increase since 1960. There is variation among the countries for both the slopes in the Y_{at} and Y_a values (**Table 3**). The differences between the two values for a given country reveal that technological advances have increased more than the yield trend line. If technology was the only factor contributing to the yield trend, then the expectation would be for the slopes of the lines to be similar; however, the slopes were significantly different ($\rho < 0.01$) using simple T-test. The standard error of the estimates was computed for each regression analysis and was quite small for all of the countries we evaluated. The Y_g values are computed on an individual year, and although there may be differences in the production area within a given country, this would be negated by the estimated Y_{at} and Y_a observations within a given year because these values are from the same land area. Yield gap analysis at the country level could be independent of the production region unless there was a major shift in the production region from good to poorer soils or from rain-fed to primarily irrigated areas. To evaluate this, we found no significant relationship between the area under production and Y_g for a given year across any of the countries. The assumption would be that trends in country-level yields would be reflective of the technology adoption within the country.

There are differences among countries. China wheat yields have shown an increase in yield; however, the slope of Y_{at} is 99.8 kg ha^{-1} year^{-1} while Y_a is at 88.3 kg ha^{-1} year^{-1}. China has demonstrated the most consistent increase in wheat productivity since 1960, suggesting that wheat production has benefited

TABLE 3 | Comparison of the slope of actual yield trends to attainable yield changes for the top wheat producing countries.

Country	Slope of the actual yield increase (kg ha^{-1} year^{-1})	Slope of attainable yield increase (kg ha^{-1} year^{-1})
China	88.3 (1.8)	99.8 (2.0)
India	44.8 (1.14)	57.6 (1.2)
United States	25.6 (0.5)	27.7 (0.6)
Russia Federation	43.9 (1.2)	48.7 (1.25)
France	83.4 (1.1)	125.9 (1.3)
Canada	31.7 (0.6	41.8 (0.9)
Germany	93.4 (2.1)	112.0 (2.1)
Australia	15.2 (0.3)	21.4 (0.4)
Pakistan	38.9 (0.7)	41.8 (1.1)
Turkey	27.3 (0.7)	28.9 (0.9)

Standard errors are shown in parentheses.

from adoption of technology across the country (**Figure 1A**). If we compare the yield trends in Australia (**Figure 1B**), Canada (**Figure 1C**), and the United States (**Figure 1D**), these national scale yields show variability among the years with the Y_{at} trends exhibiting a larger increase than Y_a. In the top wheat producing countries, the Y_{at} increase was greater than the Y_a trend (**Table 1**), with France and Germany showing the largest values in Y_a and Y_{at}. These two countries have used a combination of advanced technology in managing the crop and have a climate that is ideally suited to wheat production because of the combinations of temperature and precipitation during the growing season. Technology adoption was suggested by Fischer et al. (2014) as being a significant factor in closing the yield gap.

Yield Gaps

Each country has shown an increase in Y_a; however, the Y_g has remained relatively constant over the years. The average Y_g for the period from 1961 through 2017 for the 10 top producing countries showed a range from 0.0 in Germany to 0.24 in Australia and Canada (**Table 3**). These are the average values calculated from the annual Y_g values. There is variation in Y_g across the years for all countries with no significant trend in closing the gap between actual and attainable wheat yields, e.g., China (**Figure 2A**), Australia (**Figure 2B**), Canada (**Figure 2C**), and the United States (**Figure 2D**). China is showing a decrease in the variation in Y_g in the last decade (**Figure 2A**); however, this has not impacted the overall Y_g trend. Australia exhibits the largest Y_g values, often exceeding 0.5, and there has been no change in the Y_g values since 1960 (**Figure 2B**). This can be attributed to the large variation in the meteorological conditions during the growing season related to the El Nino Southern Oscillation (ENSO) Index and years with large negative Southern Oscillation Index (SOI) values have the largest Y_g values and large positive values showed the smallest Y_g values. However, the scatter among all of the years showed the overall Y_g record was not significantly correlated with SOI values because other factors contributed to the inability of the wheat crop to achieve its potential. Canada has the same average Y_g value as Australia and has recorded Y_g values near 0.5; however, the past 4 years have shown very small Y_g values compared to the early record because of more favorable weather, e.g., slightly warmer temperatures and above-normal precipitation during the grain-filling period for the wheat producing regions. Yield gap values in the United States average 0.12 and show a trend toward decreasing Y_g values, but this trend is not significant. These observations of Y_g in these countries represent the range of yield gaps in wheat producing countries in

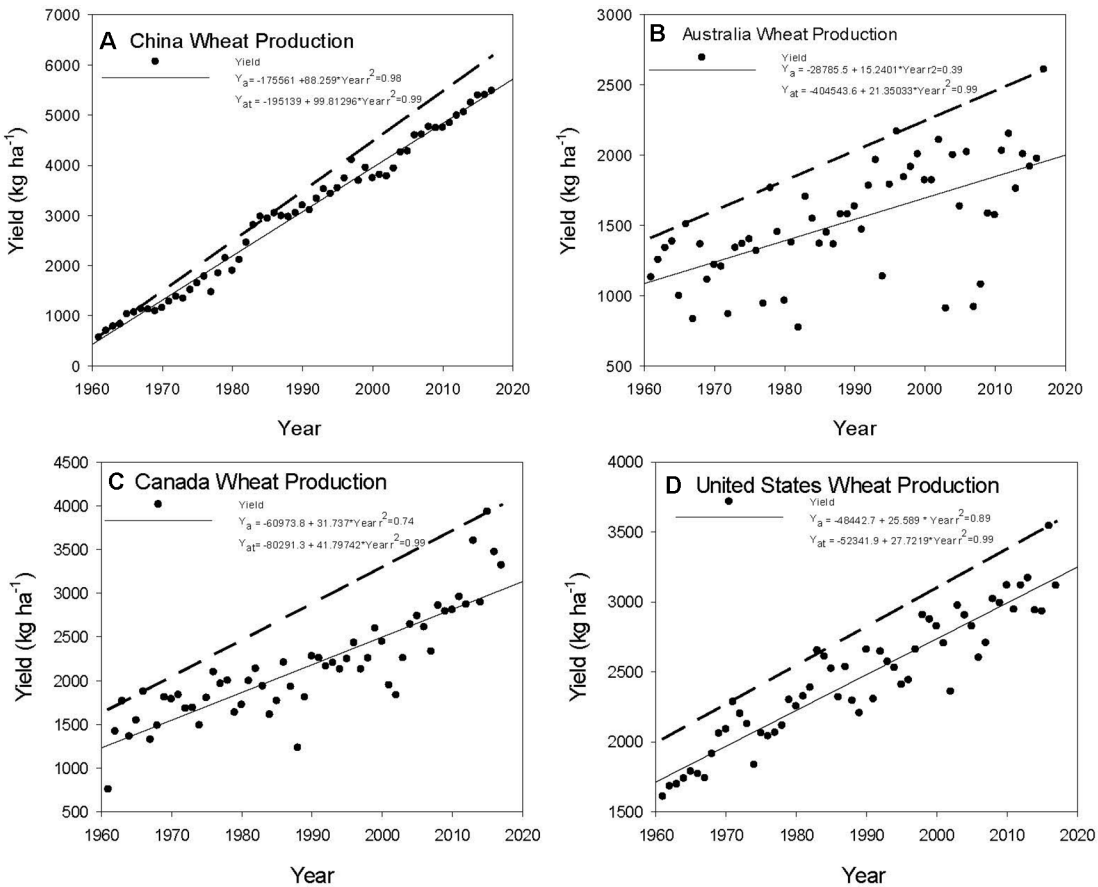

FIGURE 1 | Yield trends and attainable yield for China **(A)**, Australia **(B)**, Canada **(C)**, and United States **(D)** from 1960 through 2017. Data from FAOSTAT (www.fao.org/faostat).

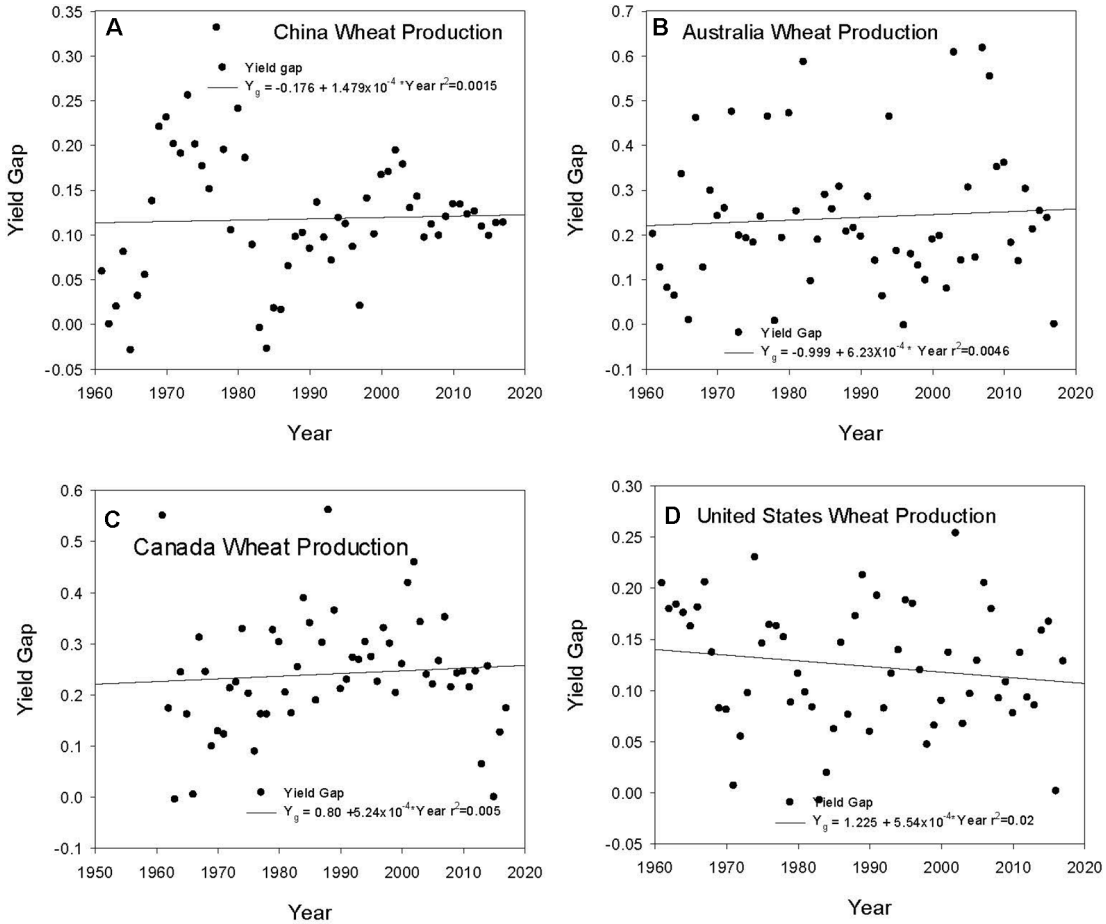

FIGURE 2 | Yield gap trends from 1960 to 2017 for China **(A)**, Australia **(B)**, Canada **(C)**, and United States **(D)** using the data obtained from FAO (www.fao.org/faostat).

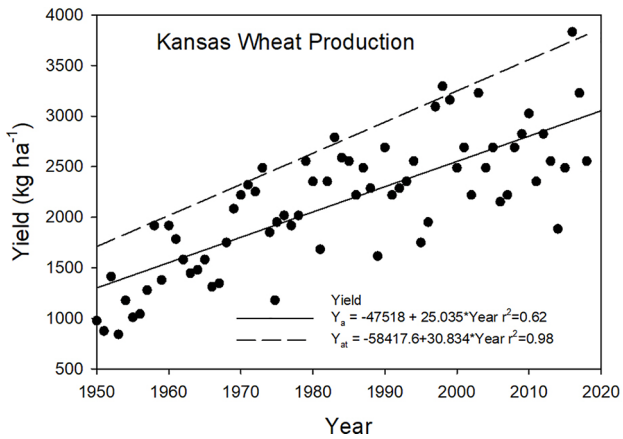

FIGURE 3 | Winter wheat yield trends and attainable yields for Kansas from 1950 through 2018. (Data from www.nass.usda.gov).

the world. It is important to realize that national scale yields are comprised of many environments and soils and reflect the large-scale impacts of technology and the weather, and it is not possible to produce any assessment other than general trends.

State- and County-Level Yields and Yield Gaps

To address the question of trends in more regional scale observations we extracted state-level data for the top three wheat producing states in the United States and computed their Y_{at} and Y_g values. The yield trends for Kansas show an increase in Y_a over time with no decrease in the Y_g values (**Figure 3**). We found the same results for North Dakota and Washington with increasing yields but no decrease in the Y_g values over time. To further refine the scale to the county level, the top three wheat producing counties in Kansas were selected, and they also showed the same pattern as the Kansas aggregate data. There were differences among the three counties in their average Y_g values (**Table 2**), with Mitchell county showing the largest Y_g average. The same results were observed by Hatfield and Dold (2018) when they examined Kansas, Oklahoma, and North Dakota wheat production and found Y_g values were related to the precipitation amounts during the grain-filling period. For these three counties, one weather event in 2007, a late spring freeze during heading was responsible for large Y_g values pf 0.64 (Mitchell), 0.76 (Saline), and 0.71 (Sumner).

Saskatchewan is the top wheat producing province in Canada and shows the same trends as the whole country of Canada

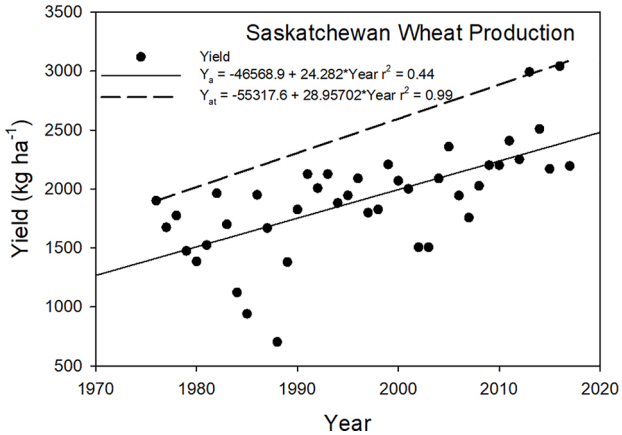

FIGURE 4 | Spring wheat yield trends and attainable yield for Saskatchewan, Canada, from 1976 through 2017.

(**Figure 4**). There is a difference in Canadian wheat production with the growth of spring wheat varieties in the western provinces. The attainable yields exhibit a larger slope than the observed yield trends revealing that weather limitations on yields reduce the effect of technology. As we change the scale of the observed yield trends, there will be greater differences in the variation around the trend line because of the more local effects of weather and soil variations and their interactions. For example, within county-level yields, the impact of a drought or freeze could be quite large; however, at the statewide or country level, these effects may not be seen because the effects would not be evident across the large area.

Yield Gap Trends

There is no discernable trend in the Y_g values across any scale we examined in this study. The Y_{at} values exhibit a larger increase than the Y_a trends, indicating that technology (agronomic and genetic) has increased the attainable yield and the potential yield; however, we are not closing the yield gap. The fact that the Y_g values have not decreased would suggest that weather remains the dominant factor limiting production around the world because the adoption of technology has provided for substantial yield increases across all countries. Since weather is the dominant effect on Y_g, the challenge will be to determine how climate resilient a cropping system can be for a given region. This will require changes in the management practices as proposed by Hatfield and Walthall (2015) where they discussed the role of the genetics × environment × management (GxExM) concept in providing a framework for increasing productivity. The scale of yield data assembled from national, province, state, or county level provides an indication of the potential progress toward reducing the Y_g at a large scale. However, this scale doesn't provide potential options for a producer to increase their productivity and reduce the yield gap. Evaluation of specific factors and potential management options for producers will have to be evaluated at a scale that represents the actual growing conditions. The analyses in this study were focused on the country-scale assessments to determine our progress toward decreasing the yield gap.

CONCLUSIONS

The concept of yield gaps provides a framework for assessing the trends in yield for all crops. Across the top wheat producing countries of the world, there are differences in the progress for increasing yield. In France and Germany, the yield increase is near 100 kg ha^{-1} year^{-1}, while in Australia, it is 15 kg ha^{-1} year^{-1}, which can be attributed to a large difference in the variation in the climate between these two regions. There is also a major difference in the magnitude of the Y_g values between these two areas. Yields are more stable in the northern Europe environments compared to the Australian continent, also reflective of the weather variation among growing seasons. Evaluating smaller-scale yields, e.g., county, reveals that weather within the growing season is the dominant factor affecting yield gaps (Lobell et al, 2009). Technological advances have increased the attainable yields at a greater level than the yield trends, indicating that to close the yield gap, wheat producers will have to adopt practices at the local scale that will allow the technology improvements to be realized. These are local decisions made by individual producers; however, efforts to demonstrate how soil and agronomic practices that increase productivity could reduce the yield variation among years will pay dividends in closing the yield gap in wheat.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

JH prepared the data analysis and JH and BB jointly prepared the paper.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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ORIGINAL RESEARCH
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The Contribution of Functional Traits to the Breeding Progress of Central-European Winter Wheat Under Differing Crop Management Intensities

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Wheat yields in many of the main producing European countries stagnate since about 20 years. Hence, it is of high interest, to analyze breeding progress in terms of yield and how associated traits changed. Therefore, a set of 42 cultivars (released between 1966 and 2012) was selected and yield as well as functional traits defined by the Monteith and Moss equation were evaluated under three levels of management intensity. The Monteith Moss equation thereby calculates grain yield as the product of incident photosynthetically active radiation, fraction of intercepted radiation, radiation use efficiency, and harvest index. The field trial was performed in a high yielding environment in Northern Germany in two seasons (2016–2017 and 2017–2018) with very contrasting rainfall rates. The three differing managements were: intensive (high N + pesticides), semi-intensive (high N – pesticides), and extensive (low N – pesticides). The results indicate that the stagnation of wheat yields in Central-Europe is not caused by a diminishing effect of breeding on yield potential. This equally applies to suboptimal growing conditions like extensified crop management and restricted water supply. Nearly all functional sub-traits showed a parallel progress but coefficients of determination of relationships between traits and year of variety release are decreasing along the hierarchy of yield formation. One exception is radiation interception which did not show a stable linear increase during breeding history. In recent years, biomass is getting more important in comparison to harvest index. Values of harvest index are slowly approaching theoretical maxima and correlations with grain yield are decreasing.

Keywords: wheat, breeding progress, harvest index, biomass, radiation interception, radiation use efficiency, high-throughput phenotyping, uav

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INTRODUCTION

Breeding progress of common wheat (*Triticum aestivum* L.) recently gained much attention because after at least half a century of continuing increase of farm level wheat yields (Calderini and Slafer, 1998) this process stagnates in many of the main producing countries, including France, the United Kingdom, and Germany (Lin and Huybers, 2012). These countries achieve above-average yields and therefore have major importance for worldwide wheat supply. An analysis of the breeding progress

of the past can help to get back on track for a much-needed increase of wheat yields.

A deeper understanding if yield formation was analyzed using the equation (1) (Monteith and Moss, 1977):

$$GY = \sum_{sowing}^{harvest} \left[R_{PAR} \times RI \times RUE \right]_{BIO} \times HI, \quad (1)$$

which calculates grain yield (*GY*) as the product of incident photosynthetically active radiation (R_{PAR}), fraction of intercepted radiation (*RI*), radiation use efficiency (*RUE*), and harvest index (*HI*). This equation can be aggregated to the term: *GY* is the product of above-ground biomass (*BIO*) and *HI*.

The amount of incident radiation is determined by the location, its seasonal weather, and the dates of sowing and harvest. The intercepted fraction of this radiation is defined by the speed of development, the final size, the longevity, and the architecture of the canopy (Long et al., 2006). A high speed of canopy development is labeled "early-vigor". Under Central-European growing conditions losses until canopy closure mainly occur during March and April, when the green area index (*GAI*) of the canopy is not sufficient for near total interception and in parallel usable incoming radiation occurs (Rose et al., 2017). A fast canopy development in this early phase can increase biomass production.

The longevity of the canopy mainly depends on its senescence dynamics. When canopies reach their final size the subsequent phase of maximal photosynthesis is rapidly replaced by the phase of senescence. Here, physiological integrity is maintained in the beginning but complete self-destruction finally terminates all growth processes (Thomas and Smart, 1993). Like the subtle process of canopy formation, its senescence is a well-programmed sequence and after the period of carbon assimilation, leaves now contribute to the grain yield by the remobilization of their nutrients (Wu et al., 2012). The visible symptom of leaf senescence is the loss of chlorophyll and genotypes which express delayed chlorophyll catabolism are named "stay-green" (Thomas and Ougham, 2014). Functional "stay-green" genotypes maintain carbon assimilation for a prolonged period during grain-filling (Thomas and Howarth, 2000; Rebetzke et al., 2016), this is often associated with considerable yield differences in wheat trials (Verma et al., 2004; Luo et al., 2006; Kichey et al., 2007; Christopher et al., 2008; Wang et al., 2008; Bogard et al., 2011; Wu et al., 2012; Christopher et al., 2016; Montazeaud et al., 2016; Pinto et al., 2016; Luo et al., 2018). In contrast, unfavorably delayed leaf senescence might result in a low nitrogen use efficiency as well as a low grain protein content (Wu et al., 2012). A tradeoff between a longer maintenance of leaf chlorophyll and a less efficient remobilization of nitrogen has been shown by Gaju et al. (2011). Therefore, Thomas and Ougham (2014) define the ideotype to "comprise late initiation of canopy senescence, to maximize C capture, followed by fast and complete mobilization of N and other nutrients".

The onset of senescence is both, part of the development process of a plant and inducible by numerous external factors (temperature, drought, nutrient supply, pathogen attack) (Buchanan-Wollaston, 1997). The developmental senescence is a consequence of phenology and induced by internal signals such as phytohormones. Stress-induced senescence in contrast is triggered by external signals (Derkx et al., 2012). These signals are primarily nitrogen depletion (Osaki et al., 1991; Mi et al., 2000; Derkx et al., 2010; Bogard et al., 2011; Luo et al., 2018), water depletion (Idso et al., 1980; Christopher et al., 2008; Thomas and Ougham, 2014; Christopher et al., 2016; Christopher et al., 2018), and pathogens (Berdugo et al., 2013). So, a "stay-green" phenotype can represent the phenological component per se but also just reflects the ability to cope with the aforementioned external factors (Richards, 2000; Rebetzke et al., 2016).

The amount of intercepted radiation is multiplied by the radiation use efficiency to get the final biomass, the measure for biological performance. This transformation efficiency includes all forms of stress (drought, pathogens, etc.) but is also affected by crop architecture (Zhu et al., 2010) and light saturated photosynthetic rates (Gaju et al., 2016). The increase of radiation use efficiency in a historical breeding set was not related to photosynthesis but shifts in canopy-level traits (Sadras et al., 2012).

The final biomass is multiplied with harvest index to get the grain yield, the measure for agronomical performance. In contrast to the preceding steps of yield formation which can be improved by the optimization of manifold biological processes, here, the quite simple parameter—fraction of biomass that is part of the harvested organs—can considerably change the final grain yield. The upper border of this fraction is restricted by an increased risk of lodging (Berry et al., 2007) and eventually occurring negative interactions with the processes of biomass production. Educated guesses for this threshold are: 0.62 (Austin, 1980), 0.64 (Foulkes et al., 2010), and 0.66 (Shearman et al., 2005).

For an adequate representation of environmental variables which influence complex traits, uncontrolled field trials are still the only adequate facility. Aerial platforms—especially unmanned drones—are an attracting platform for the use in these large-scale open field trials. Equipped with different sensors, they perform high throughput phenotyping with a high spatial resolution (Haghighattalab et al., 2016; Pauli et al., 2016; Araus et al., 2018; Condorelli et al., 2018). Additionally, in comparison to ground based methods, airborne methods often reach a higher precision because they can represent the whole plot (statistical selection can be applied to all pixels) and confounding environmental effects (temperature, sun angle etc.) are reduced through the short measurement time (Tattaris et al., 2016). This can result in higher repeatabilities for a trait like the NDVI (Condorelli et al., 2018).

The progress in the development of small unmanned drones, in combination with calibrated spectral sensors for the prediction of whole season green area indices, now allows to measure all components of the yield equation by Monteith and Moss (1977) in large field trials.

The aim of this study is to analyze the functional pathways historical breeding used to improve yield potential of winter wheat in Central-Europe. To enlighten the black box of the

preceding breeding success can help to open new perspectives for the contribution of breeding to a much-needed increase of wheat yields. The analysis is complemented by suboptimal crop management intensities and experimental years with contrasting water supply which might become more relevant due to environmental concerns and a changing climate.

MATERIAL AND METHODS

Field Trials

The field trials were conducted during two consecutive years (growing seasons 2016–2017 and 2017–2018). Sowing date was from September 20 to September 22, 2016 and on October 17, 2017. Harvest date was from August 8 to August 15, 2017 and on July 27, 2018 (**Table 1**). The experiment comprised two factors: crop management and winter wheat cultivar, and the design was laid out as a split-plot with three replications in which the factor crop management was nested within replication and the factor cultivar was nested within crop management.

The factor cultivar includes 42 levels. The set of cultivars is chosen to represent the German breeding progress in the period from 1966 to 2012 (for more details see **Table 2**). The factor crop management includes three levels: intensive, semi-intensive, and extensive. The intensive treatment received mineral fertilizer at a total N supply rate of 220 kg N ha^{-1} (fertilization adjusted for soil mineral nitrogen, N_{min}) as well as full intensity of fungicides, insecticides, and growth regulators, representing standard wheat production systems in Central-Europe. The semi-intensive treatment received mineral fertilizer at the same level as well as growth regulators, but no fungicides and insecticides, representing a scenario with no chemical plant protection. The extensive treatment received mineral fertilizer at a total N supply rate of 110 kg N ha^{-1} (fertilization adjusted for N_{min}), no fungicides and insecticides, and no growth regulators in the first season (due to problems with lodging growth regulators were applied in the second season), representing a scenario of comprehensive extensification in crop production.

To prevent patchy effects from weed cover, chemical control measures were applied across all crop management treatments (including extensive). Nutrients other than N were applied consistent across all crop managements according to requirements determined individually in each year.

TABLE 1 | Main agronomical and phenological dates during both growing seasons.

	Season 2016–2017	Season 2017–2018
Sowing date	Sep. 21 (Sep. 20–Sep. 22), 2016	Oct. 17, 2017
Ear emergence complete	Jun. 3 (May 28–Jun. 8), 2017	Jun. 1 (May 29–Jun. 06), 2018
Hard dough	Jul. 23 (Jul. 19–Aug. 1), 2017	Jul. 14 (Jul. 09–Jul. 18), 2018
Harvest date	Aug. 11 (Aug. 8–Aug. 15), 2017	Jul. 27, 2018

Values in parentheses indicate the range of the analyzed set.

TABLE 2 | Detailed information about the set of analyzed cultivars.

Cultivar	Year of release	Breeder	Quality group
Diplomat	1966	Firlbeck	A
Caribo	1968	Heidenreich und Eger	B
Highbury	1968	Plant Breeding International Cambridge (PBIC)	A
Progress	1969	Hege	A
Kormoran	1973	Lochow-Petkus	A
Disponent	1975	Bayrische Saatzuchtgesellschaft	A
Monopol	1975	Firlbeck	E
Carimulti	1975	Heidenreich und Eger	C
Vuka	1975	Franck	A
Götz	1978	Bayrische Saatzuchtgesellschaft	B
Tabor	1979	Strube	A
Kronjuwel	1980	Bayrische Saatzuchtgesellschaft	B
Urban	1980	Bauer, G.	E
Rektor	1980	Firlbeck	E
Kanzler	1980	Engelen Büchling	B
Sperber	1982	Lochow-Petkus	A
Ares	1983	Strube, Dr. H.	B
Apollo	1984	Saatzucht Breun	C
Obelisk	1987	Strube, Dr. H.	B
Alidos	1987	Saatzucht Hadmersleben	E
Greif	1989	Lochow-Petkus	B
Bussard	1990	Lochow-Petkus	E
Kontrast	1990	Saatzucht Hadmersleben	A
Ritmo	1993	Cebeco	B
Batis	1994	Strube, Dr. H.	A
Pegassos	1994	Strube Saatzucht	A
Flair	1996	Schweiger	B
Cardos	1998	Saatzucht Hadmersleben	A
Dekan	1999	Lochow-Petkus	B
Drifter	1999	Nickerson	B
Biscay	2000	Lochow-Petkus	C
Tommi	2002	Nordsaat	A
Akteur	2003	DSV	E
Hermann	2004	Limagrain-Nickerson	C
Türkis	2004	Lantmännen SW Seed Hadmersleben GmbH	A
Potenzial	2006	DSV	A
Manager	2006	Saatzucht Schweiger GbR	B
Inspiration	2007	Saatzucht Josef Breun GmbH & Co.KG	B
JB Asano	2008	Saatzucht Josef Breun GmbH & Co.KG	A
Tobak	2011	W. v. Borries-Eckendorf	B
Patras	2012	DSV	A
Elixer	2012	W. v. Borris-Eckendorf	C

Year of cultivar release, breeder, and baking quality group. German baking quality groups are: E (elite, premium quality bread wheat), A (bread wheat), B (milling wheat), and C (feed quality).

To avoid neighboring effects between plots (caused by differing plant heights) and to allow separate harvest of early and late maturing cultivars, those were grouped by expected plant height and maturation time in four incomplete sub-blocks (early/short, early/high, late/short, late/high) which were randomized within crop management. Those sub-blocks were omitted in the second season because it has shown that differing maturation time is not a problem (all sub-blocks were harvested in parallel) and plant height is quite similar when growth regulators are applied.

The experiments were part of the project BRIWECS (breeding innovations wheat for resilient cropping systems). An overview analysis for context can be seen in Voss-Fels et al. (2019).

Site, Soil, and Weather

The field trials were conducted at the Hohenschulen Experimental Farm (northern Germany, 54°18′51.2″ N 9°59′28.8″ E, 30 m a.s.l). The soil is characterized as a pseudogleyic sandy loam (Luvisol: 170 g kg^{-1} clay, pH 6.7, 13 g kg^{-1} C_{org}, 1.1 g kg^{-1} N_{org} in 0–30 cm). The climate of northern Germany is humid temperate with a long-term mean annual temperature at the location of 8.8°C and mean annual precipitation of 751 mm, whereof 396 mm occur during the main growing season (March–August).

Daily weather was recorded at a station nearby the field trials. In 2016–2017 temperatures below average occurred from the beginning of October to the mid of February with the exception of a warm period during December. A cold period appeared again from mid of April to the mid of May. After a period with low precipitation from November to March, the season was characterized by high precipitation from March until harvest. Levels of global radiation were on average.

In the season 2017–2018 temperatures above average occurred almost during the whole season with the exception of a cold period in February and March. After a period with altering phases of below and above precipitation until the end of April, a long period of very low precipitation until harvest followed. Levels of global radiation were above average in May and July.

In summary, the seasons mainly differed regarding the amount of precipitation after anthesis (**Table 3**) and the phenological development during grain filling as a result of air temperatures and drought (**Table 1**). Weather in comparison to climate during both growing seasons is shown in more detail in **Figure S1**.

Measurements and Calculations

Grain Yield, Biomass, Harvest Index, and Phenology

All plots were harvested by combine between August 8 and August 15, 2017 and on July 27, 2018, respectively. Grain yield was standardized to 100% dry matter. In addition, harvest by hand was performed at 0.5 m along the row in the first season (corresponds to 0.06 m^2) and 1 m along the row in the second season (corresponds to 0.12 m^2) to ascertain the harvest index (ratio of grain dry matter to total dry matter). Harvest by hand took place 6–13 days before combine harvest in 2017 and 4 days before combine harvest in 2018.

Small samples, like the hand harvest, are adequate to measure ratios between fractions but not absolute values. These are appreciable affected by variation inside a plot. As a consequence, we calculated biomass as the ratio of grain yield (combine) and harvest index (hand harvest) to minimize sampling errors.

Lodging and/or damage by game animals occurred in the 2017 season. Plots were visually classified and damaged ones were excluded from the analysis (12%). In the season 2018 no disturbance occurred.

For the detailed analysis of drought, the variables grain yield drop (*GY drop*) and biomass drop (*BIO drop*) are introduced. These are calculated as the difference between the stressed season (2018) and the unstressed season (2017). Consequently, the higher the effect of drought the lower the value (usually more negative).

Phenological stages ear emergence and hard dough were visually classified in the intensive crop management by frequent observations in the relevant periods. These stages refer to the states 59 and 87, respectively, in the BBCH-scale (Lancashire et al., 1991). For statistical analysis both traits were transformed to growing degree days (base temperature 0°C) to improve comparison between both seasons.

Radiation Interception and Radiation Use Efficiency

The amount of intercepted radiation can be described following Beer–Lambert law (Monsi and Saeki, 1953):

$$I = I_0 \times \left(1 - e^{-k \times GAI}\right) \quad (2)$$

where I_0 is the incoming radiation, k the extinction coefficient and GAI the one-sided area of all green plant material per ground area. To focus on interception of productive radiation, the incoming radiation was weighted by a temperature weighting factor as a function of the daily mean temperature. The function ranges between 0 and 1 and is trapezoidal with transition points at 2.5°C, 9.5°C, 20°C, and 35°C. As a consequence, I represents the intercepted effective radiation. The extinction coefficient k is ascertained to be 0.7 (unpublished own measurements) for the whole genotype set. Differences regarding k might occur but are assumed to be of minor importance for radiation interception (sensitivity of k to differing leaf angles is quite low around 45° sun angle, where most radiation occurs at the latitude of the location). Values of GAI were determined for every single plot with a high measurement frequency (at least biweekly during the main growing phase, in total 11,538 data points, **Table 4**) to provide suitable interpolated values for every single day. Calculation of total incoming effective radiation and total intercepted effective radiation starts with the mean day of sowing and ends with the mean day of the phenological stage hard dough

TABLE 3 | The Amount and distribution of precipitation as well as effective PA-radiation during the growing seasons.

	2016–2017		2017–2018	
	Before anthesis	After anthesis	Before anthesis	After anthesis
Precipitation [mm]	400	198	356	24
$PAR_{effective}$ [MJ m^{-2} d^{-1}]	595	442	599	432

TABLE 4 | Date and method of *GAI* measurements.

	Season 2016–2017	Season 2017–2018
Ortho images	Dec. 28, Mar. 9	–
Reflection measurements	Apr. 03, Apr. 19, May 7, May 15, May 23, May 29, Jun. 14, Jun. 19, Jun. 27, Jul. 3, Jul. 13	Dec. 4, Mar. 9, Apr. 9, Apr. 16, Apr. 23, May 3, May 16, May 22, Jun. 1, Jun. 6, Jun. 12, Jun. 20, Jun. 26, Jul. 5,. Jul. 13, Jul. 17

in each season. This represents the period of land use by the analyzed crop. The ratio of total intercepted effective radiation to total effective radiation is hereafter mentioned as fraction of intercepted radiation (*RI*). Radiation use efficiency (*RUE*) was calculated as the ratio of final above-ground biomass to the sum of intercepted effective radiation so the parameter describes the potential *RUE* (when temperature is optimal throughout the whole season).

Green Area Index

Measurements of *GAI* were conducted by two different methods: ortho images and reflection measurements. In the beginning of the first season *GAI* values were tracked using the ortho image method, all subsequent dates were measured using the reflection measurement method. In total, 13 measurement dates exist in the season 2016–2017 and 16 measurement dates exist in the season 2017–2018.

For the calculation of radiation interception, daily values of *GAI* are necessary. For interpolation, locally weighted scatterplot smoothing (LOESS) (Cleveland, 1979) was applied as proposed by Magney et al. (2016) instead of more functional growth curves (e.g. sigmoidal) because events like initiating drought could not be represented adequately by quite rigid growth curves. As LOESS algorithm, the homonymous function in base *R* (R Core Team, 2018) was used. The smoothing parameter α was set to 0.5 in the season 2016–2017 and 0.45 in the season 2017–2018.

Ortho images are RGB photos taken approximately 1.5 m above the ground with a view direction perpendicular to the grounds surface. All pixels are classified in plant as well as ground pixels and the ratio from plant pixels to the total number of pixels (ground cover) closely correlates with the *GAI*. Ortho-images were not taken in every plot because of restricted throughput using this ground-based method. On December 28, 2016 one image for every cultivar and on March 10, 2017 one image for every cultivar management combination was taken.

The RGB images were cropped to reduce angular effects at the border area and each pixel was classified into the groups plant and ground by a support vector machine with linear kernel using the R-package *e107* (Meyer et al., 2017) streamlined by the R-package *caret* (Kuhn, 2017). The algorithm was trained by manually classified pixels (16,629 in total, 99 different images), in doing so 80% of the images were used as training set and 20% set aside as test set. Chosen predictor variables are: red, green, blue, mean red value of the whole image, mean green value of the whole image, and mean blue value of the whole image. Predictors are centered and scaled. The tuning parameter *cost* was set to 0.04 using the largest value in a grid search with 10-fold cross validation. The trained support vector machine is reliably able to differentiate between plant and soil pixels, reaching a sensitivity of 0.88 and a specificity of 0.90 in the test set. Ground cover was calculated for each image as the ratio of plant pixels to total pixels.

Ground cover values were transformed into *GAI* values using the equation 3,

$$GAI = -\frac{\log(T)}{k}, \tag{3}$$

whereof T (transmission) corresponds to 1 – ground cover and k (extinction coefficient) is assumed to be 0.75 on 28 December 2016 and 0.65 on 10 March 2017 to account for the erecting of leaves during development.

Reflection measurements were conducted with the Sequoia camera (Parrot), a multispectral sensor which records simultaneously images in four wavebands: green (550 nm), red (660 nm), red edge (735 nm), and near-infrared (790 nm). Red edge has a bandwidth of 10 nm, all other wavebands have a bandwidth of 40 nm. The Sequoia camera has an incoming light sensor and therefore provides fractional reflection values regarding the incoming radiation. On each measurement date, images of a grayscale target were made for radiometric calibration.

The eBee Plus (senseFly) served as carrier system. It is a lightweight fixed-wing drone operated with the flight manager eMotion 3 (senseFly). The chosen resolution was 8 × 8 cm pixel^{-1} and a high degree of overlap (80% in both directions) was applied which resulted in adequate raw material for post-processing with the photogrammetry software Pix4Dmapper (Pix4D SA., Switzerland). On days with fast-moving clouds, a manual screening of the images was conducted prior post-processing to exclude those images containing both, regions with cloud shadow and full sunlight. The results were four orthogonal reflection maps, one for every waveband. With a RTK-enabled eBee, it is possible to include RINEX-files (Receiver Independent Exchange Format) in the post-flight-processing in eMotion 3. If this function was not available, the reflectance maps were georeferenced manually using the Georeferencer Plugin in *QGIS* (QGIS Development Team, 2019). The extraction of the reflectance data of the sampling spots was undertaken in *R* (R Core Team, 2018) using the package *sf* (Pebesma, 2018), whereby all pixels of a plot were summarized as median.

Reflection values were transformed into *GAI* values using the vegetation index VIQUO (Bukowiecki et al., submitted manuscript). The linear model reaches a MAE of 0.44 m^2 m^{-2} in an independent data set and showed to be stable during the whole growing season (applicability during senescence is demonstrated).

Statistical Analysis

All data processing and statistical analysis were conducted in the statistical environment *R* (R Core Team, 2018), the package *ggplot2* was used for visualizations (Wickham, 2016).

A linear mixed model was used for the analysis of variance of the relationship of cultivar, crop management as well as year with all functional traits (*GY*, *BIO*, *HI*, *RI*, *RUE*):

$$\begin{aligned} P_{ijklm} = \propto + g_i + t_j + y_k + (gt)_{ij} + (yt)_{kj} \\ + (yg)_{ki} + (ytg)_{kji} + B_l + (BT)_{lj} + (BTS)_{ljm} + \varepsilon_{ijklm}, \end{aligned} \tag{4}$$

where P_{ijklm} is the phenotype of the ith cultivar, the jth crop management, the kth year, the lth block and the mth sub-block, μ is the general mean, g_i is the fixed effect of the ith cultivar, tj is the fixed effect of the jth crop management, y_k is the fixed effect

of the kth year, $(gt)_{ij}$ is the fixed interaction of the ith cultivar in the jth crop management, $(yt)_{kj}$ is the fixed interaction of the jth crop management in the kth year, $(yg)_{ki}$ is the fixed interaction of the ith crop management in the kth year, $(ytg)_{kji}$ is the fixed interaction of the ith cultivar in the jth crop management and the kth year, B_l is the random effect of the lth block, $(BT)_{lj}$ is the random interaction of the jth crop management in the lth block, $(BTS)_{ljm}$ is the random interaction of the mth sub-block in the jth crop management and the lth block, and $\varepsilon_{\text{ijklm}}$ is the error term.

The model (and all subsequently described models with random components) was implemented with the package *lme4* (Douglas et al., 2015). Following Type II Wald chisquare test was conducted with the package *car* (John and Sanford, 2011).

For the estimation of variance components for each trait, a fully randomized model was used:

$$P_{ijklm} = \propto + G_i + T_j + Y_k + \left(GT\right)_{ij} + \left(GY\right)_{ik} + \left(TY\right)_{jk} + \left(GTY\right)_{ijk} + \left(YB\right)_{kl} + \left(YBT\right)_{kly} + \left(YBTS\right)_{klym} + \varepsilon_{ijklm}, \quad (5)$$

where P_{ijklm} is the phenotype of the ith cultivar, the jth crop management, the kth year, the lth block and the mth sub-block, μ is the general mean, G_i is the random effect of the ith cultivar, T_j is the random effect of the jth crop management, Y_k is the random effect of the kth year, $(GT)_{ij}$ is the random interaction of the ith cultivar in the jth crop management, $(GY)_{ik}$ is the random interaction of the ith cultivar in the kth year, $(TY)_{jk}$ is the random interaction of the jth crop management in the kth year, $(GTY)_{ijk}$ is the random interaction of the ith cultivar in the jth crop management and the kth year, $(YB)_{kl}$ is the random interaction of the lth block in the kth year, $(YBT)_{klj}$ is the random interaction of the jth crop management in the lth block and the kth year, $(YBTS)_{kljm}$ is the random interaction of the mth sub-block in the jth crop management and the lth block and the kth year, and $\varepsilon_{\text{ijklm}}$ is the error term. The variances of (YB), (YBT) and ($YBTS$) are summed up to the component design.

Adjusted means for every cultivar in every year were calculated prior to the analysis of relationships between traits and year of variety release as well as the stepwise analysis of the contribution of traits to the yield formation to reduce the influence of soil properties and terrain. Because the experimental design (blocks, sub-blocks) did not ameliorate sufficiently, we added a continuous variable to the model which represents the effects of soil and terrain. The variable is calculated by the Papadakis-method (type PAP-8) described by Gezan et al. (2010). The final model for the calculation of adjusted means is:

$$P_{ijkl} = \mu + g_i + t_j + \left(gt\right)_{ij} + soil + B_k + \left(TB\right)_{jk} + \left(STB\right)_{ljk} + \varepsilon_{ijkl}, \quad (6)$$

where P_{ijkl} is the phenotype of the ith cultivar, the jth crop management, the kth block and the lth sub-block, μ is the general mean, g_i is the fixed effect of the ith cultivar, t_j is the fixed effect of the jth crop management, $(gt)_{ij}$ is the fixed interaction of the ith cultivar in the jth crop management, *soil* is the continuous variable accounting for soil properties and terrain, B_k is the random effect of the kth block, $(TB)_{\text{jk}}$ is the random interaction of the jth treatment in the kth block, $(STB)_{\text{ijk}}$ is the random interaction of the lth sub-block in the jth treatment and the kth block, and $\varepsilon_{\text{ijkl}}$ is the error term.

Correlations between traits are calculated with the function *corr* in base *R* (R Core Team, 2018). The package *ggcorrplot* (Alboukadel, 2018) was used for visualizations. For the study of temporal changes, the same analysis is conducted with a 25-years sliding window over year of variety release creating multiple subsets of the dataset. Their results are assigned to the center of the considered period. The results of the first and final ten years are deleted to ensure a sufficient large subset.

The path analysis shows standardized beta coefficients (centered by mean and scaled by standard deviation) for relationships with inherent causal relationship ($GY = BIO \times HI$ and $BIO = RI \times RUE$) and Pearson's correlation coefficients for intercorrelations (*BIO* with *HI* and *RI* with *RUE*). The package *ggraph* is used for the visualization (Pedersen, 2019).

RESULTS

Grain Yield, Biomass, and Harvest Index

Grain yield (*GY*) ranged between 408 and 900 g m^{-2} over all cultivars, crop managements, and experimental years. Median values of crop managements raised from 553 g m^{-2} (extensive), over 653 g m^{-2} (semi-intensive) to 722 g m^{-2} (intensive). Median values of experimental years dropped from 663 g m^{-2} in the growing season 2016–2017 to 618 g m^{-2} in the growing season 2017–2018 (**Figure 1**).

There was a significant main effect of cultivar on *GY*, a significant main effect of crop management, and a significant main effect of experimental year. Additionally, there was a significant interaction effect between cultivar and crop management on *GY*, a significant interaction effect between cultivar and experimental year, and a significant interaction effect between cultivar, crop management, and experimental year. The interaction effect between crop management and experimental year was not significant (**Table 5**). The variance of *GY* was mainly explained by crop management, followed by cultivar. Experimental year is of exceptional low importance, almost only occurring in interaction with other predictors (**Figure 5**).

The absolute drop of *GY* due to drought (*GY drop*) was higher for high *BIO* genotypes in the unstressed season 2017 (r = −0.48), correlations of *GY drop* and the subtraits of *BIO* as well as *GY* itself were consequently strong, too (*RUE:* r = −0.47; *RI:* r = −0.3; *GY:* r = −0.38). Genotypes with later ear emergence were stronger affected by drought, but correlations were very moderate (r = −0.11). *HI* was uncorrelated to *GY drop* (**Figure S4**).

Final biomass (*BIO*) ranged between 935 and 1707 g m^{-2} over all cultivars, crop managements, and experimental years. Median values of crop managements raised from 1131 g m^{-2} (extensive), over 1322 g m^{-2} (semi-intensive) to 1393 g m^{-2} (intensive). Median values of experimental years dropped from 1422 g m^{-2} in the 2016–2017 season to 1211 g m^{-2} in the 2017–2018 season (**Figure 1**).

There was a significant main effect of cultivar on *BIO*, a significant main effect of crop management, and a significant

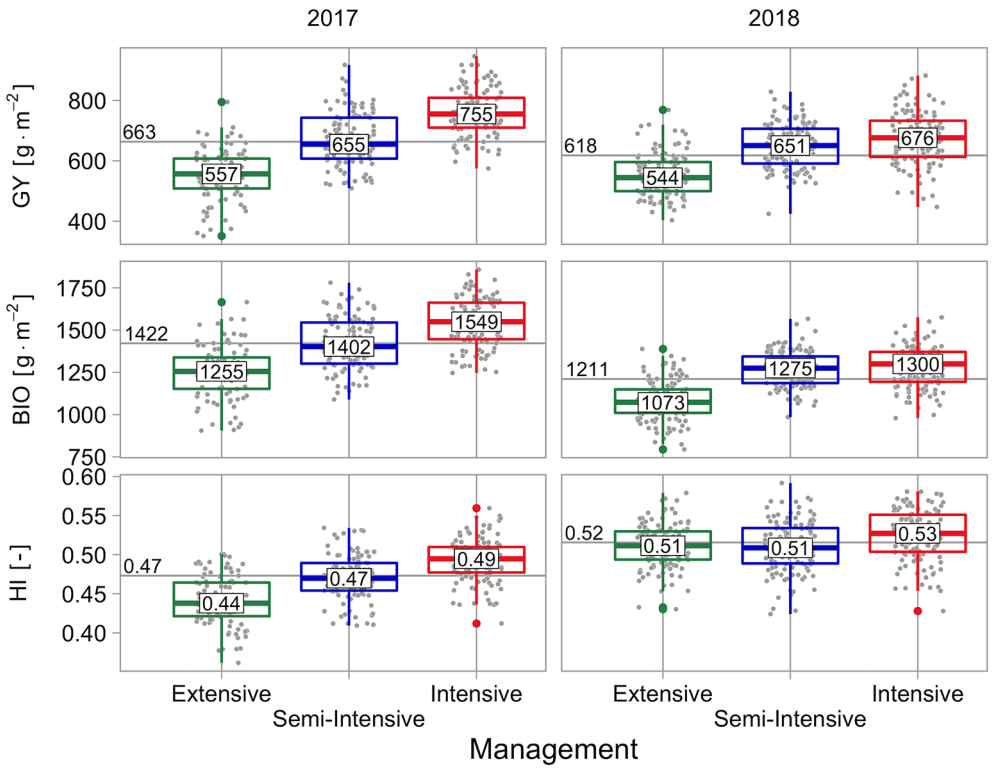

FIGURE 1 | Grain yield (*GY*), final biomass (*BIO*) as well as harvest index (*HI*), grouped by management and experimental year. Values in boxplots reflect the median value of managements within experimental years, horizontal line and its label reflect the median value of the experimental year.

main effect of experimental year. Additionally, there was a significant interaction effect between cultivar and experimental year. The interaction effects between cultivar and crop management, between experimental year and crop management, and between experimental year, crop management, and cultivar were not significant (**Table 5**). The variance of *BIO* was nearly equally explained by crop management and experimental year, whereas cultivar had a quite low contribution (**Figure 5**).

The harvest index (*HI*) ranged between 0.38 and 0.57 over all cultivars, crop managements, and experimental years. Median values of crop managements were nearly unchanged from 0.49 (extensive), over 0.49 (semi-intensive) to 0.51 (intensive). Median values of experimental years showed an increase from 0.47 in the 2016–2017 season to 0.52 in the 2017–2018 season (**Figure 1**).

There was a significant main effect of cultivar on *HI*, a significant main effect of crop management, and a significant main effect of experimental year. Additionally, there was a significant interaction effect between cultivar and experimental year and a significant interaction effect between crop management and experimental year. The interaction effects between cultivar and crop management and between experimental year, crop management, and cultivar were not significant (**Table 5**). The variance of *HI* was mainly explained by experimental year, followed by cultivar. Crop management had a comparatively low contribution and the sum of design and residual term is exceptionally low, indicating a low influence by soil differences and/or low measurement errors (**Figure 5**).

Radiation Interception and Radiation Use Efficiency

Measured values of *GAI* showed a feasible course during both seasons and the applied interpolation method was an adequate compromise between smoothing and sufficient representation of the original data (**Figure 2**). The MAE between interpolated and original data was 0.1 $m^2\ m^{-2}$ in the season 2016–2017 and 0.08 $m^2\ m^{-2}$ in the season 2017–2018, respectively.

After late sowing in the season 2017–2018, values of *GAI* were much lower in early spring but the development of canopies caught up due to a rapid development in May and maximum *GAI* values were quite similar in both experimental years. In 2016–2017 the mean values of the whole cultivar set reached as its maximum peak value: 4.35 $m^2\ m^{-2}$ (intensive), 4.43 $m^2\ m^{-2}$ (semi-intensive), and 3.23 $m^2\ m^{-2}$ (extensive). In the season 2017–2018 they reached: 4.38 $m^2\ m^{-2}$ (intensive), 4.41 $m^2\ m^{-2}$ (semi-intensive), and 3.47 $m^2\ m^{-2}$ (extensive). In late May 2018, drought became severe and *GAI* values dropped rapidly followed by a fast senescence and early ripening (**Figure 2**).

Canopies nearly reached total radiation interception when *GAI* reached its maximum, this was particular the case when abundant nitrogen is supplied (**Figure 3**). In the season 2016–2017 the mean value of the fraction of absorbed radiation over the whole cultivar set reached as its maximum peak value: 95% (intensive), 95% (semi-intensive), and 89% (extensive). In the season 2017–2018 they reached: 95% (intensive), 95% (semi-intensive), and 91% (extensive).

TABLE 5 | Results of ANOVAs for all functional traits.

		DF	$\chi 2$	*p*
Grain yield	Cultivar	41	908.62	<.001
	Management	2	75.22	<.001
	Year	1	4.13	<.05
	Cultivar × Management	82	126.96	<.01
	Cultivar × Year	41	141.60	<.001
	Management × Year	2	5.7	.058
	Cultivar × Management × Year	74	108.05	<.01
Biomass	Cultivar	41	251.28	<.001
	Management	2	51.32	<.001
	Year	1	38.79	<.001
	Cultivar × Management	82	94.78	.16
	Cultivar × Year	41	123.41	<.001
	Management × Year	2	2.9	.23
	Cultivar × Management × Year	74	92.96	.067
Harvest index	Cultivar	41	1421.02	<.001
	Management	2	168.15	<.001
	Year	1	424.64	<.001
	Cultivar × Management	82	96.2	.14
	Cultivar × Year	41	184.17	<.001
	Management × Year	2	58.99	<.001
	Cultivar × Management × Year	74	91.45	.082
Radiation interception	Cultivar	41	322.11	<.001
	Management	2	80.14	<.001
	Year	1	21.11	<.001
	Cultivar × Management	82	110.05	<.05
	Cultivar × Year	41	108.18	<.001
	Management × Year	2	1.91	.38
	Cultivar × Management × Year	74	114.30	<.01
Radiation use efficiency	Cultivar	41	231.12	<.001
	Management	2	17.07	<.001
	Year	1	30.74	<.001
	Cultivar × Management	82	92.89	.19
	Cultivar × Year	41	103.82	<.001
	Management × Year	2	2.44	.29
	Cultivar × Management × Year	74	85.66	.17

The fraction of intercepted radiation (*RI*) ranged between 0.51 and 0.72 over all cultivars, crop managements, and experimental years. Median values of crop managements raised from 0.59 (extensive), over 0.66 (semi-intensive) to 0.67 (intensive). Median values of experimental years dropped from 0.67 in the growing season 2016–2017 to 0.62 in the growing season 2017–2018 (**Figure 4**).

There was a significant main effect of cultivar on *RI*, a significant main effect of crop management, and a significant main effect of experimental year. Additionally, there was a significant interaction effect between cultivar and crop management, a significant interaction effect between cultivar and experimental year, and a significant interaction effect between experimental year, crop management, and cultivar. The interaction effect between crop management and experimental year was not significant (**Table 5**). The variance of *RI* was mainly explained by crop management, followed by experimental year. Cultivar was of low importance, and interaction components are exceptionally low (**Figure 5**).

The radiation use efficiency (*RUE*) ranged between 1.68 and 2.33 g MJ^{-1} over all cultivars, crop managements, and experimental years. Median values of crop managements raised from 1.89 (extensive), over 1.96 (semi-intensive) to 2.03 g MJ^{-1} (intensive). Median values of experimental years dropped from 2.06 g MJ^{-1} in the growing season 2016–2017 to 1.90 g MJ^{-1} in the growing season 2017–2018 (**Figure 4**).

There was a significant main effect of cultivar on *RUE*, a significant main effect of crop management, and a significant main effect of experimental year. Additionally, there was a significant interaction effect between cultivar and experimental year. The interaction effect between cultivar and crop management, between crop management and experimental year, and between cultivar, crop management, and experimental year were not significant (**Table 5**). The variance of *RUE* was mainly explained by experimental year, followed by crop management and cultivar. The

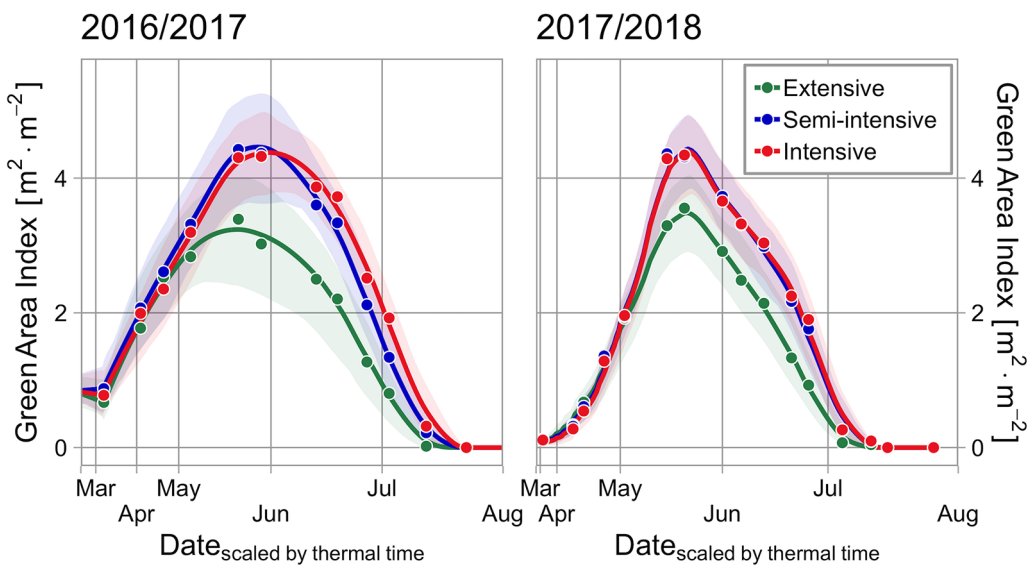

FIGURE 2 | Comparison of *GAI* courses in the season 2016/2017 and 2017/2018. Lines and points represent the mean value of different managements, the pale ribbon indicates the range between the .05 quantile and .95 quantile.

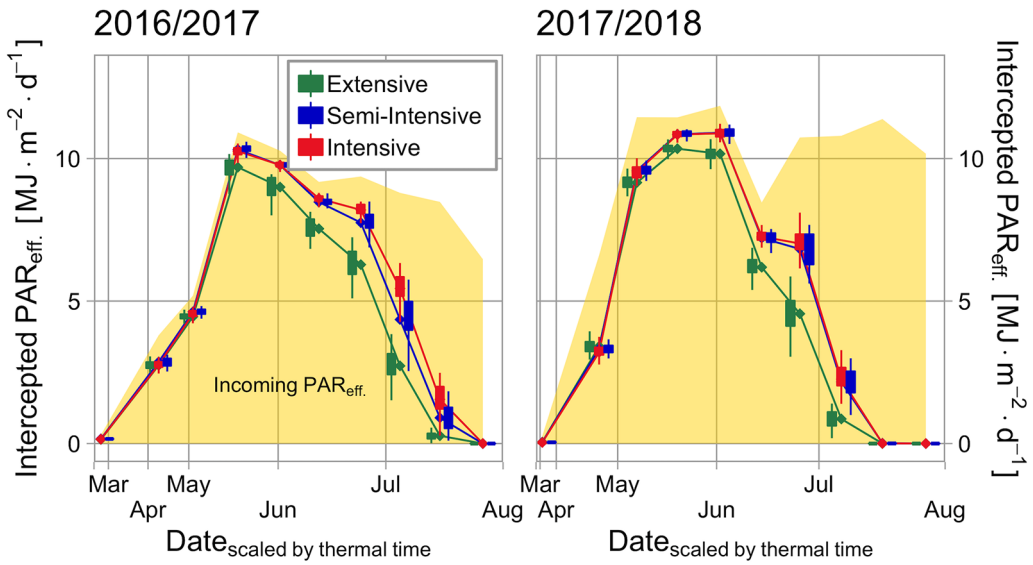

FIGURE 3 | Seasonal course of the amount of intercepted effective radiation in the cultivar set and the incoming effective radiation (yellow area). Both seasons are segmented in 10 equidistant periods and their mean values are presented. Box-whisker-plots are dodged around the mean value (diamond shape), statistical outliers are excluded.

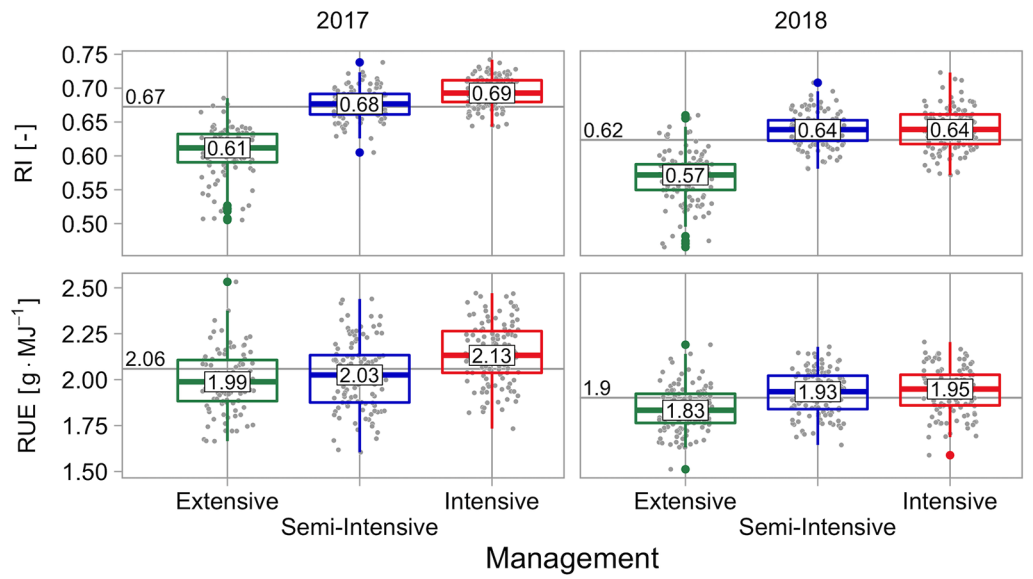

FIGURE 4 | Fraction of intercepted radiation (*RI*) and radiation use efficiency (*RUE*), grouped by management and experimental year. Values in boxplots reflect the median value of managements within experimental years, horizontal line and its label reflect the median value of the year.

sum of design and residual term was exceptionally high, indicating a high influence by soil differences and/or high measurement errors, maybe as a result of blown up errors because the calculation is based upon biomass and intercepted radiation (**Figure 5**).

Breeding Progress

To evaluate the breeding progress related to functional traits, relationships between traits and year of variety release were analyzed. The linear regression models of all traits within year and crop management showed positive slopes and the vast majority of them were significant. Non-significant slopes mainly occurred within the trait *RI* (**Table 6**). The scatterplot of this trait indicates that here, progress and regress alternated during breeding history (**Figure S2**). Progress of the highest-order trait *GY* as the mean of both years was 3.4 g m^{-2} y^{-1} in the intensive crop management, was slightly lower in the extensive management with 3.2 g m^{-2} y^{-1}, and was highest in the semi-intensive management

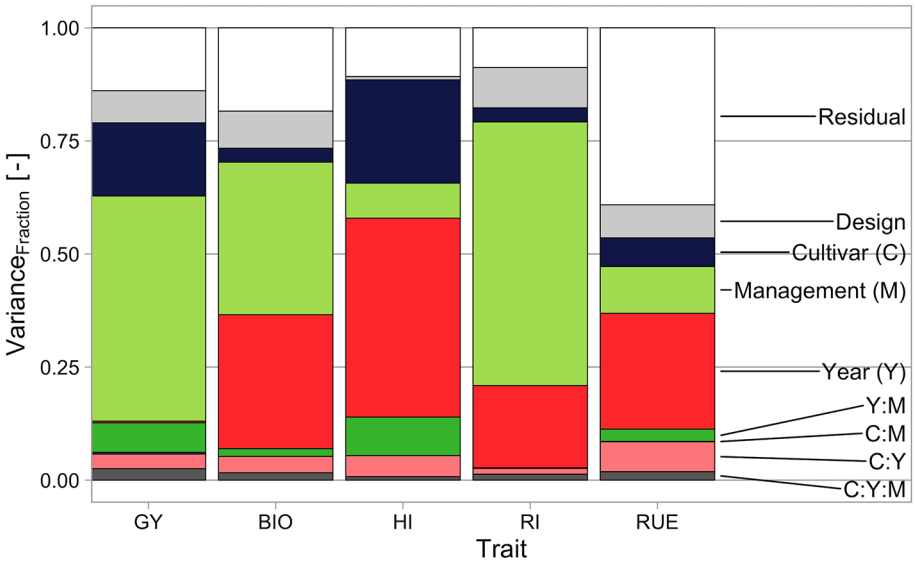

FIGURE 5 | Fraction of variance explained by different variance components for the analyzed traits. *GY*, grain yield; *BIO*, final biomass; *HI*, harvest index; *RI*, fraction of intercepted radiation; *RUE*, radiation use efficiency.

TABLE 6 | Relationship between functional traits and year of variety release.

Trait	Year	Management	R^2	P value	Slope
Grain yield [g m^{-2}]	2017	Extensive	0.58	5.10 e –09 (***)	3.9
		Semi-intensive	0.48	3.40 e –07 (***)	4.2
		Intensive	0.47	4.60 e –07 (***)	3.3
	2018	Extensive	0.47	4.80 e –07 (***)	2.4
		Semi-intensive	0.64	2.40 e –10 (***)	3.7
		Intensive	0.54	3.00 e –08 (***)	3.5
Biomass [g m^{-2}]	2017	Extensive	0.27	3.80 e –04 (***)	4.2
		Semi-intensive	0.30	1.60 e –04 (***)	5.0
		Intensive	0.10	0.038 (*)	2.3
	2018	Extensive	0.29	2.10 e –04 (***)	2.4
		Semi-intensive	0.44	1.60 e -06 (***)	3.3
		Intensive	0.32	1.00 e –04 (***)	3.0
Harvest index [–]	2017	Extensive	0.57	7.80 e –09 (***)	0.0016
		Semi-intensive	0.43	2.20 e –06 (***)	0.0013
		Intensive	0.50	1.70 e –07 (***)	0.0013
	2018	Extensive	0.37	1.70 e –05 (***)	0.0011
		Semi-intensive	0.51	1.20 e –07 (***)	0.0015
		Intensive	0.51	1.10 e –07 (***)	0.0015
Intercepted radiation [MJ m^{-2}]	2017	Extensive	0.18	0.0055 (**)	8.50 e –04
		Semi-intensive	0.07	0.086 (ns)	3.90 e –04
		Intensive	0.04	0.18 (ns)	2.80 e –04
	2018	Extensive	0.03	0.31 (ns)	2.20 e –04
		Semi-intensive	0.20	0.0031 (**)	5.40 e –04
		Intensive	0.06	0.1 (ns)	3.20 e –04
Radiation use efficiency [g MJ^{-1}]	2017	Extensive	0.20	0.0028 (**)	0.0037
		Semi-intensive	0.32	9.40 e –05 (***)	0.0061
		Intensive	0.08	0.062 (ns)	0.0023
	2018	Extensive	0.31	1.30 e –04 (***)	0.0032
		Semi-intensive	0.36	2.50 e –05 (***)	0.0034
		Intensive	0.31	1.40 e –04 (***)	0.0035
Ear emergence [°C]	2017	Intensive	0.08	0.066 (ns)	–0.63
	2018	Intensive	0.05	0.17 (ns)	–0.40

R2, P value, and slope of the linear model trait explained by year of release are shown for every trait, year, and management combination. Comments in parenthesis: P value >= 0.05 (ns), P value < 0.05 (*), P value < 0.01 (**), P value < 0.001 (***).

with 4.0 g m^{-2} y^{-1}. *GY* progress as the mean of all managements within years dropped from 3.8 g m^{-2} y^{-1} in the season 2016–2017 to 3.2 g m^{-2} y^{-1} in the season 2017–2018. Relationships between ear emergence and year of variety release were not significant.

The coefficient of determination was highest for the trait *GY*, with an R^2 value of 0.53 as the mean of all management year combinations and decreased over *HI* (R^2: 0.48), *BIO* (R^2: 0.29), and *RUE* (R^2: 0.26) to *RI* (R^2: 0.10) (**Table 6**).

This decline of the coefficient of determination—going down from grain yield to the sub- and sub-sub-traits—is reflected in a qualitative view on the cultivar set. The straight increase of grain yield was accompanied by a quite vague increase of its functional sub-traits and similar yields can be reached by quite different pathways (**Figure 6**).

	PAR	× RI	× RUE	× HI	= GY
Elixer (2012)	0.69	2.21	0.54		847
Inspiration (2007)	0.70	2.15	0.54		841
Tobak (2011)	0.67	2.10	0.55		801
Tommi (2002)	0.69	2.06	0.54		800
Dekan (1999)	0.65	2.19	0.54		797
Ritmo (1993)	0.68	2.09	0.54		796
Biscay (2000)	0.67	2.07	0.54		776
Türkis (2004)	0.68	2.10	0.53		774
Potenzial (2006)	0.68	2.11	0.52		771
Patras (2012)	0.68	1.98	0.55		769
Hermann (2004)	0.68	2.17	0.50		764
Manager (2006)	0.67	2.10	0.53		763
Drifter (1999)	0.67	2.11	0.52		762
Pegassos (1994)	0.66	2.13	0.53		756
Batis (1994)	0.67	2.19	0.50		755
Sperber (1982)	0.69	2.04	0.51		743
JB Asano (2008)	0.66	2.06	0.52		734
Flair (1996)	0.66	1.99	0.54		731
Ares (1983)	0.64	2.13	0.52		727
Greif (1989)	0.64	2.01	0.55		726
Obelisk (1987)	0.67	2.04	0.51		723
Caribo (1968)	0.67	2.09	0.50		712
Cardos (1998)	0.65	2.03	0.52		711
Disponent (1975)	0.68	2.05	0.50		709
Vuka (1975)	0.69	2.02	0.49		701
Apollo (1984)	0.68	2.00	0.50		700
Kronjuwel (1980)	0.67	1.95	0.51		696
Urban (1980)	0.67	2.05	0.49		694
Tabor (1979)	0.68	2.03	0.48		684
Götz (1978)	0.68	1.98	0.50		678
Akteur (2003)	0.66	1.94	0.51		677
Progress (1969)	0.67	2.00	0.49		677
Kanzler (1980)	0.67	1.91	0.51		671
Kormoran (1973)	0.66	1.98	0.49		670
Kontrast (1990)	0.65	1.98	0.49		661
Alidos (1987)	0.65	1.92	0.50		652
Bussard (1990)	0.66	2.00	0.48		649
Rektor (1980)	0.63	2.12	0.47		644
Diplomat (1966)	0.66	1.96	0.47		632
Highbury (1968)	0.64	1.89	0.49		620
Monopol (1975)	0.66	1.95	0.45		609
Carimulti (1975)	0.66	2.04	0.45		604

FIGURE 6 | Combination of functional traits in the cultivar set. Mean values of the intensive crop management over both experimental years are shown. Values in parentheses specify the year of release.

Besides the analysis of temporal changes of functional traits, an analysis of their importance to the formation of their higher-order traits (*GY* = *BIO* × *HI*, *BIO* = *RI* × *RUE*) is of interest. Even a trait without any temporal trend can be of high importance for the explanation of differences between cultivars.

Standardized beta coefficients of the linear model *GY* = *BIO* × *HI* were higher for *BIO* in the growing season 2016–2017, in the growing season 2017–2018 *HI* and *BIO* were roughly of equal importance, except in the extensive crop management where the relationship was nearly unchanged. Both traits were nearly uncorrelated in the intensive crop management during the first season but moderate to strong correlated in all other management year combinations (**Figure 7**).

Standardized beta coefficients of the linear model *BIO* = *RI* × *RUE* were higher for *RUE* in all management year combinations and the coefficient of *RI* was especially low in the semi-intensive management during the first season, indicating that infections primarily affected radiation use efficiency. Semi-intensive and intensive crop management behaved quite similar in the second season which reflects the low infection pressure in the second season. Coefficient of *RI* was comparatively high in the extensive crop management. Both traits were moderately correlated in the 2017 season and only weak correlated in the 2018 season (**Figure 7**).

A broader view of correlations between all functional traits showed that no negative intercorrelations existed. Except the correlation between *HI* and *BIO* (as well as *RI* and *RUE*) in the intensive crop management and the non-drought experimental year, these positive correlations were surprisingly high. In the season 2017, later ear emergence was moderately positive correlated to *RI* and *BIO* and moderately negative correlated to *HI*. In the season 2018, ear emergence was nearly uncorrelated to all other traits (**Figure S3**).

The preceding static view is complemented with a dynamic view in the intensive crop management. The importance of *BIO* outpaces the importance of *HI* around the year 1990 (**Figure 8**, left). On the contrary, the distance between *RUE* and *RI* diminished in the 90s. Interestingly, correlation between both traits increased appreciable at the same time (**Figure 8**, right).

DISCUSSION

Grain Yield, Harvest Index, and Biomass

In contrast to the yield stagnation observed in the agricultural practices (Lin and Huybers, 2012), *GY*, as the mean value of all management year combinations, increased with 3.5 g m^{-2} y^{-1} between 1966 and 2012 and the data clearly showed that this progress continues. Yield progress was usually higher when growing conditions were less optimal like it has been shown by Voss-Fels et al. (2019). The extensive crop management in the experimental year 2018 (drought) with an increase of 2.4 g m^{-2} y^{-1} was an exception. Less mineralization might have resulted in very low N supply which could have been a resource limitation for higher yields (**Table 6**). All growing conditions included, *GY* of more recent cultivars was always higher than that of older ones. This absolute yield under diverse growing conditions—unlike

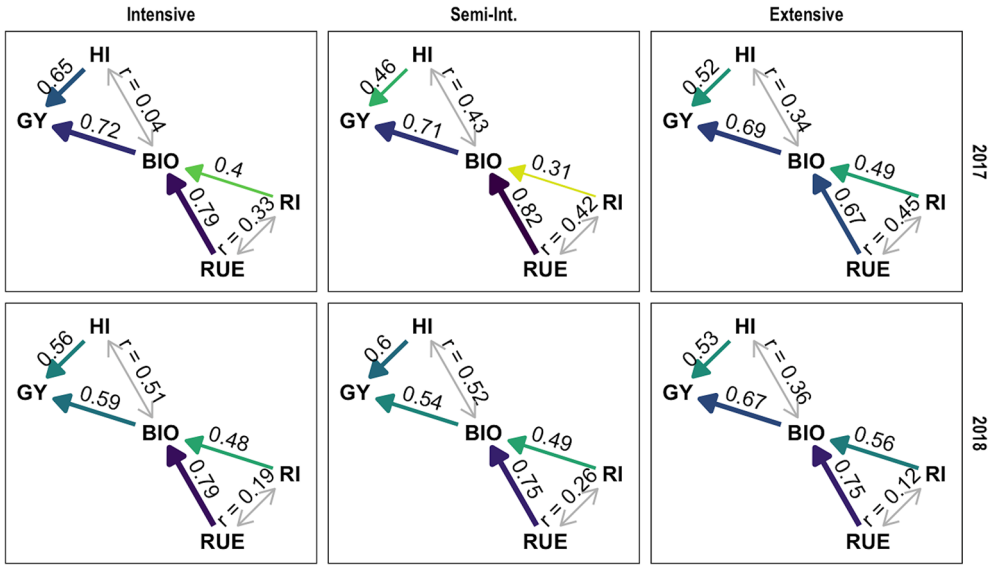

FIGURE 7 | Path analysis of functional traits during breeding history, grouped by growing seasons and crop management. Implicitly causal relationships show standardized beta coefficients (one headed arrow) other relationships show Pearson's correlation coefficient (two headed arrow).

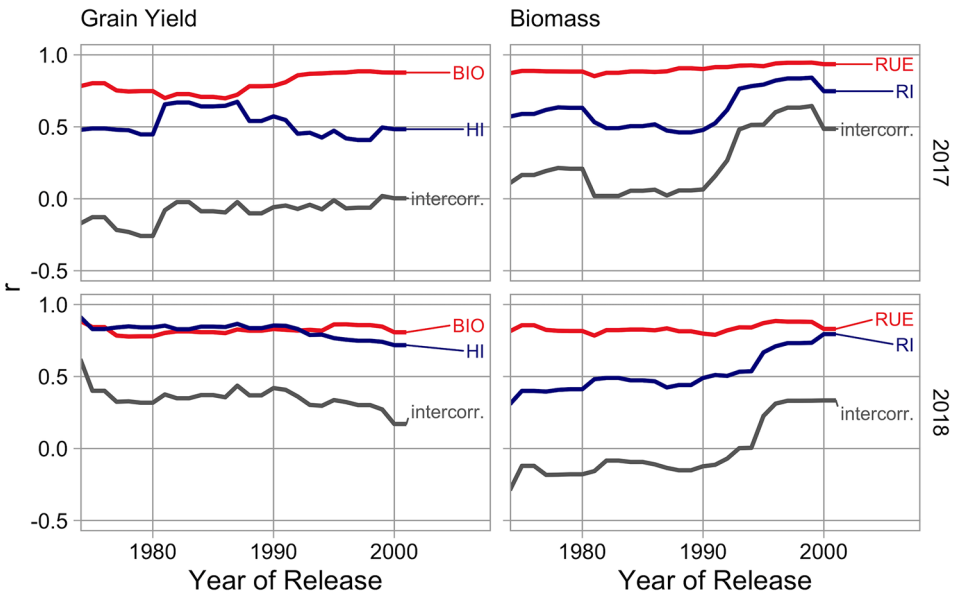

FIGURE 8 | Temporal changes of the contribution of traits during breeding history in different growing seasons in the intensive crop management. Left: Correlation between grain yield (*GY*) and harvest index (*HI*) as well as biomass (*BIO*). Right: Correlation between biomass (*BIO*) and radiation interception (*RI*) as well as radiation use efficiency (*RUE*). The component intercorr. is the correlation between explanatory variables.

some definitions of yield stability—is the most relevant measure regarding food security (Snowdon et al., 2019).

GY is mainly influenced by crop management, followed by cultivar and experimental year (mainly occurring in interaction with crop management) (**Figure 5**). The effect of drought in 2018 might be underestimated due to both suboptimal crop managements. Here, the effects are biased due to differing infection pressure and the uniform application of growth regulators in the second experimental year that shifted the *HI* of the extensive crop management considerably upwards (**Figure 1**). The yield drop of 10% in the intensive crop management represents best the observed effect of drought. Notably, the biomass drop of 16% was partly compensated by an increase in *HI* (**Figure 1**).

High biomass genotypes in the unstressed season (2017) were stronger affected by drought, reflecting the tight coupling

of biomass production and transpiration. On the contrary, *HI* is a resource neutral trait and was uncorrelated to *GY drop*. Earlier ear emergence had a small positive influence on the effect of drought (**Figure S4**).

HI showed, with a mean R^2 of 0.48 of all relationships to year of variety release, the most directional development during breeding history of all subtraits (**Table 6**). This might have two reasons: it is the most considered subtrait by breeders and it is resource neutral. Additionally, until it eventually reaches some physiological boundaries (Berry et al., 2007), it might have very little negative interactions with other subtraits.

Maximum values of *HI* reached 0.55 (**Figure 6**), a value slightly higher than previously reported ones: 0.46 (Brancourt-Hulmel et al., 2003), 0.50 (Schittenhelm et al., 2019), 0.52 (Rose et al., 2017), and 0.53 (Shearman et al., 2005). They slowly approach the theoretical thresholds, hypothesized by Austin (1980) (0.62), Foulkes et al. (2010) (0.64), and Shearman et al. (2005) (0.66).

The contribution of *BIO* and *HI* to the breeding progress of *GY* is a frequently researched question. Many studies observe an exclusive explanation of the progress regarding *GY* by an increase in *HI* (Austin, 1980; Austin et al., 1989; Siddique et al., 1989; Slafer and Andrade, 1989; Brancourt-Hulmel et al., 2003; Acreche et al., 2008; Tian et al., 2011; Zheng et al., 2011), other studies show a contribution of both traits (Hucl and Baker, 1987; Donmez et al., 2001; Shearman et al., 2005; Sanchez-Garcia et al., 2013; Beche et al., 2014; Gaju et al., 2016), and only a few studies detect no influence of *HI* (Waddington et al., 1986; Silva et al., 2014).

We observed a slightly higher correlation between *GY* and *BIO* than with *HI*. The contribution of *HI* was increased in the second experimental year with drought (**Figure 7**) and was variable in the breeding history (**Figure 8**). This dependency on environment and cultivar set corresponds to the variability of results in the literature. The contribution of *HI* decreased in recent breeding history (**Figure 8**) and latest cultivars consistently reach values above 0.5 in the intensive crop management (**Figure S2**). It seems like best cultivars recently converge to theoretical maximum values and potential for improvements are slowly diminishing but the trait should not be regarded as settled. *HI* and *BIO* were nearly uncorrelated in the intensive crop management during the first season but moderately to highly correlated in all other management year combinations (**Figure 7**), indicating that all types of stress are mainly affecting grain filling and consequently both traits in parallel.

HI was moderately negatively correlated to ear emergence (**Figure S3**), so early flowering was one component of high *HI* values, but a big part of variation was independent of it.

Radiation Interception and Radiation Use Efficiency

The challenge of an adequate mapping of *GAI* values during the whole season was implemented with a multispectral approach proposed by Bukowiecki et al. (submitted manuscript). The expansion of the application of spectral reflection measurements to the phase of senescence with vegetation indices, like the NDVI, has been shown before (Lopes and Reynolds, 2012). We extended this approach with a more functional perspective—going from the measurement of *GAI* to the calculation of *RI*. The resulting courses during senescence (**Figure 2**) are in agreement with multiple authors who interpolated this phase by some logistic-alike model with an accelerating and decelerating phase (Pepler et al., 2005; Christopher et al., 2008; Vijayalakshmi et al., 2010; Christopher et al., 2014; Christopher et al., 2016; Luo et al., 2018).

Due to nearly complete interception during full canopy development, differences in the cultivar set regarding *RI* mainly occurred in early and late season (**Figure 3**). These phases correspond to the key words "early vigor" and "stay green." High genetic variability for these traits has been shown before: "early vigor" (Turner and Nicolas, 1998; Rebetzke et al., 2001; Rebetzke et al., 2004; Maydup et al., 2013; Zhang et al., 2014), "stay-green" (Joshi et al., 2007). In comparison, "stay green" was of much higher importance because here, cultivar differences coincide with high incoming radiation. Both traits differentiated more in the season 2017–2018. This might be linked to late establishment intensified by high incoming radiation in April and May ("early vigor") (Moore and Rebetzke, 2015) and drought ("stay green") (Idso et al., 1980; Christopher et al., 2008; Graziani et al., 2014; Thomas and Ougham, 2014; Christopher et al., 2016; Christopher et al., 2018). Under reduced nitrogen supply (extensive crop management), appreciable differences of *RI* do occur in mid-season, too (**Figure 3**). Here, maximum *GAI* values are on a level where genotypic differences regarding *GAI* do result in noticeable differences for radiation interception (exponential term of Beer-Lambert law). Consequently, the importance of radiation interception for the explanation of final biomass is highest in the extensive crop management (**Figure 7**).

Like Kitonyo et al. (2017) have shown for delayed senescence, we did not detect a linear trend of radiation interception in most management year combinations with the year of variety release (**Table 6**). It seems like progress and regress alternated during breeding history regarding this trait (**Figure S2**).

We were not able to differentiate between cosmetic and functional "stay-greens" which is in general difficult in large field trials (Rebetzke et al., 2016) but a multitude of authors have shown a linking between chlorophyll content and net photosynthetic rate during senescence (Luo et al., 2006; Waters et al., 2009; Derkx et al., 2012; Naruoka et al., 2012). This indicates that the functional type of "stay green" is rather the rule than the exception in wheat. Nonetheless, occurring non parallel progression of *GAI* and photosynthesis might result in low values of *RUE*, as discussed later.

RUE ranged between 1.68 and 2.33 g MJ^{-1} over all cultivars, crop managements, and experimental years and was highly affected by all occurring forms of stress—drought, nitrogen deficiency, and pests. The effect of drought is reflected in the drop of −0.15 g MJ^{-1} from the experimental year 2017 (non-drought) to the year 2018 (drought), the effect of nitrogen deficiency in the drop of −0.1 g MJ^{-1} from the semi-intensive to the extensive crop management in the experimental year 2018 (very low infection

pressure), and the effect of pests in the drop of −0.1 g MJ^{-1} from the intensive to the semi-intensive crop management in the experimental year 2017 (high infection pressure). In comparison to management and experimental year, the variance component of cultivars is low but a quite high and significant interaction between cultivar and experimental year occurred (**Figure 5**).

The observed values are lower than reported ranges by Shearman et al. (2005) between 2.33 to 2.64 g MJ^{-1}, Sadras et al. (2012) between 1.54 to 2.68 g MJ^{-1} and the range from 2.29 to 2.57 g MJ^{-1} we observed in a preceding trial (Rose et al., 2017). The lower end of the range is highly depending on the minimum year of release of the cultivar set and the amount of occurring stresses, but the upper end should be on a similar level.

The calculation of *RUE* requires an adequate description of radiation interception, so most authors (and the mentioned studies) confine themselves to the pre-anthesis phase. Due to a new calibration of a multispectral sensor (Bukowiecki et al., submitted manuscript) we were able to expand the calculation until harvest. We hypothesize that the *RUE* during senescence is reduced due to the degradation of rubisco and assume that this is the reason for comparably low values.

RUE showed a significant linear increase during breeding history except in the intensive crop management during the season 2016–2017 (non-drought) (**Table 6**). Slopes range between 0.0023 and 0.0061 g MJ^{-1} per year and are much lower than reported values by Sadras et al. (2012), 0.012 g MJ^{-1} per year. In their Mediterranean environment, evapotranspiration is much higher than rain during the growing season. These results indicate that historical trends of *RUE* should not only be seen in the context of photosynthesis but in the context of the possibilities of genotypes to cope with adverse growing conditions (drought, nitrogen deficiency, pests). Additionally, Sadras et al. (2012) showed the link of *RUE* to canopy traits instead of photosynthesis per se. Here, a better light distribution leads to an increased canopy photosynthesis (Zhu et al., 2010).

In comparison, *RUE* is of higher importance for the explanation of *BIO* than *RI* but nearly equal levels are reached in the extensive crop management (**Figure 7**). A more detailed analysis of temporal changes in the intensive crop management showed that *RI* was clearly less important for most of the breeding history but became nearly equally important during the nineties (**Figure 8**). Both traits are positively correlated which might express that beside the phenological component of "stay green" it also just reflects the ability to cope with the external factors: drought, nitrogen depletion, and fungal infections (Richards, 2000; Rebetzke et al., 2016). Additionally, results of Zhang et al. (2006) suggest, that prolonged retention of high chlorophyll concentrations can be in certain cases an indirect indicator for higher levels of rubisco in previous phases, instead of the direct cause of increased light absorption. A lower intercorrelation in the experimental year 2018, with occurring drought, might reflect a negative relationship between water use (high radiation interception) and water supply in a later phase (low radiation use efficiency). *RI* was moderately correlated to ear emergence (**Figure S3**), so later flowering was one component of high *RI* values, but a big part of variation was independent of it.

Breeding Progress—Past and Future

Our results show that the stagnation of wheat yields in Central-Europe, is not accompanied by an ending of breeding progress. The coefficient of determination of the linear relationships with year of variety release was highest for the trait *GY*, with an R^2 value of 0.53 as the mean of all management year combinations and decreased over *HI* (R^2: 0.48), *BIO* (R^2: 0.29), and *RUE* (R^2: 0.26) to *RI* (R^2: 0.10). This reflects the main procedure in breeding—a selection for higher *GY*. The functional background is usually unknown and progress in *GY* is often accompanied by regress in some of its sub-traits (**Figure 6**). The combination of best performers in the sub-traits: *HI*, *RUE*, and *RI* for crosses is an appealing approach but negative relationships between these traits should exist. Conversely, all traits in the analyzed cultivar set are positively correlated (**Figure S3**) but it must be kept in mind that nearly 50 years of indirect parallel selection for better *HI*, *RUE*, and *RI* constitute the genetic material. Phenotyping of lower level functional traits (*RI*, *RUE*, *HI*) in combination with genotyping would help to detect QTLs which might be assignable to some quite stable trait (e.g. leaf angle, specific leaf area, initiation of senescence). This might help to understand the complex interaction of genotype and environment.

Time of ear emergence was nearly unchanged during the breeding period (**Table 6**) and showed little variation (**Table 1**) which reflects quite strict conceptions of optimal flowering time by local farmers and the consideration of this requirement by breeders.

A frequently manifested hypothesis is that plant breeding brought *HI* and *RI* close to their theoretical maxima and only *RUE*, determined by photosynthesis, is left for improvements, e.g. Long et al. (2006). Our results, representing breeding history in Central-Europe, only partly agree with this assumption. The contribution of *HI* for the explanation of *GY* diminishes since around 1990 (**Figure 8**) but modern cultivars do not finally reach theoretical maximum values (**Figure 6**). So, progress might still be possible, but a lower rate has to be expected. Regarding *RI*, in contrast to the mentioned hypothesis improvements continue and are becoming more important in recent years (**Figure 8**). Slopes of linear relationships between *RI* and year of variety release are in most management year combinations not significant (**Table 6**) and some high yielding cultivars express low values in this trait (**Figure 6**). This indicates, not a level around a theoretical maximum, but exploitable variation. As a restriction it has to be stated, that high *RI* genotypes may be more affected by drought stress and late ripening cultivars are not always accepted by farmers, especially in humid regions as the risk of high grain moisture contents at harvest increases.

The progress in the development of small unmanned drones, in combination with calibrated spectral sensors allows comparable low-cost high-throughput phenotyping of this trait. Due to its close correlation with final biomass, especially under suboptimal nitrogen supply (**Figure 7**), *RI* might serve as a proxy for biological performance in early breeding generations when yield cannot be reasonable ascertained.

As we discussed earlier, the stagnation of wheat yields in Central-Europe is not caused by a lack of breeding progress-so

other reasons have to be responsible. The analysis of variance components shows that the impact of crop management and experimental year (mainly water supply) on *GY* and its sub-traits was much higher than that of cultivar (**Figure 5**). The reasons for yield stagnation might belong in this sphere.

CONCLUSION

Our results show that the stagnation of wheat yields in Central-Europe, is not accompanied by a lack of breeding progress. This equally applies to suboptimal growing conditions like restricted pesticide applications and limited water- or nitrogen-supply. Besides the ongoing increase in grain yield (*GY*), nearly all sub-traits showed a parallel development, but relationships are weaker on the lower levels of yield formation. One exception of this steady breeding progress is radiation interception (*RI*), here, phases of progress and regress alternate. Differences in the cultivar set mainly occur in the phase of senescence. In combination with the strong contribution of *RI* to biomass production (*BIO*), the nondirectional development in the past indicates some exploitable potential for breeders. Additionally, we have demonstrated that the trait can be measured with a non-destructive high-throughput approach. Biomass itself is getting more important in comparison to harvest index (*HI*). Values of harvest index are slowly approaching theoretical maxima and correlations with grain yield are decreasing.

The detailed analysis of yield formation reveals that high-yielding cultivars often underperform in some sub-traits. A better knowledge of these functional traits during the breeding process might help to enable an even straighter yield progress.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

TR was responsible for the data acquisition in the field and all data processing as well as data analysis. HK contributed by the formulation of the main research ideas and accompanied the process of manuscript writing.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2019.01521/full#supplementary-material

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Physiological Basis of Genotypic Response to Management in Dryland Wheat

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A great majority of dryland wheat producers are reluctant to intensify management due to the assumption that lack of water availability is the most critical factor limiting yield and thus, the response to management intensification would be limited. We conducted on-farm field experiments across three locations and two growing seasons in Kansas using 21 modern winter wheat genotypes grown under either standard (SM) or intensified management (IM) systems. The goals of this study were to (i) determine whether the SM adopted is adequate to reach achievable yields by farmers in the region and (ii) identify differences in responsiveness to IM among a range of modern genotypes. Across all sites-years and genotypes, the IM increased yield by 0.9 Mg ha^{-1}, outyielding the SM system even in the lowest yielding conditions. As expected, the yield response to IM increased with the achievable yield of the environment and genotype. Across all sources of variation, the yield responsiveness to IM was related to increased biomass rather than harvest index, strongly driven by improvements in grain number (and independent of changes in grain weight), and by improvements in N uptake which resulted from greater biomass and shoot N concentration. The IM system generally also increased grain N concentration and decreased the grain N dilution effect from increased yield. Genotypes varied in their response to IM, with major response patterns resulting from the combination of response magnitude (large vs. small) and consistency (variable vs. consistent). Genotypes with high mean response and high variability in the response to IM across years could offer greater opportunities for producers to maximize yield as those genotypes showed greater yield gain from IM when conditions favored their response. For the background conditions evaluated, intensifying management could improve wheat yield in between c. 0.2 and 1.5 Mg ha^{-1} depending on genotype.

Keywords: wheat, *Triticum aestivum* L., nitrogen economy, yield components, crop management intensification, agronomic traits

INTRODUCTION

Wheat (*Triticum aestivum* L.) is critical for food security as it provides c. 20% of calories and protein of human daily nutrition requirements (Shewry and Hey, 2015). It is the crop cultivated across the largest acreage in the world (more than 200 million hectares year^{-1}; FAO-AMIS, 2018), and is mostly (80%) grown under rainfed conditions (FAO, 2003). Many of these regions produce rather variable, though overall relatively low, yields mainly due to the exposure to water stress. Rainfall in these regions is characteristically variable from season to season and is generally insufficient to maximize yield (FAO, 2003; Reynolds, 2010).

Farmers in most of these dryland regions are reluctant to intensify agronomic management. One major reason is the assumption that lack of water availability will limit yield potential and intensified management will provide no benefit, as expected from the Liebig's "law of the minimum." However, this reluctance may be unjustified as several empiric and theoretical frameworks show the inadequacy of this "law" (De Wit, 1992; Sinclair and Park, 1993). In fact, crop yields could be enhanced when there is colimitation of different factors [i.e., when different resources are similarly limiting rather than when growth is severely limited by a single factor (Sadras, 2004; Cossani et al., 2010; Cossani and Sadras, 2018)]. The proven inadequacy of Liebig's "law of the minimum" implies that the most limiting factor could be used more efficiently when increasing the availability of other factors through intensifying management (Sadras, 2005). Moreover, the high costs of inputs and low wheat market prices drive farmers to reduce investments on crop management (Jaenisch et al., 2019). Thus, conservative behavior of farmers regarding intensification of management in dryland wheat regions may prevent them from achieving higher yields, even in the lowest yielding environments. Good empirical evidence of this is that Australian wheat yields have increased consistently due to reducing biotic stresses (nematodes) and increasing N fertilization (Passioura, 2002), even though water availability has not improved in Australia (Hochman et al., 2017).

Kansas is the largest winter wheat producing state in the US (c. 15% of the total US production, growing wheat in c. 3.4 Mha; USDA-NASS, 2018a), and experiences constraints to production which are typical of dryland wheat producing regions of the globe. Average farm yields have been relatively low (c. 3 Mg ha^{-1} during the past 30 years; FAO-AMIS, 2018) mainly due to highly variable, and overall scarce level of, rainfall (Lollato et al., 2017; Araya et al., 2019). Farmers in Kansas tend to be conservatively averse to risk, limiting the use of inputs due to the expectation on inconsistent yield responses. Perhaps contributing to this conservative behavior, wheat variety trials in Kansas evaluate the performance of genotypes under farmers' standard management rather than managing varieties for their yield potential. However, similar to other wheat regions (e.g., Cossani et al., 2011), there is empirical evidence in Kansas (Jaenisch et al., 2019) that wheat yields may improve by intensifying rainfed management practices.

The two major inputs that might be inadequately managed in standard management systems in Kansas are nitrogen (N) fertilization and chemical protection against foliar fungal diseases (Lollato et al., 2019a). Nitrogen fertilization rates in Kansas average c. 60 kgN ha^{-1} (USDA-NASS, 2018b), which is considerably lower than the estimated long-term agronomic optimum rate of the region (c. 90 kgN ha^{-1}; Lollato et al., 2019b). Nitrogen limitation early in the growing season can reduce wheat tiller formation and survival, consequently reducing the number of spikes produced per unit area (Borghi, 1999; Montemurro et al., 2007) and the floret survival, resulting in reductions in grains per spike (Albrizio et al., 2010; Ferrante et al., 2013). Fertile tiller and grains per spike are major regulators of wheat yield (Slafer et al., 2014), thus lack of adequate N fertilization may limit water use and water use-efficiency (Asseng et al., 2001; Sadras and Roget, 2004; Cossani et al., 2012), even in dryland wheat production. Moreover, inadequate N availability during grain filling can reduce grain N concentration (Oury and Godin, 2007; Lollato et al., 2019a), which is a critical determinant of wheat end-use quality. Likewise, only about 25% of the wheat grown in Kansas is typically protected with foliar fungicides (USDA-NASS, 2018a). Severe incidence of foliar diseases can reduce wheat yield by lowering the source-sink ratio (Serrago et al., 2019). Moreover, even though the types and severity of fungal diseases (e.g., stripe rust [Puccinia striiformis f.sp. tritici] and leaf rust [Puccinia triticina]) vary depending on weather and genotypes, yield penalties due to diseases are common, as empirically evidenced by Jaenisch et al. (2019) and Lollato et al. (2019b). Furthermore, there has been an increase in stripe rust disease pressure and evolution of new pathogen races in recent years (DeWolf et al., 2017), which has challenged breeding programs to identify new sources of genetic resistance quickly. Thus, we believe that rainfed wheat in Kansas, and in dryland wheat growing regions in general, is likely grown under conditions that are chemically underprotected against foliar diseases that frequently reduce yield (USDA-NASS, 2018a) and where soil N availability is noticeably lower than the demand of the crop. Therefore, we hypothesize that current yields in this region are below those achievable under more intensive management in the form of higher N availability and chemical protection against diseases.

Although this hypothesis is proposed in general for modern wheat genotypes, different magnitudes of responsiveness to management intensification would be expected for specific genotypes. Thus, the hypothesis was tested considering a wide range of genotypes available to farmers in the region, allowing recognition of the level of genotypic variation and concurrently providing insight for breeding genotypes more responsive to intensive management. Future yield improvement in this (and any other) dryland region requires recognition of genetics characteristics underlying responsiveness to intensified management. Understanding agronomic traits associated with genotypic responses to management and yield determination can help breeding programs develop better adapted genotypes and enable producers to maximize yield while maintaining environmental quality.

We carried out field experiments with 21 modern winter wheat genotypes grown across three locations and two growing seasons in Kansas under either standard (SM) or intensified management (IM) systems to:

(i) determine whether the SM used in Kansas is adequate to reach achievable yields by farmers in the region by (i.a) quantifying the response to an IM system of improved N availability and protection against diseases, as well as, (i.b) ascertaining crop-physiological traits associated with yield responsiveness to IM across environments and genotypes; and
(ii) recognize genotypic differences in responsiveness to IM among a range of modern cultivars, identifying degrees of overall responsiveness (expectedly from very responsive to mostly unresponsive) together with consistency in responsiveness to IM.

MATERIAL AND METHODS

General Experiment Information

Five rainfed field experiments were established in actual farmers' fields (i.e., the background conditions were those of real farms, not experimental fields) of three locations in Kansas (Conway Springs, Ellsworth, and McPherson) during two growing seasons: 2015–2016 and 2016–2017 (**Table 1**). The soil type was Bethany silt loam (fine, mixed, superactive, thermic pachic paleustoll) for Conway and Crete silt loam (fine, smectitic, mesic pachic udertic argiustolls) for Ellsworth and McPherson. The average yield recorded by farmers for the past 3–5 years before the establishment of the field trials in these fields was 3.3 Mg ha^{-1} for Ellsworth and 4.0 Mg ha^{-1} for Conway and McPherson.

Conventional tillage was performed in the fall prior to wheat sowing in Ellsworth and McPherson, while a no-till system was used in Conway. Sowing and harvesting dates were within the optimal ranges in all cases (**Table 1**). Field trials were sown with a six-row Hege small plot cone drill. Plots were 4.6 m long and 1.5 m wide, comprised by six rows 0.25 m apart. At all sites, the seeding rate was 101 kg ha^{-1} [a weight-basis seeding rate being the usual recommendation for the region (Shroyer et al., 1997), due to the relative small variability in seed size among the most common cultivars]. Insect and weed occurrence was minimal and controlled with commercially available chemical products as needed. Weather data (**Table 2**) was collected daily (from sowing to harvest) from the Kansas Mesonet (http://mesonet.k-state.edu/) climate monitoring network from stations located near (c. 500 m) to the experimental sites. Soil fertility was evaluated within 2 weeks after sowing in all locations (**Table 3**). Soil samples were collected between plots to avoid plant and soil

TABLE 1 | Experiment information. Site-years, plot coordinates, sowing and harvesting dates, previous crop, and total N rate (kg ha^{-1}) for standard management (SM) at each location during the 2015–2016 and 2016–2017 growing seasons.

Year	Location	Coordinates	Sowing date	Harvesting date	Previous crop	N rate SM (kg ha^{-1})
2015–2016	Conway	37°27'34.94"N 97°37'43.33"W	10/13/2015	6/7/2016	soybean	157
	McPherson	38°15'56.99"N 97°35'34.04"W	10/7/2015	6/28/2016	wheat	106
	Ellsworth	38°35'37.99"N 98°19'58.18"W	10/7/2016	6/27/2017	wheat	67
2016–2017	Conway	37°27'36.7"N 97°37'48.3"W	10/11/2016	6/22/2017	corn	101
	McPherson	38°15'50.83"N 97°35'33.36"W	10/11/2016	6/20/2017	wheat	101

TABLE 2 | Weather information. Cumulative precipitation (Cum PPT) in millimeters, maximum, minimum, and average daily temperature (T) in Celsius during the growing season and average of 30 years (1981–2011), cumulative growing degree-days (Cum GDD) in Celsius, and cumulative evapotranspiration (Cum ET) in millimeters per day at each location during the 2015–2016 and 2016–2017 growing seasons.

Year	Site	Season	Cum PPT (mm)	30-yr avg Cum PPT (mm)	T max °C	T min °C	T avg °C	30-yr avg T max °C	30-yr avg T min °C	Cum GDD (°C)	Cum ET (mm day^{-1})
2015–2016	Conway	Fall	189	148	15	2	*8*	14	1	699	148
		Winter	80	133	13	–2	*5*	10	–3	658	198
		Spring	494	324	26	13	*20*	25	13	1,919	447
	McPherson	Fall	117	125	15	2	*8*	14	1	963	159
		Winter	39	119	11	–2	*4*	12	–1	772	187
		Spring	351	325	25	12	*19*	24	11	1,982	426
2016–2017	Ellsworth	Fall	30	108	15	–1	*7*	13	–1	783	*NA*
		Winter	135	102	12	–2	*5*	9	–6	615	172
		Spring	239	276	25	11	*18*	24	11	1,573	383
	Conway	Fall	36	148	15	1	*8*	14	1	566	202
		Winter	187	133	13	0	*7*	10	–3	443	244
		Spring	332	324	25	12	*19*	25	13	1,284	391
	McPherson	Fall	43	125	14	1	*8*	14	1	524	151
		Winter	132	119	12	–1	*5*	12	–1	357	221
		Spring	217	325	24	11	*18*	24	11	1,170	405

There were no solar radiation data available for the fall period at the Ellsworth site, therefore cum ET in this location was calculated from January to June (harvesting). Fall; October to December, Winter; January to March, Spring; April to Harvest.

TABLE 3 | Soil fertility information two weeks after sowing at each location during the 2015–2016 and 2016–2017 growing seasons.

	2015–2016				2016–2017					
	Conway		McPherson		Ellsworth		Conway		McPherson	
Depth (cm)	**15cm**	**45cm**	**15cm**	**45cm**	**15cm**	**45cm**	**15cm**	**45cm**	**15cm**	**45cm**
pH	6	5	6	6	6	7	6	6	6	6
NO_3-N (ppm)	7	6	31	36	33	23	13	8	49	41
NH_4-N (ppm)	13	6	27	13	16	15	8	6	16	14
P_Mehlich (ppm)	62	15	92	33	36	32	56	25	79	68
K (ppm)	239	231	383	243	365	301	226	251	370	309
Ca (ppm)	2,271	2,528	2,567	2,811	2,182	2,450	1,709	2,503	2,464	2,498
SO_4-S (ppm)	19	15	14	10	16	7	6	6	11	10
Cl (ppm)	8	4	11	12	9	8	9	6	12	16
CEC (meq $100g^{-1}$)	22	25	19	21	21	16	22	24	22	20
OM (%)	3	2	3	2	3	3	3	2	3	3
sand %	25	21	15	12	18	13				
silt %	48	42	58	56	57	56				
clay %	27	37	27	32	25	31				

Soil test includes soil pH, nitrate- (NO_3-N), and ammonium- (NH_4-N) nitrogen, Mehlich-3 extractable phosphorus (P), potassium (K), calcium (Ca), sulfate-sulfur (SO_4-S), chloride (Cl), cation exchange capacity (CEC), organic matter (OM), and percentage sand, silt, and clay in the soil at sampling depths from 0 to 15 cm and 15 to 45 cm.

disturbance within plots, using hand-probes at 0–15 and 15–60 cm depth. At each depth, 15 soil cores were combined to represent the soil characteristics of each field experiment.

Treatments and Experimental Design

Twenty-one winter wheat genotypes, commercially available to farmers in the region (**Table 4**), were tested under two management practices at each location. The management systems tested were common farmer's practice (actual management made by the specific farmer in whose field the experiments were conducted) hereafter referred to SM versus IM. In the SM treatment, there was no fungicide application, and the N management (source, rate, and timing of application) varied slightly across fields depending on each farmer's practice (**Table 1**). In general, farmers applied N at planting and at early tillering stage (stage Z26 in the scale of Zadoks et al., 1974) in the spring with a total rate sufficient to achieve a yield goal of approximately 5 Mg ha^{-1}, according to the recommendation guide from Kansas State University (Leikam et al., 2003). This rate considered soil N availability prior sowing in the topsoil layer (0–15 cm), soil NO_3

TABLE 4 | Information of agronomic traits [drought tolerance, maturity range (heading date), straw strength] and genetic resistance to most occurring fungal diseases in KS [leaf rust (*Puccinia triticina*), stem rust (*Puccinia gramini*), stripe rust (*Puccinia striiformis*), powdery mildew (*Blumeria graminis*), tan spot (*Pyrenophora tritici-repentis*), and Septoria tritici blotch (*Mycosphaerella graminicola*)] for the 21 genotypes tested in 2016 and 2017 growing seasons.

	Genotypes	Drought	Maturity	Straw strength	Leaf rust	Stem rust	Stripe rust	P. Mildew	Tan spot	Septoria
1	1863	6	5	7	7	1	3	6	6	6
2	AG Robust	7	3	2	4	5	2	*NA*	8	6
3	Bentley	*3*	4	6	5	2	5	6	6	5
4	DoublestopCL+	7	7	4	3	2	5	5	6	6
5	Everest	7	2	2	3	3	8	3	7	5
6	HotRod	7	3	2	3	5	4	4	6	5
7	Kanmark	5	5	1	2	3	6	7	6	6
8	Larry	6	6	3	7	2	2	5	5	6
9	LCS Chrome	5	8	3	2	2	3	6	4	4
10	LCS Mint	4	7	6	7	4	5	6	5	5
11	LCS Pistol	5	4	7	6	8	7	3	7	*NA*
12	SY Flint	5	4	4	6	3	4	7	7	7
13	SY Monument	6	7	5	2	2	2	5	5	4
14	T158	4	3	4	8	8	2	3	7	7
15	Tatanka	5	6	7	6	2	2	7	7	7
16	WB4303	*6*	4	1	3	1	4	5	6	6
17	WB4458	6	4	2	7	1	4	7	5	7
18	WBCedar	7	2	1	5	3	4	2	5	4
19	WB-Granfield	5	6	3	4	2	6	6	6	6
20	Winterhawk	4	6	3	7	8	6	5	6	7
21	Zenda	7	4	2	3	2	3	5	5	4

NA, not available due to insufficient information.

Legend for agronomic traits. Drought tolerance: 1 = excellent; 5 = good; 9 = poor. Maturity: 1 = early; 5 = medium; 9 = late. Straw strength: 1 = excellent; 5 = good; 9 = poor (high lodging risk). Legend for disease resistance levels: 1 = highly resistant, 3 = moderately resistance, 5 = intermediate, 7 = moderately susceptible, 9 = highly susceptible (DeWolf et al., 2017).

in the profile (0–60 cm) (both shown in **Table 2**), previous crop credits, and tillage practice (Leikam et al., 2003). The IM treatment consisted of the SM treatment in each particular field with (i) an additional N rate of 45 kg ha^{-1} of N broadcasted as urea (46-0-0) at the onset of stem elongation stage (Z30), and (ii) two fungicide applications. The first fungicide application was made when the first node was detectable (Z31) to protect leaves and stems using a two mode of action product (24 g a.i. of fluxapyroxad ha^{-1} and 49 g a.i. of pyraclostrobin ha^{-1}). The second fungicide was a three mode of action product (20 g a.i. of fluxapyroxad ha^{-1}, 139 g a.i. of pyraclostrobin ha^{-1}, and 82 g a.i. of propiconazole ha^{-1}) applied at the heading stage (Z58) to protect upper leaves and spikes. The average yield produced under the IM treatment represents the water-limited achievable yield of site-years and genotypes, as defined by Evans and Fischer (1999).

Treatments within each of the experiments were arranged in a split-plot design with genotypes assigned to the main plots and management to the subplots. Main plots were arranged in a randomized complete block design with three replications.

Measurements

Aboveground biomass was sampled at physiological maturity from 0.5 m of a middle plot-row and the number of spikes counted before the material was fractioned into stover (leaves and stems), and spike (chaff and grains). Samples were dried at 60°C for one week, and then dry weights recorded. Spikes were counted and threshed; grains were weighed and counted to estimate yield and its numerical components: grain number per unit area and 1,000-grain weight on a dry weight basis. Samples were then ground (sieve 2 mm), and plant N concentration in stover and grains was determined *via* the LECO TruSpec CN combustion analyzer. The nutrient concentration of the chaff was estimated from that of the stover. Aboveground N uptake was estimated as the product between the weighted average of N concentration among organs by biomass and reported on a dry weight basis. Harvest index (HI) was determined as the ratio of grain yield by aboveground biomass at maturity. Nitrogen utilization efficiency was estimated as the ratio of grain yield by aboveground N uptake at maturity (Moll et al., 1982).

The severity of several foliar fungal diseases was evaluated in all experimental units approximately two weeks after each fungicide application. As the main goal of our study was to evaluate the management impacts on fungal diseases in general, our discussions will be based on the average incidence of all diseases found in each site-year.

Statistical Analyses

Sources of variation in ANOVA comprised of genotype, management, site-year, and their interactions as fixed factors; and block nested within site and genotype nested within block as random effects, the latter to account for the split-plot design. Analysis of variance was conducted using the "lmerTest" package (Kuznetsova et al., 2017) in R software version 3.4.0. Descriptive statistics were calculated using the R package "doBy" (Højsgaard and Halekoh, 2016) and included mean, standard deviation (sd), and 0.25 and 0.75 percentiles for grain yield. To evaluate the impact of management on yield across genotypes and site-years, we built boxplots using the R package "ggplot2" (Wickham, 2009).

A biplot GGE model was used with yield, aboveground biomass, and HI as dependent variables to evaluate the genotypes performance and genotype and environment interactions across management and site-years (Romagosa et al., 2013).

We evaluated the relationships among measured variables by regression analyses using the "lm" function in the R package "ExpDes" (Ferreira et al., 2018). To estimate the impacts of agronomic traits on yield differences among environments and genotypes (i.e., the global responses), results are shown for all site-years and genotypes (n = 210), but also on average of genotypes for each site-year (n = 5), and on average of site-years across genotypes (n = 21).

Trait response to management within each particular background condition was estimated by subtracting the mean under IM by mean under SM. Likewise, the magnitude of genotypic yield responsiveness to management was evaluated as the difference between yield at IM and SM, averaged across background environments. The variability (i.e., lack of consistency) of genotypic response to management was assessed by the standard deviation of the mean yield response to management. The relationship between mean yield at IM and SM versus mean yield response to management was evaluated by regression analyses using the "lm" function in the R package "ExpDes" (Ferreira et al., 2018).

To investigate the causes of differences in N uptake due management we built a critical N dilution curve for each management system across all environments and genotypes by fitting the negative power function (Eq.1) suggested by (Justes et al., 1994).

$$\text{ShootNconcentration} = a \star \text{biomass}\ (-b) \quad (1)$$

where a is the shoot N concentration when biomass is equal to 1 Mg ha^{-1} and b is the dilution coefficient (i.e., rate of decrease in shoot N concentration as the biomass increases). We compared the intercepts and slopes of the relationship between grain N concentration and yield between IM and SM using the standardized major axis (SMA) analysis in the R package "smatr" (Warton et al., 2012).

General Weather and Disease Incidence Conditions

For both 2016 and 2017 growing seasons, the average daily temperature was similar to the 30-year normal (1981–2000) of each region (NCDC-NOAA, 2019), except for winter season which was warmer than expected by approximately 3°C (**Table 1**). Precipitation during the fall of the 2015–2016 growing season was similar to the long-term in McPherson and slightly above average in Conway. Moderate drought and few freeze events were observed in the winter and early spring (around flag leaf emergence [mid-April]), which was then followed by greater than normal precipitation and below normal temperatures. During the 2016–17 growing season,

fall months were drier and winter months were wetter than expected from an average year. The drier fall resulted in crops with less tiller formation (visually observed), which was then followed by a period of greater than average water availability and warm temperatures. In the spring (from flag leaf emergence and afterwards) weather was similar to those of an average year.

The fungal diseases recorded in the experiments at early season (stem elongation to flag leaf) were tan spot (*Pyrenophora tritici-repentis*), septoria tritici blotch (*Zymoseptoria tritici*), and powdery mildew (*Blumeria graminis* f. sp. Tritici). At late season, prevalent diseases were stripe (*Puccinia striiformis* Westend) and leaf rusts (*Puccinia triticina*). The greater leaf damage from foliar fungal diseases occurred after heading. Although average disease severity was similar across site-years (c. 10%), the overall disease pressure within an experiment varied due to differences in genetic resistance of genotypes. The disease severity recorded two weeks after heading under SM plots ranged from 4% to 38% in Conway 2016, from 4% to 20% in Conway 2017, from 4% to 50% in Ellsworth 2017, and from 2% to 27% in McPherson 2016. Under IM, disease severity ranged from 2% to 10% in Conway 2016, from 3% to 12% in Conway 2017, from 2% to 37% in Ellsworth 2017, and from 1% to 9% in McPherson 2016. No disease severity data was collected for McPherson 2017.

RESULTS

Overall Effect of Management System on Crop Yield

Across all sources of variation (five background environments given by the combination of sites and years and 21 cultivars grown in each of them), IM outyielded SM by an average of 0.9 Mg ha^{-1} (**Figure 1A**). Across the study, yields were normally distributed for both management systems and showed a larger standard deviation for the IM as compared to the SM (c. 0.97 and 0.67 Mg ha^{-1}, respectively; **Figure 1A**). Usually, the lowest yields achieved in both systems tended to be similar while yields under IM were clearly larger than under SM in higher yielding conditions (**Figure 1A**). Therefore, the yield advantage of IM over SM was neither uniform across background environments (the interaction between management and site-year was significant at $p < 0.05$), nor across genotypes (although the interaction between genotype and management was significant only at a $p = 0.14$). The three-way (site-year x genotype x management) interaction was not significant ($p = 0.81$). However, the magnitude of the management effect was much larger than its interaction with the background environment (the mean square for management effect was more than tenfold higher than that of the site-year × management interaction), and therefore, that interaction was not crossover. That is, the IM

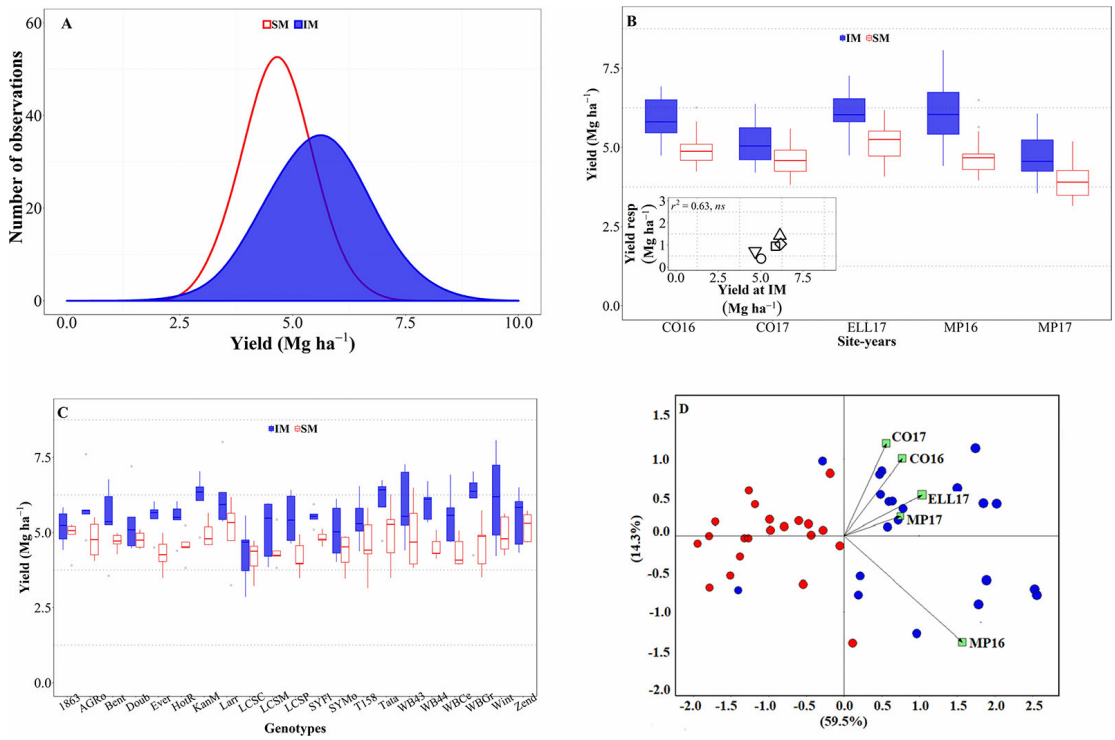

FIGURE 1 | Distribution of the mean yield across environments and genotypes for intensive (IM) and standard (SM) management systems **(A)**. Mean yield for IM and SM systems on average of genotypes for each site-year **(B)**, with an inset showing the relationship between the average yield response to IM and achievable yield (yield in IM). Mean yield for IM and SM systems on average of site-years for each genotype **(C)**. Genotype and genotype × environment (GGE) biplot analysis for yield of 21 genotypes grown in five site-years at SM and IM systems **(D)**.

always outyielded SM, though the magnitude of the difference was not uniform across sites-years (**Figure 1B**). Indeed, the response of wheat yield to the IM tended to increase with achievable yield (i.e., yield under IM) of the background environment (**Figure 1B**, inset). Regarding the overall differential response of the genotypes, we observed a consistent trend for IM outyielding SM in all genotypes, though that difference was not statistically significant in five out of the 21 genotypes (**Figure 1C**).

All these elements are clearly illustrated in the GGE biplot analysis (**Figure 1D**). In general, varieties under SM tended to have lower yields as compared to IM. The IM system seemed to have been better adapted, in terms of increased yield, than the SM across all site years (**Figure 1D**); although specific varieties were better adapted to certain particular background conditions.

Traits Associated With Yield Responsiveness to IM

There was an overall positive relationship between yield and aboveground biomass at maturity, with 45% of the variation in yield due to the combination of background environments, genotypes, and management systems explained by differences in biomass accumulation at maturity (**Figure 2A**), even though there was a clear penalty in harvest index in Ellsworth 2017 (Rhombs in **Figures 2A**, **B**, **D**, **E**). On the other hand, across all sources of variation considered, there was no relationship between yield and biomass partitioning toward the grains (**Figure 2D**), although this relationship was positive and significant within location-management combination (ranging from r2 = 0.14 in Conway 2016 to r2 = 0.60 in McPherson 2017) mainly driven by genotypic differences within each growing condition. Focusing on the background environmental conditions, the overall positive trend between yield and biomass demonstrates that differences in yield between site-years were in general due to differences in biomass accumulation (**Figure 2B**), and rather independent of site-year differences in harvest index across management systems (**Figure 2E**). Neither the relationship between yield and biomass, nor that between yield and harvest index, were significant within each management system ($p > 0.05$). It was clear, however, that biomass was more relevant than harvest index in explaining the differences in yield across sites-years, even within management systems (**Figures 2B**, **E**). Thus, the yield response to IM across sites-years was related differences between the two management systems for biomass rather than harvest index (**Figures 2B**, inset, **E**, inset). On the other hand, the yield differences between genotypes were significantly related to both biomass and harvest index across management systems, though the degree of association was substantially higher for biomass (cf. **Figures 2C**, **F**). Overall, it was clear that biomass responses to IM were the primary driver of the yield response of the genotypes. Evidence for this includes not only that coefficients of determination were more highly significant for biomass than for harvest index but also that while responses to IM of yield and biomass were always positive (**Figure 2C**, inset) in several cases, IM did not improve, and sometimes decreased, harvest index (**Figure 2F**, inset).

Changes in grain number per unit area explained 61% of the overall variation in grain yield, i.e., when accounting for environments, genotypes, and management systems together (**Figure 3A**). Although grain weight also significantly associated with differences in yield, the proportion explained was much lower (c. 6%, **Figure 3D**). Yield differences across environments were well explained by differences in grain number (**Figure 3B**), not only due to their high association across site-years (**Figure 3B**), but also because yield responses to IM within each

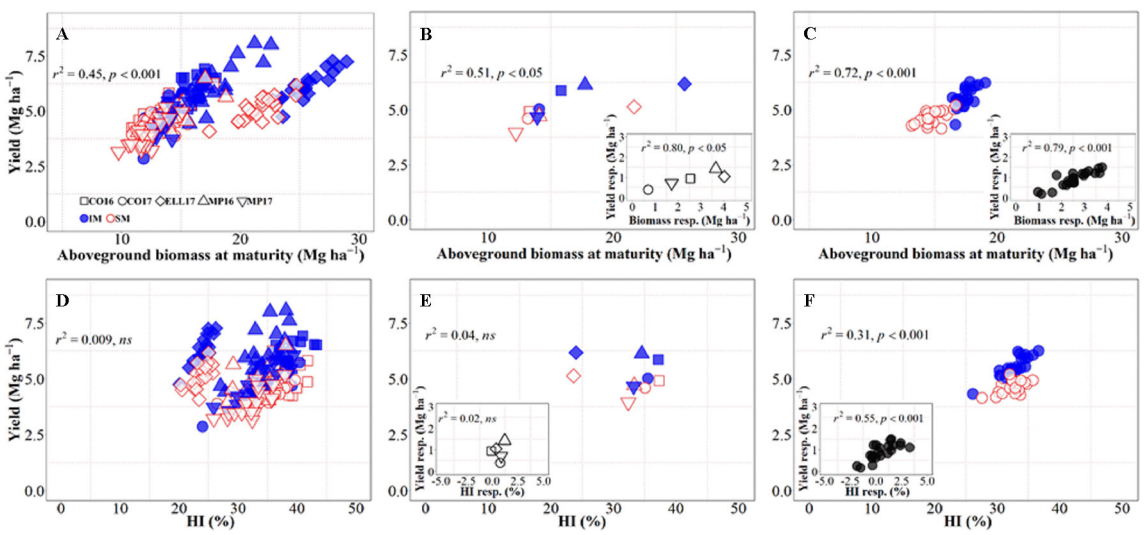

FIGURE 2 | Relationship between yield versus aboveground biomass at maturity and harvest index across environments, genotypes, and management systems [intensive management (IM) and standard management (SM)] (n = 210) **(A, D)**, on average of genotypes for each site-year **(B, E)** (n = 10), and on average of site-years for each genotype **(C, F)** (n = 42). Insets are the relationships between the responses of the variables to intensive management (difference in the variable between IM and SM) averaged across either genotypes for each site-year (B, E insets) (n = 5) or site-years for each genotype (C, F insets) (n = 21).

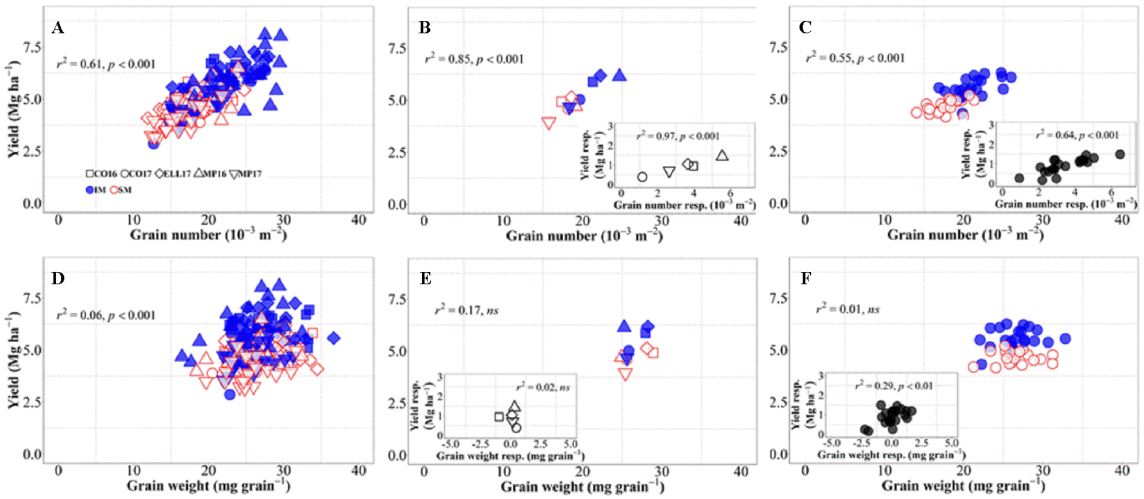

FIGURE 3 | Relationship between yield versus grain number and grain weight at maturity across environments, genotypes, and management systems [intensive management (IM) and standard management (SM)] (n = 210) **(A, D)**, on average of genotypes for each site-year **(B, E)** (n = 10), and on average of site-years for each genotype **(C, F)** (n = 42). Insets are the relationships between the responses of the variables to intensive management (difference in the variable between IM and SM) averaged across either genotypes for each site-year (B, E insets) (n = 5) or site-years for each genotype (C, F insets) (n = 21).

of the site-years were strongly driven by improvements in grain number (**Figure 3B**, inset). On the other hand, differences in yield among environments were not explained by differences in grain weight within or across management systems (**Figure 3E**). Yield responses to IM of the different background environments were rather independent of those in grain weight (**Figure 3E**, inset). Indeed, there was almost no difference in grain weight between IM and SM within each of the site-years (**Figure 3E**), and therefore neither in the response of grain weight to IM (**Figure 3E**, inset). Similarly, differences in yield among genotypes across management systems were exclusively brought about by differences in grain number (**Figure 3C**), as the relationship with grain weight was negligible (**Figure 3F**). The relationship between yield and grain number across genotypes was strong within each of the management systems, but also the yield response to IM of the genotypes was associated with increases in grain number (**Figure 3C**, inset). The lack of relationship between yield and grain weight across genotypes and management was also true within each of the two management systems (**Figure 3F**). Even though the yield response of genotypes to IM was related to their grain weight response (**Figure 3F**, inset), the relationship could hardly be mechanistic as IM always improved yields even in situations where it decreased grain weight of several genotypes (**Figure 3F**, inset).

There was an overall positive relationship between yield and N uptake at maturity. Differences in N uptake explained 64% of the variation in yield across background environments, genotypes, and management systems (**Figure 4A**). By dissecting the N uptake into shoot N concentration and biomass, we observed that differences in N uptake due to IM across site-years and genotypes were due to greater shoot N concentration under IM as compared to SM as biomass levels increased (**Supplementary Figure S1**). Conversely, changes in NUtE did not explain overall differences in yield across the entire dataset (**Figure 4D**). Considering only the differences between environments, there was a strong positive relationship reflecting that differences in yield among site-years were largely due to differences in N uptake across and within management systems (**Figure 4B**). Differences between sites-years in yield response to IM were related to their differences in N uptake response to IM (**Figure 4B**, inset). On the other hand, differences in yield between environments were not explained by their differences in NUtE (**Figure 4E**). In fact, there was a trend ($p = 0.06$) for site-years with higher yields to exhibit lower levels of NUtE (**Figure 4E**) and yield responses to IM of the different site-years was not mediated through NUtE response (**Figure 4E**, inset). Considering the differences between genotypes across management systems, there was also a positive relationship between yield and N uptake (**Figure 4C**), and differences among genotypes in yield response to IM were preceded by their differences in responses of N uptake (**Figure 4C**, inset). Yield differences between genotypes across management systems were not related to differences in NUtE (**Figure 4F**), but genotypic differences in yield within each management system were well explained by NUtE (**Figure 4F**) ($p < 0.05$, $R2 = 0.78$ for IM and $R2 = 0.26$ for SM). Although genotypic differences in yield response to IM were significantly related to their response in terms of both N uptake and NUtE, the former was the determinant of yield response, as NUtE was actually reduced (with most of values of NUtE response near or below zero) by intensifying management, partly compensating for the larger effect of management on N uptake relative to yield (**Figure 4F**, inset).

The relationship between grain N concentration and yield was weak when considering all sources of variation together and IM improved both yield and grain N concentration as compared

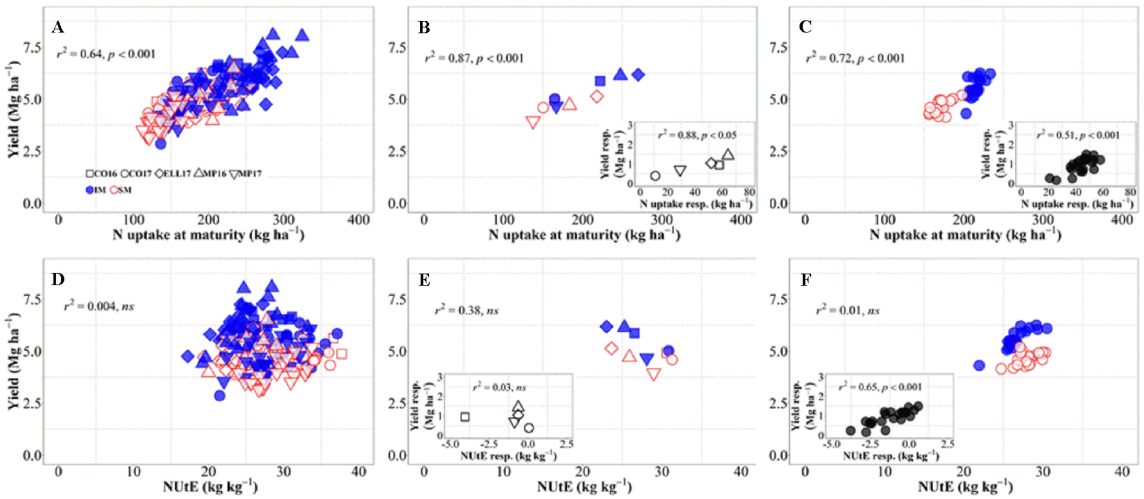

FIGURE 4 | Relationship between yield versus nitrogen uptake and utilization efficiency at maturity across environments, genotypes, and management systems [intensive management (IM) and standard management (SM)] (n = 210) **(A, D)**, on average of genotypes for each site-year **(B, E)** (n = 10), and on average of site-years for each genotype **(C, F)** (n = 42). Insets are the relationships between the responses of the variables to intensive management (difference in the variable between IM and SM) averaged across either genotypes for each site-year (B, E insets) (n = 5) or site-years for each genotype (C, F insets) (n = 21).

to SM, reducing the dilution of N in the grain (**Figure 5A**). This lack of relationship is actually hiding two contrary relationships, depending on whether the source of variation was site-years or genotypes. When considering the differences in site-years and management systems, the relationship was significantly positive, with changes in yield explaining 64% of the variation in grain N concentration across site-years and management systems (**Figure 5B**), mainly because IM improved both yield and grain N concentration in all five site-years (**Figure 5B**, inset). Conversely, changes in grain N concentration were not explained by differences in yield of genotypes considering both management systems together, though there was a significant negative relationship within management systems (**Figure 5C**) ($p < 0.05$; R2 = 0.33 for IM and R2 = 0.20 for SM). This implies that within management systems there was a general trend for higher-yielding cultivars to dilute the N in the grain and vice-versa. The fact that the relationship was not maintained when considering genotypes × management together reflects the positive effect of the IM system on both yield and grain N concentration. This may seem at odds with the fact that grain N concentration response to IM was negatively related to yield response of genotypes to management (**Figure 5C**, inset). However, the data were all in the positive quadrant: IM increased yields and grain N concentration of all genotypes; although there was a general trend for cultivars more responsive in yield to be less responsive in grain N concentration (**Figure 5C**, inset). Within each management system encompassing all sources of variation, the IM increased yield and maintained

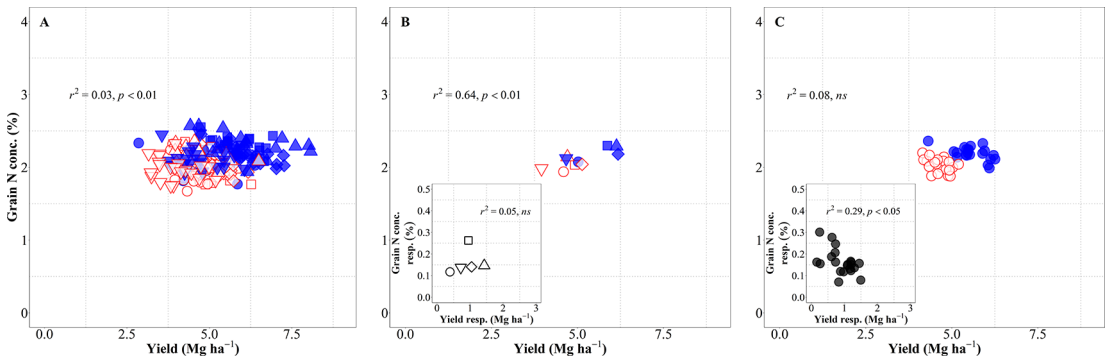

FIGURE 5 | Relationship between grain nitrogen (N) concentration and yield across environments, genotypes and management systems [intensive management (IM) and standard management (SM)] (n = 210) **(A)**, on average of genotypes for each site-year **(B)** (n = 5), and on average of site-years for each genotype **(C)** (n = 42). Relationship between grain N concentration and yield responses to IM on average of genotypes for each site-year (**B** inset) (n = 5) and on average of site-years for each genotype (**C** inset) (n = 21).

similar levels of grain N concentration while for SM there was a clear penalty in grain N concentration as yield increased (**Supplementary Figure S2** and **Table S1**).

Yield (in terms of grain dry matter) was consequently a strong determinant of the total amount of N harvested (grain N uptake). Considering the overall variation due to background environments, genotypes and management systems, changes in yield explained 86% of the variation in grain N uptake (**Figure 6A**). This relationship was also very strong when focusing on either environment, both across and within management systems (**Figure 6B**), or genotypes (**Figure 6C**). The differences in grain N uptake response to IM, both between site-years (**Figure 6B**, inset) and between genotypes (**Figure 6C**, inset), mimicked the corresponding differences in yield responses.

Genotypic Differences in Consistency of Yield Response

We restricted the analysis of the data so far to recognize differences and relationships across all sources of variation together or focusing on general responses to IM across sites-years (with averages across genotypes for each background condition) or across genotypes (with averages across background conditions for each genotype). This was done in order to determine whether an intensification of rainfed wheat management in Kansas would generally result in increased achievable yields and to assess the consistency of the outcomes (the first aim of the study). Nevertheless, genotypes varied specifically in their adaptation and responsiveness to IM. Examining overall responsiveness to IM was critical to draw general conclusions but also masked specific responses of particular genotypes. In this section we dissected these genotype- specific responses to IM, considering not only their responsiveness to IM but also their response consistency.

As mentioned above, we observed a generalized increase in yield due to IM in all genotypes, but with noticeable differences in magnitude and significance of the response (i.e., across all site-years yield increased between c. 0.2 and 1.5 Mg ha^{-1}; this overall increase was statistically significant in 16 genotypes whilst only a trend in five genotypes; **Figure 1C**). This is reinforced by analyzing the yield of each of the 21 genotypes averaged across sites-years under both management systems (**Figure 7A**). As expected from overall results previously presented (**Figure 1C**), there was a considerable diversity in performance within each of the management systems, all data-points were above the 1:1 ratio (implying that all cultivars exhibited higher average yield under IM than under SM), and the performance of cultivars under IM depended largely on their responsiveness to intensification of the management (**Figure 7B**). It is relevant that performance of cultivars under IM was generally consistent with their performance under SM (in general, low- and high-yielding cultivars under IM were also low- and high-yielding cultivars under SM; **Figure 7A**). Even though the coefficient of determination was statistically highly significant, diversity in achievable yield and responsiveness to IM was still agronomically very significant, as evidenced by the 67% of the variation in IM not explained by that in SM. Thus, the overall response to IM across site-years included genotypes with relatively low responsiveness having either low (e.g., LCS Chrome), intermediate (e.g., 1863) or relatively high yield (e.g., Zenda) under SM; as well as genotypes with high responsiveness with either of the yield scenarios in SM (e.g., LCS Pistol, WB4458, Larry) (**Figure 7A**). Thus, the yield responsiveness to IM of the genotypes was largely unrelated to their performance under SM (**Figure 7C**), indicating that overall responsiveness to IM was mostly independent of adaptation to current management practices and thus achievable yield was strongly dependent upon the inherent genotypic responsiveness to IM (**Figure 7B**; please note that not only was the coefficient of determination highly significant but also that the slope was very close to one). Not only did genotypes vary in overall responsiveness to IM across site-years but also their differences in responsiveness were largely unrelated to their consistency in response to IM (inversely assessed by the standard deviation of their average response; **Figure 7D**). Although instability in response of the genotype

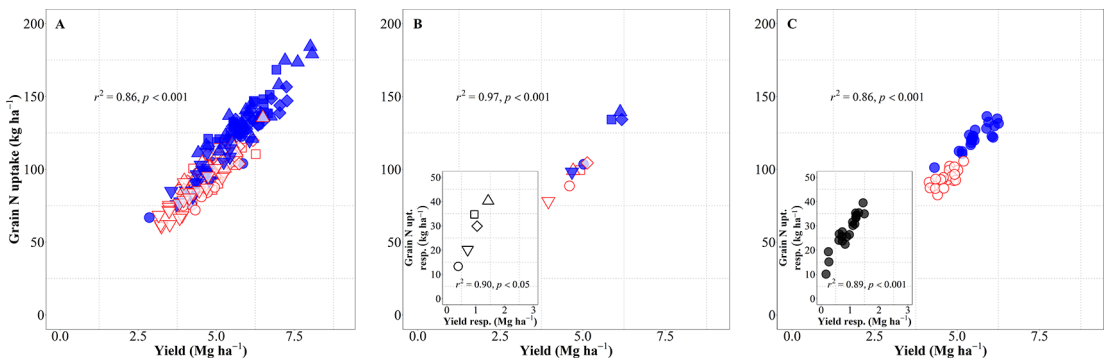

FIGURE 6 | Relationship between grain nitrogen (N) uptake and yield across environments, genotypes, and management systems [intensive management (IM) and standard management (SM)] (n = 210) **(A)**, on average of genotypes for each site-year **(B)** (n = 10), and on average of site-years for each genotype **(C)** (n = 42). Relationship between grain N concentration and yield responses to IM on average of genotypes for each site-year (**B** inset) (n = 5) and on average of site-years for each genotype (**C** inset) (n = 21).

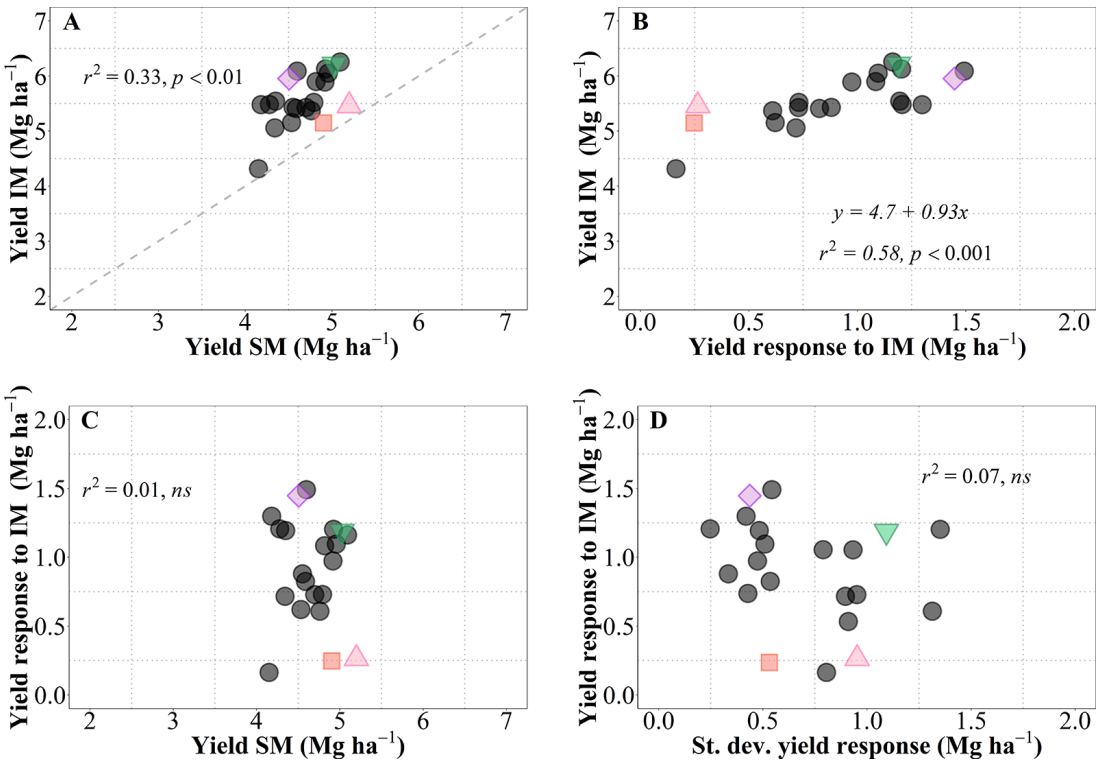

FIGURE 7 | Relationship between mean yield under intensive (IM) versus standard management (SM) for the 21 genotypes tested averaged across site-years **(A)**. Relationship between mean yield under IM and yield response to IM (i.e., yield IM minus yield SM) **(B)**. Relationships between yield response to IM and either mean yield of SM **(C)**, or standard deviation of the yield response to IM **(D)**. The different symbols shows four genotypes selected to represent contrasting behaviors in terms of average responsiveness to intensive management (IM) and in stability of that responsiveness across all site-years selected genotypes, Zenda (triangle), Larry (inverted triangle), 1863 (square), and WB4458 (rhombus).

did not contribute to the average yield in IM, it was naturally relevant to achieve the maximum yields that were equally related to the average response across sites-years and the instability in the response (**Supplementary Figure S3**). Being the variability in response (measured by the standard deviation of yield response to management) independent of the mean yield response (**Figure 7D**), maximum yields shall be obtained by genotypes combining a high average response and a high variability in response (**Figure S3**).

To illustrate the issue in more detail, we selected four cultivars representing contrasting average response to IM and contrasting stability in the response (**Figure 7D**). Cultivars 1863 and Zenda had both a small overall responsiveness but contrasted noticeably in consistency. Cultivar 1863 showed positive responses in four out of the five site-years, although with relatively small increases (from 0.18 to 0.87 Mg ha^{-1}) and, in an exceptional case, showed a yield penalty though the magnitude was small (c. 0.52 Mg ha^{-1}; **Figure 8**). On the other hand, due to its instability in response Zenda had c. 1 Mg ha^{-1} decrease in yield in Conway 2017 but also more than 1 Mg ha^{-1} yield gain in both Conway 2016 and McPherson 2016, and marginal responses in the other two environments; **Figure 8**). The same sort of lack of uniformity in consistency across sites-years was evident for genotypes with larger average responsiveness. For instance, cultivars such as WB4458 had simultaneously high and stable responsiveness to IM (**Figure 7D**), therefore responding with noticeable improvements in yield across all five site-years (ranging in response from 1 to 2 Mg ha^{-1}; **Figure 8**). Meanwhile, genotypes such as Larry were highly responsive to management on average, but their response was not stable across site-years, with a very large response in some environments (> 2 Mg ha^{-1} yield gain in McPherson 2016 and 17), a high response in other environments (> 1 Mg ha^{-1} gain in Conway 2016), but mostly unresponsive in the other two site-years (**Figure 8**).

DISCUSSION

Results reported in this paper come from a study carried out in real farmers' fields. Working in realistic farming systems instead of carrying out experiments in experimental stations implies accepting restrictions in experimental procedures and produce "noisier" datasets, such as slightly different background environments for the standard treatment; but has a clear advantage when conclusions are expected to be pertinent (Rzewnicki et al., 1988). Moreover, conclusions were reached based on a very simplistic approach of applying a single intensification measure against what farmers were

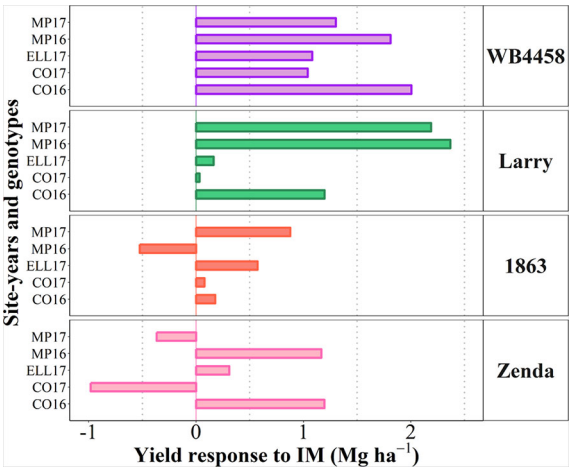

FIGURE 8 | Yield response to intensive management (IM) for the selected contrasting genotypes at each individual site-year.

actually doing regardless of the particular situation. The aim was to test yield responses to management across different site-years to determine whether farmers are too conservative and thus missing opportunities of achieving greater yields. Naturally, an optimal level of intensification would likely be different for particular fields. Therefore, this paper does not contribute a tool to define the level of intensification required but only to uncover whether or not the current level of intensification is too conservative, evidencing whether or not there are opportunities to increase yield from the baseline. Similar to our data, several studies have registered average achievable yield for the region of c. 5.5 Mg ha^{-1} in field experiments (Lollato and Edwards, 2015; Jaenisch et al., 2019), simulation studies (Lollato et al., 2017), and survey of yield contest fields (Lollato et al., 2019b).

Intensifying Management to Increase Rainfed Wheat Yield

Intensification of management practices and adoption of genotypes highly responsive to management can contribute to increasing wheat yields required for achieving food security, while improving the relatively low N use efficiency of production systems (Raun and Johnson, 1999). However, following a more conservative approach, dryland-wheat producers have been traditionally reluctant to intensify crop management and frequently prefer growing "stable" genotypes that are expected to perform relatively well under conservative conditions but are less responsive when under better growing conditions (i.e., intensified management, and fertile soils).

Climate variability affects the performance of genotypes and their response to management, challenging an effective implementation of management practices across seasons. Changes in precipitation (e.g., amount, intensity, and timing) and temperature patterns may interfere with crop adaptation (Reynolds and Ortiz, 2010), availability of resources (Chloupek et al., 2004), and enable conditions for pests to develop (Agrios, 2005; Legrève and Duveiller, 2010). Although the factors above may explain the variation in yield response to management across site-years, there was no single background condition in our study in which wheat yield, averaged across the 21 cultivars considered, decreased in response to IM. This suggests that, for the background environments evaluated, an excessively conservative attitude regarding the intensification of agronomic management is restricting farmers-yield in the region. Similar results were shown for rainfed wheat in other dryland regions (McDonald, 1989; Connor et al., 2011) as well as in other studies in the same region (Dorsey, 2014; Jaenisch et al., 2019; Lollato et al., 2019b). While we characterized the physiological basis of yield response to IM, future studies could focus on yield comparisons between IM and SM on a large number of fields to determine the most often probability of yield response and perhaps the magnitude of the yield gap.

Adequate N availability during the growing season is critical for wheat grain yield and quality (Entz and Fowler, 1989). There is usually a curvilinear relationship between yield and N rate (Simpson et al., 2016), but this relationship depends on yield potential (Savin et al., 2019) and might be linear or nonexistent (Lollato et al., 2019b). In the present study, yield was improved due to N rate and positively associated with higher N uptake and grain number, similar to previous reports which also suggested an increase in water use-efficiency (Entz and Fowler, 1989). Determining the agronomic optimum N rate is challenging in rainfed cereal production due to the variability in growing season precipitation and yield potential (Lollato et al., 2017), and leads to a dominant producer-mindset based on Liebig's "law of the minimum" that induces to underfertilize (Connor et al., 2011). Thus assuming (correctly) that water is commonly the most stressful factor limiting yield, it is overlooked that N availability may well improve water use and water use efficiency (Sadras, 2004; Cossani et al., 2012). The other factor supporting reluctance to fertilize rainfed wheat is the idea that it may bring about "haying-off" (i.e., an expected negative yield response to N fertilization of dryland wheat; van Herwaarden et al., 1998). However, it seems that this effect has been consistently reported only in Eastern Australia; as in other dryland regions this yield penalty is not evidenced beyond exceptional cases, and yield gains are frequently reported (Palta and Fillery, 1995; Asseng and van Herwaarden, 2003; Cossani et al., 2011) in line with results reported herein, with the exception of the cultivars with low overall responsiveness that may eventually exhibit a yield penalty (once again the "conservative" attitude of selecting "stable" cultivars induced to the very few cases of "haying-off" reported in the present study.

Moreover, the appearance of new populations of fungal diseases able to break genetic resistance of modern wheat genotypes (Chen, 2005) can result in need of fungicide application, in some cases even for relatively new cultivars that are expected to be resistant. The magnitude of yield loss from lack of fungicide varies according to the disease pressure, weather, fungicide management (i.e., timing and source), and genetic resistance (Thompson et al., 2014; Lopez et al., 2015;

Benin et al., 2017). Naturally, years with considerable disease pressure will result in greater yield response to fungicide (Cruppe et al., 2017; Jaenisch et al., 2019) on cultivars susceptible to the most prevalent disease in the season (Thompson et al., 2014). However, we showed that yield advantages of a management intensification, including fungicide protection, produced yield gains across a range of sites-years and modern cultivars. This indicates that in most conditions of this dryland region, the penalty imposed by foliar diseases would be significant and fungicide application would be economically viable to producers (at least within the site-years evaluated in this study and other years with similar growing conditions). Furthermore, we found a positive relationship between the yield response to IM and the achievable yield under IM, which agrees with literature suggesting that the magnitude of responses to N and fungicide applications depend on the environmental yield potential of the growing season (Cruppe et al., 2017; Lollato et al., 2019b). Thus, it seems that the consequences of the aversion to risk are worse in conditions of higher achievable yield, which can be detrimental for further yield progress.

Relevance of Yield Determining Traits in the Response of Wheat to Intensive Management

The magnitude and consistency of yield response to agronomic management can vary due to physiological aspects (e.g., ability to produce greater yields per unit of N supplied [NUE]) (Russell et al., 2017) and adaptation patterns of genotypes across different environmental conditions (Chloupek et al., 2004; Barraclough et al., 2010). In line with our results, other studies have found that genotypes more responsive to N management have greater biomass accumulation and N uptake at maturity (Kanampiu et al., 1997), and that their differences in yield are associated with differences in HI through differences in grain number produced per unit area (Calderini et al., 1995). The response of genotypes to N can be associated with their high yield potential and N use efficiencies (Ortiz-Monasterio et al., 1997). Grain yield improvements due to N management was achieved by increasing N uptake at maturity (López-Bellido et al., 2005), through improving N uptake efficiency (Barraclough et al., 2010) or utilization efficiency of genotypes (Cossani et al., 2012). However, reduction in NUtE is expected when improvements in N uptake from management occur at larger magnitude relative to yield (Gaju et al., 2011). In our data, yield increases due to IM occurred through improvements in N uptake, and the greater increase in N uptake from IM relative to yield reflected a reduction in NUtE. Although IM improved both yield and grain N concentration, genotypes with large yield gain from IM showed a reduction in grain N concentration (Giunta et al., 2019; Lollato et al., 2019a). Overall, our experiments were conducted during two growing seasons resulting in overall low grain protein concentration under SM and improved grain protein under IM, suggesting an opportunity to increase yield and maintain quality with IM. Previous research has proposed a critical value for grain protein concentration of 11.5% above which yield is not limited by N for hard red winter wheat in the region (Goos et al., 1982). In our study, average grain protein concentration for SM and IM were 11.5% and 12.5%, respectively. Thus, considering the narrower range of yield values (from 0.7 to 4 Mg ha^{-1}) in the latter study as compared to our data (from 3 to 8 Mg ha^{-1}) and the N dilution process in larger grain dry matter (Justes et al., 1994), we could postulate that yield was somewhat limited by N under SM in our study, and additional; N application would increase farmer's net return. A broader range of N rates would have to be tested to definitively make such conclusions.

Top-dress N application at late tillering stages improves yield by increasing grain number per unit area (Ercoli et al., 2013). Therefore, yield differences among genotypes are usually explained by differences in grain number as compared to grain weight at maturity (Arduini et al., 2006). The larger plasticity of grain number relative to grain weight (Sadras and Slafer, 2012; Wang et al., 2017) likely plays a role in this observation and may clarify our findings where grain number was the main yield component contributing to the response of genotypes to management (Slafer et al., 2014). Furthermore, the possible increase in late-season tiller production and survival from the N and fungicide applications may have resulted in additional formation of smaller spikes with smaller grains. Thus, the overall decrease in grain weight due to IM could be attributed to the larger number of smaller grains resulting from the late tillers, consequently decreasing the overall average grain weight in the IM relative to the SM (see Acreche and Slafer, 2006).

In general, the impacts of management on the performance of genotypes are evaluated for a small set of genotypes (Russell et al., 2017), and information about the scope of physiological determinants of genotypic responsiveness to management is usually limited. Our study utilized a large set of modern wheat genotypes differing in agronomic traits and genetic origin and characteristics, and thus, it provides insights on physiological mechanisms associated with response to the management of modern winter wheat genotypes.

Producers could consider approaches regarding the risks of intensifying management. The more risky approach is to grow genotypes with high average responsiveness to management and high variability on the response (i.e., unstable, as the standard deviation of the response was positively related to yield under IM, **Figure S3**) while the less risky approach is to grow genotypes with high mean response but stable yields in response to management. The former indicates that farmers who are willing to accept some risks to maximize productivity should select genotypes with unstable response, as those are the ones that maximize yield when the conditions favor response. In general, high yielding genotypes tended to be more unstable although with greater chance to maximize yield than low-yielding genotypes (the concept of stability can be also seen as lack of responsiveness to improvements in growing conditions; Calderini and Slafer, 1999). This is similar to the findings of Grogan et al. (2016) in which phenotypic plasticity (or the opposite of stability) of grain yield was a positive trait for 299 hard red winter wheat genotypes evaluated in the Great Plains. Indeed, breeding programs tend to select under more favorable conditions than those representing the average of the target

population of environments in which the released cultivars are to be grown (**Box 1**). This is because cultivars of higher yield potential tend to outyield low-yield potential cultivars under a rather wide range of conditions (Slafer et al., 2005 and references quoted therein). Accordingly, Voss-Fels et al. (2019) demonstrated that breeding for genotypes under high input levels resulted in genotypes able to outperform under both high and low input levels. Understanding the physiological bases at the crop level of organization determining yield can help guide breeding to select prospective parents to produce strategic crosses aiming to increase the genetic gains in yield (**Box 2**), which would in turn require higher levels of

BOX 1 | Relevance of High-Yielding Selection Environment.

Data collected in the current study allowed us to discuss on the convenience for breeding programs to select in growing conditions that are as close as possible to those of the target environments in which released cultivars are to be grown or otherwise under better growing conditions (i.e., within the best yielding conditions that can be expected in the region). For this purpose we related the overall performance in the region for each individual cultivar with the yield of each cultivar in one particular condition. To take into account the overall performance of each genotype we calculated their average yield across nine growing conditions (all locations × years × management systems, but the particular condition that was used to predict the overall performance). These particular conditions were (i) the lowest-yielding environment, in which the most resilient genotypes would perform best; (ii) the growing condition producing an average yield closest to the overall average yield of the 10 environments; or (iii) the highest-yielding environment, in which the cultivars with the highest achievable yield would perform best (**Figure B1**, from left to right, respectively).

Naturally data-points fell above and below the line representing the 1-to-1 ratio in the left and right panels, respectively; and around that line when the environment used to predict the overall performance across all other environments was the growing condition with an average yield closest to the overall average yield (**Figure B1**).

Overall performance in the region was totally unrelated to the yield in the lowest-yielding condition (**Figure B1**, left panel). This implies that the specific characteristics making cultivars particularly adapted (or unadapted) to the most stressful condition did not contribute to the overall performance across the region (in fact the cultivars with the overall highest and lowest yielding were both rather low-yielding in this particular low-yielding condition (**Figure B1** left panel). Prediction of the overall performance from a single condition improved considerably (and became statistically significant) when using yield of an environment closest to the average-yielding growing condition as independent variable (**Figure B1**, middle panel). However, prediction of the overall performance from yield of the cultivars in the highest-yielding condition was even better than that from the average-yielding condition (**Figure B1**, right panel). Although each of the other environments were more stressful (with different levels of severity), it seemed that some attributes conferring water-limited yield potential somehow also produced a constitutive improved performance under lower-yielding environments.

This result justifies that breeding programs select promising lines under field conditions that are frequently higher-yielding than those targeted population of environments in which released cultivars are to be grown. This is in agreement with previous evidence advocating that the selection would be best if performed in high-yielding environments (Cooper et al., 1997). Using an environmental yielding condition representing higher than average yield of those targeted population of environments would likely increase the predictive performance (cf. middle and right panels in **Figure B1**).

This result also concurs with the idea that an improved yield potential (that can only be selected for in high-yielding conditions) would bring about improved performance under a range of environments with different degrees of stressful conditions; even though they would be less stable (as high yield potential implies strong responsiveness to better growing conditions; Calderini and Slafer, 1999) they might also perform better than lower-yield potential cultivars (Richards, 2000; Araus et al., 2008; Cattivelli et al., 2008; Ferrante et al., 2017). Indeed, wheats selected in CIMMYT for their high yield potential were released in drought environments (van Ginkel et al., 1998). Furthermore, selecting in higher-yielding conditions would also improve the efficacy of the program through increasing the achieved genetic gains. This is because the expected differences in performance are in line with the average yield of the environment and therefore increase the confidence in the selection process (van Ginkel et al., 1998) and explains why selection for yield in low-yielding conditions slows the progress achieved by the program (Blum, 1988; Richards et al., 2002). An empirical quantitative evidence of this is the reported positive relationship between the genetic gains achieved and the environmental average yield (Calderini et al., 1999; Sadras et al., 2016).

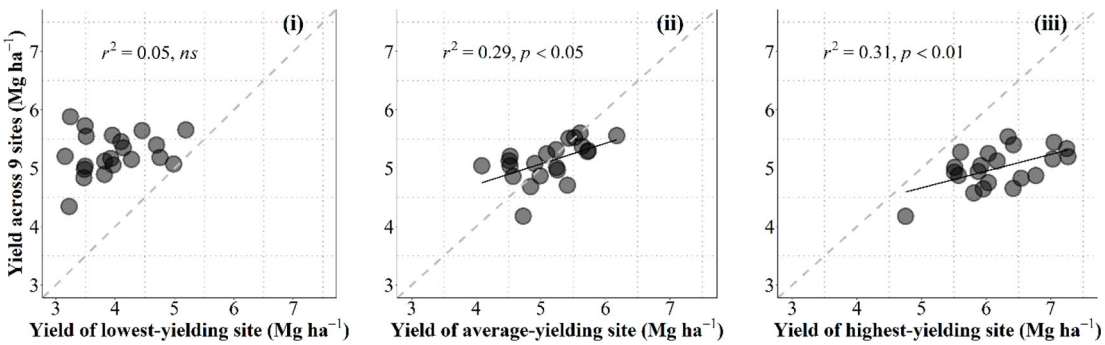

FIGURE B1 | Relationship between the overall average yield across all environments but the one being used as independent variable and yield under the lowest-yielding, mean- and highest-yielding conditions across the study (from leaf to right) for the 21 cultivars grown in 10 environments of Kansas produced by the combination of locations, growing seasons and management systems. The dashed line stands for the line representing Y = X (i.e., the 1:1 ratio) and solid lines represent the linear regression (when significant).

BOX 2 | Difficulties for achieving significant genetic gains in yield.

We analyzed the performance of commercial cultivars. That means that in a traditional historic analysis of yield gains (i.e., considering several decades of breeding), all of them would be uniformly grouped as "modern cultivars" which is relevant when comparing the breeding effect over long periods. However, analyzing the performance of cultivars released over a much shorter period may be relevant to determine the needs for maintaining/changing breeding strategies. Although far less common, analyses of short-term breeding effects (Chairi et al., 2018) are also done for this reason. Cultivars of the current study were released in the US southern Great Plains from 2007 to 2016.

Although a decade may be a rather short period to confidently analyze the performance of breeding programs, it was worrying to see no gains in yield over the whole decade, regardless of the condition in which we estimated these gains (**Figure B2**).

This evidence that recent breeding in the US southern Great Plains failed to consistently increase wheat yield is actually further supported by a previous independent study carried out in Kansas recently in which it was shown that there were virtually no yield gains since 1992 (Maeoka, 2019). Furthermore, this does not seem to be a particular case for Kansas. Conclusions derived from some studies considering in particular the most recent yield gains from long-term breeding gains (e.g., Acreche et al., 2008; Flohr et al., 2018; Lo Valvo et al., 2018; M. Sanchez-Garcia et al., 2012) or from studies exclusively focused in the recent past (e.g., Chairi et al., 2018) indicate that recent gains in yield have been much lower than in previous decades and in some cases rather marginal or inexistent. Although part of the failure in actually increasing yields could be attributed to the fact that genetic gains in environments like Kansas, characterized by low and variable yields, are more difficult to achieve (see discussion in **Box 1**), this may not be the unique cause. The studies analyzing long periods of breeding in other low and variable yield environments (Acreche et al., 2008; Sanchez-Garcia et al., 2012; Flohr et al., 2018; Lo Valvo et al., 2018) all showed clear gains in yield from mid to late 20th century, and the environments then were at least as low-yielding and as variable as they are nowadays (and for that reason they normally exhibited lower genetic gains than in high-yielding environments, but gains were clear; Calderini et al., 1999; Sadras et al., 2016). Thus, the lack of current genetic gains may well mean that a change of strategy may be required to recover the genetic gains, which are clearly needed. Identifying germ plasm possessing physiological traits that may contribute to improve yield would be ideal for strategic crosses with increased likelihood of delivering the necessary transgressive segregation required to improve yield. Thus, a physiological approach, where the physiological attributes limiting yield are recognized, complementing empirical breeding might enhance the expected gains in yield (e.g., Richards et al., 2002; Slafer, 2003).

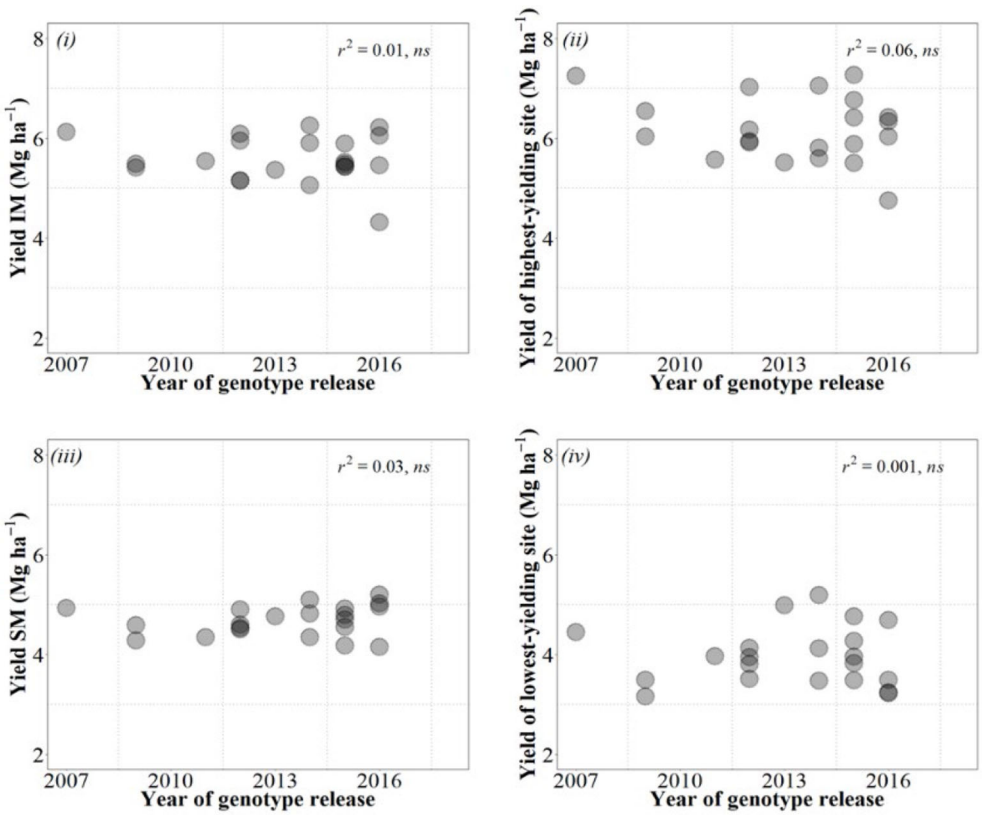

FIGURE B2 | Relationships between yield of the cultivars and their year of release considering yield under IM (top left panel), SM (bottom left panel), averaged across site-years for each management system, as well as under the highest- (top right panel) and lowest-yielding condition (bottom right panel) out of the 20 combinations of site × years × management systems.

intensification of management to reach the achievable yield of the newer cultivars produced. Thus, through understanding performance and responsiveness capacity of new genotypes, breeding programs would be more likely to identify genotypes with relatively good yield under standard conditions, but highly responsive when resources are available.

A major conclusion from this study is that the standard management of rainfed wheat in dryland Kansas consistently fall short of achievable yields, should the management be more intensive through increasing the levels of fertilization and protecting the crop against fungal diseases. In general, yield improvement due to IM was related to a greater N uptake by the crop that brought about increases in biomass accumulation with no major changes in partitioning (and in grains per m^2 with no compensation in average grain weight) determining a simultaneous increase in yield and protein concentration consistently across sites-years analysed. Identifying crop physiological mechanisms associated with the ability of genotypes to respond to management across different environmental conditions will help to develop efficient production systems, and assist breeding programs on the selection of genotypes with high yield potential and resource use efficiency. Hence, additional N fertilization and foliar fungicide application can help wheat producers to attain achievable yields in dryland systems *via* improving aboveground biomass and N uptake at maturity while maintaining HI.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

RL and AF conceived, designed, and carried out the experiments. AS performed all data collection and analysis and drafted the manuscript. GS made substantial contributions to data analysis and interpretation, as well as manuscript writing. All authors reviewed and edited the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2019.01644/full#supplementary-material

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Lessons From 20 Years of Studies of Wheat Genotypes in Multiple Environments and Under Contrasting Production Systems

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Identifying opportunities and limitations for closing yield gaps is essential for setting right the efforts dedicated to improve germplasm and agronomic practices. This study analyses genotypes × environments interaction (G × E), genetic progress, and grain yield stability under contrasting production systems. For this, we analyzed datasets obtained from three Swiss trial-networks of winter wheat that were designed to evaluate genotypes under organic farming conditions, conventional management with low-inputs (150 kg nitrogen (N) ha^{-1} with no fungicide application) and conventional management with high-inputs (170 kg N ha^{-1} with fungicide application). The datasets covered the periods from 1998 to 2018 for organic and conventional management with low-inputs and from 2008 to 2018 for conventional management with high-inputs. The trial-networks evaluated each year an average of 36 winter wheat genotypes that included released varieties, advanced breeding lines, and lines for registration and post-registration in Switzerland. We investigated within each trial-network the influence of years, genotypes, environments and their interactions on the total variance in grain yield and grain N concentration using variance components analyses. We further applied mixed models with regression features to dissect genetic components due to breeding efforts from non-genetic components. The genotype as a single factor or as a factor interacting with the environment or the year (G × E, G × year, and G × E × year) explained 13% (organic), 20% (conventional low-inputs), and 24% (conventional high-inputs) of the variance in grain yield, while the corresponding values for grain N concentration were 29%, 25%, and 32%. Grain yield has stagnated since 1990 for conventional systems while the trend under organic management was slightly negative. The dissection of a genetic component from the grain yield trends under conventional management showed that genetic improvements contributed with 0.58 and 0.68 t ha^{-1} y^{-1} with low- and high- inputs, respectively. In contrast, a significant genetic source in the grain yield trend under organic management was not detected. Therefore, breeding efforts have been less effective on the wheat productivity for organic farming conditions than for conventional ones.

Keywords: grain yield, protein yield, germplasm, variety, crop management, plant breeding, cropping systems

INTRODUCTION

In Switzerland, bread wheat is the most cultivated crop with a cultivated area of 75,830 ha in 2018. This area corresponds to 18% of the arable land and yielded 412,000 tons of grains in 2017 (Swiss Federal Statistical Office, 2018). From the area cultivated with cereals, 7.6% was cultivated under the principles of organic agriculture and this percentage is far higher than the organic cereal share of 0.6% in the world. Besides having one of the largest adoption rates of organic agriculture, Switzerland is an interesting model to study how management, driven by political and economic decisions, as well as contrasting environments influence wheat performance. The widespread adoption of contrasting production systems and pronounced differences in environmental conditions that stem from a large landscape heterogeneity renders substantial variation in limiting factors (water and nutrients), inputs (fertilizers and fungicides), and outputs (grain and protein yield). In Switzerland, as in many other countries, wheat productivity increased during the second half of the 20th century through the deployment of improved genotypes with high yield potential, enhanced tolerance to diseases and pests, and the use of mineral fertilizers and pesticides. Breeding wheat for high performance had raised wheat productivity dramatically during this period. The introduction of shorter genotypes allowed higher levels of nitrogen (N) application as well as later applications, which, influence both productivity and quality (Cruppe et al., 2017; Corassa et al., 2018). However, the achievements in productivity were accomplished to some extent at the cost of losing soil organic matter and other ecosystem services and polluting the environment (Paustian et al., 2016). To remediate these undesired effects, governments have introduced limitations for the use of certain inputs (e.g. mineral fertilizers and nocuous pesticides). In Switzerland, agricultural policy has introduced incentives for producing crops with fewer inputs or directly without some of them, as it is the case of organic agriculture with synthetic pesticides and mineral fertilizers (Lehmann and Stucki, 1997; Finger and Lehmann, 2012; Mascher and Willi, 2018). Production systems that are highly productive, resilient to changes in climate and minimize environmental harm are critically needed. A look into the genetic progress under different production systems, particularly organic ones, could be essential to identify opportunities to close gaps in productivity and in objectives (productivity vs environmental soundness).

Because the benefits of specific managements may depend on the genotype, variety trials in many countries are conducted under different cropping systems. Fischer (2009) estimated that approximately 0.6% of the 1.1% annual wheat yield gain in Australia is from improved management and 0.5% is from improved genotypes and G × management interactions. Cooper et al. (2001) examined the magnitude of G × management × environment interactions for grain yield and grain N concentration in multi-environment trials involving 272 advanced breeding lines and reported that the G × management component of this three-way interaction was the largest source of variation for both grain yield and grain N concentration. These findings not only indicate the importance of each component of the interaction to achieving high yields but also the potential to exploit such interactions to maximize grain yield and quality. However, wheat varieties registered specifically for organic agriculture rarely outperform genotypes that were bred for conventional management when both are tested under organic conditions (Przystalski et al., 2008). This has been attributed to the fact that breeding and cultivar registration for conventional management is conducted throughout several years under a broad range of environments, including treatments where pests and diseases are not controlled. Although the experimental design of most official-variety-trials do not allow quantifying G × management interactions, they can be used to quantify the relative importance of other factors (e.g. environments and genotypes) and inspect genetic progress and grain yield stability. Genotypes by Environments interaction (G × E) leads to variance differences and rank changes among genotypes (Crossa et al., 2004) and prevent higher levels of productivity and quality from being achieved (Jarquín et al., 2014). A better understanding of the impact of this interaction for different production systems may shed light on whether a breeding strategy for broad or narrow adaptability is more suitable given the production system.

The global demand for wheat is expected to rise driven by population and income growth (Charles et al., 2014). Besides a high productivity to respond to an increasing food demand, temporal and geographical stability of production will become a great challenge under a changing and less predictable climate (Schmidhuber and Tubiello, 2007). However, studies about production systems are generally focused on productivity while less attention is given to yield stability (Macholdt and Honermeier, 2017). Yet, farmers seek to reduce year-to-year variability in productivity to minimize income fluctuations. A recent study shows that the resilience of European wheat under conventional high-inputs has been declining because modern varieties have a reduced capacity as compared to older ones to respond to climatic variability and anomalies (Kahiluoto et al., 2019). Loss of resilience under a more unpredictable climate would represent a serious risk for the forthcoming future (Wójcik-Gront, 2018). Most analyses of production systems have focused on relatively short-term experiments and/or on single or few genotypes. However, studies that cover a period of 10 years or more are scarce (Kleinman et al., 2018). Furthermore, interactions between cropping systems and genotypes are well documented (e.g. Cober and Morrison, 2015) and the use of one genotype may create a bias in favor of one production system (Büchi et al., 2016).

This study analyses genotypes × environments interaction (G × E), genetic progress, and grain yield stability under contrasting production systems. We analyzed datasets obtained from three Swiss trial-networks of winter wheat designed to evaluate genotypes under organic, conventional low-inputs (150 kg N ha^{-1} with no fungicide application) and conventional high-inputs (170 kg N ha^{-1} with fungicide application) production systems.

MATERIALS AND METHODS

Data Sources

The datasets used in this study were obtained from three trial-networks of winter wheat varieties designed to evaluate genotypes in the context of three different production systems. The production systems were conventional management with low-inputs (LM), conventional management with high-inputs (HM), and organic management (OM). Besides the production system, the three networks differed in the locations where the experiments were conducted (**Table 1**) and the germplasm evaluated. The experimental sites were distributed across the wheat main production area of Switzerland (**Figure 1**). They were situated between 376 and 707 m a.s.l. and on soils that are mostly classified as Cambisols (World Resource Base, FAO) except for the site in Vouvry (**Table 1**) whose soil is classified as Fluvisol. Soil pH and organic matter content ranged between 6.7 and 8.1 and between 15 and 33 g kg^{-1}, respectively. Field trials within each site were arranged as Lattice (conventional management with low-inputs), Latin square (conventional management with high-inputs), and randomized complete block (organic management) designs and always with three replications. The experimental plots covered 7.1 m^2 (4.75 × 1.50 m) and consisted of eight rows with an inter-row distance of 0.16 m. Plots were separated by 1.3 m and sown at a rate of 350 (conventional management) and 380 seeds m^{-2} (organic management). Sowing and harvest took place each year during the months of October and June–July, respectively.

In addition, we considered data from the Food and Agriculture Organization of the United Nations (FAO, 2019) to compare the results obtained in the variety trials with those that summarize the evolution and general characteristics of wheat productivity in Switzerland. FAO grain yield data are indirectly estimated from national production quantity and total area harvested and we used it here because long-term farm-level data were not available.

Germplasm in the Swiss Winter Wheat Trial-Networks

The genotypes included released varieties, advanced breeding lines, lines submitted for registration or post-registration in Switzerland. According to the information provided by the seed companies, the vast majority of the genotypes were grown under conventional management during the selection stages of the breeding program. Selection was performed under diverse environments and across many years that exposed genotypes to variable climatic conditions. The set of genotypes also included varieties declared to have been bred and/or to be suitable for organic production.

Overall, the study considers results from 300 (conventional low-inputs), 81 (conventional high-inputs), and 102 (organic) genotypes in total. For the analyses of variance components (of

TABLE 1 | Main characteristics of the sites of the conventional low-inputs (LM), conventional high-inputs (HM), and organic (OM) trial networks of winter wheat varieties.

Site	Alt.[a]	Prec.[b] (mm)	Evap.[c] (mm)	Evaluation networks in the site	Time Span	Grain Yield (dt ha^{-1})[d]		
						Organic	Conv. low-inputs	Conv. high-inputs
Assens	707	1,107	778	LM	1998–2018	NI[e]	72.27 ± 0.36	NI
Avenches	480	838	697	OM	2005–2018	39.15 ± 0.51	NI	NI
Bünzen	441	1,356	491	OM	1998–2018	56.50 ± 0.36	NI	NI
Changins	376	971	760	LM,HM	1998–2018, 2008–2018	NI	68.17 ± 0.30	68.57 ± 0.46
Courtemelon	441	897	673	HM	2008–2018	NI	NI	78.68 ± 0.58
Dickihof	416	848	612	OM	2008–2018	46.81 ± 0.48	NI	NI
Ellighausen	537	1,030	647	LM	1998–2008	NI	72.57 ± 0.31	NI
Grangeneuve	620	898	475	LM,HM	1998–2018, 2008–2018	NI	70.86 ± 0.36	79.73 ± 0.49
Hindelbank	519	1,018	541	OM	1999–2018	51.09 ± 0.36	NI	NI
Knutwil	541	1,182	530	OM	1997–2009	50.56 ± 0.43	NI	NI
Liebegg	510	1,679	651	HM	2008–2018	NI	NI	73.12 ± 0.43
Lindau	449	1,267	669	LM,HM	2008–2018, 2008–2018	NI	74.46 ± 0.39	77.47 ± 0.50
Moudon	540	953	671	LM,HM	1998–2018, 2008–2018	NI	72.26 ± 0.27	77.19 ± 0.47
Nennigkofen	456	1,031	528	OM	2008–2018	47.65 ± 0.37	NI	NI
Neuhausen	461	850	614	HM	2008–2018	NI	NI	73.68 ± 0.46
Portalban	529	808	691	LM	1998–2018	NI	75.34 ± 0.36	NI
Rheinau	400	854	618	OM	2001–2013	34.94 ± 0.33	NI	NI
Riedholz	471	1,031	528	HM	2008–2018	NI	NI	74.71 ± 0.50
Salenstein	400	844	608	HM	2008–2018	NI	NI	71.32 ± 0.49
Seebach	420	1,037	668	OM	2008–2018	51.50 ± 0.47	NI	NI
Sulz bei Künten	420	1,356	491	LM,OM	2008–2018, 2002–2007	50.38 ± 0.50	54.70 ± 0.39	NI
Vufflens	478	1,107	778	OM	2010–2018	41.98 ± 0.46	NI	NI
Vouvry	382	966	735	LM	1998–2018	NI	64.65 ± 0.33	NI
Wegenstetten	441	1,063	720	OM	1999–2018	44.95 ± 0.35	NI	NI
Zollikofen	564	1,018	541	LM,HM	2008–2018, 2008–2018	NI	78.68 ± 0.43	85.19 ± 0.49

[a]Alt., altitude is expressed in m above sea level; [b]Prec., average annual precipitation, [c]Evap., average annual evapotranspiration, [d]Data are means across years ± standard error of the mean; [e]NI is site not included in the network.

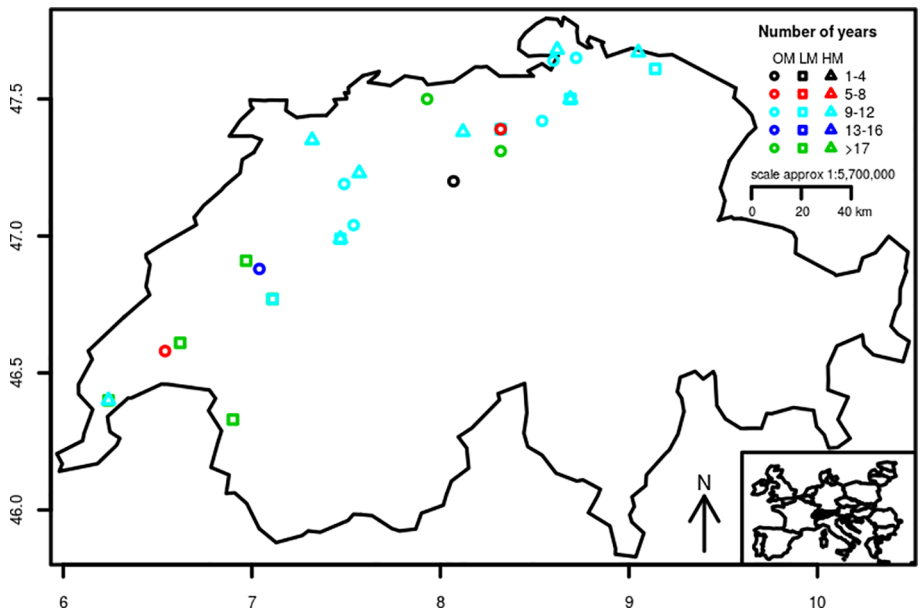

FIGURE 1 | Distribution across Switzerland of the sites of the conventional low-inputs (LM), conventional high-inputs (HM), and organic (OM) trial networks of winter wheat varieties. Colors show the number of years that experiments were repeated at specific sites.

grain yield and N concentration), yield trends, and stability, we considered only genotypes that were included at least three years in one of the trial-networks. By this, our analyses base on genotypes that fulfill the requirements to be registered in Switzerland. These genotypes may be assumed as genotypes that farmers would grow in their farms. Finally, the subset for the latter analyses included 58 (conventional low-inputs), 35 (conventional high-inputs), and 43 (organic) genotypes.

Growing Conditions

Trials under conventional management were conducted on research stations of public institutes or educational centers while trials under organic management were mostly conducted in organic farms by public research institutes. Trials under organic management were conducted under the principles of organic agriculture, namely without using synthetic inputs (i.e., no synthetic pesticides and no mineral fertilizers). Wheat was fertilized at a rate of 150 kg N ha^{-1} (conventional low-inputs), 170 kg N ha^{-1} (conventional high-inputs), and at approximately 90 kg N ha^{-1} (organic). The source of N was liquid manure for the organic management and inorganic N fertilizer split into two to three applications depending on year and site for the conventional management. Available P and K values ranged from 38 to 184 and from 99 to 318 kg ha^{-1}, respectively. Fertilization with P or K was not regularly done, except when their concentration was below the recommended soil availability. Fungicides and growth regulators were systematically applied under conventional high-inputs while no disease control or growth regulators were applied under conventional low-inputs and organic management.

Characterization of Sites

We used two statistics to characterize sites: i) repeatability (also known as single plot heritability) which provides information on how consistent is the performance of the genotypes in one site, and ii) the ability of the sites to differentiate genotypes (differentiability, hereafter).

We estimated repeatability with the following equation:

$$r_{jk} = \frac{s_g^2}{s_g^2 + s_e^2} \quad (1)$$

where r_{jk} is the repeatability in year j at site k and $s^2{}_g$ is the genotypic variance and $s^2{}_e$ the error variance. We estimated differentiability following Utz (1973):

$$d_k = 1 + \frac{\sum_i (X_{ik} - \bar{X}_{i.} - \bar{X}_{.k} + \bar{X}_{..})(\bar{X}_{i.} - \bar{X}_{..})}{\sum_k (\bar{X}_{i.} - \bar{X}_{..})^2} \quad (2)$$

where d_k is the differentiability at site k and X are mean values obtained across genotypes ($\bar{X}_{i.}$), sites ($\bar{X}_{.k}$) or both (X_{ik}) and $\bar{X}_{..}$ is the general mean.

Variance Components Analyses

We used the following model to quantify the amount of variance explained in grain yield and N concentration by specific factors:

$$t_{ijk} = \mu + v_i + s_k + y_j + vs_{ik} + vy_{ij} + sy_{jk} + vys_{ijk} + e \quad (3)$$

where t_{ijk} is the response variable (i.e. grain yield or grain N concentration) of genotype i in year j at site k; μ is the trial series

mean; v_i is the effect of genotype i; s_k is the effect of site k; y is the effect of year j; vs_{ik} is the interaction of variety i in site k; vy_{ij} is the interaction of variety i in year j; sy_{jk} is the interaction of site k with year j; vys_{ijk} is the three-way interaction among variety i, site k and year j; and e is a residual comprising variation unexplained by the previous components. The model was fitted using maximum likelihood (ML) as implemented in the R (R Core Team, 2015) package "lme4" (Bates et al., 2015).

Analyses of Trends in Grain Yield

We evaluated five statistical models (i.e. linear, quadratic, linear piecewise, logistic, and asymptotic) for their performance fitting the relationship between grain yield data from FAO and years (Grassini et al., 2013). The models were used as defined in the R packages "easynls" (i.e. quadratic), "segmented" (i.e. linear piecewise), and "stats" (i.e. logistic and asymptotic). Selection of the most suitable model was based on the AIC (Akaike information criterion) estimator (Akaike, 1998). The R function used for the linear piecewise model, estimates one or more breakpoints based on the slope parameters and changes in the linear relation. Long-term yield trends have genetic and non-genetic components which can be differentiated by a linear mixed model (Friesen et al., 2016) with regression terms (Piepho et al., 2014). Improved agronomic practices and environmental changes account for the non-genetic components while the genetic component allows characterizing the impact of breeding efforts on the productivity of released genotypes.

To account for both genetic and non-genetic effects on yield trends, we applied here the approach developed by Mackay et al. (2011) and extended by Piepho et al. (2014). The following model was fitted using restricted maximum likelihood (REML) as implemented in the R package "lme4":

$$g_{ijk} = \mu + v_i + s_k + y_j + vs_{ik} + vy_{ij} + sy_{jk} + e \quad (4)$$

where g_{ijk} is the grain yield of genotype i in year j at site k; μ is the mean; v_i is the effect of genotype i; s_k is the effect of site k; y is the effect of year j; vs_{ik} is the interaction of variety i with site k; vy_{ij} is the interaction of variety i with year j; sy_{jk} is the interaction of site k with year j; and e_{ijk} is a residual comprising both genotype × site × year interaction as well as the error of the mean. To account for genetic effects on yield trends, we explicitly incorporated regression terms to model the genetic source in the grain yield trend by using the year that each genotype entered the trials for the first time:

$$G_i = \beta y_{0i} + H_i \quad (5)$$

where β is a fixed regression coefficient for genetic trend, y_{0i} is the first year the genotype i entered the trials, and H_i models a random normal deviation of G_i from the genetic trend line.

Despite some apparent non-linear relations, in the cases where visual assessments suggested potential deviations from a linear relationship, we did not find a non-linear substitute. Therefore, we report linear regression results. These models assume that at least some sites are used across several years. All effects except μ, v_i, y_j, and y_{0i} are assumed to be random with constant variance. We estimated adjusted means with the R package "emmeans".

Some authors proposed to add regression terms to account for breakdown of disease resistance (Mackay et al., 2011; Laidig et al., 2017). Although we made such attempts, they did not improve the performance of the models. We attribute this to two reasons: i) in reality individual genotypes succumb to disease abruptly and often at non-linear rates (Mackay et al., 2011) and ii) the genotypes stayed on average for short times in the trials (Perronne et al., 2017). The average age of the genotypes was 4.57, 4.32, and 2.94 years under organic, conventional low-inputs, and conventional high-inputs, respectively.

Grain Yield Stability and Interannual Variability

Grain yield stability can be measured in different ways (Lin et al., 1986). One way to measure grain yield stability that was often used for comparing cropping systems is the coefficient of variation (CV) (e.g. Knapp and Van der Heijden, 2018), which divides the variability in grain yield (expressed as standard deviation) by the grain yield mean. The advantage of this approach is that it provides a measure of variability corrected by the level of grain yield achieved. Different approaches were also followed to study the interannual variability on the grain yield of crops. Here we followed the approach of Penalba et al. (2007) that considered the absolute values of the difference between the mean grain yield of one year and the mean grain yield of all the years throughout the duration of the study. Since genetic progress may increase grain yield with time and show deviations from the mean grain yield of all the years that are not associate to climate, we divided the aforementioned difference by the mean of the year and express this parameter as a ratio. We refer to this parameter as interannual deviation ratio. The rationale of these analyses was to determine if there were reductions in grain yield stability and increases in interannual variability due to climate change. We additionally wanted to determine if there were differences in these parameters among production systems. We used Mann-Kendall and Hartley's tests in these analyses.

Statistics and Presentation of Results

We used R (R Core Team, 2015) for all statistical analyses. Performance at the sites were evaluated using the following indicators: CV (data not shown), repeatability (**Table 2**), differentiability (**Table 2**), and the visual inspection of heat maps of grain yield for spatial patterns associated to gradients in soil fertility or another factor that may disrupt the real differences among the tested genotypes (data not shown). Repeatability, differentiability and CV were calculated per year but displayed as means across years in order to summarize results. We conducted a Hartley's test as implemented in the R's package "stats" to assess differences in variances of grain yield among production systems and a Mann–Kendall test as implemented in the R's package Kendall to determine if there were time series trends within production systems in the CV and interannual deviation ratios of grain yield.

TABLE 2 | Average repeatability (m.r.) and average ability to differentiate genotypes (m.d.) of the sites included in the study.

Site	Organic			Conventional Low-inputs			Conventional High-inputs		
	m.r. ± s.e.[a]	m.d. ± s.e.	n[b]	m.r. ± s.e.	m.d. ± s.e.	n	m.r. ± s.e.	m.d. ± s.e	n
Assens		NI[c]		0.87 ± 0.02	1.12 ± 0.11	17		NI	
Avenches	0.36 ± 0.12	0.99 ± 0.25	12		NI			NI	
Bünzen	0.60 ± 0.08	1.11 ± 0.19	20		NI			NI	
Changins		NI		0.87 ± 0.05	0.99 ± 0.10	20	0.95 ± 0.01	1.00 ± 0.12	10
Courtemelon		NI			NI		0.92 ± 0.02	1.15 ± 0.14	10
Dickihof	0.30 ± 0.12	0.79 ± 0.31	10		NI			NI	
Ellighausen		NI		0.84 ± 0.04	0.92 ± 0.11	21		NI	
Grangeneuve		NI		0.82 ± 0.04	0.93 ± 0.11	21	0.88 ± 0.03	1.03 ± 0.13	10
Hindelbank	0.60 ± 0.08	1.01 ± 0.22	17		NI			NI	
Knutwil	0.50 ± 0.11	1.09 ± 0.16	11		NI			NI	
Liebegg		NI			NI		0.94 ± 0.01	0.91 ± 0.12	10
Lindau		NI		0.84 ± 0.05	1.09 ± 0.11	9	0.91 ± 0.02	1.04 ± 0.12	11
Moudon		NI		0.76 ± 0.05	1.01 ± 0.12	21	0.87 ± 0.03	0.99 ± 0.15	11
Nennigkofen	0.70 ± 0.09	1.22 ± 0.23	11		NI			NI	
Neuhausen		NI			NI		0.90 ± 0.02	0.92 ± 0.13	11
Portalban		NI		0.89 ± 0.01	1.13 ± 0.10	21		NI	
Rheinau	0.39 ± 0.08	0.53 ± 0.18	11		NI			NI	
Riedholz		NI			NI		0.95 ± 0.01	1.02 ± 0.10	11
Salenstein		NI			NI		0.94 ± 0.01	0.95 ± 0.10	10
Seebach	0.60 ± 0.11	1.11 ± 0.24	10		NI			NI	
Sulz bei Künten	0.44 ± 0.12	1.07 ± 0.17	6	0.73 ± 0.06	0.66 ± 0.12	10		NI	
Vouvry		NI		0.92 ± 0.01	1.06 ± 0.13	17		NI	
Vufflens	0.39 ± 0.12	1.17 ±0 .27	7		NI			NI	
Wegenstetten	0.71 ± 0.07	0.96 ± 0.18	19		NI			NI	
Zollikofen		NI		0.86 ± 0.02	1.01 ± 0.10	11	0.93 ± 0.01	0.99 ± 0.12	10

[a]s.e. is standard error of the mean; [b]n is the number of years used in the calculations; [c]NI is site not included in the network. The parameter was estimated from grain yield under conventional low-inputs (LM), conventional high-inputs (HM), and organic (OM). trial networks.

RESULTS

Summary Statistics and Characteristics of Sites

Averages across sites and years (**Table 1**) show, as expected, that grain yield was the highest in the network where wheat genotypes were grown under conventional practices with high-inputs (75.97 dt ha^{-1}). They were followed by those where the genotypes were grown under conventional practices with low-inputs (70.40 dt ha^{-1}). The genotypes grown under organic practices showed the lowest grain yield mean (46.86 dt ha^{-1}). These results indicate a yield difference of 5.57 and 29.11 dt ha^{-1} for the conventional low-inputs and organic production systems, with respect to the conventional management with high-inputs. The corresponding values considering only the grain yields observed the last three years with common genotypes in the compared networks are 14.32 and 20.23 dt ha^{-1}, and in both cases these differences are statistically significant ($p < 0.05$). A comparison for both common genotypes and sites was only possible between conventional low-inputs and conventional high-inputs and it showed a difference of 11.35 dt ha^{-1}.

The CV was systematically higher under organic management, where only one site had a CV <10%. Overall, the CV was higher when the amount of inputs used was lower (organic > conventional low-inputs > conventional high-inputs) and showed always values below 10% under conventional managements. In contrast, repeatability showed the opposite ranking; values were higher when the amount of inputs used was higher (organic < conventional low-inputs < conventional high-inputs). Thus, the evaluation of genotypes tended to be more consistent across years in the sites under conventional high-inputs than low-inputs. Under organic management, there were sites with very low (i.e. Assens, Dickihof) and low (i.e. Rheinau, Sulz bei Künten, and Vufflens) repeatability, showing that evaluations in these sites tended to be more inconsistent across years than those conducted at other sites. Despite the limitations in the organic network, the sites of Bünzen and Nennigkofen show a high ability to differentiate genotypes (values >1). Similarly, the sites of Assens, Portalban, Lindau, and Vouvry under conventional low-inputs and Courtemelon and Lindau under conventional high-inputs showed an ability above the average to differentiate genotypes. In short, higher levels of inputs resulted in less variable grain yield (lower CV), higher consistency across years (repeatability), and higher ability to differentiate genotypes (differentiability).

Variance Components Analyses

Figure 2 shows the results of variance components analyses for grain yield and N concentration in the three trial-networks. Five, 13 and 17% of the variance on grain yield was ascribed to genotypes effects under organic, conventional low-inputs and conventional high-inputs, respectively. The corresponding values were 13, 20, and 24% when taking into account also other components where the factor genotypes was involved through interactions. The factor genotypes explained a higher proportion of the variance in grain N concentration than in grain

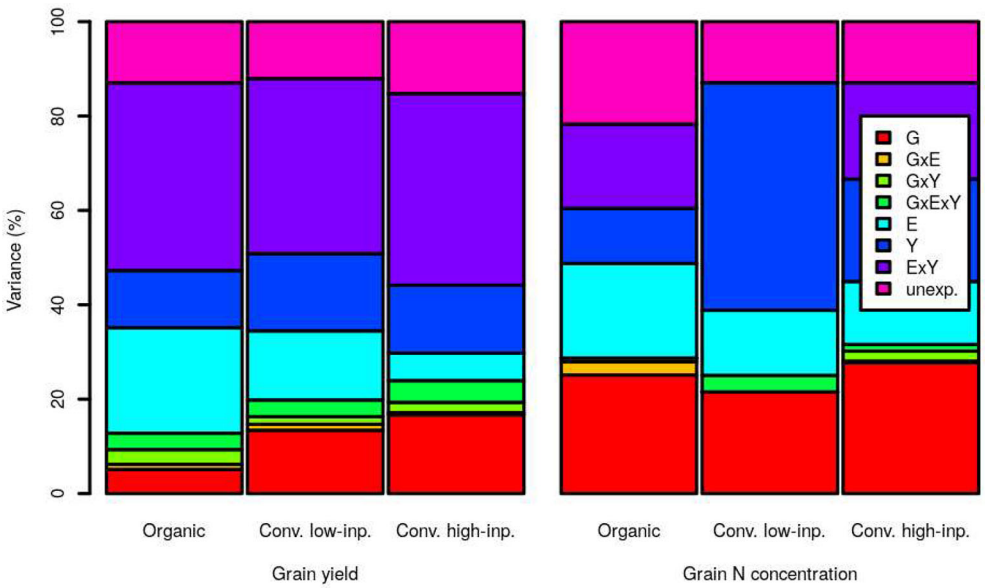

FIGURE 2 | Variance component analyses for grain yield and grain nitrogen (N) concentration within an organic (1998–2018), conventional low-inputs (Conv. low inp.) (1998–2018) and conventional high-inputs (Conv. high inp.) (2008–2018) variety-testing networks. Components considered were genotypes (G), environments (E), years (Y), the interaction genotypes by environments (G × E), the interaction genotypes by years (G × Y), the interaction environments by years (G × Y), and the interaction genotypes by environments by years (G × E × Y). We also show the amount of variance that remained unexplained by the models (unexp.).

yield, with percentages of 25, 22, and 28 in the organic, conventional low-inputs and conventional high-inputs trial-networks, respectively. The corresponding values were 29, 25, and 32% when taking into account also other components where the factor genotypes was involved through interactions.

For grain yield, the factor that explained the highest proportion of variance was the environment by years interaction and the value of this proportion was similar for the three production systems. Interestingly, the amount of variance explained by the environment as a single factor diminished as the inputs level was higher (organic > conventional with low-inputs > conventional with high-inputs). This reduction is almost equivalent to the increase in the proportion explained by genotypes alone or through interactions with increasing use of inputs (conventional with high-inputs > conventional with low-inputs > organic).

For grain N concentration, the main difference among production systems is the amount explained by years as a single factor, which was surprisingly high under conventional low-inputs. In any case, the proportion of variance explained by years was also higher for grain N concentration than for grain yield in the other two cropping systems. Interactions among factors explained a lower amount of the total variance in grain N concentration than in grain yield.

Grain Yield Trends

Figure 3 shows the average grain yield of winter wheat in Switzerland between 1961 and 2017. This figure also presents the period in which the genotype evaluations presented here took place. The linear piecewise model (AIC = 339.9) showed to be more suitable than linear (AIC = 373.9), quadratic (AIC = 427.5), logistic (AIC = 347.7), and asymptotic (AIC = 351.6) models for summarizing the relationship between grain yield and years. The breakpoint between the period of linear increase in productivity and the period of stagnating yields was estimated to be the year 1991. When only data between 1961 and 1991 was considered (line in **Figure 3**), the slope of the linear regression for the period of linear increase in productivity was 0.98 dt ha^{-1} y^{-1} (standard error of the mean 0.09 dt ha^{-1} y^{-1}).

Points in **Figure 4** show grain yields of genotypes from 1998 to 2018 (**Figure 4A**: organic system and **Figure 4B**: conventional system with low-inputs) and from 2008 to 2018 (**Figure 4C**: conventional with high-inputs). Fitting data with non-linear models did not show an advantage over linear ones. Thus, it was not necessary to replace linear regression models by non-linear ones (Lopes et al., 2012; Piepho et al., 2014). Grain yield trends and the genetic source of grain yield trends are plotted with lines. The slope of the grain yield trends observed under conventional low-inputs was not different from zero (**Table 3**) while the corresponding slope for the conventional high-inputs and organic managements were negative. However, only under organic management this slope was significantly negative. In contrast, the genetic source of the grain yield trend was positive in the three studied networks (**Table 3**) and it was significant and marginally ($p < 0.10$) significant for the conventional low-inputs and conventional high-inputs managements, respectively. While the increase in the genetic source of grain yield was almost null under organic management, genetic effects increased steadily

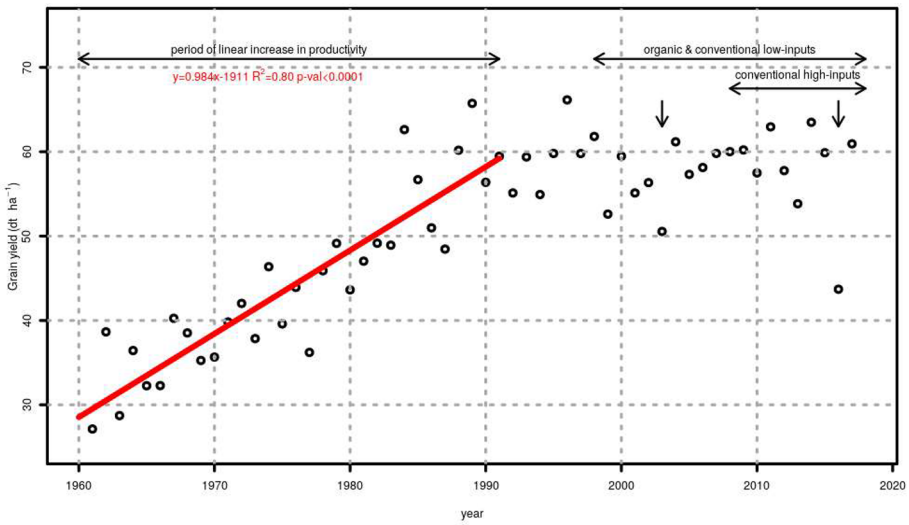

FIGURE 3 | Average grain yield of winter wheat in Switzerland between 1961 and 2017. A linear trend summarizes the evolution from 1961 to 1989 (red line). The period during which genotypes were tested under organic, conventional low-inputs and conventional high-inputs is shown using horizontal arrows while vertical arrows show years with exceptionally severe droughts.

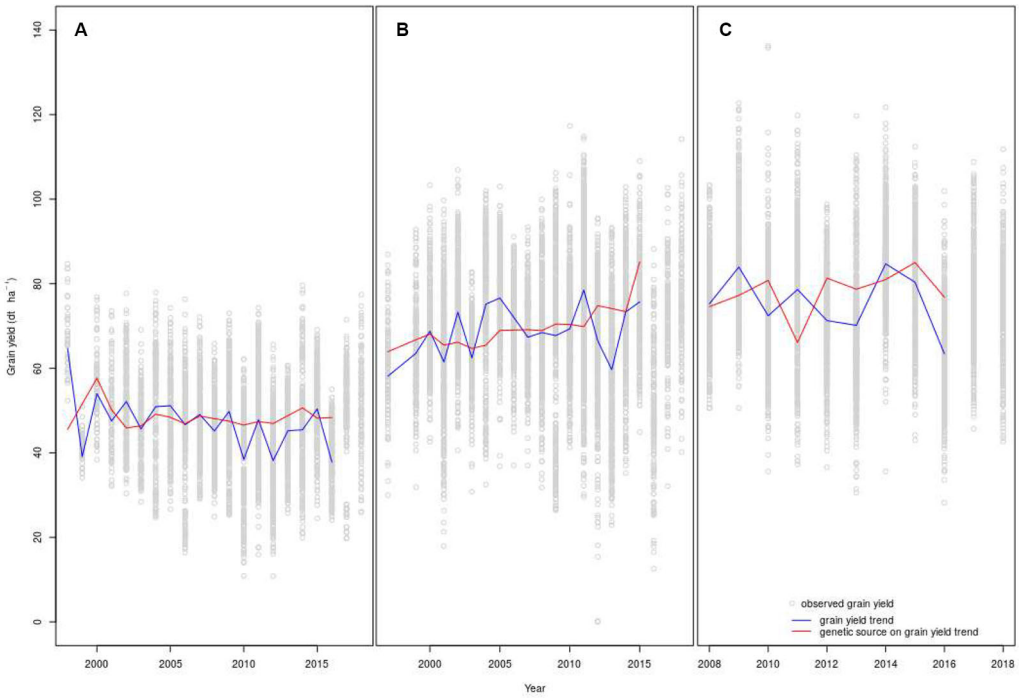

FIGURE 4 | Grain yield trends and genetic sources on the grain yield trends under organic **(A)**, conventional low-inputs **(B)**, and conventional high-inputs **(C)** management. The fit on the models is shown until 2016 because the analysis was performed on genotypes that remained in the trials at least three years. Because of this criterion, the year 2016 was the last year available to consider the year that a genotype entered the variety trials. X-axis of panels **(A–C)** have different scales.

under conventional managements. This increase represented 0.58 and 0.68 dt ha^{-1} y^{-1} with low- and high-inputs, respectively. The estimated genetic contribution to the grain yield trend under conventional low-inputs (0.58 dt ha^{-1} y^{-1}) is in the same range of the value obtained from FAO data for the period 1961-2015 (0.58 dt ha^{-1} y^{-1}). In both conventional

TABLE 3 | Regression parameters used in mixed linear models of grain yield of winter wheat to estimate the slopes for grain. yield trends and genetic sources on grain yield trends.

Trial Network	Grain yield trend (dt ha^{-1} y^{-1})		Genetic source on grain yield trend (dt ha^{-1} y^{-1})	
	Estimate ± s.e.[a]	Pr(>|t|)	Estimate ± s.e.	Pr(>|t|)
Organic (OM)	−0.35 ± 0.17	0.03*	0.09 ± 0.08	0.32ns
Conventional with low-inputs (LM)	0.16 ± 0.16	0.33ns	0.58 ± 0.13	<0.0001***
Conventional with high-inputs (HM)	−0.41 ± 0.34	0.23ns	0.68 ± 0.35	0.06†

[a]*s.e. is standard error of the mean; ns is not significant at the 0.10 probability level; †, *, *** are significant at the 0.10,0.05, and 0.001 probability levels, respectively.*

production systems, the contribution of genetics to the grain yield was often below the average before 2007, while after this year it was above the average in 8 out of 9 and in 5 out of 9 years with low- and high- inputs, respectively (**Figures 4B**, **C**). In the conventional systems, independently of the levels of inputs, the contribution of genetics to the grain yield trend was above the average in 2015, a year with a severe drought in Switzerland. This was also the case under conventional low-inputs in 2003, another year with a severe drought. In contrast, under organic management the genetic component of the grain yield trend was below the average in 2003 and 2015.

Grain Yield Stability and Variability

We inspected the yield-stability considering the CV of all the genotypes that stayed in the trial-networks for more than two years (**Figure 5A**). The average values of CV were 18.5, 16.5, and 14.0% under organic management, conventional low-inputs, and conventional high-inputs, respectively. Thus, it was systematically higher under organic than under conventional management. A Hartley's test to assess differences between variances showed marginally significant differences between conventional low-inputs vs conventional-high inputs and significant differences between conventional high-inputs and organic. We were particularly interested to know if there was a trend towards a decrease in stability (or increase in interannual variability) triggered by climate change and if there were different patterns among production systems. We tested this hypothesis in different ways. A Mann–Kendall test on the CV of grain yield through time revealed only a marginally significant trend under organic management. We considered the interannual-deviation-ratio of grain yield (**Figure 5B**) which showed positive and negative values (**Figure 5B**). Thus, it can be ruled out that deviations are due to grain yield increases from genetic progress. The consideration of absolute values for the interannual-deviation-ratio of grain yield suggests an increasing interannual variability (**Figure 5C**) also visible for the CV of grain yield under conventional low-inputs (**Figure 5A**). The onset of this increasing variability seem to be from 2007 onwards. However, the statistical tests that we considered did not reveal significant trends.

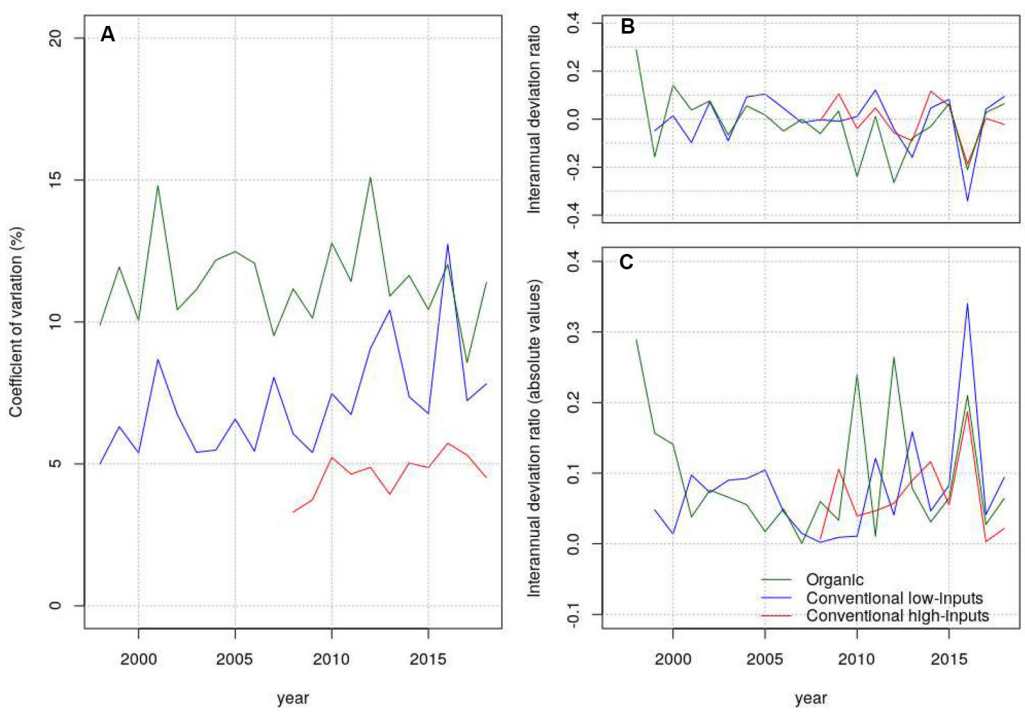

FIGURE 5 | Coefficient of variation **(A)**, interannual deviation ratio **(B)** and absolute values of the interannual deviation ratio **(C)** estimated from grain yield under contrasting production systems.

DISCUSSION

Grain yield and wheat quality are subject to unexpected outcomes from interactions between genotypes and environmental factors. This is a challenge in breeding and genotype evaluation programs (Cullis et al., 2000; Munaro et al., 2014). Among the most important environmental factors that modify genotypic performance are soil characteristics, N availability, rainfall, and temperatures during ripening. Numerous studies show the influence of G × E on wheat's grain (e.g. Bilgin et al., 2016) and protein (Finlay et al., 2007; Williams et al., 2008) yields. Grain yield was highly influenced by environment by year interaction in the three production systems considered here (**Figure 2**). The realization of the yield potential of varieties relied on the use of inputs; when the levels of inputs were higher, the variance on grain yield explained by genotypes was higher. Hence, a higher use of inputs reduced the impact of environment on this trait. This suggests that with a lower level of inputs, selection programs may need to include a larger number of environments to detect stable performing genotypes. Breeding programs for wheat cannot neglect the importance of quality and the factor genotype influenced to a higher extent protein than grain yield. This may be explained by the fact that the genetically determined composition of gluten is the main determinant of genotypic differences in grain protein concentration (Payne et al., 1987; Jiang et al., 2019). The comparable contribution of genotypes to grain N concentration across production systems suggest that selection strategies for protein concentration may be less dependent on the type of production system considered. Overall, our results agree with general conclusions by other authors that grain yield and protein concentration were highly sensitive to environmental fluctuations (Bilgin et al., 2016; Laidig et al., 2017). Here we also show that this was the case for three contrasting production systems.

According to the FAO database, productivity of wheat in Switzerland has stagnated during the last 27 years. The fact that FAO grain yield data (**Figure 3**) are estimated from national production quantities and the total harvested area, may lead to misleading conclusions such as that grain yield stagnation may not really stem from an invariable yield potential of the winter wheat genotypes but just from changes in the area harvested. This is, however, unlikely because there were no major changes in the area harvested and grain yield measured directly in genotype trials also showed stagnation (**Figure 4** and **Table 3**) for different production systems. Under organic management, the yield trend was even negative with a significant slope (**Table 3**). The question if this stagnation in the productivity shows lack of genetic improvement in winter wheat will be addressed later, demonstrating that the answer depends on the production system considered. Among causes of stagnation in wheat productivity, different reasons have been suggested. They include lack of genetic improvement (Calderini and Slafer, 1998), changes in crop management (Brisson et al., 2010), worsening of environmental conditions caused by climate change (Hochman et al., 2017), use of low input levels (Patrignani et al., 2014), lack of crop rotations (Patrignani et al., 2014), soil degradation (Patrignani et al., 2014), as well as economic (Hafner, 2003), and political (Finger, 2010) factors. Political and economic decisions may lead to changes in agricultural practices such as a reduced use of inputs. In 1992, approximately at the onset of the period of stagnated productivity, subsidies to reduce the use of fungicides, insecticides, plant growth regulators, and synthetic stimulators were introduced in Switzerland. Finger (2008) propsosed also shifts towards production systems with lower inputs as one of the main reasons for the stagnation in wheat's productivity. Another process that was observed in the last 10 years is that more farmers are targeting a market class with a higher quality requirement. The wheat varieties that they must grow to achieve these quality requirements have lower yield potential.

A possible pathway to break grain yield stagnation is through plant breeding. The contribution of breeding to increase grain yield in farms may depend however on the difference between current yields and potential yield in different regions and production systems (Battenfield et al., 2013; Patrignani et al., 2014). In the genotype trial networks, we found that yield stagnation is present independently of the production system (**Figure 4**) and the genetic component of the yield trends shows different outcomes depending on the production system considered (**Table 3**). While we found positive significant and marginally significant genetic effects on conventional low- and high- inputs, respectively, we did not detect evidence of significant genetic improvements under organic conditions. The procedure applied for conducting filial generations (F_2 to F_5) in a breeding program can affect the response of genotypes to management as shown for winter wheat for grazing vs. grain-only production systems (Thapa et al., 2010). A recent comprehensive study showed that breeding for high inputs enhances cultivar performance not only under high inputs but also in production systems with reduced agrochemical inputs (Voss-Fels et al., 2019). However, the study by Voss-Fels et al. (2019) did not include organic management. We did not find evidence that breeding for other production systems impacted genetic progress under organic management in the same extent; the genetic effects that we found under conventional management were not observed under organic management (**Table 3**). The parallel impact for conventional low- and high-inputs production systems was explained by the fact that most breeding programs expose their materials to conventional conditions of low and high inputs through the cycles of selection and testing (Voss-Fels et al., 2019). Besides the use of modern breeding techniques, continual gains in productivity and quality have been promoted by official genotype testing procedures that require trait improvement and consistency across diverse environments as a prerequisite for cultivar registration (Voss-Fels et al., 2019). Thus, traits that are important under high-inputs may be also relevant with lower inputs under the same production system and only the degree of expression of the trait may differ. In contrast, organic management may have differences in the sources and dynamics of nutrients (Lori et al., 2017) and in the spectrum of pest and diseases (Lammerts Van Bueren et al., 2011; Bilsborrow et al., 2013) compared to conventional management that may demand additional or different traits (Lammerts Van Bueren et al., 2011). An additional indication

of the likely lower breeding effort for organic management is the higher average age of the varieties; fewer genotypes are submitted each year for the test under organic conditions, which results in a 55% higher age of the genotypes under organic management than conventional with high-inputs. Since the sites under organic management differed from those under conventional management, genotypes may in addition be less adapted to the sites where they have been tested. Such hypothesis is supported by the higher impact of the factor Environment, alone or interacting, under organic management than under conventional management (**Figure 2**). Finally, agronomic limitations that prevent the yield potential to be expressed under organic management cannot be fully ruled out as well as differences in breeding goals for conventional and organic production systems.

The most widely practiced and studied alternative to high-inputs agriculture is organic management. Studies of organic agriculture have revealed better performance than conventional practices on some parameters associated to sustainability but not all (Tuck et al., 2014). The concept of yield gap (Van Ittersum et al., 2013) allows identifying unlocked yield potential and it must be kept in mind that generally full yield gap closure is not economically feasible and not environmentally advisable. The yield gap for rainfed wheat was recently estimated for Switzerland at 3.7 t ha^{-1}. This was based on an estimated yield potential for rain-fed conditions of 9.7 t ha^{-1} (Schils et al., 2018). This yield potential was determined with the WOFOST crop model considering temperature, day length, solar radiation, and genetic characteristics assuming absence of any water or other stress factors (Schils et al., 2018). The results obtained in the last three years (2015–2018) under conventional management with high-inputs shows an average performance of genotypes only 2 t ha^{-1} below the yield potential. Thus, the genotypes recently released may be reaching the biophysical potential of wheat in Switzerland. Besides the pressure from consumers and regulators to move towards production systems with fewer inputs, levering yield potential may be challenging for conventional management with high-inputs due to economic, environmental, and biophysical limitations. We estimated yield differences for organic and conventional management with low-inputs compared to conventional management with high-inputs. These differences can be considered a rough approximation because it compares results obtained in different sites, with different genotypes, and for experiments conducted throughout different periods. According to Laidig et al. (2017) it must be noted that grain yields on farms tend to be lower than in variety trials for three reasons: i) variety trials are usually ignored if they are not of sufficient quality; ii) the average age of varieties grown on-farm is usually higher than in variety trials; and iii) economic constraints imposed by the prices of inputs are usually considered on-farms but not on variety trials. Furthermore, genotype trials are generally located in the middle of fields and will not therefore suffer from the reduced grain yields at field margins from soil compaction and other limitations (Mackay et al., 2011). Although, organic agriculture originally addressed the demand of consumers for food free of synthetic pesticides and fertilizers, it has recently been proposed as a solution to revert the loss of soil organic matter and other ecosystem services (Gattinger et al., 2012). Different authors suggested that organic production systems can be a way to increase the sustainability of cereal production as long as it closes the yield gap with other production systems and meet the requirements necessary to sustain a growing world population (e.g. Trewavas, 2001). A meta-analysis by Ponisio et al. (2015) compared 1071 paired yield observations under conventional and organic agriculture and concluded that fields under organic management had on average 19.2% less yield compared to those under organic management. Cereal crops exhibited the greatest differences between organic and conventional systems, which the authors attributed to the extensive efforts since the Green Revolution for breeding high yielding varieties adapted to respond to high inputs. Early comparisons of organic and conventional systems suggested that the yield gap between organic and conventional production systems was going to decline over time (Smith et al., 2007). In the genotype trials evaluated here, which were mainly conducted in farms, there is no sign that the yield difference between organic and conventional practices declined during the studied period.

Agronomy may contribute significantly to reductions in yield gaps through a more optimized and efficient use of inputs (Chapagain and Good, 2015; Lollato et al., 2019). It might be useful to investigate explicitly and systematically how specific management practices (e.g. rotations, fertilization, and weed, diseases and pest control) could be altered in different production systems to maximize productivity and quality. The exploitation of interactions between genotype and crop management has, indeed, produced important changes in production strategies in the last century, shown for example by the use of shorter wheat varieties that can be fertilized with higher doses. Improved agronomy is necessary for production systems with reduced levels of inputs but also for those that rely on high inputs. The use of nitrogenous fertilizers presents a challenge, as the optimization of plant nutrition stabilizes yields and helps to reduce expansions in crop area but contribute substantially to the greenhouse gas emissions that promote climate change (Fowler et al., 2013).

Genotypes can contribute to attain a stable wheat production. The relative yield stability (i.e. stability assessed per unit yield produced) was the lowest with the least use of inputs. Among the differences in production systems, N availability may be a key element explaining the higher yield variation under organic management compared to conventional management with high inputs (Bilsborrow et al., 2013). Although, we observed an apparent increasing trend for CV with conventional low-inputs and for the interannual-deviation ratio, the trends were not statistically significant. This differs with other studies published (e.g. Kahiluoto et al., 2019) and we attribute this difference to the fact that we considered several genotypes instead of a few ones. The availability of adapted genotypes is therefore fundamental to achieve a stable wheat production in a given cropping system. The implementation of a strategy to use genotypes for climatic-risk mitigation will not however be easy without models that anticipate these risks or agronomic practices that rely on the use of genotypes mixtures.

DATA AVAILABILITY STATEMENT

Restrictions apply to the datasets: The datasets used in this study will be made available upon fulfilling certain requirements. However, they are not publicly available because a part of the data was obtained from a third party. Requests to use the organic, conventional high inputs and conventional low inputs datasets should be directed to LL (lilia.levy@agrscope.admin.ch).

AUTHOR CONTRIBUTIONS

LL, JH, and DP planned and designed the experiments. LL, JH, FM, DF and CB conducted the experiments and fieldwork. JMH analyzed the data. JMH, LL, FM, JH, DF, CB, RC, and DP wrote the manuscript.

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Changes in the Phenotype of Winter Wheat Varieties Released Between 1920 and 2016 in Response to In-Furrow Fertilizer: Biomass Allocation, Yield, and Grain Protein Concentration

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Plant breeding has increased the yield of winter wheat (*Triticum aestivum* L.) over decades, and the rate of genetic gain has been faster under high fertility in some countries. However, this response is not universal, and limited information exists on the physiological traits underlying the interaction between varieties and fertilization. Thus, our objectives were to identify the key shifts in crop phenotype in response to selection for yield and quality, and to determine whether historical and modern winter wheat varieties respond differently to in-furrow fertilizer. Factorial field experiments combined eight winter wheat varieties released between 1920 and 2016, and two fertilizer practices [control *versus* 112 kg ha^{-1} in-furrow 12 -40-0-10-1 (N-P-K-S-Zn)] in four Kansas environments. Grain yield and grain N-removal increased nonlinearly with year of release, with greater increases between 1966 and 2000. In-furrow fertilizer increased yield by ~300 kg ha^{-1} with no variety × fertility interaction. Grain protein concentration related negatively to yield, and the residuals of this relationship were unrelated to year of release. Yield increase was associated with changes in thermal time to critical growth stages, as modern varieties had shorter vegetative period and longer grain filling period. Yield gains also derived from more kernels m^{-2} resultant from more kernels head^{-1}. Historical varieties were taller, had thinner stems, and allocated more biomass to the stem than semidwarf varieties. Yield gains resulted from increases in harvest index and not in biomass accumulation at grain filling and maturity, as shoot biomass was similar among varieties. The allometric exponent (i.e., the slope between log of organ biomass and log of shoot biomass) for grain increased

with, and for leaves was unrelated to, year of release. The ability of modern varieties to allocate more biomass to the kernels coupled to an early maturity increased grain yield and grain N-removal over time. However, increases in grain yield were greater than increases in grain N-removal, reducing grain protein concentration in modern varieties.

Keywords: *Triticum aestivum* L., genetic progress, yield components, chronological change, biomass partitioning, harvest index, in-furrow fertilize

INTRODUCTION

Global wheat production often surpasses 750 Mt harvested from about 220 Mha, with an average yield of 3.4 Mg ha^{-1} (FAOSTAT, 2018). The development of semidwarf wheat varieties (Evenson, 2003) coupled with N fertilizer was responsible for large proportion of the yield advances over decades (Bell et al., 1995). The successful introduction of dwarfing genes carrying the alleles Rht1-B1b (Peng et al., 1999) allowed for plants with reduced height, greater response to fertilizer, and higher yields (Evenson, 2003). For irrigated spring wheat in Mexico, genetic improvement accounted for 28% and increased use of N fertilizers for 48% of the yield improvement between 1968 and 1990 (Bell et al., 1995). For dryland winter wheat in Kansas (U.S.) between 1977 and 2006, these estimates are 79% and 21%, respectively (Nalley et al., 2008).

Comparison of wheat varieties released during different historical eras returned rates of genetic gains from 0.3% to 1.1% (Austin et al., 1989; Sayre et al., 1997; Brancourt-Humel et al., 2003; Battenfield et al., 2013; Fischer et al., 2014). However, some studies showed that rates of yield gain can differ over time, and have typically decreased in recent years. For instance, genetic gain greater than 0.5% yr^{-1} during the 1960s to 2000s period was reported in the U.S., Australia, and Chile (Fufa et al., 2005; Sadras and Lawson, 2011; Del Pozo et al., 2014). Meanwhile, the genetic gain in wheat decreased or was nonsignificant in recent years in Spain, Brazil, and Argentina (Acreche et al., 2008; Beche et al., 2014; Lo Valvo et al., 2017).

Wheat yield gain is often associated with improved harvest index, kernels m^{-2}, kernels per head, reduced plant height, shoot biomass and kernel weight (Brancourt-Humel et al., 2003; Zhou et al., 2007; Fischer and Edmeades, 2010; Sadras and Lawson, 2011; Sanchez-Garcia et al., 2013; Beche et al., 2014; Wu et al., 2014; Aisawi et al., 2015; Lo Valvo et al., 2017). More recently, genetic gain in yield correlated with shoot biomass at maturity in some breeding programs (Donmez et al., 2001; Shearman et al., 2005; Xiao et al., 2012; Beche et al., 2014; Wu et al., 2014) and agronomic studies across different varieties (de Oliveira Silva et al., 2019). However, previous research has not evaluated the dynamics of biomass accumulation and partitioning during the growing season of historical versus modern varieties (Pampana et al., 2007).

The rates of genetic gain are often greater in well-fertilized, well-watered crops than in their counterparts with water and/or nutrient deficiencies (Austin et al., 1980; Slafer and Andrade, 1989; Brancourt-Humel et al., 2003; De Vita et al., 2007; Giunta et al., 2007; Barraclough et al., 2010; Tian et al., 2011; Gizzi and Gambin, 2016; Wang et al., 2017). In-furrow fertilization with nitrogen, phosphorus, sulfur, and zinc can improve early-season wheat tillering, biomass production, and yield (Rodríguez et al., 1998; Rodríguez et al., 1999; Valle et al., 2009; Lollato et al., 2013). Nitrogen can increase grain yield (May et al., 2008; Grant et al., 2016) through kernels head^{-1} (Asif et al., 2012), heads m^{-2}, and kernels m^{-2} (Marino et al., 2009). Phosphorus improves plant leaf area (Rodríguez et al., 1998) and tillering (Sato et al., 1996). Sulfur can increase grain yield and protein concentration (Tao et al., 2018), and Zn can increase pollen viability (Nautiyal et al., 2011). The combination of improved yield potential and management increased wheat yield worldwide; however, limited information exists on the changes in biomass accumulation and partitioning and on the interaction between historical and modern wheat varieties and in-furrow fertilization. Thus, our objectives were to: (i) determine grain yield increase due to genetic improvement of wheat adapted to Kansas, USA, by identifying the underlying changes in phenology, morphological, and physiological traits; and (ii) quantify how genotypes released in different eras respond to in-furrow fertilizer.

MATERIALS AND METHODS

Site and Experiment Description

Field experiments were conducted in four environments resulting from the combination of two seasons and two locations in Kansas. In 2016-2017, experiments were established on a Belvue silt loam (coarse-silty, mixed, superactive, nonacid, mesic Typic Udifluvents) in Ashland Bottoms (39°08'37.8"N, 96°37'59.8"W, elevation 315 m) and on a Crete silt loam (fine, smectitic Pachic Udertic Argiustolls) in Belleville (39°48'54.1"N 97°40'16.7"W, elevation 469 m). In 2017–2018, experiments were conducted on an Ost loam (fine-loamy, mixed, superactive, mesic Udic Argiustolls) near Hutchinson (37°55'52.4"N 98°01'47.8"W, elevation 471 m) and again in Belleville.

Eight hard red winter wheat varieties released between 1920 and 2016 (**Supplementary Table 1**) were combined factorially with two fertilization treatments. The experimental design was a split-plot with four replications, with whole plots arranged as randomized complete block design and subplots completely randomized within whole plots. Varieties were assigned to plots and fertilizer treatment to subplots. The varieties were: "Kharkof," released in 1920; "Scout 66" (1966); "Karl 92" (1992); "Jagger" (1994); "Jagalene" (2001); "Fuller" (2006); "KanMark"

(2014); and "Larry" (2016). Varieties were selected based on large adoption by growers in the period following their release. Kharkof and Scout 66 carry the alleles Rht1-B1a-Tall and will hereafter be referred to as "tall varieties"; the remaining varieties carry the alleles Rht1-B1b-Short and will be referred to as "semidwarf varieties." Due to seed germination issues, we excluded the data from Jagger during the first year. Fertilizer treatments were (i) control and (ii) 112 kg ha^{-1} in-furrow 12-40-00-10-1 (N-P-K-S-Zn) fertilizer, for a total application of 13, 45, 11, and 1 kg ha^{-1} of N, P_2O_5, S, and Zn. During the growing season, the entire experiment received the same amount of N fertilizer (see section "2.2. Agronomic management" for details) so that the only difference between treatments was the presence/absence of in-furrow fertilizer. The control treatment followed current soil fertility recommendations for P as per the nutrient "sufficiency" approach (Leikam et al., 2003), in which no in-furrow fertilizer was applied as the study locations had Mehlich-3 P above 25 mg kg^{-1} (**Table 1**). On the fertilization treatment, in-furrow fertilizer was applied at sowing through the drill with the seed.

Agronomic Management

Seeds were treated with insecticide and fungicide (15 ml 100 kg $seed^{-1}$ of imidacloprid[1] and with 0.74 ml 100 kg $seed^{-1}$ of tebuconazole[2]) to control early-season insects and diseases. Wheat was sown 18 October 2016 at Ashland Bottoms, 3 October 2016 and 2 October 2017 at Belleville, and 19 October 2017 at Hutchinson. All crops followed a previous wheat crop and were conducted under conventional tillage with surface residue cover below 10%. Plots were sown with a commercial drill (Great Plains 606-NT drill) at a seeding rate of 67 kg ha^{-1} (approximately 2.1 million seeds ha^{-1}). Subplots were 9.1-m long by 2.7-m wide, consisting of fourteen 0.19-m spaced rows. Half of the subplot (9.1 m x 1.33 m) was used for destructive sampling of biomass. The other half was used for nondestructive measurements (i.e., stem diameter and plant height), and harvested for yield.

Composite soil samples consisting of 15 individual soil cores were collected at two depths (0–15 cm and 15–60 cm) prior to sowing and analyzed for nutrient concentration (**Table 1**). Soil pH was analyzed through the procedure with water; soil P was measured through Mehlich-3; soil K, Ca, Mg, Na were measured through ammonium acetate extraction; soil $S0_4$-S was measured through calcium phosphate extraction; soil Zn was analyzed through DTPA extraction; cation exchange capacity (CEC) was calculated through summation; soil organic matter was measured through loss of ignition; and NO_3-N was measured through KCl extraction. Soil analyses were used to determine N fertilizer needs for all treatments using a yield goal of 6 Mg ha^{-1} (Leikam et al., 2003). This resulted in different total inorganic N amount in each site depending on the profile NO_3-N content (i.e., 63 to 158 kg N ha^{-1}, **Table 1**), but purposefully resulting in the same total N available to the wheat crop during the growing season. The entire trial was top-dressed with urea (46-0-0) in early spring (GS 31) under favorable weather to minimize N losses. Two foliar fungicide applications (i.e., 65.77 ml ha^{-1} of picoxystrobin[3] at jointing [GS 31] and 89.15 ml ha^{-1} of picoxystrobin[1] plus 35.63 ml ha^{-1} cyproconazole[4] at anthesis [GS 65]) ensured that genetic resistance to fungal diseases was not a confounding factor. Herbicides were sprayed during fall of both growing seasons to ensure weeds were not a limiting factor. There was no significant insect pressure, so no insecticide was applied.

Plots were machine-harvested for grain yield on 22 June 2017 at Ashland Bottoms, 28 June 2017 and 24 June 2018 at Belleville, and 6 June 2018 at Hutchinson using a Hege 140 self-propelled small-plot combine. Grain moisture was measured at harvest and grain yield was corrected for 13% moisture content.

Vegetative Development Evaluations

Phenological stages were determined using the Zadoks scale (Zadoks et al., 1974) when about 50% of the plants in the experimental unit achieved a particular stage. Shoot biomass was collected from the middle rows at tillering (GS 26), jointing (GS 31), anthesis (GS 65), soft dough stage of grain development (GS 85); and physiological maturity (GS 92) using an electric clipper (Gardena 8893-U, Gardena Co., Ulm, Germany). The sampled area was 0.76, 0.76, 0.38, 0.19, and 0.19 m^{-2}, respectively, at an average stand of 185 plants m^{-2}. Varieties differed in maturity and thus sampling occurred on different calendar days. Dry mass was determined after drying the samples at 65°C until constant weight. Shoot weight was determined at GS 26; stem and leaf weights were determined at GS 31; stem, leaf, and chaff weights were determined at GS 65; and stem, leaf, grain, and chaff weights were determined at GS 85 and GS 92. Plant parts were separated manually, except for grain and chaff, which were separated with a thresher (Wheat Head Thresher, PM Precision Machine Co. Inc., Lincoln, NE).

Stem diameter was measured at GS 85 using OriginCal IP54 digital caliper (Igaging, San Clement, CA) approximately 2.5 cm aboveground on the main stem of ten randomly selected plants per subplot. Plant height was measured at GS 92 from the soil surface until the tip of the awns of three plants per subplot. Yield components (harvest index, heads m^{-2}, kernels $head^{-1}$, kernels m^{-2}, and individual kernel weight) were measured in the sample collected at physiological maturity. Grain protein concentration (g kg^{-1}) was measured in the whole kernel from samples collected at harvest using near-infrared reflectance spectroscopy with a Perten DA 7250 (Perten Instruments Inc., Springfield, Illinois) and was reported on a 13% water basis. Grain N concentration was measured at GS 92 using the procedure of dry combustion (TruSpec CN, LECO Corporation, St. Joseph, MI,

[1] Imidacloprid: 1-[(6-Chloro-3-pyridinyl) methyl]-N-nitro- 2-imidazolidinimine), 0.95 ml 100 kg $seed^{-1}$ of metalaxyl: N-(2,6-dimethylphenyl)-N-(methoxyacetyl) alanine methyl ester.

[2] Tebuconazole: alpha-[2-(4-chlorophenyl) ethyl]-alpha- (1,1-dimethyl-ethyl)-1H-1,2,4-triazole-1- ethanol).

[3] Picoxystrobin (Methyl (∝E)- ∝-(methoxymethylene)-2-[[[6-(trifluoromethyl)-2 pyridinyl]oxy]methyl]benzeneacetate.

[4] Cyproconazole ∝-(4-chlorophenyl)- ∝-(1-cyclopropylethyl)-1H-1,2,4-triazole-1-ethanol.

TABLE 1 | Initial soil pH in water, extractable P, K, Ca, Mg, Na, SO_4-S, Zn, cation exchange capacity (CEC), organic matter (O.M.), and NO_3-N for the 0–15 and 15–60 cm soil layers at Ashland Bottoms, Belleville and Hutchinson, KS.

Year	Location	fDepth (cm)	pH	P (mg kg^{-1})	K (mg kg^{-1})	Ca (mg kg^{-1})	Mg (mg kg^{-1})	Na (mg kg^{-1})	SO_4-S (mg kg^{-1})	Zn (mg kg^{-1})	CEC (Meq $100g^{-1}$)	O.M. (g kg^{-1})	NO_3-N (mg kg^{-1})	Applied N (kg ha^{-1})
2016-2017	Ashland B.	0 –15	6.0	41	190	975	105	13	1.7	0.3	10	13	3.6	105
		15 – 60	6.9	11	90	1,375	125	12	3.7	0.4	8	8	3.5	
	Belleville	0 – 15	5.9	42	474	1,532	202	13	2.9	1.5	21	30	4.5	158
		15 – 60	5.9	12	224	2,005	245	18	2.5	1.9	24	26	2.0	
2017-18	Hutchinson	0 – 15	6.0	77	218	1,886	238	11	3.4	2.3	20	24	6.2	63
		15 – 60	6.8	55	214	2,666	237	10	3.6	2.8	16	24	8.2	
	Belleville	0 – 15	5.6	42	400	1,727	228	10	3.0	0.9	22	28	8.9	67
		15 – 60	5.9	35	342	2,452	326	37	2.3	0.8	24	27	7.7	

Amount of inorganic N applied across the entire trial in each location during each growing season is also shown.

2005). Grain-N removal was calculated as the product between grain yield and grain nitrogen concentration (Lollato et al., 2019a).

Data Analysis

Two-way analyses of variance (ANOVA) were performed to determine significant difference among treatments using PROC GLIMMIX in SAS version 9.4 **Supplementary Table 2**. (SAS Institute, Cary, NC). To determine whether site-years could be combined, we performed an ANOVA on the residuals of the combined analysis considering year, location, variety, and fertility, and their interactions, as fixed effects. Year was a significant effect for both biomass ($p < 0.05$) and grain yield ($p = 0.08$); thus, we performed all remaining analysis across locations within year. Variety, fertility, and variety × fertility were fixed effects; and replication, sites, replication nested within site, and variety × replications nested within site were random effects. We used the LINES statement for pairwise comparisons.

To evaluate historical trends across the entire data set, we calculated trait deviation from the mean of each environment (Sadras and Lawson, 2011) and fitted seven models to the deviation data as a function of year of release (i.e., logarithm, logistic, piecewise, linear, quadratic, sigmoidal, and cubic). Models were fitted with SigmaPlot version 13.0 (Systat Software, San Jose, CA). The best model was selected using the Akaike information criterion (AIC) and the coefficient of determination (R^2). We also considered the agronomic significance and interpretability of the models tested. We analyzed the residuals of these relationships for the fertilizer effect (Sadras and Moran, 2012). Because grain protein concentration is dependent on yield (Simmonds, 1995; Oury and Godin, 2007; Bogard et al., 2010), we first fitted a linear regression between deviations of grain protein and yield. Then, we analyzed the residuals of this relationship against year of variety release and fertilizer practice (Ortez et al., 2018).

Shoot biomass as affected by thermal time was first evaluated using the ANOVA procedure described above at each growth stage for whole plant biomass, and afterwards, for each individual plant component at each growth stage. Thermal time (growing degree days, GDD°C) was calculated as the sum of daily minimum and maximum temperature divided by 2 considering a base temperature of 0^0C (Gallagher, 1979). Crop growth rate was calculated as the difference in shoot biomass between two successive samplings, divided by the intervening thermal time. Allometric relationships between biomass of plant organs (leaf, stem, chaff, and grain) and shoot were evaluated using standardized major axis (SMA) in through SMATR package (SMATR version 3; Warton et al., 2012) in R software (R development Core team, 2016). Plant organs and shoot biomass were $\log_{10}$ transformed prior to this analysis (Niklas, 2006), and time trends in allometric coefficients were evaluated by regression the slope of this relationship ($\log Y = \alpha \log X$) against year of variety release. Nonlinear models and historical trends were fitted with SigmaPlot version 13.0 (Systat Software, San Jose, CA).

We performed a final, comprehensive analysis across the entire data set using seven statistical procedures (stepwise, forward, backward, least angle regression (LAR), least squared shrinkage operator (LASSO), elastic net, and conditional inference trees) to assess the influence of all measured traits and environmental conditions on grain yield. Environmental conditions were calculated for different developmental windows (i.e., the entire cycle, the 30-d period prior to anthesis, and the grain filling period) and included average maximum and minimum temperatures, cumulative precipitation, cumulative solar radiation, and photothermal quotient (Fischer, 1985). All models were built in PROC GMSELECT in SAS version 9.4 (SAS Institute, Cary, NC) except for the conditional inference tree, which was built using the *partykit* package in R (R development Core team, 2016). Intermediate node and terminal node included a minimum of 10% of total observations. A sensitivity analysis allowed less observations to form nodes, but the model fit was improved in less than 10% so the most parsimonious model was selected.

RESULTS

Weather Conditions

Seasonal precipitation ranged between 281 and 472 mm. Seasonal differences were more apparent during the fall and winter, with spring precipitation ranging between 169 and 262 mm at both growing seasons (**Table 2**). These conditions led to lower biomass in 2016-2017, precluding a combined analysis of the data. Despite lower seasonal total precipitation, favorable spring weather led to greater grain yield in 2017-2018.

TABLE 2 | Cumulative precipitation (Precip.), average maximum (T_{max}), and minimum temperatures (T_{min}), cumulative solar radiation (R_s) in (MJ m^{-2}), and average photothermal quotient (PTQ) for each portion of growing season during 2016-2017 and 2017-2018 at Ashland Bottoms, Belleville, and Hutchinson, KS.

Year	Location	Precip.			T_{min}			T_{max}			R_s			PTQ		
		Fall[a] (mm)	Winter[b] (mm)	Spring[c] (mm)	Fall[a] (°C)	Winter[b] (°C)	Spring[c] (°C)	Fall[a] (°C)	Winter[b] (°C)	Spring[c] (°C)	Fall[a] (MJ m^{-2})	Winter[b] (MJ m^{-2})	Spring[c] (MJ m^{-2})	Fall[a] (MJ m^{-2} d^{-1} °C^{-1})	Winter[b] (MJ m^{-2} d^{-1} °C^{-1})	Spring[c] (MJ m^{-2} d^{-1} °C^{-1})
2016-2017	Ashland B.	99	146	227	2	–1	12	16	11	25	1,027	1,083	1,909	0.79	0.77	1.82
	Belleville	91	74	262	–1	–3	10	14	10	24	876	996	1,938	0.64	0.56	1.71
2017-2018	Hutchinson	52	60	169	0	–5	11	14	10	26	874	1,063	1,567	0.62	0.55	1.33
	Belleville	37	36	217	–3	–8	10	12	6	24	861	1,030	1,811	0.54	0.30	1.33
30-year mean	Ashland B.	119	87	318	1	–4	12	13	9	25	792	941	1,745	0.59	0.47	1.41
	Belleville	85	71	256	–1	–6	10	12	8	24	826	1,002	1,839	0.57	0.42	1.56
	Hutchinson	125	102	264	2	–3	10	15	9	23	764	786	1,396	0.57	0.41	1.16

[a]*Fall encompasses October, November, and December.*
[b]*Winter encompasses January, February, and March.*
[c]*Spring encompasses the period between April 1st and harvest.*
The 30-year mean of each variable for each location is also shown.

Plant Height, Stem Diameter, and Phenology

Plant height decreased over time with a steep change around ~1970s from 122 cm to 93-100 cm (**Figure 1A**, **Table 3**). Stem diameter ranged from 2.87 to 3.21 mm among locations and increased with year of release, particularly from 1960s to 2000s (**Figure 1B**). Time from sowing to anthesis and to physiological maturity decreased over time (**Figures 1C, D**), and modern varieties had a longer period from anthesis to physiological maturity (**Figure 1F**). The duration of the period between anthesis and physiological maturity associated linearly and positively with harvest index (r^2 > 0.14, data not shown), suggesting that the increase in wheat yield in modern varieties was partially explained by a longer grain fill. However, varieties released in the last 30 years showed minimal developmental changes (**Figure 1**).

Grain Yield, Grain-N Removal, and Grain Protein Concentration

There were significant variety and fertility effects on wheat grain yield in both seasons, with no variety × fertility interaction (**Table 3**). Grain yield ranged from 1.7 to 4.9 Mg ha^{-1} for tall varieties and from 3.4 to 6.3 Mg ha^{-1} for semidwarf varieties. In-furrow fertilizer increased mean yield by 0.2 to 0.4 Mg ha^{-1} in relation to the control. Grain yield increased nonlinearly with year of release (**Figure 2A**), with three distinct rates. A low yield-gain period between 1920 and 1966 (17 kg ha^{-1} yr^{-1}), followed by a steep yield gain between 1966 and 2000 (62 kg ha^{-1} yr^{-1}), and a slower yield gain phase after 2000 (8 kg ha^{-1} yr^{-1}).

There were significant variety and fertility effects on grain-N removal (**Table 3**). Grain-N removal increased from tall to semidwarf varieties (c.a., 64 to 130 kg ha^{-1} in 2016-2017 and 127 to 155 kg ha^{-1} in 2017-2018). In-furrow fertilizer increased grain-N removal by 6 to 9 kg ha^{-1}. Similar to grain yield, grain-N removal deviation increased nonlinearly with year of release, with linear rates of 0.44, 1.28, and 0.11 kg ha^{-1} yr^{-1} for the aforementioned periods (**Figure 2B**).

Typically, tall varieties had greater grain protein concentration than the semidwarf varieties. In 2016-2017, there was a significant interaction between variety and fertility on grain protein concentration (**Table 3**) as most varieties increased grain protein concentration in response to in-furrow fertilizer except by the semidwarf varieties Fuller and KanMark (data not shown).

In 2017-2018, grain protein concentration in tall varieties was 142 to 150 g kg^{-1} compared to 129 to 140 g kg^{-1} in semidwarf varieties. In-furrow fertilizer decreased grain protein concentration (**Table 3**). Grain protein deviation declined linearly with grain yield deviation (**Figure 3A**), and the residuals of this relationship were unrelated to year of release (p > 0.37, **Figure 3B**).

Yield Components

There was a nonlinear relationship between heads m^{-2} and year of release, with modern varieties having fewer heads m^{-2} (greater differences between late 1980s until early 2000s, **Figure 4A**). Tall varieties had 872 and 767 heads m^{-2} while semidwarf varieties had 741 and 680 heads m^{-2} during 2016-2017 and 2017-2018 (**Table 3**). As heads m^{-2} decreased over time, kernels $head^{-1}$ increased, from 12–18 kernels $head^{-1}$ to 21–27 kernels $head^{-1}$ with greater increases after 1980s (**Figure 4B** and **Table 3**). Due to the contrasting trends in heads m^{-2} and kernels $head^{-1}$, the increase in kernels m^{-2} was slower but significant (**Figure 4C**). The tall variety Kharkof had the lowest kernels m^{-2} (i.e., 9,383 and 12,852 kernels m^{-2}) while the semidwarf variety KanMark had the highest (i.e., 17,904 and 21,041 kernels m^{-2}).

Kernel weight showed a bilinear relationship with year of release (**Figure 4D**), increasing at a higher rate until 1966 and remaining constant afterwards (**Table 3**). Harvest index increased nonlinearly over time and ranged from 0.26 to 0.51

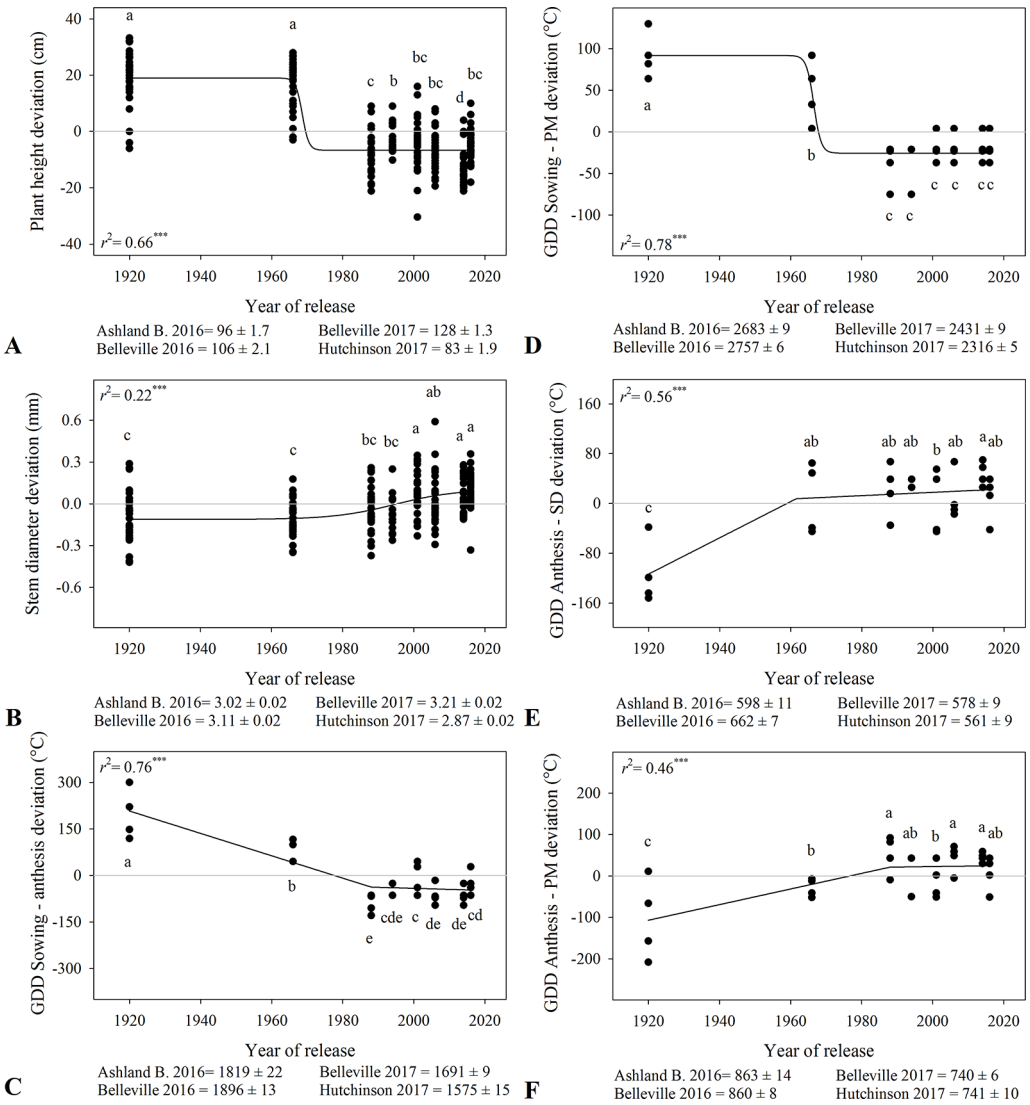


FIGURE 1 | Relationship between year of release and plant height **(A)**, stem diameter **(B)**, and thermal time from sowing to anthesis **(C),** sowing to physiological maturity **(D),** anthesis to soft dough **(E),** and anthesis to physiological maturity **(F)**. Values correspond to the data of four site-years during two growing seasons (2016-2017 and 2017-2018). Mean for all varieties in each site and year. All models are significant at P < 0.0001. Varieties followed by the same letter are not statistically different at α = 0.05.

among locations (**Figure 4E**). While harvest index increased from 0.15 to 0.33 in 2016-2017; differences were smaller in 2017-2018 (**Table 3**). Variety affected grain volume weight in both growing seasons, both with no consistent time trends (**Table 3**).

In-furrow fertilizer increased heads m^{-2} (**Figure 4A**) from 733 to 825 in 2016-2017, and from 667 to 737 heads m^{-2} in 2017-2018 (**Table 3**). However, it decreased kernels $head^{-1}$ (**Figure 4B**) from 20 to 17 in 2016-2017 and from 26 to 24 in 2017-2018 (**Table 3**). Fertilizer had no effect on kernels m^{-2} (**Figure 4C**) and decreased kernel weight (**Figure 4D** and **Table 3**) from 26.9 to 26.1 mg $kernel^{-1}$ in 2016-2017 and from 26.3 to 25.4 mg $kernel^{-1}$ in 2017-2018. There were no differences in harvest index between the fertilizer practices (**Figure 4E**), and in-furrow fertilizer showed lower volume weight than control (**Table 3**).

Shoot Biomass, Crop Growth Rate, and Biomass Allocation to Plant Components

There was no clear pattern in biomass among varieties early in the season (i.e. at GS 26 and 31), but tall varieties had greater shoot biomass than semidwarf ones at anthesis (861–1,087 g m^{-2} *versus* 658–888 g m^{-2}) (**Table 4**). These differences related positively to thermal time from sowing to anthesis (r^2 = 0.42). However, these differences were not apparent (2017-2018) or were reversed (2016-2017) at soft dough (GS 85), when semidwarf varieties showed up to

TABLE 3 | Grain yield, head number, head size, kernel number, kernel weight, harvest index (HI), plant height (PH), stem diameter, grain protein concentration (GPC) and grain volume weight (GVW) of wheat varieties released between 1920 and 2016, fertilizer treatment, and their interaction during the growing seasons 2016-2017 and 2017-2018.

Year	Variety	Year of release	Fertilizer	Grain Yield (Mg ha^{-1})	Nitrogen removal (kg ha^{-1})	GPC (g kg^{-1})	Head number (heads m^{-2})	Head size (kernels head^{-1})	Kernel number (kernels m^{-2})	Kernel weight (mg kernel^{-1})	HI	PH (cm)	Stem Diameter (mm)	GVW (kg m^{-3})
2016-2017	Kharkof	(1920)		1.7e	54d	135ab	813bc	11d	9383c	22.0b	0.13c	120a	2.88c	728e
	Scout 66	(1966)		2.4d	74c	133ab	931a	12d	10863c	26.7a	0.16c	123a	2.90c	751c
	Karl 92	(1988)		3.4c	103b	138a	854ab	14c	12221bc	26.8a	0.26b	93c	3.00b	744d
	Jagalene	(2001)		5.2a	142a	122c	755bcd	23ab	17075a	27.2a	0.34a	95bc	3.17a	770a
	Fuller	(2006)		4.5b	127a	131b	677d	23ab	15763a	27.9a	0.32ab	92c	3.16a	755bc
	KanMark	(2014)		5.2a	138a	119c	712cd	24a	17904a	26.4a	0.37a	87d	3.18a	776a
	Larry	(2016)		5.1ab	138a	121c	708cd	21b	15312ba	28.3a	0.36a	98b	3.18a	759b
			In-furrow	4.0A	114A	129	825A	17B	13946	26.1B	0.28	102	3.06	754B
			Control	3.8B	108B	128	733B	20A	14203	26.9A	0.28	100	3.07	756A
2017-2018	Kharkof	(1920)		3.9d	116d	150a	767a	17e	12852c	22.9c	0.39c	125a	3.00	723ab
	Scout 66	(1966)		4.9c	137c	142b	766a	19de	14501bc	27.4a	0.44bc	119a	3.00	712bc
	Karl 92	(1988)		5.5b	148bc	137bcd	731ab	21d	15322bc	27.3a	0.54a	100bc	3.04	731a
	Jagger	(1994)		5.9ab	155ab	139bcd	721ab	28bc	19982a	25.1b	0.50ab	104b	2.98	694de
	Jagalene	(2001)		6.3a	163a	134cde	660bc	28abc	18443a	27.3a	0.56a	103b	3.07	721ab
	Fuller	(2006)		5.5b	144bc	140bc	609c	26c	15657b	25.8b	0.52a	102b	3.02	681e
	KanMark	(2014)		6.2a	152ab	129e	698ab	30a	21041a	24.9b	0.52a	94c	3.08	718b
	Larry	(2016)		6.2a	166a	133de	666bc	29ab	19274a	26.2ab	0.55a	101bc	3.13	704cd
			In-furrow	5.8A	152Aa	137B	737A	24B	17237	25.4B	0.51	106	3.03	708B
			Control	5.4B	143Bb	139A	667B	26A	17031	26.3A	0.50	106	3.05	713A

Values followed by the same letter within growing season and treatment (lower case letters for varieties and capitalized letters for fertility) are not statistically different at $\alpha = 0.05$.
Jagger was not included in the 2016-2017 growing season analysis.
Variety and fertilizer means were averaged across locations within growing season.

30% greater biomass relative to tall varieties. There were no differences in biomass among varieties at maturity, and in-furrow fertilizer increased biomass irrespective of growth stage.

Crop growth rate was low (c.a., 0.08 to 0.3 g m^{-2}°C^{-1} day^{-1}) between tillering and jointing, and increased to about 1.3–1.5 g m^{-2}° C^{-1} day^{-1} between GS 31 and GS 65 (**Supplementary Table 2**). There were no differences among varieties early in the season, although in-furrow fertilizer increased growth rate. The growth rate in semidwarf varieties was as much as two times greater than in tall varieties from anthesis to soft dough in the first season (**Supplementary Table 3**), decreasing after soft dough.

There were no clear differences among varieties in their allocation of biomass toward leaves and stem early in the season (**Table 4**). However, at anthesis and soft dough tall varieties showed greater biomass in the stem relative to semidwarf varieties (c.a., 605 *versus* 430 g m^{-2}, and 620 *versus* 518 g m^{-2}). During 2016-2017, tall varieties also showed greater leaf biomass than semidwarf varieties at GS 65 and GS 92 (**Table 4**). Grain biomass at soft dough stage was greater in semidwarf varieties in both growing seasons, and dry matter partitioning to leaves and stem ceased at this stage regardless of year of release. Grain biomass at maturity in semidwarf varieties was as much as 470 g m^{-2} (2017-18) and no more than 345 g m^{-2} (2017-18) for tall varieties (**Table 4**). In-furrow fertilizer increased biomass irrespective of growth stage and plant component (**Table 4**); however, more biomass was allocated to vegetative tissues than to grain.

The slopes from the allometric analysis (i.e., log organ *versus* log shoot biomass) plotted against year of release showed no significant trends for leaves (**Figure 5A**). For stem, there was a significant nonlinear relationship during the 2016-2017 growing season, with no changes from 1920 to 1966 and a clear decrease afterwards (**Figure 5B**). The allometric coefficient for chaff increased with year of release in 2016-2017 (**Figure 5C**). The allometric coefficient for grain increased with year of release in both seasons (**Figure 5D**). Fertility treatment only affected the allometric coefficient for stem in 2017-18, when in-furrow fertilizer showed greater slope than control treatment (data not shown).

Association Between Grain Yield, Crop Traits and Weather Variables

In-furrow fertilizer, plant height, year of release, and kernels m^{-2} were positively, and seasonal cumulative solar radiation was negatively associated with grain yield in at least six out of seven models tested (inset table on **Figure 6**). Grain yield related positively with kernel weight, head size, stem diameter, and biomass growth rate between GS 65 and GS 85 in at least half of the models. Seasonal minimum temperature, photothermal quotient during grain filling, timing from sowing to anthesis, and biomass rate at GS 92, were negatively associated with yield. The conditional inference tree suggested that kernels head^{-1} was among the most important determinants of yield, with head size less than 12 kernels resulting in the lowest yields (**Figure 6**). There were significant interactions between head size and biomass rate at GS 92, time from sowing to anthesis, in-furrow fertilizer, and kernel number on wheat yield. The highest yields

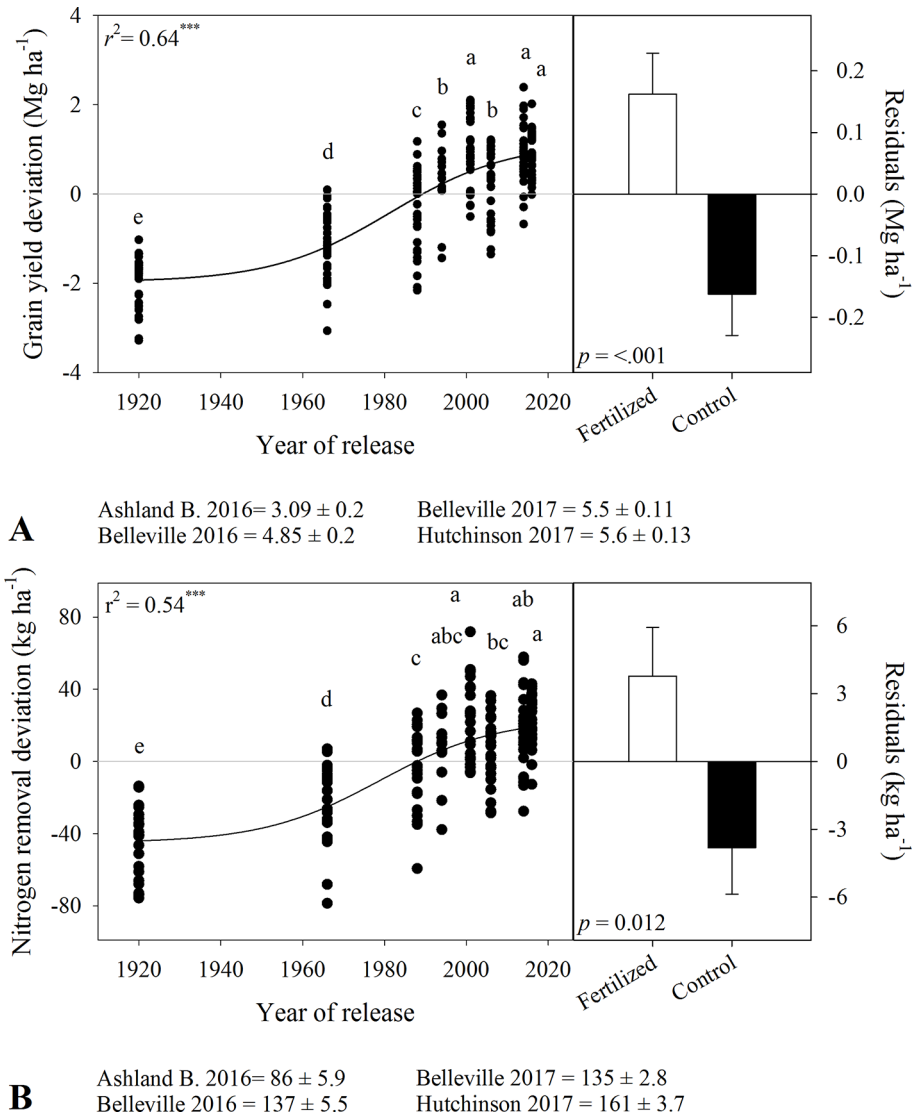


FIGURE 2 | Relationship between year of release and **(A)** grain yield deviation and **(B)** grain nitrogen removal deviation. Comparison of the residuals of the regressions for in-furrow fertilizer treatment and control (bars show mean and standard error). Values correspond to the data of four site-years during two growing seasons (2016-2017 and 2017-2018). Mean for all varieties in each site and year. Both curves are significant at P < 0.0001. Varieties followed by the same letter are not statistically different at $\alpha = 0.05$.

were attained when heads had more than 22 kernels, in crops with in-furrow fertilizer and with photothermal quotient less than 1.34 MJ m^{-2} d^{-1}°C^{-1}. In the absence of fertilizer, more kernels m^{-2} related to greater yield.

DISCUSSION

We evaluated the effects of in-furrow fertilization on grain yield, yield components, and biomass accumulation and partitioning in a set of historical and modern commercial wheat varieties adapted to Kansas, USA. Our results exemplify how direct selection for grain yield changed wheat phenotype during a ~100-year period in a dry subhumid environment. While changes in crop physiological traits in response to breeding have been reported a number of times, to our knowledge, this is the first detailed assessment of changes in biomass partitioning and rates of mass accumulation to different organs as affected by both cultivar and management (i.e., in-furrow fertilizer). Our results can help guide future selection for wheat yield in other dry-environments.

Plant Height, Stem Diameter, and Phenology

The logistic model suggested a steep decrease in plant height from historic to modern varieties, resulting in two distinct

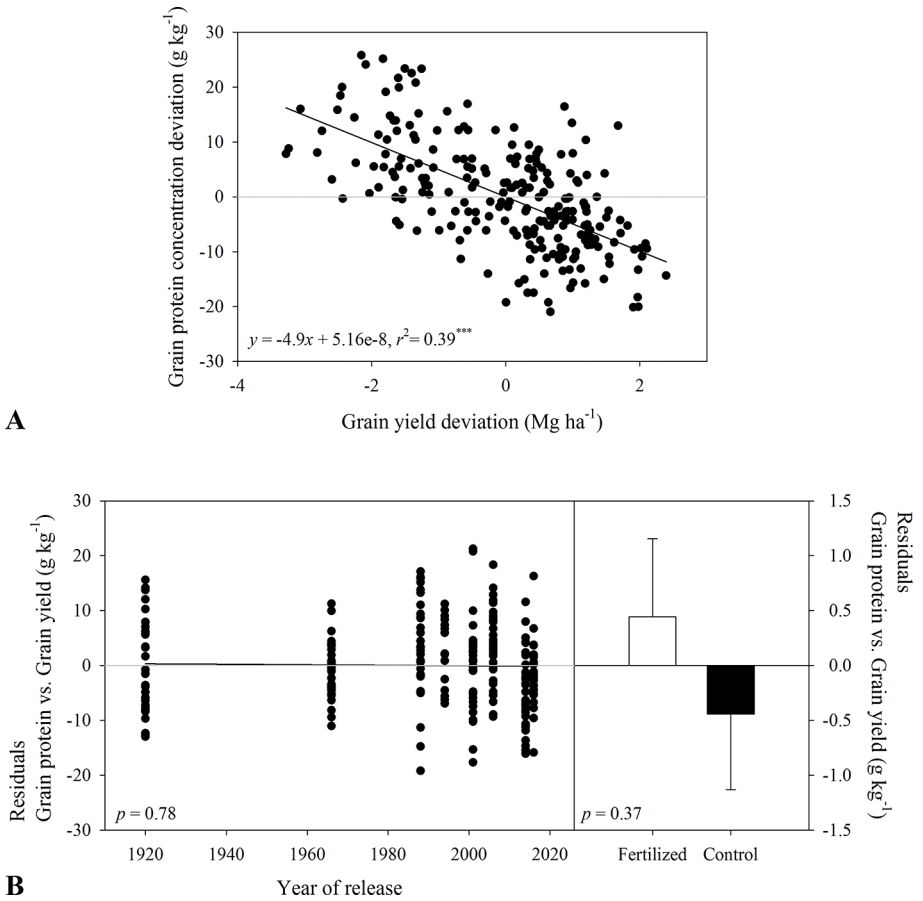


FIGURE 3 | Relationship between **(A)** grain protein concentration deviation and grain yield deviation for varieties released between 1920 and 2016. Residuals of the regression **(B)** as affected by year of variety release or in-furrow fertilizer treatment and control (bars show mean and standard error). Values correspond to the data of four site-years during two growing seasons (2016-2017 and 2017-2018).

groups. This is a consequence of the introduction of dwarfing genes in modern genotypes (Peng et al., 1999). An optimum wheat plant height between 0.7–1.0 m was described by Richards (1992) in a south-eastern Australian environment, which is shorter than the measurements in the current study. This indicates that there is still scope for shortening wheat varieties in U.S. southern Great Plains. Benefits of shorter varieties include increases in harvest index (Austin et al., 1980; Acreche et al., 2008); standability; and perhaps improvements in grain yield (Donmez et al., 2001; Brancourt-Humel et al., 2003). The logistic model representing changes in stem diameter was not as steep as that for plant height, but historical varieties with thinner stems were more prone to lodging (data not shown). Zuber et al. (1999) and Tripathi et al. (2003) found a strong negative relationship between stem diameter and lodging score. Lodging can decrease the stored photoassimilate reserves (Fischer and Stapper, 1987) and N use efficiency (Brancourt-Humel et al., 2003), reducing grain yield in as much as 35% (Fischer and Stapper, 1987).

The piecewise model suggested a large variation for flowering thermal time in the varieties included in this study between 1920 and 1988, with no substantial changes afterwards. The shorter cycle observed in semidwarf varieties derived from earliness in flowering time but similar or longer duration of grain fill. Earlier flowering associated with reduced shoot biomass at anthesis and the longer grain filling period of modern varieties associated with increased harvest index and yield. Early anthesis has been associated with genetic progress in grain yield of wheat in the U.S. Great Plains (Donmez et al., 2001), in the U.K. (Austin et al., 1980), and Mediterranean environments (Siddique et al., 1989a; De Vita et al., 2007; Giunta et al., 2007). The lack of change in flowering time since 1990s suggests that modern varieties flower at the optimal time for the region, balancing higher risks of spring freeze injury in earlier flowering and greater risks for high temperatures and drought stresses during grain fill with later flowering (Khalil et al., 1995; Sciarresi et al., 2019).

Grain Yield, N Removal, and Grain Protein Concentration

A sample of winter wheat varieties released between 1920 and 2016 in the U.S. southern Great Plains revealed different rates in yield gain in different time periods, with a small yield gain until ~1970s, accompanied by greater yield gain through ~2000s, and

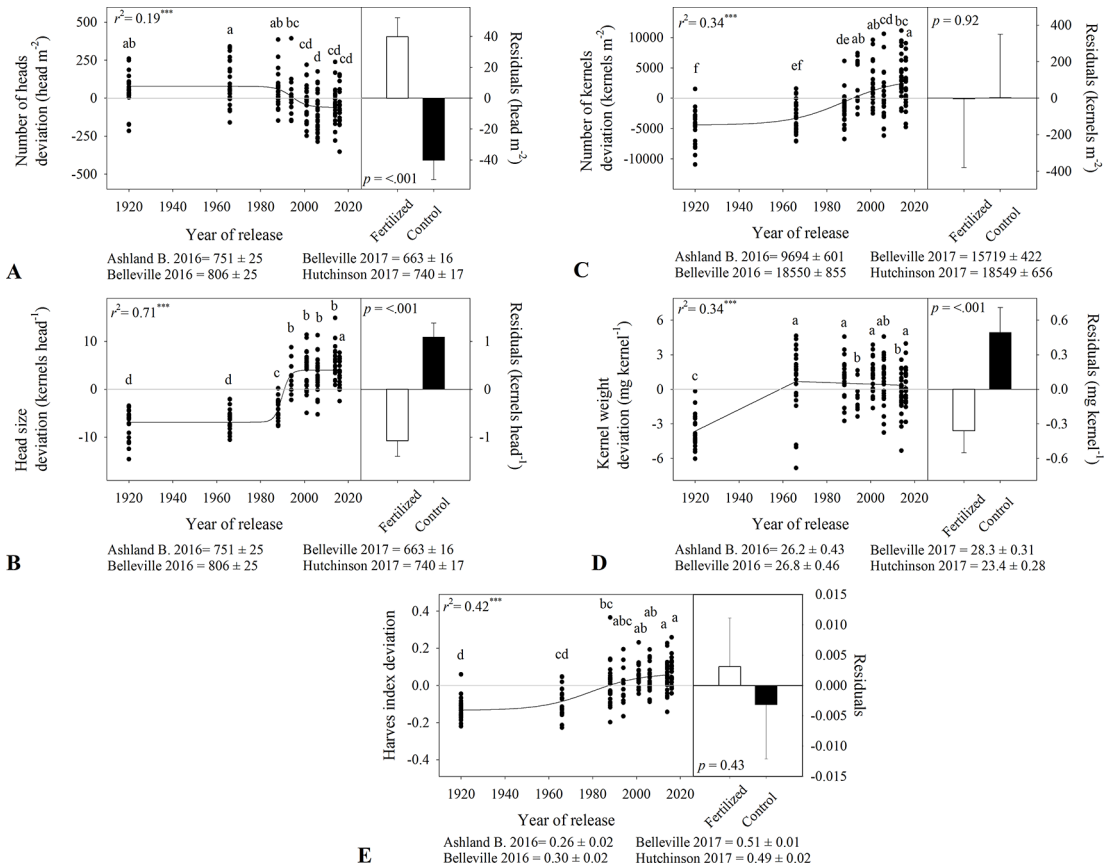


FIGURE 4 | Relationship between the year of release and yield components deviation including **(A)** heads number, **(B)** head size, **(C)** kernel number, **(D)** kernel weight, and **(E)** harvest index. Comparison of the regression residuals for in-furrow fertilizer treatment and no control (mean and one standard error). Values correspond to the data of four site years during two growing seasons (2016-2017 and 2017-2018). Mean for all varieties in each site and year. All models are significant at P < 0.0001. Varieties followed by the same letter are not statistically different at $\alpha = 0.05$.

smaller gain afterwards. This small yield progress in recent years was recently reported for a set of commercial varieties from different breeding programs in the region (de Oliveira et al., 2019). Historical sets of wheat varieties have been assessed to estimate the progress of breeding efforts and quantify the impact of management practices (Brancourt-Humel et al., 2003; Acreche et al., 2008; Del Pozo et al., 2014; Lo Valvo et al., 2017; Flohr et al., 2018). In some cases, similar historical trends occurred in different regions (Austin et al., 1980; Cox et al., 1988; Slafer and Andrade, 1989; Sanchez-Garcia et al., 2013; Beche et al., 2014; Lo Valvo et al., 2017; Flohr et al., 2018). The greater yield improvement mid-century was a result of the introduction of the dwarfing genes, which allowed for less lodging (Evenson, 2003).

The trend in yield gain found in this study contrasted with other studies that reported no clear tendency of leveling-off in yield progress (Donmez et al., 2001; Sadras and Lawson, 2011). This divergence might result from the genotype × environment interaction (Sanchez-Garcia et al., 2013), or environmental yield potential might also affect these results, especially when evaluating responses to management (Brancourt-Humel et al., 2003). Finally, the focus of the regional breeding programs may also affect the rate of yield gain (e.g., focusing solely in yield potential *versus* focusing in disease resistance and grain quality) (Fischer and Edmeades, 2010). We also acknowledge that our power to make inferences to changes in phenotype in other regions is relatively low as our data is biased toward varieties developed by a particular wheat-breeding program, and rates of yield gain vary greatly between breeding programs even within a similar geography (Rife et al., 2019). Nonetheless, our analysis offers insights into changes in wheat phenotype in response to breeding for yield in a predominantly dry environment.

Modern varieties removed more N in grain and had lower grain protein concentration than historical ones, suggesting that the decrease in grain protein concentration over time was due to greater improvements in grain yield relative to putative increase in crop nitrogen uptake and/or nitrogen harvest index (Sadras et al. (2016). As expected (Kibite and Evans, 1984; Oury and Godin, 2007; Bogard et al., 2010; Lollato and Edwards, 2015), grain protein concentration declined with grain yield. The decrease in grain protein concentration with higher yield is partially a dilution effect (Kibite and Evans, 1984). Nonetheless, when normalized for yield, grain protein

TABLE 4 | Shoot biomass in different plant components (leaves, stem, chaff, grain) at Zadoks 26, 31, 65, 85, and 92 of wheat varieties released between 1920 and 2016, fertilizer treatment, and their interaction during the growing seasons 2016-2017 and 2017-2018. Variety and fertilizer means were averaged across locations within growing season.

Year	Variety (Year of release)	Fertilizer	GS 26	GS 31		GS 65			GS 85				GS 92			
			Leaves (g m^{-2})	Leaves (g m^{-2})	Stem (g m^{-2})	Leaves (g m^{-2})	Stem (g m^{-2})	Chaff (g m^{-2})	Leaves (g m^{-2})	Stem (g m^{-2})	Chaff (g m^{-2})	Grain (g m^{-2})	Leaves (g m^{-2})	Stem (g m^{-2})	Chaff (g m^{-2})	Grain (g m^{-2})
2016-2017	Kharkof (1920)		60.8a	158.3	88.3c	243.1a	749.9a	103.2c	190.1	798.3a	148.0c	185.7c	159.5a	797.2a	154.7c	209.1c
	Scout 66 (1966)		56.7a	156.3	128.9ab	224.0ab	707.2a	131.8b	171.4	757.1a	169.5c	227.3c	144.6ab	808.9a	196.2ab	285.5bc
	Karl 92 (1988)		58.6a	131.8	134.9a	184.2b	493.0d	134.5b	151.3	730.8a	238.5ab	365.6b	103.2d	589.5b	227.5a	331.2b
	Jagalene (2001)		54.0a	150.5	102.6bc	221.1ab	603.5b	154.6a	192.3	804.7a	247.7a	582.6a	132.7abcd	611.0b	210.5ab	464.6a
	Fuller (2006)		43.1b	134.8	113.3abc	190.7b	525.5cd	133.4b	164.9	805.9a	238.7ab	492.6a	109.2cd	581.8b	202.5ab	439.3a
	KanMark (2014)		43.4b	138.3	100.9c	185.1b	458.5d	143.5ab	168.9	600.9b	247.9a	538.8a	125.9bcd	512.8b	221.9ab	474.3a
	Larry (2016)		57.9a	154.7	96.9c	221.4ab	585.6bc	144.9ab	212.8	759.5a	216.1b	514.8a	133.7abc	587.1b	189.8bc	425.6a
		In-furrow	63.5A	163.9A	126.5A	228.2A	626.5A	140.3A	198.8A	807.6A	227.0A	443.9	140.9A	674.4A	204.5	365.0
		Control	43.4B	128.9B	92.3B	191.7B	551.6B	130.0B	158.9B	694.4B	203.4B	396.8	118.8B	607.9B	196.3	386.3
2017-2018	Kharkof (1920)		36.0	102.1	55.0bc	150.4	466.7a	201.1a	112.9	471.7a	181.3	308.2d	93.6	441.5a	184.3	292.3c
	Scout 66 (1966)		30.0	118.6	80.5a	187.5	498.9a	196.5ab	103.1	451.2a	188.5	408.6c	91.1	417.2a	201.0	397.8b
	Karl 92 (1988)		38.8	97.6	69.6ab	140.1	335.7b	149.3cd	84.9	327.7b	194.1	436.1bc	72.4	299.0bc	190.1	415.3b
	Jagger (1994)		35.2	103.5	66.7ab	171.7	340.0b	142.3d	98.3	355.1b	188.6	478.6ab	94.9	351.4b	196.9	491.4a
	Jagalene (2001)		36.4	104.8	60.2b	171.0	381.0b	162.3bcd	91.0	332.5b	172.9	488.9ab	84.3	312.3bc	187.4	495.2a
	Fuller (2006)		31.9	89.4	61.5b	158.6	327.5b	144.5cd	98.3	333.3b	189.7	433.6bc	85.9	306.8bc	199.7	406.0b
	KanMark (2014)		34.1	107.0	62.2b	192.8	330.4b	178.3abc	110.9	305.4b	209.0	511.8a	100.9	297.0c	210.5	519.9a
	Larry (2016)		33.8	95.7	42.3c	199.0	349.9b	173.6abcd	99.0	343.0b	186.9	494.4ab	90.5	325.4bc	189.5	496.9a
		In-furrow	41.5A	120.5A	79.3A	193.6A	416.9A	181.8A	112.8A	405.2A	203.3A	471.2A	97.5A	365.3A	201.2A	434.8
		Control	27.4B	84.2B	45.2B	149.2B	340.6B	155.2B	86.8B	324.8B	174.5B	418.8B	80.9B	322.4B	188.7B	443.9

Values followed by the same letter within growing season and treatment are not statistically different at $\alpha = 0.05$.
Jagger was not included in the 2016-2017 growing season analysis.

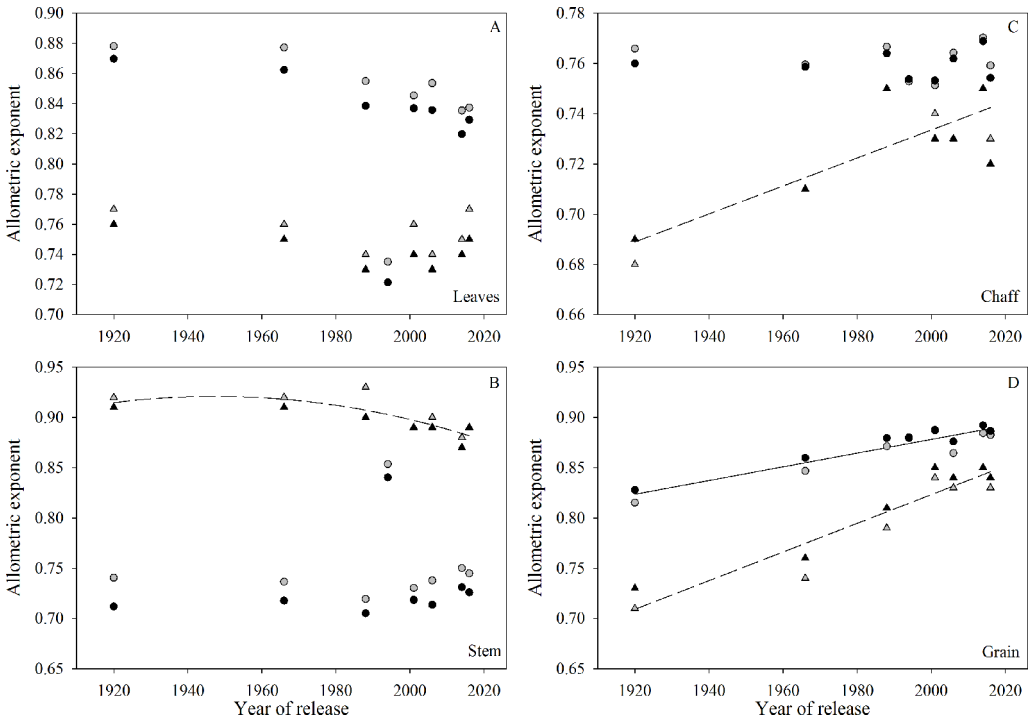


FIGURE 5 | Relationship between allometric exponent (slope of log of plant organ biomass *versus* log of shoot biomass) and year of release for each plant organ: **(A)** leaves, **(B)** stem, **(C)** chaff, and **(D)** grain. Symbols (▲▲) and dashed lines refer to the 2016-2017 growing season, symbols (●●) and solid lines refer to 2017-2018 growing season. Black symbols are the control treatment and grey symbols are the in-furrow fertilizer treatment. Only significant ($P < 0.05$) regressions are shown.

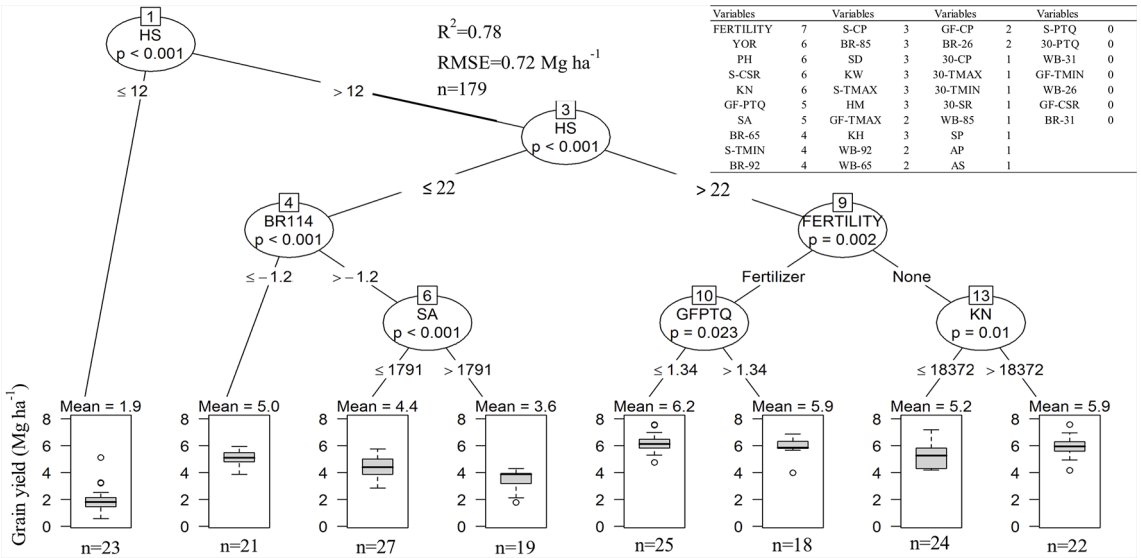
concentration did not change with year of release. This maintenance of protein concentration when corrected for yield, despite substantial increases in grain yield, is likely a response to the emphasis on wheat quality in the region (e.g., mostly bread wheat as opposed to lower quality soft wheat classes) (Baenziger et al., 2001; Fufa et al., 2005).

Morphological and Physiological Components of Yield Increase

Heads m^{-2} decreased over time in our study, with similar findings reported by Tian et al. (2011) in China. Breeding programs directly selecting for yield in dry environments (e.g., Kansas or the North China Plain) might have indirectly selected for lower tillering and fewer heads per unit area as a soil water conservation strategy (van Herwaarden et al., 1998), perhaps with the exception of dual-purpose (i.e., grazing plus grain) breeding programs for dry regions (Carver et al., 2001). In-furrow fertilizer increased heads m^{-2} by 7%–10%, likely due to greater early-season wheat biomass (Lollato et al., 2013) and tillers $plant^{-1}$ (Sato et al., 1996), increasing heads m^{-2} (Rodríguez et al., 1999). The effects of in-furrow fertilizer increasing heads m^{-2} contrasted with the trends of decreased heads m^{-2} due to breeding. This, in addition to results shown in **Figure 6**, suggests that more heads m^{-2} might not always be desirable in this dry environment, perhaps explaining the inconsistent wheat yields response to in-furrow P in the region (e.g., Lollato et al., 2013; Lollato et al., 2019b).

The increase kernels $head^{-1}$ over time corroborates with findings for other regions (Siddique et al., 1989a; Siddique et al., 1989b; De Vita et al., 2007; Del Pozo et al., 2014). Sanchez-Garcia et al. (2013) reported that the increase in kernels $head^{-1}$ was explained by an increase in spikelets $head^{-1}$ and kernels $spikelet^{-1}$. The introduction of dwarfing genes can partially explain the increase in kernels $head^{-1}$ (Flintham et al., 1997; De Vita et al., 2007), as these genes might favor partitioning of biomass into spikes (Abbate et al., 1998; Miralles et al., 1998), and enhanced survival of floret primordia (Miralles et al., 1998). Interestingly, in-furrow fertilizer reduced kernels per head, perhaps because of the increased number of heads reducing the average head size.

Kernels m^{-2} is considered a coarse-regulator of wheat yield (Slafer et al., 2014). Its progress over decades was reported to relate to improvements in kernels $head^{-1}$ (Slafer and Andrade, 1989; De Vita et al., 2007), head dry weight at anthesis (Acreche et al., 2008), partition of more photoassimilates into the developing heads (Slafer and Andrade, 1989), and growth rate (Sadras and Lawson, 2011). Kernel weight increased from 1920 until 1960s, with no major changes afterwards. While this analysis suggests that selection for yield over time did not change kernel weight (maybe because kernel weight is a fine



Variables		Variables		Variables		Variables	
FERTILITY	7	S-CP	3	GF-CP	2	S-PTQ	0
YOR	6	BR-85	3	BR-26	2	30-PTQ	0
PH	6	SD	3	30-CP	1	WB-31	0
S-CSR	6	KW	3	30-TMAX	1	GF-TMIN	0
KN	6	S-TMAX	3	30-TMIN	1	WB-26	0
GF-PTQ	5	HM	3	30-SR	1	GF-CSR	0
SA	5	GF-TMAX	2	WB-85	1	BR-31	0
BR-65	4	KH	3	SP	1		
S-TMIN	4	WB-92	2	AP	1		
BR-92	4	WB-65	2	AS	1		

FIGURE 6 | Conditional inference tree for grain yield as related to weather, crop traits, and fertiliser across the entire data set. Boxplots spans first to the third quartile, inside solid line are the means which are also shown above each boxplot. The lower and upper lines show the 5th and 95th percentile, respectively. Inset table shows a list of 37 candidate variables at influencing wheat grain yield and the number of statistical models in which each variable was significantly associated with grain yield, out of a total of seven models. Year of variety release (YOR), plant height (PH), kernel number (KN), head number (HN), stem diameter (SD), kernel weight (KW), head size (HS), thermal time from sowing to anthesis (SA), from sowing to physiological maturity (AP), from anthesis to soft dough (AS), from sowing to physiological maturity (SP), maximum (TMAX) and minimum temperature (TMIN), cumulative solar radiation (CSR), cumulative precipitation (CP), photothermal quotient (PTQ), whole plant biomass (WB), crop biomass rate (BR). Letters left to each variable represent the period, growing season (S), thirty days before anthesis (30), grain filling (GF). Values to the right to each variable represent the growth stage in the Zadoks scale, GS 26, 31, 65, 85, and 92.

regulator of wheat yield; Slafer et al., 2014), we note that there were substantial increases in kernels m^{-2} whilst maintaining kernel weight. In-furrow fertilizer decreased average kernel weight, which agrees with Tian et al. (2011). This likely results from more heads formed from later tillers due to in-furrow fertilization.

Total Biomass, Crop Growth Rate, and Allocation to Plant Components

Most studies comparing historical and modern wheat varieties report biomass at one of few growth stages, more often at physiological maturity (Brancourt-Humel et al., 2003; Giunta et al., 2007; Sadras and Lawson, 2011; Pampana et al., 2013; Wang et al., 2017). Only a handful of studies reported dynamics of shoot biomass more times in the season (e.g., Austin et al., 1980; Siddique et al., 1989a; Shearman et al., 2005; Acreche et al., 2008; Pampana et al., 2013; Flohr et al., 2018).

The similarity among wheat varieties in total biomass and initial growth rate suggests that the chronological changes in biomass accumulation responsible for greater grain yield occurred later in the season. At anthesis, tall varieties had greater total biomass, partially due to the longer period required to reach this growth stage as compared to shorter-cycled semidwarf varieties (Álvaro et al., 2008; Flohr et al., 2018). Despite a greater biomass, its partitioning into reproductive organs was less efficient in tall varieties, as the allometric coefficient consistently increased when related to varieties' year of release. Reports by Slafer et al. (1990) and Álvaro et al. (2008) agreed with our findings and showed that biomass partitioning to the chaff in wheat varieties increased over time. The same levels of biomass with greater HI in semidwarf varieties and the consistent increase in allometric coefficient for grain versus year of release across all site-years suggests that yield increases in modern wheat varieties resulted from more efficient partitioning of assimilates to the grains rather than greater biomass, possibly due to greater remobilization (Pampana et al., 2013). Likewise, previous studies have reported no substantial changes in biomass accumulation at maturity over the years (Austin et al., 1980; Calderini et al., 1995; Royo et al., 2007; Acreche et al., 2008; Kitonyo et al., 2017). The inconsistent results in allometric exponents for the different years of this study for leaves, chaff, and stem might result from different patterns of accumulation and remobilization of dry matter as affected by environment, similar to the results of Pampana et al. (2013).

Harvest index has been associated with genetic yield gain in wheat (Slafer and Andrade, 1989; Royo et al., 2007; Zhou et al., 2007). However, Austin et al. (1980) proposed that theoretical biological limit for harvest index in well-watered crops was ~0.62, suggesting that there might have room for further improvement in modern hard red winter wheat varieties in the study region (i.e., harvest index ~0.44 for semidwarf varieties), although this limit might be lower in dryland environments. Tall

and semidwarf varieties at maturity presented similar shoot biomass, suggesting that improvements in grain yield over time resulted from a greater ability of semidwarf varieties to allocate assimilates to the grain (Tian et al., 2011).

CONCLUSIONS

Kansas winter wheat varieties increased grain yield over time, but there was a decrease on the pace of progress after 1990s. Selection for yield increased kernels per area and kernels per head in modern semidwarf cultivars. Semidwarf varieties also flowered earlier than tall varieties and had longer grain-filling period, which associated with less biomass at anthesis and greater harvest index, respectively. Increases in allometric coefficient with year of release also suggested that greater yield in semidwarf cultivars resulted from a greater ability to allocate dry matter into the grain even at similar shoot mass. The decrease in grain protein concentration over time was solely a function of increases in grain yield, as there was no relationship between the residuals of grain protein concentration and grain yield *versus* year of release. While in-furrow fertilizer increased biomass and grain yield, the lack of interaction suggests that semidwarf varieties were not more responsive than tall varieties to in-furrow fertilizer when otherwise well fertilized (i.e., all plots received enough N for a 6 Mg ha^{-1} yield goal).

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

The manuscript was reviewed and approved for publication by all authors. RL and AF conceived and designed the field experiment. RM collected data, analyzed the data, and drafted the manuscript. VS, IC, and RL made substantial contributions to data analysis and interpretation, and manuscript editing. AF and DD edited the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2019.01786/full#supplementary-material

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The Integration of Spring and Winter Wheat Genetics With Agronomy for Ultra-Early Planting Into Cold Soils

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Early seeding has been suggested as a method of increasing the grain yield and grain yield stability of wheat (*Triticum aestivum L.*) in the Northern Great Plains. The point at which early seeding results in a decrease in grain yield has not been clearly identified. Changes in climatic conditions have increased frost-free periods and increased temperatures during grain filling, which can either be taken advantage of or avoided by seeding earlier. Field trials were conducted in western Canada from 2015 to 2018 to evaluate an ultra-early wheat planting system based on soil temperature triggers as opposed to calendar dates. Planting began when soil temperatures at 5 cm depth reached 0°C and continued at 2°C intervals until 10°C, regardless of calendar date. Conventional commercial spring wheat genetics and newly identified cold tolerant spring wheat lines were evaluated to determine if ultra-early wheat seeding systems required further development of specialized varieties to maintain system stability. Ultra-early seeding resulted in no detrimental effect on grain yield. Grain yield increased at sites south of 51° latitude N, and was unaffected by ultra-early seeding at sites north of 51° latitude N. Grain protein content, kernel weight, and bulk density were not affected by ultra-early seeding. Optimal seeding time was identified between 2 and 6°C soil temperatures. A greater reduction in grain yield was observed from delaying planting until soils reached 10°C than from seeding into 0°C soils; this was despite extreme environmental conditions after initial seeding, including air temperatures as low as −10.2°C, and as many as 37 nights with air temperatures below 0°C. Wheat emergence ranged from 55 to 70%, and heads m^{-2} decreased with delayed seeding while heads $plant^{-1}$ did not change. Cold tolerant wheat lines did not increase stability of the ultra-early wheat seeding system relative to the conventional spring wheat check, and are therefore not required for growers to adopt ultra-early seeding. The results of this study indicate that growers in western Canada can successfully begin seeding wheat earlier, with few changes to their current management practices, and endure less risk than delaying seeding until soil temperatures reach 10°C or greater.

Keywords: wheat, seeding, early, grain yield, cold tolerance, stability, great plains

INTRODUCTION

Canada is a globally important producer and exporter of high-quality wheat. In 2016 Canada ranked as the world's fifth largest producer of wheat (32.1 MT), and third largest exporter (19.7 MT) (FAOSTAT, 2019). Wheat production in the Northern Great Plains region of western Canada is limited by a short frost-free period which dictates the requirement for early maturing spring wheat varieties (Iqbal et al., 2007). Cutforth et al. (2004) calculated the average frost-free season in western Canada as 96 days in 1940, increasing to 114 days in 2000, a trend expected to continue. This increase in growing season length is one of many contributing factors accounting for increases in western Canadian spring wheat production from an average of 14.3 MT on 9.63 Mha from 1961 to 1970 to 19.8 MT on 6.63 Mha from 2008 to 2017 (Statistics Canada, 2019). Growth of the frost-free period has occurred as a result of both earlier final spring frosts, and later initial fall frosts (Cutforth et al., 2004), the former being correlated to calendar date and used as the current primary determinant of seeding date in western Canada. Lanning et al. (2010) reported that grain yield of the variety 'Thatcher' had increased over 56 years of comparative data and attributed this to earlier planting and longer growing seasons. However, increased average growing season temperatures that have accompanied longer frost-free periods have the potential to reduce yield due to higher temperatures during grain fill and reduced in-season moisture availability (Asseng et al., 2004; Lanning et al., 2010; He et al., 2012). Kouadio et al. (2015) identified earlier seeding in western Canada as one method to reduce the risks associated with increased temperatures during the growing season as a result of climate change. In the evaluations of Kouadio et al. (2015) the lowest yield loss was observed from the earliest seeding dates. Many studies have indicated higher grain yield from seeding wheat earlier in western Canada (Larter et al., 1971; Mckenzie et al., 2008; McKenzie et al., 2011; Lanning et al., 2012) however, few have indicated the point at which seeding earlier has a detrimental effect on yield. Thilakarathna et al. (2017) evaluated frost-seeding, or seeding prior to spring ground thaw, in Ontario, Canada and determined a grain yield benefit of up to 24% over conventional seeding times for spring wheat in that environment, despite increased plant mortality.

The objective of this study was to evaluate an ultra-early spring wheat seeding system beginning at soil temperatures of 0°C. Ultra-early seeding treatments were combined with and without specialized cold-tolerant spring wheat genetics to determine if reductions in grain yield, grain quality, or growing system stability are associated with ultra-early seeding into cold soils in the Northern Great Plains.

MATERIALS AND METHODS

Site Description, Experimental Design, and Seeding Date Determination

This study was conducted at five sites in western Canada over 4 years, 2015–2018, totaling 13 site years (**Table 1**). The treatment structure consisted of a factorial arrangement of 24 treatments based on four wheat lines, six planting dates, and four replicates blocked within replicate by planting date. The lines used were "AC Stettler" (DePauw et al., 2009), an industry standard Canada Western Red Spring (CWRS) wheat, and three cold tolerant experimental lines (LQ1282A, LQ1299A, LQ1315A) developed by intercrossing two previously identified cold tolerant lines derived from a cross between "Norstar" (Grant, 1980) Canada Western Red Winter (CWRW) wheat and "Bergen," a Dark Northern Spring (DNS) wheat grown in North Dakota (**Table 2**). The seeding dates were based on soil temperature triggers of 0, 2, 4, 6, 8, and 10°C as measured with an Omega™ TPD42 soil temperature probe at 5 cm depth at 10:00 AM each day prior to

TABLE 1 | Average precipitation, post-seeding air temperature extremes and cumulative freezing events for each location x year.

Location	Latitude/ longitude	Agroecological region	Soil zone	Average yearly precipitation† (mm)	Year	Actual precipitation (mm)	Earliest seeding date‡	Number of days with air temperature below 0°C after initial seeding date	Lowest air temperature recorded after seeding (°C)
Dawson Creek, BC	55°48'N 120°14'W	Parkland	Gray wooded	453	2015	325	April 16	12	–5.0
					2016	542	April 21	11	–6.1
Edmonton, AB	53°33'N 113°29'W	Parkland	Black	446	2015	299	April 9	12	–4.2
					2016	510	March 29	11	–3.6
					2017	416	May 5	0	2.3
Lethbridge, AB	49°41'N 112°50'W	Western Prairies	Dark brown	380	2015	251	March 6	37	–6.7
					2016	338	February 16	36	–10.2
					2017	249	March 20	17	–7.6
					2018	284	April 23	2	–1.2
Regina, SK	50°26'N 104°35'W	Western Prairies	Dark brown	397	2015	347	April 21	11	–5.0
Scott, SK	52°21'N 108°49'W	Western Prairies	Dark brown	366	2016	415	April 2	21	–9.8
					2017	300	March 31	27	–9.4
Swift Current, SK	50°18'N 107°46'W	Western Prairies	Brown	357	2015	304	April 10	23	–6.4

† 1981–2010 average yearly precipitation accumulation. ‡ Based on 0°C soil temperature trigger date.

TABLE 2 | Classification of commercial check, cold tolerant, and parent lines.

Cultivar	Parental lines	Parental lines Canadian wheat classification	Experimental designation	Reference
AC Stettler[δ]	Prodigy, Superb	CWRS[δ]/CWRS	Commercial check	DePauw et al., 2009
LQ1282A[β]	Norstar, Bergen	CWRW[θ]/DNS[θ]	Cold tolerant[†]	Larsen, 2012
LQ1299A[β]	Norstar, Bergen	CWRW/DNS	Cold tolerant	Larsen, 2012
LQ1315A[β]	Norstar, Bergen	CWRW/DNS	Cold tolerant[†]	Larsen, 2012

† Cold tolerant lines were selected from 92 double haploid lines from a Norstar/Bergen cross initially completed at AAFC Lethbridge. Cold tolerant lines were selected based on demonstrated cold tolerance using LT_{50} tests as described in Larsen (2012). Further selection criteria included yield and quality parameters.
[δ] Canada Western Red Spring
[θ] Canada Western Red Winter
[θ] Dark Northern Spring
[β] Undetermined

seeding. If soil conditions made seeding impossible at the first soil temperature trigger (0°C), each seeding date was adjusted so that there was a 2°C soil temperature differential between each successive seeding date. The initial seeding date at each site in each year is shown in **Table 1**. In general, soil conditions at the sites south of 51°N allowed seeding to occur at targeted soil temperatures, while seeding at the sites north of 51°N began as soon as planting equipment could access trial sites and continued with 2°C soil temperature intervals between seeding dates. Access to trial sites at the higher latitude locations was often limited at 0°C soil temperatures due to excessive moisture and saturated soil after snow ablation.

Cold Tolerant Wheat Lines

The cold-tolerant wheat lines used in this study were the result of work completed at Agriculture and Agri-Food Canada Lethbridge and the University of Guelph, where a proof of concept study successfully demonstrated the transfer of high levels of cold tolerance from Norstar winter wheat to spring wheat (Larsen, 2012). Briefly, spring growth habit, doubled haploid lines from a Bergen x Norstar cross were screened using an LT_{50} test to discover lines with exceptional cold tolerance. LT_{50} tests or lethal temperature tests, evaluate cold tolerance by identifying the temperature at which 50% mortality occurs among seedling plants (Fowler, 2008). Two of the best cold tolerant spring growth habit lines were intercrossed (A134 $S10 x A134$S17) to develop lines with improved agronomics. Transfer of cold tolerance to spring wheat was successful, as several lines exhibited LT_{50} values superior to some commercial winter wheats commonly grown in eastern Canada. Thirty-nine semi-dwarf $F_{5:7}$ derived cold tolerant lines were placed into a non-replicated preliminary yield trial established in Lethbridge in the fall of 2013 to identify superior lines. The same lines were increased and spring growth habit was confirmed at the Agriculture and Agri-Food Canada winter nursery in New Zealand over the winter of 2013/14. In the spring of 2014, both a yield trial and seed increase were established at Lethbridge to provide a robust data set of crop response variables (data not shown) which was used to select the three lines for this study (LQ1282A, LQ1299A, LQ1315A). In addition to cold tolerance, the selection criteria included high grain yield, grain protein content, and straw strength, and reduced plant height and maturity.

Seeding Operations, Nutrient Management, and Pest Management

Seeding equipment varied but was similar to the drill designed and built by Agriculture and Agri-Food Canada Lethbridge, which was configured with ConservaPak™ knife openers (8) spaced 24 cm apart, a Valmar™ air delivery system, a Raven™ hydraulic seed calibration and product control system, and Morris™ seed cups. Fertilizer was banded to the side and below the seed row at seeding and was applied based on soil test recommendations and regional yield expectations. All seed was treated with a fungicide seed treatment to control seedling diseases [Raxil PRO—tebuconazole ({RS}-1-p-chlorophenyl-4,4-dimethyl-3-{1H-1,2,4-triazol-1-ylmethyl}pentan-3-ol] 3.0 g L^{-1} + prothioconazole [(RS)-2-[2-(1-chlorocyclopropyl)-3-(2-chlorophenyl)-2-hydroxypropyl]-2,4-dihydro-1,2,4-triazole-3-thione] 15.4 g L^{-1} + metalaxyl [metyl N-(methoxyacetyl)-N-2,6-xylyl-DL-alanite] 6.2 g L^{-1} Bayer Crop Science Canada Inc., Calgary, AB). All wheat lines were seeded at 400 viable seeds m^{-2}.

Weed control was achieved with in-crop herbicide applications at the BBCH 12–22 stage of wheat, generally in late May. Due to variable staging between seeding dates, herbicide products with restrictive crop staging or residual properties were not used. All post-emergent herbicide applications were made using a motorized sprayer calibrated to deliver a carrier volume of 45 L ha^{-1} at 275 kPa pressure.

Data Collection

Plant counts for each plot were performed from BBCH 20 to BBCH 49 to indicate total viable plants in two one-m long areas in the second and third rows and the second and third last rows of the plot. These areas were staked and used to count the number of heads later in the growing season. Heads $plant^{-1}$ was calculated using the number of heads divided by the initial plant count for each staked area. Days to emergence were determined when 50% of plants in a plot had emerged. Crop anthesis was recorded in days from planting to when 50% of the heads in a plot began extruding anthers. Plant height was recorded from two randomly picked but representative areas of the plots and the height of five spikes, excluding awns, was measured.

The entire plot was harvested with a plot combine. The combine was equipped with a straight-cut header, pickup reel, and crop lifters. Grain yield per plot was weighed after drying the sample to 14% moisture content, and used to estimate total yield per ha (Mg Ha^{-1}). A 2 kg subsample of grain was used to determine seed mass (from 250 kernels) and grain bulk density (kg hl^{-1}). Whole grain protein concentration was determined from the same subsample using near infrared reflectance spectroscopy technology (Foss Decater GrainSpec, Foss Food Technology Inc, Eden Prairie, MN) (Irvine et al., 2013).

Statistical Analyses

Data were analyzed in the MIXED procedure of SAS, and any outlier observations were removed before a combined analysis over years and environments (site-year) was performed using site-year, replication, soil temperature at seeding, and wheat variety as variables in the CLASS statement (Littell et al., 2006; SAS Institute, 2009). Error variances were heterogeneous among the environments, and corrected Akaike's information criterion (AICc) on model fit indicated that modeling residual variance heterogeneity improved fit. Variance heterogeneity was modeled for all analyses using the random statement in PROC MIXED with the group option set to environment. Environment and the interactions associated with environment were considered as random effects, whereas the treatment effects were considered fixed and significant if $P \leq 0.05$ when the analysis was performed (Steel et al., 1997). Analyses were performed for environment groupings based on latitude. Sites north and south of 51° latitude were placed into two groups and analyzed separately (**Figure 1**).

The effect of planting date on yield was further evaluated with an analysis of covariance (ANCOVA) following the method developed by Yang and Juskiw (2011). The implementation of ANCOVA reduced the error mean square, accounted for missing data, and served to increase the precision of the resulting regression analysis. Planting date was considered a covariate and classification variable by generating a second column of data (s) identical to the planting date to be used as the covariate. Type 1 sums of squares was specified *via* the METHOD statement in PROC MIXED (Yang and Juskiw, 2011). Direct regression variables (covariates) s and s*s represent linear and quadratic responses to planting date and are part of the MODEL statement. Environment or group interactions with s and s*s are used to evaluate linear and quadratic responses that are heterogeneous relative to planting date. Initial ANCOVA analysis indicated a significant interaction between s*environment which supports the decision to analyze the environments in two groups based on latitude.

A biplot grouping methodology was used to explore system responses and variability of wheat yield as described by Francis and Kannenberg (1978). The mean and coefficient of variation (CV) across years and replications were estimated for each treatment combination. Means were plotted against CV, and used to categorize the biplot data into four quadrants/groups, which included high mean grain yield and low variability (group I), high mean grain yield and high variability (group II), low mean grain yield and high variability (group III), and low mean grain yield and low variability (group IV).

RESULTS AND DISCUSSION

Growing Season Variability and Environmental Conditions

Initial seeding date varied within locations across years. Seeding began early in 2016—February 16 in Lethbridge, March 29 in Edmonton. The 2017 and 2018 seasons experienced delayed seeding due to late spring thaw. The first seeding date in Lethbridge in 2016 was 66 days earlier than the first seeding date in 2018. The first seeding date in Edmonton in 2016 was 37 days earlier than the first seeding date in 2017. Initial seeding dates by year and location are listed in **Table 1**. The wide range of environmental conditions that were experienced through the course of this study would be considered typical for the Northern Great Plains region as reported by Shen et al. (2005) who found no long term trends for the start of the growing season, defined

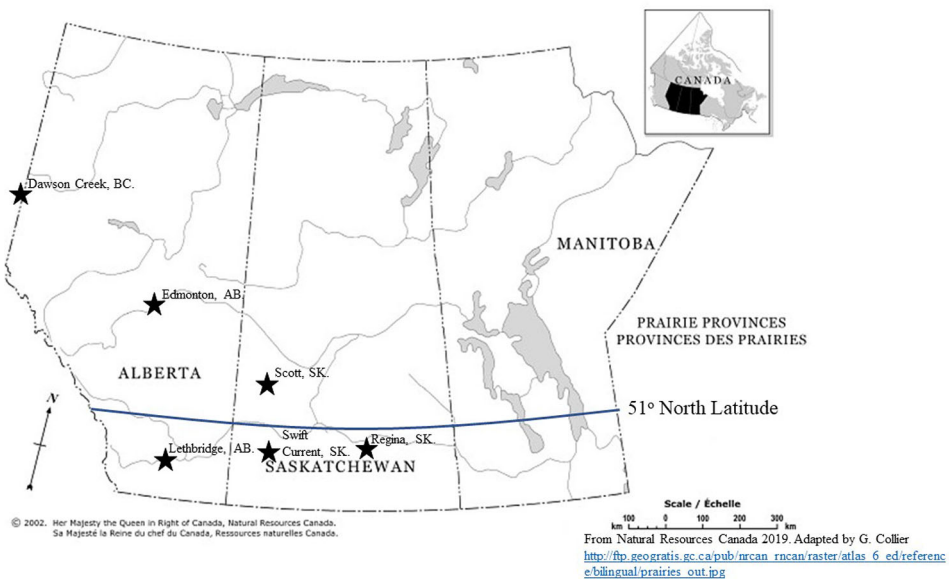

FIGURE 1 | Geographical distribution of test locations for the assessment of ultra-early wheat planting in western Canada 2015 to 2018. (The Atlas of Canada—Natural Resources Canada. http://ftp.geogratis.gc.ca/pub/nrcan_rncan/raster/atlas_6_ed/reference/bilingual/prairies_out.jpg).

as the first day of the year when five consecutive days have a mean temperature of 5°C, end of the growing season, the first day in the fall the mean temperature is below 5°C, and length of the growing season in the region. Shen et al. (2005) reported no change in the growing season despite reporting significant increases in frost free growing period, later first fall frosts, and earlier final spring frosts. The lack of an identifiable trend in growing season length, beginning, and end support the adoption of a soil-temperature-based seeding trigger system to standardize planting date from year to year and take advantage of the increased frost free period as opposed to the traditional use of calendar date as a reference point.

Precipitation varied over the duration of the study. Precipitation in 2015 was below average at all trial locations. In 2016 precipitation was above 30-year averages at all locations except Lethbridge, which was 89% of the 30-year average. All sites in 2017 and 2018 received below average rainfall (**Table 1**).

Eight of 13 site years experienced ambient air temperatures of −5°C or lower after initial seeding; some sites experienced temperatures as low as −9.8°C and −10.2°C. One site did not experience a nighttime low below 0°C after the initial seeding date. On average, sites had 16.5 nights where air temperatures reached below freezing, the most severe being Lethbridge in 2016 and 2017 where the air temperature dropped below 0°C for 37 and 36 nights respectively (**Table 1**).

After the initial planting date, nights with air temperatures below freezing averaged 21 at the sites south of 51°N and 12.5 at the sites north of 51°N. The soils at the sites south of 51°N tended to be free of snow cover and excess moisture and reached 0°C earlier than the sites north of 51°N. However, once sites north of 51°N reached 0°C they warmed faster than the sites south of 51°N, meaning planting dates were closer together at the sites north of 51°N (**Table 3**). This is due to the later disappearance of snow cover, increased available solar radiation when sites north of 51°N reached 0°C, and greater heat holding capacity of heavier texture clay loam soils relative to the sites south of 51°N (Zhao et al., 2002). The trial sites north of 51° N include soils classified as gray wooded Luvisols, orthic black chernozems, and orthic dark brown chernozems. The trial sites south of 51°N include soils of orthic dark brown chernozem and orthic brown chernozem classes.

Wheat emergence was slowed by the cool, slowly warming soils of sites south of 51°N. Wheat seeded at the earliest planting dates in the sites south of 51°N required 9.5 days longer to emerge than the earliest planting dates at the sites north of 51°N (**Table 3**).

Seeding Date Effect

Planting date did not alter yield at sites north of 51°N ($P = 0.158$) (**Table 4**). There was a yield response to planting date at sites south of 51°N ($P = 0.025$), and significant linear and quadratic effects of planting date on grain yield ($P = 0.044$ and $P = 0.03$ respectively) (**Tables 4** and **5**). The greatest grain yield occurred at the second and third planting dates, which correspond to soil temperature increase of 2 and 4°C after the earliest feasible planting date. Grain yield was lower at the earliest and latest seeding date (**Table 5**, **Figure 2**). The earliest seeding date produced less grain than the second and third seeding dates, however it did not produce less grain than the fourth or fifth

TABLE 3 | Least square means values and significance of crop development stage duration in ultra-early seeded wheat.

Planting date	Days to emergence	Days to anthesis	Days to maturity	Emergence to anthesis (days)	Anthesis to maturity (days)	Emergence to maturity (days)
Sites South of 51°N latitude[Ŧ]						
1 (Earliest)	23	79	140	56	60	117
2	22	82	138	60	56	116
3	21	76	136	56	60	115
4	18	76	135	58	59	117
5	13	69	131	55	62	117
6 (Latest)	13	65	125	53	60	113
F-Test	***	***	**	**	NS	NS
SED	1.6	2.6	3.9	1.8	NS	NS
Linear	***	***	***	*	NS	NS
Quadratic	NS	*	NS	*	NS	NS
Sites North of 51°N latitude[Ŧ]						
1	19	78	123	59	45	104
2	19	77	122	57	45	102
3	17	73	119	56	46	102
4	15	69	116	54	47	101
5	12	66	113	53	48	101
6	9	62	111	53	49	102
F-Test	***	***	***	***	*	*
SED	1.5	1.4	2.0	0.7	1.1	1.0
Linear	***	***	***	***	***	**
Quadratic	NS	NS	NS	*	NS	NS

(Ŧ) Data not reported for all environments. Sites south of 51° latitude include Lethbridge, AB. 2017, 2018. Sites north of 51° latitude include Dawson Creek, BC. 2016, Edmonton, AB. 2016, 2017, Scott, SK. 2016, 2017. (***) Significant at P < 0.001. (**) Significant at P < 0.01. (*) Significant at P < 0.05. (NS) Not significant. (SED) Standard error of the difference. (Ŧ) Planting date as determined by soil temperature trigger temperatures. Planting date (PD) 1 corresponds to a soil temperature of 0°C, or as soon after this trigger soil temperature as the site could be planted. Each successive PD corresponds to a 2°C increase in soil temperature from the previous PD.

TABLE 4 | Probability values from the analysis of variance for each dataset for the fixed effects of planting date and wheat line. Environments, replicates within each environment, and interactions between random and fixed effects are considered to be random.

Effect	Yield (Mg ha^{-1})	Protein (%)	Test weight (kg hL^{-1})	Thousand Kernel weight (g)	Height (cm)	Heads m^{-2}	Heads plant^{-1}
Sites South of 51°N latitude$^{\theta}$							
Planting Date (PD)	**0.025**	0.072	0.67	0.75	0.051	**<0.001**	0.73
Wheat Line (WL)	**0.044**	**<0.001**	**<0.001**	**<0.001**	**0.047**	**0.023**	0.86
PD_{linear}	**0.030**	**0.009**	0.54	0.26	**0.014**	**<0.001**	0.28
$PD_{quadratic}$	**0.0047**	0.18	0.14	0.33	0.47	0.36	0.78
PD x WL	0.48	1.0	0.98	0.98	0.17	0.97	0.57
Sites North of 51°N latitude‡							
Planting date (PD)	0.16	0.21	0.60	0.091	**0.008**	0.28	0.14
Wheat line (WL)	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.006**	**<0.001**	**<0.001**
PD_{linear}	0.84	**0.015**	0.22	**0.005**	0.15	**0.039**	**0.028**
$PD_{quadratic}$	0.22	0.33	0.52	0.86	**0.001**	0.31	0.54
PD x WL	0.95	0.91	0.94	1.0	0.81	0.96	0.88

θ 6 site years. Lethbridge, AB 2015, 2016, 2017, 2018. Regina, SK 2015, Swift Current, SK 2015

‡ 7 site years. Dawson Creek, BC 2015, 2016. Edmonton, AB 2015, 2016, 2017. Scott, SK 2016, 2017. Bolded values indicate a p - value of less than 0.05.

TABLE 5 | Least square means values and significance of treatment interactions for sites south of 51°N latitude.

Planting date$^{\mathbf{T}}$	Yield (Mg ha^{-1})	Protein (%)	Test weight (kg hL^{-1})	Thousand Kernel weight (g)	Height (cm)	Heads m^{-2}	Heads plant^{-1}
1 (Earliest)	2.89	12.0	77.3	30.4	70	345	1.3
2	3.04	11.9	77.6	30.5	71	362	1.3
3	3.04	12.2	77.6	30.6	71	337	1.4
4	2.94	12.1	77.7	30.3	70	286	1.3
5	2.93	12.3	77.4	30.4	68	298	1.1
6 (Latest)	2.68	12.6	77.1	29.7	69	270	1.2
F-Test	*	NS	NS	NS	NS	***	NS
SED	0.12					56	
Linear	*	**	NS	NS	*	***	NS
Quadratic	**	NS	NS	NS	NS	NS	NS
Wheat line							
LQ1282A	3.00	11.5	77.3	28.2	70	318	1.3
LQ1299A	2.90	11.8	76.4	30.9	69	307	1.3
LQ1315A	2.91	11.8	77.2	30.4	70	309	1.3
AC Stettler	2.86	13.6	78.8	31.7	71	332	1.3
F-Test	*	***	***	***	*	*	NS
SED	0.06	0.14	0.2	0.3	1	11	
Planting date x wheat line	NS	NS	NS	NS	NS	NS	NS

(***) Significant at P < 0.001. (**) Significant at P < 0.01. (*) Significant at P < 0.05. (NS) Not significant. (SED) Standard error of the difference. (Ŧ) Planting date as determined by soil temperature trigger temperatures. Planting date (PD) 1 corresponds to a soil temperature of 0°C, or as soon after this trigger soil temperature as the site could be planted. Each successive PD corresponds to a 2°C increase in soil temperature from the previous PD.

seeding dates and yielded more grain than the latest seeding date. The optimum seeding time at sites south of 51°N in the Northern Great Plains of Canada is between soil temperatures of 2 and 6°C after the first possible seeding date (**Figure 2**). The regression equation determined in this study indicates a maximum grain yield is realized when seeding occurs prior to when soil temperatures reach 3.9°C. Planting as early as possible after soil temperature has reached 0°C, will result in the same grain yield as delaying seeding until soil temperatures warm by 7.7°C (**Figure 2**). Seeding after a soil temperature of 7.7°C above the first feasible seeding date will yield less grain than seeding as early as possible after ground thaw. Seeding dates prior to spring thaw as evaluated by Thilakaranthna et al. (2017) are often met with equipment and logistical restraints in western Canada. Seeding attempts prior to soil reaching 0°C in western Canada may be better served by fall seeding of winter wheat which has additional agronomic benefits as reviewed by Larsen et al. (2018).

Grain yield at sites south of 51°N is limited by lower precipitation and greater heat stress relative to sites located north of 51°N (**Table 1**, **Figure 2**). Delayed seeding at sites south of 51°N resulted in lower grain yield due to reduced water availability and daylight hours and increased temperature during critical grain fill periods (Farooq et al., 2011). Anthesis to maturity and emergence to maturity periods were not significantly different at any seeding dates at sites south of 51°N (**Table 3**). However, anthesis to maturity and emergence to maturity periods were offset as a result of seeding date. The length of days and available solar radiation captured in the anthesis to maturity and emergence to

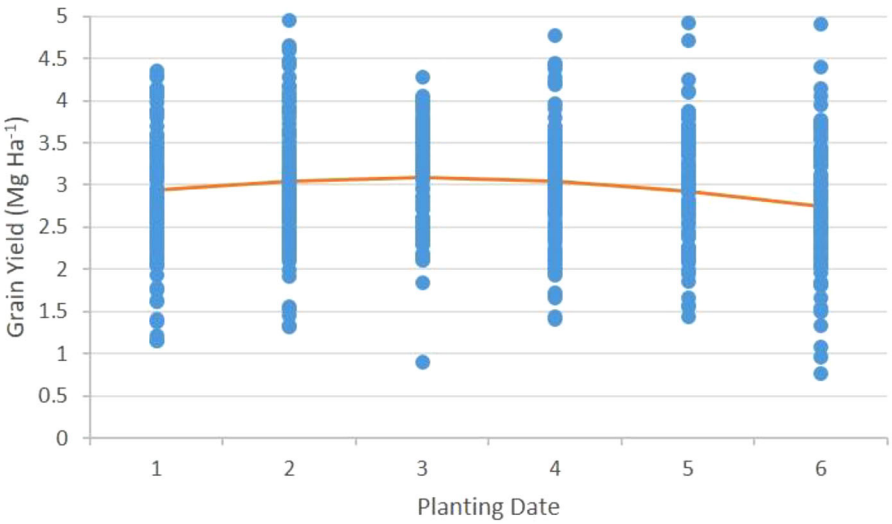

FIGURE 2 | Wheat grain yield as a function of planting date (PD) in sites south of 51°N latitude. PD 1 corresponds to a soil temperature of 0°C, or as soon after this trigger soil temperature as the site could be planted. Each successive PD corresponds to a 2°C increase in soil temperature from the previous PD.) The line represents a quadratic regression for grain yield [yield = 2.7709 + (0.2125 × PD) − (0.03624 × PD^2): R^2 = 0.61***] (***) Significant at $P < 0.001$.

maturity periods of the earlier planting dates was greater than at the later planting dates.

Sites north of 51°N had no grain yield difference as a result of seeding date. Rapid soil temperature increases decreased time differential between each seeding date. Greater moisture availability and longer periods from anthesis to maturity compensated for potential grain yield loss associated with delayed seeding (**Table 3**).

Wheat is highly amenable to ultra-early seeding into cold soils; no negative yield effect relative to later plantings north or south of 51°N was discernable. Planting as early as possible had less negative effect on spring wheat yield than delaying seeding until soils had warmed 8 to 10°C (**Figure 2**).

Grain protein concentration, grain thousand kernel weight, and grain test weight were not affected by seeding date. Ultra-early seeding did not result in changes in grain quality despite increased grain yield in some environments. Previous studies have indicated increased grain yield is associated with decreased grain protein concentration (Iqbal et al., 2007a). Further evaluation is required to determine if ultra-early seeding can consistently result in greater grain yield without decreasing grain protein concentration.

Plant height was shorter at seeding dates two, three, and four at sites north of 51°N, while earlier and later seeding treatments were taller. The effect of seeding date on plant height had a significant positive quadratic association at sites north of 51°N (**Table 6**). Plant height at sites south of 51°N was not affected by seeding date.

The number of heads m^{-2} significantly decreased with delayed seeding at sites south of 51°N (**Table 4**). A significant negative linear effect for reduced number of heads m^{-2} and no significant difference in the number of heads plant^{-1}, indicate that despite the extreme environmental conditions experienced when seeded ultra-early, the early planted wheat had better survivability than later seeded wheat, which did not initiate additional tillering to compensate for decreased plant stand (**Table 5**).

Effect of Cold Tolerant Wheat Lines

Treatment effects were present for all reported variables in sites north and south of 51°N except for heads plant^{-1} in sites south of 51°N. Significant effects are the result of class differences between AC Stettler and the cold tolerant wheat lines LQ1282A, LQ1299A, and LQ1315A (**Table 2**). AC Stettler is a milling quality wheat of the CWRS class. The CWRS class wheats have high grain protein concentration, typically over 13.5%, which reduces grain yield potential (Iqbal et al., 2007a; Prairie Grain Development Committee, 2015). The cold tolerant lines used in this study are not registered varieties and have not been evaluated by the Prairie Grain Development Committee or the Canadian Grain Commission; however, the end-use characteristics of these lines indicate a likely classification of Canada Western Special Purpose (CWSP). CWSP wheats have reduced grain protein content and greater yield potential than CWRS wheats.

AC Stettler had higher grain protein content at all sites. At sites north of 51°N AC Stettler yielded less grain than the cold tolerant lines. At sites south of 51°N AC Stettler yielded less grain than LQ1282A, but yielded the same as LQ1299A, and LQ1315A (**Tables 5** and **6**). Grain yield of longer maturing cold tolerant wheat lines at sites south of 51°N may have been limited by reduced water availability and higher temperatures during grain fill. At sites south of 51°N AC Stettler had greater thousand kernel weight, grain test weight and heads m^{-2} values than the

TABLE 6 | Least square means values and significance of treatment interactions for sites north of 51°N latitude.

Planting date ₮	Yield (Mg ha^{-1})	Protein (%)	Test weight (kg hL^{-1})	Thousand Kernel weight (g)	Height (cm)	Heads m^{-2}	Heads plant^{-1}
1 (Earliest)	5.69	12.4	79.0	35.0	82	464	2.0
2	5.35	12.6	78.8	35.4	81	460	2.0
3	5.17	12.6	78.9	35.5	79	457	1.8
4	5.54	12.9	78.8	35.6	80	454	1.8
5	5.62	12.9	78.9	36.6	82	451	1.9
6 (Latest)	5.44	12.8	78.4	36.7	83	426	1.8
F-Test	NS	NS	NS	NS	**	NS	NS
SED					1		
Linear	NS	*	NS	**	NS	*	*
Quadratic	NS	NS	NS	NS	**	NS	NS
Wheat line							
LQ1282A	5.74	11.4	78.5	33.2	82	455	1.9
LQ1299A	5.48	12.2	78.1	36.4	80	417	1.7
LQ1315A	5.51	12.1	78.8	36.2	81	447	1.8
AC Stettler	5.14	15.2	79.8	37.4	81	491	2.0
F-Test	***	***	***	***	**	***	***
SED	0.10	0.2	0.2	0.3	1	7	0.1
Planting date x wheat line	NS	NS	NS	NS	NS	NS	NS

(***) Significant at P < 0.001. (**) Significant at P < 0.01. (*) Significant at P < 0.05. (NS) Not Significant. (SED) Standard error of the difference. (₮) Planting date as determined by soil temperature trigger temperatures. Planting date (PD) 1 corresponds to a soil temperature of 0°C, or as soon after this trigger soil temperature as the site could be planted. Each successive PD corresponds to a 2°C increase in soil temperature from the previous PD.

cold tolerant lines, additionally, there were no differences in heads plant^{-1} between AC Stettler and cold tolerant lines. Greater heads m^{-2} and no difference in heads plant^{-1} indicate the survival of AC Stettler was at least as good as the survival of the cold tolerant lines under ultra-early planting conditions.

Ultra-Early Seeding System Stability

A version of the Francis and Kannenberg (1978) biplot grouping method was used to help visualize the stability of ultra-early wheat seeding systems. The biplots for yield suggest advantages to an ultra-early seeding system in sites south of 51°N. Seeding dates two and three had the greatest yield and lowest variability (**Figure 3A**). Seeding date four maintained high grain yield, but variability increased at this seeding date. Seeding dates one, five, and six tended to result in higher variability and lower grain yield than seeding dates two, three, or four. AC Stettler consistently yielded less grain than the cold tolerant lines, but the stability of yield across seeding dates was similar to the cold tolerant varieties, as indicated by similar CV values.

Seeding date did not affect grain yield at sites north of 51°N. The biplot in **Figure 3B** shows mixed system stability responses to seeding date and grain yield. All seeding dates except seeding date three are represented by at least one data point in group I (high yield and low variability). Seeding ultra-early at sites north of 51°N did not reduce grain yield or system stability relative to delayed seeding.

An ultra-early wheat seeding system on the Northern Great Plains is feasible with few changes from current management systems. Grain yield was not negatively impacted by seeding very early and in some areas resulted in increased grain yield. At sites south of 51°N where seeding date where seeding date had a significant effect on yield, the earliest seeding date did not result in different grain yield from the fourth or fifth seeding date, and resulted in a higher grain yield than the final seeding date. We conclude that seeding spring wheat in the Northern Great Plains region of Canada can begin as soon as soil temperatures are above 0°C and seeding equipment can access fields. Ultra-early seeding did not result in decreased growing system stability or lower grain yield than delaying seeding until soil temperatures warmed 8 to 10°C. In sites south of 51°N growing system stability increased with ultra-early seeding.

The use of cold tolerant lines did not increase growing system stability relative to the conventional check variety AC Stettler. Based on studies by Fowler (2008), it was postulated that the ability of the cold tolerant spring wheat lines to acclimate to a relatively low LT_{50} would provide a useful genetic resource for enhanced cold temperature protection of commercial spring wheat varieties when seeded at ultra-early seeding dates, provided that there was adequate time for cold acclimation. These results, relative to AC Stettler, showed that for ultra-early spring wheat seeding, additional genetic cold temperature protection and increased rates of cold acclimation did not confer an advantage to the crop.

Currently in western Canada crop insurance systems maintain limits for the latest seeding dates a grower can plant a crop and receive compensation. The results of this study indicate that an incentive program to encourage early seeding may limit risk, increase grain yield potential, and increase growing system stability relative to current practices.

CONCLUSIONS

Recommendations generated from this study are for growers to begin shifting to earlier spring wheat planting in western Canada —planting may begin immediately after the soil reaches 0°C, or as early as fields allow seeding operations to commence. A shift to seeding based on soil temperature triggers can normalize

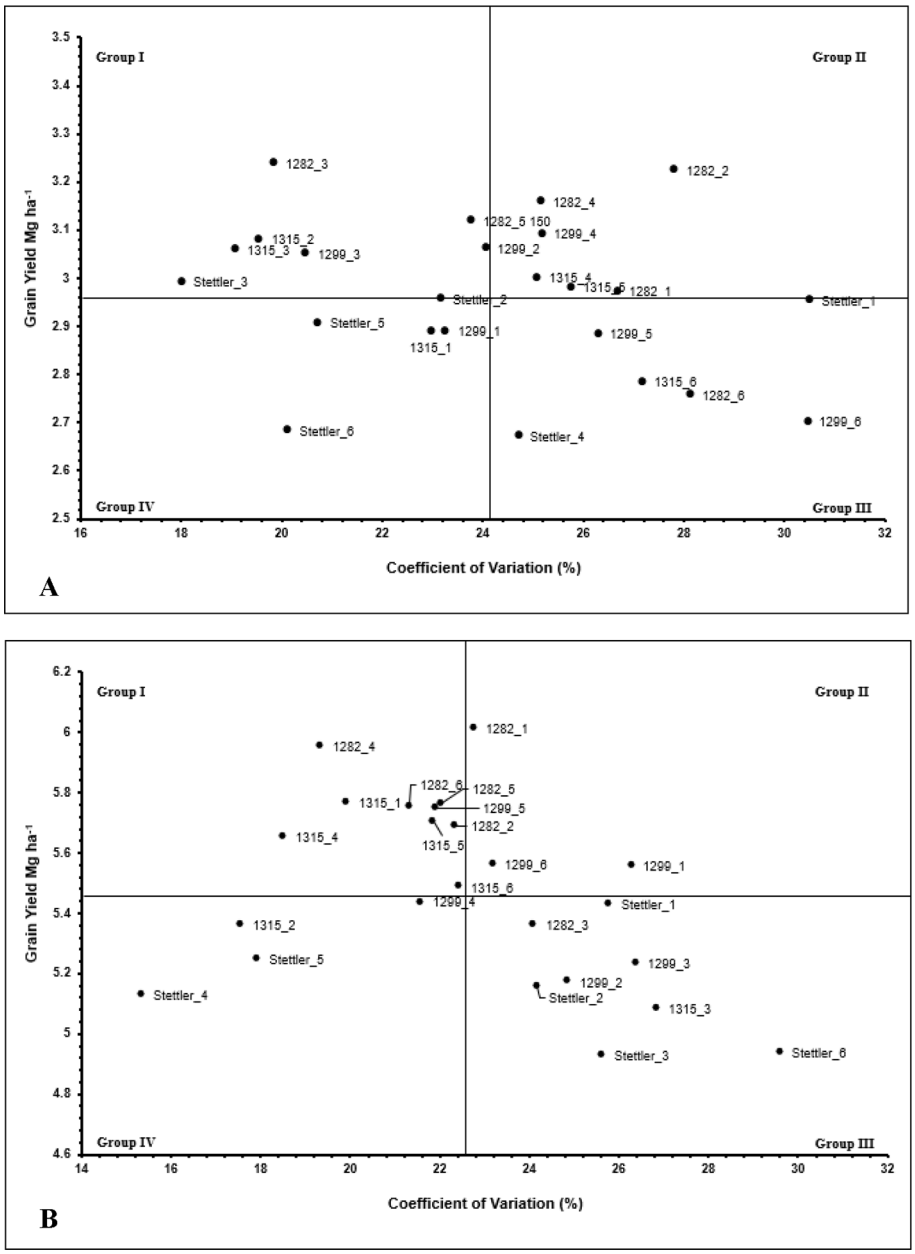

FIGURE 3 | Biplots summarizing yield means *vs*. coefficient of variation (CV) for **(A)**: sites south of 51°N latitude, **(B)** sites north of 51°N latitude. Abbreviations are as follows: I) first number/name represents the wheat line (AC Stettler, LQ1282A, LQ1299A, and LQ1315A). II) Second number represents planting date (1–6). Grouping categories: group I: high mean, low variability; group II: high mean, high variability; group III: low mean, high variability; group IV: low mean, low variability.

planting times within the growing season more effectively than seeding based on calendar date or on last expected spring frost. Special cold tolerant lines evaluated in this study did not benefit grain yield or stability of an ultra-early growing system. This study indicates that ultra-early seeding has no detrimental effect on yield on the Northern Great Plains and can potentially increase grain yield in lower latitude regions of western Canada. As indicated by Asseng et al. (2004); Lanning et al. (2010); He et al. (2012), and Kouadio et al. (2015), the risk of reduced grain yield in western Canada caused by increases in average growing season temperature and reduced precipitation can potentially be avoided by continually shifting wheat planting windows earlier. Future work will develop best management practices for an ultra-early wheat seeding system© in western Canada and evaluate the benefits of optimized agronomic systems.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

GC, Senior Author. Used project for partial fulfilment of PhD thesis requirements at the University of Alberta. Analyzed data and prepared manuscript. Participated in meetings and presented findings at conferences, field days and grower meetings. BB, Principal Investigator/Corresponding Author. Developed and conceptualized the hypotheses and field experiments. Identified and recruited Collaborators, PhD student, and led workshops to finalize proposal. Developed budget for all activities and co-supervises GC. RG, Co-Investigator. Developed cold-tolerant lines used for field experiments. Reviewed and edited manuscript. DS, Co-Investigator responsible for the field experimentation at the Edmonton sites. Co-Supervisor of GC. Reviewed and edited manuscript and mentored manuscript preparation and statistical analyses.

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Economically Optimal Wheat Yield, Protein and Nitrogen Use Component Responses to Varying N Supply and Genotype

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Improvements in market value of hard red spring wheat (HRS, *Triticum aestivum L.*) are linked to breeding efforts to increase grain protein concentration (GPC). Numerous studies have been conducted on the identification, isolation of a chromosome region (*Gpc-B1*) of Wild emmer wheat (*Triticum turgidum* spp. *dicoccoides*) and its introgression into commercial hard wheat to GPC. Yet there has been limited research published on the comparative responsiveness of these altered lines and their parents to varied N supply. There is increased awareness that wheat genetic improvements must be assessed over a range of environmental and agronomic management conditions to assess stability. We report herein on economically optimal yield, protein and nitrogen use efficiency (NUE) component responses of two Pacific Northwestern USA cultivars, Tara and Scarlet compared to backcrossed derived near isolines with or without the *Gpc-B1* allele. A field experiment with 5 N rates as whole plots and 8 genotypes as subplots was conducted over two years under semi-arid, dryland conditions. One goal was to evaluate the efficacy of the *Gpc-B1* allele under a range of low to high N supply. Across all genotypes, grain yield responses to N supply followed the classic Mitscherlich response model, whereas GPC followed inverse quadratic or linear responses. The *Gpc-B1* introgression had no major impact on grain protein, but grain N and total above ground crop N yields demonstrated quadratic responses to total N supply. Generally, higher maximum grain yields and steeper rise to the maxima (Mitscherlich c values) were obtained in the first site-year. Tara required less N supply to achieve GPC goals than Scarlet in both site-years. Genotypes with *Gpc-B1* produced comparable or slightly lower Mitscherlich A values than unmodified genotypes, but displayed similar Mitscherlich c values. Target GPC goals were not achieved at economic optimal yields based on set wheat pricing. Economic optimization of N inputs

to achieve protein goals showed positive revenue from additional N inputs for most genotypes. While N uptake efficiency did not drop below 0.40, N fertilizer-induced increases in grain N harvest correlated well with unused post-harvest soil N that is potentially susceptible to environmental loss.

Keywords: protein, wheat, *Gpc*-B1, nitrogen use efficiency, fertilizer, Mitscherlich, economics

INTRODUCTION

Global wheat (*Triticum aestivum L.*) production and consumption continues to rise (USDA FAS, 2020) as wheat continues to be a major source of human calories and protein (Mondal et al., 2016). Wheat has been the dominant crop in the inland Pacific Northwest (iPNW) USA since farming began in the late 1800's (Pan et al., 2017). Grain protein and N use responsiveness to N management in hard red wheats is well recognized (Belete et al., 2018), leading to specific unit N recommendations by wheat class (Koenig, 2005; Brown et al., 2005; Jones and Olson-Rutz, 2012; Franzen, 2018). A tremendous range in grain protein concentration (GPC) can be seen with variable N fertilizer management (Walsh et al., 2018; Beres et al., 2018). This experiment focused on recropped wheat in the transition zone of eastern Washington state, between wheat-fallow and continuous cropping agroecological zones. Recropping hard red spring wheat (HRS) after winter wheat is a strategy for crop intensification for diversifying the system and markets (Pan et al., 2017).

Economically optimal N supply is dictated by the shape of yield-protein and N use efficiency responses to N supply, the relative prices of wheat and N fertilizer, and the market premium:discount prices for GPC of hard red wheat (Baker et al., 2004). In the U.S., hard red wheat grain price premiums and discounts are often assessed at the grain elevator, based on GPC. Bekkerman (2018) used differences between prices for hard red spring wheat futures contracts on the Minneapolis Grain Exchange (MGEX) and hard red winter wheat futures contracts on the Kansas City Board of Trade (KCBT) to study how the market values protein. He found that the long-run average spread is approximately $23.15/Mg. These economic analyses indicate that building grain protein through N fertilization is not always profitable, however, depending on external factors such as the cash price of wheat, availability of high-protein wheat, and the cost of N fertilizer. As a result, improving grain protein to enhance end-use quality has long been a breeding goal in wheat breeding programs.

Improvements in wheat production and quality, and improved water and nutrient use can be achieved through integrated, environmentally-targeted cultivar selection and management efforts (Hatfield and Walthall, 2015). DePauw and Townley-Smith (1988) determined that environment and management typically overshadow genetic effects on GPC. While GPC has long-been recognized as an important grain end-use quality attribute and economic market factor, breeding improvements in wheat grain concentration has progressed slowly (Carter et al., 2012; Tabbita et al., 2017).

Wheat genetic heritability of nitrogen use efficiency (NUE) physiological traits that contribute to high NUE and grain protein (Hawkesford, 2012), particularly for low N environments, has been reviewed by Dawson et al. (2008). For example, genetic variation for wheat N uptake (Johnson et al., 1967) and translocation efficiency (Cox et al., 1986) are well established. In addition, genetic variability for post-anthesis N uptake was early recognized (Clarke et al., 1990). Early wheat breeding efforts connected high grain protein with genetic improvement of nitrate reductase activity, N uptake and translocation of the hard red winter wheat cultivar Lancota (Johnson and Mattern, 1968). Loffler and Busch (1982) correlated grain yield with harvest index and N harvest index of hard red spring wheat varieties, but GPC was negatively correlated with harvest index, and not significantly correlated with N harvest index.

Avivi (1978) identified a gene associated with high GPC in wild emmer wheat (*Triticum turgidum* spp. *dicoccoides).* Joppa and Cantrell (1990) substituted chromosomes from the wild emmer wheat into the durum wheat cultivar Langdon, producing high GPC lines. A genomic region was mapped as a QTL in a recombinant inbred line of this cultivar (Joppa et al., 1997) and then mapped as a single Mendelian locus designated as DIC *Gpc-B1* (Olmos et al., 2003). Introgression of this region into tetraploid and hexaploid wheat increased GPC (Joppa et al., 1997; Mesfin et al., 2000, Distelfeld et al., 2007).

Tabbita et al. (2017) reviewed 25 studies conducted over 10 years characterizing the allelic variation of *Gpc-B1* and its effects on wheat yield and quality. Studies were conducted over a globally diverse range of wheat genetic backgrounds and environments. A few studies linked *Gpc-B1* related increases in GPC to accelerated leaf senescence (Uauy et al., 2006; Carter et al., 2012) and more efficient N remobilization from leaves (Kade et al., 2005). Yet, the surveyed papers generally lacked examination of how genotypes with *Gpc-B1* respond to a wide range of N supply. Moll et al. (1982) defined a statistical evaluation of genotypic variation of nitrogen use efficiency (NUE) and its mathematical relationship to NUE components: N uptake efficiency (NUPE; crop N/N supply) and N utilization efficiency (NUTE; grain yield/crop N). Their analysis of corn genotypes suggested that variation in N utilization contributed to genetic differences at low N supply, whereas variation in N uptake efficiency was the major source of NUE genetic variation at high N supply. Dawson et al. (2008) suggested the possibility of developing wheat cultivars with high NUE in low N environments, when high remobilization of leaf N into grain will be critical. Therefore, the objectives of this research were to determine whether introgressing *Gpc-B1* into two commercial hard red spring wheat cultivars would improve yield, protein and NUE component responsiveness over a wide range of N supply, while reducing economically optimal N requirements.

MATERIALS AND METHODS

Experimental Conditions

This experiment was conducted over two years near Dusty in 2004 and Endicott Washington, U.S in 2005 under semi-arid, dryland conditions. The soil at Dusty, WA was an Onyx silt loam (coarse-silty mixed mesic Cumulic Haploxerolls) soil type, that received 378 mm of annual precipitation. The soil at Endicott, WA was an Athena silt loam (fine-silty mixed mesic Pachic Haploxerolls) that received 424 mm of precipitation. Genotypes were direct seeded into winter wheat stubble from fields yielding 4,200 and 3,600 kg ha^{-1} in the first and second site-years, respectively. Fall pre-fertilization soil sampling consisted of triplicate samples taken to 120 cm depths in each replicate block, and 30 cm depth increments were composited by replicate for determination of 1 M KCl exchangeable NH_4^+-N and NO_3^-N. Samples were taken with a tractor (John Deere 5425, Moline, IL)-mounted hydraulic probe (Giddings, Windsow, CO). Additional general soil fertility tests were performed on the 0-30 cm samples. Samples were stored at -15.6°C prior to inorganic N determination using flow injection autoanalysis (Quickchem 8000 Series FIA+ system, Lachat Instruments, Loveland, CO). Soil nitrate-N was measured at each depth, and soil ammonium-N was measured in the 0-30 cm samples. Net mineralization was estimated as only 17 kg N ha^{-1} following winter wheat stubble, and when added to the residual mineral N resulted in estimated soil N supplies of 46 and 39 kg N ha^{-1} in the first and second site-years, respectively.

Plant Germplasm and DNA Marker Analyses

Recurrent parents included the hard red spring wheat cultivars Scarlet (Kidwell et al., 1999), which was developed for the semi-arid region of Eastern Washington and Tara 2002, herein referred to as Tara (Kidwell et al., 2002), which was released for production in the high rainfall regions of the PNW. The donor parents were hard red spring wheat cultivar Glupro and ND683 from North Dakota (Mesfin et al., 1999; Khan et al., 2000). The high GPC region was incorporated into Scarlet and Tara using DNA markers to select for the presence of the region (Carter et al., 2012). At the time, Scarlet was a high yielding hard red spring wheat cultivar in the production region (Burns, 2002), and Tara was released based on its improved yield potential and superior end-use quality. The goal was to recover lines nearly identical (near isolines) to Scarlet and Tara with the addition of the high GPC segment from Glupro. The HRS wheat cultivar Glupro was used as the donor parent for the DIC *Gpc-B1* allele. Isolines included three BC_5F_5 marker-assisted backcross (MAB)-derived genotypes with the DIC *Gpc-B1* allele and three with the recurrent parent allele at the *Gpc-B1* locus. The backcross introgression process using DNA marker analysis to assay for the presence of the DIC *Gpc-B1* was described by Carter et al. (2012). The eight genotypes evaluated in this study were Tara, 3512-26T, 3586-6G/T, 3512-1G, Scarlet, 1519-16S, 1553-25G, 1584-12G where crosses with *Gpc-B1* have the letter G behind the cultivar; T or S indicates a near isoline of Tara or Scarlet and G/T represents the heterogeneous population.

Experimental Design

A split-plot, randomized complete block field experiment with five fertilizer nitrogen (Nf) rates (0, 45, 90, 135, 179 kg N ha^{-1}) as whole plots randomized in four replicate blocks. Eight genotypes were randomized as subplots within each N rate main plot. A basal fall application of 45 kg urea-N ha^{-1} was topdressed over all N fertilized plots and the remaining urea N fertilizer was applied in spring at planting, 10 cm below the seed. Row spacing was 18.5 cm in plots with 2.1 m x 12.2 m dimensions. Spring wheat lines were planted in late March at a 5 cm depth at a seeding rate of 78 kg ha^{-1} using a no-till drill (Fabro Ltd., Swift Current, SK, Canada).

Sampling and Data Collection

Two, 1-m rows of plant material were hand-harvested at physiological maturity in early August. Grain was harvested a week later with a small-plot combine (Wintersteiger Inc., Salt Lake, UT, USA), After collection, samples were dried at 65°C, heads were threshed and the grain was dried, weighed, and ground with a Udy mill (Udy Corp., Fort Collins, CO) to <0.5 mm. The stover was ground <2 mm Wiley mill (Thomas Scientific, Swedesboro, NJ) for nitrogen analysis. Plant samples were evaluated for nitrogen, sulfur and carbon with the above ground biomass and grain analyzed separately using a dry combustion analyzer (Leco Corp., St. Joseph, MI, USA). The GPC was calculated as GPC = grain N (g/100g) * 5.7.

Data Analysis

All data were subjected to analysis of variance using PROC MIXED procedure to compare means of the dependent variables in this study (SAS Institute Inc., 2013).

Replicate data of yield response to total N supply in individual site years were best fitted to the Mitscherlich growth factor response model using Sigmaplot (Systat Software, Inc., San Jose, CA). The Mitscherlich yield response to total N supply model (Pan et al., 2016) is defined as:

$$Y = A \times (1 - 10^{-c(X)}) \quad (1)$$

Where: Y = Gw, grain yield; X = Ns, N supply; A = maximum yield; c = efficiency constant.

Grain protein concentration (GPC), grain N yield, and above-ground crop N responses to N supply were all best-fitted with quadratic equations:

$$Y = a + b X + c X^2 \quad (2)$$

Total N supply estimated as described below (Huggins and Pan, 1993):

$$\begin{aligned} &\text{Total N supply (Ns)} \\ &= (\text{pre} - \text{plant, root zone inorganic soil N}) \\ &\quad + [\text{estimated net mineralized N (Koenig, 2005)}] \\ &\quad + (\text{fertilizer N}). \end{aligned} \quad (3)$$

The regression analyses for the Mitscherlich-modeled yield and the quadratic-modeled crop N responses included virtual observations of zero yield and zero crop N at zero N supply, added for each genotype x N supply block replicate.

N use efficiency, grain N harvest efficiency and their components were defined (Moll et al., 1982) using grain weight (Gw), above-ground crop N uptake (Nt), and grain N (Ng) as the following ratios:

N use efficiency (NUE) = Gw/Ns
N uptake efficiency (NUPE) = Nt/Ns
N utilization efficiency (NUTE) = Gw/Nt
Nitrogen harvest index (NHI) = Ng/Nt
Nitrogen harvest efficiency (NHE) = Ng/Ns

where:

$$Gw/Ns = (N_t/Ns) \times (Gw/Nt) = (Nt/Ns) \times (Gw/Ng) \times (Ng/Nt), \text{ and} \quad (4)$$

$$Ng/Ns = (Nt/Ns) \times (Ng/Nt) \quad (5)$$

These use efficiencies and components were statistically analyzed for main effects of genotype, N rate, year, and genotype × N rate.

Economic Optimization of N Inputs

Mitscherlich equations (Eq. 1) identified c and A values for each genotype's response to N supply in each year. These response models were then used with a fixed N and grain prices to obtain initial estimates of economically optimal N rates (EONR), supply (EONS), yield (EOY) and the corresponding unit N requirement (UNR) according to Fiez et al. (1995) as

$$UNR = (EONS/0.01) \times EOY \quad (6)$$

with no initial consideration of market valuation of protein. Economic optimal nitrogen rates (EONR) and total nitrogen supplies (EONS) required to achieve economic optimal grain yields (EOY) were determined by plotting a constant value (i.e. current market prices) of fertilizer N inputs (X$) at US $1.03 (kg Nf) $^{-1}$ vs. wheat grain (Y$) at $0.23 (kg grain) $^{-1}$ where dY$/dX$ = 0.23/1.03. This current market price was set as the base grain price for wheat at 140 g protein kg^{-1}, which is a typical target GPC for U.S. hard red spring wheat. Net revenue is defined here as revenue over Ns cost at the optimum. Price discounts for low protein wheat were then applied to determine the adjusted economic value of grain produced at the initial EONS. Since none of the genotypes achieved this target GPC at EONS the grain prices were then adjusted with discounts, $0.009 kg^{-1} subtracted from the base price for each 2.5 g protein kg^{-1} below 140 g protein kg^{-1}. The net revenue was then determined from the amount of additional N fertilizer required above the EONS to achieve the market target of 140 g protein kg^{-1}. Premiums ($0.009 kg^{-1}) were also added to the base wheat price (reported at 140 g protein kg^{-1}) for each 2.5 g above 140 g kg^{-1} protein achieved when N supply was increased above that required to achieve 140 g protein kg^{-1}.

Net revenue to farmers, assuming fertilizer N rate was the only varying management variable, was calculated as

$$\text{Net Revenue} = (Gw \times \text{protein based grain price}) - (Nf \times \text{N fertilizer price}). \quad (7)$$

RESULTS

Grain Yield, Grain N Yield, Crop N, and GPC Responses

Increased N supply significantly increased grain yield with a diminishing slope best represented by the Mitcherlich model, and it also increased GPC by inverse quadratic functions in both site-years (**Figures 1** and **2**; **Tables 1** and **S1**). The Mitscherlich efficiency coefficient "c", which describes the steepness of the approach to maximum "A" did not statistically vary among genotypes or by site-year (**Table 1**). Supplying fertilizer N up to an additional 179 kg N ha^{-1} enabled us to establish maximum grain yields not limited by N supply in both site-years, whereas excess N continued to increase GPC past the point of maximum yield. Modeled grain yield plateaus (A values) in the first site-year ranged from 2651to 2889 kg ha^{-1}, whereas yield plateaus in the second-site year were significantly lower based on pair-wise t tests, ranging from 2310 to 2497 kg ha^{-1} (**Figures 1** and **2**; **Table 1**). Supplying the lowest N rate input, 45 kg N ha^{-1}, increased yield compared to the no N fertilizer control, while only maintaining or decreasing GPC (**Figures 1** and **2**). The increase in GPC was steeper once optimal grain yield was achieved, as GPC levels of 16 to 17 g (100 g)$^{-1}$ were reached at the highest N supply (**Figures 1** and **2**).

Analysis of variance revealed site-year, N rate and genotype were significant for all crop parameters except crop N, which was not different across genotypes (**Table S2**). No significant interactions were detected between N rate and genotype. Backcross derived near isolines with the *Gpc-B1* region did not have significantly higher GPC averages than their recurrent parent at the economically optimal N supply and yield when the grain protein premium was not considered (**Table 2**).

Crop N and Grain N Yields

Crop and grain N responses to increasing N supply were best fitted by quadratic response functions (**Figures 1** and **2**; **Table S1**). Crop N functions were near linear, as illustrated by larger, linear coefficients that were more frequently significant than the smaller, more frequently non-significant quadratic coefficients (**Table S1**). In comparison, grain N accumulated with lower slopes (**Figures 1** and **2**) over the range of N rates, illustrating greater proportion of crop N stored in the straw with increasing N supply.

Economic Optimization

Mitscherlich response functions were initially used with fixed N and grain prices to estimate economically optimal N rates (EONR), supply (EONS), yield (EOY), and the corresponding unit N requirement (UNR), all initially ignoring market

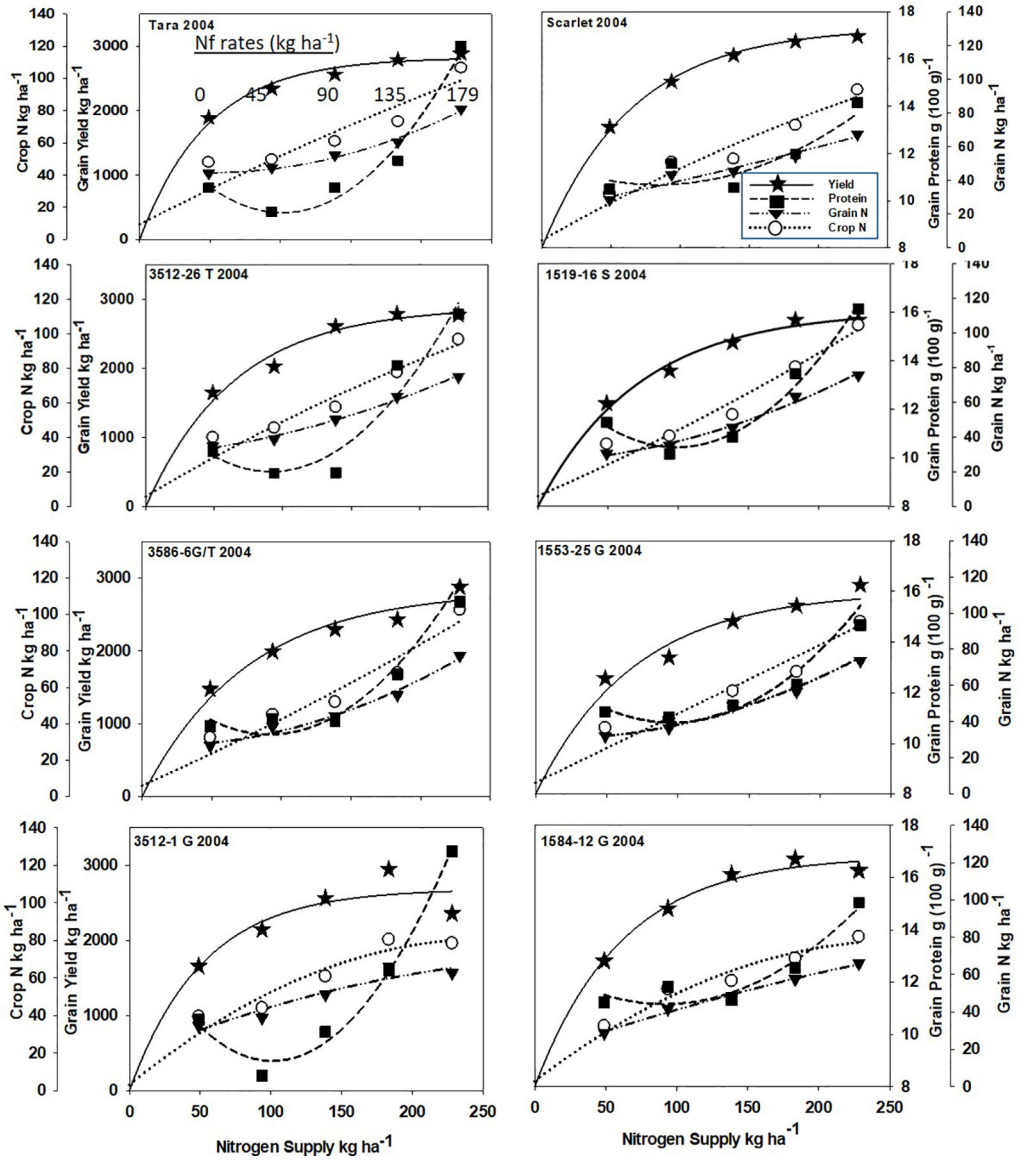

FIGURE 1 | Grain yield, grain N concentration, grain N yield, and crop N responses to increasing N supply at Dusty WA in 2004 of HRS cultivar Tara and its derivatives 3512-26T, 3586-6G/T, 3512-1G; HRS cultivar Scarlet and its derivatives 1519-16S, 519-16S, 1553-26G and 1584-12G. Symbols represent means of 4 N rate replicates. Regression coefficients of responses modeled on entire datasets of each dependent variable are presented in **Tables 1** and **S1**.

valuation of protein (**Table 1**). While EOYs were lower in the second vs. first site-year, the EONS values were only slightly lower, thus resulting in higher UNRs in the second site-year. Derivatives of Tara and Scarlet generally exhibited higher EONS and UNR than their parents in both years. Nevertheless, 3586-6 G/T was an exception in the second site-year, exhibiting lower EONS and UNR than Tara.

Since high protein goals were not achieved with the initial EONS that was estimated without regard to protein premiums or discounts, we used the Mitscherlich yield and quadratic GPC functions to assess the net revenues obtained with additional N fertilizer additions beyond the initial EONS that elevated both yield and GPC (**Table 2**). While the higher N fertilizer investment per unit yield did not pay off for Scarlet in the first site-year due to a more gradual increase in GPC beyond the EONS required to achieve the initial EOY, overall net revenues of \$25 and \$ 37 ha^{-1} were obtained with increased Ns to achieve 14 and 15 g protein (100 g)$^{-1}$ for Scarlet and its derivatives averaged over both site-years (**Table 2**). In contrast, higher net revenues of \$39 and \$54 ha^{-1} were obtained as Ns was increased to achieve 14 and 15 g protein (100 g) $^{-1}$ for Tara and its derivatives averaged over both site-years. Comparing N supply required to achieve

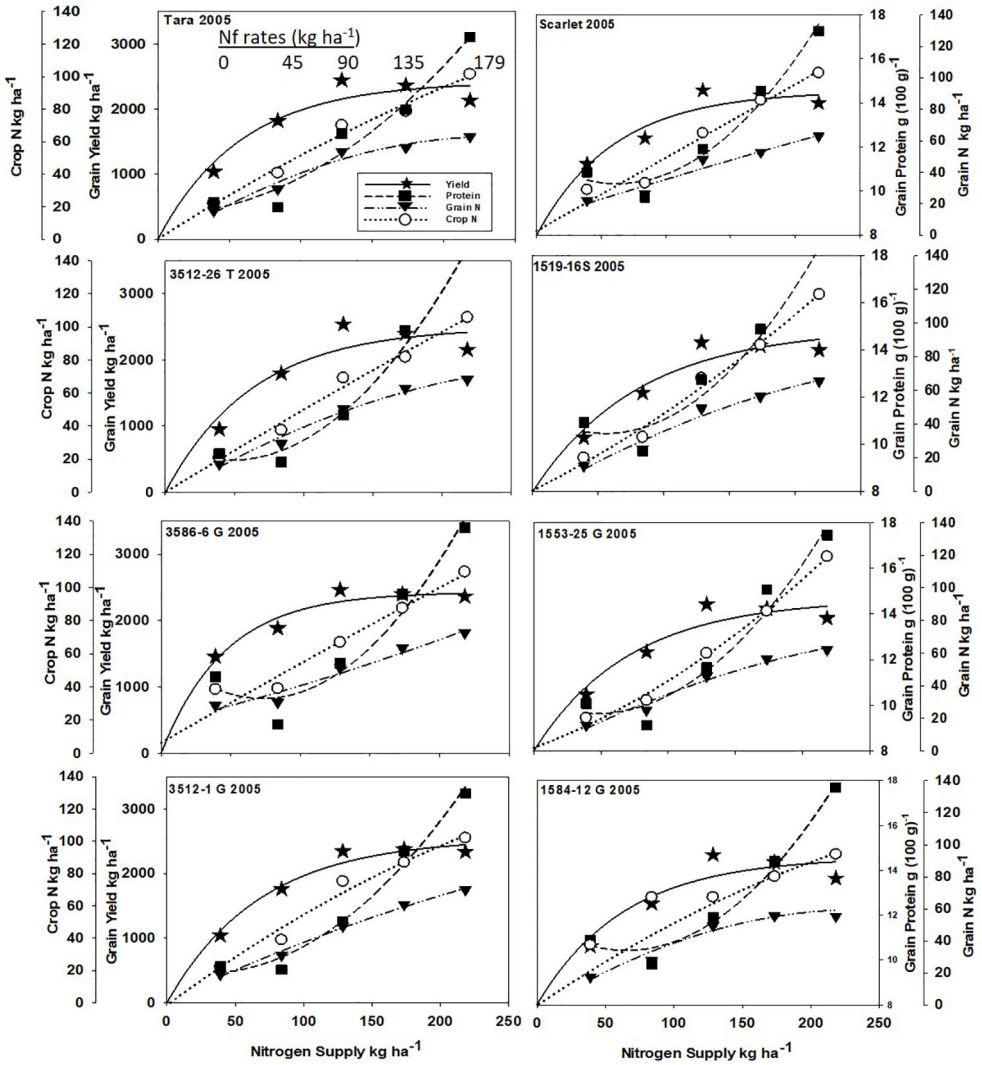

FIGURE 2 | Grain yield, grain N concentration, grain N yield, and crop N responses to increasing N supply at Endicott WA in 2005 of HRS cultivar Tara and its derivatives 3512-26T, 3586-6G/T, and 3512-1G; HRS cultivar Scarlet and its derivatives 1519-16S, 1519-16S, 1553-26G and 1584-12G. Symbols represent means of 4 N rate replicates of each dependent variable. Regression coefficients of responses modeled on entire datasets are presented in **Tables 1** and **S1**.

these protein goals of the base cultivars in the high yielding first site-year, Scarlet required 315 and 339 kg Ns ha^{-1}, while Tara only required 209 and 223 kg Ns ha^{-1} (**Table 2**). Similarly in the lower yielding second site-year, Scarlet required 172 and 186 kg Ns ha^{-1}, while Tara only required 157 and 172 kg Ns ha^{-1} to achieve protein goals of 14 and 15 g protein (100 g)$^{-1}$, respectively.

NUE and Components

Analysis of variance revealed site-year and N rate effects were significant for NUE, NUPE, and NUTE, but genotype only affected NUE and NHI (**Table S2**). No significant interactions were detected between N rate and genotype for NUE and its components. The interactions between genotype and N rate were largely non-significant, so main effects of genotype (**Table 3**) and N rate (**Table 4**) are presented. Tara exhibited higher NUE and NHE than its derivatives in the first site-year due to higher N uptake efficiency rather than higher NHI (**Table 3**). Yet in all other comparisons, the advanced lines were not significantly different than either parents for both site-years (**Table 3**). One exception was 3586-6 G/T in the second site-year was higher than its parent Tara in NUE and grain N accumulation efficiency, due to higher N uptake efficiency.

The NUE averaged over all genotypes decreased with increasing applied N for both site-years, attributable to decreases in both NUPE and NUTE (**Table 4**). Similarly, NHE also decreased with increasing N rate, most attributable to decreased NUPE, and to lesser extent, reduced NHI (**Table 4**).

TABLE 1 | Mitscherlich model correlation coefficients, A and c parameters with their standard errors for yield response to N supply of all genotypes, shown in **Figures 1** and **2**.

Genotype	r^2	A	*SD*	c	*SD*	EONS	EOY	EONR	UNR
A. Dusty, 2004									
1519-16 S	0.94	2827	146	0.0060	0.0009	157	2503	108	6.26
1553-25 G	0.89	2801	198	0.0062	0.0013	153	2487	104	6.17
1584-12 G	0.90	2651	147	0.0071	0.0013	139	2377	90	5.84
Scarlet	0.91	2802	153	0.0067	0.0012	147	2511	98	5.85
3512-1 G	0.76	2688	220	0.0084	0.0026	127	2456	78	5.16
3512-26 T	0.91	2889	167	0.0067	0.0012	149	2598	100	5.73
3586-6G/T	0.89	2829	211	0.0058	0.0012	160	2494	111	6.40
Tara	0.91	2824	121	0.0090	0.0015	124	2608	75	4.76
Site-year means		2789	171	0.0070	0.0014	143	2510	104	5.71
B. Endicott, 2005									
1519-16 S	0.92	2416	175	0.0054	0.0010	153	2056	114	7.45
1553-25 G	0.92	2326	151	0.0061	0.0011	141	2007	102	7.05
1584-12 G	0.91	2310	130	0.0068	0.0013	133	2024	94	6.59
Scarlet	0.84	2289	176	0.0073	0.0018	128	2022	89	6.33
3512-1 G	0.95	2548	121	0.0064	0.0009	144	2244	105	6.43
3512-26 T	0.89	2497	168	0.0069	0.0014	137	2216	98	6.20
3586-6G/T	0.90	2430	116	0.0095	0.0017	113	2225	74	5.08
Tara	0.92	2423	124	0.0075	0.0013	129	2164	90	5.98
Site-year means		2405	145	0.0070	0.0013	134	2126	95	6.30

Economic optimal N supply (EONS), yield (EOY), N rate (EONR), and Unit N requirement (UNR) were estimated initially using a base wheat price of $0.23/kg grain without protein discounts/premiums.

TABLE 2 | Grain protein and net revenue generated from EONS and yields described in **Table 1**, and higher EONS required to generate higher net revenues calculated when meeting 14 and 15 g (100 g)$^{-1}$ protein goals as protein price premiums are accounted.

Genotype	Varying Protein Levels at EONS				14 g (100 g)$^{-1}$ Protein Level			15 g (100 g)$^{-1}$ Protein Level		
	EONS	Yield	Protein	Revenue	EONS	Yield	Revenue	EONS	Yield	Revenue
	kg/ha		g (100 g)$^{-1}$	$/ha	kg/ha		$/ha	kg/ha		$/ha
A. Dusty, 2004										
1519-16 S	157	2503	12.8	438	175	2576	468	188	2618	488
1553-25 G	153	2487	12.6	432	182	2593	465	198	2635	483
1584-12 G	139	2377	11.7	403	208	2563	431	228	2587	441
Scarlet	147	2511	10.3	391	315	2780	375	339	2787	378
3512-1 G	127	2456	10.9	414	206	2638	451	221	2650	463
3512-26 T	149	2598	12.8	465	174	2691	496	190	2735	514
3586-6G/T	160	2494	11.4	399	210	2658	452	224	2688	469
Tara	124	2608	10.8	447	209	2787	483	223	2797	496
B. Endicott, 2005										
1519-16 S	153	2056	13.4	344	163	2096	360	177	2149	377
1553-25 G	141	2007	12.6	330	163	2089	358	176	2129	374
1584-12 G	133	2024	11.6	323	179	2170	360	193	2198	372
Scarlet	128	2022	11.7	330	172	2161	365	186	2188	378
3512-1 G	144	2244	11.8	363	185	2381	403	200	2415	417
3512-26 T	137	2216	11.7	361	174	2339	405	186	2368	420
3586-6G/T	113	2225	11.4	382	160	2357	422	173	2375	435
Tara	129	2164	12.4	373	157	2262	403	172	2299	418

Tradeoffs Between Grain Protein Production and Unused Reactive Soil N

Unused reactive soil N left behind after harvest was calculated as the difference between N supply and crop N accumulation. A linear relationship between grain protein harvested and unused reactive N was observed in both site-years, without significant N supply x site-year interaction (**Figure 3**). Unused N increased by 0.41 kg N ha^{-1} per 1 kg protein ha^{-1} increase.

TABLE 3 | Genotypic means averaged over all N rates for N utilization (NUTE), N uptake (NUPE), nitrogen use efficiency (NUE), grain N harvest efficiency (NHE), and N harvest index (NHI).

Genotypes	NUTE	NUPE	NUE	NHE	NHI
A. Dusty, 2004					
1519-16 S	39.4A	0.49B	18.94BC	0.40B	0.82BC
1553-25 G	40.5A	0.48B	19.37BC	0.41B	0.84AB
1584-12 G	40.0A	0.47B	18.77C	0.39B	0.85A
Scarlet	40.9A	0.48B	19.92BC	0.40B	0.81C
3512-26 T	39.9A	0.51AB	20.26B	0.43AB	0.84AB
3586-6 G/T	39.4A	0.47B	18.75C	0.39B	0.82BC
3512-1 G	40.3A	0.50AB	20.32B	0.42B	0.84AB
Tara	40.0A	0.56A	21.96A	0.47A	0.84AB
B. Endicott, 2005					
1519-16 S	33.1C	0.49B	15.36C	0.34B	0.71B
1553-25 G	35.8AB	0.48B	16.09C	0.33B	0.73AB
1584-12 G	33.4BC	0.49B	16.08BC	0.36B	0.73AB
Scarlet	34.7ABC	0.52AB	17.56BC	0.37B	0.72AB
3512-26 T	36.1A	0.50B	17.85BC	0.37B	0.75A
3586-6 G/T	35.1ABC	0.60A	20.71A	0.44A	0.74AB
3512-1 G	35.4ABC	0.52AB	18.08AB	0.37B	0.72AB
Tara	36.0AB	0.50B	18.14AB	0.37B	0.74AB

Same letters following means represent non-significant differences within a site-year according to the Least Significant Difference test (alpha = 0.05).

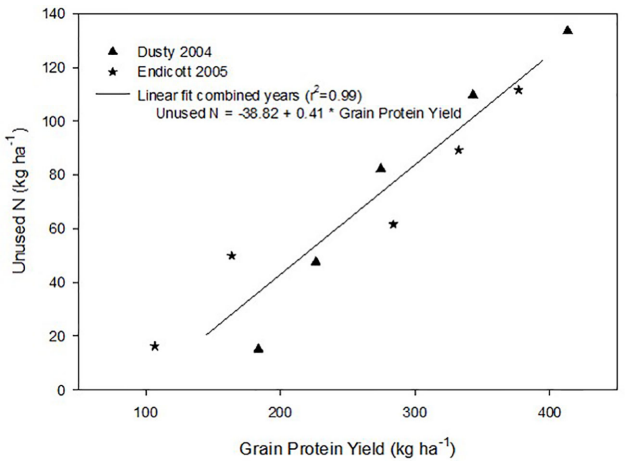

FIGURE 3 | Linear relationship between the amount of unused soil N left behind after harvest and the grain protein yield produced at each N supply over two years. Mean data averaged over all genotypes and replicates in both site years are linearly regressed.

TABLE 4 | N rate means averaged over all genotypes for N utilization (NUTE), N uptake (NUPE), nitrogen use efficiency (NUE), grain N harvest efficiency (NHE), and N harvest index (NHI).

N Rate (kg/ha)	NUTE	NUPE	NUE	NHE	NHI
A. Dusty, 2004					
0	44.4A	0.76A	32.5A	0.66A	0.87A
45	45.5A	0.49B	22.0B	0.42B	0.87A
90	44.3A	0.41C	17.7C	0.35C	0.86A
135	37.0B	0.40C	14.6D	0.32C	0.81B
179	28.7C	0.42C	11.9E	0.32C	0.77C
B. Endicott, 2005					
0	43.3B	0.62A	26.3A	0.48A	0.78A
45	46.6A	0.43C	19.6B	0.33C	0.78A
90	36.9C	0.52B	18.2B	0.38B	0.74B
135	29.2D	0.48BC	13.2C	0.334C	0.71C
179	21.2E	0.49BC	9.9D	0.30C	0.64D

Same letters following means represent non-significant differences within a site-year according to the Least Significant Difference test (alpha = 0.05).

DISCUSSION

Re-cropping hard red spring wheat after winter wheat replacing fallow is a strategy for crop intensification for diversifying the system and markets (Pan et al., 2017). However, this shortens the time of soil N mineralization that would otherwise add greater available mineral N during fallow. For example, diminished fertilizer N responses of canola were earlier observed following fallow in this region (Pan et al., 2016). Steeper initial yield responses to N fertilizer inputs were observed herein with recropped HRS, with diminishing returns with higher N inputs represented by the Mitscherlich model (**Figures 1** and **2**). The modest maximum grain yields (A values) were due to the low soil water and in-season precipitation following winter wheat compared to fallow in this transitional agroecological zone.

Before a season, farmers can impact the protein level of their wheat by genotype selection and management of nitrogen. Yield and nitrogen both impact profit, so an economically motivated farmer will apply N at rates that optimizes both yield and protein. Baker et al. (2004) found that it is not always profitable to use 14 g (100g)$^{-1}$ as the base protein goal for fertilization. Depending upon the wheat price premium/discount and the cost of N, in some scenarios profit was greater with higher yield and lower than base protein levels.

The price of N fertilizer and the protein premium/discount were held constant at current levels to assess the economic (**Table 1**) and ecosystem (**Figure 3**) impacts from varying the N supply. The GPC ranged from 10.3 to 13.4 g (100g)$^{-1}$ at solely yield-based EOYs (**Table 2**). The economic analysis that accounted for GPC premiums and discounts revealed greater economic returns from elevating N supply above that required to achieve the yield-based optimum (**Table 2**). Only Scarlet in the first site-year showed lower economic returns (**Table 2**) from raising the N supply to >300 kg N ha^{-1} necessary to achieve GPC of 14 g (100 g)$^{-1}$ (**Figure 1**).

The *Gpc-B1* introgression has been associated with earlier flag leaf senescence (Uauy et al., 2006) and greater N remobilization, along with higher N harvest index (Kade et al., 2005) that promotes higher GPC. However, as Carter et al. (2012) suggested, physiological benefit may have limited potential for improving GPC where spring wheat grain-filling periods are already shortened by environmental conditions in the inland Pacific Northwest.

Brevis and Dubcovsky (2010) demonstrated that *Gpc-B1* introgression increased protein yield in common and durum

wheat. In the present study, the physiological benefit was not observed at any level of N supply, from deficient to excessive. Varying N supply with the addition of fertilizer N within the two site-years had greater impact on protein, yield, N use and its components, and economic returns than introgression of the *Gpc-B1* allele in these two hard red spring wheat cultivars. However, advanced Scarlet lines generally had higher GPC than advanced Tara lines at EONS determined on base yield price only (**Table 2**).

Maximizing protein-based economic returns with increased N supply can incur an environmental cost, demonstrated by decreased N use and its components with increased N supply (**Table 4**), as previously observed (Huggins and Pan, 1993). Application of fertilizer N required to produce >400 kg protein ha^{-1} also left >130 kg unused N ha^{-1} (**Figure 3**), representing increased reactive N remaining in the system that has potential for negatively impacting the environment. The presence of greater reactive N requires an N management accounting and reduction of fertilizer N inputs in the next crop cycle to avoid reactive N losses to the environment (Schlesinger, 2009; Snyder et al., 2014). Field-performance and grain-quality based selective breeding lead to the release of Tara (Kidwell et al., 2002) that improved the economic returns on N investments compared to the older Scarlet cultivar. These results stress the importance of further developing genotypes with increased yield and GPC potential. While the *Gpc-B1* introgression did not further improve economically optimal yield and GPC of these hard red spring cultivars grown under these conditions, future research should further investigate new genotype × environment × soil interactions for improving N use efficiency, grain quality, and economic returns, while reducing reactive soil N.

DATA AVAILABILITY STATEMENT

The datasets analyzed in this article are not publicly available. Requests to access the datasets should be directed to WP, wlpan@wsu.edu.

AUTHOR CONTRIBUTIONS

WP prepared the initial journal manuscript, supervised data collection, analysis, and interpretation. KK developed the wheat genotypes, supervised field experimental design and maintenance, and manuscript editing. VM conducted economic analysis and manuscript editing. RB conducted experimental layout, soil and plant sample collection, Mitscherlich modelling and analysis of variance statistical evaluation. MA, graduate research assistant, organized literature review, initial methods description and draft dataset.

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SUPPLEMENTARY MATERIAL

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Winter Wheat Yield Response to Plant Density as a Function of Yield Environment and Tillering Potential: A Review and Field Studies

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Wheat (*Triticum aestivum* L.) grain yield response to plant density is inconsistent, and the mechanisms driving this response are unclear. A better understanding of the factors governing this relationship could improve plant density recommendations according to specific environmental and genetics characteristics. Therefore, the aims of this paper were to: i) execute a synthesis-analysis of existing literature related to yield-plant density relationship to provide an indication of the need for different agronomic optimum plant density (AOPD) in different yield environments (YEs), and ii) explore a data set of field research studies conducted in Kansas (USA) on yield response to plant density to determine the AOPD at different YEs, evaluate the effect of tillering potential (TP) on the AOPD, and explain changes in AOPD *via* variations in wheat yield components. Major findings of this study are: i) the synthesis-analysis portrayed new insights of differences in AOPD at varying YEs, reducing the AOPD as the attainable yield increases (with AOPD moving from 397 pl m^{-2} for the low YE to 191 pl m^{-2} for the high YE); ii) the field dataset confirmed the trend observed in the synthesis-analysis but expanded on the physiological mechanisms underpinning the yield response to plant density for wheat, mainly highlighting the following points: a) high TP reduces the AOPD mainly in high and low YEs, b) at canopy-scale, both final number of heads and kernels per square meter were the main factors improving yield response to plant density under high TP, c) under varying YEs, at per-plant-scale, a compensation between heads per plant and kernels per head was the main factor contributing to yield with different TP.

Keywords: wheat, yield environment, tillering potential, yield components, synthesis-analysis

Abbreviations: AOPD, agronomic optimum plant density; PD, plant density; TP, tillering potential; YE, yield environment.

INTRODUCTION

Wheat is one of the most important cereals in human diets, increasing its relevancy as the global population is projected to increase by 30% in 2050 (United Nations, 2019). Thus, a continuous increase in wheat demand is expected, which will be mainly satisfied by improving crop yield per unit area (Neumann et al., 2010) as expansion in cultivated land is unlikely due to negative social and environmental impacts (Foley et al., 2011). At a global scale, the wheat yield gap (deviation of actual from potential yield) was estimated at 36% (Neumann et al., 2010), but this yield gap is much larger in regions such as the U.S. southern Great Plains (Patrignani et al., 2014; Lollato et al., 2017). Among the most relevant management factors for improving wheat yields and closing the yield gap is the use of the optimum seeding rate for an appropriate plant density (PD) (Hochman and Horan, 2018; Jaenisch et al., 2019; Lollato et al., 2019).

Below-optimum seeding rates may reduce resource use efficiency, yield, and final profit (Whaley et al., 2000), depending on the level of resource availability (Lollato et al., 2019; Fischer et al., 2019). Meanwhile, above-optimum seeding rates increase cost of production and might potentially decrease yield by increasing disease pressure, insects, and lodging (Lloveras et al., 2004; Laghari et al., 2011). Consequently, defining the agronomic optimum plant density (AOPD), which is the minimum number of plants per unit area required to maximize yield, is crucial for future improvements in wheat yield. Nonetheless, one of the main challenges of determining the AOPD is that diverse yield to PD relationships have been reported in the scientific literature for wheat, which range from linear, quadratic, quadratic-plateau, and lack of response (Whaley et al., 2000; Lloveras et al., 2004; Fischer et al., 2019). Thus, it is necessary to understand yield to PD response models *via* synthesizing studies published in the scientific literature and analyzing a comprehensive field research data set.

The interplay between genotype × environment × management (G × E × M) regulates wheat plasticity and attainable yield (Geleta et al., 2002; Valério et al., 2013), rendering AOPD dependent on yield environment (YE). In this line, recent studies in soybean [*Glycine max*(L.) Merr.] (Corassa et al., 2018; Carciochi et al., 2019), canola (*Brassica napus* L. "Canola") (Assefa et al., 2018b), and maize (*Zea mays* L.) (Assefa et al., 2016; Assefa et al., 2018a) classified the data on different YE levels based on its average yield and determined the AOPD at each YE. Therefore, as was observed for canola and soybean (e.g., crops that have compensation mechanisms comparable to wheat), the AOPD in wheat could change across YEs with a greater requirement of plants to attain the maximum yield at the low YE. However, this hypothesis is yet to be tested.

Wheat yield components have a strong compensation capacity depending on the availability of resources (Whaley et al., 2000; Lloveras et al., 2004). However, this compensatory mechanism could differ across wheat genotypes (Dahlke et al., 1993; Lloveras et al., 2004). As an example, some wheat genotypes have greater tillering potential (TP) than others (Valério et al., 2013), so if the number of plants is below the carrying capacity of resources available, the number of tillers might increase to compensate the lack of plants. Thus, it is possible that the AOPD could depend on the genotype's TP within each YE. Other yield components such as kernel number and weight are modified with changes in the PD. Thus, increases in PD usually increase heads and kernel number per unit area, and decrease kernel weight and kernels per head (Geleta et al., 2002; Lloveras et al., 2004; Valério et al., 2013). However, the magnitude of these changes could depend on the availability of resources at each YE, so the variation in yield components at different YEs deserves to be studied.

The overarching objective of this study was to quantify whether the AOPD for winter wheat depended on YE and genotype TP. We used two levels of organization based on the type of data utilized in the analyses to attain this goal: i) a synthesis-analysis of existing data related to yield-PD relationship with the specific objective of providing an indication of the need for different AOPD at each YE, and ii) an analysis of a comprehensive dataset of field research studies on winter wheat yield to PD to determine the AOPD at different YEs, evaluate the effect of TP on the AOPD, and explain changes in AOPD *via* modifications in wheat yield components.

MATERIAL AND METHODS

Synthesis-Analysis

A literature review was conducted to retrieve data from published scientific research using Web of Science™ and Google Scholar. The criteria for inclusion of a paper in the database were: i) the study must have been performed with winter wheat (i.e., no spring wheat or durum wheat (*Triticum durum* L.) studies were included); ii) the study must have reported both PD (i.e., measured final number of plants per area, not only reporting seeding rates) and yield, and iii) the study must have been conducted in North America [United States (US) and Canada] and published during the period from 1980 to 2019. From all the papers screened in the research literature (**Table 1**), a database containing information on citation (author, year of publication), location, site-years, number of observations reported, average reported PD and yield (minimum and maximum) were recorded from each study. Whenever grain yield and PD were

TABLE 1 | Characterization of studies included in the synthesis analysis. Location is shown as state/province initial followed by country initial.

Citation	No. Sites, location	Pest control (W/I/D)	Site-years	Obs.	Plant density	Yield
					(plants m^{-2})	(Mg ha^{-1})
Joseph et al. (1985)	1, VA/USA	Y/Y/Y	3	24	364 (148, 872)	6.7 (5, 8.1)
McLeod et al. (1992)	2, SK/CAN	Y/Y/Y	7	20	120 (70, 170)	1.2 (0.6, 1.9)
Mian and Nafziger (1992)	1, IL/USA	NA	2	6	169 (121, 250)	3.6 (2.9, 4.5)
McLeod et al. (1996)	2, SK/CAN	Y/Y/NA	6	22	97 (54, 190)	1.3 (0.3, 2.6)
Roberts et al. (2001)	2, OK/USA	Y/NA/NA	2	6	299 (186, 444)	2.1 (1.6, 2.7)
Schaafsma and Tamburic-Ilincic (2005)	1, ON/CAN	NA/NA/Y*	2	3	613 (343, 832)	2.1 (2, 2.3)
McKenzie et al. (2007)	3, AB/CAN	Y/NA/NA	9	5	191 (154, 238)	6.4 (6.2, 6.4)
Childress et al. (2010)	5, VA/USA	NA/NA/Y	6	5	355 (237, 495)	4.6 (4.4, 4.7)
Beres et al. (2016)	9, AB, MB, SK/CAN	Y/Y*/Y*	26	22	153 (40, 340)	4.3 (1.6, 8.1)
Bhatta et al. (2017)	1, NE/USA	NA	2	6	233 (122, 365)	3.9 (2.1, 5.7)

**As part of the study treatment design.*

USA, United States of America; CAN, Canada; VA, Virginia; SK, Saskatchewan; IL, Illinois; OK, Oklahoma; ON, Ontario; AB, Alberta; MB, Manitoba; NE, Nebraska; W, weeds; I, insects; D, diseases; Y, yes; NA, not available.

Plant density and yield are shown as median (minimum, maximum).

reported in figure format, data were extracted using the WebPlotDigitizer software version 4.2.

To evaluate the response of winter wheat grain yield to PD across all studies, four different models were fit to the 1st, 50th, and 99th quantiles of the dataset using the functions *rq* and *nlrq*, for linear and non-linear regression respectively, from the package *quantreg* (Koenker, 2019) in R (R Core Team, 2019). These quantiles were chosen to represent low, medium, and high yielding conditions, respectively. Models tested were the linear, quadratic, linear-plateau and quadratic-plateau. For each quantile, the model with the lowest Akaike Information Criteria (AIC) was used to estimate AOPD.

Field Research Studies

Nine field experiments resulting from the combination of sites and years were conducted during the winter wheat growing seasons of 2015-16, 2016-17, and 2017-18 in Kansas, USA. All experiments were sown at the optimum sowing window for each location to avoid the confounding and interacting effects of sowing date and wheat seeding rate (Staggenborg et al., 2003). Treatment structure was a two-way complete factorial combination of seeding rate by winter wheat genotype, and trials were established in a randomized complete block design with four blocks. Each field experiment consisted of five to seven winter wheat genotypes sown at five target seeding rates (150, 235, 321, 408, 494 seeds m^{-2}) (**Table 2**). Five commercial genotypes were consistent across all experiments (i.e., "Joe", "KanMark", "Larry", "Tanaka" and "Zenda"), and the other two commercial genotypes, when applicable, varied with site-year and included "1863", "Ag Icon, "Bob Dole", "Everest", and "AM Cartwright". Each experimental unit was 10 m long by seven rows (0.19-m spaced) except for two site-years (Hutchinson 2015–2016 and Hays 2017–2018) that consisted of six rows (0.25-m spaced).

While row spacing and tillage practices varied with site-year (**Table 2**), crop husbandry was otherwise consistent across locations. Weeds were controlled during the fall prior to sowing and early in the spring using commercially available herbicides. Composite soil samples consisting of 15 individual soil cores were collected prior to sowing at the 0–0.15 and 0.15–0.6 m soil depth to characterize initial soil fertility and adjust N fertilizer rates (**Supplementary Table 1**). Soil analysis consisted of pH, buffer pH, ammonium, nitrate, Mehlich III P, K, Ca, Mg, Na, organic matter, cation exchange capacity, Cl, and sulfate-sulfur (Nathan and Gelderman, 2012). Diammonium phosphate (18-46-0) was applied in-furrow at sowing at a rate of 55 kg ha^{-1}. Nitrogen fertilizer was applied as urea (46-0-0) during early spring in rates sufficient to meet a yield goal of 4.7 Mg ha^{-1} following Kansas State University's recommendations that considered nitrate-N available in the 0–0.6 m profile, N derived from mineralization of organic matter in the 0–0.15 m, previous crop, and tillage practices (Leikam et al., 2003). Foliar fungicide (i.e., 85 g ha^{-1} as Picoxystrobin-Class 11 plus 34 g ha^{-1} as Cyproconazole-Class 3) and a non-ionic surfactant (1905 g ha^{-1}) was sprayed at heading (Zadoks GS 55) using a backpack sprayer with a CO_2 tank and a hand boom. The use of fungicide was justified to avoid the confounding effects of genetic resistance to different fungal diseases. Daily weather data was collected for each site year from both Climate Engine (Huntington et al., 2017) and monitoring stations from Kansas Mesonet (http://mesonet.k-state.edu/), including maximum and minimum daily temperature, precipitation, evapotranspiration, and incident solar radiation (**Supplementary Table 2**).

Measurements

Crop stand establishment was measured from one linear meter in two different places within each experimental unit approximately 20 to 30 days after sowing, and final stand on an area basis (plants m^{-2}) was calculated considering row spacing in each location. While we did not measure the stand after the winter to quantify winterkill, the studied growing seasons were not conducive to winterkill due to smooth transitions to colder temperatures, allowing the crop to acclimate and improve freeze tolerance (Bridger et al., 1994). Since the relationship between achieved and target plant densities can vary between YEs and serve as a feedback to the overall observed yield level, we evaluated the achieved/target stand ratio within each YE. At physiological maturity (Zadoks GS94), shoot biomass samples were collected from a linear meter per experimental unit. Samples were dried in an air-forced dryer at 60 °C for approximately one week. These samples were used to measure the yield components: i) shoot biomass, ii) harvest index (grain yield to total aboveground biomass ratio), iii) heads per linear meter (later transformed into heads m^{-2} using the row spacing), iv) kernels $head^{-1}$, and v) thousand-kernel weight. Grain yield was measured by combine-harvesting the entire experimental unit. Grain moisture content was measured at harvest time and yields corrected for 130 g kg^{-1} moisture content.

Statistical Analysis

Different site-years were grouped into low, medium, and high YEs (**Table 2**) using a fuzzy k-means clustering algorithm across all raw grain yield data points (n = 1160), implemented with the function *fanny* (utilizing Euclidean distance as the dissimilarity metric) from the package *cluster* (Maechler et al., 2019) in R. The final number of groups (i.e. three) was chosen because it most parsimoniously minimized intra-group variance while maximizing inter-group variance. Final site-year association into a YE group was based on the majority (> 50%) YE membership of data points within a given site-year. The generated YEs are groups that represent a simplification of site-specific characteristics impacting grain yield.

Different genotypes were grouped as having low or high TPs. For that, first the complete dataset was filtered to include only the target seeding rate treatment level of 148 seeds m^{-2} (i.e., the lowest seeding rate which resulted in an average density of 133 plants m^{-2} and varied from 57 to 335, and therefore under which TP is most expressed). This first step ensured that the TP of the different varieties could be expressed due to the low PD. Then, the average number of heads per plant was calculated for each genotype as the number of heads m^{-2} measured in the stand count [c.a., 20 to 30 days after sowing (Mehring, 2016)], and this was used in a fuzzy k-means clustering algorithm in a similar manner as previously described to segregate high- versus low TP

TABLE 2 | Geographic coordinates, yield environment classification (YE), soil type, tillage practice (CT, conventional till; NT, no-till), genotypes, and sowing date (MM/DD/YYYY) for each location and winter wheat growing season evaluated in the nine field studies.

Havrest Year	Location	YE	Latitude (°)	Longitude (°)	Soil Type	Tillage	Genotypes	Sowing date
2016	Manhattan	Low	39.218	-96.591	Kahola silt loam (Fine-silty, mixed, superactive, mesic Cumulic Hapludolls)	NT	Everest, KanMark, 1863, Zenda, Larry, Tatanka, Joe	10/08/2015
2016	Hutchinson	Medium	37.931	-98.027	Ost loam (Fine-loamy, mixed, superactive, mesic Udic Argiustolls)	CT	Everest, KanMark, 1863, Zenda, Larry, Tatanka, Joe	10/07/2015
2017		High					KanMark, Zenda, Larry, Joe, Tatanka, Ag Icon, Bob Dole	10/13/2016
2018		Medium					KanMark, Zenda, Larry, Joe, Tatanka, Bob Dole, AM Cartwright	10/19/2017
2017	Belleville	Medium	39.815	-97.672	Crete silt loam (Fine, smectitic, mesic Pachic Udertic Argiustolls)	CT	KanMark, Zenda, Larry, Joe, Tatanka, Ag Icon, Bob Dole	10/03/2016
2018	Ashland Bottoms	Low	39.127	-96.635	Wymore silty clay loam (Fine, smectitic, mesic Aquertic Argiudolls)	CT	KanMark, Zenda, Larry, Joe, Tatanka, Bob Dole, AM Cartwright	10/06/2017
2018	Great Bend	High	38.364	-98.867	Taver loam (Fine, smectitic, mesic Udertic Argiustolls)	CT	KanMark, Zenda, Larry, Joe, Tatanka.	10/12/2017
2018	Leoti	Medium	38.285	-101.211	Richfield silt loam (Fine, smectitic, mesic Aridic Argiustolls)	NT	KanMark, Zenda, Larry, Joe, Tatanka	10/13/2017
2018	Hays	Low	38.856	-99.338	Harney silt loam (Fine, smectitic, mesic Typic Argiustolls)	CT	KanMark, Zenda, Larry, Joe, Tatanka, Bob Dole, AM Cartwright	10/03/2017

genotypes. This methodology expanded on the current literature to classify varieties in high and low TP (e.g., Mehring, 2016) by using a clustering approach and by only evaluating tiller production in extremely low PD to allow for TP expression (e.g., Kuraparthy et al., 2007).

Daily weather data variables were summarized (summed or averaged) for each YE for the periods of fall (October through November), winter (December through February), jointing through anthesis (March through April), and grain filling (May through mid-June). To assess differences in weather conditions between YEs, an analysis of variance (ANOVA) was conducted for each weather variable with the explanatory variables of YE, period, and their interaction using the function *lm* from the package *stats* (R Core Team, 2019) in R. Terms in the ANOVA were deemed significant at $\alpha = 0.05$.

The AOPD for each YE × TP combination was estimated by choosing the AIC-based best-fit model describing the relationship between grain yield and PD. Models tested were the intercept-only, linear, quadratic, and linear-plateau. For the intercept-only, linear, and quadratic models, the function *lmer* from the package *lme4* (Bates et al., 2015) in R was used to include site-year as a random effect either alone (intercept-only) or in addition to PD as a fixed effect variable (linear and quadratic models). For the linear-plateau model, the function *nlme* from the package *nlme* (Pinheiro et al., 2019) in R was used to include site-year as a random effect in addition to PD as a fixed effect variable in a non-linear shape of the form

$$GY = a + b \times PD \quad (if \quad PD < tx)$$

where GY is grain yield (Mg ha^{-1}); PD is plant density (plants m^{-2}); and the coefficients a (y-intercept), b (slope), and tx (breakpoint projected on PD).

To dissect the differential yield responses to PD, winter wheat yield and its components of heads per plant, heads m^{-2}, kernels head^{-1}, kernels m^{-2}, and thousand-kernel weight were analyzed as a function of PD group, YE, and TP. For that, PD was grouped into discrete intervals of <100, 100–200, 200–300, 300–400, and >400 plants m^{-2}. A mixed-effect ANOVA model was fit with each of yield or yield components as the response variable, and the explanatory variables of YE, TP, PD, and their interactions as fixed effect terms, and block nested in site-year as random effect. Significant ($\alpha = 0.05$) ANOVA terms were further analyzed by conducting pairwise comparisons of the expected marginal means using Fisher's least significant difference test.

The overall importance of yield components in explaining grain yield variability was assessed. For that, three different random-effect models were fit where the response variable grain yield was regressed against different sets of yield component as random effects, using the function *lmer* from the package *lme4* (Bates et al., 2015) in R. The first model represented an orthogonal partition of yield components and included PD, heads per plant, kernels head^{-1}, and thousand-kernel weight; the second model represented the main yield components defining final grain yield and included kernels m^{-2} and thousand-kernel weight; and the third model represented the contribution of harvest index and aboveground biomass to total grain yield variance.

To understand how different yield components were affected by YE and TP at AOPD, the dataset was further filtered to include only observations within ± 50 plants m^{-2} of the estimated YE-TP-specific AOPD, except for high-YE high-TP. For the latter, AOPD was derived from the intercept-only model and estimated at the minimum PD, filtering to include observations within AOPD+100 plants m^{-2}. Thereafter, a mixed-effect ANOVA model was fit for each of yield or yield components as the response variable, and the explanatory variables of YE, TP, and their interactions as fixed effect terms, and site-year as random effect term. Terms in the ANOVA were deemed significant at $\alpha = 0.05$. Significant terms were further analyzed by conducting pairwise comparisons of the expected marginal means using Fisher's least significant difference test.

RESULTS

Winter Wheat Yield Response to Plant Density in North America

Ten publications with field studies conducted in North America were found in the literature reporting both winter wheat yield and PD (**Table 1**), for a total of 119 observations. Despite a relatively small number of observations, there was a large range in PD (40 to 872 plants m^{-2}) and in grain yield (0.3 to 8.1 Mg ha^{-1}) among the studies matching our inclusion criteria. Linear-plateau models had the best fit for the 1st, 50th, and 99th quantiles (**Figure 1**), and AOPD was estimated at 397, 297, and 141 plants m^{-2} for the low, medium, and high YE, respectively. Likewise, the slope of the linear phase differed among YE, suggesting that each additional emerged plant per m^2 produced more yield in the high YE (0.043 Mg ha^{-1}.plant m^{-2}) versus the medium or low YE (0.020 and 0.006 Mg ha^{-1}.plant m^{-2}). Of the ten studies included in the synthesis analysis, only three stated that weeds, insects, and diseases were controlled, two studies did not mention pest control of any sort, while most of the other studies mentioned control of only one or two pest types (**Table 1**).

Winter Wheat Yield as a Function of G × E × M

Overall across the nine field studies and 11 wheat genotypes, PD ranged from 57 to 512 plants m^{-2}, and grain yield ranged from 1.1 to 8 Mg ha^{-1}. The average grain yield and total number of observations was 2.7, 5.2, and 6.6 Mg ha^{-1} with 407, 517, and 236 observations for the low, medium, and high YEs, respectively (**Figures 2A, B**). Different genotypes were classified as low and high TP based on average heads $plant^{-1}$ for each genotype. The average heads $plant^{-1}$ was 3.4 and 4.2, and total number of observations was 723 and 437 for the low and high TP, respectively.

The ratio between achieved and target PD was greatest at the lowest target PD, and significantly decreased similarly at all YEs as target PD increased (**Figure 2C**). We also investigated whether weather pattern and variability promoted different YE, but interestingly, weather variables varied as a function of period within the growing season, but were not statistically different across YEs (**Figures 2D–F**).

Yield Response to Density as a Function of Yield Environment and Tillering Potential

To understand the effect of genotype and environment on grain yield response to PD, AOPD was estimated for each combination of YE and TP (**Figure 3**). The linear-plateau model had the best fit for all YE × TP combinations, except for high-YE high-TP where grain yield did not respond to PD. At the low YE, AOPD was higher for low-TP compared to high-TP (334 vs. 271 plants m^{-2}), while yield at AOPD (YAOPD) was the same for both TPs. At the medium YE, AOPD was similar between high- and low-TP (296 vs. 281 plants m^{-2}, respectively). This small difference in AOPD translated into a greater difference in YAOPD of 5.6 and 5.2 Mg ha^{-1} for the high and low TPs, respectively. At the high YE, a distinct and opposite response of grain yield to PD was observed for different TPs. While grain yield at high-TP did not respond to increasing plant densities and AOPD was estimated at 58 plants m^{-2}, grain yield at low-TP increased until the

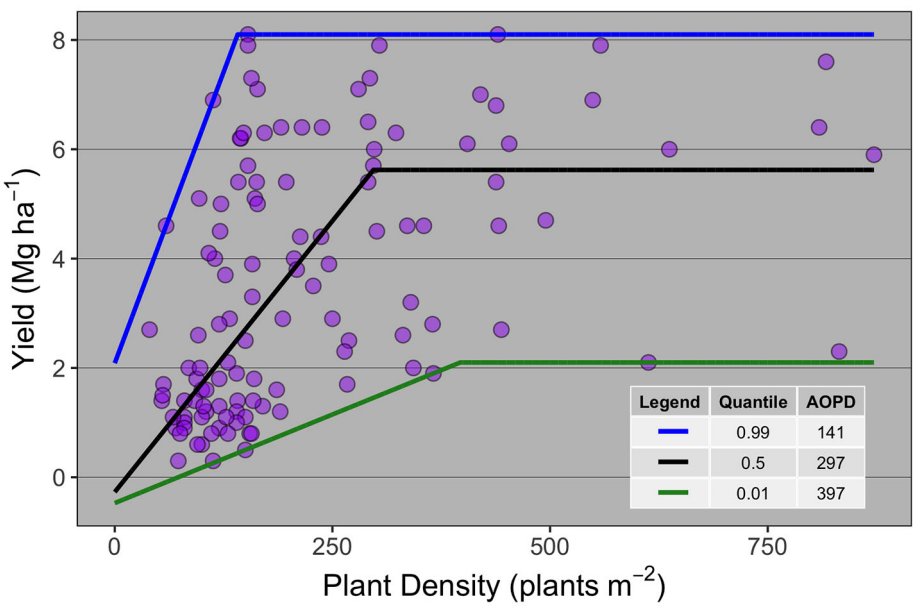

FIGURE 1 | Winter wheat grain yield response to plant density for data collected from 10 publications (n = 119). Each point represents the average yield at a given plant density as reported on the publication from which it was extracted. Different lines are the best-fit curve describing the agronomic optimum plant density (AOPD) at the 1st, 50th, and 99th quantiles.

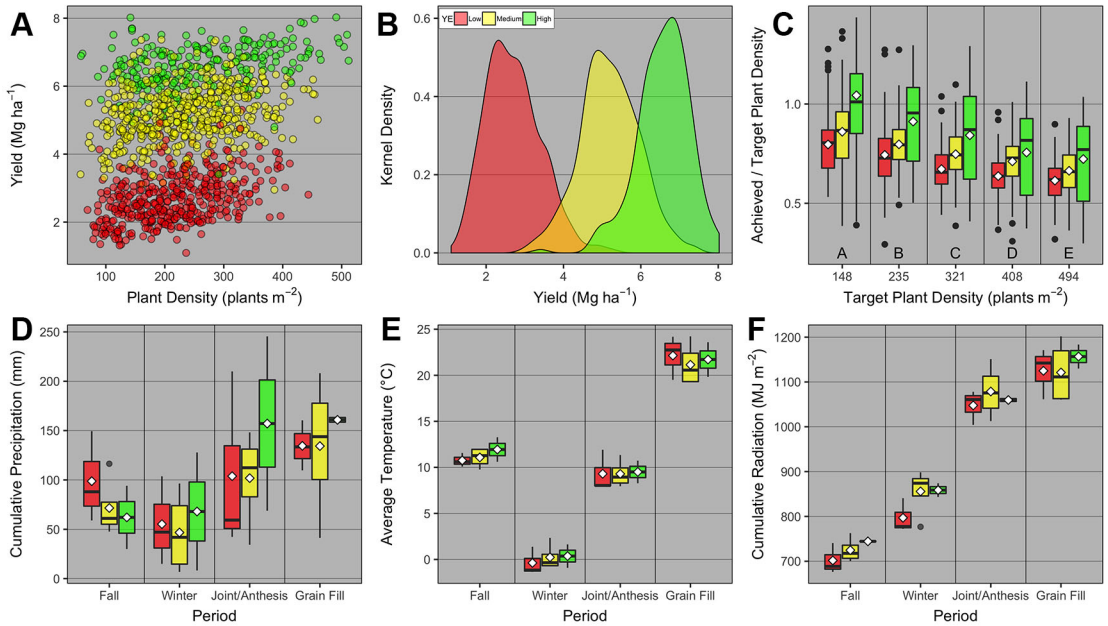

FIGURE 2 | Relationship between **(A)** winter wheat grain yield and plant density for low, medium, and high yield environments (YE); **(B)** kernel density distribution for grain yield at each YE; **(C)** achieved and target plant density ratio vs. target plant density for each YE; boxplots of **(D)** cumulative precipitation, **(E)** average daily temperature, and **(F)** cumulative daily radiation during different growing season periods [fall (Oct-Nov), winter (Dec-Feb), jointing/anthesis (Mar-Apr), grain filling (May-mid-June)] for each YE. Boxplots portray the 5th (lower whisker), 25th (bottom edge), 50th (solid black line), 75th (top edge), and 95th (upper whisker) quantiles, and mean (white diamond). On panel c, boxplots across different target plant density groups with the same letter are not statistically different (α = 0.05). On all panels, individual observations were either displayed (panel **A**), or summarized in the form of kernel density (panel b) or boxplots (panels **C–F**).

estimated AOPD of 492 plants m^{-2}. In spite of the large difference in AOPD between both TPs, YAOPD only varied slightly (6.7 vs. 6.8 Mg ha^{-1} for the high and low TP, respectively). Despite a significant increase in grain yield from the lowest to the highest population for the low TP genotypes, the increase was only 0.7 Mg ha^{-1} and seeking the highest yield might not be economical. These results expand those found in the synthesis analysis, and demonstrate that AOPD is not only a function of management (i.e., PD) and environment (i.e., YE), but also of genotype (i.e., TP).

Yield Components and Their Responses to Plant Density and Tiller Potential

Winter wheat grain yield was significantly affected by PD group, YE, TP, and YE × PD group (**Supplementary Table 3**, **Figure 4**). Averaged across YE and PD group, high-TP yielded more than low-TP (4.9 vs. 4.7 Mg ha^{-1}, respectively). Averaged across TP, grain yield levels had little overlap for all PD groups across different YEs (**Figure 4A**). The highest grain yields were observed at the PD groups >200 (2.8 to 2.9 Mg ha^{-1}) for the low YE, > 400 (5.7 Mg ha^{-1}) for the medium YE, and <100 and >300 (6.5 to 7 Mg ha^{-1}) for the high YE. For the latter, the wide range of PD able to promote high yield levels is noteworthy, and demonstrates the plasticity of winter wheat plants under near non-limiting growing conditions.

The number of heads per plant was significantly affected by PD group, TP, YE × PD group, TP × PD group, and YE × TP × PD group (**Supplementary Table 3**). Overall, heads per plant was greatest at the lowest PD group and decreased thereafter for all YE × TP combinations (**Figure 4B**). At the <100 PD group, heads per plant was greatest under medium-YE high-TP and high-YE high-TP (12 and 9.6 heads per plant, respectively). For medium- and high-YE, high-TP had more heads per plant than low-TP at the <100 PD group. At the 100–200 PD group, the numerically greatest number of heads per plant was observed under medium-YE high-TP (5.4 heads per plant). The main differences in this PD group were observed at low- and medium-YE, where high-TP had significantly greater number of heads per plant than low-TP.

The number of heads m^{-2} was significantly affected by PD group and TP (**Supplementary Table 3**, **Figures 4C, D**). Averaged across YE and TP, heads m^{-2} increased from 680 to 893 as PD group increased from <100 to >400, respectively. Averaged across YE and PD group, heads m^{-2} was greater for high-TP compared to low-TP (831 vs. 729 heads m^{-2}, respectively).

The number of kernels per head was significantly affected by PD group and TP (**Supplementary Table 3**, **Figures 4E, F**). Averaged across YE and TP, kernels per head was greatest at the <100 PD group (c.a., 26.4), and lowest when PD group >300 (c.a., 20.7 to 21.2). Averaged across YE and PD group, kernels per head was greatest for low-TP compared to high-TP (c.a., 24 vs. 22.2). The number of kernels m^{-2} was significantly affected only by TP (**Supplementary Table 3**), being greater for high-TP compared to low-TP (18,530 vs. 17,411 kernels m^{-2},

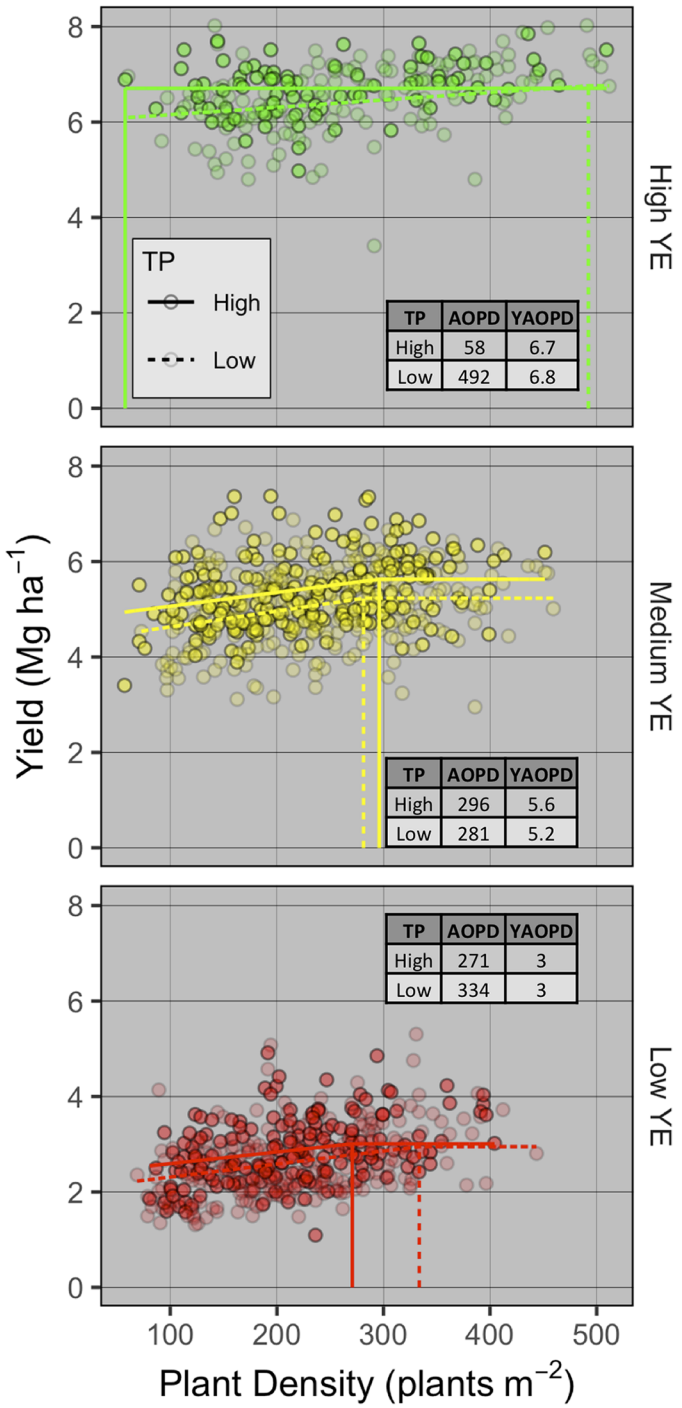

FIGURE 3 | Winter wheat grain yield response to plant density and agronomic optimum plant density (AOPD) determination for different tillering potential (TP) groups (high as solid points and lines, low as transparent points and dashed lines) within the high (top), medium (intermediate), and low (bottom panel) yield environments (YE). Dashed lines are the AOPD estimates projected on the x-axis and YAOPD refers to the yield reached at the AOPD.

respectively, **Figure 4G**). The thousand-kernel weight was not significantly affected by any of the explanatory variables (**Supplementary Table 3**) and varied from 11.8 to 36 g (**Figure 4H**).

The random effects analyses to understand the contribution of yield components to winter wheat grain yield suggested that at the plant level (model 1, orthogonal partition of yield components) the total yield variance contribution was in the

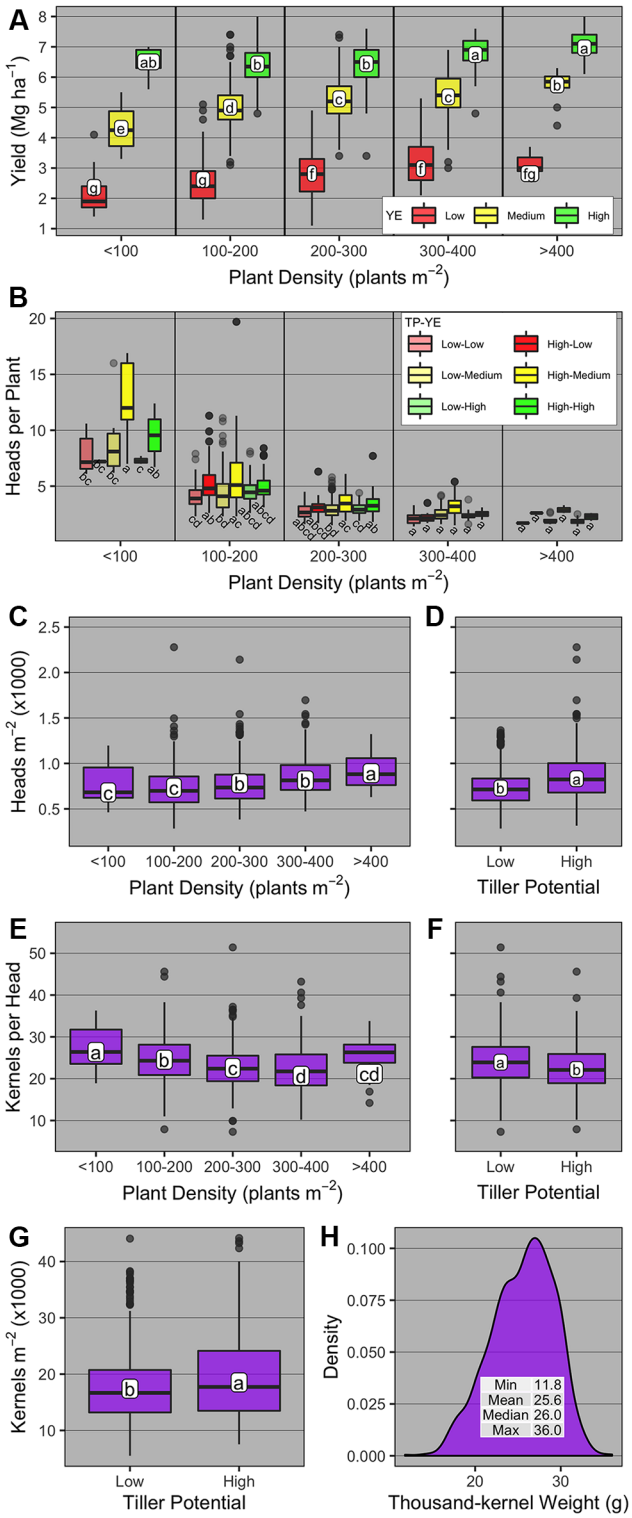

FIGURE 4 | Boxplots of **(A)** winter wheat grain yield and yield components [**(B)** heads per plant; **(C, D)** heads m^{-2}; **(E, F)** kernels head^{-1}; **(G)** kernels m^{-2}; and **(H)** thousand-kernel weight] as affected by plant density group (< 100, 100-200, 200-300, 300-400, and >400 plants m^{-2}), yield environment (YE; high, medium, and low), and tillering potential (TP; high and low). On panel b, boxplots within the same plant density group with the same letter are not statistically different (α = 0.05). On all other panels, boxplots with the same letter are not statistically different across all levels shown in the panel (α = 0.05). Boxplots portray the 5th (lower whisker), 25th (bottom edge), 50th (solid black line), 75th (top edge), and 95th (upper whisker) quantiles.

order thousand-kernel weight > kernels per head > PD >> heads per plant, with a residual variance of 46% (**Table 3**). At the canopy level, model 2 (yield components defining final grain yield) suggested that kernels m^{-2} and thousand-kernel weight explained 37 and 23% of total yield variance, respectively, while 40% remained in the residual variance (**Table 3**). Again at the canopy level, model 3 suggested that the contributions of harvest index and aboveground biomass to total grain yield variance explained 44 and 35% of the yield variance, respectively, with a residual variance of 21% (**Table 3**).

Yield At AOPD as a Function of Yield Environment and Tillering Potential

Given that AOPD was variable across different YE × TP combinations, yield and yield components at AOPD were further analyzed as a function of YE and TP (**Figure 5**). Grain yield at AOPD was significantly affected by YE and YE × TP (**Supplementary Table 4**). Grain yield varied across YEs in the order high > medium > low YE, and high-TP yielded more than low-TP only in the medium YE (5.6 vs. 5.1 Mg ha^{-1}, respectively, **Figure 5A**).

The number of kernels per head was significantly affected by TP and YE × TP (**Supplementary Table 4**). Kernels per head was numerically greatest under low-TP high-YE (26.7), yet not different from other TPs at the medium- and high-YE (**Figure 5B**). Kernels per head within the high-TP were not different across YEs, while low-TP at the high-YE was significantly greater than low-TP at low-YE.

The number of heads per plant was significantly affected by TP and YE × TP (**Supplementary Table 4**). Heads per plant was greatest at high-YE high-TP (5.9) and lowest at high-YE low-TP (1.7, **Figure 5C**). High-TP had significantly higher heads per plant than low-TP in all YEs. At the canopy-scale, the number of heads m^{-2} was significantly affected by YE × TP (**Supplementary Table 4**, **Figure 5D**). The greatest number of heads m^{-2} was observed under medium-YE high-TP (924), being only different from that under medium-YE low-TP (792). The number of kernels m^{-2} and thousand-kernel weight were not affected by YE or TP (**Supplementary Table 4**) and ranged from 5.5 to 44 kernels m^{-2}; and from 16 to 36 g, respectively (**Figures 5E, F**).

TABLE 3 | Winter wheat grain yield total variance partitioning based on different yield components models.

Model	Source of variation	Variance proportion
1	Thousand-kernel weight (g)	0.218
	Kernels per head	0.212
	Plant density (plants m^{-2})	0.111
	Heads per plant	0.001
	Residual	0.458
2	Kernels m^{-2}	0.370
	Thousand-kernel weight (g)	0.229
	Residual	0.401
3	Harvest index	0.439
	Biomass (g m^{-2})	0.350
	Residual	0.211

DISCUSSION

To the extent of our knowledge, this paper is the first effort on synthesizing literature data on winter wheat yield and its response to PD. Linear-plateau relationships were adjusted for the 1st, 50th, and 99th quantiles, differing in the slopes of the linear models and in the breakpoint to maximize yields, demonstrating the ability of wheat to capture resources differently based on environmental potential. Yield response to PD in wheat is largely driven by the competition for resources with neighboring plants (Satorre, 1988). The literature review demonstrated that when the environment is less limited in resources (high-yielding, plateau at ~8 Mg ha^{-1}), the number of plants required to maximize yield was lower relative to the medium (plateau at ~6 Mg ha^{-1}) and low (plateau at ~2 Mg ha^{-1}) yielding environments because plants utilized the resources more efficiently. We purposely limited our literature review and field experiments to winter wheat. While the results shown in this paper apply strictly to winter wheat, we also performed a literature review including spring wheat papers, which resulted in similar findings (i.e., yield plateau at 153 and 269 plants m^{-2} for HY and LY, $n = 35$ manuscripts; data not shown). Likewise, a recent study from Fischer et al. (2019) discussed the remarkable insensitivity of spring wheat yield response to PD in low latitude with ample resources. Thus, while these results might mostly apply to winter cereals (i.e., wheat, triticale), there is also some evidence that these results might also apply to spring wheat in certain growing conditions. However, we note that spring wheat grown in high latitudes or under lower resource availability, where the crop cycle and tillering potential might be limited by the number of accumulated thermal units, might warrant greater PD (Mehring, 2016). The work by Fischer et al. (2019) also portrayed the lack of data on PD below 100 plants m^{-2}. From our review, only three studies presented minimum plant densities below 100 plants m^{-2} (McLeod et al., 1992; McLeod et al., 1996; Beres et al., 2016) and the AOPD for the high-yielding environment was attained with 141 plants m^{-2}. The review from Fischer et al. (2019) highlighted a study from UK recorded by Whaley et al. (2000) that presented a maximum yield around 9.5 Mg ha^{-1} with an optimum of 100 plant m^{-2} when sowing at the optimal date. Likewise, Lollato et al. (2019) showed that yield contest winter wheat fields (e.g., high input and high yielding fields) were still able to attain their potential (c.a., 7.5 Mg ha^{-1}) when sown at ~100 seeds m^{-2} (which would result in <100 plants m^{-2}). This information confirms the main outcomes found on this first section of the review, under high-yielding and less limited resources the number of plants required to maximize yields in wheat is very low, below any commercially recommended number of plants for this crop. On the other spectrum of the frontier line (Q = 0.01), low yielding environments, a much lower efficiency and greater AOPD level

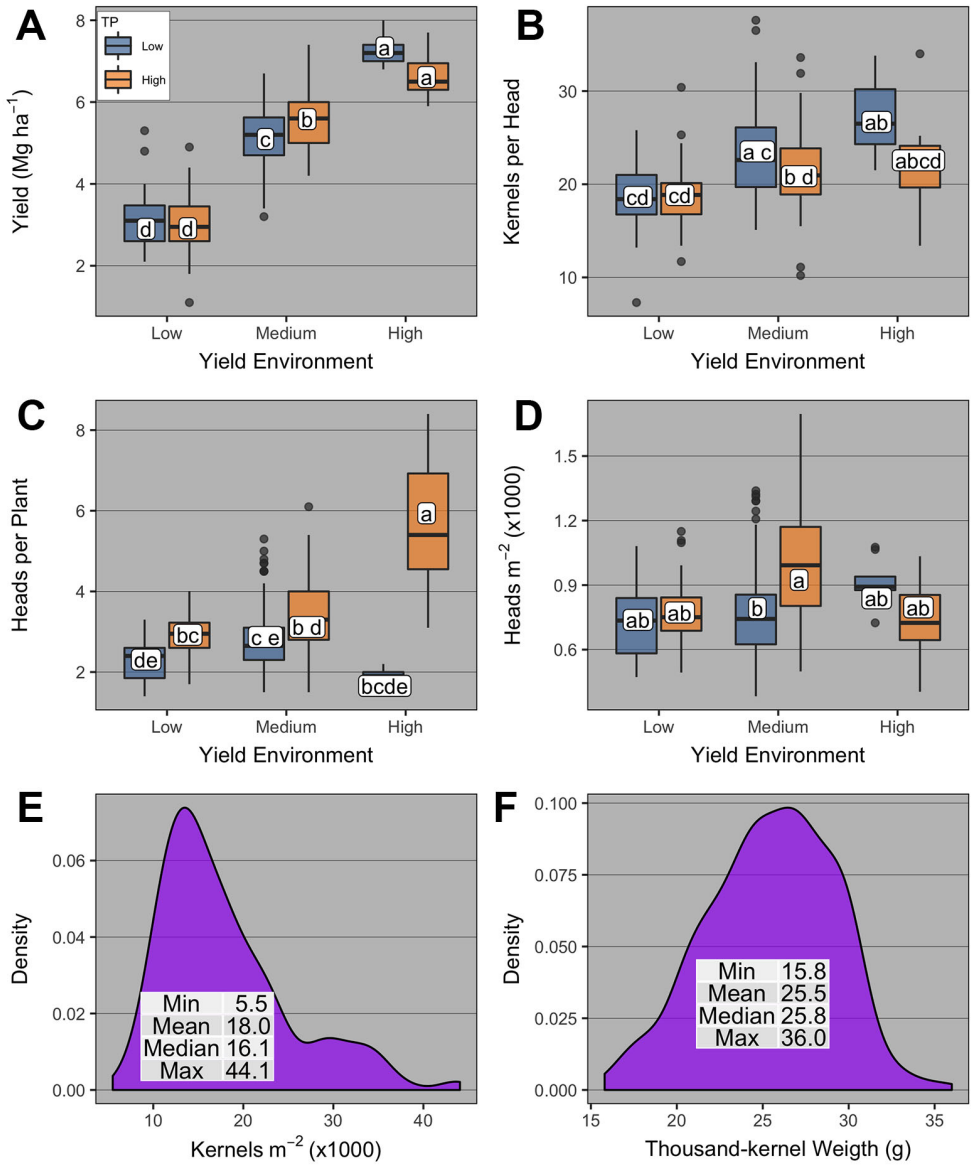

FIGURE 5 | Boxplots of **(A)** winter wheat grain yield and yield components [**(B)** kernels head^{-1}; **(C)** heads per plant; **(D)** heads m^{-2}; **(E)** kernels m^{-2}; and **(F)** thousand-kernel weight] at the agronomic optimum plant density (AOPD) as affected by yield environment (high, medium, and low), and tillering potential (TP; high and low). Boxplots with the same letter are not statistically different across all levels shown in the panel (α = 0.05). Boxplots portray the 5th (lower whisker), 25th (bottom edge), 50th (solid black line), 75th (top edge), and 95th (upper whisker) quantile.

was needed to sustain maximum yields. These results are likely a function of less resource availability and poorer growing conditions for those environments, potentially leading to lower tillering ability and less heads per unit area (Valério et al., 2013), and the need for increased plant densities.

Limitations of this review analysis were: i) the relatively small number of manuscripts included in the analysis (while many papers reported seeding rate by yield relationships, it was surprisingly rare for manuscripts to report emerged plants per unit area); and ii) the underpinning physiological mechanisms governing the yield to PD response in each YE cannot be properly dissected due to the lack of data on the yield components for each study synthesized on this dataset. In addition, lack of well-documented information on the ability of each genotype to produce tillers is also a major weakness for identifying the main causes for obtaining lower AOPD in less limited resource environments. Therefore, the dataset collected from field research studies performed in Kansas for characterizing the effect of genotype (tillering ability) by environment by management interactions was utilized on this

study to provide a more detailed physiological response to the mechanisms that play a critical role in the compensation process at lower plant densities.

Results from the field studies showed interaction between YE and TP on AOPD (**Figure 3**). As was expected, a lower AOPD was observed at high YE as compared to medium-low YE (58 vs. 284 plants m^{-2}) for the high TP genotypes. Likewise, Mehring (2016) suggested that the AOPD for hard red spring wheat decreased with increases in YE, and concluded that a high tillering genotype ('Albany') should be seeded at lower seeding rates than other genotypes with less TP to maximize yields. These findings are similar to those by Balla (1971). We also measured a lower ratio of achieved/target PD at higher seeding rates, which has been previously reported (Hanson and Lukach, 1992; Wiersma, 2002; Mehring, 2016). Anyhow, this was the case for all YEs. Even though the main effect of YE was non-significant in explaining achieved/target PD ratio, largely due to the high variability in the data, for all target PDs the numerical mean ratio followed the order high > medium > low YE. This pattern can be a consequence of suboptimal seedbed conditions (Hanson and Lukach, 1992), adverse weather and soil conditions (Mehring, 2016), or late sowing dates (Staggenborg et al., 2003). Thus, Dahlke et al. (1993); Staggenborg et al. (2003), and Lloveras et al. (2004) indicated the need to increase seeding rates with late sowing dates, because the shorter growing period reduced the individual plant growth and tiller production. In addition, Lloveras et al. (2004) reported a linear relationship between yield and PD in conditions of dry winter, showing the greater PD required to increase yield when water availability limited the crop growth. While this type of post-mortem analysis is useful in understanding the factors contributing to the yield-PD relationship, a producer will not know future weather to adjust seeding rate decisions accordingly. Within this context, the appropriate decision could take into account the yield history (past years of average yield from the same field) in each field to determine an expected YE. Nonetheless, weather uncertainty plays a major role in the outplay of various management practices, including seeding rate. A producer may respond to weather uncertainty by selecting conservative management practices, which in this case correspond to higher seeding rates, and/or utilizing genotypes with high TP.

Surprisingly, in our study it was not possible to characterize each YE with weather variables. The lack of significant weather effect was likely the result of low statistical power given that the total number of observations for a given weather variable and period was nine. Nonetheless, greater cumulative precipitation in the Fall, higher average temperature, and lower cumulative radiation during the Fall and Winter periods were evident when comparing low and high YEs (**Figures 2D, F**, respectively). We hypothesized i) that differences in intercepted solar radiation between YEs and among seeding rates within the same YE might have led to some of the observed differences in yield response (**Box 1**); and ii) that differences among site-years in nitrogen supply (e.g., either lower nitrogen supply due to losses, or higher nitrogen supply due to the mineralization of the soil organic matter) and/or nitrogen demand by the plants could have impacted the yield response at different YEs. This hypothesis is corroborated by observed site-year differences in exported nitrogen in the grain at different yield levels (**Supplementary Figure 1**).

BOX 1 | Intercepted solar radiation as affected by seeding rate and yield environments

Data on fractional green canopy cover for two YEs (low vs. medium) was collected during the 2015-16 growing season [i.e., Manhattan (average yield of 2.9 Mg ha^{-1}) and Hutchinson (average yield of 5.2 Mg ha^{-1})]. The fractional green canopy cover was measured using a methodology similar to Purcell (2000), where digital photographs encompassing one meter square were taken in eight to ten different dates in the season. Photos were analyzed using Canopeo (Patrignani and Ochsner, 2015). **Figures 6A, C** portray the growing season dynamics of fractional green canopy cover, calculated by assuming a linear increase or decrease between consecutive measurements. Incident solar radiation measured in a nearby weather station was multiplied by each respective daily fractional green cover, and a cumulative value of intercepted solar radiation for the growing season was calculated (**Figures 6B, D**).

This exploratory analysis showed that: i) fractional green canopy cover was as high as 82% in the medium YE but never surpassed 67% in the low YE; ii) cumulative intercepted solar radiation was considerably lower in the low relative to the medium YE (c. 1145 vs. 1465 MJ m^{-2}) despite similar growing season total (3710 vs. 3571 MJ m^{-2}, respectively); iii) differences in cumulative intercepted solar radiation between the lowest and the highest seeding rate were greater in the low (c. 1005 vs. 1283 MJ m^{-2}, or 28%) relative to the medium (1404 vs. 1562 MJ m^{-2}, or 11%) YE, and iv) differences in intercepted solar radiation between the low versus high TP varieties were negligible regardless of the environments and seeding rates (data not shown). Considering a radiation use efficiency of 1.4 g MJ^{-1} and a harvest index of 0.4 (Lollato and Edwards, 2015), differences in intercepted solar radiation led to differences in yield potential of 6.4 to 8.2 Mg ha^{-1} between YEs. The difference in yield potential between seeding rates was expectedly greater at the low (7.2 versus 5.6 Mg ha^{-1} for 494 and 150 seeds m^{-2}, respectively) relative to the medium YE (8.7 vs. 7.9 Mg ha^{-1}, respectively). We note in passing that the decrease in percent canopy cover measured in **Figure 6A** between days after sowing 61 (c.a., 19–33%) and 127 (c.a., 9 and 11%) resulted from losses in green leaf area due to cold winter temperatures coupled with no-till and large amounts of maize residue. This loss in canopy area was not measured in the warmer winter and conventional tillage practices in the southern location (**Figure 6C**).

A genotypic effect was observed on the AOPD, here studied by classifying the genotypes on TP groups. These results are supported by research suggesting a significant genotype by seeding rate interaction (Pendleton and Dungan, 1960; Briggs and Ayten-Fisu, 1979; Faris and De Pauw, 1980; Baker, 1982; Anderson and Barclay, 1991; Wiersma, 2002; Mehring, 2016). The field research dataset confirmed the influence of TP, more specifically in both low (~3 Mg ha^{-1}) and high (~6 Mg ha^{-1}) YEs. Clearly, for low YE, genotypes that had a greater TP resulted in a reduced AOPD by 23% relative to those classified as lower TP (**Figure 3**), while no difference between TPs were observed in the medium YE. Surprisingly, the AOPD at high YE changed with the TP. Similarly, Valério et al. (2009) reported greater seeding rates needed to obtain maximum yield for low TP genotypes, compared to high TP (417 to 555 vs. 221 to 422 seeds m^{-2}, respectively), with similar findings by Mehring (2016) and Balla (1971). Moreover, for the low TP genotypes, these authors observed linear relationships between yield and seeding rate

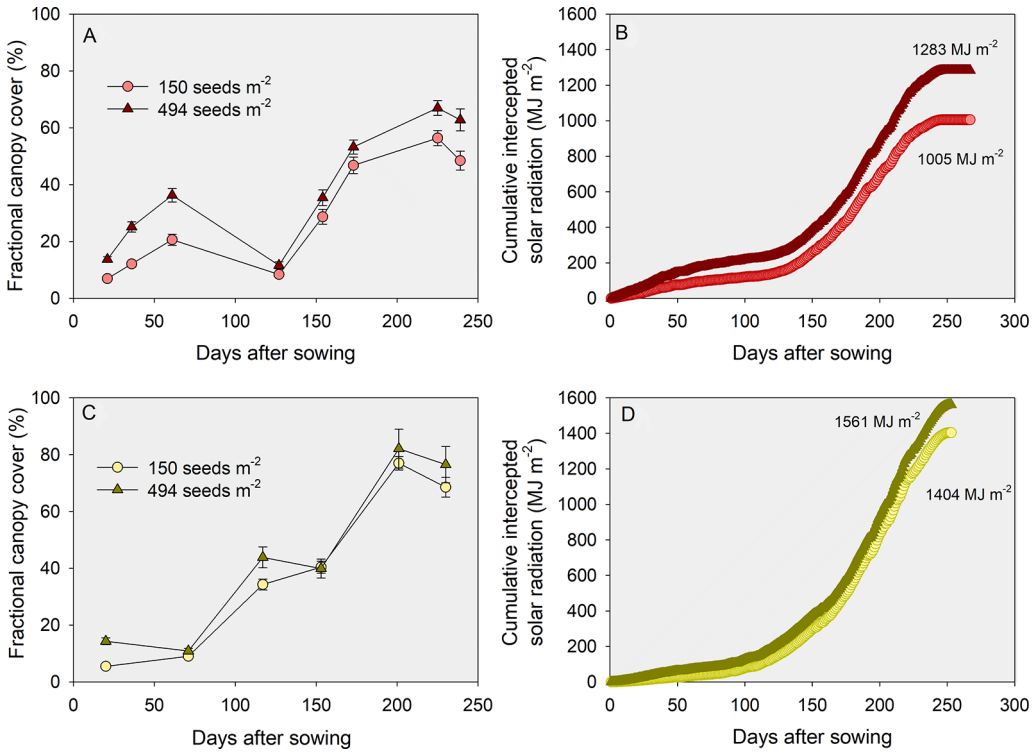

FIGURE 6 | Growing season dynamics of fractional green canopy cover **(A, C)** and cumulative intercepted solar radiation during the growing season **(B, D)**, for a low **(A**, **B)** and a medium **(C**, **D)** yield environment. Data represents the low tillering potential varieties sown at the lowest (150 seeds m^{-2}) or highest (494 seeds m^{-2}) seeding rates.

with low yields, but the relationship was mostly quadratic in site-years with greater yields. This reinforces the idea of increasing seeding rates/PDs as the environment is more restrictive for wheat growth. In spite of numerical differences, the AOPD levels observed on the field studies followed a similar trend to those found on the synthesis analysis, with a decrease in AOPD as YE changes from low to high, except for the high YE and low TP condition. The studies included in the synthesis analysis did not report on genotype TP, and thus our results cannot be validated with the same literature dataset. These differences in AOPD, especially at high YE, are significant for seeding rate decisions, and future yield-PD studies should also report information on genotypic TP. Furthermore, AOPD levels observed from the field studies for the low and medium YEs are similar to the first- (246 seeds m^{-2}) and third-quantile (304 seeds m^{-2}) of the seeding rate distribution of 100 intensively-managed wheat fields surveyed through the Kansas Wheat Yield Contest from 2010 through 2017 (Lollato et al., 2019). The authors found that in high YEs (i.e. 0.99 quantile), seeding rates greater than 305 seeds m^{-2} were negatively correlated with yield (loss of 2.7 Mg ha^{-1} for each 100-seed m^{-2} increment above 305 seeds m^{-2}). This behavior was not observed in our field studies high YE analysis, where greater seeding rates were optimal for low TP; and for high TP, while not optimal, high seeding rates were neither detrimental.

Given the YE-TP specific relationship of decreasing PD with increasing seeding rates, under the high-YE low-TP condition it would be required 686 seeds m^{-2} to achieve a PD of 492 plants m^{-2} (i.e., AOPD for this case). Assuming this seeding rate, a seed cost of US$1.54 per 100,000 seeds, a yield at AOPD of 6.8 Mg ha^{-1}, and a grain price of US$157 Mg^{-1}, the marginal profit for the high-YE low-TP condition when seeded to match AOPD is US$963 ha^{-1}, compared to US$949 ha^{-1} if seeded at a low PD of 60 seeds m^{-2} with a yield 6.1 Mg ha^{-1}. Thus, in spite of a large difference in seeding rate, the high-YE low-TP condition would still economically benefit from a seeding rate to match its AOPD of 492 plants m^{-2}. The difference in AOPD between the low and high TP genotypes can be used to anticipate the economics between conventional vs. hybrid wheat. Hybrids usually have a greater tillering potential as well as grain yield than conventional wheat (Rai et al., 1970; Curtis et al., 2002). Thus, for each YE, we assumed hybrid AOPD to be the same as that from high TP, and hybrid yield at AOPD to be 10% greater than yield at AOPD from high TP. Those numbers were compared against AOPD and yield at AOPD from low TP (representing conventional wheat). Further assuming a seed cost of US$1.54 and US$3.85 [i.e., 2.5x greater for hybrid, Curtis et al. (2002)] per 100,000 seeds for conventional and hybrid wheat, respectively, and a grain price of US$157 Mg^{-1}, the marginal profit difference

between hybrid and conventional wheat would be -30, 44, and 171 US$ ha^{-1} for the low, medium, and high YEs, respectively. Thus, under all the stated assumptions, the economic advantage of using hybrid over conventional wheat would be warranted under responsive environments, and discouraged under limiting environments.

In our research, the statistical models that usually maximized fit when representing wheat yield as affected by PD were linear-plateau. While the literature reports a wide range of models representing wheat yield as function of seeding rate (e.g., linear, quadratic, quadratic-plateau and lack of response; Whaley et al., 2000; Lloveras et al., 2004; Fischer et al., 2019), the quadratic is usually the most often reported to represent lodging and other potential yield losses due to increased pressure of insects and diseases at high populations and/or high yielding conditions (Lollato and Edwards, 2015; Mehring, 2016). In our study, diseases and insects were not a confounding factor due to prophylactic application of pesticides. Likewise, while lodging is recognized as a reoccurring issue in wheat grown under high populations (Holliday, 1960; Kirby, 1967; Faris and De Pauw, 1980; Orloff, 2014; Mehring, 2016), it ranged from non-existing to moderate in most of the site-years studied, not impacting yields (data not shown). Nonetheless, while this research grouped genotypes based on their expressed TP, future research should also investigate the effects of straw strength (Mehring, 2016), maturity (Hucl and Baker, 1988), and, when not controlled, disease and insect reactions of the studied genotypes.

Our findings related to the differential yield-PD response under varying YEs and TPs can be potentially used to guide variable seeding rate efforts. As an example, a producer could split his/her fields and sub-field regions into low-medium vs. high YEs based on historical yield trends. Then, low-medium YEs could be seeded at rates ranging from 300–350 seeds m^{-2} with the option of using high TP genotypes for greater plasticity in yield response. Moreover, high YEs could be seeded either at a low (< 100 seeds m^{-2}) or high (~500 seeds m^{-2}) rates, depending on the genotype TP, respectively. Nonetheless, this approach assumes that i) YEs remain stable through time (e.g. high YEs are high-yielding regardless of the year); ii) the yield limiting factors under low-medium YE are stationary regarding what caused them to be lower-yielding in the first place (e.g. soil texture, slope, etc.); and iii) the seed cost-to-grain price ratio remains stable. Independently of these assumptions being met, a wheat variable seeding rate technology should be site-specifically validated in order to optimize profitability.

Wheat genotypes differed in their plasticity to compensate for variations in PD by modifying different yield components, including the number of productive tillers (Lloveras et al., 2004). Wheat TP is a quantitative trait (Li et al., 2002) and thus genotypic differences in TP among wheat genotypes exist (Hucl and Baker, 1988; Anderson and Barclay, 1991; Mehring, 2016) and its expression depends on environmental conditions such as precipitation (Anderson and Barclay, 1991) and the genotypes' length of vegetative period (Hucl and Baker, 1988). Then, seems likely that under restrictive growing conditions (low YE), genotypes with a greater TP allowed to reach the maximum yield with a lower number of plants per unit area, while low TP genotypes were not able to fully compensate for the decreased number of plants by increasing the number of tillers per plant. Therefore, genotypes with lower TP are more dependent on seeding rate/PD for maximizing yield (Geleta et al., 2002; Valério et al., 2013).

Variations in yield components could explain the effect of YE and TP on AOPD. Our results showed that tillers and consequently heads per plant increased with reductions in PD, but overall, the increment was greater for the high TP genotypes compared to the low ones (**Figure 4B**). Consequently, the high TP genotypes could compensate the reductions in plants with more tillers and head per plant, avoiding a great reduction in heads number per unit area. Thus, a lower reduction in heads per unit area due to low PD occurred at high YE compared to low YE. Similarly, Mehring (2016) suggested that higher tillering genotypes had more tillers per plant than lower tillering genotypes at the two lowest out of five seeding rates evaluated. Wheat crops growing at low PD increased green area per plant and the duration of tiller formation (Whaley et al., 2000), which explains why yield did not decrease proportionally to PD variations. A reduction in PD decreased the number of heads per unit area but increased the number of kernels per head. However, some differences in these mechanisms were observed between TP groups. For the low TP, the increase in kernels per head was not enough to compensate the reduction in heads per unit area, and consequently, the number of kernels per unit area was reduced, negatively affecting the yield. In agreement, Arduini et al. (2006) observed an increase in the number of kernels per head with the decrease of seeding rate, but this yield gain was not

BOX 2 | Grain quality parameters as affected by plant density and genotypes

The effect of PD on grain quality was assessed by evaluating the relationships between: i) grain protein concentration and PD as a function of genotype; iii) test weight and PD as function of genotype; and iv) TKW and PD as a function of genotype. For each analysis, a range of models with different covariates (site-year, YE, genotype, TP) main and interacting effects were evaluated, and the one with the lowest AIC was chosen. Models residuals were diagnosed, and when necessary, outliers (less than -3 standardized residuals) were removed, and/or within-group error variances were allowed to vary according to site-year in order to address residual variance heteroscedasticity.

Overall, results suggested that i) grain protein concentration decreased with increasing PD at the same rate for all genotypes, with a genotype-dependent *y*-intercept (**Figure 7A**); ii) test weight increased with increasing PD at the same rate for all genotypes, with a genotype-dependent *y*-intercept (**Figure 7B**); and iii) TKW did not vary with increasing PD, but had a genotype-dependent main effect on the *y*-intercept (**Figure 7C**). First, similarly to available literature (Otteson et al., 2008; Williams et al., 2008; Rozbicki et al., 2015), these results highlight the importance of genotype on wheat quality determination, as using actual genotype rather than its TP explained much greater proportion of the variability in quality parameters. Regarding management, our results are also supported by Roth et al. (1984) and Geleta et al. (2002), who suggested that wheat test weight increased with increases in seeding rate due to the greater proportion of primary spikes compared to secondary tillers as seeding rate increased. Greater test weight on the primary spikes compared to tillers have been reported by Gautam et al. (2012).

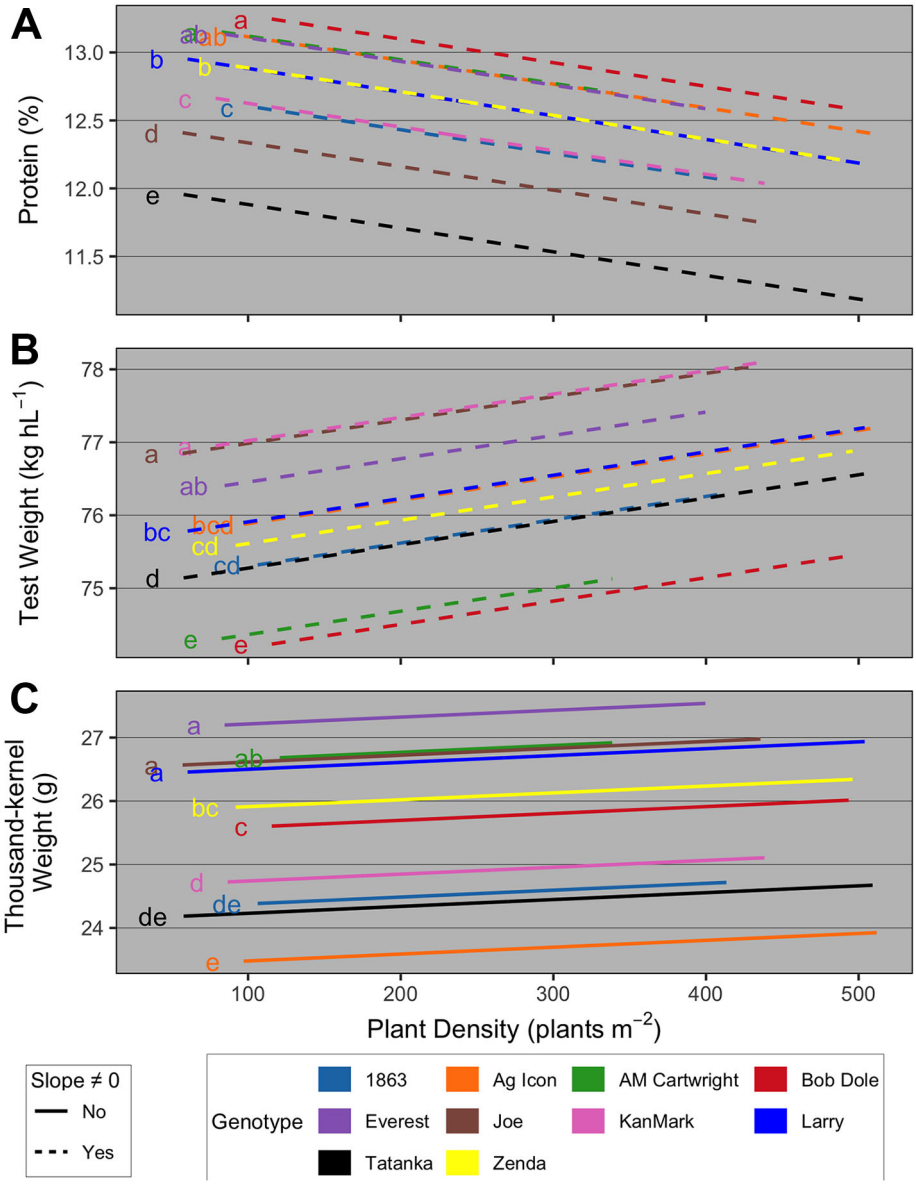

FIGURE 7 | Relationship between **(A)** grain protein concentration and plant density as a function of genotype; **(B)** test weight and plant density as function of genotype; and **(C)** thousand-kernel weight and plant density as a function of genotype. Different line types represent slopes that were significantly different than zero (dashed) and not significantly different than zero (solid). At each panel, the y-intercept of regression lines followed by the same letter are not statistically different (α = 0.05).

enough to fully compensate for the lower number of heads per unit area. Moreover, Arduini et al. (2006) and Slafer et al. (2014) reported how yield is regulated by yield components and environment, and stated that number of kernels per area is a coarse and seed weight is a fine regulator of wheat yield. While AOPD estimation prioritizes grain yield, grain quality parameters are an important consideration when evaluating yield-PD responses. In the current research, the relationships between PD and grain protein concentration, test weight, and thousand-kernel weight were genotype-dependent (**Box 2**).

Our study provides a unique perspective on the AOPD needed for maximizing wheat productivity at different yield levels. The data collected from both the review and the field research studies confirmed that AOPD is lower under high-yielding and less resource limited environments. The latter has been recently reported by Fischer et al. (2019) in a high fertility, irrigated environment; concluding that the great plasticity in wheat by tillering appears to explain the lower number of plants required to maximize light interception and increase yields. Nonetheless data on TP was not reported by Fischer et al.

(2019). Therefore, this study closes this unknown research gap on the need of lower AOPD for high-yielding environments by demonstrating with the field research data set that greater tillering ability from diverse wheat genotypes is a main factor for improving yields at very low plant densities.

CONCLUSIONS

Major findings of this study were: i) the review analysis portrayed new insights of differences in AOPD at varying YEs, reducing the AOPD as the attainable yield increases (with AOPD moving from 397 plants m^{-2} for the low YE to 191 plants m^{-2} for the high YE); ii) the field dataset confirmed the trend observed in the review but expanded on the physiological mechanisms underpinning the yield response to PD for wheat, highlighting the following points: a) high TP reduces the AOPD mainly in high and low YEs, b) at canopy-scale, both final heads and kernel number were the main factors improving yield response to PD under high TP, c) under varying YEs, at per-plant-scale, a compensation between heads per plant and kernels per head were the main factors contributing to yield with different TP genotypes.

As evidenced by the synthesis-analysis and expanded by the field studies to include TP, AOPD varies as a function of YE primarily, and to a lesser extent as a function of TP, except at high YE where TP is an important modulator of yield. Based on this, a producer may select different seeding rates and genotypes with varying levels of TP depending on a given field YE and the producer risk aversion. Either increasing seeding rates or selecting high TP genotypes could be used to decrease weather-related production risk. However, the former may not be the most economical practice if adverse weather does not happen and a lower seeding rate may have produced equally well. Therefore, we demonstrated with this work aspects of management and genotype that producers can select to better match their profitability and risk potential.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the author(s).

AUTHOR CONTRIBUTIONS

LB and WC performed the statistical analyses and drafted the manuscript. RL and AF designed the field experiment and, aided by BJ, CR, and GZ, conducted the field experiments. LB and IC coordinated data collection and led the review synthesis analysis, and LB, RL, and IC guided statistical analysis and development of the entire manuscript. All authors contributed, reviewed and edited the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2020.00054/full#supplementary-material

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Cultivar, Trait and Management System Selection to Improve Soft-Red Winter Wheat Productivity in the Eastern United States

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Wheat growing regions and seasons are diverse, mandating different varietal adaptation and management practices. Grain yield is the primary target for soft-red winter (SRW) wheat, due to lower protein content requirements. The growing season for SRW wheat in the eastern United States takes up to 9 months under variable environments, highlighting the importance of variety and management. In this study, we present the results of a 2-year field-based investigation of yield response of 30 wheat lines to different nitrogen treatments by dissecting yield to its components. For 5 out of the 30 lines, we performed in-tissue nitrogen analysis. Spring nitrogen (N) treatments were two levels of 0 kg N ha^{-1} (low N) and 112 kg N ha^{-1} (high N). On average, application of 112 kg N in the spring, in addition to fall N fertilizer, increased phytomass by 22% at maturity, enhanced fertile tiller numbers by 16%, and increased grain yield by 18% that coincided with a 26% increase in grain number per unit area. N in the grains, or the nitrogen harvest index, was lower (36% of total) in high N than in low N (40% of total) treatment, which indicated plants did not increase the in-grain utilization of N. The 18% higher grain yield with 112 kg N treatment occurred without considerable change in grain N content. However, lines with greater biomass produced greater yields in low N. Therefore, increasing tiller numbers and grain numbers for SRW wheat are the targeted traits for improving grain yield under N management, with less emphasis on the utilization of N in grains because N content is not critically influential for the marketability of soft wheat grains.

Keywords: soft-red winter wheat, nitrogen use efficiency, yield components, grain number, kernel weight, nitrogen harvest index, glutenin subunits

INTRODUCTION

Wheat cultivation occupies 22% of the major croplands globally, and covers the temperate latitude of both hemispheres, consisting of the Great Plains in United States, Canadian Prairie Provinces, western Europe, the Indus and the upper Ganges valleys, southern South America, eastern Africa, eastern China, southern Australia, and along the Kazakhstan and Russia border (Leff et al., 2004).

Wheat grown throughout the world consists of either spring or winter wheat. Winter wheat requires a vernalization period to transition from vegetative to reproductive stage (Dubcovsky et al., 2006). The vernalization requirement is genotype specific, with variations in time (15–45 days) and temperature (0–5°C) (Crofts, 1989). Some wheat producing regions manage autumn-grown wheat that are not considered winter types. These regions use the mild but elevated winter temperatures to grow wheat for higher yield potential. Examples of these locations are Mexico, California, and parts of the Middle East. Winter wheat is typically not viewed as a cover crop but has dual grain and grazing purposes in targeted regions such as Oklahoma and Texas (Maulana et al., 2019).

A key characteristic of wheat is the unique properties of forming dough from flour (Shewry, 2009). Quality is indicated by the performance of a cultivar at specific protein levels for defined end use products (Bushuk et al., 1997) and viscoelastic properties (Shewry, 2009). Wheat classes are defined by grain hardness, protein content, and growth habit. Hard wheat has hard endosperm texture and higher protein content. Soft wheat has soft endosperm texture, low levels of damaged starch granule upon milling, and weaker dough strength that is suitable to make biscuits, cookies, and cakes (Bushuk et al., 1997). Protein composition in the endosperm is made of monomeric gliadins and polymer glutenins subunits (Porceddu et al., 1997). Glutenins are further divided into high molecular weight (HMW) and low molecular weight (LMW) subunits. The composition of high and low molecular weight glutenin subunits is the key quality determinant for dough (Bushuk et al., 1997). In addition to genetics, protein quantity and quality is dependent on environmental conditions (Luo et al., 2000; Cooper et al., 2001).

Management practices in wheat have substantial impacts on crop productivity and environmental stewardship. In both winter and spring wheat cropping systems, nitrogen (N) fertilizer applications are routinely applied pre-planting or during leaf formation (Zadoks 15) with additional N top-dress application in the stem elongation stage (Zadoks 30) or post-anthesis (Zadoks 69) (Woodard and Bly, 1998; Otteson et al., 2007). Developing a site-specific understanding for fertilizer expenses, environmental impacts such as leaching and volatilization, and efficient use of N by crops are pillars of crop profitability in relation to N management. Previous work by Koch et al. (2004) described the economic benefits for site-specific and environment-specific management practices for variable rate nitrogen applications, but further research is needed in the area of targeted genotype by environment by management practices for improved economic and environmental outcomes.

Nitrogen is necessary for growth of canopy, intercepting solar radiation, and photosynthesis in green tissues (Barraclough et al., 2014). Nitrogen use efficiency (NUE) is the amount of grain produced per unit of N available in the soil (Moll et al., 1982). In other words, the ability to increase grain yield per N applied. The two main components of NUE are uptake efficiency and utilization efficiency. Nitrogen uptake efficiency (NUpE) is the plant's ability to absorb N available in the soil, and nitrogen utilization efficiency (NUtE) is the efficiency of which the absorbed N is utilized to produce grain (Moll et al., 1982). NUtE is also described as the ratio between crop yield and total N absorbed by the plant (Todeschini et al., 2016), indicative of the output of grain yield based on the amount of N taken up by the plant.

It is nearly impossible to identify and recommend a single variety that is the "best" across multiple environments due to the infinite interactions that can cause unstable phenotypic characteristics (Allard and Bradshaw, 1964). Yield is the most economically important trait, making both pre-planting and in-season crop management (Kirkegaard and Hunt, 2010) critical to maximize this market for growers and suppliers. The end-use quality traits such as protein content and endosperm texture are also influenced by N availability during plant growth. Farm profitability is primarily dependent on grain yield and quality. With approximately 7.8 million metric tons of soft-red winter wheat produced in the United States in 2018, accounting for ∼15% of total wheat production, it is paramount to strategically manage the cost and benefits to increase yields. The goal of our study was to identify traits responsive to N in a typical soft-red winter wheat breeding population under two contrasting N management and identify potential useful genetic solutions for the long term goal of managing wheat with reduced nitrogen fertilizer. To accomplish our goal, we evaluated grain yield, yield determining traits and N components under low N and high N environments and assessed protein quality.

MATERIALS AND METHODS

Field Experiments and Nitrogen Management

Thirty experimental breeding lines, designated as PU01–PU30, from Purdue University's soft-red winter wheat breeding program were selected based on their variation in grain yield (from 3,500 to 6,500 kg ha^{-1}). These 30 lines were planted in the Purdue Agronomy Farm (40.43° N, 86.99°W) for two seasons: 2016–2017 and 2017–2018. The experimental layout included two N rates arranged in a split plot design with 4 blocks, where N rate was main-plot and line was sub-plot. Each experimental unit measured 1.22 m × 3.05 m, with 7 rows spaced 15 cm apart with a targeted planting density of 370 seeds m^{-2}. The soil type at the Agronomy Research Farm is a combination of Rockfield silt loam (fine-silty, mixed, superactive, mesic Oxyaquic Hapludalfs), Fincastle silt loam (fine-silty, mixed, superactive, mesic Aeric Epiaqualfs), and Toronto silt loam (fine-silty, mixed, superactive, mesic Udollic Epaqulafs) (USDA Web Soil Survey). Experiments were planted in late September following corn and harvested late June of the following year. The experiments were planted using a Hege (Wintersteiger, Austria) drill planter and plots harvested with a Wintersteiger (Wintersteiger, Austria) plot harvester at physiological maturity.

In the fall, 224 kg ha^{-1} of mono-ammonium phosphate (11-52-0) was applied based on soil test (Mehlich-3) recommendations. The plot area was then chisel cultivated. Approximately 100 kg ha^{-1} of potassium chloride was added to the entire experimental area as recommended by soil analysis. Emergence began approximately 6 days after planting. Spring

nitrogen applications of 112 kg N ha^{-1} of urea (46-0-0) was broadcast applied to the main plots, designed as high-N treatment, at stem elongation (Zadoks 30) growth stage. Prior to application, urea was treated with Limus (BASF, Germany), a urease inhibitor which prevents urea from being broken down via urease enzymes and lost through volatilization. The main plots, designated for low-N treatment, received zero spring N. Herbicide (Harmony Extra [thifensulfuron + tribenuron], DuPont, 35 g ha^{-1}) was applied in mid-April to minimize weed pressure. Weather information including average monthly precipitation and temperature, as per iClimate (2019), are shown in **Supplementary Table S1**.

Agronomic Traits

Days to heading (HD) and days to physiological maturity (MD) were recorded when 50% of the plot showed head emergence and maturity, respectively, and expressed as the number of days from January 1 of the current year. Plant height (PLH), from the ground to the top of the uppermost spikelet, was measured at four locations within the plot at physiological maturity. Thousand kernel weight was measured and the average weight for a single kernel was calculated (KW). Grain yield (YLD) was measured on a whole plot basis, corrected for 13% moisture.

The aboveground biomass (BIO) was estimated by cutting 0.25 m × 0.30 m (2 rows) from the middle of each plot for all treatments at heading (Zadoks 58), anthesis (Zadoks 60–68), and maturity (Zadoks 91) and dried to constant weight. Number of spikes per cut area (NS) was estimated by averaging the count of spikes at heading, anthesis, and maturity from the samples of cut area (0.25 m × 0.30 m). Yield component traits were measured from the same cut area sample at physiological maturity. Five random spikes were chosen to measure spike length (SPL), and hand-threshed to obtain the number of kernels per spike (KNS), kernel weight per spike (KWS), and grain number per cut area (GN). Fruiting efficiency (FE) was calculated by the number of kernels produced by each spike divided by the spike weight at anthesis. Lastly, harvest index (HI) was determined by the dividing the grain yield by the aboveground biomass at maturity.

We chose 5 out of 30 lines, based on earlier yield data, to analyze N concentration in biomass and grain. These lines showed a range of grain yield over 5 years and three locations in Indiana. The entire aboveground biomass (phytomass) was analyzed at heading and anthesis. At maturity once leaf senescence was complete, plant biomass was divided into grain and leaves plus straw. All samples were dried for 72 h at 49°C.

Plant samples were ground with cutting mill (Model E3703, Eberbach Corp., Bellevile, MI, United States) and UDY grinder (Udy Corp., Fort Collins, CO, United States) and passed through a 1.0 mm screen. Thirty milligrams of each sample were sent for flash combustion analysis (Flash EA 112 Series, CE Elantech, Lakewood, NJ, United States). The N concentration of phytomass at heading (NCPH) and anthesis (NCPA) were measured on whole plant samples. The nitrogen concentration of phytomass at maturity (NCPM) was measured on leaf and straw tissues. The nitrogen concentration of grains at maturity (NCGM) was measured on the grain samples.

For NUE measurement, we adopted the methods presented by Moll et al. (1982), and Foulkes et al. (2009).

$$\text{NUE} = \frac{\text{Grain dry matter}}{\text{Available N}}$$

where Grain dry matter is the grain yield (kg ha^{-1}) of plots at maturity (Zadoks 92), and available N, based on the formula, is the nitrogen available from the soil and fertilizer. Residual N was not tested and is not included in the study and calculation of NUE. In this estimation, instead of available N, we used the amount of N applications in each treatment. Both low-N and high-N environments received the same fall N application of 25 kg N ha^{-1} as monoammonium phosphate. A spring N application of 112 kg ha^{-1} N was applied to the high-N environment only. The total N supplied in low-N environment was 25 kg ha^{-1} N, while the total N supplied in the high-N environment was 137 kg ha^{-1} N. N uptake was calculated as the total nitrogen in the aboveground biomass including grain. NUtE was measured as grain dry matter produced per gram of plant N uptake. Nitrogen harvest index (NHI) was estimated as amount of nitrogen that was recovered in grains relative to overall N uptake of the plants.

Phenotyping Grain and Flour Characterization

A subsample of grains from each N environment were subjected to Single Kernel Characterization System 4100 (SKCS) (Perten Instruments, Sweden) analysis. A single replicate was performed for each linein each N environment. The SKCS weighs and crushes individual kernels and converts the force-crush profile to a unit-less Grain Hardness Index (GHI). Whole-meal flour samples were also prepared with a UDY Cyclone mill (Udy Corp., Fort Collin, CO, United States) with a 0.5 mm screen. Sodium dodecyl sulfate (SDS) sedimentation volume was carried out according to the modified protocol described in Pena et al. (1990) using 1 g of flour.

Glutenin Subunits and the Rye Translocation

Allelic variation of glutenin subunits and the presence or absence of the rye translocation were evaluated by sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE) for all 30 lines following method described by Peña et al. (2004).

Statistical Analysis

Combined year analysis of variance (ANOVA) was performed with PROC GLM in SAS 9.4 (SAS Institute, Cary, NC, United States) similar to the model presented by Iannucci et al. (2008), where sources of variations are year, nitrogen, year × nitrogen interaction, genotype, year × genotypes, nitrogen × genotypes, and year × nitrogen × genotype

interaction effects, each tested against appropriate error term (**Table 1**).

$$Y_{ijkl} = \mu + Yr_i + rep(Yr)_{li} + N_j + NYr_{ji} + rep^{*}N(Yr)_{lji} + G_k + GYr_{ki} + GN_{kj} + GNYr_{kji} + \varepsilon_{ijkl} \quad (1)$$

Where Y_{ijkl} is the phenotypic observation of the lth replicate of the kth genotype, in the jth nitrogen treatment, observed in the ith year. μ is the grand mean, Yr_i is the effect of ith year, $rep(Yr)_{li}$ is the effect of the lth replicate in the ith year. The effect of year was tested against $rep(Yr)_{li}$. N_j is the effect of the jth nitrogen treatment and NY_{ji} is the interaction effect of the jth nitrogen level with the ith year. These two terms were tested against the interaction effect of nitrogen by replicate within the year [$rep^{*}N(Yr)_{lji}$]. G_k represents the effect of the kth genotype. Remaining interactions were tested against the residual error. Tukey's studentized range test (HSD) was implemented for comparison of means using the MEANS statement in PROC GLM (SAS 9.4) and significant differences reported with $p < 0.05$.

Least squares means was estimated using '*lsmeans*' package (Lenth, 2016) in R environment (R Core Team, 2019) for genotypes and N levels with combining years and implemented for phenotypic analysis. Heritability, in the broad sense (H^2) (Nyquist, 1991; Piepho and Möhring, 2007), was estimated for each nitrogen environment by restricted maximum likelihood (REML) variance and covariance components using PROC MIXED (SAS Institute Inc., 2013) with random effect model in equation 2.

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + + \frac{\sigma_{gy}^2}{y} + \frac{\sigma_\varepsilon^2}{yr}} \quad (2)$$

With σ_g^2 representing variance component of genotype (genetic variance), σ_{gy}^2 the variance component of genotype × year interaction, and finally σ_ε^2 the residual error. Denominators represent years (y = 2), and replications (r = 4).

TABLE 1 | ANOVA for year (Y), nitrogen level (N), and genotype (G).

		Grain yield (YLD)		
Source of variation	**d.f.**	**Mean square (× 10^4)**	***F*-value**	**Pr > *F***
Year (Y)	1	1286	5.23	ns
Residual 1	6	246		
N levels (N)	1	11144*	12.75*	*
Y × N	1	40.4	0.05	ns
Residual 2	6	874		
Genotype (G)	29	281***	8.31***	***
Y × G	29	132***	3.89***	***
N × G	29	53.5*	1.58*	*
Y × N × G	29	43.7	1.29	ns
Residual	348	33.9		
Total	479			

*Significance: <0.001 = ***, ≤0.05*, and >0.05 = ns.*

Pearson's correlations were calculated for low-N and high-N environments separately using *cor* function in R environment (R Core Team, 2019). The linear relationship among measured traits was evaluated by Pearson's correlation coefficient (r). Principal component biplot analysis was used to visualize relationships among traits and lines by using the '*factoextra*' (Kassambara and Mundt, 2016) package and '*factoMineR*' (Lê et al., 2008) package in R environment (R Core Team, 2019).

RESULTS

Agronomic Traits

On average, the lines took approximately 130 days (from first of January) to head, and 168 days to reach physiological maturity (**Supplementary Table S2**). N effect was significant on biomass accumulated at physiological maturity (**Supplementary Table S3**). For example, biomass at maturity (BIO_{MD}) was ∼22% greater in high N compared with low N.

The effects of G and N × G were significant for number of spikes (NS) (**Supplementary Table S3**). We observed correlations of $r \geq 0.21$ between NS and BIO_{MD} in both N treatments (**Supplementary Table S4**), as more tillers produces more biomass. The lines showed variations in their number of tillers and biomass (**Supplementary Table S2**). PU10 and PU14 showed an average of approximately 60 NS across both N treatments, and BIO_{MD} greater than 95 g (**Supplementary File S1**). In comparison, PU21 and PU29 averaged 43 NS and BIO_{MD} of 87 and 88 g, respectively, showing a difference of 20 spikes and 10 g of biomass per cut area.

Number of spikes had the highest significant positive correlation observed with yield (r = 0.64* in low N; r = 0.36* in high N). On average, 8 more effective spikes per sampled area were observed in high N compared to low N, which resulted in 275 more kernels per sampled area in high N compared to low N (**Supplementary Table S2**). The grain number per unit area was a result of NS and effective tillers, which in our study, was significantly impacted by N. However, the weight of individual kernels was unaffected by N treatment (**Supplementary Table S3**). The mean KW was 36 mg, with a range of 25–47 mg across lines and environments (**Supplementary Table S2**). PU14 was the only line to have a KW above 40 mg in low N and high N (**Supplementary File S1**). We observed a negative correlation between GN and KW under both treatments (r = −0.34 low-N; r = −0.30 high-N) (**Supplementary Table S4**).

The effect of N, G, Y × G, and N × G were significant on YLD (**Table 1**) and the interaction of Y × N was not significant. On average, YLD was 976 kg ha^{-1} less in low N compared to high N (**Supplementary Table S2**). In the high-N treatment, YLD had a mean of 6,335 kg ha^{-1} and ranged between 3,799 and 8,090 kg ha^{-1}. Difference in YLD resulted from producing more GN per treatment based on NS where N, G, N × G, and Y × N × G had significant effects on GN (**Supplementary Table S3**). Y, G, and G × Y had significant effects on HI. Across genotypes in environments, HI ranged from 0.21 to 0.55 (**Supplementary Table S2**). The 5 lines selected for in-tissue N analysis revealed

TABLE 2 | Nitrogen analysis and grain quality assessment of five subset lines.

	PU08	PU10	PU15	PU17	PU21
Low-N					
Yield (kg ha^{-1})	5,698	5,527	5,874	4,696	4,928
NUE (kg ha^{-1} grain/kg ha^{-1} N supply)	227.96	221.10	235.01	187.84	197.12
NCPH (mg g^{-1})	10.5	11.0	11.4	12.4	9.9
NCPA (mg g^{-1})	8.5	8.4	9.0	8.8	8.5
NCPM (mg g^{-1})	3.4	3.3	3.7	4.3	3.3
NCGM (mg g^{-1})	16.1	16.2	16.0	18.1	18.3
N uptake (g)	0.83	0.85	1.00	1.00	0.63
NUtE (g g^{-1})	42.84	41.47	42.97	34.56	37.53
NHI (%)	69	66	67	62	68
GHI	14	14	13	24	16
SDS-Sed	4.8	4.0	4.3	5.0	5.0
High-N					
Yield (kg ha^{-1})	7,391	7,320	7,098	5,483	5,567
NUE (kg ha^{-1} grain/kg ha^{-1} N supply)	53.95	53.43	51.81	40.03	40.64
NCPH (mg g^{-1})	15.7	15.6	15.8	16.3	15.6
NCPA (mg g^{-1})	11.8	11.3	12.1	12.1	12.9
NCPM (mg g^{-1})	4.5	3.7	5.8	5.2	4.1
NCGM (mg g^{-1})	18.9	18.4	17.9	19.1	19.6
N uptake (g)	1.56	1.29	1.53	1.30	1.35
NUtE (g g^{-1})	35.11	36.76	33.45	31.24	34.22
NHI (%)	65	68	57	58	66
GHI	20	17	9	17	19
SDS-Sed	4.8	5.5	5.3	4.8	5.3

Nitrogen concentration at heading (NCPH; mg g^{-1}), anthesis (NCPA; mg g^{-1}), maturity (NCPM; mg g^{-1}), in grains (NCGM; mg g^{-1}), nitrogen uptake (g), nitrogen utilization (NUtE; g g^{-1}), and nitrogen harvest index (NHI; %) determined from in season tissue analysis for five lines. Grain hardness index (GHI) based on single kernel characterization (SKCS). SDS Sedimentation (SDS-Sed) based on whole grain flour meal.

a range of grain yield. For example, PU08, PU10, and PU15 exhibited YLD greater than the mean across both environments, and PU17 and PU21 exhibiting less YLD than average (**Table 2**).

Spike traits were investigated by measuring SPL and the KNS in both environments. The effect of N and G were significant on SPL and KNS (**Supplementary Table S3**). SPL ranged from 5.9 to 10.5 cm (**Supplementary Table S2**). The mean SPL was 7.8 cm in low N and 8.4 cm in high N. Positive correlation was observed between SPL and KNS at 0.53 in high N and 0.59 in low N, respectively (**Supplementary Table S4**). The mean KNS in high N was 32, in comparison to the mean KNS of 29 in low N. However, the range was similar under both N levels, from 20 to 50 KNS. PU28 produced the most KNS in high N with average of 41, and PU15 produced the most KNS under low N (**Supplementary File S1**). The percent reduction of SPL and KNS from high-N to low-N treatments were, on average, 7.7 and 10.3%, respectively. In most cases, larger SPL values were associated with larger KNS values, suggesting that the length of the spike could be a primary determinant of the number of kernels per spike.

Lines were significantly different for fruiting efficiency (FE) (**Supplementary Table S3**); however, N did not affect FE. FE was highly heritable across environments ($H^2 > 0.50$) (**Supplementary Table S2**). In high N, FE showed a mean of 87 kernels per gram of dry matter spike at anthesis (range 21–186) (**Supplementary Table S2**). Genotypes PU02 and PU20 had the lowest FE of 57 and 62 in high-N environment, well below the average. PU07 and PU19 showed FE above 100 in both low-N and high-N treatment (**Supplementary File S1**).

In-Tissue Nitrogen Analysis

N treatment had significant effects on N concentration in phytomass at heading, anthesis, and maturity, as well as in grains for the 5 subset genotypes (**Supplementary Table S3**). On average, N concentration in biomass at heading was 11.1 mg g^{-1} in low N (**Supplementary Table S2**) where genotype PU17 showed the maximum in-biomass N concentration (**Table 2**). In high N, plants were able to accumulate N concentration of 15.8 mg g^{-1} in biomass at heading (**Supplementary Table S2**). The amount of in-biomass N concentration decreased to 8.8 and 12.1 mg g^{-1} by anthesis in low-N and high-N treatments and in-phytomass N concentration decreased to 3.5 and 4.7 mg g^{-1} by maturity in low-N and high-N treatments, respectively (**Supplementary Table S2**).

From anthesis to maturity, the amount of N in phytomass decreased. The effect of N and Y was significant for N concentration at anthesis and maturity (**Supplementary Table S3**) where PU21 displayed the largest loss of 8.8 mg g^{-1} N from anthesis to maturity in high N, while PU15 lost 5.3 mg g^{-1} in low N (**Table 2**). This signifies the translocation of N into the grains. Genotypes were only significantly different at maturity stage for N concentration in phytomass and in grains (**Supplementary Table S3**). The maximum NHI of 69% was observed in PU08 in low N. While the minimum NHI of 57% was observed in PU15 in high N (**Table 2**). The sum of N in phytomass and grain at maturity was approximately 22.0 mg g^{-1}, on average (**Supplementary Table S2**). The total N at anthesis was approximately 10.5 mg g^{-1} across environments. We observed that pre-anthesis N concentration was correlated with grain N concentration ($r = 0.51$; p-value < 0.001) among the 5 lines (data not shown).

Nitrogen Use Efficiency

Nitrogen use efficiency was estimated for all 30 lines across N treatments. N, G, Y × G, N × G, and Y × N × G were significant for NUE (**Supplementary Table S3**). Due to the level of N application, and method of calculation, NUE estimates were higher in low N (**Supplementary Table S2**). For example, NUE averaged 209.92 kg ha^{-1} grain per kg ha^{-1} N supplied in low-N environment. PU03 had the lowest NUE of 179.78 kg ha^{-1} grain per kg ha^{-1} N, with PU13 the highest at 243.62 kg ha^{-1} grain per kg ha^{-1} N (**Supplementary File S1**). In high N, NUE averaged 46.05 kg ha^{-1} N. PU08, PU10, and PU15 had the greatest NUE in high N (**Table 2** and **Supplementary File S1**). We further quantified N uptake, NUtE, and NHI in 5

selected genotypes in this study (**Table 2**). The effect of N was significant on N uptake (**Supplementary Table S3**). N uptake average 1.42 and 0.87 g in high N and low N, respectively (**Supplementary Table S2**). This was a 38% reduction in whole plant N uptake. However, the effect of G and G × N was not significant, indicating that lines responded similarly to their N uptake across the two environments (**Supplementary Table S3**). The effects of Y, N, G, and Y × G were significant on NUtE (**Supplementary Table S3**). NUtE was significantly greater in low N (compared to high N) by 14% (**Supplementary Table S2**). The effects of N, G, Y × G, and N × G was significant on NHI (**Supplementary Table S3**). NHI ranged from 42 to 75% across years and environments.

Glutenin Subunits and the Rye Translocation

Loci for HMW glutenin subunits *Glu-A1*, *Glu-B1,* and *Glu-D1* and LMW subunits *Glu-A3, Glu-B3,* and *Glu-D3* and presence of 1B/1R translocation (**Table 3**) were characterized (**Supplementary Figure S1**). In the thirty lines tested, the common *Glu-A1* allele was the *1* subunit with only six genotypes possessing the *2** allele. The variants observed in *Glu-B1* locus were *7, 7 + 8, 7 + 9, 13 + 16,* and *32 + 33* subunits. Two alleles *2 + 12* and *5 + 10* were found for *Glu-D1* locus at almost equal frequency. For LMW, the *Glu-A3c* subunit and *Glu-D3a* subunit were the most frequent (**Table 3**), while *Glu-B3* showed a wide allelic variation. The 1B/1R rye translocation was identified in 17 out of 30 genotypes. When we compared genotypes with translocation with those without the translocation by using two-sample *t*-test, the difference was not significant (p-value > 0.05) (data not shown). Genotypes with the 1B/1R translocation varied in allelic variation for HMW and LMW subunits (**Table 3**).

Grain Quality Indicators

The GHI values greater than 59 are indicative of hard while GHI values less than 33 specify soft endosperms. Because we analyzed

TABLE 3 | Allelic variation of high (HMW) and low molecular weights (LMW) for glutenin subunits and presence of 1B/1R translocation for each line.

	Low-N	High-N	HMW			LMW				Low-N		High-N	
Germplasm	Yield	Yield	Glu-A1	Glu-B1	Glu-D1	Glu-A3	Glu-B3	Glu-D3	Translocation	GHI	SDS-Sed	GHI	SDS-Sed
PU01	5,001	6,296	1	7	2 + 12	f	j	a	1B/1R	10	4.0	13	4.8
PU02	5,405	6,292	2*	32 + 33†	5 + 10	c	j	b	1B/1R	6	4.8	12	5.5
PU03	4,494	5,842	1	7	5 + 10	c	f,g	a	–	9	4.8	12	5.8
PU04	5,340	5,900	1	7	5 + 10	d†	b	a	–	9	4.0	13	4.3
PU05	5,426	6,780	1	7 + 9	2 + 12	d	f,g,j†	c/b	1B/1R	2	6.0	4	6.3
PU06	5,571	6,485	1	13 + 16†	2 + 12	c	f,g	a	–	7	4.3	13	5.8
PU07	4,668	6,328	1	7	2 + 12	f	j	a	1B/1R	13	4.3	16	5.0
PU08	5,699	7,392	2*	7	2 + 12	g	j	a	1B/1R	14	4.8	20	4.8
PU09	5,875	6,479	1	7	2 + 12	c	b	a	1B/1R	10	5.0	12	6.3
PU10	5,528	7,320	2*	7 + 9	2 + 12	g	j	a	1B/1R	14	4.0	17	5.5
PU11	5,269	6,105	1′±	13 + 16	5 + 10	c	h	a	–	20	6.3	17	7.3
PU12	5,270	5,656	1	7	5 + 10†	c	f†	b†	1B/1R	12	5.3	17	6.3
PU13	6,090	6,817	1′±	13 + 16	5 + 10	c	h	a	–	16	5.5	17	7.0
PU14	4,917	6,151	0	7 + 8	2 + 10.1 ±	c	g	a	–	19	5.5	20	7.0
PU15	5,752	7,099	1	7	2 + 12	c	b	a	1B/1R	13	4.3	9	5.3
PU16	5,638	6,710	1	7 + 9†	2 + 12†	c	j†	c†	1B/1R	13	3.8	16	4.0
PU17	4,696	5,484	1	7	2 + 12	c	j	a	1B/1R	24	5.0	17	4.8
PU18	5,870	6,707	1	7 + 8	2 + 12/5 + 10	c	b	b	–	12	4.5	9	5.0
PU19	5,650	6,148	2*	7 + 9	2 + 12	c	j	c	1B/1R	23	4.8	29	6.3
PU20	5,742	6,676	2*†	7 + 9	2 + 12†	c	h†	a	–	11	3.8	16	5.0
PU21	4,928	5,568	1	7†	2 + 12	f	j†	a	1B/1R	16	5.0	19	5.3
PU22	5,617	6,242	1	7 + 8	2 + 12	c	b′	a	–	22	4.8	18	5.8
PU23	5,619	6,402	1	7	2 + 12	d	b′	a	–	12	5.0	14	5.3
PU24	4,719	5,851	1′±	13 + 16†	2 + 12	c	h/b	a	–	25	5.3	31	4.8
PU25	5,979	6,866	2*	7	2 + 12	g	j	a	1B/1R	17	4.3	21	5.3
PU26	5,802	6,170	1	7 + 9†	2 + 12†	c	j	c†	1B/1R	19	3.8	25	4.3
PU27	5,358	6,230	1	7 + 8	5 + 10†	c	b	b±†	–	15	5.0	16	5.3
PU28	4,901	5,938	1	7 + 8/32 + 33	5 + 10/2 + 12	c	f, g, j†	b†	1B/1R	6	4.8	9	4.8
PU29	5,040	6,059	1	7 + 9	2 + 12	c	j	c†	1B/1R	16	5.3	19	4.8
PU30	5,080	6,065	1	7 + 8	5 + 10/2 + 12	d	b′	b	–	7	4.5	12	5.0

*±Indicates similar to the allele showed but not confirmed with a proper check. †Indicates that the allele was not identified with certainty. Grain hardness index (GHI) and SDS-Sedimentation (SDS-Sed) evaluated under both nitrogen environments for each line. *Indicates of an allele variation.*

only single replicate grains with SKCS, we could not perform ANOVA or any significance test among genotypes. GHI averaged 13.8 ± 1.03 (standard error of the mean) in low N. In high N, GHI averaged 16.1 ± 1.05 (**Table 3**). PU24 showed maximum GHI values of 25 and 31 in low N and high N, respectively. In contrast, PU05 showed the minimum GHI values less than five in both treatments.

For SDS-sedimentation, higher values indicate better bread-making quality (Moonen et al., 1982). SDS tested whole meal flour samples of each line performed in duplicate showed sedimentation mean of 5.4 ± 0.15 in high N in contrast to 4.7 ± 0.12 sedimentation mean observed in low N (**Table 3**). PU16 showed minimum SDS-sedimentation while PU11 showed the maximum.

Germplasm with the 1B/1R translocation showed a lower grain hardness and lower SDS-sedimentation (**Table 3**). For example, PU05 and PU16 had the minimum GHI and the minimum SDS-sedimentation across environments, respectively, while PU11 and PU24 which do not carry the translocation show maximum GHI and SDS-sedimentation for whole grain flour meal. PU10 and PU15 exhibit the translocation and were among the highest yielding lines in high N and low N, with lower protein in both environments and a lower SDS-sedimentation score than average in low N (**Table 3**).

Nitrogen × Genotype Interaction

Five traits including grain yield, grain number, number of spikes, nitrogen use efficiency, and nitrogen harvest index showed significant N × G interaction effect (**Supplementary Table S3**), indicating that lines performed differently in response to nitrogen environments. In particular, when we assessed grain yield with ranks, a cross over interaction was observed for lines PU08 and PU13. PU08 was the first rank line in the high-N environment while PU13 was the first rank in the low-N environment (**Figure 1**). The change was evident as only 4 of 30 genotype held the same rank across environments. One specific genotype, PU26, is an example of the importance of phenotyping in low input environments. Under high N, PU26 yielded 6,170 kg ha^{-1}, below average, and ranked as the 18th best genotype based on yield performance. However, in low N, PU26 yielded 5,802 kg ha^{-1}, above average, and moved up 12 spots to the 6th best yielding genotype (**Supplementary File S1**). The change in ranking was indicative of genotype by nitrogen interaction.

Principal Component Analysis (PCA) – Biplot Analysis

The interrelationship among traits and genotypes in the form of biplots in each environment is shown in **Figure 2**. Principal component analysis (PCA) was performed on the 12 traits measured and all 30 lines in both environments. In low N, PC1, and PC2 explained 34.8 and 32.5% of phenotypic variations, respectively. In high N, PC1 and PC2 explained 32.6 and 22.0% of phenotypic variation, respectively. The number of spikes was significantly and positively associated with grain yield in both environments (**Figure 2** and **Supplementary Table S4**). Kernel weight was not positively associated with any other trait but had significant negative correlations with harvest index and fruiting efficiency. Lines are also visually shown in PCA-biplot. Two high yielding lines in both environments, PU08 and PU10, were in the same direction as grain yield and number of spikes.

DISCUSSION

Of the estimated 31.8 million acres of winter wheat planted in 2019, approximately 5.54 (∼17%) million acres are estimated to be planted as soft-red winter wheat in the eastern United States. A record low harvest area is expected in New Jersey, Ohio, and Virginia (USDA, 2019). The decline in wheat cultivation area in the United States is due to an increase in acreage and production of maize and soybean. In maize, nitrogen dynamics and optimizations under varying environments have been studied extensively to increase productivity with efficient fertilization, management, and less environmental footprint (Bänziger et al., 1997; Ciampitti and Vyn, 2012). Studies in wheat took a variety of objectives from improving wheat for low-nitrogen input in order to reduce environmental impacts (Ortiz-Monasterio et al., 1997; Delogu et al., 1998; Le Gouis et al., 2000; Brancourt-Hulmel et al., 2005), breeding for productivity gains and cost-effectiveness under low input environments (Bänziger and Cooper, 2001), and nitrogen use efficiency in soft-red winter wheat (Van Sanford and MacKown, 1986; Hitz et al., 2017; Brasier et al., 2018). The ability to identify nitrogen efficient soft-red winter wheat germplasm will have the potential to reduce N applications, therefore saving time, resources, and management costs.

Yield and Yield Component Responses

The rank change of lines across environments, e.g., from high N to low N (**Figure 1**), can indicate the potential profit loss or gain. For example, the profit made by PU17, which yielded 4,696 and 5,484 kg ha^{-1} under low N and high N, would be below the average profit margins across all 30 lines and displays the potential loss in comparison to other higher yielding lines (**Supplementary File S1**). This data seems to suggest breeding

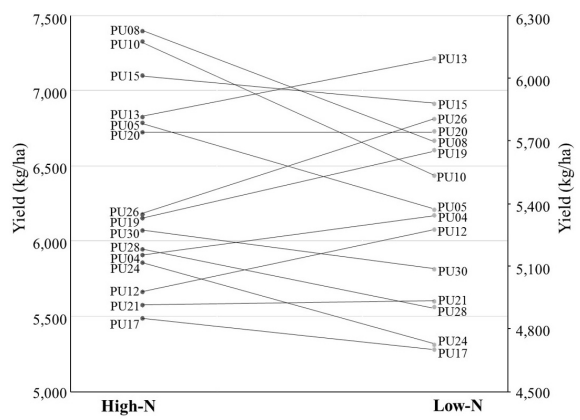

FIGURE 1 | Genotype ranking and interactions based on grain yield (kg ha^{-1}) in low-N and high-N environment for 15 out of 30 genotypes.

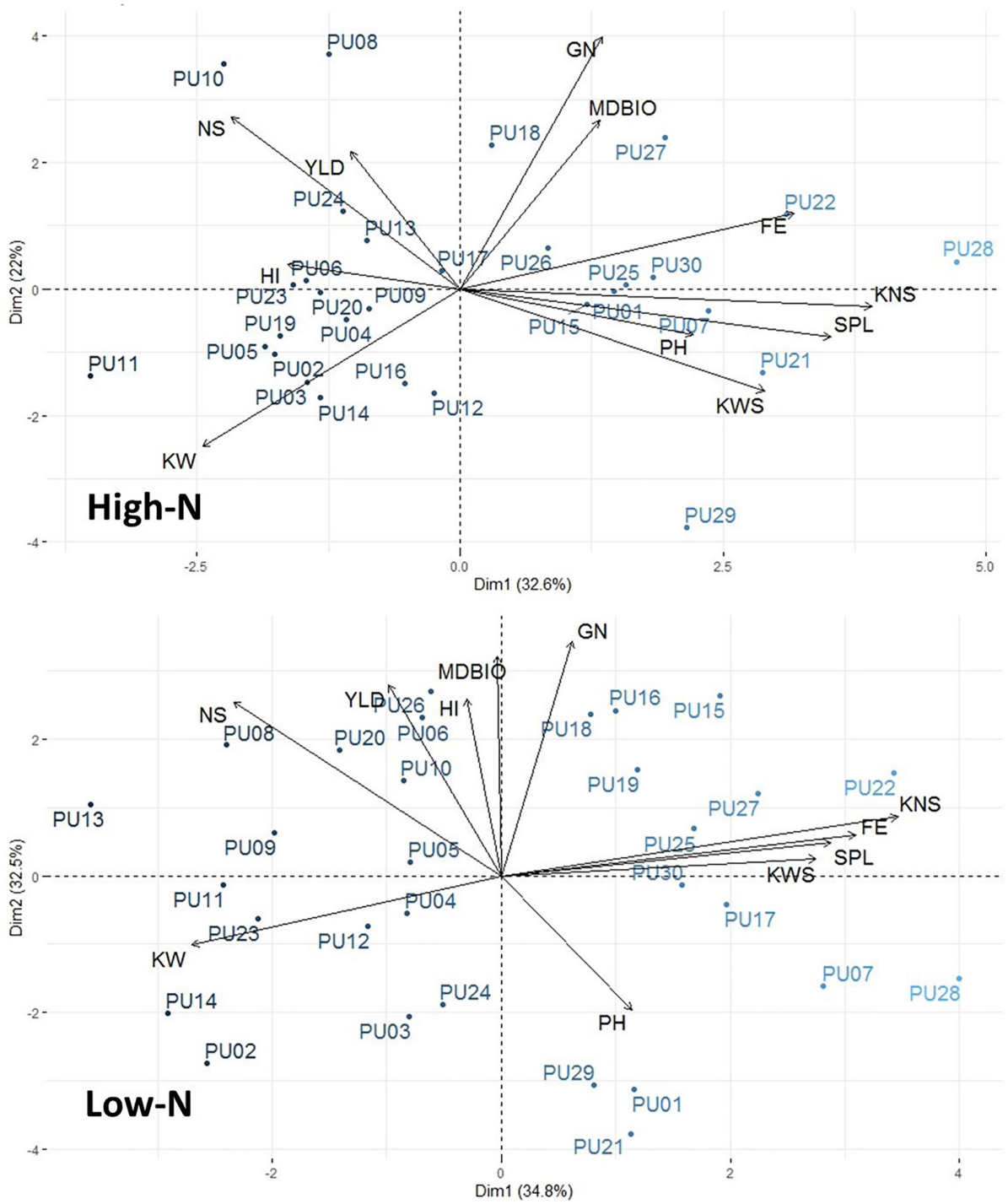

FIGURE 2 | Principal component analysis (PCA)-biplot analysis among 12 agronomic traits and 30 genotypes. PCA-biplots were performed in both high-N and low-N environments.

specifically for separate environments by using beneficial founder individuals for each environment. A PCA-biplot that shows trait and line associations (**Figure 2**), can be useful for shortlisting of founder individuals. For example, in low N, unlike in high N, the biomass at maturity has a close association and higher correlation (**Supplementary Table S4**) with grain yield, showing that, under limited nitrogen, the decreases of biomass (tillers and leaves), is the bottleneck for grain production later in the season. Therefore, it seems that the negative effect of low N is through reduction in canopy size and radiation use. Yield potential is expressed

as a function of light interception, radiation use efficiency, and harvest index, where the critical underlying trait common to all three components is above-ground plant biomass. An increase in biomass is associated with an increase in radiation use efficiency, grain number, and ultimately grain yield (Reynolds et al., 2005). In spring wheat, Caviglia and Sadras (2001) observed nitrogen deficiency reduced light interception and radiation use efficiency, ultimately because of smaller leaf area index due to decrease tillering and less shoot dry matter (biomass). Calderini et al. (1997) identified wheat cultivars reached a maximum leaf area index between the booting and terminal spikelet growth stage, implying the importance of establishing a wheat canopy earlier in the growth season as leaf area index and dry matter decreases post-anthesis when the wheat transitions from vegetative growth to reproductive growth for grains.

In our study, the difference in spike number can be attributed to the lack of tiller initiation in the spring or the loss of an emerging tiller in winter. The decreases in biomass due to low-N treatment resulted in reduction of grain number via decreases of number of spikes, and kernel per spike, similar to previously reported observations (Le Gouis et al., 2000; Terrile et al., 2017). Grain number, as an important yield component, is positively related to pre-anthesis dry matter accumulation (Duan et al., 2018) and was shown to respond directly to N supply to the spike (Abbate et al., 1995). Our results indicate grain number and biomass are highly correlated (**Supplementary Table S4**) and are associated with genotypes producing more grain in low and high N (**Figure 2**). Despite responsiveness of grain number, our study indicated that kernel weight is more stable under environmental conditions with higher heritability (H^2 = 0.88 and 0.89), implying that the physiological mechanisms that control grain filling are able to fill the number of grains that were determined earlier. Even though a contradicting report of kernel weight was described as the main determinant of grain yield (Major et al., 1988), we observed grain number as the primary contributor for grain yield. Similar to our observation, other physiological studies reported similar behavior for environmental responsiveness of grain number and kernel weight (Sadras and Slafer, 2012; Slafer et al., 2014; Ferrante et al., 2017).

End-Use Quality Determinants

One aspect of genotypic differences in responses to low N is end-use quality traits. Protein content, gluten quality, and endosperm texture in wheat are the driver of end-use products. Several studies evaluated the relationship between grain yield to protein content and quality. For example, experimental evidence is indicative of a negative correlation between grain yield and protein (Cooper et al., 2001; Magallanes-López et al., 2017). We used several measures to understand the dynamics of protein quality under the two contrasting N regimes.

Contrary to changes that we observed for grain yield under different N management, our study only indicated a slight decrease in SDS-sedimentation and grain hardness index. This is an opportunity for developing low-N efficient soft-red winter wheat breeding because these traits were minimally affected by the lack of sufficient N. Contrary to our results of soft-red winter wheat, N fertilizer was previously shown to have significant effect on SDS sedimentation in hard wheat (Luo et al., 2000; Saint Pierre et al., 2008).

Gluten quality is a function of allelic variation of HMW and LMW subunits. For example, *Glu-A1(2*)* and *Glu-D1(5 + 10)* HMW subunits are considered high gluten quality alleles. Line PU02 revealed high yield and possessed *Glu-A1(2*)* and *Glu-D1(5 + 10)* HMW subunits. One of the highest yielding lines under low N, PU15, possessed *Glu-A1(1)* and *Glu-D1(2 + 12)* subunits, which are not considered the highest glutenin quality alleles. Selection of lines as breeding parents with reasonable yield under low N condition and high glutenin subunits as parents of breeding populations, may be a way to maintain the quality under low N in the breeding population.

Germplasm with the 1B/1R translocation showed a lower grain hardness and lower SDS-sedimentation. For example, PU05 and PU16 had the minimum GHI and the minimum SDS-sedimentation across environments, respectively, while PU11 and PU24 which do not carry the translocation show maximum GHI and SDS-sedimentation for whole grain flour meal. PU10 and PU15 exhibit the translocation and were among the highest yielding lines in high N and low N (**Figure 1**), with lower protein in both environments and a lower SDS-sedimentation score than average in low N (**Table 3**). Morris and Paulsen (1985) analyzed hard winter wheat under two contrasting treatments. In deficient N, the low levels of vegetative N resulted in a significant decreased in total grain N after anthesis. In comparison, high N maintained 37 mg N plant^{-1} throughout grain filling but increased grain N dramatically (Morris and Paulsen, 1985). Parts of the N that is in the grain comes from senescence of leaves (remobilization of existing N compounds) (Hawkesford, 2014). Tolley and Mohammadi (2020), showed significant differences for grain N at maturity in seven diverse wheat accessions. The grain N in low-N treatment was 23.3 mg g^{-1} while grain N in high-N environment was 27.8 mg g^{-1}. Our study did not detect any significant genotypic variation of N uptake in spite of previous studies showing genetic variation in nitrogen uptake and assimilation previously described in wheat (Cox et al., 1985; Ortiz-Monasterio et al., 1997; Le Gouis et al., 2000).

Breeding for Low-N Environments

A comparative view of the crop produced per nitrogen used in this study indicates that breeding and selection for performance under low-N environment has the potential for minimizing N use and environmental impacts. In our study each additional kg ha^{-1} of spring N fertilizer resulted in a grain yield increase of 9 kg ha^{-1}, with the G × N effect for grain yield being significant, indicating that lines responded differently (**Table 1**). For example, PU10 responded maximally and PU04 responded minimally by increasing 16 and 5 kg ha^{-1} of yield per each kg ha^{-1} of nitrogen applied (**Supplementary File S1**).

Most breeding programs and variety testing are historically performed under optimal conditions and sufficient N applications for evaluating yield potential. N applications have the negative environmental impact of leaching, pollution, and runoff into the water, as nitrate is the most commonly detected agricultural chemical in the water. Wu et al. (1996) estimated an average annual runoff and leaching of 4.47 and

4.57 kg N ha^{-1}, respectively, in the midwestern and northern plain regions under corn, sorghum, soybean, wheat, or legume hay cultivation, accounting for about 5.5 and 5.6% of N applied.

This result indicates that establishing breeding and selection for specifically performance under low-N cropping systems has the potential to produce reasonably well under low-N conditions while decreasing the environmental footprint. The former was evident by changes in rank analysis of lines in both environments (**Figure 1**). Change of rank in differential environments was previously used in drought (Li et al., 2011; Lopes et al., 2014), salinity (Salam et al., 1999; Chamekh et al., 2015), and other nutrient deficiencies (Torun et al., 2000; Murphy et al., 2008; Zhao et al., 2018), to postulate a need for environment specific management and breeding practices. For example, van Bueren and Struik (2017) described breeding for grain crops and vegetables under diverse N management for genotype adaptation and interaction with availability of N.

Our data seems to suggest that the lines PU05, PU08, PU10, PU13, PU15, PU19, PU14, PU20, and PU26 have the potential to be the founder of a breeding population for low-N environment (**Figure 1**). For this selection we used criteria such as higher ranks in low-N conditions, higher kernel per spike in low-N, higher kernel weight, superior *Glue-A1* (*2**) allele, the rye 1B/1R translocation, and higher NHI and FE. Another related trait that can help wheat breeding for low-N system is the use higher grain protein content trait. It has been shown that greater translocation of nitrogen to grains from increased fertilizer N results in a higher grain protein concentration (Delogu et al., 1998; Saint Pierre et al., 2008). A grain protein content (GPC) locus, *GPC-B1*, has been identified on chromosome 6B in wheat (Distelfeld et al., 2006). *Gpc-B1* increases protein content via N remobilization from leaves and senescence (Uauy et al., 2006).

CONCLUSION

In conclusion, we propose the first ideotype for breeding N-efficient cultivars specifically for the United States midwest wheat. In soft-red winter wheat, where grain yield and relatively lower grain protein content is desired, we believe that in-tissue concentration of nitrogen, which traditionally represents uptake and utilization of N, may not be a good indicator of nitrogen use efficiency.

In fact, a superior and N-efficient genotype is one which uses the available N to produce a canopy allowing for maximum radiation use efficiency, producing dry matter that is required for fertile tiller and grain numbers. Therefore, for a grain crop where protein content is not critical, a good indicator of nitrogen use efficiency is fixation of carbon, efficient use of radiation, and developing a productive canopy, per unit of nitrogen used. The rank differences among lines in contrasting environments is a testament to the opportunity to select and breed for more crop per same N (or same crop with less or optimized N). In this context, the success of wheat breeding for N-deficient environments needs management strategies that enable supplying continuous availability of N in the field post-anthesis and during grain fill.

Our study resulted in identification of traits and variants that will lead to increases of yield and maintaining of yield under lower nitrogen conditions, and therefore can be regarded as "the breeder's toolkit for developing N-efficient soft-red winter wheat varieties." For breeding soft-red winter wheat for high-N environment, PU08, PU10, and PU15 would be advantageous due to responsiveness to N with significant increases in grain number, biomass, and number of spikes, which led to the increase in grain yield. Since N treatment did not significantly impact end-use quality of the grains, N management in soft-red winter wheat can focus on the best practices for canopy enhancement, grain number per unit area, and yield.

GERMPLASM AND DETAILED DATA

Seed and detailed data for each line evaluated in this study is available via the wheat breeding program, Purdue University.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

BR and MM planned and designed the research, and wrote the manuscript. BR collected field measurements and analyzed the data. CG performed gluten quality measurements. BR, CG, and MM edited and revised the manuscript. All authors read and approved the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2020.00335/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Cultivar × Management Interaction to Reduce Lodging and Improve Grain Yield of Irrigated Spring Wheat: Optimising Plant Growth Regulator Use, N Application Timing, Row Spacing and Sowing Date

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Severe lodging of irrigated spring-wheat in sub-tropical Australia has previously caused yield loss of between 1.7 and 4.6 t ha^{-1} (20–60% of potential yield). In response, agronomic management options were assessed for their ability to reduce lodging and increase grain yield, namely plant growth regulators (PGRs), timing of nitrogen (N) application, row spacing and sowing date, in combination with long and short duration cultivars across 15 irrigated environments from 2012 to 2016. Our study identified significant interaction between genotype, environment and agronomic management (G × E × M) for grain yield and lodging, although some combinations of agronomic techniques were broadly applicable across cultivars. PGR application improved grain yield of most cultivars in well-irrigated fields that had more than 120 kg ha^{-1} N (mineral N + fertiliser N) at sowing, with yield gains of up to 0.5 t ha^{-1} observed in both lodged and non-lodged fields. However, PGRs had little effect on grain yield when soil + fertiliser N at sowing was less than 80 kg ha^{-1} N. In-crop N application (compared to sowing N application) often improved grain yield of short duration, lodging resistant cultivars, but reduced the yield of long-duration, lodging susceptible cultivars in some environments. Narrow row spacing of 19 cm had the highest grain yield across cultivars in low lodging environments. At a severely lodged environment, narrow rows were the highest yielding for five out of six cultivars when PGRs were used, but was the highest yielding for only half of the tested cultivars when PGRs were not used. Cultivar × sowing date interaction for grain yield was also associated with the occurrence of lodging. Neither early nor late sowing had a consistent yield benefit across a range of cultivars, as lodging severity varied between sowing date depending on the timing of storm-induced lodging events. Lodging resistant long-duration cultivars had more stable grain yield across

environments and increased grain yield in response to early sowing. Further research is needed to determine the optimum management strategy for new cultivars, because farmers do not always choose the most lodging resistant cultivars for reasons of cultivar disease resistance, grain quality and seed availability.

Keywords: G × E × M, wheat, irrigation, PGR, canopy management, in-crop N, crop duration

INTRODUCTION

Irrigation of wheat on broad-acre farms in sub-tropical (i.e. between 23.5 and 31°S) eastern Australia has historically been uncommon due to the greater profitability of irrigated cotton (Hulugalle et al., 1999). Nevertheless, significant areas of irrigated spring-wheat were sown in the region in 2008, due to high grain prices and water availability. Unfortunately, substantial lodging occurred soon after anthesis in most production fields. Lodging related losses were estimated at 1.7 t ha^{-1} on average, with yield losses as high as 4.6 t ha^{-1} in extreme cases (Peake et al., 2014). Peake et al. (2016) found that high levels of soil nitrogen (N) and high seeding rates were probably responsible for the severe lodging experienced in 2008. These factors have previously been identified as increasing lodging risk in high-yielding winter and spring wheat production regions around the world (Stapper and Fischer, 1990; Easson et al., 1993; Sylvester-Bradley et al., 1997; Hobbs et al., 1998; Sylvester-Bradley et al., 2000; Berry et al., 2004).

Following these initial studies, additional research was conducted that aimed to decrease lodging and improve grain yield of irrigated wheat production systems in north-eastern Australia. Peake et al. (2014, 2016) identified traditional long duration cultivars as being more susceptible to lodging and lower yielding than short duration cultivars in the region. Subsequently, Peake et al. (2018) demonstrated that newly released long duration cultivars had a consistent yield benefit in comparison to short duration cultivars, when cultivars were sown at different times to achieve synchronised anthesis during the optimal anthesis window. However, the long duration cultivars were still more prone to lodging than short duration cultivars, and improved agronomic management is therefore still needed to minimise lodging in the region.

Several agronomic management options often referred to as canopy-management practices (Sylvester-Bradley et al., 1997; Sylvester-Bradley et al., 2000) are known to reduce lodging risk and severity. Reduced light quality and quantity (i.e. increased shading) has been shown to weaken the stem base and surface roots, thus increasing lodging risk (Sparkes and King, 2008; Sparkes et al., 2008). Avoiding excessive canopy development during vegetative growth has been shown to reduce lodging risk without reducing grain yield (Sylvester-Bradley et al., 2000; Peake et al., 2016). Reducing crop height also reduces lodging risk by reducing leverage applied to the stem base during windstorms (Baker et al., 1998; Berry et al., 2003). Canopy management practices used to reduce lodging around the world include plant growth regulator (PGR) application (Herbert, 1982; Knapp et al., 1987; Crook and Ennos, 1995; Tripathi et al., 2003), in-crop N application (Mulder, 1954; Kheiralla et al., 1993; Crook and Ennos, 1995; Berry et al., 2000; Islam et al., 2002; Tripathi et al., 2003; Peake et al., 2016; Wu et al., 2019), wider row spacing (Stapper and Fischer, 1990; Din et al., 2017) and delayed sowing (Hanley et al., 1961; Stapper and Fischer, 1990; Berry et al., 2000; Spink et al., 2000).

Few studies have been conducted to assess the suitability of these practices for broad-acre irrigation farms in sub-tropical Australia. Peake et al. (2016) determined that the optimal N management strategy for a representative Vertosol soil (Isbell, 2016) was for the soil to contain 50–70 kg N/ha (mineral N + sowing fertiliser N) at sowing, with the remainder of the crop N requirement applied during the cropping season. This strategy induced visible N stress during tillering which reduced vegetative growth prior to in-crop N application at floral initiation and flag leaf emergence, and subsequently achieved a significant reduction in lodging. However, their study used two outdated cultivars that were subsequently assessed as having moderate to high levels of lodging susceptibility, and was only conducted across two seasons in a single environment. No research has been conducted on the ability of row spacing or PGRs to control lodging in conjunction with the range of cultivars available to farmers in the region. And while the previously mentioned study of Peake et al. (2018) demonstrated the benefits of long duration cultivars for irrigated wheat production in the region, early sowing is known to cause increased lodging risk in high yielding wheat production regions such as Europe and New Zealand. In these environments, late sowing is promoted as a lodging control method for high risk (e.g. high soil fertility) conditions.

This study extends the study of Peake et al. (2018) and reports the findings of a long-term cultivar × agronomy research program, which aimed to identify the optimum agronomic management practices for cultivars adapted to irrigated, broad-acre spring-wheat production regions of sub-tropical Australia.

MATERIALS AND METHODS

Experiments were conducted at multiple locations from 2012 to 2016. **Table 1** details experiments conducted to investigate the interaction of cultivar with PGR application, while **Table 2** details experiments examining the interaction of N application timing, row spacing and sowing date. Due to the large number of cultivars and agronomic treatments, factorial experiments did not include all combinations of cultivar and agronomic management at each location. The majority of experiments were conducted at Spring Ridge (31.3871°S; 150.2469°E) and Gatton (27.54°S; 152.33°E), chosen for their representation of two environmental extremes within the target population of environments. Spring Ridge is a cooler, higher latitude environment with a longer growing season

TABLE 1 | Summary of experiment details, factor entries and PGR effect on grain yield and lodging for PGR × cultivar experiments between 2012 and 2016.

Experiment details[1]				Factor entries					PGR effect on grain yield			Grain yield (t ha^{-1})		Grainfill lodging (%)	
Lodging severity	**Location and season**	**Cultivar duration**	**Sowing N status**	**PGR**	**Yr**	**DG**	**Cv**	**PGR factor significance (Grain Yield)**	**Positive**	**NS**	**Negative**	**Expt. Mean**	**PGR effect (min, mean, max)**	**Expt. Mean**	**PGR effect (min, mean, max)**
High sowing N experiments															
No lodging	Em12	Short	High	2	1	1	16	N.S.	0	16	0	5.64	NA	Nil	Nil
No lodging	SR15/16	Long	High	2	2	1	4	Cv × PGR	3	1	0	8.22	(0, 0.68, 1.16)	Nil	Nil
No lodging	SR15/16	Short	High	2	2	1	8	Cv × PGR	6	2	0	7.89	(0, 0.40, 0.71)	Nil	Nil
Negligible	Brz13	Long/short[2]	High	2	1	2	36	Main effect	36	0	0	5.42	0.56	1.9	(−5.3, −1.0, 0)
Negligible	Em13	Short	High	2	1	1	12	Cv × PGR	2	9	1	6.56	(−0.6, 0.2, 0.91)	1.2	(−5.3, −1.3, 0)
Negligible	Nar13	Long	High	2	1	1	16	Cv × PGR	1	15	0	6.60	(0, 0.13, 1.48)	2.5	(−13.9, −1.3, 6.4)
Negligible	Gat15/16	Short	High	2	2	1	6	Cv × PGR	2	4	0	6.75	(0, 0.06, 0.39)	2.1	(−0.8, −0.1, 0)
Moderate	Brz12	Long	High	2	1	1	22	Main effect	22	0	0	6.81	0.41	7.1	NA
Moderate	Nar13	Short	High	2	1	1	16	N.S.	0	16	0	6.85	NA	6.9	(−3.2, −1.3, 0)
Severe	Gat13	Short	High	2	1	1	15	Main effect	15	0	0	5.79	0.52	11.9	(−28.3, −12.3, 0)
Moderate sowing N experiments															
Negligible	Em13	Short	Moderate	2	1	1	12	Cv × PGR	2	9	1	6.56	(−0.6, 0.2, 0.91)	1.2	(−5.3, −1.3, 0)
Negligible	SR15/16	Long	Moderate	2	2	1	4	Cv × PGR	2	2	0	8.22	(0, 0.2, 0.54)	Nil	Nil
Negligible	SR15/16	Short	Moderate	2	2	1	8	Cv × PGR	4	3	1	7.89	(−0.5, 0.28, 0.6)	Nil	Nil
Negligible	Gat16	Short	Moderate	2	1	1	3	Cv × PGR	0	3	0	6.75	(0, 0, 0)	2.1	NA
Severe	SR14	Long/short[2]	Moderate	2	1	2	12	Cv × PGR	8	3	1	7.17	(−0.53, 0.41, 0.87)	24.5	(−10.6, −3.0, 4.6)
Low sowing N experiments															
Negligible	Brz13	Long	Low	2	1	1	18	N.S.	0	18	0	5.35	NA	1.2	(−1.6, −1.3, −1.0)
Negligible	Brz13	Short	Low	2	1	1	18	Cv × PGR	3	15	0	5.48	(0, 0.3, 1.1)	0.4	(−0.7, −0.5, −0.3)
Negligible	Gat15	Short	Low	2	1	1	3	Cv × PGR	0	3	0	6.75	(0, 0, 0)	2.1	NA
Mild	Brz12	Long	Low	2	1	1	22	N.S.	0	22	0	6.92	NA	4.8	NA
Partially irrigated experiments															
Negligible	Brk13	Long	Moderate	2	1	1	12	Main effect	0	0	12	4.80	−0.21	Nil	Nil
Negligible	Brk13	Short	Moderate	2	1	1	12	N.S.	0	12	0	5.15	NA	Nil	Nil

PGR = plant growth regulators, Yr = year (or season), DG = duration group (i.e. grouped long and short duration cultivars sown on different sowing dates), Cv = cultivar, Em = Emerald, SR = Spring Ridge, Nar = Narrabri, Brza = Breeza, Gat = Gatton, Brk = Brookstead, N.S = no significant effect ($p > 0.05$), Cv × PGR: significant interaction was observed between cultivar and P GR treatment ($p < 0.05$), main effect: the main effect of PGR was significant ($p < 0.0\ 5$) and no higher order interactions involving PGR were significant ($p > 0.0\ 5$). [1] = Each line of the table represents a single statistical analysis conducted at a single location, with multi-year and duration group factors also listed where relevant. [2] = Cultivar was nested within duration group for these experiments.

TABLE 2 | Summary of experiment details, factor entries and results summary for grain yield and lodging, for the N timing, sowing date and multi-factor row-spacing experiments between 2014 and 2016.

Experiment details[1]		Sowing Soil N (kg ha^{-1})	Factor entries							Date of sowing	Highest signif.* effect	Experiment mean yield (t ha^{-1})/ grainfill lodging (%)		
Location and season	Cv duration/ sow date	Yr 1/Yr 2	N	RS	PGR	Yr	Env	Sow	Cv			2014	2015	2016
N timing experiments														
Gat15/16	Long/early	50/140	5	1	–	2	1	1	4	15-May/17-May	Cv × N[2]	–	6.95/17.2	6.64/17.2
Gat15/16	Short/late	50/140	5	1	–	2	1	1	2	29-May/25-May	N[3]	–	6.70/17.3	6.98/10.2
SR15/16	Long/early	140/160	5	1	–	2	1	1	2	18-May/19-May	Cv × N × Yr	–	8.58/1.0	8.26/1.6
SR15/16	Short/late	140/160	5	1	–	2	1	1	4	19-May/14-Jun	Cv × N × Yr	–	7.32/0.3	7.00/nil
Row spacing multi-factor														
SR14	Long/early	130	1	3	2	1	1	1	2	19-May	PGR × RS × Cv	8.03/20.3	–	–
SR14	Short/late	130	1	3	2	1	1	1	4	11-Jun	PGR × RS × Cv	7.10/23.1	–	–
Gat15/16	Short/late	50/140	2	2	2	2	1	1	3	29-May/25-May	PGR × Cv × N	–	6.71/2.7	6.79/1.7
SR15/16	Long/early	140/160	2	3	2	2	1	1	2	18-May/19-May	PGR × RS × Cv × N × Yr	–	8.33/nil	8.47/nil
SR15/16	Short/late	140/160	2	3	2	2	1	1	4	19-Jun/14-Jun	PGR × RS × Cv × N × Yr	–	8.06/nil	7.97/nil
Sowing date (multienvironment analysis of all 5 experiments)														
Em14	L + S/E + L	260	1	1	–	1	5	2	6	13-May/30-May	Sow × Cv × Env (multi-env. analysis)	6.04/19.5	–	–
Nar14	L + S/E + L	170	1	1	–	1		2	6	15-May/30-May		7.50/6.8	–	–
SR14	L + S/E + L	130	1	1	–	1		2	6	19-May/11-Jun		8.31/25.0	–	–
Nar15	L + S/E + L	140	1	1	1	1		2	6	8-May/9-Jun		–	7.12/1.4	–
SR15	L + S/E + L	140	1	1	1	1		2	6	18-May/19-Jun		–	7.90/nil	–

*Cv = cultivar, Yr = year, N = nitrogen, RS = row spacing, PGR = plant growth regulator, Env = environments (i.e. location × year combinations), Sow = sowing dates, L + S = long and short, E + L = early and late, SR = Spring Ridge, Em = Emerald, Nar = Narrabri, Gat = Gatton. * = Significant at $p < 0.05$ unless otherwise stated. [1]Each line of the table represents a single statistical analysis conducted at a single location, except where indicated otherwise. [2]$p = 0.056$, [3]$p = 0.086$.*

and high yield potential, while Gatton is a warmer, lower latitude environment with a shorter growing season and moderate yield potential (Peake et al., 2014, 2016). Additional locations were Narrabri (30.3324° S; 149.7812° E), which has a slightly shorter growing season than Spring Ridge, and Emerald (23.5273° S; 148.1646° E) near the Tropic of Capricorn and having a shorter growing season than Gatton.

Agronomic Treatments

A wide range of germplasm was screened in initial experiments (2012 and 2013) before conducting multi-factor experiments with a smaller set of high-performing cultivars from 2014 to 2016. When comparing cultivars in combination with three of the agronomic treatments investigated (PGRs, N application timing and row spacing), cultivars were sown on one of two available sowing dates (i.e. early or late) as recommended for each cultivar in that specific location, to allow them to reach anthesis approximately during the optimum flowering window for each location. The cultivars LRPB Cobra and LRPB Trojan (hereafter referred to as Cobra and Trojan) were classified as short duration cultivars at the cooler southern environment (Spring Ridge) but as long duration cultivars at the warmer environment (Gatton). All the cultivars discussed within this study are protected by Plant Breeders Rights legislation within Australia. Other agronomic treatments consisted of combinations of the following.

Plant Growth Regulators (PGRs)

The PGR treatment consisted of 1000 ml/ha chlormequat chloride mixed with 200 ml/ha trinexapac-ethyl, applied approximately at GS31 (Tottman, 1987). This PGR-mix was applied on the same day for all cultivars in each experiment, hence the application occurred approximately when mean crop stage of all cultivars was GS31. Variation in crop development between cultivars thus meant that the application was not applied precisely at GS31 for each cultivar in all experiments. A control treatment (i.e. no PGR applied) was also included for all cultivars, in all PGR experiments.

N Application Timing

Two N strategies (sowing N and in-crop N) were compared for their effect on grain yield and lodging. The aim of the in-crop N application strategy was to apply no fertiliser N [other than small quantities of starter fertiliser such as mono ammonium phosphate (MAP)] until GS31 (Tottman, 1987). This involved surface-spreading of urea to ensure that the crop had been supplied with 200 kg/ha N (taking both soil mineral N at sowing and fertiliser N into account) by GS31. The remainder of the N fertiliser required to achieve target yield potential was applied at GS39. The in-crop N strategy was compared with an alternate 'sowing N' strategy, where all N was applied either prior to, or within 2 weeks of sowing. Three other in-crop N strategies were also tested which created five N treatments in total; however, only the two described above are reported herein. Total season N supply ranged from 275 to 400 kg N ha^{-1} depending on location and potential yield. This strategy achieved non-limiting N status through grainfilling as evidenced by the grain protein being in excess of 13% in all experiments (Goos et al., 1982; Holford et al., 1992).

Row Spacing

A range of row spacing was tested at multiple locations, with the exact spacing depending on the capability of local sowing equipment. Typically, the wide row spacing was 38 cm, the intermediate spacing was 25 or 28 cm and the narrow row spacing was 19 cm.

Sowing Date and Cultivar Duration

Six cultivars were compared on both an early and late sowing date in 2014 and 2015, at three locations (Emerald, Narrabri and Spring Ridge) to determine whether late sowing could be used to reduce lodging risk and increase grain yield. The cultivars were Cobra, Trojan, Kennedy, EGA Bellaroi (hereafter referred to as Bellaroi), Caparoi and Suntop. Sowing dates were approximately 2–3 weeks apart (**Table 2**).

Due to the importance of sowing on time and the requirement for a sowing irrigation at some locations, sowing date treatments were sown in adjacent but separate areas. This avoided the problem experienced by Peake et al. (2016) in which late sown areas of split plot experiments were irrigated on the first sowing date, subsequently experienced rainfall, and were then too wet to sow on the optimal late sowing date thus preventing synchronisation of anthesis.

Plot Management and Statistical Analysis

Plots at Narrabri, Breeza, Emerald and Gatton were 2 m wide × 7 m long and trimmed to 5 m long at harvest. Longer, narrower plots 1.4 m wide × 12 m long were sown at Spring Ridge and trimmed to 10 m at harvest. Seeding rate was 110 seeds per m^2. Edge rows were not trimmed due to the similarity of lateral plot dimensions with the 2 m bed configuration commonly used on furrow-irrigated farms within the region. The gap between outside rows of neighbouring plots was 50 cm at all locations except Narrabri where it was 60 cm. Yield was calculated by multiplying final plot length by the distance between the centre of neighbouring plots, and grain yield is reported at 12% moisture. Pests and diseases were effectively controlled using a range of agrochemicals as preferred by local co-operators, except for a powdery mildew (*Blumeria graminis*) outbreak that became noticeable during late grain filling at Narrabri in 2014.

Overhead irrigation systems (i.e. lateral move irrigators or hand-shift sprinklers) were used for all experiments except those conducted at Breeza, where experiments were furrow irrigated. Irrigation scheduling was timed to avoid water stress by applying irrigation weekly to fully replace crop evapotranspiration (locally known as 'full irrigation'). The effectiveness of implementation varied between locations and seasons due to climate variation (i.e. evaporative demand and rainfall), logistical issues and individual soil characteristics. The experiments at Brookstead 2013 were ultimately water-stressed due to an unexpectedly reduced supply of irrigation water and are thus referred to as 'partially irrigated' experiments.

Lodging was calculated as 'average grainfill lodging' as described by Peake et al. (2016). This involved rating lodging where possible on the first day after each potential lodging event (rainfall or irrigation), and every 5–7 days between lodging events. Lodging score for a given day were similar to those used by Mulder (1954), i.e. the average stem angle from vertical (divided by 90 and expressed as a %) for the whole plot and ranged from 0% (no lodging) to 100% (completely lodged). These data were then used to calculate the average lodging during grainfill (also referred to as 'grainfill lodging') by multiplying each daily score by the number of days before the next score was taken, and then averaging these over the number of days between anthesis and harvest. This method quantifies the likelihood that lodging may have caused physiological disruption to the crop. By contrast, the lodging score at harvest (Stapper and Fischer, 1990) may be wholly due to a single, late lodging event immediately before harvest, and not reflect on the development of lodging through the season.

Experiments were generally arranged as randomised complete block designs incorporating a latin square design to avoid the same treatments occurring in the same row/column. The exception was at the Narrabri 2014 sowing date experiments (**Table 2**) which were implemented as split-plot experiments, with the agronomic treatments randomly allocated at the main plot level and cultivars at the sub-plot level. All experiments had three replications for each combination of cultivar, sowing date and agronomic treatment.

Combined experiment analyses were conducted using the REML (residual maximum likelihood; Patterson and Thompson, 1971) procedure in GENSTAT (19th Edition, VSN International, 2017), using linear mixed models with individual trial designs and separate residual variances fitted for each trial. Location and season were considered random effects, while agronomic treatments and cultivars were fitted as fixed effects. Square-root transformation was necessary before analysis of average lodging during grainfill for some experiments, and the results reported have been back-transformed. In all analyses, the level of significance was set at $P = 0.05$ unless stated otherwise. The least significant difference (LSD) procedure was used to compare levels of an effect if the F-test was significant.

RESULTS

Interaction of Cultivars With Plant Growth Regulator

Significant grain yield increases were observed in most of the PGR × cultivar experiments (**Table 1**). Significant interactions between cultivar and PGR for grain yield meant that no specific cultivar consistently achieved increased grain yield in response to PGR application. Out of 251 comparisons from the fully irrigated experiments conducted using a range of cultivars, locations, seasons and sowing N availability, 106 showed a yield advantage associated with PGR application, 141 were not significantly different, and 4 showed a significant yield decrease. Cultivars that showed a significant yield decrease at Emerald 2013 (Merinda), Spring Ridge 2014 (Lancer) and Spring Ridge 2015/2016 (Cobra) all achieved a significant positive yield response to PGRs in at least one other experiment. All cultivars used across multiple experiments had a significant increase in grain yield in response to PGR application in at least one experiment. In the two partially irrigated experiments at Brookstead in 2013, PGRs did not increase grain yield of the short-duration cultivars, and significantly decreased grain yield by 0.21 t ha^{-1} in the long duration cultivars (**Table 1**).

The benefits of PGR application were most clearly demonstrated at Gatton in 2013, where a significant positive relationship was observed between the PGR-associated yield gain and lodging reduction, across a range of cultivars (**Figure 1**). The maximum PGR-associated yield gain for an individual cultivar in this experiment was 1.1 t ha^{-1}. However, PGR application did not always reduce grainfill lodging and even increased lodging occasionally, as seen at Spring Ridge 2014 (**Figure 2**) where a significant linear trend was also observed between lodging reduction, and the yield increase attributed to PGR application. In this experiment the x-intercept of the regression line was −15, with one cultivar lodging more severely in response to PGR application, and several cultivars having yield increases of 0.25–0.5 t ha^{-1} in association with PGR application despite having no decrease in lodging. The maximum PGR-associated yield gain for an individual cultivar in this experiment was 1.75 t ha^{-1}.

The probability of observing PGR-associated grain yield increases was greatest in the fully irrigated experiments where sowing N status was high or moderate (**Table 1** and **Figure 3**). Nearly 60% of cultivar × PGR comparisons displayed a significant grain yield increase when sowing N (i.e. mineral

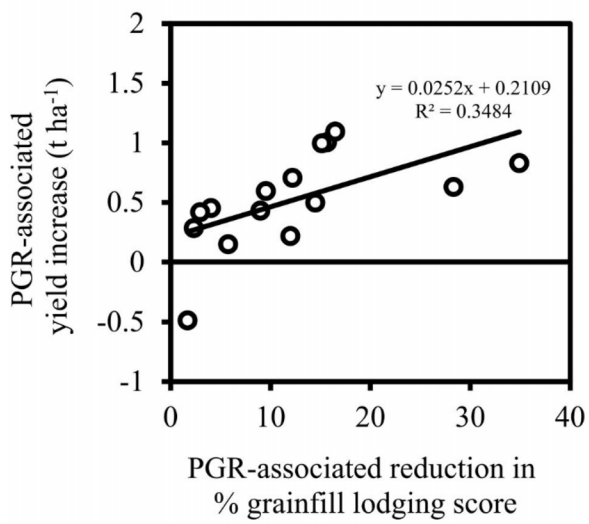

FIGURE 1 | Grain yield increase associated with PGR-mix application (i.e. the difference between predicted grain yield of PGR treated and control plots of the same cultivar) vs. reduction in grainfill lodging score (i.e. the difference between grainfill lodging score of PGR treated and control plots for the same cultivar) of the equivalent plot comparisons, for 15 cultivars tested at Gatton in 2013. The solid line represents the significant (F_{prob} = 0.021) linear regression.

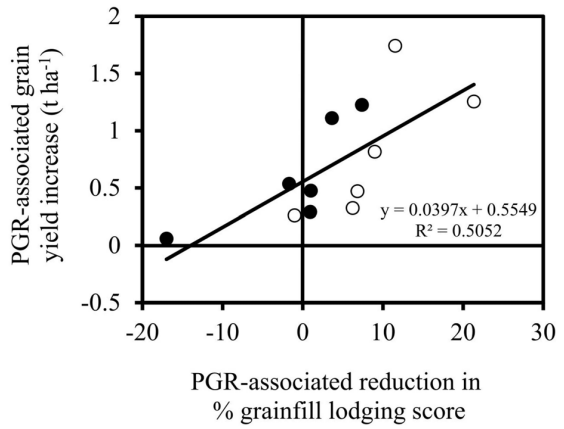

FIGURE 2 | Grain yield increase associated with PGR-mix application (i.e. the difference between predicted grain yield of PGR treated and control plots of the same cultivar) vs. reduction in grainfill lodging score (i.e. difference between grainfill lodging score of PGR treated and control plots for the same cultivar) of the equivalent comparisons, across six cultivars and two sowing dates at Spring Ridge in 2014. The solid line represents the significant (F_{prob} = 0.01) combined linear regression of data from early (•) and late (○) sown experiments.

N + fertiliser N) was greater than 250 kg ha^{-1}, and 41% had a significant grain yield increase when sowing N was between 120 and 150 kg ha^{-1}. No significant difference was observed between the PGR and control treatments for most remaining cultivar × PGR combinations in experiments with high or moderate sowing N status. A negative grain yield response to PGR application was observed in three out of 39 comparisons in the moderate sowing N experiments, and one of the 151 comparisons in the high sowing N experiments. At low sowing N experiments (where between 50 and 80 kg N ha^{-1} was available from sowing for vegetative growth), only 5% of cultivar × PGR comparisons achieved a significant yield increase in response to PGR application, while the remainder (95%) had no significant difference in grain yield between PGR treatments (**Figure 3**). A chi-squared test confirmed that the ratio of positive, non-significant and negative grain yield differences between PGR × cultivar combinations was significantly different between the high, moderate and low sowing N fields (data not shown).

Gatton 2013 and Spring Ridge 2014 possessed high and moderate sowing N, respectively, and were the two most heavily lodged experiments. These experiments contained two of the biggest grain yield increases associated with PGR application across a range of cultivars (0.52 and 0.41 t ha^{-1} respectively; **Table 1**). Yet PGR application also increased grain yield by approximately 0.5 t ha^{-1} in some experiments with high or moderate sowing N when lodging was negligible, e.g. Breeza 2013, Spring Ridge 2015 and 2016 (**Table 1**).

Interaction of Cultivars With N Application Strategy

Significant N treatment effects were observed either as main effect or as interactions with cultivar and/or season for grain yield and lodging in the cultivar × N timing experiments conducted at Spring Ridge and Gatton in 2015 and 2016 (**Table 2** and **Figure 4**). Only results for cultivars that were included both at Spring Ridge and Gatton are reported. Suntop and Cobra both achieved significantly increased yield of 0.4–0.6 t ha^{-1} in conjunction with in-crop N application at Gatton in both seasons, but only Cobra yielded significantly more at Spring Ridge in 2015. Mitch did not have a significantly different yield between N treatments in any of the experiments. Grain yield of Lancer and Trojan was significantly decreased in response to in-crop N application in both seasons at Spring Ridge (by 0.3–0.4 t ha^{-1} for Lancer and 0.5 to 0.8 t ha^{-1} for Trojan), but was not significantly different between N treatments at Gatton.

The significant yield increases associated with in-crop N application for Cobra and Suntop were not accompanied by significant reductions in lodging, with the exception of Suntop at Gatton in 2015 (**Figure 4**). Surprisingly, lodging

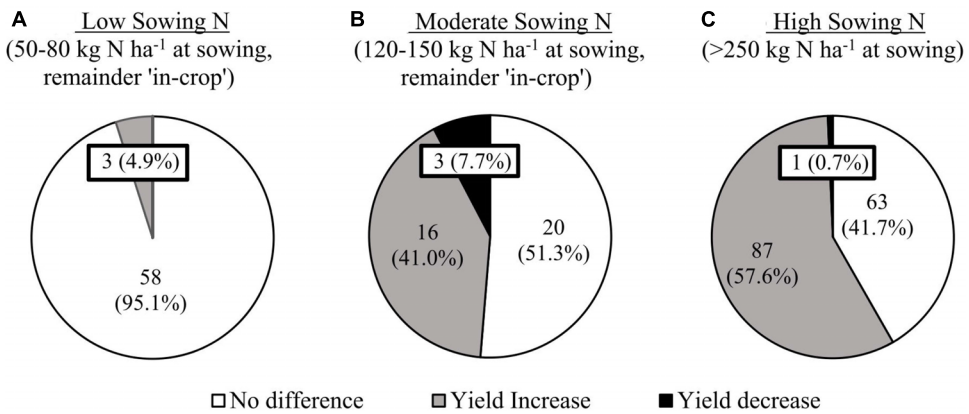

FIGURE 3 | Pie chart showing PGR response (significant grain yield increase, no change, significant grain yield decrease) across cultivar comparisons grouped into **(A)** low, **(B)** moderate and **(C)** high sowing N fields. Results collated from all experiments listed in **Table 2** except for the partially irrigated experiments at Brookstead 2013.

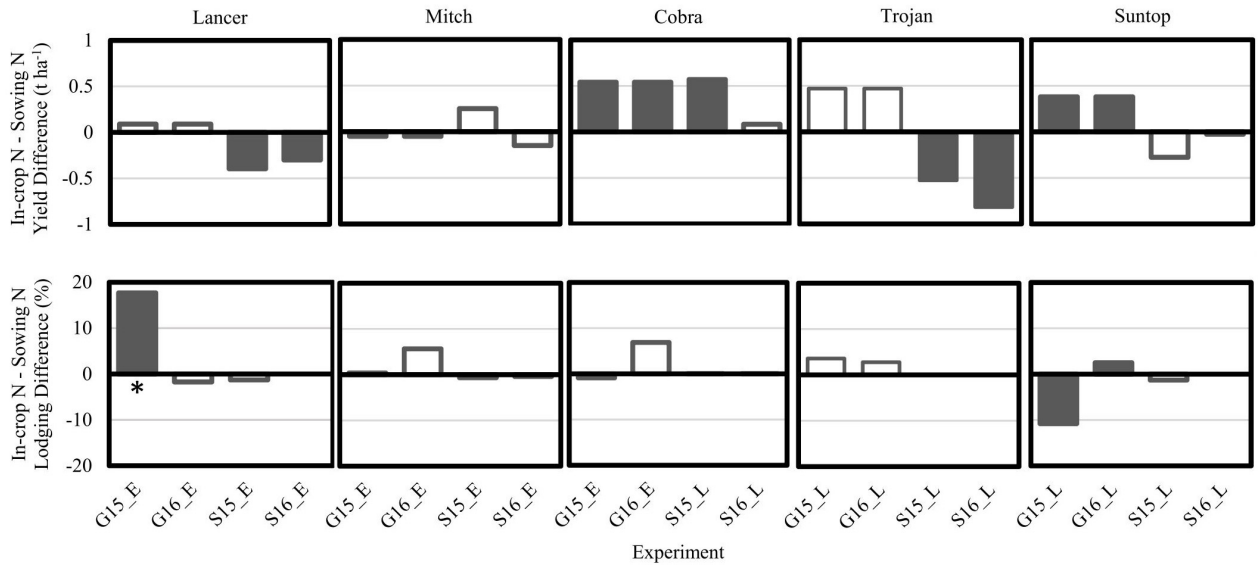

FIGURE 4 | Difference between in-crop N application and sowing N application strategies for grain yield and lodging score for the five cultivars sown at both the Gatton (G) and Spring Ridge (S) sites in the early (E) or late (L) sown N timing × Cultivar experiments in 2015 and 2016. Filled bars indicate that the difference between N treatments was significantly different ($p < 0.05$); empty bars were not significantly different ($p > 0.05$). A positive value indicates larger absolute values for the in-crop N treatment, meaning that bars above the line in the lodging graphs demonstrate more severe lodging associated with the in-crop N treatment. ∗Lodging for Lancer at Gatton 2015 began first in the sowing N treatment, but stems straightened to the extent that average grainfill lodging was ultimately worse in the in-crop N treatment which lodged heavily later in the season.

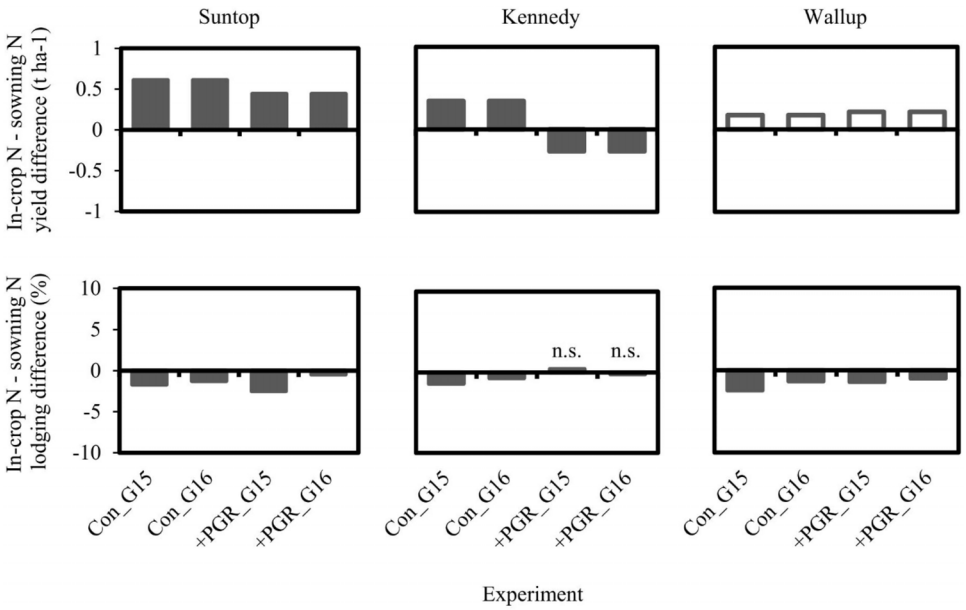

FIGURE 5 | Difference between in-crop N application and sowing N application strategies for grain yield and lodging score for three short duration cultivars in the N timing × row spacing multi-factor experiments from Gatton (G) in 2015 and 2016. A positive value indicates larger absolute values for the in-crop N treatment, meaning that bars above the line in the lodging graphs demonstrate more severe lodging associated with the in-crop N treatment. Filled bars were significantly different ($p < 0.05$) and empty bars were not significantly different ($p > 0.05$). 'Con' = Control (i.e. no PGRs applied), ' + PGR' = PGR mix applied. 'n.s.' = not significantly different ($p < 0.05$).

in Lancer was significantly worse in association with in-crop N application at Gatton in 2015. Close examination of the timing of lodging revealed that the Lancer sowing N treatment lodged before the in-crop N treatment, but the stems then straightened in a phototropic response. The in-crop N plots lodged later but did not recover as well due to the later

growth stage, leading to the greater average lodging score during grainfilling.

In a second experiment conducted using short duration cultivars at Gatton, significant interaction was observed between cultivar, PGR treatment and N application strategy for grain yield and lodging. The short duration cultivars in this experiment exhibited different responses to PGR and N treatments (**Figure 5**). Grain yield of Suntop was significantly increased in response to in-crop N application compared to sowing N application (by approximately 0.5 t ha^{-1}) regardless of whether PGRs were applied, while grain yield of Wallup was not significantly different between N treatments in combination with either PGR treatment. In-crop N application increased grain yield of Kennedy compared to sowing N application when no PGRs were applied (0.35 t ha^{-1}), but decreased grain yield of Kennedy (−0.27 t ha^{-1}) when combined with PGR application. Lodging was significantly reduced for in-crop N compared to sowing N for all three cultivars when no PGRs were applied, and also for Suntop and Wallup when PGRs were applied.

Interaction of Cultivars With Row Spacing, PGRs and N Timing

Significant cultivar × PGR × row spacing interaction for grain yield was observed at Spring Ridge in 2014 (**Table 2** and **Figure 6**) where 130 kg ha^{-1} of N was available at sowing and severe lodging occurred. The long duration cultivars Lancer and Mitch both displayed similar interactions of row spacing and PGRs, with the narrowest row spacing (19 cm) being the highest yielding of all row spacing treatments when PGRs were applied, but the lowest yielding when PGRs were not applied (**Figures 6A,B**). These trends were not directly associated with severity of lodging (**Figures 6D,E**) as lodging was more severe in conjunction with PGR application for these two cultivars. The short duration cultivar Caparoi also had increasing yield with narrower row spacing when PGRs were applied (**Figure 6C**) but the intermediate row spacing exhibited the greatest yield in the absence of PGR application. Lodging in Caparoi was not significantly different between PGR and control plots (**Figure 6F**).

Bellaroi and Wallup exhibited different yield response patterns across row spacings (**Figures 6G,H**) compared to Lancer and Mitch at Spring Ridge in 2014. Narrow row spacing gave a small (non-significant) yield increase when PGRs were applied, but a large, significant yield increase when PGRs were not applied that was associated with reduced lodging in the narrow row spacing (**Figures 6J,K**). Bellaroi and Wallup had substantially less lodging when PGRs were applied on average across row spacings (**Figures 6J,K**). Merinda (**Figures 6I,L**) exhibited different yield response patterns across row spacings to the other cultivars, with the intermediate row spacing (25 cm) being the highest yielding regardless of whether PGRs were used. Despite the significant interactions with row spacing and cultivar, PGR application was generally associated with significantly greater grain yield compared to the untreated control across the range of cultivars (**Figure 6**), in agreement with the experiments reported in Section 'Interaction of Cultivars With Plant Growth Regulator'.

At Gatton in 2015 and 2016 where only mild lodging occurred, there was a near-significant higher order interaction ($p = 0.057$) of row spacing with season, PGR application and cultivar for grain yield. Grain yield was not significantly different between wide and narrow row spacing for 10 out of the 12 comparisons (data not shown). However, grain yield was significantly greater in the wider (35 cm) row spacing by 0.16 t ha^{-1} for the cultivar Suntop in 2015 when no PGRs were applied, and also by 0.34 t ha^{-1} for the cultivar Kennedy in combination with PGR application in 2016. Grain yield trends across treatments were not associated with treatment differences for lodging within this experiment.

Significant grain yield increases were observed in conjunction with narrow row spacing at Spring Ridge in 2015 and 2016 (**Figure 7**), where negligible lodging was experienced in both seasons. A significant five-way interaction of cultivar, row spacing, N regime, PGR treatment and seasons was observed for grain yield within both the long and short duration cultivar groups (**Table 2**). The significant five-way interaction was predominantly exhibited as variability between the low yielding agronomic factor combinations (data not shown) that are less favoured by growers in the region (e.g. no PGRs applied). In particular, in 2016 when in-crop N application was used and PGRs were not applied, both Cobra and Suntop had a reverse trend where grain yield decreased with narrower row spacing. This trend was isolated as it was not evident in the previous season, or within the same season when PGRs were used.

On average across PGR and N treatments, significant grain yield increases were observed in conjunction with narrow row spacing at Spring Ridge in 2015 and 2016 (**Figure 7**). In particular, the 19 cm row spacing showed a 0.7–0.8 t ha^{-1} grain yield increase compared to the 38 cm row spacing, on average across the long duration cultivars (Lancer and Mitch) in both seasons and the short duration cultivars (Bellaroi, Cobra, Trojan and Suntop) in 2015 (**Figures 7A,B**). The highest grain yields were achieved at Spring Ridge by combining the 19cm row spacing with PGR application and sowing N application (**Figure 7C**).

Interaction of Cultivar and Crop Duration With Sowing Date and Environment

Significant cultivar × sowing date × environment interaction was observed for grain yield (**Table 2** and **Figure 8**) when comparing six cultivars across two sowing dates and five environments. The early sowing date achieved the highest grain yields at three environments (Emerald 2014, Narrabri 2015 and Spring Ridge 2015) while the late sowing date had the highest yields at two environments (Narrabri 2014 and Spring Ridge 2014). Lodging was more severe on the early sowing date at Narrabri 2014 and on the late sowing date at Emerald 2014, potentially contributing to the yield difference at these environments. At Spring Ridge 2014 the highest yielding sowing date (late sowing) also experienced the greatest lodging. Lodging at this location was initially worse on the early sowing date, but a severe late lodging event affected the late sown experiments more than the early sowing (data not shown). At Emerald 2014, the increased lodging associated with late sowing was probably related to the timing of storms.

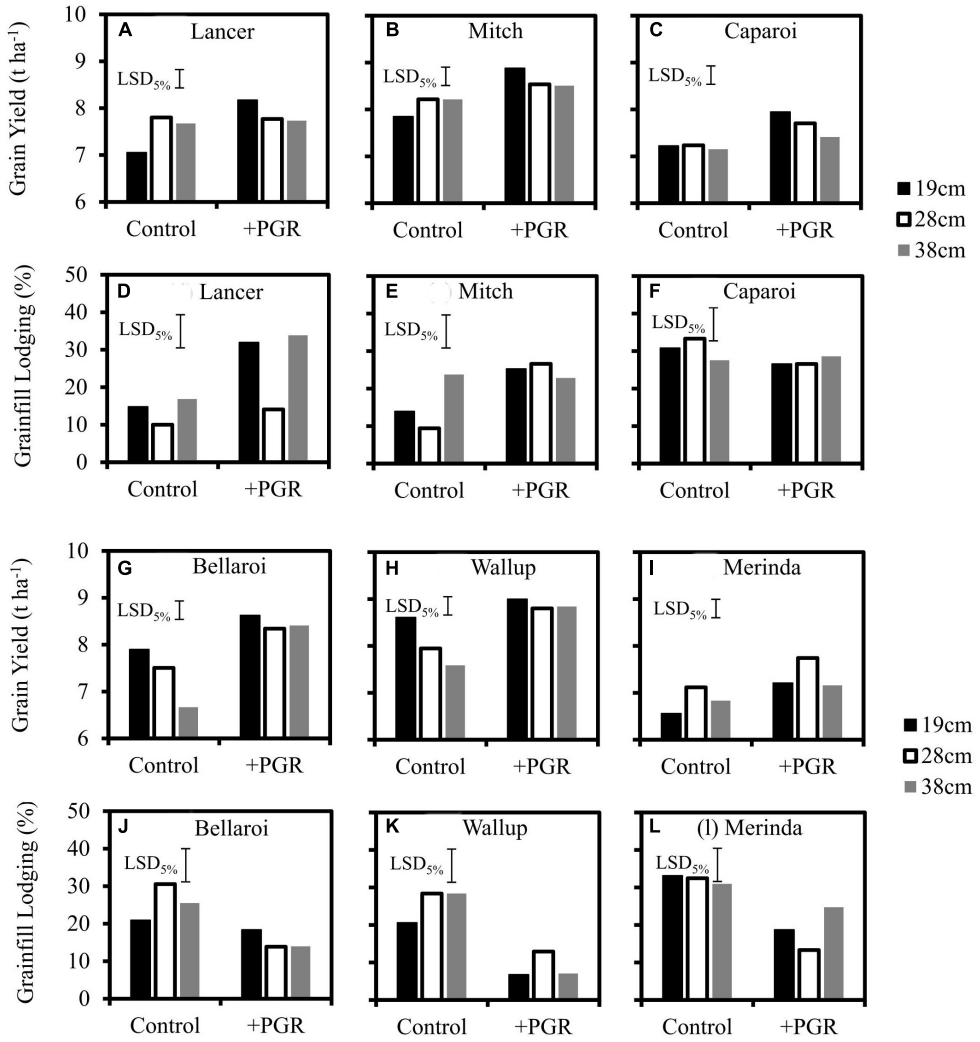

FIGURE 6 | Grain yield and grainfill lodging for three row spacings in response to plus and minus PGR-mix treatments in six cultivars sown on their optimum sowing date at Spring Ridge in 2014. $LSD_{5\%}$ represents the average LSD across all pairwise comparisons. Maximum LSD was 5% greater than average LSD, while minimum LSD was 10% below average LSD. **(A–F)** Grain yield and lodging for Lancer, Mitch, Caparoi. **(G–L)** Grain yield and lodging for Bellaroi, Wallup, Merinda.

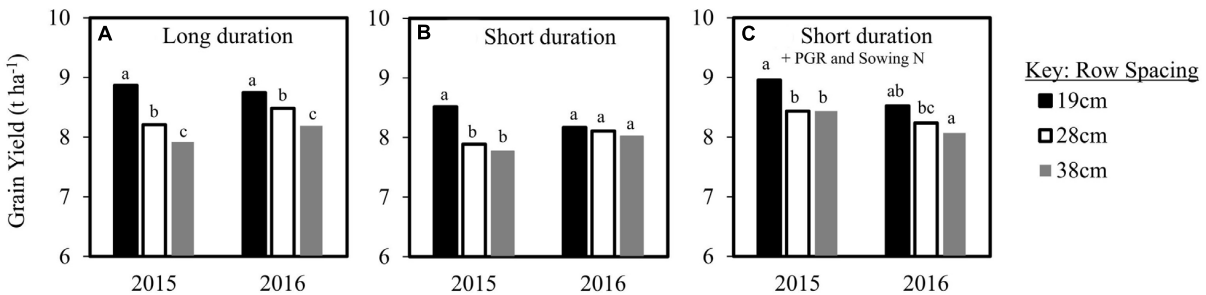

FIGURE 7 | Grain yield of row spacing treatments from a combined analysis of Spring Ridge across the low-lodging seasons of 2015 and 2016 for **(A,B)** long and short duration cultivars on average across PGR and N treatments, and **(C)** short duration cultivars in combination with the site-specific highest yielding management practices of sowing N application in combination with application of the PGR-mix.

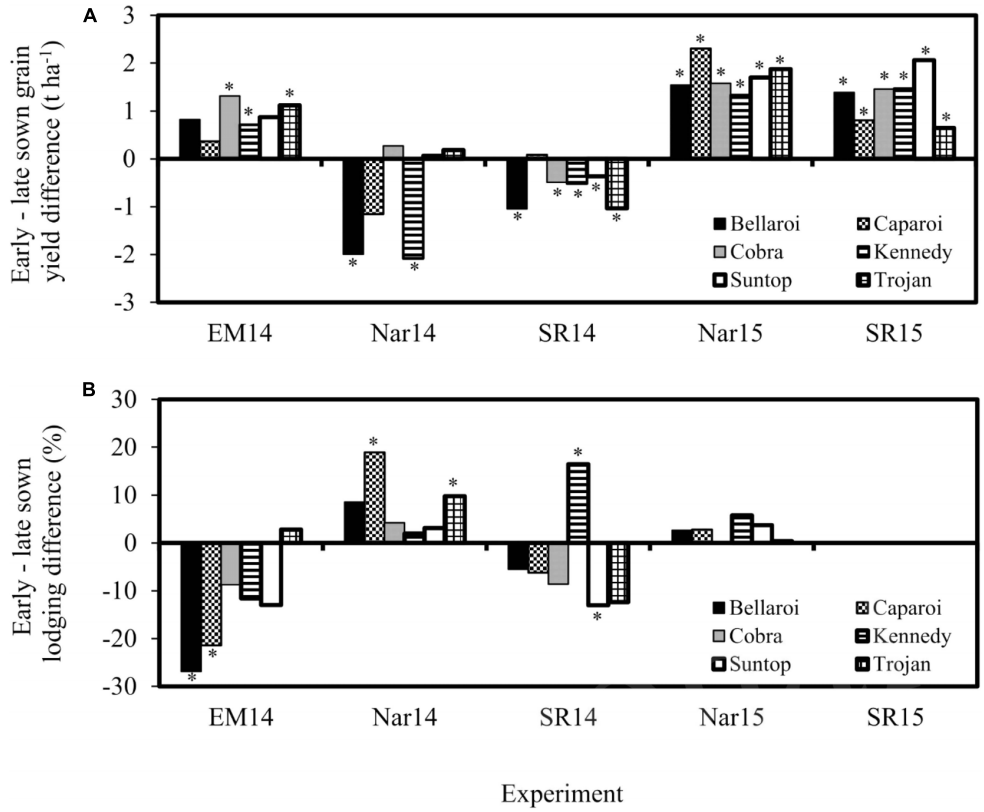

FIGURE 8 | Difference between early and late sown grain yield **(A)** and lodging score **(B)** of six cultivars sown at 5 environments in 2014 and 2015 (EM = Emerald, Nar = Narrabri, SR = Spring Ridge). A positive value indicates larger absolute values for the early sowing treatment, meaning that bars above the line in the lodging graphs demonstrate more severe lodging associated with early sowing. An asterisk '∗' signifies that the difference between early and late sowing was significant ($p < 0.05$).

These caused more severe lodging in the late sown experiment in comparison to the early sown experiment (**Figure 9**).

Cultivar × sowing date interaction was more apparent at Narrabri 2014. Three cultivars (Cobra, Suntop and Trojan) had similar grain yield between the sowing dates, while the remaining cultivars had substantially decreased grain yield (>1.0 t ha^{-1}) on the early sowing date. The largest and most consistent yield increases associated with early sowing were at Narrabri and Spring Ridge in 2015. As discussed by Peake et al. (2018), the early sown treatments at these locations probably experienced less water stress during grainfilling due to the development of deeper root systems. This stress occurred during heat wave conditions, when irrigation infrastructure could not supply enough water to equal potential evapotranspiration.

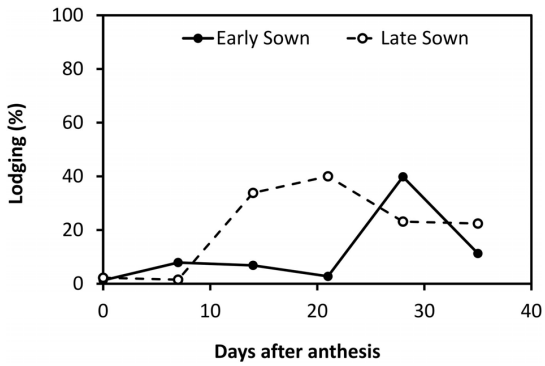

FIGURE 9 | Mean lodging score vs. days after anthesis from the early (•) and late (○) sown experiments at Emerald in 2014. A 14-day difference was recorded between the date of 50% anthesis for the two sowing dates, hence storm-related lodging was experienced at an earlier growth stage in the late sown experiment.

DISCUSSION

The results of the study showed that G × E × M (genotype by environment by management interaction) is present within irrigated, sub-tropical wheat production systems. Some agronomic practices (PGRs and narrow row spacing) generally improved grain yield across a wide range of applicable cultivars and environments, particularly when used together. Other practices (in-crop N application and early/late sowing) increased grain yield for specific cultivar, management or environment combinations. Interaction was also observed between multiple management practices, and it is important to understand the

specific circumstances under which each management practice was associated with increased grain yield. Trends in grain yield were sometimes (but not always) related to the variation in lodging between environments and/or seasons.

Application of PGRs induced four main types of response: increased grain yield in fields where lodging was moderate to severe; increased grain yield when lodging was negligible; no grain yield increase when lodging was negligible and rare instances where yield was decreased in response to PGR application. The first two responses (increased grain yield) occurred when sowing soil N levels were greater than 120 kg ha^{-1}. The third response (no grain yield effect) was mostly associated with fields where either (i) soil N at sowing was low (i.e. 50–70 kg ha^{-1}) and in-crop N application was used to reduce lodging risk, or (ii) experiments were only partially irrigated. The fourth response (negative grain yield response) was rare, occurring in just 2% of comparisons in fully irrigated fields with moderate or high sowing N, and in one of the partially irrigated experiments.

It is important for farmers in the region to understand their management options when growing irrigated wheat on fields with high soil N, such as those of north-eastern Australia where > 200 kg ha^{-1} of N has been frequently observed at sowing (Peake et al., 2014). These soil N levels arise through a combination of residual N from previous crops, and mineralisation of N over the multi-year fallows that can occur due to irregular water supply. Our study found that PGR application had a positive or neutral effect on grain yield in high N environments. The effect was not strictly dependant on the occurrence of lodging, with large yield increases (0.5 t ha^{-1}) recorded in response to PGR application in some environments where lodging was negligible. This gives confidence to farmers that PGR application can increase yield and reduce lodging of a wide range of cultivars when soil N at sowing is high. The variable response of cultivars to PGR application was potentially due to variability in the power of statistical analysis between experiments and the difficulty of applying PGRs at a consistent growth stage for each cultivar in each experiment. Precise application of PGRs at the optimum growth stage to individual cultivars may achieve more consistent yield gains than observed herein. In rare instances, a negative yield response was observed in high or moderate N fields. This may have occurred because the increased yield potential associated with PGR use increases weight (and leverage) at the top of the plant (Berry et al., 2004) which can subsequently worsen late season lodging, leading to eventual yield losses. The same mechanism probably explains the increased grainfill lodging that was occasionally observed in association with PGR application.

The increased grain yield we observed in response to PGR application when lodging was negligible has previously been observed in studies using the same PGR-mix at slightly different rates (Matysiak, 2006; Zhang et al., 2017). Similar results have also been observed in studies using chlormequat chloride alone for either winter wheat (Pinthus and Rudich, 1967; Mathews and Caldicott, 1981) or spring wheat (Harris, 1978). However, none of these studies reported both soil mineral N and fertiliser N available to the experimental treatments, and it was not possible to ascertain trends in the literature in relation to impact of N availability on PGR efficacy. Future studies of PGR efficacy should ensure that both soil N at sowing and fertiliser N regime are reported, to allow more detailed assessment of environmental factors influencing yield gains in the presence or absence of lodging.

The mechanism of PGR-associated yield increases in the absence of lodging is also unclear. PGR application to crops during vegetative growth has been reported to reduce height and above-ground biomass for a range of PGR products (Berry et al., 2004). It has been demonstrated that maximum grain yield of winter wheat was obtained by having a moderate canopy density, achieved by reducing N supply (Sylvester-Bradley et al., 1997). In the absence of lodging, PGR application (and the subsequently reduced canopy size) might increase grain yield due to more efficient light interception through the entire canopy (Duncan, 1971; Burgess et al., 2017), or more efficient use of undetermined scarce resources (e.g. micronutrients or water). Further study is necessary to determine the mechanisms causing increased grain yield in response to PGR application, in the absence of lodging.

In the third PGR response category, our results indicated that PGR application rarely increased grain yield in fields where low sowing N (i.e. 50–80 kg soil mineral N ha^{-1}) was used in conjunction with in-crop N application to minimise lodging. It is probable that successful implementation of in-crop N application (i.e. canopy management) eliminated the excessive crop canopy size that underpins PGR response. The use of either (but not both) of these practices is therefore recommended for irrigated wheat production on vertosol soils in north-eastern Australia. The fourth PGR response occurred most noticeably when decreased grain yield was observed in a partially irrigated experiment at Brookstead 2013, where water supply was limited, and grain yield was below 6 t ha^{-1}. This result contrasted with the results of Barányiová and Klem (2016) who found that chlormequat chloride or trinexapac-ethyl used individually could increase grain yield of winter wheat under water deficit. Their findings are potentially related to the results of De et al. (1982) who found that application of chlormequat chloride could lead to an increase in root:shoot ratio, potentially decreasing the effect of water stress through reduced above ground biomass and a larger root system. However, Green (1986) presented evidence showing both positive and negative yield responses to PGR application in water deficit scenarios. In our partially irrigated experiment, the reduced grain yield associated with PGRs may have been caused by application at a sub-optimal growth stage or an unknown negative interaction between PGR application and the environmental conditions experienced at this particular site.

In-crop N application is commonly used to reduce lodging risk and increase grain yield of high yielding production fields for both spring and winter wheat (Mulder, 1954; Kheiralla et al., 1993; Crook and Ennos, 1995; Berry et al., 2000; Islam et al., 2002; Tripathi et al., 2003; Ercoli et al., 2013; Pampana et al., 2013; Peake et al., 2016). However, the results of the current study demonstrated that G × E × M interaction exists, as the grain yield response was variable between cultivars and location. Cultivars such as Suntop and Cobra had consistently positive grain yield responses to in-crop N application, while Mitch,

Lancer, Trojan and Wallup displayed neutral or negative grain yield responses. Additionally, the cultivar Kennedy exhibited increased grain yield and reduced lodging in response to in-crop N application in a warm sub-tropical environment when used without PGRs, but had decreased grain yield in comparison to sowing N application at the same location when PGRs were also used. This result agreed with those above that showed little benefit of PGR application when used in conjunction with in-crop N application on a low N soil.

Interestingly, the four cultivars rated as resistant (Cobra) or moderately resistant to lodging (Suntop, Mitch and Wallup; Peake et al., 2017) were the cultivars that showed the greatest and most consistent grain yield responses to in-crop N application (or in the case of Mitch, a neutral response). Alternatively, two cultivars with greater lodging susceptibility (Trojan and Lancer) displayed decreased grain yield in response to in-crop N application at Spring Ridge 2015 and 2016 where there was negligible lodging.

While in-crop N application has been shown to decrease lodging of susceptible cultivars in severe lodging seasons (Peake et al., 2014), the small lodging reductions achieved by in-crop N application herein may not have been responsible for the grain yield increase in the lodging resistant cultivars. This is particularly evident given that Cobra had increased grain yield in response to in-crop N application, that was not associated with a significant reduction in lodging. It is possible that lodging resistant genotypes possess a canopy structure (e.g. reduced leaf:stem ratio, or a smaller angle between leaf and stem) that interacts with improved late-season N availability to increase grain yield. In-crop N application has previously been advocated in sub-tropical Australia to increase grain yield of irrigated wheat through reduced lodging risk. However, the practice may now be more important for its role in a G × M combination (i.e. in-crop N + lodging resistant cultivars) that increases grain yield of lodging resistant cultivars through improved N availability during the critical period for yield formation. This possibility was also evident in the seminal studies of canopy management in winter wheat production (Sylvester-Bradley et al., 1997, 2000).

It is noteworthy that the in-crop N regimes used across environments and seasons were not identical because soil N at sowing varied noticeably between site/year combinations. Some fields had more N available at sowing than is recommended for the region (50–70 kg N/ha of mineral N + sowing fertiliser N; Peake et al., 2014) which reduces the effectiveness of the in-crop N strategy (Peake et al., 2016). However, it is possible that alternative in-crop N strategies exist which may work effectively for the long-duration cultivars or high levels of sowing N. It is therefore recommended that future studies into optimum N regime should be conducted after first using cover crops to reduce soil N, so that uniform levels of soil N can be achieved across locations. Nevertheless, the results demonstrated the importance of assessing G × E × M interaction though multi-environment testing of multiple genotypes. Optimum N application strategy varies with cultivar and environment, and further research is necessary to determine the optimum N application strategy for new cultivar releases at localities relevant to irrigated wheat production in sub-tropical Australia.

The study also demonstrated the importance of row spacing in managing the balance between lodging risk and increasing yield potential. The complex G × E × M interactions showed that while narrow row spacings were most likely to increase grain yield, some cultivars and management practices could require alternative row spacings to optimize grain yield. When lodging was negligible at a more temperate environment (Spring Ridge), large yield increases were generally achieved by using the narrowest row spacing for all cultivars. This trend was particularly evident for the highest yielding agronomic treatment combination (i.e. PGR application in conjunction with sowing N application). However, when lodging was severe at the same location in 2014, grain yield response across row spacing varied significantly with cultivar and PGR treatment. Application of PGRs in conjunction with the narrowest row spacing was the highest yielding agronomic treatment for most cultivars in this environment, with the exception of the cultivar Merinda which consistently displayed the highest grain yield on the intermediate (28 cm) row spacing. Ongoing testing on newly released cultivars is necessary to determine whether narrow rows in conjunction with PGR application would achieve maximum grain yield, under similarly severe lodging pressure.

In contrast, narrow row spacing did not lead to an increase in grain yield at the subtropical environment, where only short duration cultivars were tested. Our results therefore contrast with the results of Hussain et al. (2013) from a similar latitude (Multan, Pakistan) who found that short statured, low-tillering cultivars had the highest grain yield under irrigation at 10 cm row spacing compared to 20 or 30 cm. Nevertheless, our results are similar to those of Fischer et al. (2005, 2019) also at a similar latitude in the Yaqui Valley (Mexico), who found that cultivars released after the late 1980s could compensate almost completely for a 44 cm gap between outside rows of adjacent raised beds. Our results showed that in the absence of lodging, narrower rows were better suited to take advantage of the greater yield potential and longer growing season available at a more temperate environment, but row spacing did not have an effect on grain yield in a lower yielding, subtropical environment.

The interaction of sowing time and cultivar duration is the subject of considerable research in Australian winter cereal production systems. This is due to the rapid change between seasons that is bordered by the occurrence of damaging frosts just prior to anthesis, and heat stress during grainfilling (Flohr et al., 2017). Studies in both rainfed and irrigated environments have demonstrated that long duration cultivars showed increased grain yield compared to short duration cultivars, when sown at their respective optimum dates to ensure they both reached anthesis during the same optimum flowering window (Coventry et al., 1993; Moore, 2009; Hunt et al., 2015; Flohr et al., 2018; Peake et al., 2018; Hunt et al., 2019). In a study conducted at many of the same irrigated environments used herein, Peake et al. (2018) showed that the yield advantage of long duration cultivars (sown early) was 0.7 t ha^{-1} on average across environments, and up to 1.5 t ha^{-1} in environments that experienced greater levels of water stress. Water stress occurs frequently on commercial irrigated farms where poorly designed infrastructure, labour shortages or mechanical failure can all limit water supply to

the crop. Long duration cultivars (sown early) likely developed deeper root systems (Barraclough and Leigh, 1984; Incerti and O'Leary, 1990; Thorup-Kristensen et al., 2009) that allowed them to better withstand the intermittent water stress experienced at some environments. However, Peake et al. (2018) showed that the yield advantage associated with early sowing was smaller or even absent in environments where lodging was more severe. The potential increase in grain yield by sowing early in irrigated production fields must therefore be weighed with the potential for increased lodging. Later sowing has generally been promoted as an effective control method to reduce lodging risk in both winter and spring-wheat production systems (Hanley et al., 1961; Stapper and Fischer, 1990; Spink et al., 2000).

Our results showed that when comparing the same cultivars across two sowing dates, early sowing often (but not always) increased grain yield. The significant cultivar × sowing date × environment interaction for grain yield was partially attributed to differences in cultivar lodging susceptibility. At two of the heavily lodged environments (Narrabri and Spring Ridge 2014), the lodging resistant cultivars Suntop and Cobra showed little difference in grain yield between sowing dates, but the lodging susceptible cultivars (Bellaroi, Caparoi, Kennedy and Trojan) all had significantly decreased grain yield associated with early sowing in at least one of these environments. In contrast, all cultivars had greater yield associated with early sowing at the two low lodging environments (Narrabri and Spring Ridge in 2015), where yield response was more dependent on meteorological conditions during flowering and grainfilling.

Interestingly, later sowing was associated with increased lodging at two locations: at Emerald 2014, where early sowing was associated with a smaller yield advantage than that observed at Narrabri and Spring Ridge 2015; and at Spring Ridge 2014 where most cultivars had lower yield when sown on the early sowing date. Lodging was worse for these late sowing dates because the crops were at an earlier (more lodging susceptible) growth stage than those sown on the early sowing date on the day that thunderstorms occurred. This contrasts with results from the United Kingdom where later sowing almost always reduces lodging risk (Berry et al., 2004). However, the summary of Pinthus (1973) compiled from a range of locations showed that late sowing and early sowing could both reduce lodging depending on environment and germplasm. Rather than recommend one practice or the other, they recommended that 'adopting a suitable sowing date may contribute to the prevention of lodging'. The results from our study are significant to farmers and researchers in sub-tropical Australia, who should be aware that late sowing may not reduce lodging risk due to the increased frequency of thunderstorms during grainfilling.

It is important to understand that lodging susceptible cultivars are often preferred by farmers due to improved quality traits and/or disease resistance, or sometimes because seed availability is greater. Additionally, management techniques such as in-crop N application, narrow row spacings or early sowing are sometimes unavailable to farmers due to equipment limitations, or environmental influences (e.g. rainfall) that prevent operations from occurring at the optimal time. Ongoing research is necessary to ensure that new cultivar releases are assessed for their lodging susceptibility in combination with the range of agronomic management options available to farmers. Such knowledge will help maximise farm profitability in the context of the G × E × M interaction that exists for grain yield and lodging in high-yielding, spring-wheat production systems.

CONCLUSION

The results of our study indicated the existence of significant interaction between cultivar, environment and agronomic practice (G × E × M) for grain yield and lodging in irrigated spring wheat, although some practices were broadly applicable across a range of cultivars. The application of PGRs and the use of narrow row spacing, early sowing and in-crop N application were relatively consistent in improving grain yield when used in optimum combination with other management techniques and/or lodging resistant cultivars. However, grain yield increases were less consistent and decreased grain yield was sometimes observed when in-crop N application was used in conjunction with certain long duration cultivars, or when sowing date (either early or late) increased lodging severity in susceptible cultivars. The optimum agronomic practice for farmers in the region must vary depending on the cultivar they choose to grow, a choice that varies for reasons of local adaptation (e.g. disease pressure), target grain quality specifications and seed availability. Ongoing study of the interaction of future cultivars with the range of management practices available to farmers is therefore imperative to ensure that farmers possess the tools and tactical management options necessary to maximise profitability in variable climates such as those of sub-tropical Australia.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

AP conceived, designed and implemented experiments, interpreted data and prepared the manuscript. KB designed and conducted the statistical analyses and assisted with manuscript preparation. RF assisted with experimental design, data interpretation and manuscript preparation. BD assisted with data analysis and interpretation and manuscript preparation. MG and NP assisted with experimental design and conduct and data interpretation. MM assisted with design and conduct of the statistical analyses.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Deep Soil Water-Use Determines the Yield Benefit of Long-Cycle Wheat

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Wheat production in southern Australia is reliant on autumn (April-May) rainfall to germinate seeds and allow timely establishment. Reliance on autumn rainfall can be removed by sowing earlier than currently practiced and using late summer and early autumn rainfall to establish crops, but this requires slower developing cultivars to match life-cycle to seasonal conditions. While slow-developing wheat cultivars sown early in the sowing window (long-cycle), have in some cases increased yield in comparison to the more commonly grown fast-developing cultivars sown later (short-cycle), the yield response is variable between environments. In irrigated wheat in the sub-tropics, the variable response has been linked to ability to withstand water stress, but the mechanism behind this is unknown. We compared short- vs. long-cycle cultivars × time of sowing combinations over four seasons (2011, 2012, 2015, and 2016) at Temora, NSW, Australia. Two seasons (2011 and 2012) had above average summer fallow (December–March) rain, and two seasons had below average summer fallow rain (2015 and 2016). Initial plant available water in each season was 104, 91, 28, and 27 mm, respectively. Rainfall in the 30 days prior to flowering (approximating the critical period for yield determination) in each year was 8, 6, 14, and 190 mm, respectively. We only observed a yield benefit in long-cycle treatments in 2011 and 2012 seasons where there was (i) soil water stored at depth (ii) little rain during the critical period. The higher yield of long-cycle treatments could be attributed to greater deep soil water extraction (<1.0 m), dry-matter production and grain number. In 2015, there was little rain during the critical period, no water stored at depth and no difference between treatments. In 2016, high in-crop rainfall filled the soil profile, but high rainfall during the critical period removed crop reliance on deep water, and yields were equivalent. A simulation study extended our findings to demonstrate a median yield benefit in long-cycle treatments when the volume of starting soil water was increased. This work reveals environmental conditions that can be used to quantify the frequency of circumstances where long-cycle wheat will provide a yield advantage over current practice.

Keywords: evaporation, fallow rainfall, harvest index, transpiration efficiency, water use efficiency

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INTRODUCTION

In southern Australia, fast developing spring wheat crops are traditionally established following the hot, dry summer fallow period on rains that fall in late autumn (April–May), and grow through the cool winter months to flower at an optimal time in early spring (September–October) during which collective damage from water stress, frost and heat are minimized (Richards, 1991; Zheng et al., 2012; Flohr et al., 2017). The drying trend recorded during austral autumn in semi-arid regions of the Southern Hemisphere (Pook et al., 2009; Cai and Cowan, 2013) unfortunately aligns with the optimal sowing window for short-cycle wheat cultivars, which combined with increasing farm size has prompted Australian growers to start sowing crops earlier (Fletcher et al., 2016; Flohr et al., 2018c).

Early sowing systems are facilitated by management that improves capture and storage of summer fallow rain including weed control, stubble retention and no-till farming to allow early germination, and the use of slow developing wheat cultivars (Hunt et al., 2013; Kirkegaard et al., 2014). Slow developing cultivars have a photoperiod or vernalization requirement that impedes progress through the crop's life cycle such that flowering remains aligned to the optimal period despite earlier sowing dates (Pugsley, 1983). The combination of slow development and early sowing confers a longer crop life-cycle (long-cycle). Hunt et al. (2019) propose that by exploiting a much wider sowing window and longer growing season, long-cycle wheats can increase Australian national yields by 0.54 t/ha under current climate conditions, whilst managing the logistics of timely sowing on large farms. In response, and with the aid of a deeper understanding of genetic control, Australian breeders have begun to release a new generation of slow developing cultivars suitable for early sowing (Hunt, 2017).

Field experiments conducted over many decades have given conflicting results when comparing yield of long- and short-cycle treatments with synchronized flowering time across a range of environments (Penrose, 1993; Gomez-Macpherson and Richards, 1995; Penrose and Martin, 1997; Hunt, 2017; Peake et al., 2018). The study of Gomez-Macpherson and Richards (1995), and others reviewed by them (Batten and Khan, 1987; Connor et al., 1992) revealed that while long-cycle treatments accumulated more dry matter, yields were equivalent to short-cycle treatments due to lower harvest index (HI) in early sown cultivars. They postulated that while this could have been due to rapid growth in early sown crops depleting soil water so that little remained after flowering for grain fill (Passioura, 1977; Fischer, 1979), they ultimately suggested that long-cycle crops were taller and had more leaves. They proposed that competition for carbohydrates between the developing spike and elongating stem was responsible for reducing grain number and thus lower than expected yields and HI in early sown crops. In below average seasons in a high rainfall environment, Riffkin et al. (2003) reached a similar conclusion, finding over two seasons that long-cycle was inferior to short-cycle. Under high yielding irrigated conditions, Stapper and Fischer (1990) found yield of long-cycle was further reduced by a higher incidence of lodging. Also under irrigation and using isogenic lines, Fischer (2016) found that long-cycle treatments were equivalent or inferior to short-cycle treatments. The study of Coventry et al. (1993) demonstrated a yield advantage of early sown long-cycle treatments, but only in one (1986) of the two seasons (1985 and 1986) studied.

Peake et al. (2018) suggested that in most of these studies that a deficiency of nitrogen may have limited grain yield, therefore long-cycle wheats with greater dry matter may have been discriminated against by experiencing greater nitrogen stress. Peake et al. (2018) applied best practice agronomy under sub-tropical irrigated conditions and achieved synchronized flowering between short and long-cycle treatments in multiple site and year experiments between 2014 and 2016 (7 experiments in total). Results from these experiments showed a yield advantage (0.5–1.5 t ha^{-1}) in 70% of experiments for long-cycle treatments over short-cycle treatments. Simulation modeling was used to infer that long-cycle had a yield advantage when imperfect irrigation timing resulted in crops experiencing short periods of drought stress. They concluded that the yield advantage was due to long-cycle treatments being better able to withstand drought stress, but did not take the measurements necessary to identify the mechanisms responsible.

Hunt (2017) hypothesized that long-cycle treatments may only have a yield advantage in seasons when the soil profile has water that is accessible at depth, and limited water at shallow depths due to limited rainfall so that the potentially deeper root growth of long cycle treatments becomes advantageous. Whilst the study of Peake et al. (2018) supports this hypothesis, it has not been tested in experiments with measurements of soil water and dry matter accumulation. The aim of this study was to clarify the environmental conditions that confer an advantage to long-cycle crops in a rain-fed environment, and identify the mechanisms responsible for any observed yield advantages.

METHOD

Field Sites

Field experiments were conducted in four seasons (2011, 2012, 2015, and 2016) at sites near Temora, New South Wales (NSW, **Table 1**). Temora has a mean annual rainfall of 520 mm (1963–2013) with 312 mm on average falling during the wheat growing season (April–October) and 208 mm falling during the summer fallow period (November–March). Experiments were split-plot (whole plot = time of sowing, sub-plot = cultivar) with four replicates, and either randomized complete block or row: column designs. Sowing date was randomized within replicates. Soil type at all sites the was a red chromosol (Isbell, 2002), with plant available water capacity (PAWC) as per **Table 1**. In 2015 and 2016 the soil type was per profile number Temora No. 913 in the APSoil database[1]. Rainfall summaries and site details for the four experimental growing seasons are reported in **Table 1**.

Cultivar × Sowing Date Selections

Each experiment had four cultivars that were selected as being highest yielding milling (Australian Hard) spring wheat cultivars

[1]https://www.apsim.info/Products/APSoil.aspx

TABLE 1 | Site details for each year of the experiment, including soil plant available water capacity (PAWC), plant available water (PAW) at sowing, summer fallow (Dec-Mar), growing season (Apr-Oct) rainfall and rainfall in the 30 days prior to the start of the optimal flowering period (OFP).

Site detail	Year			
	2011	2012	2015	2016
Location	S 34.49°, E 147.51°	S 34.73°, E 147.54°	S 34.41°, E 147.53°	S 34.41°, E 147.53°
PAWC (mm) and depth of measurement	203 (1.85 m, Hunt et al., 2016)	196 (1.85 m)	206 (1.6 m, Wang et al., 2018)	206 (1.6 m, Wang et al., 2018)
PAW at sowing (mm)	104	91	28	27
Summer fallow (Dec-Mar) rainfall (mm)	408	386	206	113
Growing season (Apr-Oct) rainfall (mm)	200	169	279	588
Rainfall 30 days prior start of OFP (mm)	8	6	14	190
Soil mineral nitrogen at sowing (kg/ha)	207	52	209	89
N fertilizer (kg/ha N) applied as urea	74	171	46	198

for four development types (**Table 2**, fast, mid, slow, and very slow developing) based on yield performance in National Variety Trials for south eastern NSW (ACAS, 2007). The alleles of major development genes for each cultivar are as described by Bloomfield et al. (2018) and are presented in **Table 2**. Alleles for the major genes indicate that the four cultivar's development is moderated from fastest to slowest by an increasing number of vernalization and photoperiod sensitive alleles. In 2015 and 2016 a fast spring (Sunstate) and very slow spring (W16A) near-isogenic pair (Hunt et al., 2019) were also included in experiments.

Crop Management

All crops were direct-drilled in small plots (1.8 m × 9 m) on 305 mm row spacing with press wheels to give six crop rows per plot. Seeding depth was ∼40 mm depending on seed bed moisture. Each experiment had 4 sowing dates spaced at 10 day intervals commencing in mid-April and ending in mid-May, but only data for the treatments that flowered concurrently and within the optimal flowering period for Temora (25 September–10 October as per Flohr et al., 2017) are shown (**Table 3**). Sowing date is defined as the calendar date at which seeds become imbibed and begin the process of germination, i.e., either the date on which they are planted into a moist seed bed, or the date on which they received rainfall/irrigation after being sown into a dry seed bed. Seed bed moisture was insufficient to establish all sowing dates at Temora in 2011 and 2016, and at the early and mid-May sowings either 8 mm (2011) or 15 mm (2016) of water was applied to the sown furrow using drip irrigation. As this small amount was applied to very dry soil and did not penetrate deeply, it is assumed not to have contributed to crop transpiration and yield. In all experiments, chemical fertilizers and pesticides were applied such that nutrient limitations, weeds, pests or diseases did not limit yield. Grain protein in all experiments exceeded 11.1% indicating N deficiency was unlikely (Goos et al., 1982; Holford et al., 1992).

To compare crop development rates between the four experimental seasons, degree days, i.e., Thermal time (TT) = $\Sigma\ ((T_{min} + T_{max})/2) - T_{base}$ accumulated using 0°C as the base temperature and starting from the first sowing date were calculated for each season, using data available from the Commonwealth Bureau of Meteorology (BoM) website (Australian Government, 2017).

Management of Treatments to Manipulate Harvest Index

Previous experiments in southern Australia have demonstrated that long-cycle wheat has lower HI than short-cycle treatments (Batten and Khan, 1987; Connor et al., 1992; Gomez-Macpherson and Richards, 1995; Riffkin et al., 2003). Modified agronomic management can be used to alter carbohydrate partitioning and early dry matter accumulation in order to improve HI. To this end, two plant density treatments ("high" = ∼100 plants/m^2 and "low" = ∼50 plants/m^2) were imposed at the optimal sowing date for each cultivar in 2011 and 2012 experiments. In 2011 a plant growth regulator (PGR) treatment designed to reduce stem height and consisting of 50 g/ha trinexapac-ethyl + 757 g/ha chlormequat chloride applied at development stage 30 (Tottman, 1987) was compared to a control in a

TABLE 2 | Genotypes used in experiments and alleles at five major development loci using nomenclature after Bloomfield et al. (2018).

Cycle length	Development	Cultivar	Ppd-B1	Ppd-D1	Vrn-A1	Vrn-B1	Vrn-D1
Short	Fast	Lincoln	b	a	a	a	v
	Fast	Condo	a	a	v	a	a
	Fast	Sunstate	a	a	v	a	a
	Mid	Gregory	b	a	v	v	a
Long	Slow	Bolac	b	a	a	v	v
	Very slow	Eaglehawk	b	b	b	v	a
	Very slow	W16A	b	b	e	a	a

For Ppd genes "a" indicates insensitive allele and "b" indicates sensitive. For Vrn genes "a" and "b" denote different spring alleles, and "v" winter (wild type) allele.

factorial design with plant density at the optimal time of sowing of each cultivar. In 2012, two defoliation treatments (control and Z30 defoliation as per Kirkegaard et al., 2015) were used in a factorial design with plant density at the optimal time of sowing of each cultivar. The effect of all treatments on yield and other parameters were uniformly small and often not significant. The effect of the treatments on all data were analyzed using either one or two-way analysis of variance (ANOVA) assuming a split plot design in the GenStat 15 software package (VSN International, 2013). Significance is assumed at the 95% confidence level. If management treatments to increase HI had a significant interaction with cultivar x sowing date combinations on any variate, they were not included in the analysis of that variate and only control treatments ("high" plant density, no PGRs and no defoliation) were used. If the interaction was not significant, then pooled means incorporating the management treatments were used in the comparisons and figures below.

Plant and Soil Measurements

Day of flowering was recorded as the date when 50% of the spikes in each plot had at least one visible anther DC65 (Z65, Zadoks et al., 1974). Dry matter (DM) was measured at Z89 (maturity) by cutting all above ground plant parts in a quadrat 0.39 × 1.2 m (four middle rows from plots) in 2011, 2012, and 2016, and a quadrat 0.83 × 1.2 m (four middle rows from plots) in 2016 per replicate. At DC69 and DC89, 20 stems were partitioned into stem, leaf, spike and dried at 70°C for at least 48 h to record a dry weight. Stem weight was not recorded in 2012. Individual grain weight was measured by weighing 200 grains dried at 70 °C for at least 48 h. Harvest index was calculated as the ratio of the grain to the total DM of the sample taken at maturity. In 2012 grain yields were measured by machine harvest of the inside four rows of six row plots and are reported at oven-dry moisture content. In 2011, 2015, and 2016 yield was measured by hand harvesting and threshing a quadrat of either 0.39 × 1.2 m (2011 and 2015) or 0.83 × 1.2 m (2016) taken from the inside four rows of six row plots and are also reported at oven-dry moisture content. Harvest grain moisture was determined via Near Infrared (NIR) technology, and grain yield was divided by grain weight (also 0% moisture) to calculate grain/m^2.

A neutron moisture meter (NMM) access tube was installed centrally to a depth of 1.8 m in April of each year to allow in-crop measurements of soil water. Recordings using an NMM (CPN International, Martinez, CA) were taken at 0.1 m increments to depth of 1.6 m and volumetric water content was calculated using an existing calibration (Hunt et al., 2016). To determine plant available water (PAW) in April, the change in soil water content between sowing and crop maturity was used to estimate the crop lower limit.

In 2011 and 2012 groundcover was estimated using regular readings of NDVI recorded using a GreenSeeker® (Trimble Inc., Sunnyvale CA), and then used to estimate PAR light interception based on an existing unpublished relationship developed for wheat at Temora (PAR = 1.60*NDVI - 0.39, R^2 = 0.92). In 2015 and 2016 canopy light interception PAR was recorded around solar noon using a ceptometer (AccuPAR LP-80; Pullman, WA, United States) at 4 positions per plot at the time of DC39 and DC70 DM sampling. Values of daily fractional PAR interception were obtained by interpolation between readings of interception (Monteith, 1972) and then used to estimate daily soil evaporation (E_s) based on FAO56 values of potential evapotranspiration (obtained from www.longpaddock.qld.gov.au, ET_o) and days since last rain fall (d) after the method used by Siddique et al. (1990) where

$$E_s = ET_o{}^*(1/d)$$

Daily evaporation under each cultivar (E_{sc}) was then estimated from

$$E_{sc} = E_s{}^*(1 - a)$$

where a is the daily interpolated PAR interception.

Daily estimates of E_s were summed from the day on which initial NMM soil water measurements were made (early April) to maturity to estimate seasonal soil evaporation. Seasonal transpiration was calculated as the difference between seasonal crop water use and evapotranspiration (i.e., crop water use - E_{sc}), and this was used to calculate transpiration efficiency (TE) for dry matter. The NMM measurement was taken on the same date regardless of sowing date. Water use efficiency (WUE) was calculated by dividing total dry matter at maturity by total crop water use. NMM measurements made at flowering were used to calculate the proportion of water used pre- and post-flowering. In 2015 and 2016 these were calculated for the near-isogenic lines only (W16A and Sunstate), as neutron moisture meter tubes were only installed in these treatments. Evapotranspiration is defined

TABLE 3 | Target and actual sowing dates in 2011, 2012, 2015, and 2016.

Treatment	Target sow date	Cultivar	Actual sowing dates			
			2011	2012	2015	2016
Long-cycle	Mid-April	Eaglehawk	15 Apr	18 Apr	17 Apr	15 Apr
	Mid-April	W16A			17 Apr	15 Apr
	Late-April	Bolac	27 Apr	26 Apr	27 Apr	27 Apr
Short-cycle	Early-May	Gregory	9 May	8 May	27 Apr	6 May
	Mid-May	Lincoln/ Condo	19 May	17 May	15 May	15 May
	Mid-May	Sunstate			7 May	15 May

as rainfall plus the change in soil water content between sowing and crop maturity.

Statistical Analysis

Similar to the analysis of Peake et al. (2018), treatments were grouped by long- and short-cycle cultivars that flowered synchronously during the optimal flowering period defined by Flohr et al. (2017). In each year, a two-sample *t*-test (GenStat 19 user interface, VSN International, 2013) was used to test for significant differences between pooled means of long- and short-cycle treatments. For each season, long-cycle and short-cycle treatment yields were used to calculate the yield difference of long-cycle treatments over short-cycle treatments, which were plotted against the soil water extraction from between 1.0 and 1.6 m depth for each block. Linear regression analysis was used to determine relationships between the yield benefit of long-cycle treatments and soil water extraction below 1.0 m, and between HI and proportion of water used after flowering. Non-linear regression analysis was used to fit grain yield and grain number data.

Investigation of Yield Differences Between Long and Short Cycle Treatments Under Different Levels of Starting Soil Water Using Simulation

The Agricultural Production Systems Simulator (Holzworth et al., 2014) was used to evaluate yield differences between long- and short-cycle treatments under different levels of starting soil water in seasons between 1997 and 2016. The APSIM modules used in the analysis were Wheat (wheat crop growth and development), SoilWat (soil water balance), SoilN (soil nitrogen dynamics), SurfaceOM (surface residue dynamics), and Manager (management rules) as described by Hunt and Kirkegaard (2011). In order to validate APSIM's ability to simulate the differences between long- and short-cycle treatments, it was parameterized for the Eaglehawk sown mid-April (long-cycle) and Lincoln sown mid-May (short-cycle) treatments in the field experiments described above. Soil input data for the 2011 site were derived from a detailed characterization conducted at the experimental site and is reported by Hunt et al. (2016). Soil data for 2012 were derived from measurements of drained upper limit and crop lower limit made in an adjacent field reported by Kirkegaard et al. (1994). Initial soil water and mineral N were measured from intact soil cores taken across each site to a depth of 1.65 m and segmented 0–5 cm then every 10 cm below that. Crop specific inputs (sowing depth, plant density, row spacing) were used from measurements recorded in the experiment. The parameterization for Eaglehawk available in the released version of APSIM gave good agreement between observed and simulated flowering dates and was used to simulate that cultivar. The released parameterization for Lincoln was found to under predict flowering time by ∼10 days, and a new parameterization was created to optimize flowering date with observations (**Supplementary Figure S1**). Daily minimum and maximum temperatures were recorded using iButton datalogers (Maxim Integrated, San Jose, CA) housed in a wooden radiation screen at 1.5 m. Daily rainfall was recorded using a tipping bucket rain gage. All other meteorological inputs were obtained from the SILO Patched Point Dataset (Jeffrey et al., 2001) for the nearby Australian Bureau of Meteorology station 073038 (Temora Research Station). The APSIM yield prediction assumes phosphorus and all nutrients other than N are non-limiting and does not incorporate the effects of the presence of pests, disease, weeds, or heat and frost shock.

To extend the field experiments described here across a greater range of seasons and levels of starting soil water, a simulation experiment was conducted with short- (Lincoln sown 15 May) and long-cycle (Eaglehawk sown 15 April) treatments at two locations (Temora and Griffith) defined by SILO Patched Point Dataset for Australian Bureau of Meteorology stations 073038 (Temora Research Station) and 075041 (Griffith Airport AWS). Griffith was selected as the second site as it has a similar soil type and latitude as Temora but is warmer (mean annual temperature 17.0 vs. 15.5°C) and drier, receiving an average (1958–2018) annual rainfall of 401 mm, with 237 mm falling during the growing season. The Temora 2011 site soil type was used at both sites. Crop growth and yield was simulated at different levels of starting soil water by resetting soil water at 5, 25, 50, 75, and 100% of plant available water capacity (203 mm) filled from the top each year of the simulation. There was also a sixth "natural" treatment in which the soil water was set at 0% of PAWC in the first year of the simulation and not reset after that. The years 1987–2016 were simulated, but the first 10 years discarded in order to allow soil water in the "natural" treatment to equilibrate. In all simulations NO_3 in the top three soil layers were maintained above 50 kg/ha such that N supply did not limit yield. Crops in both treatments were planted at 100 plants m^{-2} on 305 mm row spacing. Output variables reported included yield, root_depth, seasonal soil evaporation, seasonal transpiration.

RESULTS

Growing Conditions

The four growing seasons studied contrasted in their pattern of seasonal water availability (**Table 1**). NMM measurements made on 7, 3, 14, and 15 April in each growing season, respectively, determined average initial PAW across the site to be 104, 91, 28, and 27 mm. Rainfall 30 days prior to the start of the optimal flowering period (25 September as per Flohr et al., 2017) in each year is reported in **Table 1**. This period is assumed to correspond to the critical period for yield determination in wheat (Fischer, 1985). The disparate patterns of rainfall gave three different season types;

1. Deep stored soil water present (from summer rain) and drought during critical period (2011 & 2012).
2. No deep stored soil water and drought during the critical period (2015).
3. Deep stored soil water present (from in-crop rain) and no drought during the critical period (2016).

The monthly TT accumulation (°C) in the year of experiment for each site is summarized in **Figure 1**. Accumulation of thermal

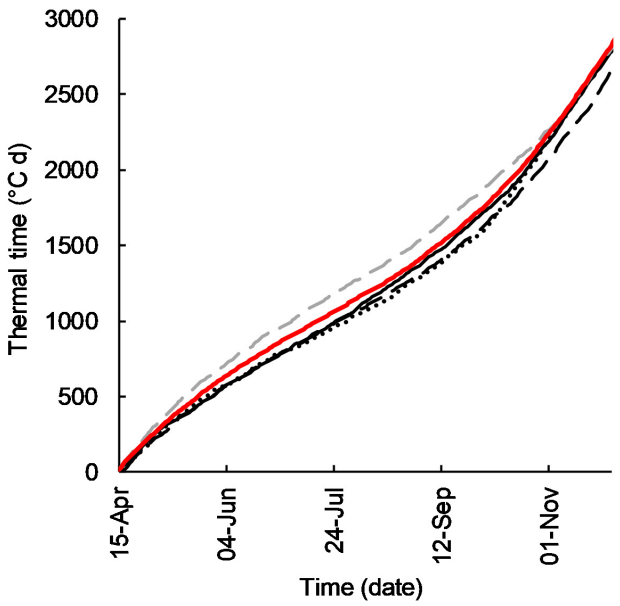

FIGURE 1 | Cumulative thermal time (°C d) for Temora, NSW in growing seasons 2011 (-), 2012 (- -), 2015 (•••), 2016 (- -), and average 2005–2016 (-).

time was near average in 2011, lower than average in 2012 and 2015, and above average in 2016.

Synchronization of Flowering Dates and Grain Yield

Whilst the precise target sowing dates were not achieved (**Table 3**), flowering of cultivars sown at their optimal time was satisfactorily concurrent in 2011, 2012, and 2015 (**Table 4**). In 2011 and 2012 flowering occurred within a range of 3 days, and in 2015 within 8 days. In 2016 flowering dates ranged by 20 days. In 2016 the very slow developing types (EGA Eaglehawk and W16A) flowered 6–12 days after the optimal flowering period when sown at the earliest sowing date, all other development types flowering within the optimal period (25 September–10 October as per Flohr et al., 2017). This behavior was possibly due to the warmer than average conditions experienced that season (**Figure 1**) hastening development of most cultivars, whilst the strong photoperiod sensitivity of EGA Eaglehawk and W16A impeded development despite above average temperatures. As W16A and EGA Eaglehawk did not flower at a comparable time to the other cultivars nor within the optimal period in 2016 (**Figure 2**), they were both excluded from the long vs. short cycle analysis for all variates except crop water-use in that year. The short cycle NIL pair of W16A (Sunstate) was also excluded so as not to bias in favor of long-cycle by retaining a line that is not an elite cultivar. W16A and Sunstate were still used to calculate crop water use in 2016 as these were the only treatments in which NMM tubes were installed.

In all growing seasons, highest yields were achieved in treatments that flowered within the optimal flowering period defined by Flohr et al. (2017) (**Figure 2**).

Grain Yield, Number, Grain Size, Dry Matter, and HI

In 2011 and 2012 long-cycle treatments yielded significantly more than short-cycle treatments. In 2015 and 2016 there was no significant difference in grain yield between short- and long-cycle treatments (**Table 5**). In all growing seasons long-cycle treatments had higher grain number and this was significant in three of four seasons. In 2011 and 2012 growing seasons, long-cycle treatments accumulated more dry-matter than short-cycle treatments. Higher yields in long-cycle treatments were due to higher grain number at similar (2012) or even lower grain weight (2011, **Table 5**). Higher grain number in long-cycle cultivars in 2016 did not result in higher grain yield, and short-cycle treatments had greater grain weight (**Table 5**). There was no significant difference in HI or stem weight % of total dry-matter at flowering in all growing seasons.

There was a positive correlation between HI and the percentage of water used after flowering (**Figure 3**) and this was in good agreement with the relationship derived by Passioura (1977) from pot experiments. A HI of 0.50 was observed when 35% of water was used after flowering, and a progressively lower HI as the percentage of water used after flowering decreased.

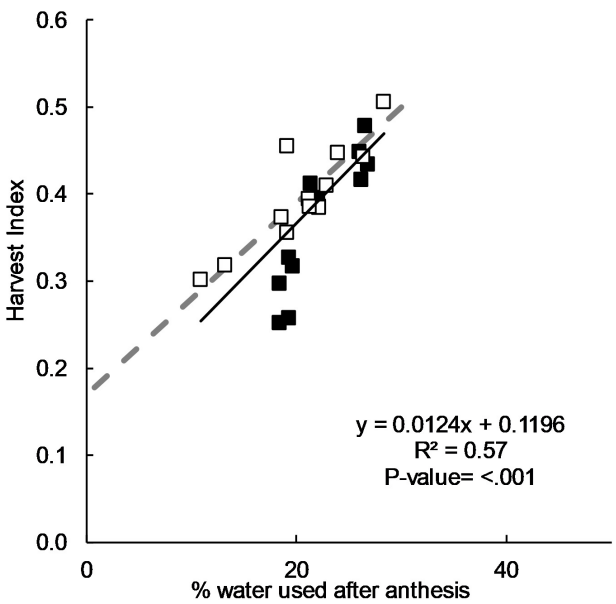

FIGURE 3 | Relationship between harvest index and post-flowering water use as a ratio of seasonal water use for long-cycle (■) and short-cycle (□) cultivars grown in 2011, 2012, 2015, and 2016. The same relationship postulated by Passioura (1977)(- -).

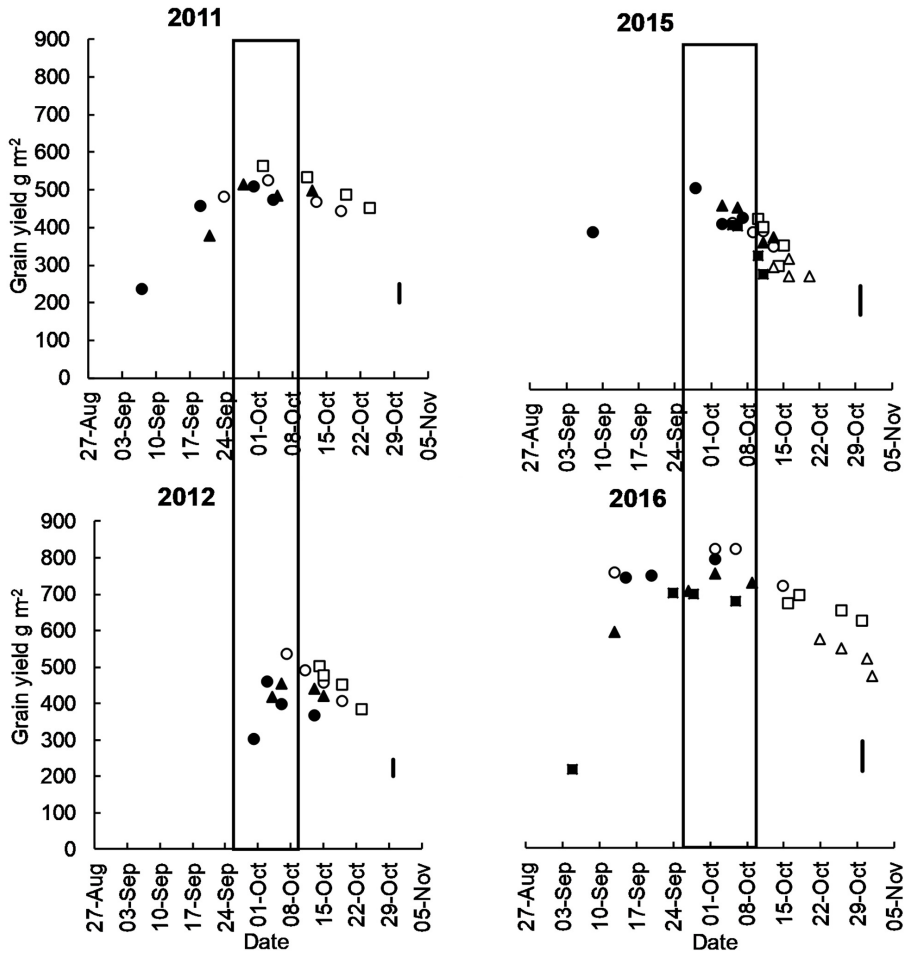

FIGURE 2 | Mean grain yield of long cycle (Eaglehawk □, W16A △, Bolac ◯) and short cycle (Gregory ▲, Lincoln/Condo ●, Sunstate ■) cultivars plotted against flowering date at Temora in 2011, 2012, 2015, and 2016. Box represents the optimal flowering period as per Flohr et al. (2017). Each marker represents a different time of sowing (from mid-April to mid-May) and sowing date moves later from left to right. The vertical line is LSD, and the *P*-Value of ToS x cultivar interactions at all sites is <0.001.

Crop Water Use

In the presence of deep stored soil water and terminal drought, there were no significant difference in crop water use in 2011, but in 2012 long-cycle treatments used more water than short-cycle (**Table 6**). This was due to deeper root growth (see Kirkegaard et al., 2015 for root measurements from these experiments in 2012) in the long-cycle treatments. Long-cycle treatments lost less water to evaporation in all (not significant in 2016) seasons due to earlier canopy development (**Table 6**). WUE for dry matter was higher for the long-cycle treatments compared to short-cycle treatments in 2011 and 2012, due to both less evaporation and higher TE for dry matter in 2012.

In a growing season with no deep stored soil water and drought during the critical period (2015), and a season with above average rainfall (2016), there was also greater crop water use by long-cycle treatments (not

TABLE 4 | Flowering dates (Z65 – 50% of ears with anthers extruded) for the different maturity groups in 2011, 2012, 2015, and 2016.

Cultivar	Development type	Cycle length	2011	2012	2015	2016
EGA Eaglehawk	Very slow	Long	2-Oct	14-Oct	10-Oct	16-Oct
W16A	Very slow	Long			13-Oct	22-Oct
Bolac	Slow	Long	5-Oct	11-Oct	5-Oct	2-Oct
EGA Gregory	Mid	Short	5-Oct	13-Oct	6-Oct	2-Oct
Lincoln/ Condo	Fast	Short	4-Oct	13-Oct	7-Oct	2-Oct
Sunstate	Fast	Short			10-Oct	6-Oct

significant in 2016), but this did not result in a higher grain yield (**Table 6**).

Use of Stored Soil Water and Yield Response

There was a significant positive linear relationship between the yield benefit of long-cycle treatments and soil water used below 1.0 m (**Figure 4**). Although there was variance unaccounted for ($R^2 =$ 0.51), yield of long-cycle cultivars increased by 3.1 g m^{-2} mm^{-1} (or 31 kg $ha^{-1}mm^{-1}$) of soil water extracted below 1.0 m.

Grain Number Drives Increased Grain Yield in Long-Cycle Treatments

In both 2011 and 2012, there was an asymptotic relationship between grain number and grain yield (**Figure 5**). In both years, the asymptotes approached the water limited potential yield calculated for each site as per Sadras and Angus (2006) where water limited yield potential (PY_w) = (ET-60)*22.

Simulation of Long and Short Cycle Treatments Under Varying Levels of Starting Water

There was good agreement between simulated and observed yields of long- and short-cycle treatments in 2011 and 2012 (**Supplementary Figure S1**). When simulated over 19 seasons there was a clear positive relationship between median yield benefit of long-cycle and increasing starting soil water on 15 April at Temora and Griffith (**Figure 6**). The median yield benefit was ∼100–175 g m^{-2} when the soil profile was 50% filled on 15 April, and ∼250–300 g m^{-2} when the soil profile was 100% filled on 15 April. There was also a positive relationship between biomass, root depth, transpiration benefit and increasing stored soil water on 15 April at both sites. There was no trend for a benefit from a reduction in evaporation in long-cycle treatments in the simulations.

DISCUSSION

Environment Determines Yield Response of Long-Cycle Treatments

The yield advantage of long-cycle treatments over short-cycle treatments was strongly related to seasonal pattern of water availability. Requisite environmental conditions for a yield benefit in long-cycle treatments were (a) the presence of accessible deep soil water and (b) low rainfall during the critical period for yield determination in wheat. In 2011 and 2012 there was ∼70 mm more PAW stored at sowing compared to 2015 and 2016. In 2011 and 2012, drought during the critical period for yield determination forced greater reliance on deep soil water for crop growth, and long-cycle treatments were able to access more of this due to longer duration of root growth and thus root depth (Kirkegaard et al., 2015). In seasons where no soil

TABLE 5 | Mean values for long- and short-cycle treatments grown in Temora, for dry-matter at maturity, grain yield, harvest index, grain number, stem weight at flowering and grain weight in each growing season.

Year	Maturity dry matter (g m^{-2})		Grain yield (g m^{-2})		Harvest index		Grain number (m^{-2})		Stem weight % of total dry-matter at flowering		Grain weight (mg)	
	Long	Short	Long	Short	Long	Short	Long	Short	Long	Short	Long	Short
2011	1,243	1,163	499	461	0.40	0.40	16,692	12,258	64	68	32	38
2012	1,078	887	483	403	0.44	0.45	15,977	12,341			30	32
2015	1,353	1,300	405	438	0.30	0.34	17,060	15,705	56	56	25	28
2016	1,806	1,613	698	655	0.39	0.41	22580	15046	66	68	31	44

*Shaded cells indicate that long- and short-cycle treatments are significantly different at the 95% confidence level, P-values are available in **Supplementary Table S1**, and standard deviation around the mean in **Supplementary Table S2**.*

TABLE 6 | Mean values for long- and short-cycle treatments grown in Temora for crop water use, estimated evaporation, post-flowering water use, transpiration efficiency (TE) for dry matter at maturity and water use efficiency (WUE) for grain yield in each growing season.

Year	Crop water use (mm)		Estimated evaporation (mm)		Post-flowering water use (mm)		TE maturity dry matter (g m^{-2} mm^{-1})		WUE for maturity DM (g m^{-2} mm^{-1})	
	Long	Short	Long	Short	Long	Short	Long	Short	Long	Short
2011	329	319	78	96	68	76	5	5.1	3.8	3.7
2012	332	321	59	66	88	80	4.1	3.7	3.4	2.9
2015	374	356	80	91	73	51	4.6	4.4	3.6	3.6
2016	604	592	92	99	119	112	3.5	3.3	3.1	2.7

*Shaded cells indicate that long- and short-cycle treatments are significantly different at the 95% confidence level, P-values are available in **Supplementary Table S3**, and standard deviation around the mean in **Supplementary Table S4**.*

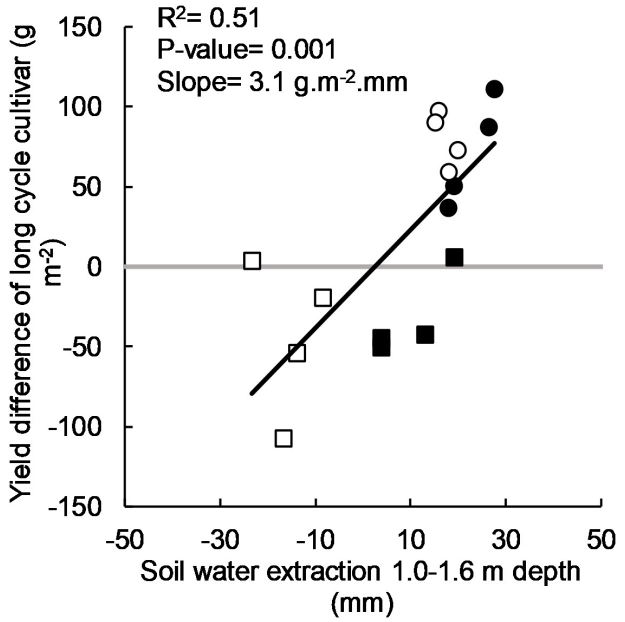

FIGURE 4 | Yield difference of long-cycle cultivars (Eaglehawk, Bolac, W16A) over short-cycle cultivars (Gregory, Lincoln, Condo, Sunstate) in 2011 (●), 2012 (○), 2015 (●), and 2016 (□) and soil water extracted from 1.0 to 1.6 m depth by the long-cycle treatment. Each symbol represents values for individual blocks (replicates) within each experiment. *P*-value and R^2 relates to the regression fitted to the data.

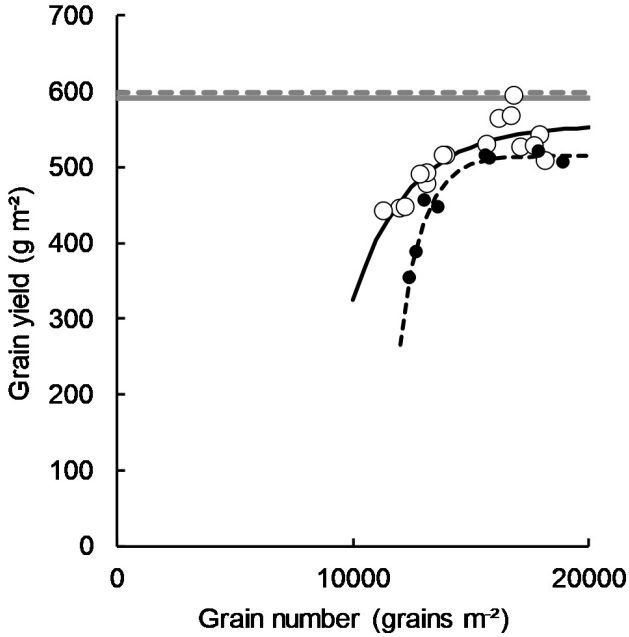

FIGURE 5 | Grain number plotted against grain yield in 2011 (○, $y = 556\text{-}14084*(0.999^X)$, $P = <0.001$, $R^2 = 0.72$) and 2012 (■, $y = 515\text{-}5.3 \times 10^7*(0.999^X)$, $P = <0.001$, $R^2 = 0.94$) referenced against the water limited yield potential as per Sadras and Angus (2006) for each 2011 (solid gray line) and 2012 (broken gray line). Data points are contributed by four sowing time x cultivar treatments (two long-cycle, two short-cycle) and the management applied to increase HI as per section Management of Treatments to Manipulate Harvest Index (plant density and PGR treatments in 2011 and density treatment in 2012).

water was available at depth (2015) or enough rain fell during the critical period to meet crop demand from shallow soil layers (2016), long cycle had no yield advantage despite universally lower evaporation, and generally greater dry matter accumulation and higher grain number. Our results support the findings of Peake et al. (2018), who found that long-cycle treatments had a yield advantage only in environments where there was water stress during the critical period. Similarly, Coventry et al. (1993) found a yield advantage in long-cycle treatments in one growing season out of a 2 year experiment. While insufficient nitrogen application may have contributed to the variable yield response in these experiments, above average winter rainfall in 1986 would have filled the soil profile to depth, increasing water availability making greater rooting depth an advantage in long cycle treatments.

The efficiency in converting soil water stored below 1 m into grain yield reported in this study (31 kg $ha^{-1}mm^{-1}$) is in close agreement to the marginal water-use efficiency for deep soil water reported by Lilley and Kirkegaard (2007) of 30–36 kg $ha^{-1}mm^{-1}$ and Angus and Van Herwaarden (2001) of 33 kg $ha^{-1}mm^{-1}$. It is less than the 60 kg/ha.mm reported by Kirkegaard et al. (2007) for efficiency of water use after flowering in one site year where complete terminal stress was established with a rainout shelter, but is close to the average calculated through simulation of 30–40 kg $ha^{-1}mm^{-1}$ in the same study. Other authors (e.g., Connor et al., 1992) reported no difference in water extraction at depth between different cycle length, but this may have been due to the presence of sufficient shallow water to meet crop demand as observed here in the 2016 season, or a shallow soil with physical or chemical constraints that limit root depth.

Greater water uptake at depth in 2012 was associated with deeper root growth. Kirkegaard et al. (2015), Figure 3 of that paper report root length density (RLD) for one of the long-cycle treatments (EGA Eaglehawk sown 18 April) and short-cycle treatments (Lincoln sown 17 May) in 2012. There were no roots found in the short-cycle treatment below a depth of 1.4 m, but RLD in the long-cycle treatment exceeded 0.2 $cm.cm^{-3}$ to the deepest sampling depth of 1.8 m. As a result, EGA Eaglehawk was able to extract 21 mm more water than Lincoln. In addition, it was able to convert this water to dry matter more efficiently under terminal drought (3.4 vs. 3.1 g m^{-2} mm^{-1}).

Greater rooting depth and deep soil water extraction was achieved in this experiment through a combination of genotype (G, slow development) and management (M, early sowing) resulting in longer life-cycle and thus duration of root growth. However, it only resulted in a yield benefit in specific environments, i.e., in the presence of deep soil water and drought during critical growth period. Other authors have proposed increasing rooting depth by genetic means alone as a useful trait to target for low rainfall environments (Dreccer et al., 2002; Wasson et al., 2012; Rich et al., 2016). However, the magnitude of increase by this mechanism may not be as great as that demonstrated by synergistic G x M interaction here. The

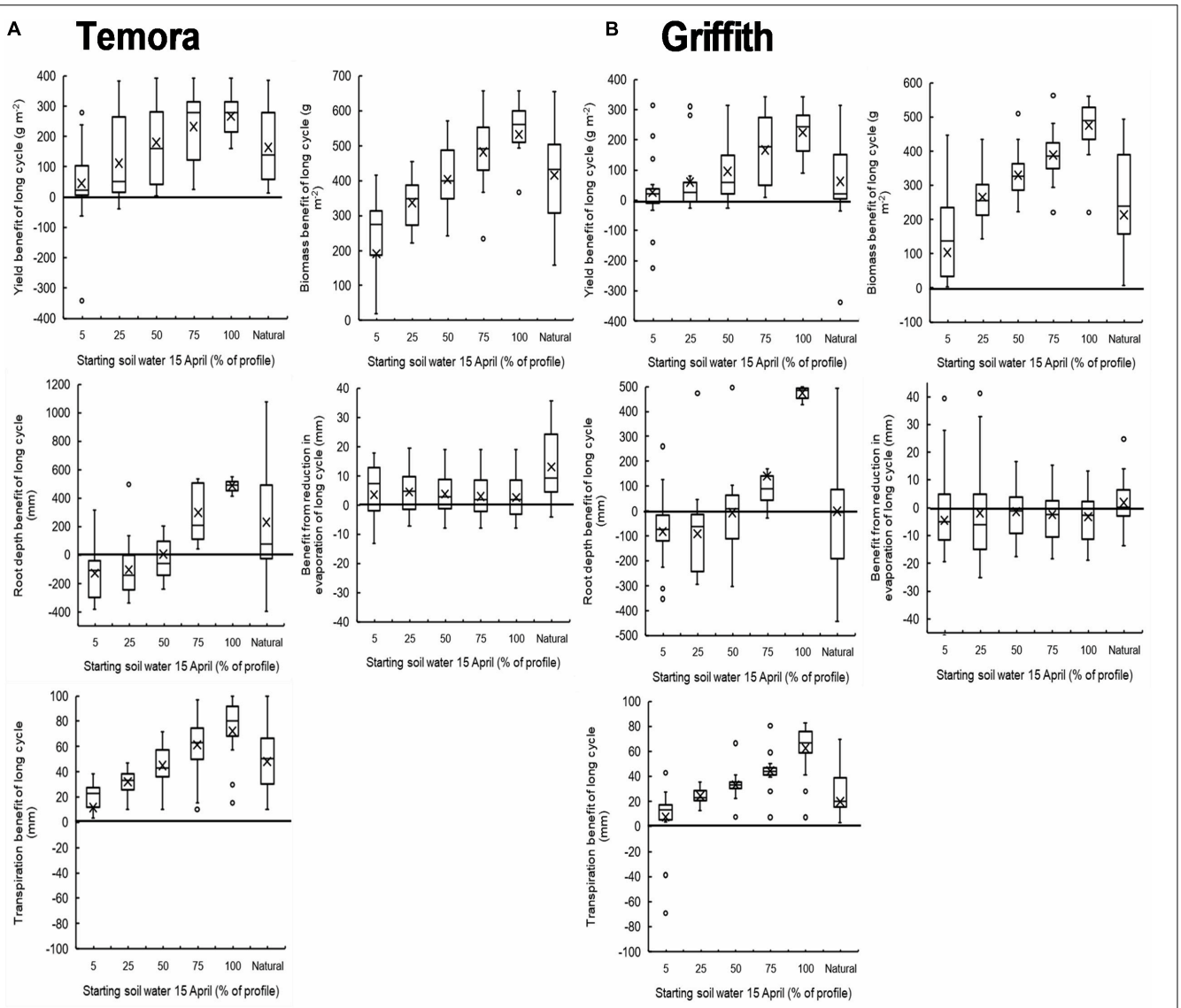

FIGURE 6 | Box and whisker plots showing the simulated yield benefit (1997–2016) of long cycle treatment (Eaglehawk sown 15 April) over the short cycle treatment (Lincoln sown 15 May) at different levels of starting plant available water on 15 April at both Temora **(A)** and Griffith **(B)**.

findings from the 4-year field experiment are supported by a 19-year simulation experiment conducted at two locations. The simulation study showed that as soil water at the start of the growing season was increased, the yield benefit of long-cycle also increased. As presented in **Figure 6**, there is considerable variation around the median yield benefit of long-cycle at both locations. This is driven by seasonal variability, and it is likely that in seasons where there was greater long-cycle benefit there was little rainfall in the 30 days preceding the optimal flowering period, and in years where there was little yield advantage over short cycle treatments, there was no spring drought. Our results support other studies that also indicate that deeper roots are only of benefit in environments where soils are able to hold water deep in the profile, rainfall distribution enables deep soil wetting and drought during the critical period and grain filling forces reliance on deep soil water to support growth (Kirkegaard et al., 2007; Lilley and Kirkegaard, 2007, 2016). Our results are limited to a single region with a similar environment. Yield benefits from stored soil water are likely to differ in environments where soil water holding capacities are lower or there is an impediment to root growth, and in environments where rainfall (particularly during the summer fallow) is lower and thus soil water is unlikely to be stored at depth (Lilley and Kirkegaard, 2016).

Potential for Genetic Improvement of Long-Cycle Cultivars

Our data showed good agreement in the relationship between HI and proportion of water used after flowering proposed by Passioura (1977), who reported that irrespective of the total water

supply, HI is optimized when around 30% of the water supply was used after flowering. However, there was no significant difference in the distribution of pre- and post- flowering water use between long- and short-cycle treatments. This implies that imbalance between pre-and post- flowering water use is unlikely to be the reason for low HI in long-cycle treatments observed by other researchers (Gomez-Macpherson and Richards, 1995). Based on our data, it also seems unlikely that competition for assimilates between the elongating stem and developing spike during the critical period reducing grain number is responsible for low HI. Stem weight as a proportion of dry matter was not significantly different, and grain number was never lower in the long-cycle treatments despite equivalent yields. Equivalent yields in 2015 and 2016 were due to lower grain weight, implying greater post-flowering stress in long cycle treatments or an imbalance between source and sink reducing grain weight.

There was an unusual relationship between grain number and yield in the 2 years in which long-cycle treatments showed a yield advantage over short-cycle (**Figure 5**). Relationships between these two parameters are typically linear (Calderini et al., 1995; Slafer et al., 2005) but both these seasons showed an asymptotic relationship. We hypothesize that this relationship is due to gradual imposition of a sink limitation other than grain number on grain yield as water limited potential yield is approached. It implies an imbalance between source and sink in long-cycle treatments, with sink ultimately limiting yield. Reynolds et al. (2017) demonstrated that substantial yield gains were possible by crossing high dry matter lines (source) with lines selected for strong sink traits (grain number, harvest index, water soluble carbohydrate mobilization) to improve source/sink balance. This raises the possibility that yield could be increased in long-cycle cultivars (which have high biomass through G x M interaction) via genetic improvement of sink traits other than grain number, such as HI, grain size or accumulation of translocatable carbohydrates. Flohr et al. (2018b) demonstrated that historic yield gains in this environment have largely been achieved through increases in HI and that this trait was decoupled from cycle length, supporting the potential for such a breeding strategy to improve yields. HI and grain weight are traits that lend themselves to early generation selection in spaced plants (Fischer and Rebetzke, 2018), and this technique could be used to improve the speed and precision of breeding for high yield in long-cycle cultivars.

Management for Yield Advantage in Long Cycle Cultivars

Management strategies that improve the capture and efficient use of summer fallow rain (residue retention, summer fallow weed control) are likely to synergize with long-cycle treatments (Kirkegaard et al., 2014). An analysis by Chenu et al. (2013) illustrated that different sowing dates, stored soil water at sowing and genotype development patterns can affect the drought pattern experienced by a crop. It is possible that G × M factors can be further manipulated to increase the yield advantage of long-cycle treatments. Fischer and Armstrong (1990) demonstrated that stored soil water accumulated during fallow periods increases the probability of gaining early sowing opportunities. As practiced in the United States Pacific Northwest (Schillinger, 2016), other authors (Oliver et al., 2010; Flohr et al., 2018a) also surmized that crop rotation and fallow length can be altered in different rainfall zones to increase early sowing and establishment opportunities, and also amount of stored soil water. Farmers intending to use long-cycle cultivars could manage rotations such that soil water accumulation is maximized, i.e., by extending fallow periods to increase both sowing opportunities and the likelihood of achieving a yield advantage with long-cycle. However, this could have negative implications elsewhere in the farming system. In the context of mixed cropping and livestock enterprizes where dual-purpose cropping is possible, long-cycle treatments will provide additional biomass production even from levels of starting water where a grain yield benefit is not observed (**Figures 6A,B**). Therefore when making decisions regarding when it is profitable to sow long-cycle crops, the value of feed should also be considered rather than for grain harvest alone (Sprague et al., 2018).

Future climates may favor the early sowing x slow developing cultivar x fallow management synergy. Australian agencies (BOM and CSIRO, 2018) reported that while April-October rainfall has declined by 11% since the late 1990s, in the future there will be an increase in intense heavy rainfall events with longer periods spent in drought. Verburg et al. (2012) determined that rainfall in excess of 20–30 mm is needed to infiltrate below the evaporative zone at the soil surface for storage for subsequent crop growth, and an increase in intensity may improve storage. Sowing ultra-long cycle cultivars early into stored soil water could alleviate the on-farm impacts of the decline in April-May rainfall by allowing growers to establish crops using stored soil water from summer fallow rain, rather than relying on the declining in-crop rainfall. In seasons where stored soil water cannot be manipulated with management, or where there is inadequate summer fallow rainfall prior to sowing, growers would be best to sow short-cycle treatments at the optimal sowing date (Flohr et al., 2017).

An analysis of the amount of rainfall required in different environments on soils with different water holding capacities to achieve a yield advantage in long-cycle crops would improve our understanding of environmental suitability. An accurate long-term forecast would enable growers to better decide on long- or short-cycle cultivars (Lilley et al., 2019). Further consideration and analysis is required to determine the legacy effect of growing long-cycle crops that have greater rooting depth and leave the soil in a drier state (Lilley and Kirkegaard, 2016), and on the summer fallow rainfall required to recharge deep stored water.

CONCLUSION

Field and simulation results demonstrated that long-cycle cultivars possessed a yield advantage over short-cycle cultivars in seasons where two conditions are met (1) water is stored deep

in the soil profile, and (2) where little rain subsequently falls during the critical period for yield determination which increases the reliance on deep water to maintain growth. Early sowing of long-cycle cultivars, and management to maximize accumulation of soil water during fallow periods are complementary practices which will assist to maintain current yield levels in southern Australia under projected future climates. Greater yield gains may be possible in the future by selecting for sink traits other than grain number in long-cycle cultivars.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

JH and BF conceptualized, designed and analysed the experiments and interpreted the results. BF and JH wrote the manuscript and designed and prepared figures and tables. JH and BF managed the collection of data from field experiments, and with assistance from TS, BR, LG, and MB. JH conducted the simulations and BF prepared the figures. JK and JE contributed valuable comment to the final manuscript and interpretation of results.

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SUPPLEMENTARY MATERIAL

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Effect of Plant Density on Wheat Stem Sawfly Sex Ratio

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The wheat stem sawfly (*Cephus cinctus* Norton) has plagued wheat production for over a century in North America. Host plant resistance in the form of wheat cultivars with a solid pith is a key management strategy. In this study we assessed the interaction of plant density, stem thickness and sawfly sex allocation using the most recent bread wheat cultivar with the resistant trait registered in Canada. The resistant cultivar with the solid stem trait was Lillian and it was compared to triticale and Go wheat, both of which lacked this trait. We confined 1 meter square crop plots using cages and half of the area in some cages was thinned manually to obtain thicker stems. We hypothesized that plant densities would affect stem diameters and solid pith expression, and these would affect host choices by the sawfly and sex ratio allocations. Our data showed that stems with a thicker diameter consistently produced more females compared to thinner stems that were more likely to produce males regardless of wheat cultivar. Shifting the plant population to lower average stem diameters in the resistant cultivar Lillian resulted in a male biased sex ratio, but not consistently. Further field studies are needed to test the hypothesis that at low plant densities of a resistant cultivar, the sex ratio would be more even due to higher female mortality in thicker stems.

Keywords: ***Cephus cinctus*, sex ratio, fitness, yield, solid stem**

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INTRODUCTION

Two species of grass stem mining sawflies (Hymenoptera: Cephidae) are significant pests of wheat in temperate regions. *Cephus pygmaeus* L., the European wheat stem sawfly from Eurasia, is an intermittent pest in that region (Özberk et al., 2005). In the Northern Great Plains of North America, the endemic *Cephus cinctus* Norton, the wheat stem sawfly (hereafter WSS), if by far a more serious pest and has been researched intensively for over a century (Beres et al., 2011d). Historically, WSS has threatened wheat production in the southern prairies of Canada, and Montana and North Dakota in the USA. Recent molecular studies (Lesieur et al., 2016) have revealed three population clusters of wheat stem sawfly: northern (on spring wheat, Canadian prairies, and adjacent northern USA), mountain (winter and spring wheat in western Montana) and southern (spring and winter wheat, north USA, and as far south as Colorado) (Lestina et al., 2016). Specific phenology of each cluster varies depending on the region and the host. In all cases, larvae mine inside the stem feeding on parenchymous tissue and near the end of the summer migrate to the base of the stem where they notch it to construct an overwintering chamber (Criddle, 1923). Mature larvae overwinter below the crown zone and complete pupation the following spring. Adults chew a hole through the plug on top of the stub and emerge ready to mate and with a full complement of eggs (Holmes, 1979). Like all hymenoptera, WSS are haplodiploid

so that unfertilized eggs produce males (Mackay, 1955). Adults only live around a week and emerge intermittently, thus making management with chemicals ineffective (Holmes, 1979).

Yield losses to WSS can be substantial during outbreak cycles and require mitigation strategies. Losses stem from larval mining and unrecovered toppled stems and can reach 30% (Holmes, 1977; Beres et al., 2007). Both the European and the North American WSS can reduce grain yield by about 2 kg/ha with every increase in percent of stems cut (Özberk et al., 2005; Beres et al., 2007). Beres et al. (2011d) estimated that annual losses caused by WSS in North America can reach $350 Million. These authors recommended an integrated pest management approach (IPM) centered on host plant resistance in the form of wheat cultivars with solid stem pith (Farstad, 1940). Other key components of the IPM package (Beres et al., 2011b) include crop rotations to diversify agricultural landscapes (Rand et al., 2014), conservation biological control (Shanower and Hoelmer, 2004), trap crops with semiochemicals (Weaver et al., 2009; Buteler et al., 2010), and cultural methods such as residue management (Beres et al., 2011a) and planting cultivar blends (Cárcamo et al., 2016). Despite considerable progress toward IPM of this pest, in some regions of the USA it remains a major threat to wheat production and its resurgence still constitutes a biotic threat for cereals in Canada.

Host plant resistance is a key strategy in insect pest management. For WSS, several lines of durum and bread wheat with some level of WSS resistance have been developed in North America. All rely on the development of solid pith in the lumen that reduces egg laying (Varella et al., 2017), survivorship of immatures (Holmes and Peterson, 1958) or reduces adult fitness (Morrill et al., 2000; Cárcamo et al., 2005). Local environmental conditions and agronomic practices can interact with genetic expression of the solid pith so that in some cases it is poorly expressed and plants are damaged (Holmes, 1984). At high plant density (over 350 plants/m^2), cultivars with the solid pith trait can have weak expression and incur economic damage (Beres et al., 2011c); this may also happen under rainy or cloudy conditions (Platt, 1941). Thus, there is a need for more case studies under a variety of environments to better understand genotype by environment interactions relevant for WSS pest management.

Hymenopteran insects such as WSS can alter the sex ratio of their progeny in relation to host quality. For example, parasitoids lay more female than male eggs in better quality hosts, such as larger ones (Wang et al., 2008). This phenomenon has also been documented for some herbivores, including WSS, although the effects of cultivars on sex ratios are inconclusive (McGinnis, 1950; Holmes and Peterson, 1963). Within cultivars, however, some authors have noted that more females than males emerge from wheat stems that have higher average diameters (Wall, 1952; Cárcamo et al., 2005). Stem diameter (= stem thickness) is expected to increase with decreasing plant density, which can also influence pith expression (Beres et al., 2011c). Holmes and Peterson (1963) noted more male emergence from the solid stem cultivar Rescue than from hollow stem cultivars. They explained the difference as follows: (1) early in the flight period there are more mated females than later in the season when males have died, (2) these mated females lay female eggs fertilized with sperm, but some are killed by the solid pith as eggs or larvae, (3) scarcity of males later in the flight period results in unfertilized eggs that yield more males which go on to survive because some of the earlier cohort dies in solid pith cultivars. The authors dismissed stem thickness effects or cultivar preferences. However, an earlier study by McGinnis (1950) noted clear cultivar differences in the damage of two hollow stemmed cultivars (Red Bobs and Thatcher) and some evidence for sex ratio effects. Furthermore, recent studies by Weaver et al. have clearly demonstrated that plant volatile differences have differential attractiveness to WSS (Weaver et al., 2009). It is quite likely that resulting sex ratios are driven my multiple factors that include differential attraction to the host through plant volatiles as shown by Weaver et al. (2009), varying survival of the males and females in relation to host quality (Cárcamo et al., 2005), and the mating biology of WSS (Cossé et al., 2002), which limits the availability of sperm throughout its short adult life.

The goal of the current study was to continue to improve our understanding of sawfly-plant interactions that influence the pest population dynamics, particularly sex ratios. To this end, we confined WSS with plants in cages and manipulated host plant densities with and without the solid pith trait. Our objectives were to determine if stem thickness would interact with the solid pith trait to influence wheat stem sawfly sex ratio. More specifically we wanted to test the following hypotheses: (1) female sawflies choose thicker stems over thin stems to lay female eggs, therefore, the sex ratio from stands dominated by thicker stems in our cages should be female biased in a hollow stem cultivar; (2) stands dominated by thicker stems of a resistant cultivar with more solid pith would have a less female biased sex ratio because of potential higher mortality of female larvae in these stems. Finally we were interested in corroborating the effect of sawfly damage on individual wheat stem yield.

MATERIALS AND METHODS

This study was conducted in southern Alberta, Canada in 2009 and 2010. In 2009 it was located 1 km east of Lethbridge (49°41′ N, 112°44′ W) on research plot land of Agriculture and Agri-Food Canada (AAFC). In 2010, it was located 10 km west of Lethbridge at the wheat stem sawfly nursery (49°44′ N, 112°57′ W) near Coalhurst established by AAFC researchers (Peterson et al., 1968; Beres et al., 2005). Both sites are in the Moist Mixed Grassland Ecoregion within the Prairies Ecozone. This semiarid region has a long term mean annual air temperature around 5°C and 350–400 mm precipitation with soils classified predominantly as Orthic Dark Brown Chernozem clay loams. Annual precipitation in the Lethbridge area was 208 mm in 2009 and 367 mm in 2010.

The cereal hosts included wheat and triticale. In 2009, triticale (x *Triticosecale*, cultivar Pronghorn) and red spring wheat (*Triticum aestivum*, cultivar Lillian) were used. In 2010 triticale was replaced with the hollow stemmed wheat cultivar Go. Triticale was included because of the potential to develop this crop for industrial purposes and the need to understand its risk of damage by sawflies. Pronghorn triticale (Salmon et al.,

1997) is an early maturing cultivar well-adapted to the southern Prairies; it is high yielding and the check standard to measure new cultivars, but a known host of WSS (Beres et al., 2013). Go was used in 2010 because it was one of the most widespread red spring cultivars in the region at the time and a well-documented host of WSS (Cárcamo et al., 2016). Lillian is a solid-stemmed cultivar with sufficient resistance to WSS and high yield (DePauw et al., 2005) with a high degree of adoption by growers in years with high sawfly pressure. In some regions, depending on weather conditions the solid pith expression can be inconsistent, therefore, this cultivar could be considered semi-resistant.

A cage assay was conducted both years to manipulate stand densities to obtain thicker stems and assess impact on wheat stem sawfly sex ratio, stem infestation, and interactions with yield. In 2009 triticale and Lillian wheat were planted in adjacent strips on 21 May at a rate of 200 seeds per meter square. Four, one meter square areas were designated within each of the strips and half of each area was thinned manually to remove tillers, by clipping with scissors, two times prior to the stem elongation stage (Zadok 32). Cages (1 m square and 1.2 m tall, clear nylon screen with 12 threads/cm) were deployed on 30 June 2009 and kept until crop maturity. Therefore, each cage in 2009 contained both a sparse (thinned) stand and a high density plant stand each about 0.5 m^2.

In 2010, 4 wheat strips were planted at the Coalhurst site to include a high and a low seeding rate for two cultivars (**Figure 1**). Two adjacent strips of Go wheat were planted at 450 and 150 seeds per m square, and two similar strips of Lillian were planted immediately west at the same two seeding rates. For the high seeding rate strips, the same treatment performed in 2009 was executed: 4 cages in each of the two strips had half of the area inside each cage thinned manually by clipping the tillers with scissors. This treatment was intended to provide a choice of thin vs. thick stems for the sawfly to lay eggs within a cage. An additional 4 cages were set up in these same strips (alternating pattern) and left intact at high plant densities. Finally, at each of the wheat strips planted at low densities, four cages were set up, and all tillers were removed as described above in the entire 1 m square (**Figure 1**). These last two treatments were intended to deny an oviposition choice to WSS so that they would encounter mostly thin or mostly thick stems. For both years of the study each treatment was replicated 4 times and represented by 4 cages that were deployed on a certain cultivar strip and received a particular plant density manipulation.

Cages were deployed on 29 June 2010 and similar to 2009, they were left until plant maturity. To inoculate the cages with WSS, plant stubs (damaged plants with overwintered sawfly larvae) were collected from a field near Taber (about 50 km east of Lethbridge) on 24 June 2009 and from the Coalhurst nursery on 30 June 2010. The plant remains were sorted in the laboratory and 50 wheat stubs were "planted" in the middle of each caged area. Parasitoid wasps (*Bracon cephi*) were aspirated from the cages as much as possible to minimize sawfly mortality. A subsample

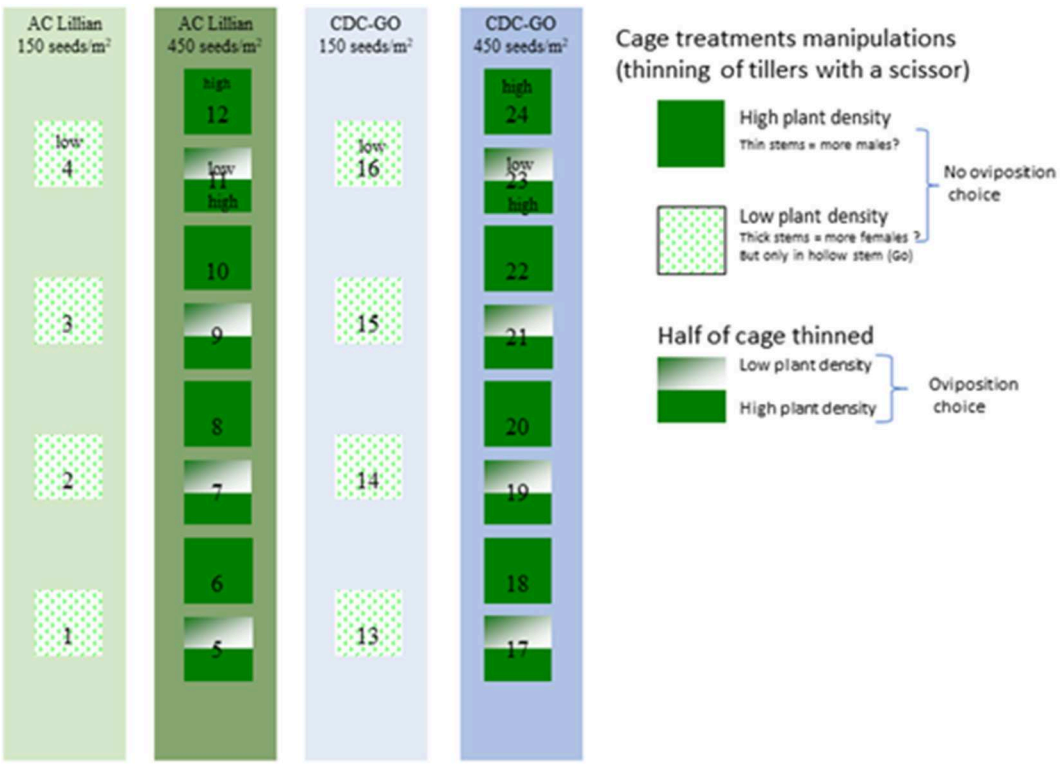

FIGURE 1 | Layout of the cages within the adjacent strips of CDC Go and Lillian wheat planted at 150 or 450 plants/m^2 near Coalhurst, Alberta Canada. Some cages were thinned manually with scissors completely or only half to obtain thicker stems and assess effects on sawfly sex ratio.

of 100 stubs were set up for emergence in the laboratory to estimate population size and sex ratios introduced into the cages. Survivorship from this subsample showed about 90% emergence and over 70% were females.

Several response variables were measured each year. Prior to crop senescence, cages were removed and all plants were dug out carefully, and placed in large paper bags. A random subsample of at least 20 stems from each cage or manipulated half was taken to measure the stem diameter at 3 angles using a digital caliper. Cut stems were measured 1 cm below the cut area and for uncut stems 1 cm below the second node. In 2010, a similar sample size of uncut stems were dissected longitudinally and each undamaged internode was given a rank where zero was a completely hollow lumen and 5 was completely solid. Both years, cut stubs expected to have mature larvae were placed to overwinter in a room at 10°C and 8:16 h, L:D regime from late September until late March. At this time, each stub was placed in a plastic vial with moistened sand and moved to room temperature (22°C) and long light:dark photoperiod regime (16:8 h). The sex of each adult that emerged was recorded. A similar sample size of mature plants were collected from an uncaged area in each of the strips to estimate effects of the cage on stem diameter (both years) and pith expression (2010 only) and potential interactions with WSS.

Statistical Analysis

Stem diameter, pith and grain weight were analyzed using the GLIMMIX procedure in SAS (2013). The mixed models included cage as the random factor and location, variety, and plant density as fixed factors. An additional analysis was conducted using type of sawfly damage as a fixed factor nested within plant density and cages. Fixed factors were included where they were warranted based on the $p < 0.05$ of the F-test (fixed factors and their interactions). The inverse Gaussian or the Gamma distribution were selected to model the stem diameter data based on the model fit statistics, i.e., the Bayesian information criterion (BIC). For pith and grain weight, the beta-binomial and Gaussian (normal) distribution were selected, respectively. The relationship between female proportion and stem diameter for each cereal crop or cultivar was modeled using a modified Weibull function (SAS PROC NLIN):

$$Female = 1 - e^{(-Ad^B)},$$

where F indicates the proportion of females and d indicates the stem diameter. The number of males vs. females in each of the plant density and cultivar treatments were integer counts and as such they were assumed to be Poisson distributed for comparison using a t-test:

$$t_{\alpha[\infty]} = \frac{Y_1 - Y_2}{\sqrt{Y_1 + Y_2}}$$

The corresponding P-values were calculated in R using the pt function with df = Inf and lower.tail = FALSE (R Core Team, 2019).

In all cases, Bonferroni's adjustment for multiple comparisons was used when there were fewer than seven categorical levels, and Scheffe's adjustment was used when there were seven or more levels.

RESULTS

Stem diameter for the plant population sampled inside the cage or at an adjacent open patch was affected by some of the treatments in 2009 (**Figure 2**), but not in 2010 (**Figure 3**). In 2009, Lillian stems were over 2 mm thick in the low plant density stand and under 2 mm in the area with higher plant density, outside, or inside the cage [$F_{(1,458)} = 45.59$, $P < 0.0001$]. Triticale stems were thicker than those of Lillian [$F_{(1,458)} = 18.54$, $P < 0.0001$]. In 2010 there were no significant differences with respect to stem diameters for any of the treatments inside or outside the cages. Most stems were between 1.5 and 3.0 mm in diameter below the second internode.

Pith solidness was assessed only in 2010 and it was affected by the cages and cultivar [$F_{(8, 614)} = 41.08$, $P < 0.0001$], but not by plant density treatments inside cages (**Figure 4**). The highest pith rating was around 3 out of 5 for Lillian grown in the open and higher than Lillian plants confined with cages. Inside the cages, Lillian had significantly higher solid pith at 2.2 than Go at 1.6 [$F_{(8,614)} = 40.23$, $P < 0.0001$].

Stem diameter influenced host acceptance for wheat, but not for triticale. In 2009, Lillian infested stems were significantly thicker than un-infested stems (**Figure 5**, Bonferroni adjusted comparison, $t_{1,458} = 2.69$, $P = 0.0442$). In 2010 (**Figure 6**), infested stems (cut or not cut by sawfly), were significantly thicker than un-infested stems in both wheat cultivars [$F_{(2, 724)} =$

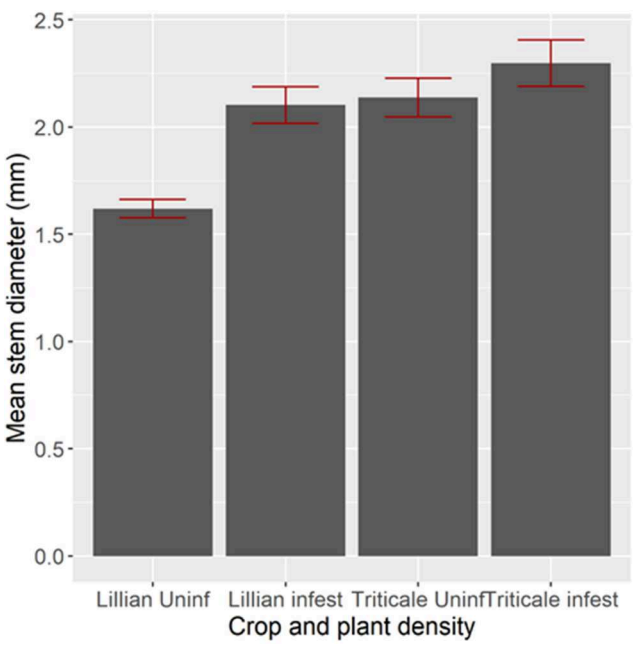

FIGURE 2 | Stem diameters (mm) of wheat and triticale in stands with tillers removed (Low) or left at high density (High) in 2009 inside cages. Four cages were used to replicate the plant density manipulation.

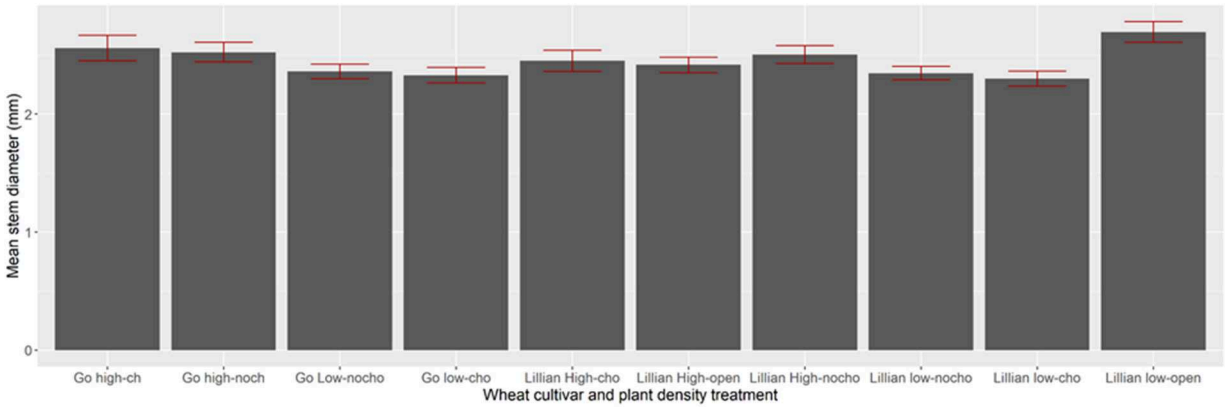

FIGURE 3 | Stem diameters of two wheat cultivars outside (0) or inside (1) cages near Coalhurst, Alberta in 2010. Density Choice: refers to the stand density, high or low, in half the cage (choice) or the entire stand in the cage (no choice). HighChoi, high with choice; LowChoic, low with choice; HighNoch, high with no choice; LowNoCho, Low no choice. Four cages were used to replicate the plant density manipulation for each cultivar.

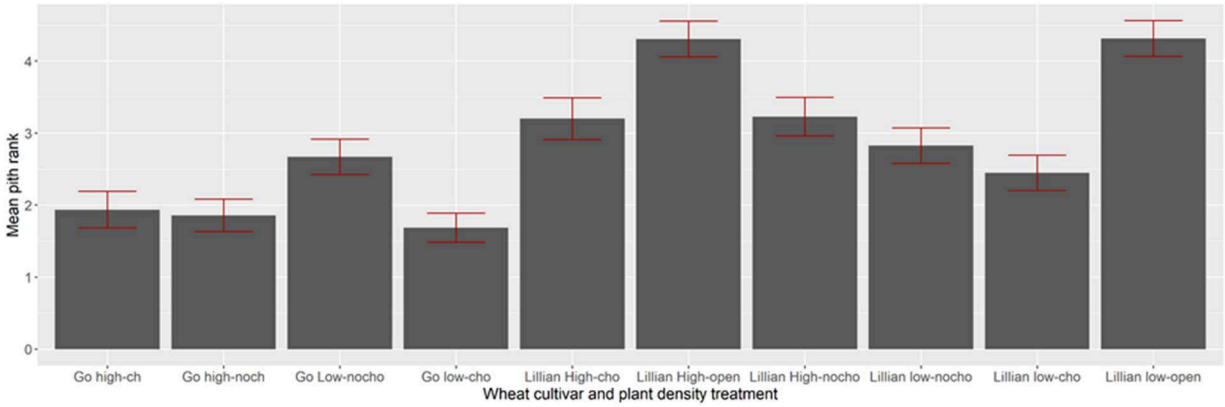

FIGURE 4 | Pith of the stem lumen (solidness rank) of wheat cultivars in 2010 inside and outside cages. Entries are means and standard errors. Refer to **Figure 3** for abbreviations. Four cages were used to replicate the plant density manipulation for each cultivar.

84.15, $p < 0.0001$]. Grain weight followed the same pattern as the stem diameters: sawfly-infested, thicker stems, had significantly higher seed weights than un-infested thinner stems [$p < 0.001$, **Figure 7**, $F_{(2,1494)} = 67.97$, $p < 0.0001$].

Female and male counts differed significantly in the plant density treatments within cultivars in 2009 (**Table 1**, *t*-test, $p < 0.05$). In 2009, from the 130 adults reared, there were more females than males from the low plant density stands in the cages of Lillian wheat, but this pattern was reversed from the high density stand for this cultivar, which had a lower average stem diameter than the former. For triticale, both areas within the cages, with high or low plant densities, produced more females than males, but the overall number of sawfly adults was lower than those from wheat. In 2010, 232 adults emerged from the Go and Lillian wheat cultivars combined. With one exception, the sex ratios were female biased and ranged from about 0.6 to 0.7. The number of females was significantly higher than males only from the high plant density treatment of Lillian without the stand choice ($p = 0.0092$). The only treatment with an even sex ratio was for the low plant density treatment for Lillian with no stand choice, but only 4 adults emerged from these cages (**Table 1**).

The relationship between stem diameter and female proportion (weather a female or male emerged from a given stem) was further explored using non-linear functions. A Weibull non-linear function (**Figure 8A**) explained the relationship and showed different responses for Lillian ($\widehat{Female} = 1 - e^{(-0.0120 \times d^{6.1213})}$) and triticale ($\widehat{Female} = 1 - e^{(-0.0641 \times d^{3.1220})}$); in this equation, $\widehat{F}$ is the female proportion and d is the stem diameter. A stem diameter near 2.0 mm and about 2.2 mm were required for a near even sex ratio of sawfly emerging from Lillian and triticale, respectively. To achieve a female dominance close to 80%, only an increase of 0.3 mm in stem diameter would be needed in Lillian, but almost a full mm was required to reach this proportion of females in triticale. In 2010, a similar non-linear relationship between sex ratio and stem diameter was observed for the two wheat cultivars Lillian and Go (**Figure 8B**), but it approached linearity for Go.

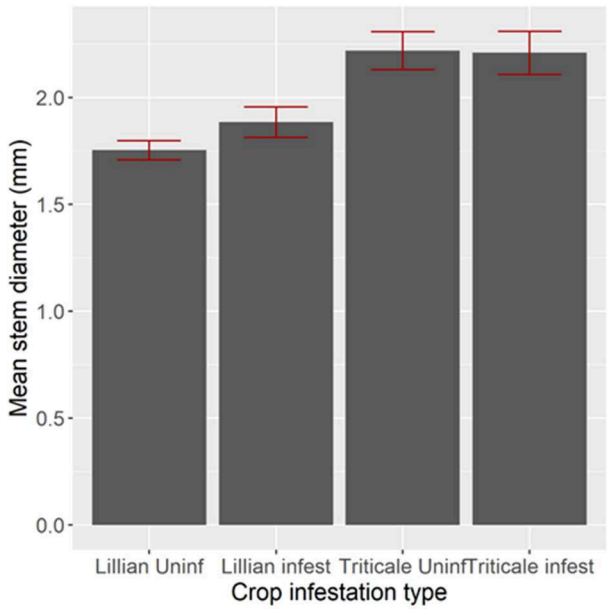

FIGURE 5 | Stem diameter of Lillian wheat and triticale infested or un-infested by wheat stem sawfly confined with cages in 2009 near Lethbridge, Alberta. Four cages were used to replicate the plant density manipulation for each cultivar.

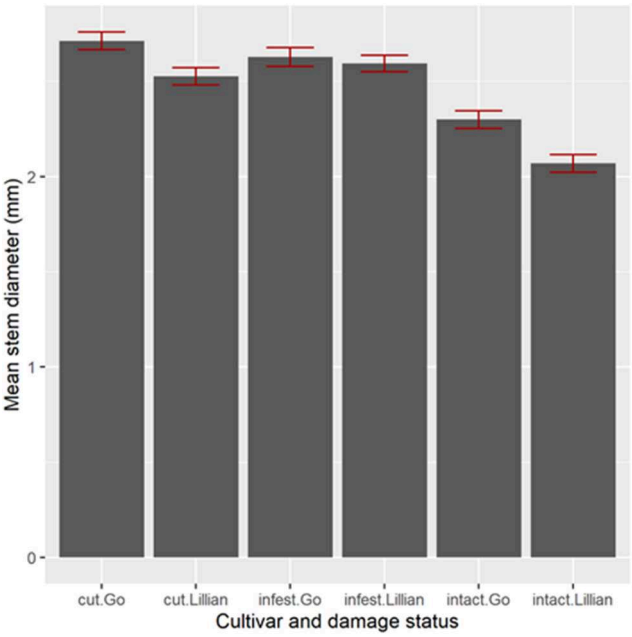

FIGURE 6 | Stem diameters of wheat infested, cut or un-infested by wheat stem sawfly inside cages in 2010. Four cages were used to replicate the plant density manipulation for each cultivar.

For both cultivars, slightly thicker stems over 2.2 mm were required to produce an even sex ratio. Stems around 3 mm in thickness resulted in a highly biased female sex ratio near 80% in Lillian similar to 2009; for the cultivar Go, stems around 3 mm had a female proportion under 70%.

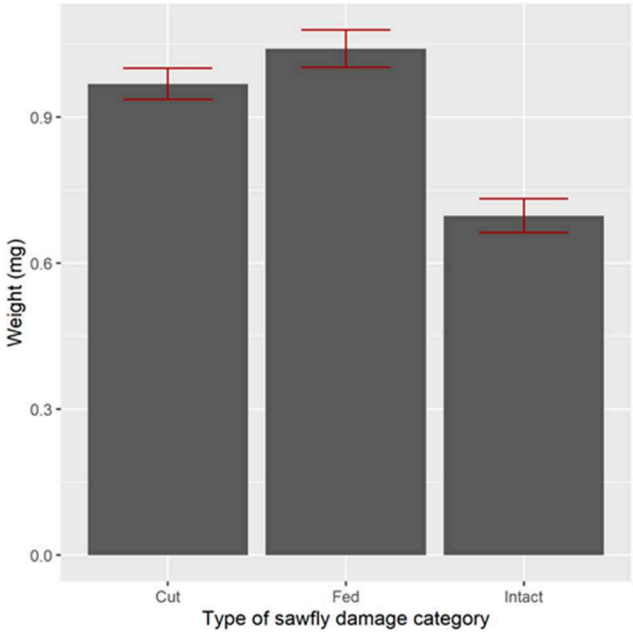

FIGURE 7 | Average weights (mg) of wheat seed weights in relation to wheat stem sawfly infestation in a cage study in 2010 near Coalhurst, Alberta. Entries are arithmetic means and ± 1 standard error. Four cages were used to replicate the plant density manipulation for each cultivar.

DISCUSSION

Host quality can influence host selection and sex ratios of haplo-diploid Hymenoptera such as wheat stem sawfly. For this sex determination system, unmated females lay male eggs, and those mated can allocate gender depending on host quality. This trait may be exploited for management of herbivorous insect pests such as the wheat stem sawfly. In this study we manipulated plant densities by varying seeding rates and also inside cages through manual thinning. We used the latest bread wheat solid stem cultivar registered in Canada, Lillian, and compared it to a hollow stemmed host, triticale in 2009 and Go wheat in 2010. We expected that at lower plant densities, average stem diameter should be greater than at higher densities. A number of studies have shown that more females emerge from stem stubs with higher diameter than from thinner stems (Wall, 1952; Morrill and Weaver, 2000; Morrill et al., 2000; Cárcamo et al., 2005). In general, over the 2 years of the study, sex ratios were female biased in most treatments with only two exceptions. In 2009, Lillian stems from the high plant density stand inside cages had a significantly male biased sex ratio compared to the low plant density stand that produced significantly more females than males. Clipping tillers to reduce plant density inside cages may have changed the volatile profile (Weaver et al., 2009) and induce stronger defenses in the main stems of these

TABLE 1 | Sex ratio of wheat stem sawfly that emerged from wheat or triticale stubs in 2009 and 2010.

Year	Cultivar	Plant density	Stand choice*	Female counts	Male counts	Female proportion (%)	Bonferroni corrected *p***
2009	Lillian	Low	Yes	33	13	71.7	0.0064
		High	Yes	12	28	30.0	0.0228
	Triticale	Low	Yes	10	2	83.3	0.0418
		High	Yes	24	8	75.0	0.0094
2010	Lillian	Low	Yes	18	8	69.2	0.0998
		High	Yes	17	8	68.0	0.1437
		Low	No	2	2	50.0	2.0000
		High	No	32	13	71.1	0.0093
	Go	Low	Yes	35	20	63.6	0.0847
		High	Yes	12	9	57.1	1.0000
		Low	No	10	4	71.4	0.2174
		High	No	25	17	59.5	0.4344

**stand choice: yes means that half of the cage was thinned manually; **t-test to compare counts of females and males, with p-value corrected for 4 comparisons.*

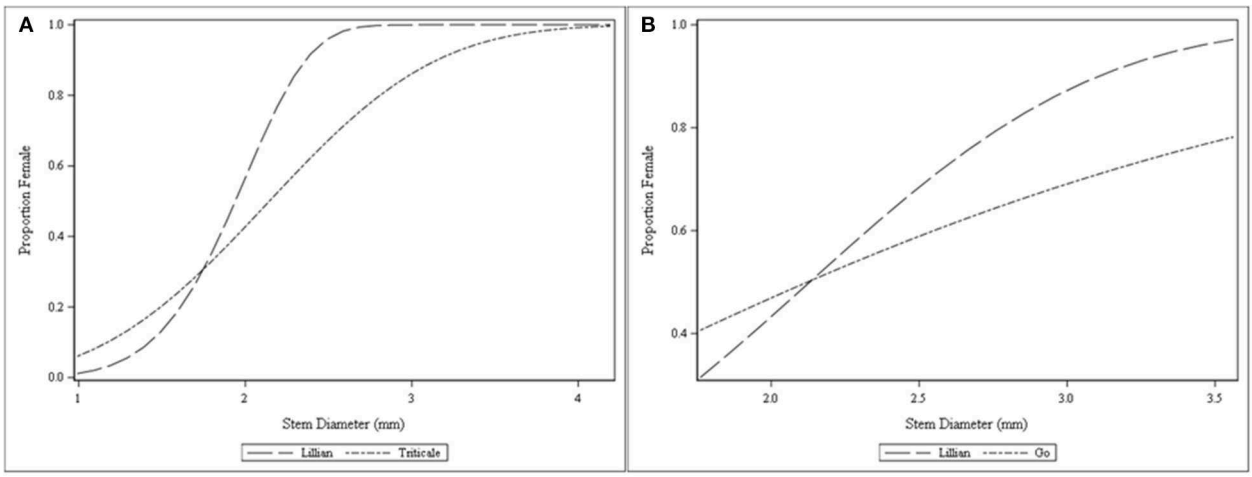

FIGURE 8 | Modified Weibull functions explaining the relationship of cereal host stem diameter and wheat stem sawfly sex ratio (female proportion) from the cage study near Lethbridge in 2009 **(A)** and 2010 **(B)**. Four cages were used to replicate the plant density manipulation for each cultivar.

plants that could affect larval survivorship (Karban et al., 2000). However, the fact that more females than males emerged from the main stems suggests that this was not the case because it is known that females are more sensitive than males (Morrill et al., 2000) to reductions in host quality presumably associated with higher defenses.

We suggest that four hypothesis may explain the pattern of male biased sex ratios in stands with more thin stems. (1) Our data lend support to the hypothesis that in a stand composed of mainly thin stems, females lay mostly male eggs rather than allocating the gender on a relative stem thickness basis (Cárcamo et al., 2005). (2) Alternatively, female larvae may not have survived if their nutritional requirements were not met in stems that were not thick enough to meet their higher nutritional requirements. This hypothesis is supported by the studies of Morrill et al. (2000) and Morrill and Weaver (2000) who showed that females are more sensitive to host quality than males. (3) Solid pith may result in higher female mortality if WSS laid more female eggs in stems that are slightly thicker, which under ideal environmental conditions should have more pith than thinner stems. The latter hypothesis is unlikely because the sex ratios were female biased in the low plant density stands of Lillian that had stem diameters over 2 mm in 2010. (4) A fourth explanation cannot be ruled out from our design: higher plant densities may have reduced light intensity inside the cages and influenced WSS mating behavior and confounded progeny sex ratio. WSS may have mated less frequently inside cages with a higher stand density due to poor light (McGinnis, 1950). If this was the case then they would have laid more unfertilized male eggs, thus biasing the sex ratio. A field experiment under natural light conditions is needed to overcome this confounding factor. The only other instance of non-female biased sex ratio was in 2010

in the Lillian treatment with low plant density that had 2 males and 2 females in total. It is not known why survivorship was so poor in this treatment, but it could not be related to solid pith because this trait was poorly expressed inside the cages regardless of plant density. The poor development of solid pith may be explained by the shading inside the cage because it is known that environmental conditions can limit expression of this trait (Platt, 1941). Teasing apart these hypotheses presents considerable logistical challenges.

Local mate competition and mating status can be a strong determinant of sex ratio in Hymenoptera (Henter, 2004). We did not control the founding sex ratios in our study, but expect that there were enough males to fertilize females. However, it is possible that some did not mate and may show less discrimination between thick and thin stems. The effect of mating status on sex ratio allocation in relation to host quality has not been studied extensively. However, Gerling et al. (1987) showed that unmated females of *Encarsia deserti* (Hymenoptera: Aphelinidae), a parasitoid of *Bemisia tabaci* (Homoptera: Aleyrodidae) failed to discriminate between parasitized and un-parasitized hosts, unlike those that had mated and could lay female eggs. A challenging controlled study that provides very high light intensity in cages with various ranges of stem diameters with treatments including mated and unmated females as well as varying proportions of founding sex ratios would help answer this question for WSS.

Cereal species and cultivar may interact with stem diameter to influence sex ratios. Triticale has relatively larger stem diameters averaging 2.9 mm compared to Lillian wheat with an average of around 2.2 mm in our low density treatment. These differences translated to corresponding differences in sex ratios: 80 and 50% females, respectively, when the plant density treatments were combined. This suggests that sawfly may lay more female eggs in crops with thicker stems as supported by the studies by Morrill et al. (2000); even at the high plant densities, average stem diameters of triticale were likely high enough to entice females to lay fertilized female eggs. This hypothesis is further supported by the extensive behavioral observations by Buteler et al. (2009) showing that female WSS assess host quality prior to oviposition. In the case of solid stem cultivars, attractive thick stems may present a dead end trap for sawfly immatures, and reduce female dominated sex ratio (Holmes and Peterson, 1963; Buteler et al., 2010). Furthermore, Varella et al. (2017) demonstrated that quantitative trait loci associated with the solid stem phenotype influence oviposition behavior of WSS. Also, Beres et al. (2011c) showed that Lillian maximizes solid pith in the stem lumen at densities below 250 plants per square meter. One of our objectives was to test the idea that for solid stemmed wheat cultivars at low plant densities, thicker stems of Lillian would have more solid stems that would kill more females thus reducing the female dominated population. We were unable to test this hypothesis because of the poor expression of solidity of the lumen in this cultivar during our study years. A field study without cages remains to be done to assess cereal crop and variety interaction effects on sex ratio. Such a test should include representative cultivars with alternative source of solid pith found in durum wheats such as Golden Ball (*Triticum durum* var Golden Ball), which have relatively thick stems and solid lumens, yet seem to produce female biased sex ratios (Farstad et al., 1949). Unknown germplasm factors not related to pith or stem thickness, likely affect WSS sex ratio as suggested by the studies by McGinnis (1950) with two hollow stemmed bread wheat cultivars, Red Bobs and Thatcher.

Our analysis of stem diameter and female emergence relationships suggested that the response can be non-linear and varies with the crop species. Both type of responses, linear or non-linear, showed that a female-dominated sex ratio is ensured even when the crop species or cultivar has an overall lower stem diameter. Our results corroborate those reported by Morrill and Weaver (2000) where they also showed clear effects of stem diameter on WSS sex ratio. Triticale and Go wheat have thicker stems than Lillian and it seems that a female dominated sex ratio would occur at a lower stem diameter for the cultivar that had the thinner stems. For example, 70% female emergence occurred around a stem diameter of 2.5 mm for Lillian but over 3 mm for the other two cultivars. This ensures that even if a wheat stand is dominated by thin stems a sawfly may still lay a large number of female eggs to maximize its fitness. A similar non-linear relationship and similar levels of stem thickness to achieve 70% female dominance was noted by Morrill et al. (2000) at a Montana (USA) site. This relationship is similar to the pattern of sex ratio in relation to host quality in some parasitoid wasps. For example *Tetrastichus julis* (Eulophidae), consistently lays a female dominated clutch regardless of cereal leaf beetle instar host size, but similar to our case study, the sex ratio becomes even more female dominated with the size of its host (Kher, Dosdall and Carcamo unpublished data). Thus, it appears that at some level, insects that control progeny gender follow a relative sex allocation rule to ensure female dominance. It would be of interest to test for a lower limit and force females to lay eggs on hosts that are far below the usual host size to see if there is a point where only males are laid. Further study of the host germplasm in terms of pith expression and stem diameter are still warranted, particularly in environments that maximize solid pith.

Plant traits such as stem diameter and height affect the initial host selection by wheat stem sawfly (Buteler et al., 2009) and confounds individual stem comparisons of plant yield. Regardless of cereal species or cultivar, it was clear in our study that sawfly preferentially attacked stems with larger stem diameter compared to thinner stems. Furthermore, seed weights were consistently higher in infested stems than in those not attacked by the sawfly. This is expected to result from the inherently higher yield potential of larger stems than smaller stems. Detailed studies of photosynthesis in infested stems have shown clear reductions of kernel weight attributed to larval feeding (Macedo et al., 2007; Delaney et al., 2010). Delaney et al. (2010) reported a reduction in yield loss for a solid stem cultivar compared to a hollow stem cultivar and speculated for potential compensation in such cultivars. The pattern of higher yield in infested than un-infested stems has been observed in previous studies. Wu et al. (2011) used stem diameter as a covariate to attempt to standardize effects of a parasitoid attack to wheat stem sawfly on grain yield in main stems and tillers in several cultivars. They still found that for most comparisons, un-infested stems had lower seed weights

than those that were infested by sawfly or where the immature sawfly had been killed by the parasitoid. A similar pattern of lower yield potential from un-infested stems than those infested had been reported in earlier studies (Holmes, 1977). Yet, the sawfly is a serious pest of wheat and at the plant population level, there are well-documented yield reductions both from larval stem mining [around 10% according to Holmes (1977)] and unrecovered grain from lodging (14% as per Beres et al., 2007). These losses have been documented when susceptible cultivars with hollow stem lumen are compared side by side with more resistant solid stem lumen cultivars (Beres et al., 2007). These authors and Özberk et al. (2005) demonstrated a very strong negative relationship between *C. cinctus* or *C. pygmaeus* damage and yield, which was equivalent to about 2 kg/ha of loss yield for every incremental percentage of stems cut by sawfly. Clearly, despite the confounding effect of stem diameter on yield when comparing individual stems, the sawfly is a destructive economical insect pest.

CONCLUSIONS

Our objectives were to continue elucidating complex insect-plant interactions between cereal crops and wheat stem sawfly. We hypothesized that plant densities would affect stem diameters and solid pith expression, and these would affect host choices by the sawfly, and sex ratio allocations. Our data showed that stems with a thicker diameter consistently produced more females compared to thinner stems that were more likely to produce males regardless of wheat cultivar. Shifting the plant population to lower average stem diameters in the resistant cultivar Lillian resulted in a male biased sex ratio, but not consistently. In this study solid pith expression in cages was poor and we were unable to test the hypothesis that at low plant densities of the resistant cultivar, the sex ratio would be more even due to higher female mortality in thicker stems. A field test needs to be conducted at several sites with sufficient natural sawfly populations to elucidate this interaction.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/supplementary material.

AUTHOR CONTRIBUTIONS

HC, BB, and XW conceptualized, designed the study and participated in its execution and data collection. TL and XW did most of the data collection. TS did the statistical analysis. HC wrote the first draft and BB, XW, TL, and TS edited it.

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frontiers in Plant Science

REVIEW
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Agroecological Advantages of Early-Sown Winter Wheat in Semi-Arid Environments: A Comparative Case Study From Southern Australia and Pacific Northwest United States

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Wheat (*Triticum aestivum* L.) is the most widely-grown crop in the Mediterranean semi-arid (150–400 mm) cropping zones of both southern Australia and the inland Pacific Northwest (PNW) of the United States of America (United States). Low precipitation, low winter temperatures and heat and drought conditions during late spring and summer limit wheat yields in both regions. Due to rising temperatures, reduced autumn rainfall and increased frost risk in southern Australia since 1990, cropping conditions in these two environments have grown increasingly similar. This presents the opportunity for southern Australian growers to learn from the experiences of their PNW counterparts. Wheat cultivars with an obligate vernalization requirement (winter wheat), are an integral part of semi-arid PNW cropping systems, but in Australia are most frequently grown in cool or cold temperate cropping zones that receive high rainfall (>500 mm p.a.). It has recently been shown that early-sown winter wheat cultivars can increase water-limited potential yield in semi-arid southern Australia, in the face of decreasing autumn rainfall. Despite this research, there has to date been little breeding effort invested in winter wheat for growers in semi-arid southern Australia, and agronomic research into the management of early-sown winter wheat has only occurred in recent years. This paper explores the current and emerging environmental constraints of cropping in semi-arid southern Australia and, using the genotype × management strategies developed over 120 years of winter wheat agronomy in the PNW, highlights the potential advantages early-sown winter wheat offers growers in low-rainfall environments. The increased biomass, stable flowering time and late-summer establishment opportunities offered by winter wheat genotypes ensure they achieve higher yields in the PNW compared to later-sown spring wheat. Traits that make winter wheat advantageous in the PNW

may also contribute to increased yield when grown in semi-arid southern Australia. This paper investigates which specific traits present in winter wheat genotypes give them an advantage in semi-arid cropping environments, which management practices best exploit this advantage, and what potential improvements can be made to cultivars for semi-arid southern Australia based on the history of winter wheat crop growth in the semi-arid Pacific Northwest.

Keywords: winter wheat, climate change, adaptation, vernalization, deep sowing, yield gap, drought

INTRODUCTION

The cropping systems of Mediterranean semi-arid southern Australia are diverse, resilient and responsive to change. Bread wheat (*Triticum aestivum* L.) is the most widely grown crop in the region and is important for both local consumption and export. The effects of anthropogenic climate change, including rising maximum temperatures, decreasing minimum temperatures and growing season rainfall and a delayed onset of autumn rain sufficient for germination (referred to as the "autumn break" or "breaking rain") present new challenges to which growers will need to respond in order to maintain farm yields and profitability (Pook et al., 2009; Cai et al., 2012; Crimp et al., 2016b; Hochman et al., 2017). Within a context of rising business costs and increased income risk these effects have already been visible across southern Australia since 1990, decreasing water-limited potential wheat yield (PY_W) and increasing the difficulty of establishing crops during autumn, the traditional sowing period for spring wheat (Pook et al., 2009; Hochman et al., 2017). A resilient response to the challenges of a changing environment is unlikely to be achieved through a singular technical or genetic development. Historic increases in Australian wheat yields have not been the result of individual advancements in crop genotype or crop management, but instead when the combination of crop genotype, environment and management has created synergies through which yield is increased more than can be accounted for through each development alone (Kirkegaard and Hunt, 2010; Hunt et al., 2019a).

The effects of anthropogenic climate change on southern Australia, both visible and predicted (including reduced growing season rainfall and establishment opportunities during autumn), have caused cropping conditions in semi-arid regions to converge with those of the inland Pacific Northwest (PNW) of the United States. For over a century, growers in the PNW have successfully grown wheat in drier conditions than those of semi-arid southern Australia, including in the absence of sufficient late summer and autumn rainfall to establish crops. This paper argues that although differences exist between the environmental conditions and production systems of the two regions, there is a benefit in applying some of the genotype × management synergies that have been successful in the low-rainfall regions of the PNW to wheat production in semi-arid southern Australia.

This is particularly the case for winter wheat, which has long been grown in the PNW, but only recently become of interest to growers in low-rainfall Australian environments, who more frequently grow spring wheat (Hunt, 2017). Winter wheat is differentiated from spring wheat by an obligate vernalization requirement, meaning that it must accumulate sufficient vernal time when temperatures are cool (−1.3 to 15.7°C, Porter and Gawith, 1999) in order to begin reproductive development. Many of the synergies used by PNW growers to increase yield have been facilitated by advantages winter wheat offers over spring wheat, and also have potential benefits for southern Australian growers.

This paper compares semi-arid cropping conditions in southern Australia and the inland PNW and demonstrates the confluence between the two environments. Focusing on the prevailing and emerging constraints inherent in the crop production environments (E) of both regions, we then discuss how specific genotype (G) × management (M) synergies offered by winter wheat cultivars are used to overcome each of these constraints in the PNW, and how they could similarly be employed in southern Australia. Finally, we consider barriers that may prevent implementation of early-sown winter wheat in southern Australia, and the conditions that would need to be met for widespread adoption of the practice.

INLAND PACIFIC NORTHWEST

Cropping Environments

The inland PNW is commonly divided into three annual precipitation zones: (i) low, <300 mm of precipitation; (ii) intermediate, 300–450 mm of precipitation, and; (iii) high, 450–600 mm of precipitation (**Figure 1**). Dryland wheat is grown on approximately 3,350,000 hectares in the inland PNW of which 1,557,000 hectares is in the low-precipitation zone (Schillinger et al., 2006). The low-precipitation zone, where early sowing of winter wheat is practiced, is most comparable to semi-arid southern Australia and is therefore the focus of the PNW portion of this paper. Precipitation intensities and volumes are low, usually not exceeding 2–3 mm/h and 10–20 mm per event. About 70% of annual precipitation occurs from October through March and 25% from April through June. July through September is the driest period (**Figure 2**). The Mediterranean-like climate of the inland PNW is largely influenced by frontal weather systems moving with prevailing westerly winds from the Pacific Ocean. The Cascade Mountains to the west impose a rain shadow effect. The driest part of the inland PNW is just east of the Cascade Mountains where average annual precipitation drops to 125 mm and gradually rises west to east with increase in elevation to 600 mm in the Palouse region.

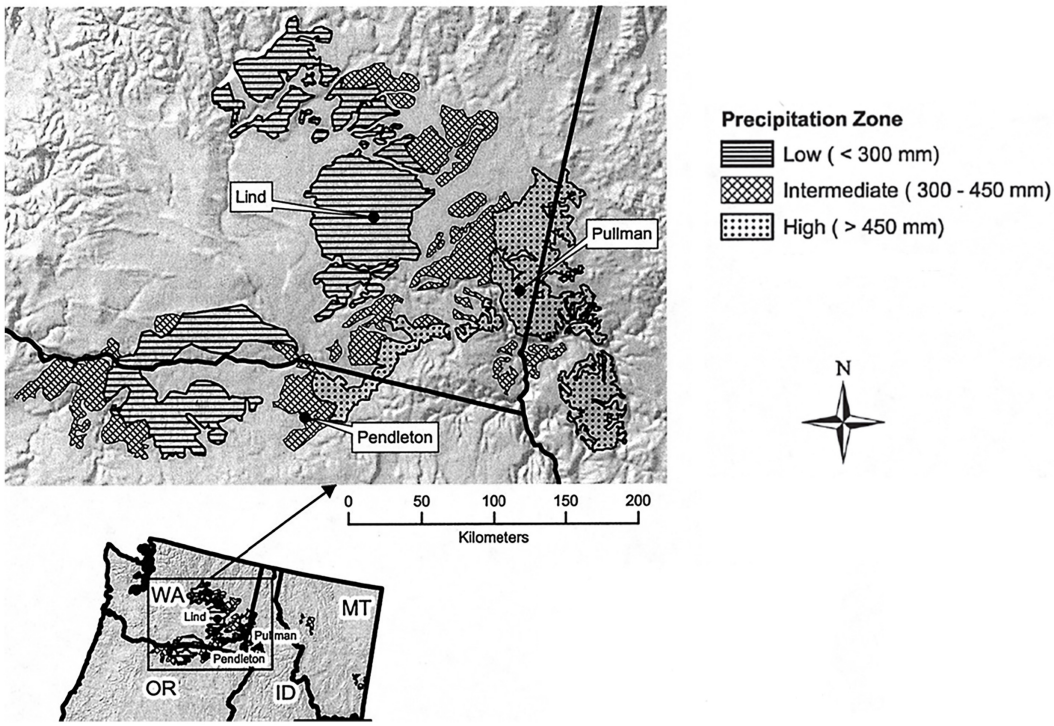

FIGURE 1 | Map showing the low (<300 mm annual precipitation), intermediate (300–450 mm) and high (>450 mm) precipitation zones of the inland PNW. Reprinted from Schillinger et al. (2006) with permission.

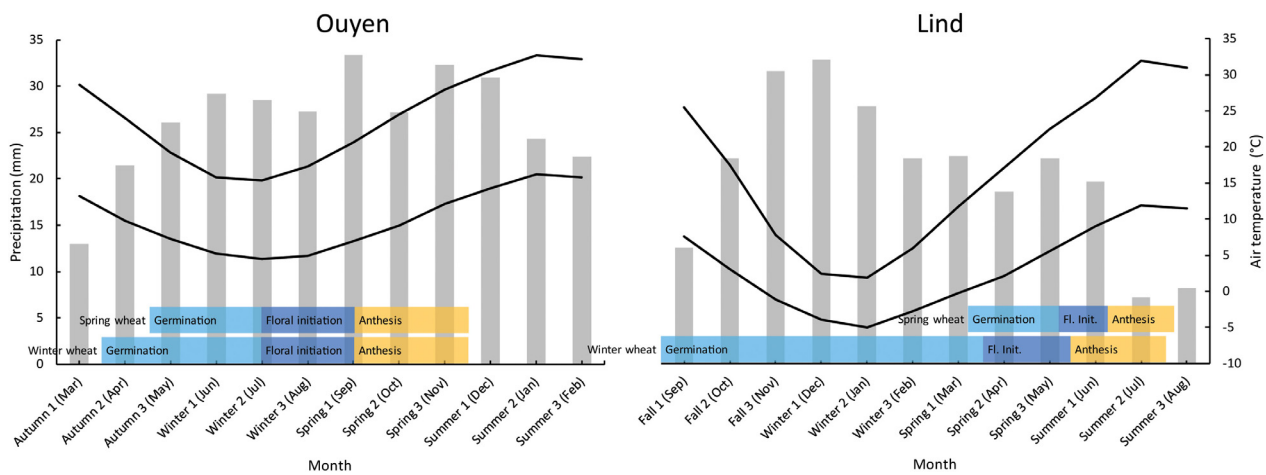

FIGURE 2 | Comparison of seasonal temperatures and precipitation for Ouyen in southern Australia and Lind, WA in the PNW, and seasonal fit of winter wheat and spring wheat life cycles under current management.

Winter weather is cool to cold with mean daily temperature in December and January of −1 and −2°C, respectively, but occasionally dropping to −24°C or lower. During extreme cold, soil not covered with snow may freeze to depths of 40 cm which can lead to heavy water runoff and soil erosion when weather changes bring rain or cause rapid snow melt. During summer, high-pressure systems dominate, leading to warm, dry conditions and low relative humidity. Average maximum temperatures in summer range between 20 and 35°C.

In the PNW, anthropogenic climate change has resulted in warming of air temperatures, however, no shifts in precipitation amounts have yet been documented (Schillinger and Papendick, 2008; Karimi et al., 2017). Climate models predict increases in winter precipitation but drier summers in the PNW. Combined with elevated CO_2, which promotes crop growth and improves its

transpiration efficiency, wheat grain yield potential in the PNW is predicted to increase (Stöckle et al., 2018), despite the otherwise dire global environmental consequences of such climate change.

Wheat Production

Winter wheat has been grown in PNW since the early 1890s. Before then, growers planted spring wheat annually (i.e., only a short 7-month fallow between crops) and grain yields were highly variable. Beginning in 1890, cold-hardy wheat cultivars brought in by rail from the eastern United States were planted and survived the winters but were not widely adopted by growers due to severe shattering loss before grain harvest. However, in 1896, growers experimenting with Jones Winter Fife, a soft red cultivar bred in New York and brought in by train, found this cultivar could both survive the winter and reach maturity with minimal shattering. Growers were soon convinced that the best grain yields could be achieved by planting winter wheat (Schillinger and Papendick, 2008). Soon thereafter, seed of Turkey Red, a hard-red winter wheat cultivar developed in the Crimea, was introduced to the region by homesteading immigrants arriving to the PNW from the United States Great Plains. Today, the major class of wheat produced is soft white with 90% exported to overseas markets from ship loading facilities in Portland, Oregon where it is used to make cakes, noodles, flatbreads, breakfast cereal, pastries and other products (Washington Grain Commission, 2019).

Winter wheat in the PNW drylands is planted in late summer, fulfils its vernalization requirement during winter before entering reproductive growth in spring and then matures in summer (**Figure 2**). Growers are generally hesitant to plant any spring crop because yields are highly variable and are not nearly as economically viable as winter wheat. For example, continuously cropped spring wheat (i.e., one crop per year and no 13-month fallow) at Lind, WA (244 mm annual precipitation) consistently produces less than 40% of the grain yield of winter wheat after a 13-month fallow (Schillinger, 2016) and at Ritzville, WA (292 mm p.a.) 55% of the grain yield of winter wheat after fallow (W. F. Schillinger, unpublished). Several studies have shown that late-sown winter wheat and spring wheat (as well as other spring-sown crops), by a wide margin, are not economically competitive with early-sown winter wheat in the drylands of east-central Washington (Juergens et al., 2004; Schillinger et al., 2007; Bewick et al., 2008).

Dryland wheat farming is practiced in areas of south-central Washington that receive as little as 150 mm average annual precipitation; this is considered the lowest for dryland wheat production in the world. A 2-year rotation of winter wheat followed by a 13-month fallow (only one crop every 2 years) is widely practiced in the low-precipitation zone. Experience to date shows that all winter crops in the drylands require a preceding 13-month fallow period so that they may be sown into stored moisture in late August-early September to produce an economically viable yield. Average winter wheat (one crop every other year) yields range from 1.3 to 4.4 t/ha with 150 and 300 mm of annual precipitation, respectively. Wheat grain yields have continued to increase linearly since the 1950s due to advances in breeding and genetics, modern farm equipment, and agronomic practices. In the past 10 years, growers in the low-precipitation zone have begun planting some acreage to winter pea (*Pisum sativum* L.), winter canola (*Brassica napus* L.), and winter triticale (× *Triticosecale Wittmack*). Details on dryland farming throughout the PNW are found in Schillinger et al. (2006) and possible future shifts in PNW cropping systems in response to climate change are outlined in Karimi et al. (2017) and Stöckle et al. (2018). **Tables 1–3** summarize the environmental, genotypic and management contexts of the low-precipitation PNW, and compare them to conditions in semi-arid southern Australia.

SEMI-ARID SOUTHERN AUSTRALIA

Cropping Conditions

Rainfall distribution in southern Australia is Mediterranean, with wet winters (June–August) and dry summers (December–February). Annual precipitation in cropping regions ranges from 281 mm at Waikerie on the dry fringe of the low rainfall zone to 747 mm at Millicent in the high rainfall zone (BOM, 2019a,c). Cropping in low-precipitation (<400 mm p.a.) environments occurs in central and south-western New South Wales, the Mallee districts of north-western Victoria and eastern South Australia, the Upper North and Eyre Peninsula of South Australia and much of south-western Western Australia (**Figure 3**). Periods of low rainfall during summer are accompanied by high temperatures (**Figure 2**). Annual precipitation in these low-precipitation regions is highly variable seasonally and across locations, ranging from 179 mm in 2012 to 573 mm in 2010 at Ouyen, Victoria (BOM, 2019b).

Since 1990, temperatures in southern Australian have increased, and growing season rainfall decreased by 11%; both phenomena have been linked to anthropogenic climate change (Murphy and Timbal, 2008; BOM and CSIRO, 2018). Much of this decline in rainfall has occurred during autumn (March–May). These trends have been attributed to a poleward expansion of the subtropical dry zone (Cai et al., 2012) and declining frequency of cold-cored, cut-off low synoptic systems (Pook et al., 2009; Cai et al., 2012). Autumn-breaking rains, used to establish crops, are also occurring later. Pook et al. (2009) demonstrated that the number of days until an "ideal" break occurs has increased by 6.3 days per decade since the 1890s. These factors have contributed to an estimated 27% decrease in water-limited potential yield across southern Australia since 1990 (Hochman et al., 2017), bringing potential yield closer to yields seen in the PNW. While advances in crop agronomy and plant breeding have prevented on-farm yields from declining over the same period, further advancements will be required to maintain or improve both actual yields and water-limited potential yield in the future.

Wheat Production

Cereal production is the most common land use in semi-arid cropping regions of southern Australia, with wheat the primary crop, followed by barley (*Hordeum vulgare* L.). Cereal crops are grown in rotation with non-cereal crops, with canola being the most common (Collins and Norton, 2019). Common pulse

TABLE 1 | Comparative analysis of case studies: environmental conditions.

Factor	Inland pacific northwest	Semi-arid southern Australia
Annual rainfall	Low rainfall zone: <300 mm Intermediate RZ: 300–450 mm High RZ: 450–600 mm	280–400 mm
Growing season length	Winter wheat: 11 months (September–July) Spring wheat: 6 months (April–August)	Winter wheat: 8 months (April–November) Spring wheat: 7 months (May–November)
Optimal flowering period	Late spring (May)	Early spring (September)

TABLE 2 | Comparative analysis of case studies: genotypic conditions.

Factor	Inland pacific northwest	Semi-arid southern Australia
Vernalization requirement of common wheat cultivars	Obligate vernalization requirement (winter wheat)	No obligate vernalization requirement (spring wheat)
Coleoptile length	<90 mm	<70 mm
Number of suitable winter wheat cultivars available	>20	3 (released 2016–2019)
Grain quality and products	Soft white (cakes, noodles etc.)	Hard white (bread and noodles)

TABLE 3 | Comparative analysis of case studies: management conditions.

Factor	Inland pacific northwest	Semi-arid southern Australia
Sowing time	Winter wheat: late summer (August–September) Spring wheat: late winter-early spring (March–April)	Winter wheat: early autumn (March–April) Spring wheat: late autumn (May)
Driver of winter wheat emergence	Stored soil moisture	Rainfall
Common rotation with wheat	Long fallow (13 months)	Barley, canola, pulse crops, long fallow (17 months)
Winter wheat sowing depth	100–180 mm	20–50 mm

crops include chickpea (*Cicer arietinum* L.), field (dry) pea, lentil (*Lens culinaris*) and narrow-leaf lupins (*Lupinus angustifolius*). As the growing season is shorter in southern Australia than the PNW (**Figure 2**), a long fallow (where a field is out of crop for one whole growing season) lasts 16–18 months, compared to 13 months in the PNW. The widespread availability of crop species suitable to rotate with wheat means that long fallows are less common on modern southern Australian farms compared to their PNW counterparts.

In southern Australia, the British colonialists of the late 18th century attempted to grow winter wheat but found their life cycle poorly matched seasonal conditions in semi-arid regions, and production was restricted to the few high rainfall regions with soils and terrain suitable for crop production. Spring wheat cultivars have been the mainstay of Australian wheat production since the beginning of the 20th century, and their development at this time revolutionized the industry and allowed reliable wheat production in semi-arid areas (Pugsley, 1983).

With a relatively mild winter, spring wheat can be sown in late autumn or early winter, begin reproductive development at the end of winter and mature in early summer (**Figure 2**). This contrasts to the PNW where winters are cold enough to kill spring wheat in tillering or early stages of reproductive development, and spring wheat must be planted in spring. However, although temperatures in Australia have been on a warming trend since the 1960s, incidences of frost, particularly late in the growing season, have increased in parts of southern Australia (Crimp et al., 2016a). The change has been most pronounced in semi-arid cropping regions of southern Australia, where simulation shows yield reductions due to frost were 20–60% higher from 1986–2013 compared to 1960–1985 (Crimp et al., 2016b). Environmental conditions during winter are therefore trending toward those found in the PNW, albeit less severely.

Crop establishment relies on the 'autumn break', which is the first significant rainfall event of the growing season, and has been variously defined as either 25 mm of rainfall within a 3-day period, or 30 mm over 7 days (Pook et al., 2009). A more mechanistic definition is provided by Unkovich (2010) who described it the first week in autumn where precipitation exceeds pan evaporation. A wheat crop may be sown following these rains in late autumn or early winter (late April–June; **Figure 2**), or 'dry sown' ahead of rainfall to ensure timely establishment once sufficient rainfall to induce germination has occurred (Fletcher et al., 2015). Flowering occurs during early spring (September) and harvest in early summer (November–December). The hot, dry summers of semi-arid southern Australia prevent any crop growth from December to March. Under best practice, fields are kept free of growing plants from the harvest of one crop until sowing the following year to maximize accumulation of water from irregular rainfall events for subsequent crop use (Hunt et al., 2013).

In recent years, there has been revived interest in winter wheat amongst growers, researchers and breeders in the semi-arid regions of southern Australia (Hunt, 2017). Firstly, the decline in autumn rainfall described above has coincided with the optimal timing of establishment for the popular fast developing spring wheat cultivars. Secondly, no-till farming has allowed sowing time to move earlier (by 30 days over 3

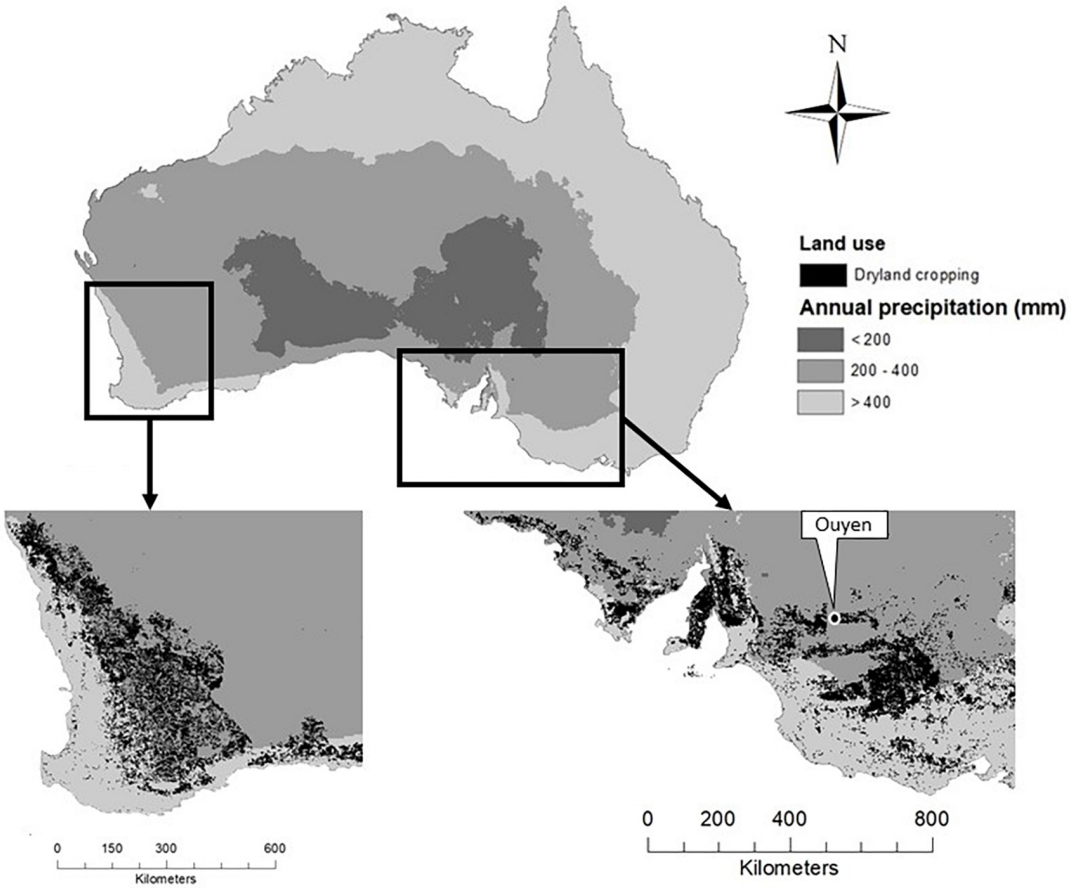

FIGURE 3 | Map of Australia showing semi-arid regions (200–400 mm annual precipitation; mid-gray) and dryland cropping sites in southern Australia (black).

decades, Anderson et al., 2016) to the point where sowing times for fast spring cultivars are optimal for the first time (Flohr et al., 2018). For growers to sow any earlier, cultivars that are slower to develop through their life cycle are required (Hunt et al., 2019b). Incentive for growers to continue the trend for earlier sowing has been driven by a continual increase in farm size and cropping intensity (Fletcher et al., 2016), and in conjunction with winter wheat, can increase water limited yield potential by ∼15% compared to later sown spring wheat (Hunt, 2017). However, breeding companies in Australia have only recently responded to the demand for winter wheat in semi-arid regions (**Table 2**).

Changes in autumn precipitation patterns and grower shifts toward early sowing have caused the farming systems of southern Australia to converge with those of PNW. One potential lesson would be a deeper understanding of the role that early sown winter wheat plays in PNW production systems, and how improved breeding of winter cultivars and optimized management can lead to increased yield and manage environmental constraints. There are several emerging environmental challenges that Australian growers will need to overcome in order to increase on-farm yield. These challenges will not have simple, one-dimensional solutions and overcoming them will require the synergy of genotypic and management strategies (**Table 4**).

NARROW OPTIMAL FLOWERING PERIODS IN MEDITERRANEAN SEMI-ARID ENVIRONMENTS (E)

A major determinant of wheat yield in water-limited environments is flowering time (Fischer et al., 1990; Gomez-Macpherson and Richards, 1995; Bodner et al., 2015). In the Australian wheat belt, low radiation, cold temperatures and frost during winter, as well as hot, dry conditions in late spring and summer, define a period of least harm, known as the optimal flowering period (OFP; Flohr et al., 2017). During the OFP, the risk of yield reductions caused by frost, heat, or drought is balanced and, on average, yield damage is minimized. Less work has been done defining an OFP for growing regions in the PNW, but there are certain yield penalties for wheat that encounters freezing air temperatures during flowering in mid-to-late May or has not finished reproductive growth by the onset of hot, dry weather in late June (Gizaw et al., 2018).

TABLE 4 | Current and emerging environmental constraints (E) to wheat production in Mediterranean semi-arid environments and the corresponding genotype (G) and management (M) advantages offered by winter wheat cultivars.

Environmental constraint (E)	Genotypic advantage of winter wheat (G)	Management strategies to maximize winter wheat yield advantage (M)
Low water-limited potential yield	Increased biomass Increased rooting depth	Early sowing
Few establishment opportunities in autumn		Deep sowing Long fallow
Reproductive frost risk	Winter hardiness	
Narrow optimal flowering period	Stable flowering time Winter hardiness	Early sowing
Increasing business costs and production risk	Stable flowering time	Grazing Whole-farm timeliness

In temperate regions, OFPs tend to be broad, meaning wheat can flower across a wider range of dates and still maximize yield. However, the southern Australian growing season is immediately succeeded by a distinct hot, dry season, creating a much narrower OFP than more temperate climates. The importance of timely flowering is therefore more heavily weighted in semi-arid Mediterranean regions such as those found in the southern Australian wheat belt.

While OFPs have perhaps not been as well defined for the PNW, the period of least harm for flowering crops is similarly narrow, as winter and early spring weather conditions are harsher than those found in southern Australia, and frosts often occur in draws and other low-lying areas in mid-to-late May during the booting and flowering stages of early-sown winter wheat with resulting severe decline in grain yield (Donaldson, 1996). The risk of heat and drought conditions in late spring and early summer during grain development is similarly high to that in southern Australia (**Figure 2**).

Stable Flowering Time (G)

In Australia, early sown winter wheat flowering time is stable relative to spring wheat across a range of sowing dates (Flohr et al., 2018). The European winter wheat cultivars brought to Australia by British colonists flowered much later than spring wheat established in late autumn, and were more likely to suffer heat and drought damage than spring wheat. However, modern winter wheat bred under Australian conditions, when established early, can develop fast enough to flower at a similar time as spring wheat sown later, and thus there is no increased risk of drought, heat and frost damage compared to spring wheat (Flohr et al., 2018). This has been achieved by shortened crop lifecycle due to reduced vernalization requirement and photoperiod sensitivity.

Winter wheat in semi-arid southern Australia therefore offers an advantage in environments with narrow OFPs. Winter wheat and spring wheat planting opportunities overlap in Australia. In seasons when soil moisture is sufficient for establishment prior to the traditional sowing period (late autumn), sowing spring wheat is untenable due to the high risk of early flowering, frost damage and reduced yield potential. In contrast, sowing of a winter wheat cultivar enables early establishment and timely flowering. Winter wheat established early generally yields more than spring wheat established late, particularly in years where the soil profile is filled with water and root growth is optimal (Coventry et al., 1993; Penrose, 1993). Sowing winter wheat therefore not only increases flowering time stability, but also yield stability (Flohr et al., 2018). The flowering time stability of winter wheat also operates across seasons, reducing yield penalties associated with chronically high air temperatures and accelerated development (Hunt et al., 2018).

Cold temperatures during winter in the PNW ensure that winter wheat always fulfils its vernalization requirement. While freezing temperatures are still common during early spring, risk of frost has diminished considerably by mid-May and booting and flowering during this period balances the risk of frost with the risk of heat and drought damage, which is common in late spring and early summer. Early-sown winter wheat in the PNW will always flower earlier than spring wheat (**Figure 2**). Even given suitable sowing opportunities, it is rare for spring wheat to finish flowering before the onset of often hot and dry conditions in June. High temperatures and water stress during the critical period of yield determination prevent spring wheat yields from rivaling those of winter wheat, and increase the risk associated with spring sowing.

As severe winter conditions prevent the sowing of spring wheat until at least late winter, and there has been little success in breeding cultivars fast enough to match the phenology of early-sown winter cultivars, winter wheat cultivars will continue to have a developmental and, very likely, a yield advantage over spring wheat in the PNW drylands. In this respect, growers have greater flexibility in Australia as similar yields and flowering in the optimal period can be obtained from both early sown winter wheat and May-sown spring wheat. In the future, the fast spring phenology of wheat cultivars developed for late sowing in southern Australia may play a role in developing faster spring cultivars to achieve timely flowering from a spring sowing date in the PNW.

Winter Hardiness (G)

While wheat is most susceptible to cold stress during the reproductive phase, extreme cold temperatures can also damage or kill plants during vegetative stages. While winter cultivars are more suited to survival and growth in cold conditions, there is also variation within winter cultivars for winter hardiness. Cox and Shelton (1992) found that under conventional tillage across five seasons in North Dakota, the hardiest winter wheat cultivar (Norstar) had a winter survival rate of 74%, whereas

other cultivars had survival rates of as low as 36%. Winter in the PNW is often harsh, with average minimum temperatures below 0°C. Crowns of winter-hardy cultivars can be held at −12°C for 15 days or longer with little or no damage (Skinner and Garland-Campbell, 2014). As little as 2–4 cm of snow cover provides the insulation necessary to trap residual soil heat and buffer against air temperature extremes that prevent killing temperatures in the crown, even during periods when air temperatures drop to −24°C. Fields with ample surface residue from the preceding crop trap snow more effectively than conventionally tilled fields (Cox et al., 1986; Papendick and McCool, 1994). In addition, the deep furrows created with deep sowing [see section "Deep Sowing (M)"] trap snow more effectively than a smooth surface.

Soil temperature at crown depth, not air temperature, is the critical factor affecting plant survival (Donaldson, 1996). Although extreme cold may kill the aboveground portion of the plant, recovery is still possible if the crown is alive. The most winter hardy PNW cultivars set crowns as deep as 3 cm below the soil surface (Donaldson, 1996).

Cold hardiness is not a static condition, but rather changes with time, temperature, and soil moisture status. Winter wheat is at most risk of winterkill when extreme cold is preceded by warm or mild conditions. Winterkill events in PNW mostly occur when cold air masses move south from Canada and are frequently associated with winds of 11 m/s (40 km/h) or greater. Wheat plants without snow cover desiccate under such cold and wind. Without snow cover, even fully hardened plants generally cannot withstand air temperatures of −23°C for more than 10 h. Severe winterkill events in the PNW drylands, which cause total crop loss, occur on average about once every 15 years.

Winter conditions in southern Australia are much milder than those of the PNW (**Figure 2**), and both winter and spring wheat cultivars are suitable for sowing in autumn. The increase in frequency and severity of frosts in southern Australia during winter and spring in recent decades has coincided with the recent trend in earlier sowing. As a result of these management and climatic changes, growers frequently experience losses due to frosts that occur early in the reproductive phase (stem elongation) which are referred to as stem frosts. Cold temperatures can cause pre-heading stem damage if air temperatures approach <-6°C, and if the spike emerges after such a frost event, this damage often presents as a bleached section with incomplete spike structure and aborted florets as explained in Frederiks et al. (2015). However, the increased incidence of stem elongation frost damage in southern Australia favors winter cultivars similar to the winterkill conditions commonly experienced in the PNW.

Reproductive frost induced sterility is best described in Martino and Abbate (2019). Previous recommendations for growers have been to delay sowing of spring wheat cultivars to ensure crops flower after the high frost risk period in early spring, despite reducing length of crop lifecycle and yield potential. Genotypic frost tolerance of cultivars can therefore be synergistic with crop management, as it allows cultivars to be sown earlier without encountering unacceptable frost risk; modeling conducted by An-Vo et al. (2018) showed that improving frost threshold temperature from 0 to −1°C would move the optimum sowing date 35 days earlier at a site in semi-arid southern Australia. The availability of suitable winter wheat cultivars has enabled growers in frost prone environments to capture early sowing opportunities, achieving stable flowering time, increased yield potential and avoidance of stem frost. The incorporation of winter wheat in the sowing program is commonly used as a frost mitigation tool in southern Australia.

Early Sowing (M)

Sowing date is one of the most important management practices determining yield in low-rainfall environments (Bodner et al., 2015), and in combination with cultivar selection is one of the few options available to growers to reduce the risk of frost, heat and drought damage. Late sown wheat not only limits the amount of biomass wheat can accumulate, but also increases the risk of drought and exposure to high temperatures during the reproductive period.

For the PNW, if satisfactory winter wheat stands cannot be achieved from deep sowing in late August-early September, growers will wait and sow at a shallow depth of 2–3 cm into dry soil (referred to as 'dusting in') around mid-October and wait for the onset of fall rains. Such late sowing reduces winter wheat grain yields by 35–40% compared to early-sown winter wheat in east-central Washington (Higginbotham et al., 2011, 2013). If fall rains do not arrive until late November, grain yield potential of late-sown winter wheat will likely be reduced by 50% or more compared with early-sown winter wheat (Schillinger, 2016). Delayed sowing is not nearly as detrimental to grain yield potential in north-central Oregon (Bolton, 1983; Machado et al., 2015), where temperatures are warmer in the fall, winter, and spring.

The reduced reliability of autumn breaking rains in southern Australia has delayed the earliest sowing opportunity within the traditional sowing window, at a cost to biomass development and protection from heat and drought stresses. The practice of 'dry sowing' (the antipodean equivalent of dusting in, see Fletcher et al., 2015) has emerged partly in response to these reduced establishment opportunities. Seeds are sown into a dry seedbed on a set date, rather than in response to rainfall. Dry sowing on a fixed date has been shown to increase farm-level production without increasing production risk (Fletcher et al., 2015). This practice is complementary to the early sowing of winter cultivars in improving overall timeliness of flowering on farms (Hunt et al., 2019b).

Kirkegaard and Hunt (2010) used simulation to compare modern wheat management practices with a conventional tillage system at a site near Kerang in the Victorian Mallee from 1969 to 2009. Moving the start of the sowing period from late May to late April increased wheat yield by 467 kg/ha (30%) compared to the conventional system; when combined with complementary practices of stubble retention, control of summer fallow weeds and rotation with a forage pea crop, the total yield increase was 2,403 kg/ha.

The flexibility of growers in these regions to adapt sowing dates in response to early rainfall is currently constrained by a lack of suitable winter cultivars. When early sowing is combined with current high-yielding spring cultivars, flowering often occurs earlier than the OFP for a particular region

(Flohr et al., 2018). This reduces average yield by exposing wheat to frost during the flowering period. Early sowing needs to be combined with suitable cultivars with an obligate vernalization requirement (i.e., wheat with high flowering date stability discussed above).

DECLINING WATER-LIMITED YIELD POTENTIAL (E)

In a well-managed production environment free from other constraints, modern elite wheat cultivars have a maximum water productivity of 2.5 kg of grain per cubic meter of transpired water (25 kg ha^{-1} mm^{-1}) (Sadras and Lawson, 2013). This places an upper limit on yield based on the available water supply during a cropping season (French and Schultz, 1984; Sadras and Angus, 2006). Water-limited potential yield (PY_W) therefore refers to the maximal attainable yield when only water limits crop production, and optimal cultivars and agronomy practices are used, and abiotic and biotic stresses are minimized (Fischer, 2015). Water supply therefore places an upper limit on yield in semi-arid environments.

As mentioned above, growing season rainfall in southern Australia has declined in recent years, contributing to a 27% decrease in PY_W since 1990 (Hochman et al., 2017). Top growers have been able to maintain yields using modern cultivars and better management but are now approaching the most economically efficient yield (van Rees et al., 2014, 2015; Hochman et al., 2017). For these growers, future advances in yield will need to come from an increase in PY_W, either through the extension of the growing season to capture more precipitation, an increase in stored soil water at the beginning of the season, and/or the release of new cultivars with a higher transpiration efficiency for grain than currently available cultivars. The development of winter wheat cultivars adapted to semi-arid cropping regions has the potential to achieve these goals when managed correctly, thus increasing yields above current limits (Hochman and Horan, 2018).

Although potential wheat yields are predicted to increase in the PNW due to anthropogenic climate change (Karimi et al., 2017; Stöckle et al., 2018), PY_W has traditionally been lower in the PNW compared to southern Australia, and the synergies offered by early-sown winter-type wheat have been used in the PNW for over a century to increase yield potential compared to later-sown wheat.

Increased Biomass Compared to Spring Wheat (G × M)

Lengthening crop life cycle is one of the simplest ways to improve crop yield potential through increased biomass and grain number. Due to their vernalization requirement, winter cultivars spend a longer time period in the vegetative phase compared to spring cultivars. This means more leaves and potential tillering sites are initiated and early-sown winter wheat accumulates more vegetative biomass than spring wheat sown at the optimal time. Grain yield and grain number potential is predominantly determined by biomass accumulation during the critical growth period prior to anthesis (Fischer, 1985), while grain weight is a function of water use and temperature immediately prior, during and post anthesis (Savin et al., 1999; Plaut et al., 2004). The greater biomass accumulated by winter wheat cultivars is theoretically an advantage over spring wheat, especially those sown late.

Experiments conducted in Australia by Gomez-Macpherson and Richards (1995) and in reviewed experiments of others (Batten and Khan, 1987; Connor et al., 1992) found that grain yields of slow developing cultivars were equivalent to faster developing cultivars sown later despite similar or greater biomass in early sown cultivars due to a lower harvest index. More recent results in south-eastern Australia have demonstrated that the grain yield of slow developing wheat sown early has been equivalent to that of faster developing cultivars with a similar flowering time but with a lower harvest index (Flohr et al., 2020).

Similarly, in the PNW, early sowing always increases straw production, with August sowing dates more than doubling straw produced from the later (October) sowing in all years (Donaldson et al., 2001). In these environments the harvest index (HI) is inversely related to straw production, which means that early sowing always results in the lowest HI; similar to Australian production systems. In the PNW, early sowing of winter wheat is associated with a high number of spikes per unit area, higher grain weight, but lower number of grains per spike (Thill et al., 1978). More recent studies by Donaldson et al. (2001) found that spikes per unit area were consistently higher from earlier planting dates resulting in higher grain yields as there were limited compensatory trade-offs in grain weight and grain per spike.

It has been possible in the PNW to increase both straw yield and grain yield. Improving biomass should be viewed as an opportunity for winter wheat production in semi-arid environments. While it was possible in the PNW to further increase straw production in tall standard-height cultivars this also resulted in lower HI and grain yield (Donaldson et al., 2001) similar to the experiences currently being observed in Australia. A likely explanation is that increased plant height and more leaves lead to competition for carbohydrates between the developing spike and elongating stem of early sown crops (Gomez-Macpherson and Richards, 1995). Genetic solutions such as the development of winter wheat cultivars that can maintain improved biomass production from earlier sowing and more effectively partition accumulated biomass into grain yield will be able to maximize the synergy between early sowing and biomass accumulation, increasing grain yield above current standards (Porker et al., 2020).

Increasing Harvest Index (G × M)

In the PNW, increased straw production is considered advantageous for erosion control and for enhancing the capture of winter precipitation in the soil. Management solutions such as sowing rate have been proposed in both PNW and Australia as a strategy to increase straw production, HI, and yield.

Donaldson et al. (2001) at Lind, WA investigated the effect of sowing rate on straw production and HI. Medium (135 seeds m^2) to high (195 seeds m^2) seeding rates were favored for increased straw production. Lower sowing rates (65 seeds m^2) increased HI and achieved similar yields to higher seeding rates but this reduced straw production and lowered spikes per unit area.

Therefore, lower seeding densities (<70 plants m^2) were not recommended for the PNW.

In Australia, reducing plant density has also been proposed as a way of reducing early DM accumulation and improving HI in early established slow developing cultivars for improved grain yield (Hunt et al., 2012; Kirkegaard et al., 2014). However, few studies have demonstrated an advantage from reducing plant density in early sown winter wheat in Australia, and effects have been generally small (Porker et al., 2020). Sowing rate responses appear much larger in the PNW relative to Australia. In the PNW the effects of sowing rate on plant growth and development were so large they masked any differences in cultivars responding differently (Donaldson et al., 2001). In Australia, higher seeding densities are favored in early sown winter wheat for dual purpose use (used for early season forage), and in situations where greater weed competition is required.

The long vegetative phase of slow developing wheat also suggests that deferring nitrogen inputs until after the start of stem elongation could significantly increase yield. Few published experiments have reported a consistent effect of N fertilizer timing on crop yield in winter cultivars under Australian conditions from early sowing dates due to other confounding factors such as high residual N and stem frost (Porker et al., 2020), though studies in other Mediterranean-type environments suggest a benefit to grain yield and protein through splitting N application between sowing, GS15 and GS30 (Ercoli et al., 2013).

Increased Rooting Depth Compared to Spring Wheat (G × M)

As root length and mass is influenced by sowing date and phase duration (Barraclough and Leigh, 1984; Kirkegaard et al., 2015), early-sown winter wheat has more and longer roots compared to later sown spring wheat (Entz et al., 1992; Kirkegaard and Lilley, 2007; Williams et al., 2013). Although the roots of winter and spring cultivars penetrate soil at a similar rate, the longer period of root proliferation increases subsoil specific root length and maximum rooting depth in early-sown winter cultivars (Entz et al., 1992; Kirkegaard and Lilley, 2007; Thorup-Kristensen et al., 2009). Maximum rooting depth is highly correlated to the maximum depth from which water is extracted (Entz et al., 1992). Kirkegaard and Lilley (2007) suggested that this advantage of winter wheat is only pronounced in years with sufficient precipitation to wet the entire soil profile. Flohr et al. (2020) demonstrated this experimentally in slow developing spring cultivars, with the added condition that low rainfall is required during the critical period to force reliance on deep stored water.

In the PNW, winter wheat effectively extracts soil water to a depth of 150 cm or more. This increased rooting depth allows the crop to access more water during anthesis and grain fill, during which time water use efficiency of subsoil water averages 35 kg/ha.mm, compared to a water use efficiency of 20–25 kg/ha.mm across the entire growing season (Kirkegaard et al., 2007; Flohr et al., 2020). During grain fill, water in the surface 100 cm has often been depleted and there is little likelihood of any substantial rain. Entz et al. (1992) found that winter wheat had access to more total water at anthesis in seasons with dry finishes, whereas when significant rainfall occurred late in the growing season, post-anthesis water availability was similar in spring and winter cultivars.

REDUCED ESTABLISHMENT OPPORTUNITIES (E)

If autumn rainfall continues to decline, southern Australian growers will regularly need to be able to establish wheat outside the traditional sowing window. Sufficient rainfall to create early sowing opportunities does not occur in every year, and the probability of receiving an early sowing opportunity varies among locations across southern Australia. The opportunity to establish wheat independently of rainfall offers growers the ability to extend the establishment window and creates flexibility in crop selection. There are whole-farm benefits to establishing wheat in the absence of rainfall, as the remaining crops can be sown in a timelier fashion.

Establishing wheat on stored soil water is common practice in the PNW and has been for many decades. Deep sowing may in future years become practiced in semi-arid southern Australia, where growers have the opportunity to learn from the advancements in genotype, sowing machinery and farm management that have made this technique possible in the PNW (Hunt et al., 2019a).

Deep Sowing (M)

There is a fundamental farming system synergy between 13-month fallows, winter wheat, and deep sowing in the drylands of the PNW. Very little rain falls from July to September and what does fall generally evaporates from the soil surface within a few days. As described above, winter wheat established in October (after 15 months of fallow) or November when the surface has been wetted by rain suffers a large yield penalty in comparison to stands established into stored soil moisture in late summer. Planting back-to-back winter wheat (i.e., without the long fallow) is a recipe for disaster (Schillinger, 2016) that no dryland growers practice.

The system practiced by PNW dryland growers is deep sowing of winter wheat into stored fallow moisture using deep furrow drills (**Figure 4**). This enables growers to achieve optimal establishment times for winter wheat without having to rely on rainfall to wet seed beds. Pacific Northwest winter wheat cultivars can germinate at water potentials as low as −1.25 MPa (Wuest and Lutcher, 2013; Wuest, 2018), but a minimum water potential of −0.55 to −0.65 MPa is generally required for winter wheat seedling emergence through more than 12 cm of soil cover (Lindstrom et al., 1976; Schillinger et al., 1998). Due to thick soil cover over the seed, it is not the coleoptile that emerges from the soil but rather the first leaf after pushing through the tip of the coleoptile. The first leaf is thin and spindly and, since most often emerging under low soil water potential, lacks much emergence force or lifting capacity (Lutcher et al., 2019). The drier the soil in the seed zone and the deeper the soil cover, the longer it takes seedlings to emerge (Lindstrom et al., 1976).

FIGURE 4 | A prototype deep-furrow drill fabricated at the Washington State University Lind Dryland Research Station. Commercially available deep-furrow drills cannot pass through heavy surface residue without plugging and are not sturdy enough for seed openers to penetrate through the hard, dry surface of no-till summer fallow. Growers and scientists seek a dual-purpose drill to sow winter wheat into heavy residue in both tilled and no-till fallow conditions. Hoe-type openers of the drill must be able to place seed as deep as 20 cm below the surface to reach adequate soil moisture for germination and emergence. The purpose of the deep furrow is to reduce the thickness of soil covering the seed to enhance seedling emergence. Photos by W. F. Schillinger.

The ability to emerge from depth is an essential trait for winter wheat adapted to the PNW drylands, and there has been strong selection within winter wheat breeding programs for this trait. In the Washington State University (WSU) winter wheat breeding program, F3 plots from crosses targeting the drylands are deep sown at the Lind Dryland Research Station and selections made from these. In this way, emergence from depth is selected before any other trait, including yield.

In contrast, in southern Australia deep sowing has been limited in practice until recent times. Following autumn rainfall decline, inadequate moisture at ideal sowing depth has led to growers sowing deeper to 'moisture-seek' (placing seed into moist soil below a layer of dry soil) to make use of residual moisture stored from summer rains or an 18-month long fallow. Their ability to do this is currently restricted by the availability of sowing equipment capable of placing seeds into moist soil at depth, and the ability of plants to emerge from depth.

Ability to Emerge From Depth (G)

Coleoptile length is an important trait determining the ability of seeds to emerge from depth and has been studied in Australia (Rebetzke et al., 2007; Bovill et al., 2019). In the PNW, all current soft white winter wheat (SWW) cultivars are semi-dwarfs that carry emergence-impeding Rht1 or Rht2 dwarfing genes but developing standard height (i.e., no dwarfing genes) SWW cultivars is a high priority of the WSU winter wheat breeding program. Standard height hard red winter wheat cultivars are available to growers in the very dry (150–220 mm annual precipitation) areas of south-central Washington.

The long outdated standard height SWW cultivar Moro (Rohde, 1966) had a coleoptile length of 90 mm and had excellent emergence from deep sowing depths. Moro was the number one winter wheat planted by dryland growers in east-central Washington for more than 20 years (Schillinger and Papendick, 2008). In 12 deep-sowing experiments, Moro always emerged faster and better with 11–16 cm of soil covering the seed compared to semi-dwarf SWW cultivars (Schillinger et al., 1998). In addition to a long coleoptile, Moro had a first leaf length of 207 mm compared to an average of only 130 mm first leaf length for other SWW cultivars (Schillinger et al., 1998). Mohan et al. (2013) conducted a comprehensive deep-sowing emergence field trial at Lind, WA with 662 wheat cultivars collected from around the world. These cultivars had coleoptile lengths ranging from 34 to 114 mm; a length of 90 mm was ideal as emergence declined for cultivars with coleoptiles longer than 90 mm.

Modern Australian semi-dwarf wheat and barley cultivars show poor emergence when sown deep (greater than 8 cm) due to shortened coleoptiles (Rebetzke et al., 2007). Warmer soils in the future may further exacerbate poor establishment with deeper sowing (Rebetzke et al., 2016).

Pre-experimental modeling indicates substantial benefits for crop yield in southern Australia if machinery and cultivars could be developed that allowed placement and emergence of seed at depth (Kirkegaard and Hunt, 2010; Flohr et al., 2018). Rebetzke et al. (2016) have argued the case for Australian breeders to use novel dwarfing genes, such as Rht8, that do not suppress coleoptile length.

Long Fallow (M)

Inland Pacific Northwest

Late summer or early autumn planting of winter wheat requires sufficient stored soil moisture to ensure establishment of a crop in the absence of precipitation. In the PNW drylands, winter wheat is grown in rotation with 13-month fallow to accumulate moisture. On average, 65% of overwinter precipitation is stored in the soil but, due to high evaporation during the dry summer months, only an average of 30% of precipitation that occurs during the 13-month fallow is stored in the soil by late August.

Following harvest in late July or early August, winter wheat stubble is generally left standing and undisturbed until at least April, using a non-selective herbicide in late winter or early

spring to control weeds. In mid-April or later most growers till fallow ground with an undercutter sweep implement or field cultivator to a depth of 10–13 cm to break soil capillary pores, creating a dry surface soil mulch to slow the upward flow of water and to thermally reduce heat flow into the soil. In the hot and dry summer months, the transfer of heat from the surface to water below is a primary driver for evaporation. Liquid water will move upward to the depth of tillage where thereafter it moves through the dry soil mulch via vapor flow. Near-surface soil water loss with no-till fallow is generally greater than with tilled fallow during the dry summer and the drying front with no-till fallow often moves below the depth that can be reached with deep-furrow drills. The physics of soil water dynamics in tilled versus no-till fallow in the PNW drylands has been reported in dozens of journal articles in the past 100 years and is well summarized by Hammel et al. (1981) and Papendick (2004).

A huge downside to tilled fallow is the risk of wind erosion, which is a major soil and air quality concern in the PNW drylands. In recent decades, most growers take care to leave ample surface residue and maintain a cloddy surface during fallow, but dust storms are still frequent, especially when straw production (and yield) of the preceding crop was low. No-till fallow is ideal for wind erosion control and acreage of no-till fallow is increasing. For example, in the milder climate of north-central Oregon where early October is an optimum sowing date (Bolton, 1983), more than 75,000 hectares of no-till summer fallow is practiced (Machado et al., 2015). No-till fallow is also practiced in the <200 mm average annual precipitation of south central Washington where storing adequate water during fallow for early sowing is not achievable most years. Additionally, no-till fallow is becoming increasingly popular in the relatively cool climate of Douglas County in north central Washington where the glacial soils farmed there are only 45–90 cm deep. However, tillage-based fallow is still the most common practice in the PNW drylands due to the seed-zone water phenomena discussed above.

Two back-to-back years of fallow is infrequently practiced in the PNW during drought periods when soil water accumulation during the first fallow year is poor. This extended fallow is called "double fallow" as it captures two winters of precipitation. With double fallow spring wheat is sown after a 20-month fallow or winter wheat after a 25-month fallow. A double fallow is inherently inefficient because: (i) the percentage of precipitation captured in the soil during the second winter is much lower than during the first winter, and (ii) spring wheat sown after an 18-month fallow will generally have significantly lower grain yield that winter wheat planted after a 13-month fallow (Young et al., 2015).

Semi-Arid Southern Australia

Sowing spring wheat in late autumn following an 18-month fallow was a widespread practice in semi-arid southern Australia until the mid-1980s (Ridge, 1986), but in recent decades cereal crops have been more commonly grown in rotation with profitable break crops such as canola or pulses. In these continuous cropping systems, an annual 5-month fallow is maintained from the harvest of one crop in early summer to the sowing of the next in late autumn (Hunt and Kirkegaard, 2011).

An 18-month fallow generally increases the yield of wheat compared to wheat grown following another wheat crop. This fallow is functionally equivalent to the 13-month fallow found in the PNW, as a field is left out of production for one growing season while precipitation from one winter is stored in the soil. The yield advantage of wheat grown on an 18-month fallow is higher in fields with a high plant-available water capacity, and the relative benefit of the practice is therefore more advantageous in south-eastern Australia than the sandier western cropping regions (Oliver et al., 2010). Unlike equivalent sequences in the PNW, total production is usually higher in continuous cropping systems than wheat-fallow rotations (Angus et al., 2015), but there are several whole-farm benefits, including reduced input costs, increased timeliness of sowing, and decreased income risk that increase the favorability of including a strategic 18-month fallow in crop sequences (Cann et al., 2020).

These yield and management advantages also work in synergy with the yield and management advantages offered by winter wheat. Flohr B. et al. (2018) simulated twelve different genotype × management strategies for spring and winter wheat production at three low-rainfall zones in southern Australia from 1997 to 2016. The highest yielding strategy at all three sites was a long coleoptile winter wheat grown following a long fallow. At Walpeup, in the Victorian Mallee, this strategy achieved a higher simulated yield than continuous production of both a short coleoptile spring wheat variety and a long coleoptile winter wheat in 16 of 20 years. The average yield of the long coleoptile winter wheat cultivar increased from 3.2 to 4.5 t/ha when rotated with long fallow as opposed to continuous wheat production; a relative yield increase of 1.3 t/ha. On the other hand, the yield of a continuously cropped long coleoptile fast spring wheat increased from 2.7 to 3.6 t/ha when rotated with long fallow; a relative yield increase of only 0.9 t/ha. This demonstrates that the adoption of multiple genotypic and management practices can have an additive effect, and that the yield of winter wheat is maximized when G × M is optimized.

INCREASING BUSINESS COSTS AND RISK

While in recent years, the top growers of southern Australia have successfully reduced the gap between on-farm yields and PY_W to an economically optimal level (van Rees et al., 2014; Hochman et al., 2017), whole-farm profit margins have stagnated. While farm incomes in semi-arid southern Australia increased by 82% from 1994–1998 to 2008–2012, total costs increased by 89% (van Rees et al., 2014, 2015). Income volatility has also increased. In Victoria, wheat revenue variance was greater for 1992 to 2009 (0.38 – linear area trend) than 1973 to 1991 (0.14) or 1955 to 1975 (0.15) (Kingwell, 2011). Growers in semi-arid Western and South Australia, where 85–95% of grain is exported, are also further exposed to the volatility of international markets (Laurie et al., 2018). Increasing profit in the future will require not only the release of cultivars with higher water-use efficiency and therefore increased yield potential, but also potential changes at the system or whole-farm level – including farming more land and diversifying through the inclusion of livestock.

Although these management strategies have the potential to increase whole-farm profit, they also carry increased risk – increasing cropped area increases the time needed for seeding to achieve timely sowing, while incorporating livestock into the enterprise requires supplementary feeding during times of low pasture availability (predominantly autumn in southern Australia). In this context, the development pattern of winter wheat is potentially advantageous in reducing income risk and increasing whole-farm yield.

In the PNW, increasing costs have until recently been offset by increased resource-use efficiency of cultivars, machinery and fertilizers. However, increased investment in land area is also necessary to maintain or improve profit margins (Schillinger and Papendick, 2008). Income risk has increased for PNW growers with increasing year-to-year variability of grain price since 1975. However, one core difference between the economies of southern Australian and PNW cropping enterprises is the role of the government. Compared to Australian growers, PNW growers have greater access to government-sponsored subsidies and incentives (Barnard et al., 1997), such as subsidized multi-peril crop insurance available for wheat, canola, dry pea, and triticale. The Conservation Reserve Program provides eligible landowners 10-year paid contracts to plant perennial grasses and shrubs in lieu of cropping. The Environmental Quality Incentives Program, managed at the local (County) level, provides incentives to adopt environment-friendly cropping practices such as direct seeding into no-till fallow. Such federal government programs reduce risk, help stabilize farm income, and buoy cropland values; albeit at considerable expense to US taxpayers.

Grazing (M)

In Australian mixed-farming systems, winter cultivars are commonly sown early as dual-purpose crops, whereby they provide livestock forage during the vegetative stage, and later regrow for grain production (Virgona et al., 2006; Harrison et al., 2011). When sown early, the vernalization response of winter cultivars results in an extended vegetative phase, which provides a grazing opportunity during autumn and winter when comparative growth rates of other pastures are slow (Virgona et al., 2006). Additionally, grazed crops are able to recover to achieve similar yields to non-grazed crops (Dove and McMullen, 2009), increasing the net economic gains from these crops by 25–75% (Bell et al., 2014). Other farming system benefits of dual-purpose crops that have been reported include reduction in crop height, risk of lodging and post-harvest stubble loads (Harrison et al., 2011). Flexibility in sowing time and delayed phenological development after grazing can reduce risk of frost damage in frost-prone environments (Porker et al., 2020), as well as enabling spelling of pasture paddocks during autumn and winter, increasing whole-farm feed supply and production (Bell et al., 2015).

Cattle grazing of winter wheat during its vegetative stage of development during the fall is also possible in the PNW with no reduction in subsequent grain yield compared to non-grazed wheat. However, grazing is practiced on only a small scale. Farms today are large and specialized on crop production; most PNW dryland wheat growers do not raise cattle.

Whole-Farm Timeliness (G × M)

Average farm size in southern Australia and the PNW, both in corporate and family owned farms, has increased steadily for several decades (Anderson et al., 2016). Timely sowing is required to maintain whole-farm yield (Fletcher et al., 2015). Increased farm size requires increased investment in machinery in order to sow a crop in timely fashion. Alternatively, in southern Australia sowing winter wheat when favorable sowing opportunities arise allows growers to expand the sowing window and increase timeliness of sowing at the whole-farm level (Fletcher et al., 2019; Hunt et al., 2019b). As farm size continues to increase, the opportunity to extend the sowing window by growing early-sown winter wheat will continue to grow in appeal as a mode of maintaining whole-farm yield.

In the PNW drylands, where winter wheat after a 13-month fallow dominates, the optimum sowing window is only 2–3 weeks. It is common for growers to have two or more tractor-drill units sowing concurrently and/or conduct their sowing operations 16–24 h per day 7 days a week. Sowing winter wheat during this time window is, by far, the most time-critical and important (and stressful) field operation for PNW dryland wheat growers.

POTENTIAL BARRIERS TO UPTAKE AND IMPLEMENTATION

Winter wheat production in semi-arid southern Australia is currently in its early stages, with winter cultivars sown only by those considered "innovators" or "early adopters" by Rogers' diffusion of innovations theory (Rogers, 2010). While the grower population in semi-arid southern Australia has historically been responsive to new technology and management practices (D'Emden and Llewellyn, 2006; Llewellyn et al., 2012; Fletcher et al., 2016), there are a number of key obstacles that remain in the way of the widespread early sowing of winter wheat cultivars in the region.

Lack of Suitable Cultivars

Following a wave of privatization in the early 2000s, Australian breeding programs and therefore objectives have almost exclusively been dominated by private breeding companies (Lindner, 2004). The release of wheat cultivars in Australia is therefore tied to profitability for breeding companies (through end-point royalties), rather than increasing sowing flexibility. Spring wheat cultivars, which have greater adaptation across environments compared to winter wheat lines (Porker et al., 2019), have therefore dominated cultivar releases in recent decades.

Despite the above, Australian breeders have recently reacted to growing interest from dryland growers for suitable winter wheat cultivars. Longsword, a fast winter wheat designed for semi-arid environments, was released in 2018 by Australian Grain Technologies (AGT) as a feed-quality cultivar (Flohr et al., 2018). AGT have also established a dedicated winter wheat breeding program at Wagga Wagga in southern Australia, and the first cultivar from this program (Illabo) was released in

2018. Several other breeding companies have also signposted upcoming releases of winter lines. While early innovators in semi-arid environments have taken to sowing winter wheat lines including Longsword, early-sown winter wheat will not be grown by a majority of growers until cultivars are released that are suited to the growing environment and can meet the requisite milling quality checks to maximize profit margin. Similarly, sowing of winter cultivars into stored subsoil moisture will not be possible until winter varieties with the ability to emerge from depth have been released. Future winter wheat breeding programs will therefore have to address not only current grower preferences, but also identify and fulfill emerging and future opportunities for G × M synergies to increase yield.

Specialized wheat breeding programs have been ongoing in the PNW since 1894 (Schillinger and Papendick, 2008). Unlike the Australian system, state land-grant university breeding programs are common in the United States and have been responsible for the release of hundreds of wheat cultivars. Wheat cultivars released in recent years by university breeding programs are no longer "public" cultivars (i.e., no royalty fee), but rather growers must pay a seed royalty fee to the university and are not allowed to store their harvested grain for seed. This has resulted in head-to-head competition with private wheat breeding companies who have developed many excellent lines. Winter cultivars bred for the PNW are unlikely to be suitable for Australian growers due to target markets for grain, region-specific fungal and nematode pathogens and the development speed of cultivars, which are still likely to be too slow to ensure flowering within the narrow OFPs in southern Australia. Winter wheat breeding programs will need to be specific to Australian climates to ensure that released cultivars have a stable flowering time (through vernalization) but also a fast development rate to ensure flowering is completed before the onset of hot, dry conditions, a requirement that will grow in importance as average temperatures continue to rise.

Environmental Specificity of Cultivars

Australian growers will require greater diversity in winter wheat for a range of flowering environments compared to spring cultivars. Although the optimal flowering period is different from region to region even within low-rainfall cropping zones, growers across these regions have traditionally manipulated sowing date of high yielding spring cultivars to ensure they flower during the OFP. Due to the stable flowering time of winter cultivars, adaptation will be driven by cultivar flowering time and coincidence with optimal flowering periods in the different environments (Hunt et al., 2019b; Porker et al., 2019). A change in development pattern (genotype) rather than sowing time (management) will be required for each different flowering time environment. This means breeding programs and growers will need to target development patterns to suit different flowering environments – fast for warm, low rainfall environments and mid to mid slow for cool medium rainfall environments. This limits the potential profitability of winter wheat lines for plant breeders, who need to invest the same (if not more) resources into winter wheat candidates for specific regions as they do for spring lines which can be grown across a wider range of environments. As released winter wheat cultivars are only likely to flower within the optimal flowering period and therefore achieve optimal yield across a smaller range of environments, their uptake is already restricted by their phenology.

There have been several suggested solutions for this problem. For environments with a narrow OFP, where frost can cause major yield reductions, sowing a slower winter wheat with heat and drought tolerance can ensure firstly that reproductive frost events are avoided by late flowering, and secondly that the impact of drought and heat events are minimized (Hunt et al., 2019a). Such cultivars would have more widespread geographic adaptability than other winter wheat cultivars, as they would be suitable for sowing not only in environments where they flower during the OFP, but also environments where they flower "too late," as long as their heat and drought tolerance prevents large yield reductions from stress events. Recent research has also suggested that the phenology of some wheat cultivars can be "reset" through induced vegetative stress or heavy grazing. This may extend the use of some winter wheat cultivars, particularly those suitable for use as dual-purpose wheat, but more research is needed to explain how management can be used to manipulate the phenology of winter wheat.

Implications for Agronomic and Whole-Farm Management

While some whole-farm factors such as timeliness of sowing favor the inclusion of early-sown winter wheat into farming systems, there remain several considerations that need to be accounted for when including winter wheat in a cropping program. One major traditional impediment to early sowing has been weed control. Historically, growers would need to wait until weeds had emerged in mid-autumn to control them, using either tillage or more recently knockdown herbicides (glyphosate and paraquat). In both southern Australia and the PNW, the advent of pre-emergent herbicides that can be applied before sowing means that growers no longer need to wait until weeds have emerged to begin control methods.

Additionally, while winter wheat cultivars offer increased sowing time flexibility, growers also need to have seed on hand in preparation for sowing. This becomes increasingly problematic in environments where early sowing opportunities are unreliable, as harvested seed needs to be held on farm in readiness for an early sowing opportunity that may not eventuate for several years. However, the stable flowering time and yield advantage of winter wheat potentially outweighs the additional inconvenience of storing winter wheat seed on farm. This problem is not encountered in the PNW due to the widespread availability of winter cultivars.

A transition to a system in which winter wheat is established on stored soil water rather than rainfall will also require the contemporaneous development of suitable cultivars, machinery and management skill. In the PNW, the deep placement of winter wheat seed is only suitable for cultivars that can emerge

through 10–15 cm of soil cover (Schillinger et al., 2017). The development of deep-furrow split-packer drills that allowed this deep placement in the mid-1960s occurred almost simultaneously with the release of the cultivar Moro, a cultivar with excellent emergence from depth. Availability of similar machinery in a southern Australian environment would not only require significant whole-farm expenditure from growers, but also need to be accompanied by high-yielding cultivars with excellent seedling emergence in order to facilitate widespread uptake. Access to PNW machinery and winter wheat germplasm would likely accelerate this process if emergence traits were to be incorporated into southern Australian breeding objectives. It would also be imperative that deep sowing into fallow moisture fit into the no-till and stubble retained farming systems which now dominate in southern Australia and have been extremely effective at reducing wind and water erosion and delivered many production benefits. The machinery challenges of sowing into uncultivated heavy soil types common in much of southern Australia would likely be greater than into the sandy silt loam soils of the PNW drylands.

CONCLUSION

The history of winter wheat production across the inland Pacific Northwest of the United States provides insight into how early-sown winter wheat cultivars can be established in the absence of precipitation, flower during the optimal flowering period and significantly out-yield later-sown spring wheat genotypes. As cropping conditions in southern Australia begin to converge with those of the PNW, Australian growers have the opportunity to learn from both the successes and the challenges of winter wheat production in the PNW, and adopt the most advantageous components whilst still exploiting the benefits of conserved crop residues and crop rotations. The yield advantage of winter wheat in the PNW has been the result of several genotype × management synergies, some of which are inherent to winter genotypes, but others which have been developed in response to the nature of the environment in which they are grown. Future semi-arid southern Australian cropping systems may therefore be able to increase flexibility by sowing winter wheat cultivars after early rainfall, increase profitability and decrease risk by grazing dual-purpose winter wheat, and establish crops independently of rainfall by deep-sowing winter cultivars with long coleoptiles into stored soil water during late summer or early autumn.

AUTHOR CONTRIBUTIONS

DC conceptualized the manuscript and wrote most of the analysis pertinent to southern Australia. WS contributed sections relevant to PNW. JH, KP, and FH made substantial written contributions to sections on southern Australia. DC, WS, and JH prepared the figures. All authors reviewed and edited the manuscript.

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Interactions of Spring Cereal Genotypic Attributes and Recovery of Grain Yield After Defoliation

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Dual-purpose crops are grazed during their vegetative phase and allowed to regrow to produce grain. Grazing slow-developing winter cereals (wheat, barley, and triticale) is common, but there is also potential to graze faster-developing spring cereals used in regions with shorter-growing seasons. Defoliation in faster-developing genotypes has risks of larger yield penalties, however, little is known about genotypic characteristics that may improve recovery after grazing. Four experiments examined 7 spring wheat and 2 barley cultivars with differing physiological attributes (phenological development rate, putative capacity to accumulate soluble carbohydrates, and tillering capacity) that may influence the capacity of spring wheat to recover after defoliation. Defoliated and undefoliated crops were compared to assess physiological differences between cultivars including recovery of biomass, leaf area and radiation interception at anthesis, and subsequent crop grain yield and yield components. All genotypes had similar responses to defoliation treatments indicating that the physiological attributes studied played little part in mitigating yield penalties after defoliation. Despite some differences in yield components amongst cultivars, defoliation did not adversely affect cultivars with different yield component combinations under non-water limited conditions. Later and intense defoliation (around GS30/31) resulted in large yield penalties (40%) which reduced both grain number and kernel mass. However, earlier defoliation (before GS28) induced small or insignificant yield penalties. Defoliation often reduced canopy radiation interception and crop biomass at anthesis but this rarely translated into large yield penalties. These studies further demonstrate that shorter season spring cereals can provide valuable forage (up to 1.2 t DM/ha) for grazing during early vegetative growth without inducing large yield penalties. This study suggests that beyond appropriate phenology, there were no other specific characteristics of cultivars that improved the recovery after grazing. Hence farmers don't need specific dual-purpose cultivars and can still focus on those that optimize grain yield potential for a particular environment and sowing date. The timing and intensity of defoliation appear to be larger drivers of yield recovery in spring cereals and better understanding of these relationships are needed to provide grazing management guidelines that mitigate risk of yield penalties in dual-purpose cereal crops.

Keywords: regrowth, radiation interception, yield components, tillering, grazing, soluble carbohydrates

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INTRODUCTION

Grazing cereal grain crops during their vegetative phase and then allowing the crop to recover to produce grain yield (dual-purpose crop) offers the potential to substantially increase productivity, profitability and flexibility on mixed crop-livestock farms (Dove and Kirkegaard, 2014). Dual-purpose crops have been used for many years and are widely adopted in south-eastern Australia (Harrison et al., 2011a) and in the Great Plains of the United States (Cutler et al., 1949; Carver et al., 2001). Traditionally these systems have involved grazing slower-developing winter cereals which have a significant vernalization requirement to generate a longer vegetative period for grazing, as well as an extended period for post-grazing recovery of crop biomass and grain yield. Consequently, the winter cultivars are developed to suit environments with early sowing opportunities and longer growing seasons with higher rainfall (Bell et al., 2015b) and breeding is focused on winter phenology, and resistance to disease resistance and weather damage (Carver et al., 2001; Hunt, 2017). In these regions, mixed farms obtain large benefits from the highly valuable forage for livestock production, and the additional revenue and income diversification provided by the grain production (Bell et al., 2015a). However, recently there has been increasing interest in the potential to obtain valuable grazing from high protein wheat crops on mixed farms in environments with shorter growing seasons, where faster developing spring wheats are better suited and more commonly grown. In these cases, the income from grain is the focus, however, economically valuable grazing potential has been demonstrated in both simulation (Moore, 2009; Bell et al., 2015b; Hussein et al., 2017) and experimental studies (McMullen and Virgona, 2009; Seymour et al., 2015; Sprague et al., 2018) from a range of different cultivars without yield penalties with careful grazing management.

Avoiding large grain yield penalties from the grazing is critical in order to maximize the value of dual-purpose crops. Recent reviews of historical studies on dual-purpose crops have shown that grazing reduces grain yield by about 7% (Edwards et al., 2011; Harrison et al., 2011a; Bell et al., 2014). Amongst previous studies large yield penalties can occur and are generally related to late and severe defoliation (or grazing), when either the reproductive structures (developing spikes) are directly removed, tiller number was significantly reduced and/or there was insufficient time for adequate crop recovery to achieve the required canopy cover to set the same yield potential (grain number) as the un-grazed crops (Harrison et al., 2011c; Butchee and Edwards, 2013). Grazing prior to the initiation of reproductive development [*equiv.* growth stage (GS) 31, stem elongation or jointing; Zadoks et al., 1974] is recommended to avoid grain yield reduction through direct removal of heads or tillers (Virgona et al., 2006). These general observations related to late grazing are consistent for winter cereal cultivars that have been used for dual-purpose. However, relatively little has been done to understand the dynamics of regrowth and physiological factors and processes involved in recovery after grazing in different genotypes (Harrison et al., 2011b,c). Some experiments have found larger trade-offs between grazing and grain yield for spring cultivars than in slower-developing winter cultivars (Sprague et al., 2018), while others have found similar responses in winter and spring types (Royo and Romagosa, 1996; Royo, 1997). Taller genotypes have been found to have less yield reduction from grazing than newer semi-dwarf cultivars, due to differences in susceptibility to lodging and yield potential (Winter and Thompson, 1990), but differences in growth habit amongst semi-dwarf genotypes (erect vs. prostrate) were not shown to differ in response to defoliation (Butchee and Edwards, 2013). This is likely to be related to interactions with environment and possibly physiological differences between cultivars in their yield setting attributes. In spring cereals, where both the grazing and recovery periods are short, there is a greater risk of yield penalties than for winter cereals in longer-season environments. The faster development through the vegetative period means they have less time to recover after defoliation and it is therefore more difficult to achieve critical radiation interception or biomass during the critical period determining grain number (Fischer, 1985). Hence, a better understanding of crop recovery and the genotypic attributes or management interventions that may mitigate risks of yield penalties after grazing are of interest.

Most research investigating the factors affecting recovery after defoliation has been conducted in slow-developing winter cereals, with far less understanding in faster-developing spring varieties (Harrison et al., 2011a). Some preliminary assessments of grain yield recovery among commonly grown spring wheat cultivars have been conducted in a range of environments across western (Seymour et al., 2015) and southern Australia (Frischke et al., 2015; Latta, 2015). There were variable amounts of recovery after defoliation, which were not clearly related to seasonal conditions nor to specific cultivars. In addition, many of the studies implemented defoliation treatments (mowing or grazing) across all cultivars at the same time, so that the timing of defoliation in relation to the phenological growth stage of the crop was not consistent across all genotypes. Confounding defoliation timing with crop development stage makes it difficult to determine whether varietal characteristics other than phenology were related to the outcome. Further, these defoliation treatments also often interact with water supply to the crop which can induce different responses after grazing (Virgona et al., 2006).

Given the lack of knowledge and inconsistent results in previous studies where recovery after defoliation in spring cereals has been investigated, we aimed to investigate cultivar differences based on putative physiological or morphological attributes thought to infer a greater capacity to recover and re-establish yield potential after grazing. Firstly, yield penalties are often associated with a reduction in tiller number as a driver of grain number, so that cultivars with a greater tillering capacity may provide greater resilience to defoliation. Secondly, crop phenology may also influence recovery independently of the interaction with grazing time (i.e., pre-GS31). Finally, some cultivars have a greater tendency to accumulate soluble carbohydrates (CHO) in the stem prior to anthesis and rely on these resources to fill the grain

(van Herwaarden et al., 1998). It is likely CHO accumulation will be reduced by vegetative defoliation (Tian et al., 2012; Hu et al., 2019), so that cultivars with a greater reliance on stem CHO may incur greater yield penalties. Here we report on a series of experiments which hypothesized that we would expect physiological differences between cultivars to bring about either improved or reduced capacity for yield recovery after defoliation. Such characteristics may provide breeding targets, or varietal selection guides for those wishing to utilize spring cereals as a dual-purpose crop. Our experiments were implemented in a way that mitigated the interactions of environment (water and nitrogen supply), and hence aimed to draw out the genotype by management interactions in the absence of the confounding influences of water or nutrient stresses.

MATERIALS AND METHODS

Experimental Approach

Four experiments were conducted between 2011 and 2013 in southern Queensland, Australia to examine the effect of defoliation on regrowth and grain yield recovery of different cultivars of spring wheat and barley. Cultivars of wheat and barley were chosen to evaluate whether specific traits or characteristics influenced grain yield recovery after defoliation. Traits compared amongst genotypes included the rate of phenological development (e.g., faster- vs. slower-developing types), tillering capacity and accumulation of water-soluble carbohydrates in stems prior to grain fill (**Table 1**). All cultivars chosen were commercially relevant at the time of the study and grown by farmers across the region. Defoliation was implemented using a self-propelled sickle-bar mower at approximately 3 cm height to simulate an intense grazing event. Timing of defoliation was tailored to match phenological stages in each cultivar (i.e., defoliation may occur on different days). Thus, the confounding effect of cultivars being defoliated at different development stages was minimized, as this is already known to have a significant influence on grain yield recovery. In some cases, sowing date was altered to try to achieve synchronous flowering between cultivars to remove another significant confounding factor on yield development. All crops were grown using agronomic recommendations for grain-only production systems (e.g., sowing densities 100–170 plants/m^2, sowing times) and were exposed to only a single defoliation event corresponding with the rationale that these short-season spring wheats would be grown for grain production and provide only opportunistic grazing for a short period (2–3 weeks).

All experiments were conducted on black vertosol soils (Isbell, 1996) which are widely used for grain production in this region of Australia. These are moderate-heavy clay soils with high water-holding capacity (200–260 mm plant-available water-holding capacity), high fertility (Colwell $P > 50$ mg/kg, organic matter $> 3\%$) and neutral pH (7–8). Three of the experiments were conducted under irrigation to remove any confounding influences of water stress in response of different genotypes. One experiment (Experiment 2) was rainfed but was sown on a full soil profile and crops did not experience moisture stress that would significantly reduce yield potential. All experiments were managed to ensure N was not limiting by applications of urea at sowing and throughout the growing season prior to irrigations. All experiments were maintained weed free through the application of broadleaf selective herbicides approximately 6 weeks after sowing, hand weeding as necessary, and preventative insect and rust sprays were applied during the season. The cultivar Gregory was used across all experiments to allow for inter-comparisons between them.

Experimental Implementation and Details

Experiment 1. Phenology × Defoliation Stage (Gatton, 2011)

The field experiment was conducted at Gatton Research Station, Queensland between May and November 2011, under fully irrigated conditions. Four replicates (2 × 10 m) in a randomized complete block design of four defoliation treatments GS25, GS28, and GS31 (dates provided in **Table 2**) and an uncut control were implemented on two cultivars. The cultivars Gregory (slower-developing) and Crusader (faster-developing) were sown in 25 cm rows on 16 May and 3 June 2011, respectively, aiming to achieve synchronous flowering time (7 September 2011), based on thermal time differences between cultivars. Hence, the different defoliation timings occurred at 50, 57, and 67 days after sowing for Gregory and 39, 49, and 55 days after sowing for Crusader. A plant population of 170 plants/m^2 was established in both cultivars. The experiment was provided with regular weekly irrigation (overhead sprinklers) to balance potential evapotranspiration to ensure the crops were not water stressed during recovery.

Experiment 2. Phenology and CHO Accumulation (Norwin, 2012)

The experiment was conducted in a farm field at Norwin, Queensland between May and November 2012 under rainfed conditions. The experiment included cultivars paired for phenology type (slower and faster developing cultivars) which are known to have a higher or lower tendency to accumulate water soluble carbohydrates (CHO) that can be translocated during grain filling (Ruuska et al., 2006; Neil Fettell, personal communication). Water-soluble carbohydrate accumulation was not measured here. The experimental design was a split-plot design with three replicated blocks with cultivars as main plots and defoliation treatments sub-plots (15 × 2 m). The slower developing cultivars (Gregory and Yenda) were sown on 17 May, and faster developing cultivars (H45 and Crusader) were sown on 23 June. Lack of sowing rain at the appropriate time meant this difference in sowing date was larger than anticipated to achieve synchronous flowering. All cultivars were sown in 25 cm rows and established 100–120 plants/m^2. Cultivars were defoliated at GS30/31 at 54 days after sowing, on 10 July for the slower developing cultivars and 16 August for the faster developing cultivars. The earlier sown cultivars reached anthesis

TABLE 1 | Experimental design, locations, and cultivars used to compare phenology (fast *vs*. slow), soluble carbohydrate accumulation (CHO) and tillering capacity related to response after defoliation in spring wheats.

Exp. #	Design	Location	Latitude, Longitude	Year	Water regime	*Varietal attributes*		
						Phenology		
1	Phenology × Defoliation timing	Gatton, QLD	27°32.5′S, 152°20.3′E	2011	Irrigated	Slow	*cv. Gregory*	
						Fast	*cv. Crusader*	
2	Phenology × CHO accumulation	Norwin, QLD	27°33.0′S, 151°19.6′E	2012	Rainfed		**High CHO**	**Mod. CHO**
						Slow	*cv. Gregory*	*cv. Yenda*
						Fast	*cv. H45*	*cv. Crusader*
3	Phenology × CHO accumulation	Brookstead, QLD	27°43.4′S, 151°17.5′E	2013	Irrigated		**High CHO**	**Mod. CHO**
						Slow	*cv. Gregory*	*cv. Yenda*
						Fast	*cv. H45*	*cv. Crusader*
4	Phenology × Tillering capacity	Brookstead, QLD	27°43.4′S, 151°17.5′E	2013	Irrigated		**Low tillering**	**High tillering**
						Fast	*cv. Gregory*	*cv. Sunvale*
						Slow	*cv. Gladius*	*cv. Bolac*
						Barley	*cv. Scope*	*cv. Hindmarsh*

on 14 September and the later sown cultivars on 28 September. The site had been managed as a long fallow (18 months) prior to the experiment and had a full soil profile (250 mm plant available water) with high levels of soil nitrogen (>400 kg NO_3/ha) at sowing.

Experiment 3. Phenology and CHO Accumulation (Brookstead, 2013)

This experiment was located on a farm at Condamine Plains, near Brookstead on the eastern Darling Downs, Queensland in 2013. It repeated the treatments in Experiment 2 but implemented them under irrigation. A fully randomized block design with three replicates and 8 plots (2 × 12 m) included a defoliated and undefoliated treatment for 4 cultivars. All genotypes were sown on the same date (18 June 2013), with a row spacing of 40 cm and an established plant density of 90–110 plants/m^2. There was little difference in early phenological development of cultivars, so all genotypes were defoliated on 6 August (49 days after sowing) when still vegetative and at GS 26 (Zadoks et al., 1974). Irrigation was applied to ensure no water limitations with a total of 40 mm of water supplied per week (balanced for any rainfall). Water soluble carbohydrates were not measured here.

Experiment 4. Phenology and Tillering Capacity (Brookstead, 2013)

This field experiment was established at Condamine Plains, near Brookstead on the eastern Darling Downs, Queensland in 2013 (at the same farm as Experiment 3). In this experiment four spring wheat and two spring barley cultivars were chosen to represent a range of varying tillering capacity (i.e., the number of ears produced per m^2 at maturity) (see **Table 1**). The same experimental design (three replicates in randomized block design) and crop management was implemented as in Experiment 3. The tiller dynamics of defoliated and undefoliated crops were monitored up until anthesis to determine any differences in tiller development between cultivars under defoliation (details outlined below).

Crop Measurements

Crop Biomass, Yield and Yield Components

In all experiments, biomass removed during defoliation from mowing at approximately 3 cm height and residual biomass was measured by taking quadrat cuts (0.6 – 1.0 m^2) before and after defoliation. At maturity, larger quadrat cuts (1.5 – 2.0 m^2) were taken to ground level from the center of each plot to determine grain yield and maturity biomass; any senesced leaf material was also collected. These samples were dried for 3 days at 80°C before being weighed. The number of ears in each sample was counted to determine ear number per m^2 and these were subsequently threshed and cleaned. Grain samples were then dried at 80°C and weighed and a subsample of 100 grains from each sample was taken and weighed to determine average kernel mass. Calculations of other yield components were then based on these measured attributes; harvest index (grain yield/maturity biomass), grain number per m^2, kernels per ear.

Tiller Dynamics

In Experiments 1 and 4, the number of primary, secondary and senesced tillers were recorded between the initiation of reproductive development and anthesis. After defoliation was implemented the number of tillers emerging was monitored on a set of 7–10 marked plants in each plot. At booting (GS45) and/or start of anthesis (GS60) a destructive sample (quadrat 0.5–1.0 m^2) was taken to determine the number of tillers present at these times. Primary tillers were identified as those that had produced a flag leaf or started anthesis at these respective times, while secondary tillers had not reached these development stages

TABLE 2 | Biomass removed and subsequent leaf area index (LAI), radiation interception (R_i) and tillers at anthesis (#/m^2) for two spring wheat cultivars with different phenological development rate (mid-season; *cv.* Gregory – Greg. and: *cv.* Crusader – Crus.) following defoliation at different growth stages compared to an undefoliated control (Experiment 1 – Gatton, 2011).

Defoliation timing	At defoliation						At anthesis											
	Date[A]		Removed biomass (t/ha)		LAI			R_i			All tillers (#/m^2)			Main tillers (#/m^2)			Minor tillers (#/m^2)	
	Crus.	Greg.	Crus.	Greg.	Crus.	P	LSD	Greg.	Crus.	P	LSD	Greg.	Crus.	P	LSD	Greg.	Crus.	Greg.
Uncut					6.37	6.00	0.97	0.96	1110	1380	770	890	340	470				
GS 25	12 July	5 July	0.55	1.16	4.67	4.02	0.93	0.90	1330	1840	1030	920	310	920				
GS 28	22 July	12 July	0.78	1.73	3.45	3.17	0.94	0.82	1230	1680	940	870	290	800				
GS 31	28 July	22 July	2.03	2.28	2.33	2.70	0.74	0.75	990	1380	550	640	460	720				
			P	LSD	P	LSD	P	LSD	P	LSD	P	LSD	P	LSD	P	LSD	P	LSD
Genotype			<0.001	0.25	0.323		0.623		<0.001	168	0.641		<0.001	118				
Defoliation			<0.001	0.31	<0.001	0.67	<0.001	0.067	0.005	235	<0.001	168	0.084	168				
Genotype × Defoliation			0.124		0.464		0.925		0.740		0.92		0.029	252				

P score (P) for main effects of genotype, defoliation treatment and the interaction are provided below and least significant difference (LSD at P = 0.05) for these effects when they are significant. [A]Defoliation was timed to achieve the same growth stage for the two cultivars, sown on different dates.

yet. The ratio of the number of tillers compared to the final ear numbers gave some indication of the proportion of tillers that had senesced during grain filling.

Crop Leaf Area Index and Radiation Interception

Crop radiation interception and predicted leaf area index (measured with a Decagon's AccuPAR model LP-80 PAR/LAI Ceptometer) was measured at anthesis (GS 65) in all experiments. Two measures above canopy height were matched with four measures at ground level below the canopy spanning 3 or 4 plant rows in each plot. Leaf distribution value (X) was set to 0.96 as recommended for wheat (Decagon Instruction Manual).

Statistical Analysis

Statistical analysis used two-way analysis of variance in GenStat version 19.1 (VSN International Ltd), with the main effects of genotype and defoliation treatments. Interactions between these two factors were expected if they responded differently to defoliation treatments. Fischers' protected least significant difference (LSD) was used for mean separation where appropriate. Experiment 4 was also analyzed for species and excluding the two barley genotypes to see if any differences amongst the four wheat genotypes were evident. As there were no genotype by defoliation interactions across experiments, using data from all genotypes and experiments, causal relationships of defoliation effects on plant growth (post-defoliation growth, anthesis biomass and canopy interception, post-anthesis growth), yield and yield components (grain yield, maturity biomass, harvest index, grain number per m^2, kernel mass, kernels per ear, ears per m^2) were explored through multiple regressions. To allow for comparisons across experiments where the magnitude of effects differed, we calculated the relative value of the defoliated crop as a proportion of the undefoliated crop. Where there was likely causation and significant correlations ($P < 0.05$) the line-of-best-fit between the predictor and response variable was derived using Microsoft Excel using least squares regression.

RESULTS

Experiment 1. Phenology × Defoliation Timing (Gatton, 2011)

Delaying defoliation timing until later phenological stages allowed significant increases in biomass removed in both cultivars. Gregory had more biomass than Crusader at each of the defoliation timings as this occurred 8–12 days after sowing later than in Crusader (**Table 2**). The defoliation treatments significantly reduced LAI at anthesis compared to the undefoliated control in both cultivars, and later defoliation had lower LAI. Radiation interception (Ri) at anthesis was also significantly reduced in both cultivars after the latest defoliation timing, but there was no significant difference in earlier defoliation times in Crusader, or the earliest timing in Gregory.

At anthesis the number of tillers per plant was increased by earlier defoliation (GS25/28) compared to the undefoliated control. This was particularly evident in the higher tillering cultivar Gregory due to an increase

in the number of secondary tillers. In both cultivars, later defoliation (GS31) had a similar number of tillers at anthesis to the undefoliated treatments but there was a reduction in primary tillers and more secondary tillers in this treatment.

Both cultivars had similar grain yields and maturity biomass across the defoliation treatments and there was no significant interaction between cultivar and defoliation treatments (**Table 3**). There was a 40% reduction in both crop biomass and grain yield following defoliation at GS31. The earliest defoliation treatment did not reduce grain yield significantly (<10%), but the defoliation at GS28 reduced grain yield and crop biomass. Reductions in grain number were the main driver of the yield reductions particularly in the latest defoliation, with kernel mass also significantly reduced in the latest defoliation time in both cultivars. The two cultivars responded differently to defoliation in terms of grain number reduction, as shown by the significant interactions for both ears/m^2 and kernels/ear. Gregory maintained ear number in all but the earliest defoliation timing (GS25), where ear number was reduced by 24%. This was compensated through an increase in kernels/ear (20%) but grain number was still reduced. The reason for this reduction is unclear. In Gregory the later defoliation did not reduce ear number but did reduce kernels per ear and hence reduced grain number. In Crusader, late defoliation (GS31) reduced ear number more than for Gregory, but the kernels per ear were less affected.

Experiment 2. Phenology and CHO Accumulation (Norwin, 2012)

All cultivars had similar biomass removal (0.94–1.25 t DM/ha) when defoliated at GS 30 (54 days after sowing), even though this occurred on different dates in the different phenology types (**Table 4**). Defoliation reduced crop biomass, LAI and radiation interception at anthesis significantly in all cultivars. Faster developing cultivars produced less biomass and leaf area by anthesis than the earlier sown slower developing cultivars, but there was no significant interaction with defoliation for anthesis biomass and LAI. There was very low radiation interception and leaf area in the defoliated later-sown fast-developing genotypes and the penalty was significantly larger than in the slower developing genotypes. There was large variance in the onset of flowering amongst tillers in these fast-developing genotypes and further leaf area accumulation occurred after our sampling allowing the crop to compensate further after defoliation.

Despite the significant reductions in anthesis biomass and radiation interception, by crop maturity there were no significant effects of defoliation on crop grain yield, biomass or yield components (**Table 5**). Grain yield and biomass varied <8% across all genotypes, and similar levels of variation occurred for the various yield components. While there were genotype differences in crop yield, biomass and yield components demonstrating different combinations of yield components amongst the cultivars, there was no interaction between defoliation and genotype for any of these attributes (**Table 5**).

Experiment 3: Phenology and CHO Accumulation (Brookstead, 2013)

All cultivars produced similar biomass at the time of defoliation (0.4 – 0.5 t/ha), but this was less than observed in the similar experiment the previous year due to an earlier defoliation timing (GS26) and a later sowing date. Despite this smaller biomass removal, there was a significant reduction in anthesis DM in all cultivars (0.9–2.0 t/ha), but this was not reflected in radiation interception at anthesis (**Table 6**). The faster-developing cultivars (H45 and Crusader) had lower LAI and radiation interception than the slower-developing cultivars at this time.

As observed in the previous similar experiment 2, there was no significant effect of defoliation on grain yield or maturity biomass across the cultivars (**Table 7**). Grain yield and maturity biomass varied <8% across all genotypes except for Yenda. Yenda had greater differences between defoliated and undefoliated treatments in grain yield, biomass and particularly in grain number per m^2, but these were not statistically significant. There was a significant reduction in kernel mass due to defoliation, but all other grain yield components were unaffected. Again, there were clear genotypic differences in crop yield, biomass and yield components demonstrating different combinations of yield components amongst cultivars, but there was no interaction between defoliation and genotype for any of these attributes (**Table 7**).

Experiment 4: Phenology and Tillering Capacity (Brookstead, 2013)

At defoliation (GS26), the barley cultivar Scope has significantly more biomass than the all other wheat and barley genotypes (**Table 8**). Generally, the higher tillering cultivars had a less erect habit which reduced the amount of biomass removed by mowing, but this was not statistically significant.

Defoliation had no effect on the total number of tillers produced at booting (**Table 8**). The number of primary tillers was significantly reduced in the higher tillering cultivars (Sunvale, Scope, and Hindmarsh) and compensated by more secondary tillers, but no differences were observed in the lower tillering cultivars. The number of tillers at booting (GS39) did not necessarily correspond to the expected classifications across the various genotypes, but the final ear numbers per m^2 (**Table 9**) did, indicating that the higher tillering varieties produce more secondary tillers that result in grain producing ears. The two barley cultivars and wheat cv. Sunvale had significantly more tillers (both primary and secondary tillers) than the other wheat genotypes.

Defoliation significantly reduced anthesis biomass, LAI and radiation interception at anthesis (**Table 8**). All genotypes had similar anthesis biomass, but defoliation reduced this by 1.0-1.9 t/ha across all genotypes except Hindmarsh barley. There were genotype differences in LAI and radiation interception and a significant interaction between genotype and defolation for radiation interception. This interaction showed that the higher-tillering genotypes (wheat and barley)

TABLE 3 | Grain yield and yield components at harvest of two spring wheat cultivars with different phenological development rate [slower: *cv*. Gregory (Greg.) and faster: *cv*. Crusader (Crus.)] following defoliation at different growth stages compared to an undefoliated control (Experiment 1 – Gatton, 2011).

Defoliation timing	Grain yield (t/ha)		Biomass (t/ha)		Harvest index		Grain no. '000/m^2		Ears/m^2		Kernels/ear		Kernel mass (mg)	
	Crus.	Greg.	Crus.	Greg.	Crus.	Greg.	Crus.	Greg.	Crus.	Greg.	Crus.	Greg.	Crus.	Greg.
Uncut	6.24	6.00	14.5	15.1	0.43	0.40	19.4	14.9	490	444	39.9	34.2	32.2	40.4
GS 25	5.88	5.35	13.5	12.1	0.43	0.44	17.9	13.7	492	339	36.7	40.7	32.9	39.2
GS 28	5.13	5.40	11.3	12.0	0.45	0.45	15.7	14.3	431	424	36.6	33.8	32.6	37.7
GS 31	3.53	3.71	8.1	8.9	0.44	0.42	11.9	10.7	395	449	30.3	23.6	29.8	35.0
	P	***LSD***	***P***	***LSD***	***P***	***LSD***	***P***	***LSD***	***P***	***LSD***	***P***	***LSD***	***P***	***LSD***
Genotype	0.728	–	0.667	–	0.042	0.01	<0.001	1.5	0.125	–	0.042	2.7	<0.001	1.1
Defoliation	<0.001	0.67	<0.001	1.4	0.001	0.02	<0.001	2.1	0.440	–	<0.001	3.8	<0.001	1.5
Gen. × Defol.	0.574	–	0.314	–	0.086	–	0.233	–	0.040	99	0.033	5.4	0.166	–

P-score (P) for main effects of genotype, defoliation treatment and the interaction are provided below and least significant difference (LSD at P = 0.05) for these effects when they are significant.

TABLE 4 | Biomass removed and subsequent biomass, leaf area index (LAI), and radiation interception (R_i) at anthesis of four spring wheat cultivars following defoliation at GS30/31 (DEF) compared to an undefoliated control (UN) (Experiment 2 – Norwin, 2012).

Phen.	CHO accum.	Cultivar	At defoliation		At anthesis						
			Date	Biomass removed (t/ha)	Date	Biomass (t/ha)		LAI		Ri	
						UN	DEF	UN	DEF	UN	DEF
Slow	High	Gregory	10 July	1.22	14 September	10.90	9.18	6.18	5.05	0.94	0.88
	Low	Yenda	10 July	1.25	14 September	10.00	8.07	5.83	4.55	0.91	0.84
Fast	High	H45	16 August	0.94	28 September	8.24	5.29	3.46	1.96	0.74	0.55
	Low	Crusader	16 August	1.25	28 September	8.91	5.69	3.34	2.05	0.71	0.56
				P		***P***	***LSD***	***P***	***LSD***	***P***	***LSD***
Genotype				0.541		<0.001	0.53	<0.001	0.35	<0.001	0.04
Defoliation						<0.001	0.38	<0.001	0.25	<0.001	0.03
Genotype x Defoliation						0.127		0.717	–	0.003	0.05

Cultivars differ in phenological development rate (slower: cv. Gregory, Yenda, and faster: cv. Crusader, H45) and capacity to accumulate water soluble carbohydrates (CHO) in biomass before flowering. P score (P) for main effects of genotype, defoliation treatment and the interaction are provided below and least significant difference (LSD at P = 0.05) for these effects when they are significant.

had a greater reduction in radiation interception than the lower-tillering group.

Defoliation significantly reduced grain yield and maturity biomass across all genotypes, however, the reductions in grain yield were small (**Table 9**, 0.36 t/ha on average, ranging from 0.04 to 0.72 t/ha). Scope barley had lower yield than the other genotypes which all achieved a similar yield. There was no genotype by defoliation interaction in grain yield and maturity biomass, but there was a significant effect on harvest index. This interaction was because defoliation increased harvest index significantly ($P < 0.01$) in the barley genotypes but not in the wheat genotypes.

Of the yield components, defoliation reduced kernel mass significantly but there was no significant effect of defoliation on yield components related to grain number (i.e., ear number per m^2 and kernels per ear). Among the genotypes, there were clear differences in yield components. As expected, the barley genotypes had less kernels per tiller and lower grain number per m^2, but larger kernels. The wheat cultivars Sunvale and Bolac had significantly higher grain number but smaller kernels (24–25 mg) than Gregory and Gladius (29–31 mg). Cultivars Sunvale and Gladius had lower kernels per ear (30–31/ear) than Bolac and Gregory (35–36/ear), but these differences were compensated by differences in ear number per m^2. Despite these apparent differences in tillering and yield components there was no significant interactions between genotype and defoliation (**Table 9**).

Further exploration of this data to examine if there were any significant effects related to tillering capacity (by grouping genotypes with similar tiller numbers) found no interactions, though there were differences between groups in ear number and kernels per ear, as indicated above. As the barley genotypes (particularly Scope) provided the main differences in the statistical analysis, a further analysis was conducted omitting the barley genotypes. However, this

TABLE 5 | Grain yield and yield components at harvest of four spring wheat cultivars following defoliation at GS30 (DEF) compared to an undefoliated control (UN) (Experiment 2 – Norwin, 2012).

Phen.	CHO accum.	Cultivar	Grain yield (t/ha)			Biomass (t/ha)			Harvest index			Grain no. ('000/m^2)			Ears/m^2			Kernel mass (mg)			Kernels/ear		
			UN	DEF	*LSD*	UN	DEF	*LSD*	UN	DEF	*LSD*	UN	DEF	*LSD*	UN	DEF	*LSD*	UN	DEF	*LSD*	UN	DEF	*LSD*
Slow	High	Gregory	4.52	4.16		14.2	13.0		0.32	0.32		14.5	13.5		463	434		31.1	30.8		31.4	31.1	
	Low	Yenda	3.74	3.54		12.7	12.0		0.29	0.29		15.9	15.6		428	463		23.3	22.5		36.8	34.0	
Fast	High	H45	5.10	5.27		11.1	12.2		0.46	0.44		17.8	18.3		426	476		28.7	28.7		41.7	38.2	
	Low	Crusader	4.71	4.55		11.1	11.7		0.42	0.39		18.7	17.4		534	520		25.5	26.0		34.9	33.1	
			P		*LSD*	*P*		*LSD*	*P*		*LSD*	*P*		*LSD*	*P*		*LSD*	*P*		*LSD*	*P*		*LSD*
Genotype			<0.001	0.70		0.027	1.5		<0.001	0.03		0.003	2.4		0.001	44		<0.001	1.6		<0.001	3.2	
Defoliation			0.584			0.952			0.101			0.525			0.516			0.793			0.067		
Genotype × Defoliation			0.890			0.429			0.415			0.868			0.220			0.844			0.737		

Cultivars differ in phenological development rate (slower: cv. Gregory, Yenda, and faster: cv. Crusader, H45) and capacity to accumulate water soluble carbohydrates (CHO) in biomass before flowering. P-score (P) for main effects of genotype, defoliation treatment and the interaction are provided below and least significant difference (LSD at P = 0.05) for these effects when they are significant.

did not reveal any further statistical differences amongst wheat genotypes.

Cross-Experiment Analysis of Defoliation Effects

Combining results across experiments demonstrate some of the critical drivers of grain yield reduction as a result of defoliation in spring cereal genotypes (**Figure 1**). There was a negative relationship between the amount of biomass removed by defoliation and the leaf area index (LAI) that was subsequently recovered by anthesis (**Figure 1A**). Every 1 t/ha of biomass removed resulted in a 25% reduction in LAI at anthesis. However, reductions of >40% in LAI at anthesis were required to dramatically reduce grain number, while lesser reductions in LAI had only small impacts on grain number (<10% decrease) (**Figure 1C**). The relative grain number (i.e., the ratio of grain number in defoliated vs. undefoliated crops) was closely correlated to relative grain yield, demonstrating that these reductions in grain number or sink limitations are the primary cause of yield penalties in defoliated crops (**Figure 1B**). The capacity for crops to compensate for the lower LAI and biomass at anthesis to achieve similar grain yields was shown by an increase in post-anthesis growth as the deficit in anthesis biomass increased (**Figure 1D**). However, this additional production was only 0.33 kg/kg of anthesis deficit so was not enough to fully recover maturity biomass.

DISCUSSION

We hypothesized that amongst spring cultivars with similar phenology, differences in physiological traits that influence how they establish grain yield would see them respond differently during recovery after defoliation. However, the experiments revealed no such evidence of genotypic differences in crop recovery after defoliation. There was no genotype by defoliation interactions on grain yield and few interactions in yield components between cultivars under defoliation compared to undefoliated crops. This result contrasts with studies on winter wheats that have shown differences in cultivar responses to defoliation (Thapa et al., 2010). Despite this lack of interaction between genotypic traits and defoliation, there was significant effects of defoliation timing on yield recovery. This indicates that genotype has less to do with the ability of the crop to recover after grazing than how the grazing is managed. It is clearly critical to manage the grazing to avoid later and more severe grazing to allow recovery of enough biomass and resources to maintain grain number and fill grains effectively. The research also clearly shows that spring wheat and barley genotypes could be used as a valuable forage source with little or no yield penalty associated with forage removal up to 1.2 t/ha and before GS31, even in environments which drive rapid crop development and with minimal terminal drought. However, the amount of biomass available for grazing is significantly less than that available from winter genotypes sown earlier (Dove and Kirkegaard, 2014; Hunt, 2017; Sprague et al., 2018).

TABLE 6 | Biomass removed and subsequent biomass, leaf area index (LAI), and radiation interception (R_i) at anthesis of four spring wheat cultivars following defoliation at GS26 (DEF) compared to an undefoliated control (UN) (Experiment 3 – Brookstead, 2013).

Cultivar	Removed biomass (t/ha)	Anthesis DM (t/ha)		Anthesis LAI		Anthesis Ri	
		UN	DEF	UN	DEF	UN	DEF
Gregory	0.37	8.51	7.62	6.58	6.44	0.94	0.94
Yenda	0.48	7.61	6.51	7.03	6.41	0.96	0.94
H45	0.40	8.08	6.07	4.79	4.56	0.88	0.88
Crusader	0.42	8.56	7.68	4.57	3.82	0.86	0.82
	P	***P***	***LSD***	***P***	***LSD***	***P***	***LSD***
Genotype	0.541	0.019	0.84	<0.001	0.93	<0.001	0.05
Defoliation	na	<0.001	0.59	0.176	–	0.286	–
Gen. x Def.	na	0.449		0.874	–	0.701	–

Cultivars differ in phenological development rate (slower: cv. Gregory, Yenda, and faster: cv. Crusader, H45) and capacity to accumulate water soluble carbohydrates (WSC) in biomass before flowering. P-score (P) for main effects of genotype, defoliation treatment and the interaction are provided below and least significant difference (LSD at P = 0.05) for these effects when they are significant.

TABLE 7 | Grain yield and yield components at harvest of four spring wheat cultivars following defoliation at GS26 (DEF) compared to an undefoliated control (UN) (Experiment 3 – Brookstead, 2013).

Cultivar	Grain yield (t/ha)		Biomass (t/ha)		Harvest index		Grain no. ('000/m^2)		Ears/m^2		Kernel mass (mg)		Kernel no./ear	
	UN	DEF	UN	DEF	UN	DEF	UN	DEF	UN	DEF	UN	DEF	UN	DEF
Gregory	4.33	4.58	12.7	12.5	0.34	0.37	14.1	15.7	476	479	30.8	29.3	29.6	32.8
Yenda	4.46	3.85	13.6	12.1	0.33	0.32	19.0	17.7	543	514	23.6	21.7	34.9	34.6
H45	5.56	5.10	12.1	11.1	0.46	0.46	17.3	17.5	421	408	32.1	29.4	41.2	43.0
Crusader	4.82	4.44	11.0	10.6	0.44	0.41	17.1	16.4	446	462	28.3	26.7	38.1	35.6
	P	***LSD***	***P***	***LSD***	***P***	***LSD***	***P***	***LSD***	***P***	***LSD***	***P***	***LSD***	***P***	***LSD***
Genotype	0.029	0.75	0.046	1.55	<0.001	0.03	0.125		0.010	62	<0.001	3.2	<0.001	3.6
Defoliation	0.220		0.161		0.661		0.963		0.778		0.084	2.2	0.684	
Gen. × Def.	0.614		0.769		0.230		0.736		0.861		0.974		0.388	

Cultivars differ in phenological development rate (slower: cv. Gregory, Yenda, and faster: cv. Crusader, H45) and capacity to accumulate water soluble carbohydrates (WSC) in biomass before flowering. P-score (P) for main effects of genotype, defoliation treatment and the interaction are provided below and least significant difference (LSD at P = 0.05) for these effects when they are significant.

Genotype Effects on Grain Yield Response After Defoliation

The cultivars tested varied in three main attributes (phenological development rate, water soluble carbohydrate accumulation, and tillering capacity) which were thought to interact with defoliation, to either mitigate or intensify the effects on subsequent grain yield. However, across all experiments defoliation didn't induce differential grain yield responses amongst different genotypes despite significant genotypic differences in resource allocation (e.g., harvest index, tiller number) and yield components in all experiments (e.g., grain number, ear number, kernel mass, and kernels per ear). Two cases were observed where certain yield components were impacted differently between cultivars. The unexpected reductions in ear number in Gregory at one defoliation time in Experiment 1; but these were compensated by increased kernels per ear so that grain number and grain yield was maintained. The only other case of differential responses to defoliation amongst genotypes was in Experiment 4, where the low harvest index of the undefoliated Scope barley was increased significantly by defoliation. The lack of interactions amongst the various yield components provides strong evidence that different genotypes responded very similarly to defoliation across these studies.

Previous defoliation studies have found that reductions in tiller number or ear number, which limit grain number and yield potential are often a key driver of yield reductions in defoliated crops (Kelman and Dove, 2009; Tian et al., 2012; Kirkegaard et al., 2015; Sprague et al., 2018). Genotypes with greater tillering capacity were thought to have greater plasticity in terms of recovering tillers after defoliation, to maintain grain number and yield, compared to genotypes with less tillering capacity (Kelman and Dove, 2009). However, across all experiments here, defoliation before GS30 did not reduce ear number significantly in any genotypes (except in Experiment 1, as discussed above). This is consistent with current understandings in winter wheats (Fieser et al., 2006; McMullen and Virgona, 2009; Harrison et al., 2011a) and is confirmed again here in spring cereals (Seymour

TABLE 8 | Biomass removed, tillers per m^2 (major and minor) present at booting and subsequent biomass, leaf area index (LAI), and radiation interception (R_i) at anthesis of four spring wheat cultivars following defoliation at GS26 (DEF) compared to an undefoliated control (UN) (Experiment 4 – Brookstead, 2013).

Crop	Tillering	Cultivar	Removed DM (t/ha)	Anthesis								Booting					
				Biomass (t/ha)		LAI		Ri		All tillers (#/m^2)		Major tillers (#m^2)		Minor tillers (#/m^2)	
				UN	DEF	UN	DEF	UN	DEF	UN	DEF	UN	DEF	UN	DEF
Wheat	Low	Gregory	0.43	8.30	6.45	5.79	5.44	0.93	0.92	705	563	378	302	327	261
		Gladius	0.44	7.69	6.64	3.59	3.54	0.76	0.76	566	562	293	302	273	260
	High	Sunvale	0.35	7.74	6.12	6.41	5.34	0.95	0.89	1053	1108	466	557	587	551
		Bolac	0.31	7.47	5.68	5.40	4.05	0.90	0.83	436	460	221	248	215	212
Barley	Low	Scope	0.95	8.05	6.15	6.73	6.20	0.95	0.95	888	1212	382	643	505	569
	High	Hindmarsh	0.52	7.72	7.47	5.95	5.14	0.94	0.88	878	1467	364	822	513	644
			LSD	P	LSD	P	LSD	P	LSD	P	LSD	P	LSD	P	LSD
Genotype			*0.28*	0.232	–	<0.001	0.56	<0.001	0.03	<0.001	220	<0.001	96	<0.001	163
Defoliation				<0.001	0.49	<0.001	0.32	<0.001	0.02	0.074	–	<0.001	58	0.960	
Genotype × Defoliation				0.315	–	0.211	–	0.038	0.04	0.298	–	0.005	134	0.941	

Cultivars differ in tillering capacity but have a similar phenological development rate. P-score (P) for main effects of genotype, defoliation treatment and the interaction are provided below and least significant difference (LSD at P = 0.05) for these effects when they are significant.

et al., 2015). Experiment 4 tested genotypes with a wide range of tillering capacity (from 650 to 450 tillers/m^2), and the high tillering barley produced twice as many ears as lower tillering wheat genotypes, yet there was no effect of defoliation on final ear number across any of these genotypes. A possible explanation is that defoliation well before GS30/31 is unlikely to remove or damage the main tillers and hence, later defoliations where this occurs may generate a greater response between genotypes varying in tilling capacity. In support of this, we only saw a reduction in main tiller numbers when defoliation occurred after GS30 (see **Table 2**), and early defoliation before GS 30 increased the total number of tillers per plant at anthesis in higher tillering cultivars (see **Tables 2**, **8**). This increase in tiller production is likely due to increased light infiltration to the lower canopy after defoliation (Sparkes et al., 2006). Further, all the present experiments had no nitrogen or water stress during the period of tiller number determination, and hence the crop had sufficient resources to support the majority of tillers to maturity. It is plausible that combinations of water and/or nitrogen stress with defoliation may reduce assimilation sufficiently to reduce tiller survival during this critical period; this has not been examined here or by others to our knowledge.

Genotypic differences in accumulation of stem CHO prior to anthesis and translocation of these during grain filling is a trait associated with improved conversion of biomass to grain yield under terminal drought conditions (van Herwaarden et al., 1998). Severe defoliation during the vegetative phase can reduce the accumulation of these carbohydrates by removing biomass and reducing crop leaf area (Muir et al., 2006; Hu et al., 2019). Hence, reduction of CHO reserves could reduce the capacity of such genotypes to maintain grain yield after defoliation. However, the two experiments here included genotypes known to vary in this trait, but found no differences in their grain yield recovery after defoliation. We did not confirm the actual differences in CHO reserve accumulation between genotypes and how this may have been altered by defoliation, but further research may examine this. In the experiment under fully irrigated conditions (Experiment 3), the crops may not have been sufficiently source-limited after anthesis for previously stored CHOs to provide a significant benefit during grain filling. However, in this experiment kernel mass was reduced by defoliation (P = 0.08), which may indicate that defoliated crops were less able to fill the total grain sink. The varietal trait of accumulating CHO is known to offer greatest benefit under conditions of moisture stress during grain filling (van Herwaarden et al., 1998), and it is likely that there may be a strong seasonal interaction with defoliation reducing these reserves in wheat crops. While no response may be expected under irrigation (Experiment 3), a larger effect of CHO accumulating traits would be expected under rainfed conditions (Experiment 2). In experiment 2, while soil water was depleted quickly during grain filling, there was minimal moisture stress as the crops were still able to produce similar yields (>4.5 t/ha) and kernel mass as the fully irrigated experiment (Experiment 3). Hence, the full effects of stored CHO may not have expressed themselves under these conditions either. While CHO reserves may be reduced this may not actually reduce the total CHO that are translocated to grain during grain filling

TABLE 9 | Grain yield and yield components at harvest of four spring wheat and two spring barley cultivars following defoliation at GS26 (DEF) compared to an undefoliated control (UN) (Experiment 4 – Brookstead, 2013).

Crop	Tillering	Cultivar	Grain yield (t/ha)		Biomass (t/ha)		Harvest index		Grain no. '000/m^2		Ear no./m^2		Kernel no./ear		Kernel mass (mg)	
			UN	DEF	UN	DEF	UN	DEF	UN	DEF	UN	DEF	UN	DEF	UN	DEF
Wheat	Low	Gregory	5.01	4.54	13.4	12.0	0.37	0.38	16.7	16.0	458	455	36.5	35.2	30	28
		Gladius	4.88	4.16	12.0	10.4	0.41	0.40	14.8	14.1	446	477	33.3	29.5	33	29
	High	Sunvale	4.91	4.73	12.4	12.0	0.40	0.39	19.3	19.0	618	657	31.3	28.8	25	25
		Bolac	4.73	4.04	13.3	11.4	0.35	0.35	18.5	17.9	527	520	35.3	34.4	26	23
Barley	Low	Scope	3.47	3.48	12.1	9.5	0.29	0.37	8.5	9.2	652	640	13.1	14.4	41	38
	High	Hindmarsh	4.75	4.71	11.9	10.0	0.40	0.47	11.9	13.3	774	758	15.4	17.7	40	35
			P	*LSD*	*P*	*LSD*	*P*	*LSD*	*P*	*LSD*	*P*	*LSD*	*P*	*LSD*	*P*	*LSD*
Genotype			<0.001	0.50	0.001	0.99	<0.001	0.025	<0.001	1.2	<0.001	80	<0.001	2.25	<0.001	2.4
Defoliation			0.016	0.29	<0.001	0.57	0.002	0.014	0.752	–	0.824	–	0.185	–	<0.001	1.4
Genotype × Defoliation			0.552	–	0.25	–	0.002	0.035	0.387	–	0.964	–	0.104	–	0.583	–

Cultivars differ in tillering capacity but have a similar phenological development rate. P-score (P) for main effects of genotype, defoliation treatment and the interaction are provided below and least significant difference (LSD at P = 0.05) for these effects when they are significant.

(Hu et al., 2019). Further, defoliation is known to slow the rate of water use leaving more soil water available at anthesis compared to the undefoliated crop (Harrison et al., 2011b); this was also observed in Experiment 2 (data not presented). This additional water available during grain filling is used more efficiently and is likely mitigating the effects of defoliation by offsetting any reductions in stored assimilates accumulated at anthesis.

Finally, we hypothesized that defoliation would have less effect on slower-developing genotypes with more time to recover leaf area and biomass than on faster-developing genotypes. However, we observed little evidence of this in these experiments although differences in development rate were relatively small. In Experiment 1, where we were able to reasonably synchronize flowering between the two cultivars, this amounted to a difference of $<7 \pm 3$ days in the period between defoliation and anthesis between the fast and slower developing cultivars. These small differences are further confounded by difficulties in achieving synchronous development stages between different genotypes, meaning different genotypes are exposed to different environmental conditions. Here in Experiment 2, the two groups were sown too far apart (due to surface moisture conditions) or in Experiment 3 were sown on the same date, so key development phases did not coincide. Our results here add to many other studies that have found both different and similar responses to defoliation across wheat genotypes varying in their phenological development (Royo and Romagosa, 1996; Royo, 1997; McMullen and Virgona, 2009; Sprague et al., 2018). This lack of consistency suggests this is a problematic relationship to unravel experimentally as it is very difficult to isolate the environmental conditions from genotypic effects and their interactions. An appropriately characterized crop growth model which integrates both regrowth and phenological effects on the crop may be able to add deeper understandings on how defoliation intensity and timing may influence the capacity of different genotypes to compensate. While others have attempted to model the trade-offs between grazing and grain yield in wheat crops (Zhang et al., 2008; Harrison et al., 2012), these models have not mechanistically captured the phenological development changes and how this would interact with environmental or genotypic differences in cultivars. Characterizing the physiological processes driving regrowth after defoliation in wheat (and other crops) is possible in models like APSIM (Holzworth et al., 2014) and hence examining interactions of genotype with water and nitrogen availability and grazing management would inform further experimental work and/or better inform agronomic recommendations.

Defoliation Effects on Crop Regrowth and Yield

Across all experiments, when crops were defoliated before GS30 yield penalties were less than 0.7 t/ha and relative yields (% of undefoliated crops) were greater than 85%; the average yield penalty across all experimental treatments was 0.36 t/ha. These yield penalties are like other studies where cereal crops are grazed or defoliated prior to stem elongation (Edwards et al., 2011; Harrison et al., 2011a; Frischke et al., 2015; Seymour et al., 2015).

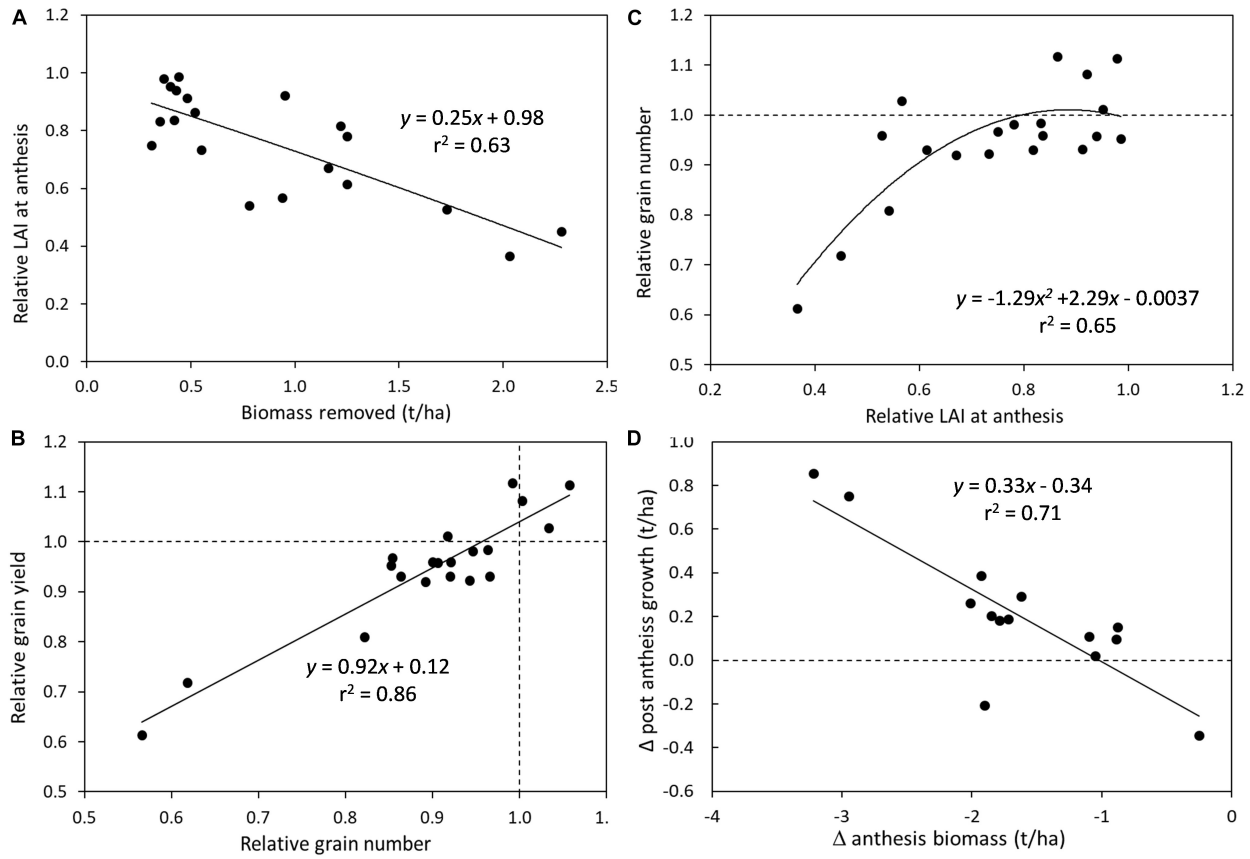

FIGURE 1 | Crop defoliation effects on determinants of grain yield across experiments in spring cereals under water- and nitrogen-unlimited growing conditions: **(A)** Crop biomass removal effects on the relative leaf area index (LAI) at anthesis (defoliated/undefoliated); **(B)** Relationship between relative grain number and relative grain yield (defoliated/undefoliated); **(C)** Relative LAI at anthesis impacts on relative grain number (defoliated/undefoliated); and **(D)** change in anthesis biomass impacts on the change in post-anthesis growth.

Larger yield penalties were observed in Experiment 1 where severe defoliation occurred after GS30, as has been reported by others (Harrison et al., 2011a). Defoliation reduced biomass at anthesis by 1-2 t DM/ha (20% reduction on average) in almost every genotype (excluding Hindmarsh barley in Experiment 4). Maturity biomass was reduced by a similar magnitude. These reductions were typically much larger than the removal of biomass by defoliation in each experiment, showing that there is an extended influence of slower plant growth after defoliation, associated with lower leaf area and accumulated radiation interception (Harrison et al., 2011c). Defoliated crops also often had a reduced LAI and Ri at anthesis; however, this was not universal across all experiments and treatments. While maximizing radiation interception at anthesis is regarded as critical to maximize grain number (Fischer, 1985), here we only observed a significant reduction in grain number (and hence grain yield) when Ri was reduced by more than 0.2 after later defoliation treatments. Most previous studies have observed reductions in kernel number after defoliation, associated with lower final ear number and/or reduced kernels per ear. Crops able to more efficiently fill this sink can compensate to maintain grain yield. In contrast, defoliation resulted in a reduced kernel mass in 3 of the 4 experiments reported here (all irrigated), while grain number was unaffected. In other studies, increases in crop harvest index have been reported after defoliation, which is typically influenced by undefoliated crops having a low conversion of biomass into grain, often associated with post-anthesis water stress. The lack of moisture stress in the present experiments may have enabled undefoliated crops to effectively fill their grain sink and defoliated crops were unable to 'catch-up' due to lower leaf area and biomass at the start of grain filling. This is further supported by calculations of the ratio of grain yield to post anthesis growth, where the undefoliated wheat crops were always higher (average of 1.37) than the defoliated wheat crops (average of 0.93), meaning that yield of the defoliated crops were more reliant on growth potential after anthesis. Together these data suggest that under plentiful water and nitrogen supply, the reduction in leaf area and biomass after defoliation is likely to have a detrimental effect on post-anthesis growth potential, while under stressful post-anthesis conditions, defoliated crops are more likely to be able to compensate. Experiments where water supply is manipulated to induce stress in combination with defoliation would help further our understanding of these interactions.

Potential for Dual-Purpose Use of Spring Cereals

This research shows that spring cereals can offer potential as dual-purpose graze and grain crops in growing environments with a short growing season (e.g., <5 months) where longer duration cultivars are unsuited (Bell et al., 2015b). In all experiments here the crops provided small but valuable amounts of high-quality forage (0.3–1.2 t DM/ha) before stem elongation, with limited risks of substantial yield reductions. These levels of biomass available were similar to those measured in lower rainfall environments in southern Australia (Frischke et al., 2015; Latta, 2015; Seymour et al., 2015). Based on an allowance of 1.5 kg of biomass per sheep per day this translates into 200–800 DSE grazing days/ha, which is consistent with the predictions of grazing from spring wheats using APSIM (Bell et al., 2015b). This translates into an additional AU$ 120–480/ha of income that can be obtained by grazing (assuming $2/kg LW and 0.3 kg LW/d when grazing wheat). This income from grazing is sufficient to offset yield reductions of 0.5 to 2.0 t grain/ha (assuming AU$240/t of wheat), which is more than the yield penalties for any of the defoliation treatments implemented here except when defoliated after GS30 (Experiment 1). Further, this lack of yield penalties was despite most of these experiments being managed under fully irrigated conditions, where post-anthesis moisture stress did not occur to reduce the harvest index of the undefoliated crops relative to the defoliated crops. In conditions with terminal drought where defoliation may help with slowing soil water use until after anthesis, yield reductions are likely to be smaller. Defoliation may actually increase grain yield, particularly in systems where crops are grown on stored soil moisture (e.g., subtropical regions) and delaying its use until post anthesis can greatly enhance efficiency of grain fill (Zhu et al., 2004). Despite the potential shown here, the defoliation in our experiments was implemented mechanically and other yield reducing factors (e.g., plant trampling, plant removal or soil surface compaction) may impact further on the crops ability to recover yield, although in cases where grazing and mechanical defoliation have been compared there has been found to be little difference (Pumphrey, 1970; Francia et al., 2006; Harrison et al., 2011a).

Longer season wheat cultivars sown earlier also provided more biomass by GS 30, however, there was little difference in biomass accumulation amongst cultivars where they were sown and defoliated at the same time. These results are consistent with model predictions of grazing potential from different spring wheat cultivars across environments, where slower spring cultivars (e.g., Gregory) can be sown slightly earlier and provide more grazing potential than later sown fast spring cultivars (e.g., Crusader, H45) (Bell et al., 2015b). Similar to other studies we also found that barley has a higher vegetative biomass production potential than wheat when sown at the same time (Francia et al., 2006; Latta, 2015; Sprague et al., 2018). Further, barley grain value is often lower than wheat, so less grazing is needed to offset any potential yield penalties. Hence, barley may provide a preferable dual-purpose option in shorter-growing season environments with limited capacity to sow earlier to allow for a longer grazing period.

CONCLUSION

Differences in physiological attributes of cereal cultivars were found to have little influence on the capacity of spring wheat to recover after defoliation. Hence, amongst genotypes with similar fast phenological development that are bred and grown primarily for grain yield attributes there seems to be little practical difference in their capacity to recover after defoliation. Other research has shown that longer-season winter cultivars developed for dual-purpose use are likely to provide greater grazing potential and have longer time to recover enough leaf area and biomass to achieve similar grain yields and hence cultivar selection may be more important (Carver et al., 2001; Thapa et al., 2010). Our research demonstrates that even in fast developing spring cultivars in warm growing environments, opportunistic removal of small amounts of biomass prior to stem elongation (GS31) can be achieved without significant reductions in grain yield. Further research should focus more on grazing management or defoliation timing and intensity before this critical point, to explore how these interact with crop recovery, rather than testing a range of cultivars under inconsistent management. Providing more rigorous guidelines and tools for farmers to make decisions about when to stop grazing or how much biomass to retain during grazing will minimize the risk of yield penalties from grazing and enhance the dual-purpose use of crops across a range of environments. In particular, understanding the residual biomass and time required to recover enough biomass and/or leaf area prior to anthesis to mitigate potential losses in grain number which is well known to be the main effect of defoliation (Royo and Romagosa, 1996; Edwards et al., 2011; Harrison et al., 2011b; Tian et al., 2012). This research clearly shows that in addition to the slower-developing winter-type genotypes widely used for grazing, the faster-developing spring cultivars can also be safely grazed. However, more effort is needed to understand if more diverse phenology types (e.g., winter vs. spring types) require different grazing recommendations.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

LB coordinated and implemented the experiments, wrote the manuscript, and conducted the data analysis. JK inputs into experimental design, edited the manuscript, and led the project. LT implemented one of the experiments and conducted the

data analysis. SM implemented one of the experiments and conducted the data analysis. JL contributed to implementing three of experiments.

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A Decision Support System to Guide Grower Selection of Optimal Seeding Rates of Wheat Cultivars in Diverse Environments

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Seeding rate in hard red spring wheat (HRSW; *Triticum aestivum* L.) production impacts input cost and grain yield. Predicting the optimal seeding rate (OSR) for HRSW cultivars can eliminate the need for costly seeding rate research and growers using OSRs can maximize yield and seeding efficiency. Data were compiled from seeding rate studies conducted in 32 environments in the Northern Plains United States to determine the OSR of HRSW cultivars grown in diverse environments. Twelve cultivars with diverse genetic and phenotypic characteristics were evaluated at five seeding rates in 2013–2015, and nine cultivars were evaluated in 2017–2018. OSR varied among cultivar within environments. Cultivar *x* environment interactions were explored with the objective of developing a decision support system (DSS) to aid growers in determining the OSR for the cultivar they select, and for the environment in which it is sown. A 10-fold repeated cross-validation of the seeding rate data was used to fit 10 decision tree models and the most robust model was selected based on minimizing the value for model variance. The final decision tree model for predicting OSR of HRSW cultivars in diverse environments was considered the most reliable as bias was minimized by pruning methods, and model variance was acceptable for OSR predictions (RMSE = 1.24). Findings from this model were used to develop the grower DSS for determining OSR dependent on cultivar straw strength (as a measure of lodging resistance), tillering capacity, and yield of the environment. Recommendations for OSR ranged from 3.1 to 4.5 million seeds ha^{-1}. Growers can benefit from using this DSS by sowing at OSR relative to their average yields; especially when seeding new HRSW cultivars.

Keywords: seeding rate, decision support system, modeling, straw strength, tillering capacity, maximum yield, decision tree

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INTRODUCTION

Genetic improvement through continued breeding efforts leads to the development of new hard red spring wheat (HRSW) cultivars that typically provide a yield advantage over cultivars released in prior years (Austin et al., 1980). Adaptations in plant growth habit, phenotypic traits, or physiological processes related to stress, are a few examples of ways that newer cultivars may

provide increased yield potential over older cultivars (Austin et al., 1989; Christopher et al., 2008; Reynolds et al., 2012). Growers have shown preference for newer cultivars, primarily driven by the opportunity for increased grain yield potential and protein content (Dahl et al., 2004). This prompts public and private seed organizations to continuously release new HRSW cultivars, resulting in the subsequent "retirement" of older cultivars. When these new cultivars are first released, they are not accompanied by a seeding rate recommendation. Growers rely on accurate recommendations for optimal seeding rates (OSR) to avoid economic losses due to uncaptured yield or excess seed waste. With the continual release of new cultivars (and subsequent discontinuation of older cultivars), growers may benefit from knowing OSR that are specific to cultivar and environment type, as this will aid growers in maximizing seeding efficiency and improve wheat yield potential.

University extension specialists commonly provide seeding rate recommendations for new cultivars based on prior seeding rate studies of cultivars released in the preceding years. After these new cultivars are subsequently tested in multi-year seeding rate studies, the actual OSR can greatly differ from the original extension recommendation. These differences can reveal 2 + years of reduced yields and economic losses due to genotype x management (GxM) interactions (Mehring et al., 2020). Although this reinforces the importance of proper seeding rate selection, with the continued release of new cultivars (and discontinuation of older cultivars), determining OSR for each cultivar is expensive, time-consuming, and repetitive research. Furthermore, the potential for genotype x environment x management (GxExM) interactions is apparent as environment-specific factors (e.g., yield potential, annual precipitation, and seasonal temperature) impact cultivar yield, and can have an interactive effect on seeding rate (Fischer, 1985; Geleta et al., 2002; Lloveras et al., 2004). Briggs and Ayten-Fisu (1979) noted the importance of including diverse environments in seeding rate studies of new cultivars; especially as some environment and cultivar combinations favor lower seeding rates. Identifying factors that may aid in predicting OSR for new varieties can eliminate the need for costly experimentation, and help growers maximize productivity and economic return. This demonstrates the importance of exploring GxExM interactions by evaluating cultivar yield and agronomic response at different seeding rates, and in diverse growing conditions, to ensure robustness in the OSR recommendation for a cultivar.

Decision support systems (DSS) have been developed to address agricultural production problems related to soil, nutrient, and precipitation, with the objective to reduce economic losses for growers and promote sustainability by minimizing environmental impact (Bonfil et al., 2004; Wang et al., 2010). These type of systems can provide environment-specific management recommendations based on location and field-specific information provided as inputs in a computer-based algorithmic model. For example, Small et al. (2015) developed a DSS to aid growers in managing late blight disease in potatoes (*Solanum tuberosum* L.). Weather data, crop information, and grower management practices were all variables incorporated into this system that would alert growers when conditions were favorable for late blight, so growers could ensure timely management for disease prevention. Most DSS developed to date have focused on nutrient or disease management. Other DSS have been developed that are specific to crop management, but they are commonly modeled in high productivity regions (i.e., southern United States), and thereby likely to be highly-sensitive to even slight changes in input variables.

Developing a predictive model for determining OSR for new cultivars could eliminate the time lag, expense, and repetition of the current method with field trials. This type of model could be coupled with environment-specific data and incorporated into a DSS to allow for the varying effects of environmental interactions to be accounted for when determining an OSR for a new cultivar.

Regression functions (linear and non-linear) are commonly used to model agronomic responses in seeding rate studies (Geleta et al., 2002; Lemerle et al., 2004). Regression equations from these models are useful when considering yield tradeoffs relative to seeding rate changes and can also be used to determine an estimate for OSR (Wiersma, 2002). However, when these models are fit to only one set of data, predictions produced by the model can be greatly biased and parameters have large standard error (Jones and Carberry, 1994). Various methods of splitting of datasets can be used to minimize these errors when conducting statistical analyses (Crowley, 1992). A prior HRSW seeding rate study conducted in ND and MN produced regression models predictive for grain yield by dividing the original dataset into two subsets (Mehring et al., 2020). This method represents the validation set approach.

When using the validation set approach, only a portion of the dataset (training set) is used to fit a predictive model. The other portion of the dataset (validation set) is then used to test the fit of the training model. Results for this test include the root mean squared error (RMSE) value, which provides an estimate for model accuracy as it represents the test error associated with differences in predicted and observed values. Akin to using several regression functions to identify a regression model best-fit for data, comparisons among models produced by various statistical learning methods can be readily accomplished by evaluating RMSE values (James et al., 2014). This process of evaluating the accuracy (fit) of these predictive models is called model assessment. Model assessment is critical for identifying and selecting the machine learning method that will best represent the data, while minimizing bias and error.

The validation approach is an efficient way to develop and test a predictive model. However, decreasing the number of observations used to train the model will inherently decrease the power of the test, increasing the likelihood of committing a Type-II error (fail to reject the null hypothesis, when the null hypothesis is false). As it is unlikely that training set data will be exactly representative of the validation set data, validation-trained models are likely to have higher RMSE values compared to models fit to only one dataset. To address these issues, cross-validation approaches are used in place of the traditional validation approach. Cross-validation is a resampling method that is used to perform multiple "model-training" iterations prior to producing a final model that is based on the average fit of these iterations. Wu et al. (2012) demonstrated the benefits

of cross-validation in regression-based modeling as they noted reduced bias in predicted values and a lower RMSE value compared to one-time regression analysis. An improvement on this method can be made by dividing the original dataset, and performing multiple cross-validation iterations on each subset, then averaging these results to determine a final model. This k-fold cross-validation method is a considerable improvement on the validation approach, as it can provide for a stable, reliable predictive model. The application of the k-fold cross-validation method has been demonstrated previously in various ecological and agricultural studies (Wiens et al., 2008; Yost et al., 2018).

Numerous algorithms have been developed to guide classification of data to produce decision trees that are user friendly as they do not require extensive knowledge to interpret. In experiments with multiple levels for each independent variable, the classification and regression trees (CART) algorithm can be used to readily produce decision trees. The use of this approach was demonstrated by Waheed et al. (2006), as they applied the CART decision tree algorithm to classify experimental plots based on irrigation use, weed management, and fertilization.

The objective of this research was to develop a DSS to improve grower selection of OSR for newer HRSW cultivars sown in the varying growing environments throughout North Dakota and Minnesota. This DSS will benefit HRSW growers by providing them with a tool to promote optimal seeding efficiency and maximum yield for sustainable production.

MATERIALS AND METHODS

Site and Experiment Description

Data from seeding rate trials conducted in North Dakota (ND) and Minnesota (MN) in the northern United States from 2013–2015 and 2017–2018 (32 total environments) were compiled for this research. Four locations were from 2013–2015 experiments at Prosper, ND and Crookston, Hallock, and Perley, MN. Two locations were from 2014 and 2015 experiments at Kimball, and Lamberton, MN. Experiment locations in 2017 and 2018 included Dickinson (2018 only), Hettinger, Minot, and Prosper, in ND, and Crookston, and Lamberton, in MN. Location and site descriptions for combined dataset are detailed in **Table 1**.

The OSR was determined for each cultivar x environment combination based on regression equation output from SAS 9.4 (PROC REG). The model considered best fit for data (linear or quadratic) was determined by maximizing R^2 and minimizing RMSE values. For linear fits, OSR was the seeding rate treatment at which maximum yield was observed. For quadratic fits, OSR was determined by evaluating the coefficients of the equation. Quadratic equations with a negative linear coefficient (second term) were assigned the lowest seeding rate treatment as the OSR. For all other quadratic models, the OSR was calculated by solving the first derivative of the quadratic equation.

Data Structure

Environments and cultivars were characterized prior to modeling. Environments were characterized based on latitude and longitude (decimal degrees), planting date (d of the year), and average HRSW yield (Mg ha^{-1}) observed in environment for the respective year (**Table 2**). These factors were selected as they can be readily determined by growers (or estimated based on field records from prior years) to be used as inputs in a DSS. The use of continuous variables to represent environments was used to minimize bias when grouping similar data across environments, and reduce model overfitting, that could increase error in OSR prediction. This also ensured models were robust, and thereby relevant to a greater number of growers.

Specific phenotypic and genetic traits were used to characterize the HRSW cultivars evaluated in this study (**Table 3**). Twelve cultivars were evaluated in 2013–2015 (Albany, Briggs, Faller, Kelby, Knudson, Kuntz, Marshall, Oklee, Rollag, Sabin, Samson, and Vantage) and nine cultivars in 2017–2018 (LCS Anchor, Lang-MN, Linkert, Prevail, Shelly, Surpass, SY Valda, ND VitPro, and TCG Wildfire). Data specific to each cultivar included gene expression for *Ppd-D* (photoperiod response), *Rht-B* and *Rht-D* (semi-dwarfing genes), and phenotypic characteristics for plant height, tillering capacity, straw strength (as a measure of lodging resistance), and heading date. Genotyping of the cultivars was done by the Wheat Genotyping Center at the USDA-ARS Cereal Crops Research utilizing polymerase chain reaction (PCR) methods. Agronomic measures compiled from published HRSW variety trial data from ND (NDSU, 2014–2018) and MN (Univ. of MN, 2008–2018) were used to characterize cultivars for phenotypic traits. A Z-score analysis approach [similar to that demonstrated by Laundre and Reynolds (1993); Ellsworth et al. (1998), and Rahman et al. (2009)] was utilized to determine cultivar tillering capacity (Stanley, 2019). Tillering capacity was based on Z-score standardized values from tillering evaluations of HRSW cultivars at spaced plantings by Stanley (2019); where cultivar tillering capacity rating is: High ($Z > 0.67$), Moderate ($0.67 \leq Z \geq -0.67$), or Low ($Z < -0.67$).

Statistical Analysis and Model Development

Analysis and modeling were completed in R 3.5.3 statistical software (R Development Core Team, 2019) using the *caret* package (Kuhn et al., 2016). Variable independence was verified by Pearson's correlation test prior to modeling. Highly correlated variables ($r \geq |0.8|$) were excluded to minimize multicollinearity and overfitting of models. Various machine learning approaches were considered for use in fitting a robust model that would support a grower DSS, including ridge regression, elastic net, least absolute shrinkage and selection operator (LASSO) regression, stepwise regression, decision tree, and random forest. These techniques were considered as they have been demonstrated in numerous agronomic and production-focused studies (Williams et al., 1979; Piaskowski et al., 2016; Sharif et al., 2016; Qin et al., 2018; Ransom et al., 2019). The decision tree machine learning technique was considered the most appropriate for this study as the primary objective of this study was to develop a DSS for growers, and results from this technique were readily transferrable to a DSS. Additionally, based on

TABLE 1 | Location and soil characteristics† of environments in seeding rate study.

Location‡	Soil series	Taxonomy	Slope (%)
North Dakota			
Dickinson	Arnegard	Fine-loamy, mixed, superactive, frigid Pachic Haplustolls	0–2
Hettinger	Shambo	Fine-loamy, mixed, superactive, frigid Typic Haplustolls	0–2
Minot	Forman	Fine-loamy, mixed, superactive, frigid Calcic Argiudolls	3–6
	Aastad	Fine-loamy, mixed, superactive, frigid Pachic Argiudolls	3–6
Prosper	Kindred	Fine-silty, mixed, superactive, frigid Typic Endoaquolls	0–2
	Bearden	Fine-silty, mixed, superactive, frigid Aeric Calciaquolls	0–2
Minnesota			
Hallock	Northcote	Very-fine, smectitic, frigid Typic Epiaquerts	0–1
Perley	Fargo	Fine, smectitic, frigid Typic Epiaquerts	0–1
Crookston	Wheatville	Coarse-silty over clayey, mixed over smectitic, superactive, frigid Aeric Calciaquolls	0–2
Lamberton	Webster	Fine-loamy, mixed, superactive, mesic Typic Endoaquolls	0–2
	Normania	Fine-loamy, mixed, superactive, mesic Aquic Hapludolls	0–2
Kimball (2014)	Fairhaven	Fine-loamy over sandy or sandy-skeletal, mixed, superactive, mesic Typic Hapludolls	0–2
Kimball (2015)	Dakota	Fine-loamy over sandy or sandy-skeletal, mixed, superactive, mesic Typic Argiudolls	2–6
	Ridgeport	Coarse-loamy, mixed, superactive, mesic Typic Hapludolls	2–6

†*Soil data obtained from NRCS-USDA, 2018.* ‡*Ordered by longitude, west to east.*

prior knowledge of environment interactions with both seeding rate and HRSW cultivars (Stanley, 2019) and the diversity of wheat production environments throughout the Northern Plains region, a tree-based approach would minimize bias when determining groupings of environments in the dataset. Therefore, the methods and results of this study are focused on the decision tree algorithm utilized in *R*.

To ensure robustness in the final decision tree model, preliminary models were fit to data split into k random subsets, with k-1 subsets used as a training set, and the remaining subset withheld from the training step and used as the validation set; repeated for k iterations. Utilizing an approach similar to James et al. (2014), a k-fold repeated cross-validation was performed with two different settings for k ($k = 5$ and $k = 10$) to produce resampling measures for assessing models and determining tuning parameters for each model. The model with the lowest RMSE value was selected as the optimal model (Breiman et al., 1984).

Utilizing an approach demonstrated in other studies (Mohammadi et al., 2010; Hitziger and Ließ, 2014), Mallows' complexity parameter (Cp) statistic was used in *R* to guide variable selection at each split in the decision tree to prevent overfitting of a model (Sreenivasulu and Rayalu, 2018). The variable producing the lowest Cp value at a split was selected as the primary variable at that branching point. Variable importance measures were selected for inclusion in *R* output, with variables ranked according to level of impact on OSR prediction based on the absolute value of the t-statistic for each model parameter (Strobl et al., 2007; Ruβ and Brenning, 2010).

RESULTS AND DISCUSSION

Cultivar and environment variables were considered independent, as values for Pearson's correlation coefficient were all acceptable ($r \leq |0.8|$). Initial models were prone to overfitting to specific latitude and longitude, so these variables were excluded from analyses. This coincides with the objective of this study, to develop a predictive model that is relevant to a broad audience of growers. Additionally, models overfit to individual locations or environments are not robust, and likely to be poor predictors of OSR for the same location in future years.

The 10-fold repeated cross-validation provided a training dataset that was most representative of the whole dataset, as the decision tree models fit by the 10-fold repeated cross-validation was more accurate at predicting OSR than models fit by the 5-fold (average RMSE of 1.250 and 1.264, respectively). This is because the additional subsets in the 10-fold provided for a more robust model, as the ratio of data comprising the training and validation sets were 316:35 samples for the 10-fold, and 281:70 samples for the 5-fold. With greater representation of cultivar and environment data in each 10-fold train set, and fewer samples in each validation set, the final decision tree model was fit after "viewing" the dataset from multiple angles.

For the decision tree algorithm, the 10-fold repeated cross-validation provided a selection of 10 decision tree models. The model selected for the final decision tree had a RMSE of 1.2386 (**Table 4**). As RMSE values are reported in the same units as OSR (million seeds ha^{-1}), and OSR observations were recorded to three decimals in the seeding rate dataset, one may postulate that any of the models from iterations 6, 8, or 9 could have been selected for the final decision tree. To avoid bias in this decision, the final model for the decision tree was automatically selected in *R*, by including a data step for making the selection based on the iteration with the lowest RMSE value. Mallows' Cp value used to guide variable selection (to prevent overfitting of the decision tree model) at each potential branching point was 0.0151 (**Table 4**). Branching ceased when all variables at a potential branch point produced a Cp value > 0.0151. The OSR at

TABLE 2 | Location and year details for 32 environments in North Dakota and Minnesota.

Location† Year	Latitude	Longitude	Previous crop	Planting date	Harvest date	Yield (Mg ha^{-1})
Dickinson, ND	46.981	−102.824				
2018			HRSW‡	2-May	13-Aug	3.82
Hettinger, ND	46.012	−102.647				
2017			Soybean	26-Apr	3-Aug	1.94
2018			Soybean	27-Apr	16-Aug	3.09
Minot, ND	48.180	−101.304				
2017			Soybean	21-Apr	19-Aug	1.81
2018			Soybean	3-May	8-Aug	4.31
Prosper, ND	47.003	−97.116				
2013			Soybean	16-May	22-Aug	4.69
2014			Soybean	27-May	3-Sep	4.43
2015			Soybean	9-Apr	21-Aug	4.67
2015			Soybean	22-May	25-Aug	3.62
2017			HRSW	22-Apr	21-Aug	4.51
2018			HRSW	30-Apr	31-Jul	4.22
Hallock, MN	48.802	−96.982				
2013			Soybean	16-May	3-Sep	7.27
2014			Soybean	23-May	6-Sep	5.45
2015			Soybean	16-Apr	13-Aug	5.62
Perley, MN	47.151	−96.752				
2013			Soybean	8-May	16-Aug	5.80
2014			Soybean	22-May	2-Sep	6.00
2015			Soybean	13-Apr	11-Aug	7.03
Crookston, MN	47.815	−96.616				
2013			Soybean	10-May	8-Aug	6.14
2013			Soybean	29-May	26-Aug	6.38
2014			Soybean	17-May	27-Aug	4.95
2014			Soybean	4-Jun	27-Aug	4.55
2015			Soybean	23-Apr	21-Aug	6.35
2015			Soybean	22-May	25-Aug	5.38
2017			Soybean	3-May	29-Aug	5.09
2018			Soybean	7-May	8-Aug	3.23
Lamberton, MN	44.241	−95.312				
2014			Soybean	21-Apr	20-Aug	5.14
2015			Soybean	4-Apr	12-Aug	5.62
2015			Soybean	27-Apr	12-Aug	4.55
2017			Soybean	17-Apr	23-Aug	3.69
2018			Soybean	7-May	10-Aug	2.52
Kimball, MN	45.417	−94.324				
2014			Soybean	26-Apr	14-Aug	5.54
2015			Soybean	8-Apr	31-Jul	5.97

†*Ordered by longitude, west to east.* ‡*HRSW, hard red spring wheat, Triticum aestivum, L.; Soybean, Glycine max (L.) Merr.*

each terminal node (leaf) is the mean OSR of the data comprising that node (**Figure 1**).

The global model from the decision tree algorithm was predictive of OSR with 67% accuracy (based on 1–mean absolute percent error). The R model output for the decision tree algorithm revealed variables impacting OSR (**Figure 1**). Nodes (branching points) included both phenotypic characteristics (straw strength, tillering capacity) and environment (yield of the environment). Based on variable importance measures (Pratt, 1987) reported in *R* (scaled relative to 1), the primary variable influencing OSR in the decision tree model was straw strength, with a relative variable importance of 25.7% (**Figure 1**). Other variables affecting OSR included yield of the environment (21.0%), tillering capacity (17.6%), and plant height (17.3%). *Rht-D* and *Rht-B* partially influenced OSR determined by the decision tree at 13.4% and 5.0%, respectively. According to the decision tree model, cultivar differences in expression for *Ppd-D* (gene for photoperiod response) did not influence OSR.

The root node in the decision tree represented GxM influences on yield, as OSR were differentiated based on cultivar straw

TABLE 3 | Genetic and phenotypic characteristics of HRSW cultivars.

Cultivar	Photoperiod response (*Ppd-D1*)	Semi-dwarf gene	Tillering capacity	Plant height†	Straw strength	Heading
			z-score	cm	1 to 9‡	DAP§
Albany	Insensitive	*Rht-B1*	1.33¶	77.0	5	63
LCS Anchor	Sensitive	*Rht-D1*	−0.23	71.9	4	58
Briggs	Insensitive	*Wild-type*	−1.03	83.3	7	57
Faller	Insensitive	*Rht-B1*	1.70	83.3	5	61
Kelby	Sensitive	*Rht-D1*	−1.10	72.6	4	58
Knudson	Sensitive	*Rht-B1*	0.63	78.0	5	60
Kuntz	Sensitive	*Rht-D1*	−0.37	75.4	4	60
Lang-MN	Sensitive	*Wild-type*	0.37	82.6	5	61
Linkert	Insensitive	*Rht-D1*	−0.83	72.9	2	59
Marshall	Insensitive	*Rht-D1*	0.73	78.2	4	63
Oklee	Sensitive	*Wild-type*	−0.80	80.5	6	58
Prevail	Sensitive	*Wild-type*	0.67	78.2	4	58
Rollag	Insensitive	*Rht-D1*	−0.73	75.9	3	59
Sabin	Sensitive	*Wild-type*	1.47	78.0	6	61
Samson	Sensitive	*Rht-B1*	−1.77	73.9	3	60
Shelly	Insensitive	*Rht-B1*	1.07	77.0	5	62
Surpass	Insensitive	*Wild-type*	−0.27	79.8	6	57
SY Valda	Insensitive	*Rht-D1*	−0.90	75.9	4	60
Vantage	Insensitive	*Wild-type*	−0.07	77.5	2	64
ND VitPro	Insensitive	*Rht-B1*	1.33	80.0	4	59
TCG Wildfire	Sensitive	*Rht-B1*	−1.20	86.6	4	60

†*Agronomic measures for phenotypic traits averaged from HRSW variety trial results (NDSU, 2014–2018; Univ. of MN, 2008–2018).* ‡*1–9; 1 is erect, 9 is lying flat.* §*DAP, days after planting.* ¶*Rating based on Z-score analysis approach described by Stanley (2019); High, Z ≥ 0.67; Moderate, 0.67 ≤ Z ≥ −0.67; Low, <0.67.*

strength rating (**Figure 1**). This follows previous reportings of differences in OSR for cultivars varying in straw characteristics that affected lodging potential (Faris and De Pauw, 1980). The model also indicated GxExM interactions, as differential effects on OSR were dependent on straw strength and average yield of the environment (**Figure 1**). This is similar to what Otteson et al. (2007) documented for GxE interactions, where different seeding rates were considered optimal for yield. For HRSW cultivars with a favorable straw strength rating ≤4 (where 1 is best, 9 is poor), tillering capacity was a determinant of OSR, but only in environments with average yield ≥3.2 Mg ha^{-1} (**Figure 1**). This revealed differences in management practices that are optimal for yield due to GxE interactions (demonstrated by cultivar phenotype expression as determined by growing conditions). This is explained by the understanding that in resource-limited environments (e.g., water or nutrient deficiencies), expression of plant phenotype(s) associated with yield can be severely restricted (Richards et al., 2010; Wasson et al., 2012). This is further demonstrated by findings of Hucl and Baker (1990) for HRSW cultivars grown in semi-arid environments in Canada (average yield of 3.55 Mg ha^{-1}). Though cultivars differed in tillering capacity, OSR for maximum yield was similar among cultivars in environments with average yield ≥3.2 Mg ha^{-1}. Variables absent from the final decision tree were plant height and all of the genetic traits (*Rht-B*, *Rht-D*, and *Ppd-D*). However, as previously indicated, all of these variables (except *Ppd-D*) were of importance to the decision tree model, thereby of influence on OSR (**Figure 2**).

TABLE 4 | Modeling summary from the 10 iterations of the decision tree algorithm in *R* analyzing the seeding rate dataset (*n* = 351).

Iteration	RMSE†	Cp
1	1.2650	0.0057
2	1.2629	0.0060
3	1.2633	0.0063
4	1.2537	0.0077
5	1.2487	0.0083
6	1.2395	0.0097
7	1.2386	0.0151
8	1.2390	0.0187
9	1.2411	0.0433
10	1.2669	0.0734

†*RMSE, root mean squared error; Cp, Mallows' complexity parameter.*

Based on the decision tree model, growers seeding in high yielding (average yield ≥ 5.5 Mg ha^{-1}), or moderate yielding (average yield 5.4 to 3.2 Mg ha^{-1}) environments, should seed at a rate of 4.5 million seeds ha^{-1}, unless growers are seeding a cultivar with known phenotypic characteristics requiring a lower seeding rate [i.e., poor straw strength (rating ≥ 5) or high tillering capacity] (**Figure 1**). Growers in low yielding environments (average yield < 3.2 Mg ha^{-1}) can maximize yield by seeding HRSW

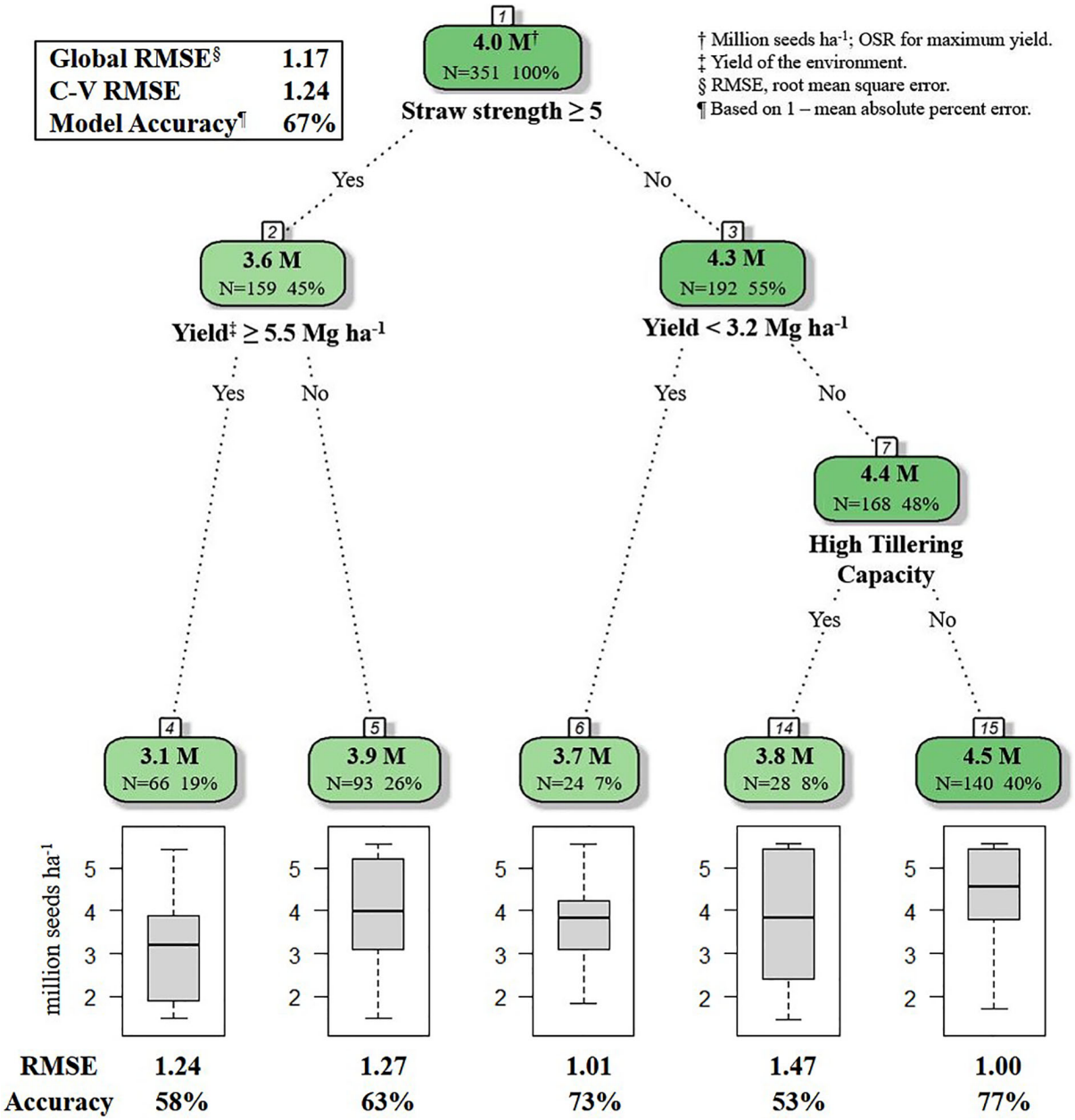

FIGURE 1 | *R* decision tree model for selecting optimal seeding rate for HRSW cultivars in differing environments in ND and MN (n = 351). Straw strength rating (1–9; 1 is erect, 9 is lying flat) for varieties in HRSW variety trial publications from North Dakota State University Extension, 2018 and University of Minnesota, 2018. Tillering capacity determined from Z-score standardized values from tillering evaluations of HRSW cultivars at spaced plantings by Stanley (2019); where cultivar tillering capacity rating is: High ($Z > 0.67$), Moderate ($0.67 \leq Z \geq -0.67$), or Low ($Z < -0.67$). Number of samples and percent of whole dataset are reported for root, nodes and leaves. Model Accuracy = 1–mean absolute percent error.

at a rate of 3.7 million seeds ha^{-1} (**Figure 1**). In general, OSR for these environment types differentiated by average yield are similar to recommendations made by Holliday (1960) and Donald (1963), where environments with greater resource availability are expected to have higher OSR. **Figure 3** was produced to provide growers with a DSS to readily determine OSR based on their selection for HRSW cultivar and the environment in which it is sown.

Though the level of variance was slightly higher for the decision tree model compared to linear regression models, the trade-off was for reduced bias in OSR predictions produced by the decision tree model. Similar to the other algorithms included in this study, the accuracy of the OSR produced by the decision tree model are greatly dependent on the data used to develop the model. This is why it was important to utilize the same resources when characterizing cultivars. Additionally, with the

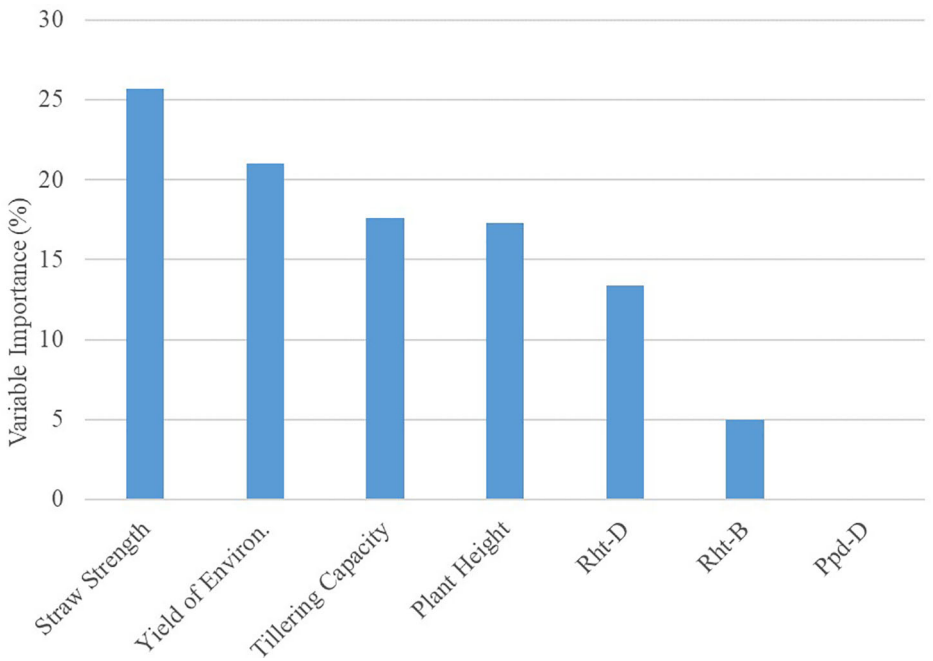

FIGURE 2 | Results for Variable Importance output from decision tree model analyzing seeding rate dataset (*n* = 351) in *R*. Importance is relative to 100%.

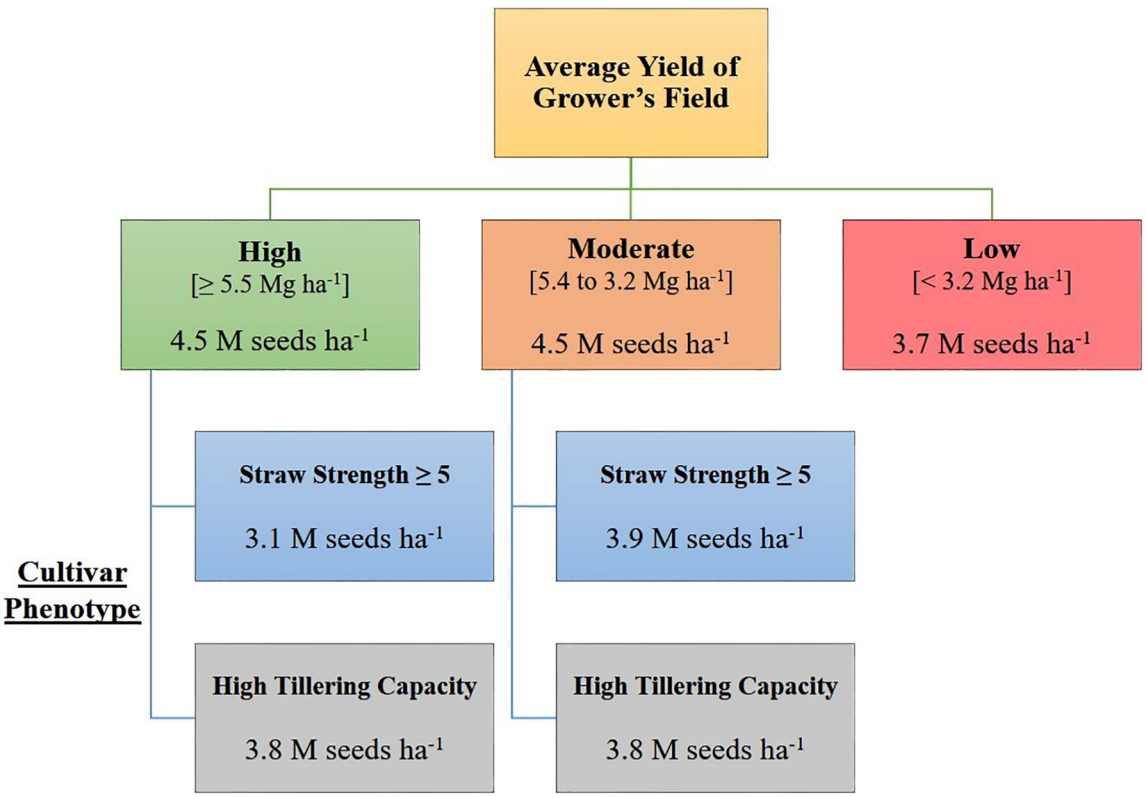

FIGURE 3 | Decision support system (DSS) for growers to determine optimal seeding rates for HRSW cultivars sown in diverse yielding environments in ND and MN. Based on decision tree model in *R* from analysis of seeding rate dataset (*n* = 351).

expectation for year-to-year variability in environmental factors (i.e., temperature, rainfall accumulation, and growing season length) influencing wheat growth in each environment, average grain yield was used to characterize environments (Slafer et al., 2014; Alvarez Prado et al., 2017). This is primarily because yield as a model parameter allows growers to readily determine OSR based on yields on their individual operations.

The recommendations outlined in the DSS improve the accuracy of predictions for OSR (Model RMSE = 1.17 million seeds ha^{-1}; Cross-validation RMSE = 1.24 million seeds ha^{-1}) in comparison to the current generalized recommendation of Wiersma and Ransom (2017) for 3.8 to 4.1 million seeds ha^{-1} (RMSE = 1.27 million seeds ha^{-1}). However, as RMSE values for the terminal nodes (leaves) in the decision tree model ranged from 1.0 to 1.5 million seeds ha^{-1}, there are apparent limitations in these findings due to the amount of error in predicted versus observed OSR values. Variability in the OSR recommendations at each terminal node could be reduced by allowing additional branching points, however, this would lead to overfitting of the decision tree model and reduce the scope of these findings. This indicates that growers should not simply default to the OSR indicated by the DSS, but rather utilize information from this tool to guide seeding rates of newer HRSW cultivars. Growers can adapt seeding rates as needed, to account for operational differences in agronomic and environmental factors influencing OSR relative to yield (**Figure 2**).

CONCLUSION

Environment and phenotypic characteristics for straw strength and tillering capacity, influence the seeding rate that is optimal for yield in HRSW production. For environments where average yield is $\geq$3.2 Mg ha^{-1}, the OSR is generally higher in comparison to OSR for lower yielding environments (4.5 versus 3.7 million seeds ha^{-1}), and when seeding cultivars with high tillering capacity. Adjustments to OSR can also be expected when seeding cultivars with poor straw strength (rating $\geq$ 5). Breeders and agronomists should utilize this information to focus efforts on characterizing advanced breeding lines and new cultivars for specific genetic and phenotypic traits influencing OSR. Growers can benefit from these findings by adapting seeding rates relative to their average yields; especially when seeding new HRSW cultivars.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

JS drafted the manuscript and was the doctoral student working on the project. GM, JW, and JR edited the draft and provided considerable contributions to the seeding rate dataset.

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Conflict of Interest: GM was employed by the company Bayer CropScience after completion of the 2013–2015 experiments.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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REVIEW
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Can Crop Models Identify Critical Gaps in Genetics, Environment, and Management Interactions?

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Increasing food demand under climate change constraints may challenge and strain agricultural systems. The use of crop models to assess genotypes performance across diverse target environments and management practices, i.e., the genetic × environment × management interaction (GEMI), can help understand suitability of genotype and agronomic practices, and possibly accelerate turnaround in plant breeding programs. However, the readiness of models to support these tasks can be debated. In this article, we point out modeling and data limitations and argue the need for evaluation and improvement of relevant process algorithms as well as model convergence. Under conditions suitable for plant growth, without meteorological extremes or soil limitation to root exploration, models can simulate resource capture, growth, and yield with relative ease. As stresses accumulate, the plant species- and genotype-specific attributes and their interactions with the soil and atmospheric environment generate a large range of responses, including conditions where resources become so limiting as to make yields very low. The space in between high and low yields is where most rainfed production occurs, and where the current model and user skill at representing GEMI varies. We also review studies comparing the performance of a large number of crop models and the lessons learned. The overall message is that improvement of models appears as a necessary condition for progress, and perhaps relevancy. Model ensembles help mitigate data input, model, and user-driven uncertainty for some but not all applications, sometimes at a very high cost. Successful model-based assessment of GEMI not only requires better crop models and knowledgeable users, but also a realistic representation of the environmental conditions of the landscape where crops are grown, which is not trivial given the 3D nature of water and nutrient transport. Models remain the best quantitative repository of our knowledge on crop functioning; they contain a narrative of plant, soil, and atmospheric functioning in computer language and train the mind to couple processes. But in our quest to tame GEMI, will they lead the way or just ride along history?

Keywords: improvement, crop models, uncertainty, GxExM, simulation performance

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INTRODUCTION

Increasing demand for higher quality and quantity of food under a changing climate with more frequent and severe heat, drought, and flood events poses a significant challenge for agriculture. It is also expected that agriculture meets this increasing demand while polluting less. The use of crop models to assess genotypes performance across diverse target environments and management practices, i.e., the genetic × environment × management interaction (GEMI), can help understanding genotype suitability, best agronomic management, and possibly provide a valuable tool for fast-turnaround in plant breeding programs. This paper is concerned with the role of crop models in assessing GEMI. Our perspective is from the viewpoint of crop model development and their adaptation for current and emerging applications. These applications can be divided in different types, for example those attending breeding program needs and pertaining to field and landscape management. Ideally, there should be no boundary between these applications, but research teams have had and still have different missions that make for diverging modeling strengths.

Process-based crop models integrate mathematical descriptions of the mechanisms leading to growth and yield of crops in response to environmental and management conditions. Through the twentieth century, the experimental and conceptual understanding of main processes allowing quantitative descriptions of crop growth advanced steadily. With the advent of personal computers in the early 1980s, these processes were integrated as concise algorithms in crop simulation models able to deal with some aspects of GEMI. These modeling systems keep evolving, integrating crop rotations, tillage, soil carbon, and other nutrients cycling. Advances in database management, spatial analysis tools, and cluster and cloud computing are creating new opportunities for model development and applications.

For decades, crop simulation models have been touted as tools with potential to evaluate crop genotype responses to changes in the environment and management (O'Toole and Stockle, 1991; Boote et al., 2001; Rötter et al., 2015). Boote et al. (2001) discussed several ways to use crop models to aid in plant breeding and remarked on the need for the improvement of models to describe cultivar-specific tolerances for drought, cold, heat, diseases, and pests. Rötter et al. (2015) reviewed the use of crop models in supporting ideotype breeding, providing several examples. Rincent et al. (2017) proposed a criterion to optimize multi-environment trials that combines crop simulation models and genomic selection models, which would result in more efficient evaluation of GEMI. Cooper et al. (2014) argued that future scaling of breeding programs would come from integration of germplasm knowledge, high-throughput genotyping and phenotyping, and modeling and prediction methods. Data acquisition, analysis, and prediction of performance of new genetic materials in multiple target environments will require tools such as remote and near-ground sensing, Internet of Things, cloud networking, algorithms and models, artificial intelligence, and other emerging technologies to assist rapid plant selection.

There has been increasing interest in combining crop and genetic simulation models. It has been proposed that plant breeding can be assisted by linking gene expression to traits that can be modeled, with the latter serving as input parameters of models to evaluate the performance of potential cultivars in multiple environments (e.g., Hammer et al., 2002; White and Hoogenboom, 2003). Cooper et al. (2014) reviewed the topic and present models as a component of the breeding strategy. Among several examples, Chapman et al. (2003) illustrated the use of models to evaluate genotype performance across multiple environments based on 15 genes controlling four adaptive traits and a quantitative genetic model simulating near isogenic lines for different combinations of traits. Messina et al. (2018) discussed the integration of crop models with whole genome prediction methodologies, which are applied in breeding to enable prediction of traits for new genotypes. These constitute the most advanced efforts in this area and provide a useful blueprint for modelers interested in integrating modeling with breeding. The integration of crop models with whole genome prediction is expected to open the potential for prediction of GEMI for breeding and product placement and for increasing the size of plant breeding programs without expanding expensive field testing (Technow et al., 2015; Messina et al., 2018). From a different perspective, Araus et al. (2018) reviewed strategies for improving and translating high-throughput phenotyping into genetic gain, including the use of crop models. To meet these expectations, the degree of detail and complexity of the processes represented in crop models and their performance require careful debate (Messina et al., 2009).

The success at making crop models useful for the assessment of GEMI depends on the effectiveness of modelers, breeders, and agronomists working together. But in any case, it is important that modelers assess model capabilities and input data quality realistically.

PERFORMANCE OF CROP MODELS IN RECENT EVALUATIONS

In recent years, under the umbrella of Agricultural Model Inter-comparison and Improvement Project (AgMIP), crop modelers have engaged in studies to evaluate model performance and provide avenues for the improvement of models (Ruane et al., 2017). Multi-model comparisons have been conducted for major staple crops, including wheat (Asseng et al., 2013), maize (Bassu et al., 2014), rice (Li et al., 2015), and potato (Fleisher et al., 2017). The standard approach has been to calibrate many models in selected world sites with increasing level of experimental observations made available to modelers. Even when complete calibration information is available to all modeling teams, important variation compared to observations and among models has been found. For example, Bassu et al. (2014) compared 23 maize models in four locations representing a wide range of maize production conditions (Lusignan, France; Ames, USA; Rio Verde, Brazil; and Morogoro, Tanzania), with individual models differing considerably in yield simulation at the four sites (2–4 Mg/ha for the 25 and 75 percentile with

low level of information for calibration, and around 1 Mg/ha with high level of information). Similarly, Asseng et al. (2013) compared 27 wheat models at four sites (the Netherlands, Argentina, Australia, and India), obtaining a large variation in simulated grain yields when limited information was provided for calibration. After full calibration, the variation among models was reduced, and many models (>50%) simulated yields with uncertainties within 14% of the mean coefficient of variation found in over 300 wheat field experiments, indicating that model calibration and the choice of models for use in particular applications are important factors. A comparison of 13 rice models with multi-year yields obtained experimentally at four locations (Los Baños, Philippines; Ludhiana, India; Nanjing, China; and Shizukuishi, Japan) resulted in yield predictions by individual models differing by as much as twofold when low levels of information were provided for calibration (Li et al., 2015). When more complete calibration information was provided, the model variation was reduced, but no single model consistently provided reliable predictions of yield across sites and years.

Evaluations of model performance against experimental data [as by Basso et al. (2016) and Gaydon et al. (2017)] are steps in the right direction toward model improvement, as they may help uncover deficiencies. Based on the review of 215 papers including data from 43 countries, Basso et al. (2016) reported normalized RMSE of ~10, ~20, and ~10% for yield of maize, wheat, and rice, respectively, across all testing conditions. Better and worst performances were reported for individual cases, and for grain yield components and other variables. Gaydon et al. (2017) evaluation included 12 countries and diverse environments, crops, and management practices. They reported RMSE of 1,084 kg/ha for the combined rice data sets compared with the standard deviation (SD) among the observed data and replicates of 2,038 kg/ha. Similarly, RMSE and SD of 845 and 1,794 kg/ha for wheat and 1,004 and 2,408 kg/ha were reported. Gaydon et al. (2017) argued that the performance of a model is adequate if it can simulate the observed behavior within the bounds of experimental uncertainty. They also pointed out that good model performance requires overcoming significant challenges in the estimation of input parameters that may indicate deficiencies and the need for model improvement. The problem with these assessments is that they coalesce individual evaluations into broad-scope statistics that obscure many details or less than stellar performance. For example, Figure 2 in Gaydon et al. (2017) depicts a reasonable overall prediction trend including 326 pairs of simulated and observed wheat yields across diverse environments. However, the large departure from the 1:1 line of many pairs of points should give us pause if we consider the need for accurate assessment of the performance of genotypes in diverse environments.

The variation among model simulation results further increases when comparing projections in response to changing climate scenarios, including warming and elevated atmospheric CO_2 (Asseng et al., 2013; Bassu et al., 2014; Li et al., 2015). In these comparisons, the variation among crop model outputs increases as temperature and CO_2 move further from current conditions and represent a greater proportion of the uncertainty in climate change impact projections than variations among general circulation models (e.g., Asseng et al., 2013). These results indicate the need to improve crop models and can be interpreted as a warning call of their limitations for more demanding GEMI assessments. Understanding the underlying causes of such variations and identification of the best approaches to model individual processes, rather than just trusting the average, will speed up progress.

Multi-model comparisons have also demonstrated that the use of model ensembles based on the mean or median of all model outputs improves predictions. Bassu et al. (2014) reported close agreement between the mean of observed and the mean of simulated maize grain yields in the four locations used for evaluation, and this good agreement was obtained both with low and high levels of information available for calibration. The mean of an ensemble of rice models resulted in grain yield prediction uncertainty of about 5% of measurements across four locations, while no single model provided predictions with uncertainties of <10%. Asseng et al. (2013) and Fleisher et al. (2017) reported similar results.

Although for certain conditions, multi-model ensembles might be better than relying on individual model simulations for projecting future crop yields, Carter (2013) pointed out that finding the minimum number of required models is not simple, and as indicated by Wallach et al. (2018), multi-model ensembles are not a substitute to model improvement. Multi-model ensembles, which paraphrasing Quételet (Eknoyan, 2008) put their faith in "l'modèle moyen," might be comforting as a means of reducing uncertainty in some applications, but their use is challenging or impractical for the routine application of crop models to evaluate GEMI. Just considering the scientist-time invested in multi-model comparisons for relatively simple cases should make that point clear.

WHERE ARE MODEL IMPROVEMENTS REQUIRED?

We focus on the major components of crop development and growth within crop models: phenology, which determines which resources the crop will access and to which stresses it might be exposed; solar radiation interception, which is determined by the green canopy development and its architecture and by the progression of senescence; water and nitrogen capture and use, which is determined by soil and root properties; net photosynthesis and biomass gain, which is determined by plant properties and limitations imposed by the environment; and biomass partitioning, which determines allocation of carbon and other elements to aboveground, belowground, and harvestable portions of the plant. Estimating the potential biomass production in a location is relatively simple when based on climate forcing. Once a suitable growing season length is defined, the available radiation, temperature, and dryness of the atmosphere bound the potential production of biomass. Most of the difficulties in modeling biomass production and yield with accuracy arise from defining the actual patterns of radiation interception, the

effective soil volume explored by the roots, the interactions among stresses, and the switches or threshold-like responses that determine pollination failures or abortion. In what follows, we review the modeling components that determine potential growth and limitations based on resource capture, use efficiency as well as the definition of the sink size.

Phenology

Crop growth simulation requires prediction of the timing of significant growth stages. These predictions are mostly based on thermal time accumulation modulated by photoperiod and in some cases vernalization. Models represent phenology satisfactorily (e.g., Aslam et al., 2017; Gaydon et al., 2017) mostly when calibrations and use are local, but are far from accurate even for crops with a wealth of information like maize (Kumudini et al., 2014) or winter wheat and after systematic careful calibration (Ceglar et al., 2019).

The calibration procedure also matters. Wallach et al. (2019) evaluated the prediction skill of the phenology components of 27 wheat models with special attention to the role of calibration. The data were from two check varieties in multi-year trials at multiple locations across France. The authors concluded that, overall, the models provided good predictions, with the median of mean absolute error of 6.1 days. Calibration compensated to some extent for differences between modeling approaches, while different calibration approaches caused differences in prediction error between similar modeling approaches.

Success in predicting relatively coarse patterns of development but difficulties obtaining accurate predictions when outside the calibration domain should hardly be a surprise. Slafer and Rawson (1994) stated in a thorough review that the controls of phenology in wheat are complex and subject to a degree of GxE that makes modeling and forecasting challenging. Our understanding of the controls of phenology has increased considerably. For example, Legris et al. (2016) have shown that phytochrome B is not only related to photoperiod but also to temperature sensitivity. Baumont et al. (2019) relate leaf appearance rate with carbohydrate availability and claim that the photoperiod effect of leaf appearance rate could be a surrogate for carbohydrate availability. And one could think that as our knowledge of the gene network controlling phenology improves, models will improve as well; but will models accelerate the uncovering of these networks? Models can help identify ideal development patterns for a given location: e.g., flowering early enough to escape heat and water stress but late enough to escape a late frost (e.g., Hunt et al., 2019), but it can be more difficult to assess GEMI beyond these broad brushstrokes.

Canopy Development

Correct modeling of the canopy leaf area and architecture is essential for modeling solar radiation interception, and therefore crop growth and water use as well as soil shading (affecting soil water evaporation). The canopy architecture, the prevailing angle of the leaves within the canopy, modulates radiation interception and the distribution of radiation among the canopy elements. Defining the canopy greenness throughout the growth cycle is critical to compute transpiring (green area) and non-transpiring fractions of the canopy. Leaf development is largely a function of temperature and carbohydrates availability (Baumont et al., 2019), but leaf expansion is also controlled by water and nutrient stress.

Many models develop leaf area by simulating leaf appearance rate as a function of thermal time, and leaf expansion as a function of temperature and water and nitrogen status. In single stems of determinate crops such as wheat, leaf expansion ends near anthesis. Senescence of individual leaf segments may begin before anthesis and continues from anthesis to maturity. Thorough evaluations of canopy development simulations are scarce. Yoshida et al. (2007) evaluated model parameterization approaches to simulate leaf area development of nine rice genotypes grown under diverse environments. The different approaches resulted in relative root mean square deviation (normalized between 0 and 1) from 0.16 to 0.21 during calibration, and from 0.18 to 0.33 during evaluation with an independent data set. A comparison of 29 maize models resulted in large simulation departures from measurements of maximum leaf area index (LAI) in 8 years of measurements (Kimball et al., 2019). Cammarano et al. (2016) comparison of 16 wheat simulation models for four world locations shows large differences of simulated LAI between models and in comparisons with measurements (for example, maximum LAI twentieth and eightieth percentiles of 2-5 m^2 leaf m^{-2} ground in Australia).

The fraction of the assimilated carbon (usually treated as biomass) that is apportioned to leaves is calculated through different means, all of which are empiric and are based directly or indirectly on phenology. Villalobos et al. (1996) followed a matrix partitioning approach for sunflower, where the fraction apportioned to leaves decreases in three steps from emergence to beginning of flowering, when it becomes zero. Jones and Kiniry (1986) and Hammer et al. (2009) calculated this fraction (biomass basis) in maize and sorghum, respectively, using the number of fully extended internodes as the basis for partitioning biomass to leaves (at 10 internodes, the fraction is ≈0.5), but there is significant dispersion in the regression (Figure 5 in Hammer et al., 2009). This approach has some semblance to that of the functional-structural model of Drouet and Pagès (2003), and provides a continuous change in the partitioning coefficient compared with the phasic approach in sunflower. Stöckle et al. (2003) followed an allometric approach, tying the partitioning of biomass to leaves to the biomass accrual per unit area. Fortunately, the largest impact of deviations in leaf area simulation occur when the leaf area index is lower than 3 m^2 leaf m^{-2} ground, for beyond this threshold further increases in LAI cause proportionally smaller errors in radiation interception (unless the row structure is too sharp and "hedgerow" models are needed). Yet, connecting these parameters with the gene network controlling the processes defining leaf growth and development (Lastdrager et al., 2014) is still a challenge. Coarse phenology-based or allometry-based approaches are far from this level of detail. Understanding and modeling biomass allocation is likely one the areas that requires the most research and a better theoretical framework.

Large departures in canopy development can introduce uncertainties in other crop growth and resource capture processes and vice versa. While, the relatively simple models currently in use can provide a satisfactory stratum to test how changes in other processes affect the ultimate determination of yield, the network of genes that determine any process would at some point intersect the network of processes directing leaf development and expansion in greater detail. This is exemplified by the relationship between stem length and grain size (Miralles and Slafer, 1995); but how many of the less obvious linkages remain undetected? There is a risk in confusing a well-calibrated model with a model able to represent the level of detail in complex gene networks that are not even completely known, for example to model ABA-induced stomatal closure (Albert et al., 2017).

Biomass Production

Mechanistic models of photosynthesis simulate gross photosynthesis and subtract growth and maintenance respiration to calculate net carbon assimilation. Carbon is partitioned into aerial (stems, leaves, and grains) and root portions, and expressed as biomass based on its carbon requirement and chemical composition, which are associated with growth and maintenance respiration (Penning de Vries et al., 1983). An advantage of these models is that photosynthesis and transpiration are linked *via* stomatal conductance, the latter responding to environmental conditions such as light, CO_2 concentration, and humidity (e.g., Kremer et al., 2008). These models provide excellent explanatory frameworks, but their usefulness may be challenged by the large number of parameters, the correlation among parameters, uncertainties associated with their values, the need to integrate photosynthesis and transpiration throughout the crop canopy, and the growth-photosynthesis feedback.

Simulation of biomass production as a function of daily crop intercepted solar radiation multiplied by a conversion factor to biomass (e = radiation-use efficiency, g MJ^{-1}) as defined by Monteith (1995) simplifies the prediction of crop biomass gain. This framework has been adopted by many modeling teams. The value of e can be determined in field experiments (Sinclair and Muchow, 1999; Stöckle and Kemanian, 2009) and while there is a general consensus on the maximum attainable e, for example for C_3 and C_4 cereals, there are studies often reporting e that can be 20% or more higher than somewhat accepted high values. Kukal and Irmak (2020) have reported maize e of 4.8 and 5.1 g/MJ of intercepted PAR, while the review by Stöckle and Kemanian (2009) reported a maximum e of 4 g/MJ (converting solar- to PAR-based e). Without unwarranted dogmatism, it is hard to operate when supposedly conservative scalars are assumed or accepted to vary to such extent.

The large differences in e for different locations and environments in which the soils would not suggest water stress as a limiting factor have been mainly associated to difference in the vapor pressure deficit of the air (D, kPa). Stöckle and Kiniry (1990) summarized e data for maize across diverse world locations, and found that e fluctuating from 2.9 to 4.4 g/MJ PAR was negatively correlated to D. This relationship was further supported by Kiniry et al. (1998), who pooled additional data for maize and sorghum, by Manrique et al. (1991) in potatoes, and by Kemanian et al. (2004) in wheat and barley. The main reason for such a response is that, as D increases and transpiration increases, stomata close (Monteith, 1995). It is difficult to separate diffuse radiation from D effects (Stöckle and Kemanian, 2009). Most of the sources of e variations are known (the same ones that affect photosynthesis), including environmental factors such as temperature, radiation and its distribution in the canopy, and air humidity, or by plant factors such as nutritional and water status, ontogeny, and source-sink regulation (e.g., Stöckle and Kemanian, 2009). However, the game of responses is seldom incorporated in crop models. There are conceptual similarities but important differences in a bottom up model that regulates stomatal conductance based on relative humidity (e.g., Collatz et al., 1991), lumped models that rely on D to define a maximum e (Williams, 1990), and models that use other controls over e (Villalobos et al., 1996).

Another approach to simulate biomass gain is based on the concept of transpiration-use efficiency (w), which is used in a limited number of models (e.g., Stöckle et al., 2003; Steduto et al., 2009). Good relationships between biomass gain (B) and transpiration (Tr) have often been reported, which improve by normalizing transpiration using climatic evaporative demand (e.g., de Wit, 1958) or D (e.g., Bierhuizen and Slatyer, 1965). Tanner (1981) and Tanner and Sinclair (1983) formalized this relationship deriving an expression accounting for the common stomatal pathway for carbon assimilation and water loss from crop canopies stating that $w = k/D$, where k is a crop/genotype parameter. This parameter was assumed constant for a given genotype, in large part because the ratio of internal (leaf) to external (air) CO_2 concentration was assumed to be constant. Therefore, $B = w \times Tr$. The value of k can be determined experimentally if Tr can be measured. However, the stomatal optimization hypothesis of Cowan and Farquhar (1977) states the marginal water use efficiency leans toward a constant; based on this assumption, it can be shown that w is proportional to the square root of D ($w = k/D^{\beta}$ with $\beta = 0.5$) and that the ratio of internal (leaf) to external (air) CO_2 concentration decreases as stomata close. Kemanian et al. (2005) showed that this relation seems to hold true for many species and estimated that $\beta = 0.59$ for barley and wheat; Kremer et al. (2008) estimated that $\beta = 0.44$ for maize. Although the apparent alignment of theory and data is pleasing, there is substantial dispersion in any k estimation and variation among genotypes is hard to quantify and requires a refined understanding of the environmental interactions (Condon et al., 1993).

A shortcoming of the e approach is the decoupling between biomass production, the canopy energy balance, and the crop water use. The consequences of this decoupling can be exacerbated by deviations in simulation of crop water use discussed below. This occurs because biomass gain calculations based on e depend on intercepted PAR radiation, but do not consider the canopy energy balance, the soil-plant-atmosphere continuum, and ensuing changes in stomatal conductance. The consequences of this decoupling are significant (e.g., Basso and Ritchie, 2018). In the model CropSyst (Stöckle et al., 2003),

this is resolved, at least for the growth estimation, by using the minimum of the growth estimated derived from radiation or transpiration.

Both *e* and *k* are, to some extent, negatively correlated. High *e* under low *D* would reflect a high stomatal conductance and high *k* may reflect lower stomatal conductance and therefore high *w*. These parameters, if used in combination, can be helpful to discern if aggressive water use (high *e* and high *Tr*) should be favored over a conservative use of water (high *k* and low *Tr*). Once again, these macro approaches can be robust enough (if well used) to simulate growth and can help define stress environments, and with expert use can suffice to explore the biological boundaries to growth. Beyond this relatively simple step, the task of evaluating the potential to genetically manipulating the expression of these traits belongs to more detailed photosynthesis models (e.g., Kannan et al., 2019; Wu et al., 2019). In our opinion, the expert user of a detailed simulation models must have a profound understanding of simplified approaches that retain core explanatory power and shed peripheral processes.

Crop Water Use

Comparative studies have uncovered a large variation in model simulation of crop water use (Cammarano et al., 2016; Kimball et al., 2019), which stems from the combination of several factors. For example, models use a variety of approaches to determine atmospheric evaporative demand, to be referred to as crop potential evapotranspiration (CPET). This accounts for the energy available to evaporate water, and the conductance for water vapor between the exchange surface and the atmosphere per unit of land area, driving crop transpiration (mostly through plant stomata), soil water evaporation, evaporation of water intercepted by crop canopy and residues, and snow sublimation. The most biophysically complete approach to calculate CPET is the Penman-Monteith evapotranspiration (P-M ET) equation (Allen et al., 1998), which has been shown to outperform several other approaches when compared with lysimetric observations (e.g., Allen, 1986; López-Urrea et al., 2006; Benli et al., 2010). The Penman-Monteith ET equation is based on the combination of the energy balance and vapor and heat transfer equations to estimate water fluxes of crop canopies modeled as a "big leaf". The P-M ET equation is not a perfect approach to model the complexity of water and heat fluxes from cropped surfaces, particularly the assignment of resistances to canopy and soil surface contributions before canopy closure. Limitations of the application of the P-M ET equation to real canopies have been addressed with engineering approaches using empirical adjustments, mostly based on lysimetric data (Allen et al., 1998).

Other methods to approximate CPET fluxes have been developed based on increasing simplifications of the P-M ET equation to accommodate the use of weather data with less variables than required. However, each simplification deviates from the physical transparency of the P-M ET approach and forces incorporating empirical coefficients whose values are not easy to assess without careful calibration and still produce CPET estimates that depart from PM-ET. Kimball et al. (2019) highlight this problem. These authors compared potential ET from 29 maize models, reporting huge differences among them (Figure 10 in Kimball et al., 2019), which obviously propagated to the simulation of actual evapotranspiration, crop transpiration, and beyond.

There are also many models to simulate crop water uptake (normally equated to *Tr*), including a wide range of complexity (e.g., van den Berg et al., 2002; Wang and Smith, 2004; Camargo and Kemanian, 2016). Evaluation of the performance of these models or sub-models decoupled from complete crop models often reveals important differences that can be obscured when comparing aggregated variables like yield. Camargo and Kemanian (2016) compared the water uptake methods implemented in six crop models, ranging from simple empirical to more mechanistic approaches, in scenarios with different evaporative demand, soil texture, and water distribution with depth. They found that each method responded differently to these scenarios, affecting the onset of water stress, the cumulative water uptake, the shape of the soil drying front, and the response to high transpiration demand. If root depth progression and water uptake were genotype-agnostic, then crop models could be calibrated and used for GEMI analysis of other traits without much concern for the roots. But we know that is not the case, and the interaction of the type of model used for modeling root colonization of the soil profile and algorithms to simulate water uptake are of critical importance in any analysis, and more so for GEMI assessment which demands a fine slicing of differences among genotypes.

Uncertainty in the calculation of potential *Tr* and realized crop water uptake is compounded by two-way feedbacks with canopy and root growth, affecting biomass growth and yield projections. Cammarano et al. (2016) quantified variations among 16 wheat models in the simulation of actual evapotranspiration, water use efficiency, transpiration efficiency, crop transpiration, soil water evaporation, and grain yield at increased temperature and elevated atmospheric CO_2 concentration. The uncertainties in the simulation of evapotranspiration and *Tr* were greater with high temperatures and in combination with elevated CO_2. They concluded that the simulation of crop water use should be improved and evaluated with field measurements before models can be used to project future crop water demand (Cammarano et al., 2016). The logical follow up question is what to do next. Is it really the case that models need to be improved to simulate water use? Perhaps soil input information needs to improve, and the consideration of plant-soil interactions needs to improve, but modeling approaches should converge to those with a defensible theoretical and empirical basis.

Crop Nitrogen Use

The N content in plants is typically modeled in two steps: (a) crop N demand and (b) soil/root N supply, with the minimum of the two reflecting crop N uptake (Stöckle et al., 1994, 2003). Above ground N demand is often calculated based on three standard N concentration curves evolving daily as a function of aboveground biomass (Greenwood et al., 1990; Stöckle and Debaeke, 1997): maximum (upper limit), critical (below which growth begin to be affected), and minimum (growth stops). The daily crop N concentration and biomass

growth reduction, if any, is defined by soil N supply. These standard concentration curves are determined from experiments including different levels of fertilization (Stöckle and Debaeke, 1997). A model by Jamieson and Semenov (2000) simulates N demand separately for structural N (low N concentration), green area N (high N concentration), and storage (luxury N consumption), not requiring the standard curves. In either case, the amount of N apportioned to roots must be calculated. The N supply is simulated based on the N mass, root density, and soil water content of all soil layers explored by roots. The supply of N is reduced as soil N mass and water content decrease from optimum values, eventually not meeting N demand and affecting leaf area expansion and radiation-use efficiency. Both demand and supply processes in crop models are empirical and potentially subject to large uncertainties.

In the case of wheat and other grain cereals, N accumulation in grains and projection of protein content are important. Most models are limited to the prediction of N concentration, which is converted to a protein content, although models that simulate the content of storage proteins are also available (Martre et al., 2006). A robust allometric relationship between grain N concentration, harvest index, and N concentration in aboveground biomass at harvest was shown by Kemanian et al. (2007a) for maize, sorghum, wheat, and barley, which indicates that the timing of N uptake and biomass accretion has lesser influence on the correlation between final C and N partitioning to grain.

Implementing different approaches to represent crop N use results in substantial diversity when outputs from different models are compared. A comparison of three spring wheat models in Canada showed that all models provided good predictions for average plant N when precipitation was near normal and recommended N rates were applied, but performance decreased when N was applied at lower rates or in the presence of mild precipitation deficit or excess early in the season (Sansoulet et al., 2014). A comprehensive study evaluated 11 crop models for spring barley in Jokioinen, Finland, under different N fertilization rates (Salo et al., 2016). The models differed widely in process description. Although detailed data were provided for calibration, the authors showed that model performance decreased for N-limited conditions and when environmental conditions deviated strongly from the calibration conditions.

Models provide opportunities to evaluate hypotheses of plant N dynamics (e.g., Sinclair and Amir, 1992; Jamieson and Semenov 2000), but the use of models for GEMI evaluation faces challenges. Multi-model comparisons indicate large variations in model responses, indicative that some models may have inadequate representation of processes or/and unsatisfactory selection of input parameters by users. The problem gets compounded by hydrologic and soil processes affecting the movement of nitrate in the soil, and other processes affecting the soil C and N dynamics responsible for N mineralization and immobilization as well as N transformations.

Yield

Grain yield is often modeled using yield components, which are affected by environmental factors. However, the ability of crop models to simulate grain number, grain weight, and translocation of stem reserves is often inadequate (e.g., Moreno-Sotomayor and Weiss, 2004; Dettori et al., 2011; Gaydon et al., 2017). Dettori et al. (2011) reported simulated grain yield with an average normalized root mean square error (nRMSE) of 27–20% compared with observed yields for three wheat cultivars and at two sites under Mediterranean conditions in Italy. Evaluation of a rice model simulations of grain yield based on 11 studies resulted in an average normalized RMSE of 23%, with two studies reporting a value of 3%, five in the range ~21–18%, and four in the range of 32–23% (Timsina and Humphreys, 2006). The same study reported eight studies for wheat, with normalized RMSE of simulated grain yields of 13%, and a range of 17–2%.

The prediction of grain yield is the result of numerous processes occurring during the growth cycle. Jamieson et al. (1998) concluded that for yield prediction the accurate simulation of phenological development and LAI is much more important than the components of the yield. Sinclair and Jamieson (2006) argued that the correlation between growth rate at a time before anthesis and grain numbers, and between the latter and grain yields led to models with unnecessary complexity. Under no N limitation, a mechanistic model of biomass accumulation and a harvest index for partitioning to grain accounted for most of the variability in wheat grain yield over a 10-year period (Amir and Sinclair, 1991). A similar argument underpins the Kemanian et al. (2007b) model to calculate the harvest index in determinate crops; the model has a logical foundation, a minimum number of parameters, but requires that phenology and growth be modeled accurately.

While it is tempting to argue that simple models are likely more robust than yield-component based models to predict yield, it is easy to see that these models can be of limited use when the interest is understanding the controls of the grain number and size and GEMI. Bustos et al. (2013) showed experimentally that high grain number can be combined with high grain weight in wheat, showing impressive yield gains in a high yielding environment. Interestingly, the high yields were associated with extremely high e compared with check wheat cultivars or any C_3 crop and suggests a strong sink control over photosynthesis. To our knowledge, most models simulate first the photosynthesis rate (or the lumped surrogates $e \times S_t$ or $w \times T$) or how much biomass will be available for the growth of each organ, and do not include a feedback from growth potential to photosynthesis, a feedback that in any case is challenging to model.

Another factor introducing uncertainty in grain yield prediction is the effect of drought and cold and heat stress on grain set and growth. We are specifically referencing to effects that are independent or in addition to the impact of these stresses on photosynthesis. Prasad et al. (2017) reviewed the effect of short episodes of heat stress on 20 field crops, showing reduction of grain set and harvest index with temperatures above crop-specific thresholds, ≈32°C in the case of wheat. The ability of crop models to simulate grain yield under conditions of heat stress appears constrained, which can be a significant limitation considering global warming scenarios.

Liu et al. (2016) compared four wheat models with 4 years of environment-controlled phytotron data with two cultivars under heat stress, concluding that all models needed improvements in simulating heat stress during anthesis. Schlenker and Roberts (2009) and Hoffman et al. (2020) analyses of large panel of county level yields reveal threshold-like responses to temperature for maize, sorghum, soybean, and cotton. Furthermore, maize and soybean seem to have broad plateaus in which temperature has a moderate effect on yield, while sorghum has a more sensitive response with almost no plateau that is more sensitive in the cold end but slightly more adapted in the hot end of the data domain (Hoffman et al., 2020). It is not clear if current models represent these nuances with fidelity.

Roots and Soils

The root-soil complex is likely one of the most understudied components and one that is represented with simplicity in simulation models. Much like foliage development, the root exploration of the soil volume depends on intrinsic properties of a given genotype that define the 3D structure of the root system, i.e., the progression of the rooting front and proliferation of roots in the explored volume, and the feedback response to soil properties that may limit or promote root growth. Roots need to intercept water or nutrients that can move through the medium or need to reach water or nutrients that are moving slowly through the soil. Lynch and collaborators (e.g., Lynch, 2011) have performed some of the most fundamental work on root architecture and its relationship with phosphorous (P) and N capture. This body of work shows that significant differences among genotypes within a species exist in root architecture and nutrient acquisition. Structural-functional models of root systems have been incorporated in models that, however, do not simulate full crop cycles (Schneider and Lynch, 2018), are not integrated in comprehensive crop models, and like any model carry the risk of conflating model assumptions with emergent properties. These models are far from representing the uneven exploration of soil layers by roots and the impact of compacted soil layers on actual water use patterns (Breslauer et al., 2020). New efforts at mechanistically modeling water uptake in soil layers with clusters of roots (uneven root distribution) are fortunately emerging in the literature (Graefe et al., 2019).

Most importantly, these models have little feedback from soil properties that may limit root growth. Ernst et al. (2016), working with wheat, and Stefani-Fae et al. (2020), working with soybean, have shown that crop yield responds strongly to soil physical properties that are best related to field measured soil hydraulic conductivity. Field measured saturated hydraulic conductivity can exceed that obtained from pedotransfer functions usually used in models by a factor of 10–20 (Stefani-Fae et al., 2020). To our knowledge, no model can yet represent this response mechanistically or derive these responses just by looking at a soil description. In the assessments of GEMI in conditions in which the yield variation is dominated by soil factors other than depth to bedrock, there are plenty of opportunities for uncertainties in root-soil processes to override genotypic variation as represented in crop models. These concerns are of lesser importance in irrigated and well-fertilized crops but become more important as soil limitations become more relevant. It is plausible that using remote sensing and machine learning algorithms (Azzari et al., 2017) to support earlier efforts at model inversion (Paz et al., 1998) can mitigate some of the soil-derived uncertainty, but clearly there is a long distance to travel to make models useful for GEMI assessments while at the same time assuaging concerns about uncertainty derived from soil variation.

THE LARGER CONTEXT FOR IMPROVING AND APPLYING MODELS FOR GEMI ASSESSMENTS

Crop models can potentially be useful for GEMI assessment, although uncertainty in output results will always exist depending on the specific model and growth conditions, and as reviewed above, with many possible interacting factors. Therefore, it is important for users (and developers) to carefully evaluate the context in which the models are applied as well as to be mindful of areas of model limitations. The context for improving and applying models includes the nature of the models themselves and appropriate knowledge of the environmental and management conditions under which crop model simulations are conducted.

The Nature of Crop Models and Their Use

Crop models are often not well balanced in the treatment of the large number of processes and interactions that are needed. This usually reflects the modeling team composition, which leans toward more emphasis on quality and details of the mathematical formulation of processes in their areas of expertise, while other components are (much) less developed. Cooperation between modeling teams would be highly desirable for progress toward better models, including sharing of code and concepts and continued testing of models. Studying what has been done before embarking in large modeling undertakings seems to be of critical importance to accelerate innovation. Increased cooperation has been fostered by communities of crop modelers such as AgMIP (Ruane et al., 2017), MACSUR (Ma et al., 2014), and others. Activities in these communities have mostly focused on model comparison, with the shortcoming that emphasis has been placed on the performance of complete crop ("branded") models, and much less on processes. The large diversity of model outputs in these comparisons (reviewed above) and underlying causes are difficult to identify, with multiple interactions and error propagation among different components defying quantification. The lack of experiments purposely designed to produce data for process comparisons is a barrier. Nevertheless, even comparison of individual processes using prescribed weather/soil scenarios and state variables affecting the target process would be extremely useful. This would require the selection of different approaches used in

crop models, and coding them into a common platform for comparison (Jara and Stöckle, 1999; Camargo and Kemanian, 2016).

Another factor affecting the performance of crop models, often ignored, is the proficiency of model users. Choosing model parameters requires an understanding of the crops and environments involved, and knowledge of the model structure, processes, mathematical formulations, and sensitivity of model responses to changes in parameter values. Confalonieri et al. (2016) argued that one should not speak of evaluation of a model but rather of a model-user combination, where a major role of the user is in determining the method of calibration and the selection of crop input parameter values. This was explicitly shown in model simulations of crop evapotranspiration (Kimball et al., 2019), with very different results obtained by the same models operated by different users.

One barrier for judicious evaluation of potential model limitations is that model descriptions are often incomplete or lacking sufficient detail. Furthermore, model developers are continuously adding new capabilities and expanding their portfolio of projects in response to ever-growing demand for new applications from multiple users. However, if attention to the basic issues discussed in this article do not receive sufficient priority, crop models run the risk of losing credibility and relevancy.

The Model Application Landscape

Successful model-based assessment of GEMI not only require the use of the better crop models, but an adequate representation of the environmental conditions on the landscape where crops are grown, and good knowledge of the management practices used. For regional or basin-scale assessments, the information on management practices is normally insufficient, starting with such simple facts as the temporal and spatial variation of planting dates. Similarly, weather and soil data are often inadequate, incomplete, or available at too large scales. Under these conditions, thorough crop model calibration is not always possible, and in fact the contrary is normally true. How do we calibrate models with imperfect information? Part of the answer is in the use of robust crop models whose state variables do not jump outside reasonable limits of variation under extreme or new conditions, as well as greater emphasis on crop input parameters that are observable.

Landscape topography, local and basin surface and sub-surface hydrology, presence of shallow water tables, field flooding, soils with physical or chemical challenges for roots colonization or crop growth, variations of carbon and nitrogen cycling, the effect of crop rotations, cover crops and residue management, and other factors are part of the landscape context where models must be applied for GEMI assessment. These are not trivial barriers that could be partially mitigated by hydrologic models, linking crop models with spatial models of water and nutrient transport, carbon and nitrogen cycling models, remote sensing data, and other tools. But these also have their own uncertainties and require expertise outside the interest of crop model users. An example, which is perhaps extreme, is the yield variation in the loess deposits of the Palouse region in Washington, Oregon and Idaho (Huggins et al., 2014). Because of the interaction of topography and landscapes, the soils represent almost contrasting climates. All these variations reflect not only in yield but also in nutrient dynamics and grain N concentration of the wheat and barley typically grown in this region. In this physical context, 1D models can be useful to represent trends but are relatively hopeless at capturing granular, topographically driven variation.

There is also an agronomic and biological context to consider. Not many models can simulate crop rotations, cover crops, and residue management. Crop models do not consider the large number of organisms and the continuously changing pressure from weeds, pests, and diseases; and if they do, properly capturing the biological variation and known responses to the environment of these bio-stressors is an additional challenge. Nonetheless, recent work with large data panels and machine learning (Schlenker and Roberts, 2009; Hoffman et al., 2020) indicate that a substantial fraction of the yield variation can be captured with relatively simple models. This indicates that some putatively complex interactions are not always relevant or that aggregation at certain scales (e.g., counties) dampens the expression of these interactions in the data.

FINAL REMARKS

This article represents a view from a crop modeler perspective looking into the progress needed to further model applications addressing GEMI. Depending on the type of application, some but not all models may perform reasonably well under well-constrained conditions. Both model and user performance often deteriorate when the simulated conditions depart from the calibration domain or typical testing scenarios. This challenge has been addressed for some applications using model ensembles. While model ensembles provide cover against model and sometimes input uncertainty, further progress needs to break free from ensembles to assess models' weaknesses and knowledge gaps critically.

Modeling teams may focus on the following: (1) There must be convergence on how to model biophysical processes for which the basic understanding has been in place for decades. (2) While model development always demands sagacity to integrate principles and empirical knowledge, the space requiring the most work is likely the root-soil interaction to determine root exploration and water uptake as well as nutrient acquisition. Sometimes maximum rooting depth or root distributions are imposed without empirical support or calibrated with substantial supervision. Yet being able to predict rather than impose how roots explore the soil (or how much water is accessible) is of critical importance for practical applications. (3) Sewing trait expression and modeling to gene transcriptional and posttranscriptional controls will require a tight bottom-up and top-down coordination of models, and that requires teams with balanced expertise. This is difficult to accomplish. (4) Most crop models are 1-D, while many landscape processes depend on the interaction of topography and soil properties. This is one of the areas with the potential to truly exploit

GEMI for a more refined management of the landscape. (5) Models cannot become even more difficult to use; setup, calibration, and application should be seamlessly integrated, otherwise the user may have more influence on the output than the model. (6) Data assimilation strategies that allow ingesting data at runtime and updating state variables while conserving mass and energy will be critical to integrate models to a flexible data-model. In this context, it is conceivable that the integration of sensors, artificial intelligence, and other technologies will be helpful to reduce uncertainty, but improvement remains a sine-qua-non condition for crop models success as research and applied tools.

The question "Can crop models identify critical gaps in genetics, environment, and management interactions?" has many angles, requiring careful work by multidisciplinary teams to overcome the limitations discussed in this article. The context for crop model applications is complex, requiring ingenuity, dedication, and good judgment to advance GEMI assessments and other applications.

AUTHOR CONTRIBUTIONS

Both authors contributed substantially to write this article.

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Evaluation of G × E × M Interactions to Increase Harvest Index and Yield of Early Sown Wheat

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Harvest index (HI) is the ratio of grain to total shoot dry matter and is as a measure of reproductive efficiency. HI is determined by interactions between genotypes (G), environment (E), and crop management (M). Historic genetic yield gains due to breeding in wheat have largely been achieved by increasing HI. Environmental factors are important for HI and include seasonal pattern of water supply and extreme temperatures during crop reproductive development. Wheat production in Australia has been dominated by fast-developing spring cultivars that when sown in late-autumn will flower at an optimal time in early spring. Water limited potential yield can be increased by sowing slower developing wheats with a vernalization requirement (winter wheat) earlier than currently practiced such that their development is matched to environment and they flower at the optimal time. This means a longer vegetative phase which increases rooting depth, proportion of water-use transpired, and transpiration efficiency by allowing more growth during winter when vapour pressure deficit is low. All these factors can increase biomass accumulation, grain number and thus grain yield potential. However higher yields are not always realized due to a lower HI of early sown slow developing wheats compared to fast developing wheats sown later. Here, we evaluate genotype × management practices to improve HI and yield in early sown slow developing wheat crops using 6 field experiments conducted across south eastern Australia from 2014 to 2018 in yield environments ranging from ~1 to ~4.7 t/ha. Practices included low plant densities (30–50 plants/m^2), mechanical defoliation, and deferred application of nitrogen fertilizer. Lower plant densities had similar yield and HI to higher plant densities. Defoliation tended to increase HI but reduce yield except when there was severe stem frost damage. Deferring nitrogen had a variable effect depending on starting soil N and in crop rainfall. All management strategies evaluated gave variable HI and yield responses with small effect sizes, and we conclude that none of them can reliably increase HI in early sown wheat. We propose that genetic improvement is the most promising avenue for increasing HI and yield in early sown wheat, and postulate that this could be achieved more rapidly through early generation screening for HI in slow developing genotypes than by crop management.

Keywords: winter wheat, defoliation, management, plant density, vernalization

INTRODUCTION

Wheat production in Australia is dominated by fast-developing spring cultivars. For over a century wheat breeding programs have been selecting for faster developing cultivars to escape drought and high temperatures (Davidson et al., 1985; Eagles et al., 2009), and growers have been sowing progressively earlier since the widespread adoption of no-till farming in the 1990s (Anderson et al., 2016). Consequently, flowering times of commercial crops have become earlier for genetic and management reasons, and are currently optimal in many environments (Flohr et al., 2017). In southern Australia, the optimal flowering period is defined by a relatively narrow period in which the combined damage from lack of radiation, frost, drought, and heat are minimized. Optimal flowering periods differ for each ecological zone depending on climate and generally occur during the first half of spring (late August to mid-October). Moving crop flowering progressively closer to this period has led to sustained increases in harvest index (HI) and water-use efficiency and has helped maintain farm yields despite declining water-limited potential yields (Hochman et al., 2017). Fast developing spring wheats are typically sown in late autumn (early May) to flower during this optimal period. However, recent research has demonstrated that water limited potential yield can be further increased by sowing winter or slow-developing spring wheats earlier than currently practiced such that they still flower at the optimal time but have a longer vegetative phase (Hunt et al., 2019). This can only reliably be achieved with cultivars with an obligate vernalization requirement, i.e., winter habit (Penrose and Martin, 1997; Fischer, 2011; Hunt, 2017; Hunt et al., 2019) sown in mid-autumn (April). Winter genotypes have previously been overlooked by growers, agronomist, and breeders due to later sowing in evaluation and agronomy trials and the Genetic (G) × Environment (E) × Management (M) opportunities to maximize yield have not been fully explored. A new generation of winter cultivars have been released in Australia from 2016 onward suitable for planting before 20 April (Hunt et al., 2019). While our understanding of genetic controls of vernalization (Trevaskis, 2010) and importance of achieving optimal flowering times (Flohr et al., 2017; Flohr et al., 2018b) has improved, crop management, and yield physiology of early sown winter cultivars has received little attention.

Due to their vernalization requirement and early sowing, winter cultivars spend longer in the vegetative phase compared to spring cultivars sown later. This means more leaves and potential tillering sites are initiated, and a lengthening of the growing period has the potential to increase water use due to greater rooting depth and thus soil water extraction. It may also increase the proportion of water-use transpired; and transpiration efficiency by allowing more growth during winter when vapour pressure deficit is low (Flohr et al., 2020). All these factors increase dry matter (DM) accumulation, grain number, and thus potential grain yield (GY). However, experiments conducted by Gomez-Macpherson and Richards (1995) and in reviewed experiments of others (Batten and Khan, 1987; Connor et al., 1992) found that GYs of slow developing cultivars were only equivalent to faster developing cultivars sown later despite similar or greater DM in early sown cultivars due to a lower HI. In some instances, yields of early sown slow developing wheats are less than spring wheats due to a lower HI and lodging (Stapper and Fischer, 1990; Riffkin et al., 2003). This presents an opportunity to improve yields in early sown slow developing cultivars by improving HI.

There is scope to improve the HI of early sown wheat. HI is the ratio of the yield of grain to the total shoot DM and can be used as a measure of reproductive efficiency (Donald and Hamblin, 1976). Environmental factors are important determinants of HI and include seasonal pattern of water supply and extreme temperatures during crop reproductive development. One plausible explanation for a reduced HI in early sown slow developing cultivars is related to pattern of water use. In glasshouse experiments, the ratio of pre- and post-anthesis water use has been demonstrated to be strongly related to HI (Passioura, 1977). When established early, winter wheats have a long duration of pre-anthesis growth, and in water-limited environments can use too much water before anthesis such that HI is low compared with spring wheats established later (Gomez-Macpherson and Richards, 1995). Deferred water use trades off against the higher DM accumulation of early established winter cultivars which drives high grain number and produces water-soluble carbohydrates (WSCs) that can be translocated to grain, such that yield of early established winter wheats is at least equivalent to faster spring cultivars established later.

The second explanation is that increased plant height and more leaves lead to competition for carbohydrates between the developing spike and elongating stem of early sown crops (Gomez-Macpherson and Richards, 1995). Genetic improvement is one approach to remove these limitations. Since the green revolution, improvement in wheat GY in many environments has been due to an increase in the number of grains per unit area and HI (Siddique et al., 1989; Hay, 1995; Sayre et al., 1997; Shearman et al., 2005; Flohr et al., 2018a). Increasing the sink size or improved partitioning to spike growth may provide a pathway for the improvement of the HI of wheat (Foulkes et al., 2010). While there may be potential to further adjust phasic development to alter the timing and duration of spike development, a recent study by Flohr et al. (2018a) showed that HI improvement was not due to phase duration and suggests other factors are involved such as partitioning traits. Previous studies in many crops have outlined any genetic or management solution that could either increase the grain growth rate or enhance the remobilization of assimilates from vegetative tissues to grains after anthesis usually leads to a higher HI within a crop (Sadras and Connor, 1991; Yang et al., 2000; Kemanian et al., 2007; Fletcher and Jamieson, 2009; Zhang et al., 2012).

Crop management also has the capacity to modify the pattern of water use and biomass partitioning. There are many examples where variation in HI are mainly attributed to differences in crop management (Kemanian et al., 2007; Peltonen-Sainio et al., 2008). While delayed sowing is a management factor known to increase HI, this is counterproductive for slow developing

cultivars as they will flower outside of the optimal window, produce less DM, and have reduced yield potential. Management factors that can improve HI and yield from an early sowing date (prior to April 20) have not yet been explored.

Over supply of nitrogen (N) early in crop development stimulates vigorous vegetative growth and can lead to water deficit in later reproductive phases. Excessive vegetative growth induced by excessive N is commonly known to lower GY and HI in water limited environments and is associated with reduced post-anthesis carbon assimilation in response to a lack of soil water (Van Herwaarden et al., 1998). The water deficit also contributes to poor re-translocation of pre-anthesis reserves. Deferring nitrogen inputs until after the start of stem elongation in winter types therefore has the potential to conserve water use and manage early biomass production. To the best of our knowledge there are no published experiments that have reported on the effect of N fertilizer timing on crop yield in winter cultivars sown early under Australian dryland conditions.

Reducing plant density has also been proposed as a way of reducing early DM accumulation and improving HI in early established slow developing cultivars (Kirkegaard et al., 2014). Early sown winter cultivars provide additional farming system benefits; a longer vegetative period means more DM is accumulated for forage, and there is more time available for stock to graze before the onset of the reproductive phase (Bell et al., 2015). It is often thought that defoliation could be used as a management technique to reduce vegetative growth and early water use. While this would imply an increase in HI, it also trades off against reduced DM accumulation by anthesis as shown by Kirkegaard et al. (2015). There have been some measured instances of deferral of water use assisting recovery of wheat yield (Virgona et al., 2006; Harrison et al., 2010), but the review of Harrison et al. (2011a) found that defoliation on average reduces GY most likely due to reduced DM accumulation.

To our knowledge, there are no reported factorial experiments combining all management factors such as plant density, nitrogen timing, crop defoliation, and genotype to assess their influence on GY and HI. Here, we evaluate the effect of these management practices on HI and GY of four different winter wheat genotypes sown early in two contrasting environments.

MATERIALS AND METHODS

Field Sites

Three field sites were chosen for evaluation of management practices for early sown winter wheat representative of the major medium-low rainfall environments in which wheat is grown in SE Australia (**Table 1**). Experiments were conducted during 2014 and 2015 at Temora and 2017 and 2018 at both Yarrawonga and Loxton. Yarrawonga and Temora have a similar annual rainfall at 470 and 520 mm, respectively, whereas Loxton is considerably drier at 266 mm. Sites will be referred to as Temora 2014 (Te14), Temora 2015 (Te15), Yarrawonga 2017 (Ya17), Yarrawonga 2018 (Ya18), Loxton 2017 (Lo17), and Loxton 2018 (Lo18) from here on. Air temperature was measured at each site using a TGP-4017 TinyTag (Gemini data loggers UK Ltd) temperature logger installed in a radiation screen at a height of 1.2 m. Rainfall was measured with a tipping bucket rain gauge (Tekbox) connected to a Wildeye data logger and telemetry unit.

Cultivar, Sowing Date, and Crop Management

Winter cultivars were selected based on suitability for early sowing. Prior to the release of new generation winter wheats in 2016, only one cultivar Wedgetail (mid-developing winter) was chosen for Temora in 2014 and 2015. At all other sites three winter cultivars were chosen based on three contrasting development patterns Longsword (fast winter), Kittyhawk (mid-winter), and DS Bennett (mid-slow winter) and planted in mid-April which is optimal for winter cultivars in all environments (**Table 2**). All cultivars have an obligate requirement for vernalization (winter wheat) and weak photoperiod sensitivity.

At all sites if the seedbed was too dry to allow emergence, plots were irrigated with ~10 mm of water applied using pressure compensating drip-line placed in seeding furrows to germinate

TABLE 1 | Mean annual, summer fallow (Nov–Mar) and growing season (Apr–Oct) rainfall (1984–2018) from nearest Bureau of Meteorology weather station in comparison to rainfall recorded at experimental sites for the relevant growing seasons.

Site	Year	Annual rainfall (mm)	Nov–Mar rainfall (mm)	Apr–Oct rainfall (mm)
Temora	Mean	520	208	312
	2014	436	158	250
	2015	481	169	276
Yarrawonga	Mean	470	197	273
	2017	473	140	276
	2018	336	161	135
Loxton	Mean	266	96	170
	2017	274	120	135
	2018	178	83	92

TABLE 2 | Experimental site characteristics including locations, year, coordinates, sowing date, soil mineral N at sowing, genotypes included in experiment, and total N applied.

Site Location/ Year (ID)	Coordinates	Sowing Date*	Soil mineral N at sowing (kg/ha), and depth (m)	Genotypes	Total N applied as urea (kg/ha)
Temora 2014 (Te14)	34°43'42"S 147°33'4"E	8 April	86 (1.6)	Wedgetail	100
Temora 2015 (Te15)	34°24'4"S 147°31'12"E	20 April	208 (1.6)		46
Loxton 2017 (Lo17)	34°31'49"S 140°31'59"E	18 April*	48 (0.9)	Longsword Kittyhawk	46
Loxton 2018 (Lo18)	34°30'25"S 140°34'06"E	18 April*	86 (0.9)	DS Bennett	46
Yarrawonga 2017 (Ya17)	36°04'04"S 145°54'43"E	13 April*	137 (0.9)		82
Yarrawonga 2018 (Ya18)	36°04'04"S 145°54'43"E	16 April*	47 (0.9),		82

*Sites received supplementary irrigation at sowing.

seed and allow emergence. Seeding depth was approximately 30 mm depending on seed bed moisture. Sowing date is defined as the calendar date at which seeds become imbibed and began the process of germination, i.e., either the date on which they are planted into a moist seed bed, or the date on which they received rainfall/irrigation after being sown into a dry seed bed. In all experiments, chemical fertilizers and pesticides were applied such that nutrient limitations, weeds, pests or diseases did not limit yield. Nitrogen applications were managed according to treatments and the rate depended on site (**Table 2**) average potential yields. Grain protein in all experiments exceeded 11.1% indicating N deficiency was unlikely (Goos et al., 1982; Holford et al., 1992).

All crops were direct-drilled in small plots at Loxton (1.37 m × 7 m) on 228 mm row spacing with press wheels to give six crop rows per plot. Yarrawonga (1.8 m × 15 m) on 225 mm with press wheels to give eight rows per plot. Temora (1.83 m × 10 m) on 305 mm row spacing with press wheels to give six rows per plot.

Management of Treatments to Manipulate Harvest Index

Management practices were imposed to alter early DM accumulation and partitioning in an attempt to improve HI. Management practices evaluated at all sites included; 1) two nitrogen timings (seedbed N and deferred N) ensuring either adequate N supply at sowing or deferred until early stem elongation (development stage 30–31; Tottman, 1987); two defoliation treatments to simulate grazing (control and defoliation) applied by mechanical mower twice during tillering before DC30; and two plant density treatments (low and high) targeting 50 and 150 plants/m^2, respectively. Management factors were applied to each cultivar in a factorial fully randomized complete block experiment which equates to eight management combinations per cultivar per site with four replications.

Measurements

The onset of stem elongation (DC30) was determined by dissection of the main stem on 5 plants at regular intervals using criteria of Tottman (1987). Day of flowering (DC65) was recorded as the date when 50% of the spikes in each plot had at least one visible anther extruded. Total above-ground biomass at maturity (DM) and yield components were estimated by cutting all above ground biomass from a quadrat 0.9 m × 0.5 m (four middle rows from plots) per replicate at maturity (DC89). Plants were cut at ground level and the number of spikes counted to determine the spike density per unit area (SD). A subsample of 50 randomly selected spikes from the quadrat sample were dried at 70°C for 48 hours and threshed by hand and weighed to determine the number of grains per spike (GPS) and grain number per unit area (GN). HI was calculated as the ratio of grain weight to total biomass. Individual grain weight (KW) was measured by weighing 200 grains dried at 70°C for at least 48 h. GYs were measured by machine harvest of the inside four rows of six row plots and are reported at 12.5% moisture content. Harvest grain moisture and grain protein was determined *via* near infrared (NIR) spectroscopy. Plant height (Hght) was measured from the base of stem up until the tip of emerged spike (excluding awns) at physiological maturity. Groundcover was estimated using regular readings of NDVI recorded using a GreenSeeker® (Trimble Inc., Sunnyvale CA).

The severity of reproductive frost stress was estimated by randomly selecting 10 spikes per plot and frost-induced sterility (FIS) was assessed on the outside florets of each spikelet excluding the terminal, basal, and supernumerary spikelets by the method proposed by Martino and Abbate (2019). FIS is the number of sterile florets per spike expressed as a percentage of the total number of possible grains that could have formed in the outside florets. The % of fertile culms (culms with a viable head relative to culms with unviable head) was measured at sites suspected of stem damage from frost.

Statistical Analysis

Principal component analysis (PCA) was used to interpret and summarize the major patterns of variation due to environment, genotype and management on phenology measurements, yield, and yield components. PCA was calculated based on genotype means for each trait under each environment, to study the inter-relationships among the components conducted using the Unscrambler software (version 10.3, CAMO, Norway). Means were standardized using 1/SD in order to account for the effect of scale.

The effect of all treatments on yield and other parameters were analysed individually using mixed linear models or across environment using ANOVA with site year, cultivar, nitrogen, defoliation, and plant density as factors/fixed effects and block structure as random effects in the statistical package GenStat for Windows (2018) 19th ed. (VSN International Ltd., Hemel Hempstead, UK). Significance is assumed at the 95% confidence level. If management treatment effect sizes were small and explained less than 3% of the variance combined, the factors were pooled (i.e., plant density and nitrogen timing as one management factor) for subsequent analysis and the factorial interactions limited to three-way interactions for interpretations of G × E × M. If the interaction was not significant, then pooled means incorporating the management treatments were used in the comparisons and figures below.

Linear regression between DM and GY was performed on each individual site using GenStat for Windows (2018) 19th ed. (VSN International Ltd., Hemel Hempstead, UK). Data was interpreted in two ways, firstly by comparing the slope and allometric constants (intercept) of genotypes across all E × M combinations. Secondly the deviation (standardized residual) of each variety × management combination from the fitted regression of DM and GY from each site was used in ANOVA to test the significance of the variety and management effect on GY deviations away from the DM/GY regression. For comparison with traditional agronomic analyses, HI of each genotype at each management combination was computed at the plot level.

RESULTS

Environment and Flowering Conditions

Summer fallow rainfall at Temora was 40 and 50 mm below average, and growing season rainfall was 62 and 36 mm below average in 2014 and 2015, respectively. The amount and distribution of rainfall at Loxton and Yarrawonga were consistent with long term rainfall averages in 2017. Both sites were considerably drier in 2018 - summer fallow rainfall was close to average being 36 mm less at Yarrawonga, and 13 mm less at Loxton but growing season rainfall was 50% below average at Yarrawonga and 46% at Loxton (**Table 1**). This led to severe spring drought at both sites.

Cold stress events were apparent in all environments, the most severe events occurred at Temora in 2014, and Yarrawonga in 2018 where minimum temperatures reached < −5.0°C in August (**Table 3**). Temperatures below −4°C are likely to cause stem frost damage and occurred at these sites during stem elongation. All sites recorded significant cold events during heading and flowering during September but were least severe at Loxton in 2017. There were few frosts during October at all sites. Heat events were minimal at Yarrawonga in both seasons, however temperatures above 32°C were common at Loxton and in 2017/2018 and Temora in 2014 (**Table 3**). Detailed temperature profiles of Temora 2014 and Yarrawonga 2018 can be found in **Supplementary Figure 1** and **Supplementary Figure 2**.

At Loxton and Yarrawonga, flowering time behavior of winter cultivars were consistent across locations and years (**Table 4**), Longsword was 5–10 days earlier than Kittyhawk, and 10–15 days earlier than DS Bennett at Loxton and ~5 days earlier at Yarrawonga. Within cultivars at each environment the flowering time range was small between 2–5 days suggesting there is little effect of management or seasonal conditions on flowering time. At Temora, flowering date was difficult to assess due to stem frost damage. In 2015 undefoliated treatments of Wedgetail flowered on 7 Oct, and defoliated treatments flowered 5–7 days later.

TABLE 3 | Number of days below 0°C (cold stress), lowest recorded minimum temperature and number of days above 32°C (heat stress), and highest recorded maximum temperature during August, September, and October at all environments.

Site	Year	Cold stress events no. of days temperature < −0°C (Min Temperature)			Heat stress events no. of days temperature > 32°C (Max Temperature)		
		Aug	Sep	Oct	Aug	Sep	Oct
Temora	2014	17 (−4.9)	13 (−2.9)	2 (−0.1)	0	0	8 (34.5)
	2015	8 (−3.5)	7 (−2.2)	0	0	0	1 (34.3)
Yarrawonga	2017	11 (−2.5)	5 (−2.4)	1 (−1.3)	0	0	0
	2018	7 (−6.0)	9 (−3.0)	0	0	0	1 (33.3)
Loxton	2017	7 (−1.7)	3 (−1.1)	0	0	1 (32.8)	6 (34.6)
	2018	5 (−3.6)	13 (−3.7)	1 (−1.0)	0	0	7 (36.8

TABLE 4 | Range (earliest to latest) in anthesis dates for Longsword, Kittyhawk, DS Bennett, and Wedgetail across all management combinations within environments.

Environment	Longsword	Kittyhawk	DS Bennett	Wedgetail
Loxton 2017	12–16 Sep	20–24 Sep	28 Sep–2 Oct	
Loxton 2018	12–15 Sep	19–24 Sep	2 Oct–7 Oct	
Yarrawonga 2017	5–9 Oct	8–14 Oct	13–14 Oct	
Yarrawonga 2018	3–7 Oct	2–8 Oct	5–10 Oct	
Temora 2015	–	–	–	7 Oct–15 Oct

Relationship Between DM, GY, and HI

There was a strong positive relationship between HI and GY at stem frosted sites Yarrawonga in 2018 and Temora in 2014 explaining up to 86% and 76% of the variation in yield respectively. At other sites, HI was not correlated with GY (**Figure 1**). This means in the absence of severe frost damage a higher HI did not always result in higher GY and specific G × M combinations may be able to achieve a high HI and GY.

DM and GY were positively associated at all sites except for Temora in both 2014 and 2015 (**Figure 2**). The strong relationship with DM and GY within treatments of similar HI at Yarrawonga in 2017, and Loxton (2017 and 2018) suggest that total biomass can be improved along with maintenance of a high HI using G × M strategies to improve crop yield. The lack of relationship at Temora (2014 and 2015) suggests other factors maybe be driving yield responses.

Management Interactions on GY, DM, and HI

There was significant variation in GY, DM, and HI across experiments. The largest amount of variation and effect size

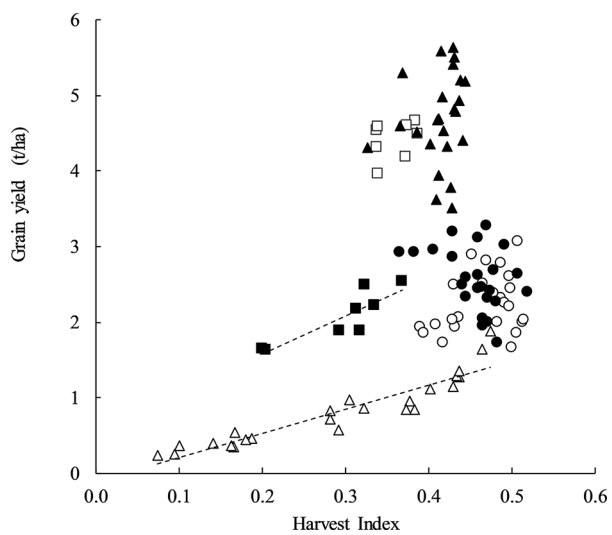


FIGURE 1 | Harvest index plotted against grain yield at Temora 2014 (■, y = 5.0868x + 0.5564, P = < 0.001, R^2 = 0.76), Temora 2015 (□, P = ns), Loxton 2017 (●, P = ns), Loxton 2018 (○, P = ns), Yarrawonga 2017 (▲, P = ns), and Yarrawonga 2018 (Δ, y = 3.1897x − 0.1031, P < 0.001, R^2 = 0.86). Data points are contributed by all of the genetic × management combinations applied to increase HI (n = 112).

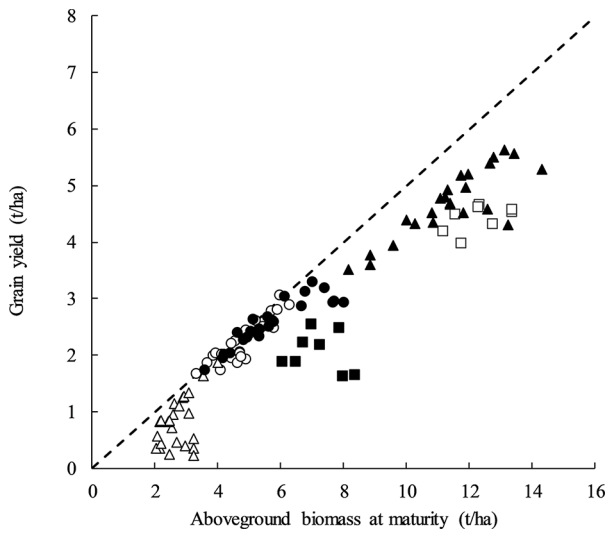


FIGURE 2 | Aboveground biomass at maturity (t/ha) plotted against grain yield (t/ha) at Temora 2014 (■, P = ns) Temora 2015 (□, P = ns), Loxton 2017 (●, y = 0.3021x + 0.8403, P < 0.001, R^2 = 0.82), Loxton 2018 (○, y = 0.444x + 0.1014, P <0.001, R^2 = 0.79), Yarrawonga 2017 (▲, y = 0.3283x + 0.9569, P < 0.001, R^2 = 0.72), and Yarrawonga 2018 (Δ, y = 0.5273x – 0.5928, P < 0.05, R^2 = 0.34). Data points are contributed by all the management × genetic combinations applied to increase HI (n = 112). The dashed line represents a harvest index of 0.5.

TABLE 5 | Mean values for DM at maturity, grain yield (GY), harvest index (HI) in each growing environment, and pooled means for management factors plant density, defoliation, and nitrogen timing.

Factor		Grain yield (t/ha)	DM at maturity (t/ha)	HI
Environment	Lo17	2.6[b]	5.7[d]	0.46[a]
	Lo18	2.2[d]	4.8[e]	0.47[a]
	Te14	2.1[c]	7.2[c]	0.29[d]
	Te15	4.4[a]	12.3[a]	0.36[c]
	Ya17	4.7[a]	11.4[b]	0.41[b]
	Ya18	0.8[e]	2.7[f]	0.29[d]
Plant density	Low	2.7	7.1[a]	0.39
	High	2.7	7.4[b]	0.38
Defoliation	Control	2.8[a]	7.9[a]	0.35[b]
	Defoliated	2.5[b]	6.4[b]	0.40[a]
Nitrogen timing	Seedbed N	2.7[a]	6.9[b]	0.40[a]
	Deferred N	2.8[b]	7.4[a]	0.37[b]

Letters a–d indicate means are significantly different at the 95% confidence level.

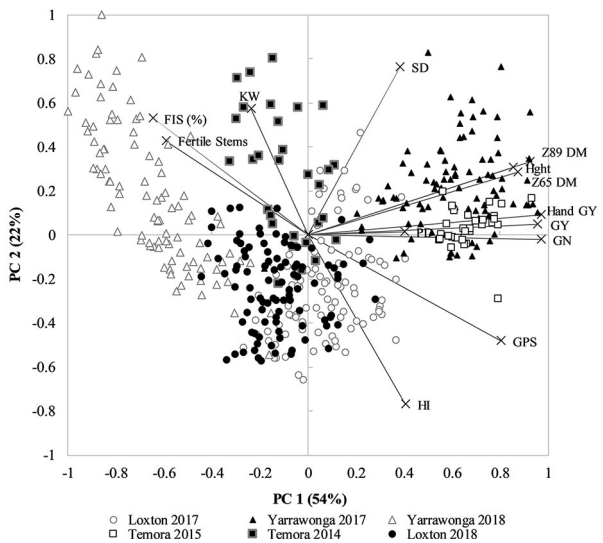


FIGURE 3 | PCA plot of all environment and management combinations for plot grain yield (GY), hand harvest grain yield (hand GY), spike density (SD), plant height (Hght), above ground dry matter at anthesis (Z65 DM), above ground dry matter at maturity (Z89 DM), Harvest Index (HI), Grains per spike (GPS), % sterile florets (%FIS), % Fertile Stems, kernel weight (KW), and grain number (GN). Environments are Temora 2014 (■) Temora 2015 (□), Loxton 2017 (●), Loxton 2018 (○), Yarrawonga 2017 (▲), and Yarrawonga 2018 (Δ). Data points are contributed by the management × genetic combinations applied to increase HI across all replicates (n = 448).

was due to environment (**Supplementary Table 1**) and while the environment × management factors (seeding density and nitrogen timing) were significant they explained less than 3% of the variance combined and was used to justify pooling plant density and nitrogen timing as one management factor for subsequent analysis.

Site mean GYs ranged from 0.8 t/ha at Yarrawonga in 2018 to 4.7t/ha at Yarrawonga in 2017, DM ranged from 2.7t/ha at Yarrawonga 2018 to 12.3t/ha at Temora in 2015. Site mean HI ranged from 0.29 at Temora 2014 and Yarrawonga 2018 to 0.47 at Loxton in 2018. Higher HI was achieved at Loxton compared to Yarrawonga in both seasons. On average across all experiments defoliation reduced DM by 1.5t/ha and increased HI by 0.05 which resulted in a GY penalty of 0.3 t/ha. Lower density reduced DM by 0.3 t/ha but on average GY and HI were similar between low and high density. Early applied N improved HI by 0.03 and reduced GY by 0.1 t/ha (**Table 5**).

To dissect the relationship between HI, GY, other crop canopy traits and environment an exploratory PCA analysis showed PC1 explained 54% and PC2 22% of the variation in the dataset, which could largely be attributed to environment (**Figure 3**). The strong influence of environment is clear as well as the strong association between GY, GN, Hght, and DM at DC65 and DC89. Importantly, HI was negatively associated to higher sterility (floret and stem), lower kernel weight (KW), and lower spike densities (SD). The PC plot also suggests there is little relationship between HI and GY across environments. HI was only positively associated with GY in environments where frost dramatically reduced the number of grains per spike (GPS) or kernel weight (KW), such as at Yarrawonga in 2018, and Temora 2014 which were associated with a higher % infertile stems, % infertile florets, and lower KW.

The PCA score and loading plot suggest it is possible to achieve both a relatively high HI and GY yield within each environment as directly shown by, **Figure 1** and that this is likely due to management and genetic interventions that are positively correlated to GN and DM.

G × E × M for Grain Yield, Yield Components and Harvest Index

All genotypes interacted with environment (**Supplementary Table 2**) for GY, DM, HI, GN, SD, and Hght, whereas G × M were limited to a small difference in KW, and the G × defoliation responses depended on environment. Defoliation was the most reliable management strategy to increase HI, however yield responses were still small and variable (including yield reductions) and interacted with environment and cultivar.

Plant density and nitrogen timing effects were small as outlined in *Management Interactions on GY, DM, and HI* and **Supplementary Table 1** and therefore pooled into one management factor titled canopy management (CM). CM interacted with G × E for GY but the G × E × CM interaction was not significant for HI (**Supplementary Table 2**). The yield responses visualized in **Figure 4** demonstrate the variable nature of the yield responses to canopy management strategies and the small effect sizes relative to genotype and environment. There is no clear pattern in the responses measured apart from the differences observed in genotypic performance. The fast-developing winter cultivar Longsword sown at lower density was the highest yielding treatments at Loxton in 2017 and 2018 irrespective of N management. Whereas at Yarrawonga, the slower developing cultivar DS Bennett sown at higher densities was the higher yielding treatment.

Canopy management × environment interactions were significant for HI and DM across all genotypes however this was largely due to the two stem-frosted sites Temora 2014 and Yarrawonga 2018 (**Figure 5**). Deferred N increased HI at these sites irrespective of planting density. At other sites, there were not any significant differences between canopy management treatments. DM responses varied with environment and the effect sizes were small. DM increased with seedbed N at Loxton in 2017 and lower densities and seedbed N increased DM in favorable conditions at Yarrawonga in 2017 and Temora 2015.

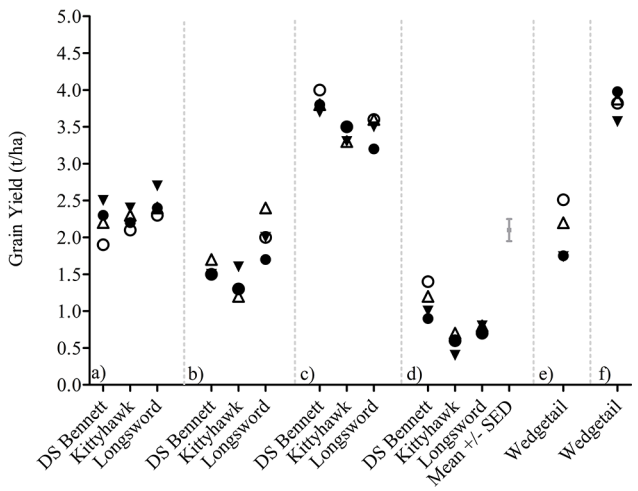


FIGURE 4 | G × E × CM interactions for grain yield at Loxton 2014 **(A)**, Loxton 2015 **(B)**, Yarrawonga 2017 **(C)**, Yarrawonga 2018 **(D)**, Temora 2014 **(E)**, and Temora 2015 **(F)** in genotypes DS Bennett, Kittyhawk, and Longsword. Canopy Management (CM) factors are ▼ Low Density and Seedbed N, Δ Low Density and Deferred N, ● High Density and Seedbed N, and ○ High Density and Deferred N.

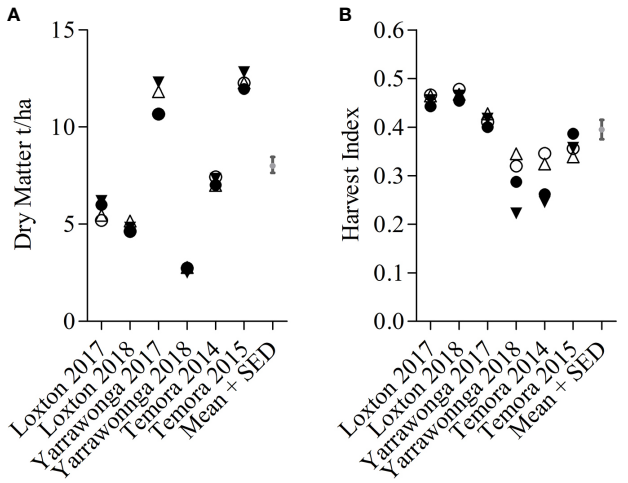


FIGURE 5 | E × CM interactions for DM **(A)** and HI **(B)** at Loxton 2014, Loxton 2015, Yarrawonga 2017, Yarrawonga 2018, Temora 2014 and Temora 2015 for pooled genotypic means. Crop Management factors are ▼ Low Density and Seedbed N, Δ Low Density and Deferred N, ● High Density and Seedbed N, and ○ High Density and Deferred N.

G × E × Defoliation Responses

In 8 out of 14 G × E combinations, defoliation increased HI, but increased GY in only 2 combinations. GY was similar between treatments at 7 out of 14 combinations and decreased in 5 combinations (**Table 6**). HI was never decreased by defoliation and remained the same as undefoliated controls in the other 6 G × E combinations.

Where GY was reduced by defoliation this was associated with a reduction in total crop biomass and grain number. It was possible to increase HI in Kittyhawk at Loxton, and in Longsword at Yarrawonga in 2017 but yield decreased due to a large reduction (>2 t/ha) in DM and a combination of reduced grain number and kernel weight. On these occasions reductions in plant height were also greater than 10 cm. Whereas in the example of DS Bennett at Loxton and Yarrawonga in 2017 HI remained similar to the control when defoliated but GY decreased due to a reduction in grain number and either DM or kernel weight and plant height effects were small (± 2–3 cm).

Where defoliated GY were similar to the undefoliated controls such as Loxton in 2018, this was due to the ability of genotypes to maintain grain number. When HI was increased by defoliation and there were small reductions in biomass and or height, and thus grain number remained similar to undefoliated treatments. There were also three combinations were HI and GY were similar and genotypes recovered all their yield without any negative tradeoffs.

Genotypic differences were evident and despite larger reductions in biomass Longsword generally recovered more

TABLE 6 | Mean grain yield (GY), harvest index (HI), above ground dry matter at maturity t/ha (DM), grain number (GN), kernel weight (KW), plant height (Hght) of winter cultivars across environments, and the management effect size when defoliated.

G × E	Control trait means						Management effect (defoliation)					
	GY(t/ha)	HI	DM(t/ha)	GN(no/m^2)	KW(mg)	Hght(cm)	GY(t/ha)	HI	DM(t/ha)	GN(no/m^2)	KW(mg)	Hght(cm)
Loxton 2017												
DS Bennett	2.4^b	0.46^a	5.8^b	9922^a	27.3^c	65^c	−0.3	ns	−1.0	−1,064	−1.7	2
Kittyhawk	2.5^b	0.43^b	6.9^a	9050^a	32.8^b	73^b	−0.5	0.04	−2.5	−1,433	−3.9	−13
Longsword	2.5^b	0.41^c	7.0^a	7344^b	38.4^a	78^a	ns	0.09	−1.8	ns	−4.1	−13
Loxton 2018												
DS Bennett	1.6^b	0.50^a	4.4^b	6882^b	32.2^b	58^b	ns	ns	ns	ns	ns	ns
Kittyhawk	1.3^c	0.42^c	4.5^b	4905^b	38.1^a	61^a	ns	ns	ns	ns	1.5	ns
Longsword	2.0^a	0.47^b	5.7^a	7079^a	37.3^a	61^a	ns	0.03	ns	ns	ns	-6
Yarrawonga 2017												
DS Bennett	5.1^a	0.42^a	12.1^b	14795^a	34.4^b	98^a	−0.5	ns	ns	-950	ns	−2
Kittyhawk	4.8^b	0.41^a	11.8^b	12706^b	39.8^a	89^b	−0.6	ns	−2.1	−1728	−1.2	−3
Longsword	4.7^b	0.36^b	13.0^a	11961^b	39.1^a	90^b	−0.3	0.07	−3.3	ns	ns	−10
Yarrawonga 2018												
DS Bennett	1.2^a	0.38^a	3.3^a	3780^a	34.5^c	59^a	ns	0.04	ns	ns	ns	−2
Kittyhawk	0.3^b	0.11^c	3.0^a	912^b	40.2^a	58^a	0.5	0.18	ns	1023	ns	ns
Longsword	0.5^b	0.17^b	2.4^b	1126^b	37.4^b	53^b	0.4	0.2	ns	1314	ns	ns
Temora 2014												
Wedgetail	2.1	0.26					ns	0.07	−1.3			
Temora 2015												
Wedgetail	3.8	0.35					ns	ns	−1.3			

Different letters in superscript within a site indicate significant differences and ns indicates no significant effect of management at the 95% confidence level for each trait relative the control trait.

yield from defoliation than other cultivars. This is reflected in HI as Longsword was the most responsive cultivar to defoliation (increased HI at all sites), whereas DS Bennett was the least responsive but increased HI at the stem frosted site (Yarrawonga 2018), defoliation increased HI in Wedgetail when stem frosted at Temora 2014. At sites where DS Bennett had a greater HI, it always had reduced biomass compared to Longsword meaning yields between cultivars were often similar at high and low HI. Despite the inconsistent effects of management and the strong influence of the environment, genotypic differences in HI were stable and consistent across sites and management. DS Bennett tended to have higher HI than both Kittyhawk and Longsword.

G × M Interactions Under Frost and Heat Shock

Stem frost damage was only evident at Temora 2014 and Yarrawonga 2018 when temperatures were below −4°C in August (**Table 3**). At Temora, seeding density and defoliation had no significant effect on the number of infertile stems (data not presented), however deferring N reduced damage by 7% relative to the seedbed N (31% infertile stems). Yield was rarely increased by defoliation but on the occasions it was associated with increased HI and GNO at similar DM to undefoliated controls. This only ever occurred at Yarrawonga in 2018 in the early mid-winter cultivars which were Longsword (+0.5t/ha) and Kittyhawk (+0.4t/ha) which were more by affected by severe stem frost, and defoliation reduced frost damage. At Yarrawonga seeding rate had little impact on stem frost damage, genotypic differences had the largest effect which could be potentially attributed to genetic differences in tolerance, developmental differences and crop architecture. Longsword had the greatest amount of stem damage under all management combinations, Longsword was also the first cultivar to reach DC30 and DC65 (**Figure 7**), followed by Kittyhawk, and DS Bennett. Management effects were significant, compared to seedbed applied N the management intervention of defoliation and deferred N reduced the damage from 63% to 53% in Longsword, from 51% to 36% in Kittyhawk, and from 36% in DS Bennett to 33% which wasn't significant (**Figure 6**). The same management intervention of deferred N and defoliation applied at Yarrawonga 2018 delayed the timing of stem elongation by 10 days in Longsword, 15 days for Kittyhawk, and 6 days for DS Bennett (**Figure 7**).

Management and genotype had a significant effect on the amount of floret sterility depending on the environment and severity of the damage. The effect of management was not significant at Loxton in 2017 and 2018, and Yarrawonga in 2017. However genotypic differences were significant, Longsword had on average 19% (Lo17), 2% (Lo18), and 7% (Ya17) sterility. Kittyhawk was 12%, 5%, and 5%, whereas DS Bennett always trended lower 11%, 2%, and 1%, respectively. The effect of genotype × management was significant at Ya18, seeding rate was insignificant but defoliation and deferred N reduced the amount of sterility relative to the untreated controls. This management combination reduced floret sterility in DS Bennett from 42% to 23%, from 70% to 16% in Kittyhawk, and 40% to 21% in Longsword (**Figure 6**).

Management practices N, defoliation, plant density, and genotype had a significant effect on NDVI and canopy cover at Yarrawonga in 2018 (data not presented). To explain the observations in **Figure 6** of frost damage there was significant differences in canopy structure as measured by NDVI during the timing of severe stem frost. There wasn't any significant G × defoliation × N timing three way interaction at any time of the

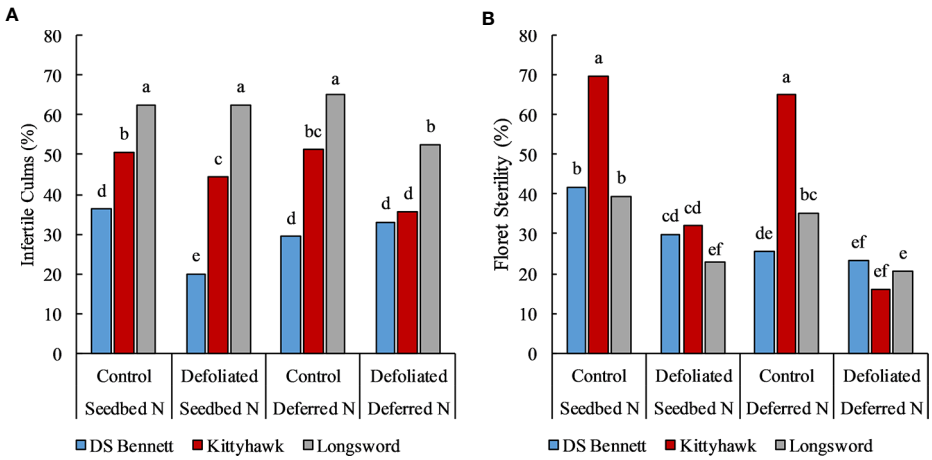


FIGURE 6 | The % of infertile culms **(A)** and % of sterile florets **(B)** in response to management factors deferring Nitrogen (N) and defoliation for winter genotypes DS Bennett, Kittyhawk, and Longsword at Yarrawonga 2018. Different letters indicate significant differences at the 95% confidence level.

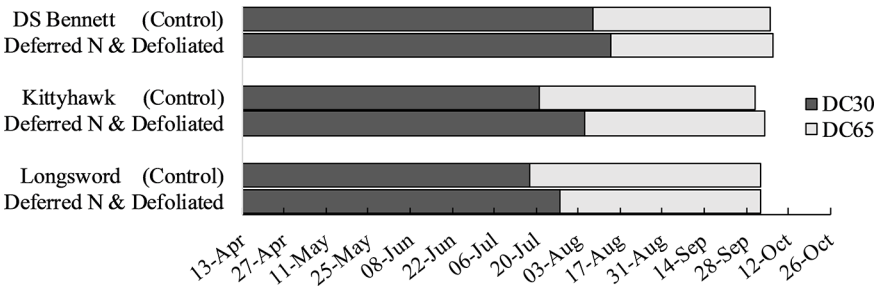


FIGURE 7 | Timing of the onset of stem elongation (DC30), and flowering (DC65) in seedbed applied N control treatments for genotypes DS Bennett, Kittyhawk, and Longsword relative to the management intervention deferring N and defoliation at Yarrawonga 2018.

year, however defoliation × N timing significantly changed the canopy structure to the largest degree in all three genotypes after defoliation and in the month of August (**Figure 8**).

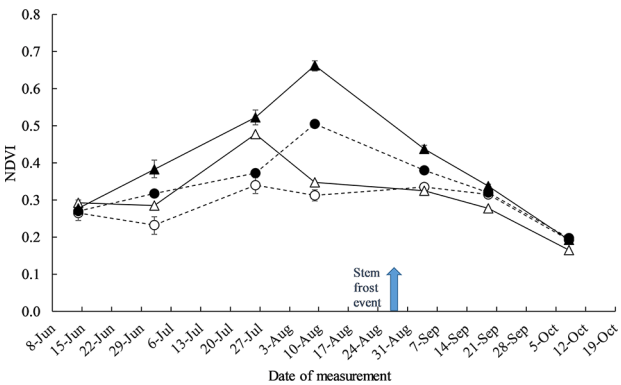


FIGURE 8 | The effect of crop management practices defoliation and deferring N on recorded canopy NDVI measurements at Yarrawonga 2018. Crop management factors are ▲ Control and Seedbed N, ● Control and Deferred N, Δ Defoliated and Seedbed N, and ○ Defoliated and Deferred N. The arrow indicates the timing of a severe stem frost event (−6°C). Data is averaged across all plant density and genotypes, the error bars represent the SED.

DISCUSSION

All crop management strategies evaluated gave variable HI and GY responses with small effect sizes which interacted unpredictably with environment. We conclude that none of the management strategies evaluated here can be used to reliably improve yield in early sown winter cultivars, whereas improved understanding of G × E interactions could reliably increase yield and HI in early sown wheat.

HI and Yield Responses to G × M in Water Limited Environments

The HI results have shown examples of early sown slow developing cultivars approaching 0.5 (**Figure 1**) which is nearing the values consistently reported in well managed fast developing spring cultivars sown later in autumn such as 0.45 by

Flohr et al. (2018a) and the maximum of 0.56 reported by Unkovich et al. (2010). While it was possible in our experiments, HI's close to 0.5 were not routinely achieved, and when they were it was often negated by a reduction in DM. The data presented here is an improvement compared to HI previously reported at Condobolin and Cowra in NSW from 0.28 to 0.31 for April-sown plots to 0.38–0.42 for June-sown plots (Batten et al., 1999), but there is still significant room for improvement in early sown wheat.

The highest yielding treatments at each environment occurred in cultivars that could maintain high DM and high HI. Defoliation had the most reliable positive effect on HI but also tended to reduce DM accumulation which negated increases in HI resulting in neutral yield responses. These results are consistent with previously published studies which have shown that that defoliation often increases HI of winter crops, but mainly though reduced total shoot biomass rather than increased GY because at maturity, grazed crops typically have lower stem and leaf DM, but spike DM remains similar to controls (Harrison et al., 2011b). Therefore, yield responses to defoliation are variable, but tend to decrease yield compared with un-grazed controls (Harrison et al., 2011a).

Responses to plant density and nitrogen timing were variable and had small effect sizes. Deferring N had very little impact on yield, even comparing the two extremes of canopy management (high plant density and early N compared to low plant density and delayed N). There appeared to be no responses resembling "haying off" that have been reported in fast developing wheat (Van Herwaarden et al., 1998) to suggest high plant density and early N are leading to excessive vegetative growth and water use. Reducing plant density has also been proposed as a way of reducing early DM accumulation and improving HI in early established slow developing cultivars (Kirkegaard et al., 2014). We found very limited evidence to suggest low plant densities increased HI or yield of early sown wheat suggesting lower plant densities are not saving anymore water for post-anthesis use. This may be due to the capacity of winter wheats to tiller and negate any significant changes in plant density compared to the shorter vegetative period of fast developing wheats. Spike densities were slightly lower at lower plant densities and deferred N applications; however, grain number was maintained by increases in grains per spike in lower density and deferred N treatments. This partially implies that winter cultivars maybe source limited and relatively inefficient at partitioning to spike growth during the critical period. This could suggest a breeding target for improved yield in winter cultivars. Our results add to the body of field experiments outlined in the review of Hunt (2017) that have found no positive effect on yield of reducing plant density in early established winter cultivars across either high, medium, and low water limited yield environments.

The lack of significant large effects of N timing and plant density highlights breeders can select from a broad range of early sown environment × management combinations, and growers have great flexibility in how they manage early sown crops. There is some evidence to suggest deferring N could increase yield in Longsword at Loxton 2018, and in Wedgetail at Temora 2014. There were two instances where defoliation increased HI and yield at Yarrawonga in 2018, due to increased grain number from reduced damage from stem frost in faster developing winter cultivars. These findings nonetheless highlight across a large range of yield environments and stresses that responses to plant density, deferring N, and defoliation are likely to be yield neutral or small and may offer a benefit in frost prone landscapes.

Improving HI and Yield in Frost Prone Landscapes

The only sites were HI was positively correlated to yield were severely frosted. The G × E × M responses to frost damage observed at Yarrawonga and Temora suggests the severity of stem frost damage can be partially managed with agronomy and genetics to increase HI and yield under these circumstances. Cold temperatures can cause pre-heading stem damage if temperatures approach < −6°C similar to Ya18 and Te14, and if the head emerges after such a frost event, this damage often presents as a bleached section with incomplete ear structure and aborted florets as explained in Frederiks et al. (2015). The improvement in yield, HI, and reduced stem damage from deferring N and grazing in fast mid-developing cultivars Longsword, and Kittyhawk at these sites relative to DS Bennett is likely due to a combination of phenology, and canopy structure. Grazing and deferred N delayed the onset of stem elongation and led to differences in crop canopy structure (**Figure 8**). Differences in crop canopy structure can affect the flow of air movement leading to different heat fluxes in the canopy around the stems and exposed spikes (Gusta and Wisniewski, 2013; Frederiks et al., 2015). Practices that are aimed at reducing the density of the canopy and increasing heat storage bank and thus radiance of the soil have been proposed before (Rebbeck et al., 2007). However, quite often management strategies that reduce or change canopy structure such as defoliation may also lead to decreased yield potential by reducing grain number per unit area as evidenced in DS Bennett at Kittyhawk in sites that were not severely frosted. The faster developing cultivar Longsword managed to maintain grain number at non frosted sites when N was deferred and plants defoliated and increased grain number at frosted sites. This strategy for fast and mid-developing winter cultivars needs further mechanistic investigation.

It is not entirely clear whether the improved stem frost tolerance from defoliation is due to phenological avoidance or a greater thermal insulation from changes in canopy structure. Genetic differences may also exist for frost tolerance but these have not been evaluated in depth here and are limited in the literature (Frederiks et al., 2015). Phenological avoidance or frost escape is a likely explanation for the reduced damage and lack of management responses observed in DS Bennett as it flowers later than other cultivars but still managed to maintain high yields. However, phenological avoidance alone for reproductive frost damage for the fast mid-developing cultivars seems an unlikely explanation as none of the management factors significantly delayed flowering date by more than four days at any site in

Longsword and Kittyhawk but there were marked reductions in sterility in response to management.

Future Improvement in HI and GY Within a G × E × M Framework

With the exceptions of environments that were characterized by severe stem frost, the management factors presented here have shown limited scope to improve HI and yield in early sown crops. Nonetheless, the responses of the cultivars in these series of experiments do suggest future yield gain may be able to be achieved through further increases in partitioning of assimilates to the growing spike that lead to increased grain number (Slafer et al., 2015). In the past, breeders have indirectly selected for lines with reduced pre-flowering senescence that invest an increasing amount of resources toward reserve and reproductive organs, which ultimately translates in greater yield (Sadras and Lawson, 2013). Since yield has largely been improved by indirect selection for higher HI, direct selection for partitioning traits may accelerate HI and GY increases in early sown slow developing wheat (**Box 1**).

The fast-developing cultivar Longsword's response to defoliation provided some insight into other strategies that can increase HI and GY. Relative to other cultivars Longsword increased HI and recovered more yield from defoliation (compared to the nil control) in 2017. This was achieved by reducing both DM and height but maintaining grain number. The increased tillering capacity of slow developing wheat could have implications for source sink relationships and increased plant height may not be required. While our experiments fall within the optimal height of 0.7–1 m for modern wheat cultivars proposed by Richards (1992), the same analysis has not been undertaken for early sown winter wheat despite the yield increase observed from shorter wheats (Sayre et al., 1997). Increased plant height and more leaves lead to competition for carbohydrates between the developing spike and elongating stem of early sown crops (Gomez-Macpherson and Richards, 1995). Increasing partitioning to spike growth at the expense of stem and other structural organs (rachis, glumes and palea) within the spike may provide an avenue for the improvement of the HI of wheat (Foulkes et al., 2010). Decreased competition for resources between stem growth and the developing spike may be possible with further reductions in plant height through genetic manipulation or management practices that have less effect on DM accumulation such as plant growth regulators. Further studies should investigate the modulation of WSCs particularly as higher apparent translocation ratio of stem WSC might mitigate yield penalties caused by defoliation (Hu et al., 2019). Remobilization of WSC stored in the stems and leaf structures at the timing of anthesis to the grains contributes to a high HI, especially when carbon assimilates for grain filling are limited by water stress during grain fill (Foulkes et al., 2007) and can be an important source of carbohydrates for grain filling in the absence of post-anthesis stress, indicating the importance of remobilization of WSC to high HI even under favorable conditions such as the UK and higher rainfall zones (Foulkes et al., 2002; Shearman et al., 2005; Zhang et al., 2012).

While flowering time should not be ignored, fine tuning of pre anthesis phases is unlikely to further improve HI, as Flohr et al. (2018a) demonstrated HI was decoupled from phase duration. The genotypes used in this study all flowered within the optimal period for each environment. The faster developing Longsword at Loxton, Mid-developing Wedgetail at Temora, and the slower developing DS Bennett at Yarrawonga as outlined in other experiments at these sites. The breeding interest in HI is important as fast developing cultivars are approaching the upper limit of HI, and future yield gains will have to be sought through increased DM production in spring wheat. Flohr et al. (2018a) proposed future yield gains may be achieved by combining the superior partitioning of modern fast developing cultivars with the longer duration of growth and thus greater DM production of early sown winter cultivars. Further enhancement in HI without compromising DM would increase GY in early sown winter wheat, in the same way it has been achieved in the past with spring wheats, South Australian cultivars released after the early 1980s accumulated more DM (Sadras and Lawson, 2011) and other key studies show that breeding has increased HI with little effect on total DM production (Perry and D'antuono, 1989; Siddique et al., 1989; Calderini and Slafer, 1999; Flohr et al., 2018a). It is acknowledged in the UK that future improvements in yield will require more crop biomass (Mitchell and Sheehy, 2018), there is evidence in the literature of HI in the UK of as high as 0.6 (Shearman et al., 2005) and while we recognize Australian conditions are more water limited than the UK it is therefore feasible to assume that 0.6 could be achieved and falls within theoretical maximums of 0.62 proposed by Austin et al. (1980), 0.64 by Foulkes et al. (2010), and 0.66 by Shearman et al. (2005).

The longer growing period of early sown slow developing wheat would imply that there is the potential to lift wheat yields through increasing DM production and focusing on partitioning traits (**Box 1**) such as HI and fruiting efficiency (Slafer et al., 2015). Early generation direct selection for HI in single spaced plants was proposed by Fischer and Rebetzke (2018) as a means of accelerating increases in potential yield. The breeding effort for winter wheat is still relatively immature in Australia and breeders are still considering the most cost effective phenotyping strategies to increase genetic gain in yield of winter wheat. It is for this reason we believe the method we propose of selecting for a high HI in single plants will accelerate yield gain in Australian winter wheats and should be considered by Australian breeders. Breeders would however need to be conducting screening within the context of the right management as discussed in this study, that is in early sown crops and selecting for appropriate flowering time in addition to selecting for a high HI and partitioning traits.

CONCLUSION

Given the limited effect of management strategies found here, we propose that genetic improvement is the most promising avenue for increasing HI and yield in early sown wheat, and postulate

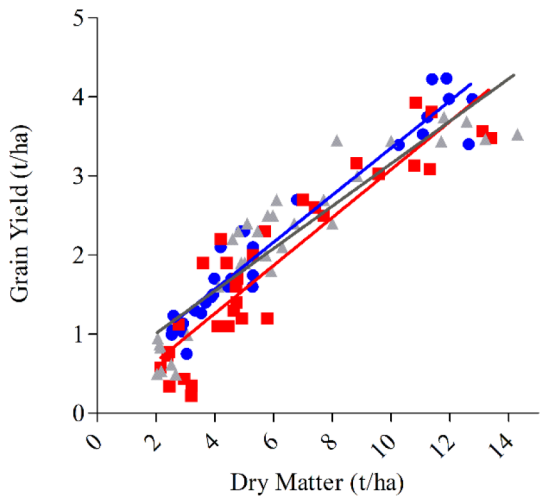
BOX 1 | Breeding and allometric relationships of cultivars

Within the context of early sowing our results have demonstrated that crop management practices of nitrogen timing, plant density, and defoliation are unlikely to provide the necessary increases in HI required to further increase yield in early sown crops. The lack of significant relationship observed between HI and GY means a higher HI did not always result in higher grain yield. Qin et al. (2013) concluded that breeders should focus on reproductive allometry of individuals when interpreting HI and select for allometric patterns that are most advantageous in a given agronomic context, especially when there is large variation in productivity among individuals, locations, or years.

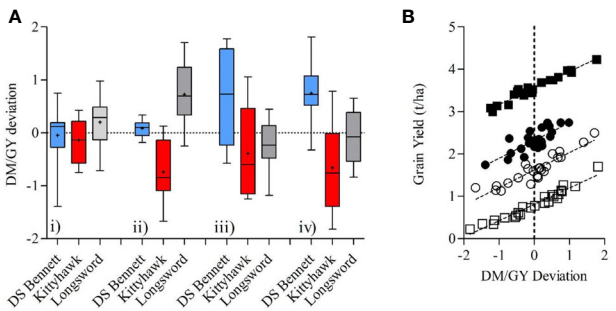
Given responses to management were small and inconsistent, it may be more useful to study allometric relationships between DM and GY within genotypes across a broad range of management practices and environment. Using an allometric approach it may be possible to increase HI by selection for high DM and grain yield. In this study, the slope of the relationship between DM and GY was similar for genotypes across all pooled means combining environment and management, meaning the genotypic differences in the ability to convert DM to yields is relatively consistent across a broad range of environments that differ in potential yield and biomass production (**Box Figure 1**). However, intercepts differed significantly between cultivars. Longsword had a significantly ($P < 0.01$) higher intercept than DS Bennett and Kittyhawk, this means Longsword is partitioning biomass more efficiently than other genotypes in low yielding environments and the slower developing cultivar DS Bennett had a higher HI and yield at Yarrawonga as it partitioned biomass more efficiently at higher yielding environments.

Monaghan et al. (2001) proposed that the deviation from the regression line between grain yield and grain protein could be used to identify genotypes having a lower or higher protein than expected from their GY. A similar approach could be used for grain yield and dry matter. Using mean deviation values obtained from across a wide range of environments it was possible to identify cultivars that deviated positively or negatively from the regression line regardless of the management factor, showing DM/GY deviation has a genetic basis. Genotypes with a positive deviation consistently yielded higher than those with a negative deviation (**Box Figure 2**). Longsword had a higher mean deviation at Loxton in both seasons and DS Bennett was higher at Yarrawonga meaning they partitioned biomass more efficiently at those respective sites. The negative deviation in the genotype Kittyhawk describes its poor partitioning and it achieves lower grain yield for a given dry matter compared to other varieties.

The G × E interaction observed in these data is likely a function of flowering time and highlights why adapting phasic development to the environment to ensure an optimal flowering time remains one of the critical factors in achieving a high HI in water-limited environments and should not be overlooked in the quest for higher HI through partitioning traits. This enables the crop to produce sufficient biomass by anthesis and minimizes losses in floral fertility from heat, frost and water stress, while leaving sufficient water for grain filling (Passioura and Angus, 2010; Flohr et al., 2018b). The flowering stability and improved biomass potential of cultivars like Longsword and improved grain number potential of DS Bennett pave the way for more genetic progress on other traits strongly correlated to improved HI



BOX FIGURE 1 | The aboveground biomass at maturity (t/ha) plotted against grain yield (t/ha) for genotypes DS Bennett (● $y = 0.30x + 0.37$, <0.001, $R^2 = 0.93$), Kittyhawk (■, $y = 0.30x + 0.043$, and <0.001, $R^2 = 0.84$) Longsword (▲, $y = 0.26x + 0.47$, <0.001, $R^2 = 0.84$). Data points are contributed by management × environment combinations applied to increase HI within each genotype (n = 32 per genotype).



BOX FIGURE 2 | (A) Boxplots comparing the variation in the DM/GY residual deviation of three cultivars DS Bennett, Kittyhawk, Longsword over 4 environments Loxton 2017 (i), Loxton 2018 (ii), Yarrawonga 2017 (iii), and Yarrawonga 2018 (iv) contributed by all management practices at each site to increase HI. **(B)** The relationship between the DM/GY deviation and grain yield across all G × M combinations at 4 sites, Loxton 2017 (●, $y = 0.42x + 2.32$, $P < 0.001$, $R^2 = 0.64$), Loxton 2018 (○, $y = 0.41x + 1.62$, $P < 0.001$, $R^2 = 0.83$), Yarrawonga 2017 (■, $y = 0.39x + 3.56$, $P < 0.001$, $R^2 = 0.96$), and Yarrawonga 2018 (□, $y = 0.38x + 0.81$, $P < 0.001$ $R^2 = 0.94$). (n = 24 per site).

that this could be achieved more rapidly through continued selection for phenology adapted to target environments and possibly early generation selection of partitioning traits such as HI and fruiting efficiency.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

KP and JH conceived and designed the experiments. KP, MS, and JH conducted the experiments and performed the data collection. KP performed data analysis and drafted the manuscript. JH made substantial contributions to data analysis and interpretation, as well as manuscript writing. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2020.00994/full#supplementary-material

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Impacts of G x E x M on Nitrogen Use Efficiency in Wheat and Future Prospects

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Globally it has been estimated that only one third of applied N is recovered in the harvested component of grain crops. This represents an incredible waste of resource and the overuse has detrimental environmental and economic consequences. There is substantial variation in nutrient use efficiency (NUE) from region to region, between crops and in different cropping systems. As a consequence, both local and crop specific solutions will be required for NUE improvement at local as well as at national and international levels. Strategies to improve NUE will involve improvements to germplasm and optimized agronomy adapted to climate and location. Essential to effective solutions will be an understanding of genetics (G), environment (E), and management (M) and their interactions (G x E x M). Implementing appropriate solutions will require agronomic management, attention to environmental factors and improved varieties, optimized for current and future climate scenarios. As NUE is a complex trait with many contributing processes, identifying the correct trait for improvement is not trivial. Key processes include nitrogen capture (uptake efficiency), utilization efficiency (closely related to yield), partitioning (harvest index: biochemical and organ-specific) and trade-offs between yield and quality aspects (grain nitrogen content), as well as interactions with capture and utilization of other nutrients. A long-term experiment, the Broadbalk experiment at Rothamsted, highlights many factors influencing yield and nitrogen utilization in wheat over the last 175 years, particularly management and yearly variation. A more recent series of trials conducted over the past 16 years has focused on separating the key physiological sub-traits of NUE, highlighting both genetic and seasonal variation. This perspective describes these two contrasting studies which indicate G x E x M interactions involved in nitrogen utilization and summarizes prospects for the future including the utilization of high throughput phenotyping technology.

Keywords: wheat, G x E x M, nitrogen use efficiency, yield, long-term experiments, phenotyping

INTRODUCTION

Evaluation of crop performance needs to consider genetic variation (G), environmental conditions such as climate (including annual variability) and location (E), together with farm agronomic management (M). It is the combination of these parameters and their interactions (G x E x M) which will determine sustainable and secure crop yields. Each parameter is composed of, or determined by, specific factors as indicted in **Figure 1**. Breeders continually seek to improve performance in terms of yield potential, improved quality and resistance to stress, both biotic and abiotic, by introducing new, mostly higher yielding varieties to compete and succeed in a commercial environment. In addition, management practices evolve, making better use of improved technology and knowledge as well as new varieties. Principal challenges are tackling pest and disease resistances whilst having to cope with a reducing range of pesticides, due to legislation banning some chemistry and requirements for increased environmental protection, thereby setting limits on chemical use. At the same time, reducing farmer incomes in many regions, with costs increasing disproportionately to output prices, alters the economics of wheat production, with a greater yield response required to cover input costs such as fertilizers.

Globally, wheat yields have steadily increased over time as a result of genetic improvement and better agronomy. Regional wheat yields also differ considerably across the globe and locally vary on an annual basis, primarily depending upon fluctuating climatic conditions, but also as a result of pest and pathogen pressures. Plant breeding seeks to increase yield potentials and produce more resilient germplasm able to resist these abiotic and biotic stresses. Agronomic practice also seeks to negate or at least moderate the influence of these factors and enable farmers to approach yield potentials for any particular crop and environment. In recent years the trend of increasing annual yields of some crops may have plateaued in some environments, for example wheat in northwest Europe (Grassini et al., 2013). Whilst the reasons for this are multifold, overcoming such yield limitations will require both genetic and agronomic approaches and will need to account for the influence of climate change. Whilst major agronomic developments have had large impacts on yield in the past, in more recent times genetic improvement has been increasingly important for crops such as wheat (Mackay et al., 2011). Anticipating future climatic impacts on yield will require the understanding of genetic, management and environmental effects, and importantly their interactions.

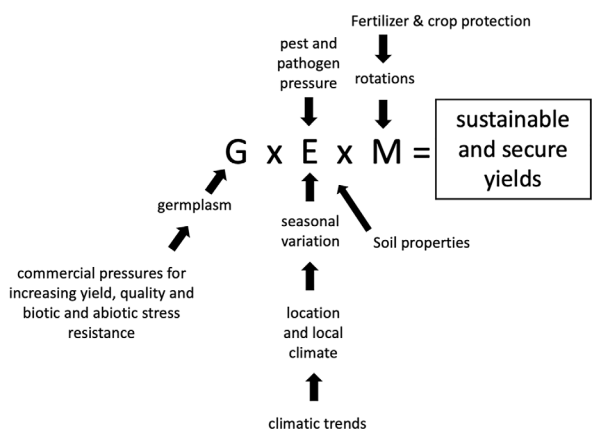

FIGURE 1 | G x E x M is influenced by multiple factors but ultimately determines sustainable and secure crop yields.

The need to improve yields with efficient fertilizer use has led to a number of G x E studies on breeding trends for wheat crop improvement and NUE traits specifically. For example studies have focused on partitioning of N between tissues (Foulkes et al., 1998; Gaju et al., 2011; Barraclough et al., 2014), variation in photosynthesis and impacts on yield potential (Gorny et al., 2006; Gaju et al., 2016), and kinetics of senescence which influence both yield potential and nitrogen remobilization and partitioning (Gaju et al., 2011). Variation in NUE traits has also been shown in an analysis of historical wheats and substantially explained by phenological and morphological traits such as flowering time and height (Guttieri et al., 2017). Other germplasm studies have focused on traits relating to abiotic stresses such as water use efficiency, simultaneously linking environmental stress to grain N traits (Sadras and Lawson, 2013). Quality traits, including those associated with N content, may be genetically controlled, or may be strongly influenced by environment, as shown by an analysis of data on 316 German varieties (Laidig et al., 2017).

A widespread management strategy which has a major impact on crop performance and has implications for NUE is crop rotation. Individual crops should not be considered in isolation and NUE should be evaluated as part of the whole cropping system when considering economic or environmental impact. For example, one modeling study highlighting the importance of looking at the cropping system and not just individual crops, clearly identifies that NUE of one crop will impact on succeeding crops (Dresboll and Thorup-Kristensen, 2014).

Further management practices critical in influencing NUE will be the variable utilization of N-fertilizer depending on timings, amounts and chemical formulation. For example, coated urea for controlled release of N, more effective timing of applications, and appropriate dose rates, taking into account soil N supply, to optimize yield and quality whilst minimizing losses and avoiding contravening legislation. A recent overview outlining strategies for reducing crop N requirements highlights the importance of taking a holistic view combining elements of improved germplasm and agronomy (Swarbreck et al., 2019).

DEFINING NITROGEN USE EFFICIENCY

To consider the impacts of G x E x M, as individual factors as well as in combination, on NUE, it is necessary to define NUE and consider how the key constituent components may be affected individually and as a whole. NUE may be considered

as the efficiency of nitrogen recovery from applied fertilizer, or from the N available to the crop, and this gives rise to the 33% efficiency of crop recovery (Raun and Johnson, 1999; Zhang et al., 2015). Alternatively, it is often considered as a productivity index and defined as the yield produced per unit of available N (Moll et al., 1982; Barraclough et al., 2010). Another distinct definition of NUE is to consider nitrogen responsiveness in combination with dose response curves to identify economic N-optima (Swarbreck et al., 2019).

Whichever definition is used, plant growth and yield require nitrogen, and furthermore are dependent upon multiple physiological processes (**Figure 2**). From this perspective, it is useful to use the productivity index and the component traits of this index (Barraclough et al., 2010) to consider impacts on G x E x M. NUE may be considered the top level trait and for wheat is the yield of grain produced per unit of N available to the crop; it is expressed as kg yield per kg of available N; it is also the product of the two second level traits, N uptake efficiency (NUpE) and N utilization efficiency (NUtE). NUpE, or sometimes biomass NUpE (BioNUpE) is the ratio of N taken up by the crop compared to what is available from the soil and applied fertilizer, and is expressed as kg N (in the crop) per kg N (available). N in the roots is ignored, but the N in the aerial biomass for wheat is that in the grain and straw combined. NUtE

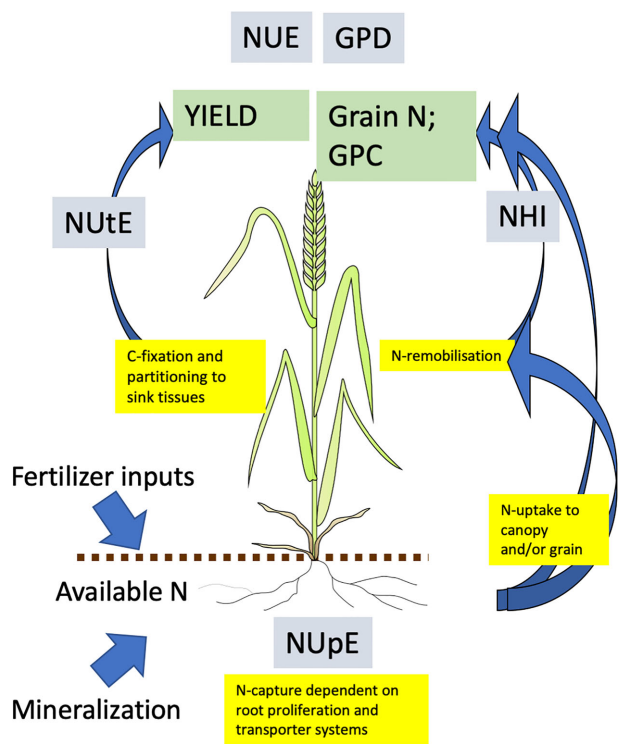

FIGURE 2 | Processes contributing to and determining NUE in wheat. Measures of nitrogen use efficiency shown in grey boxes; primary traits in green boxes; physiological process in yellow boxes. All abbreviations are in the text. Arrows indicate movement of N. Adapted from (Hawkesford, 2011).

or grain NUtE is the amount of grain produced per unit of N taken up, and is also kg (grain) per kg N. NUE is mathematically the product of NUpE x NUtE. An interaction between N-management and genetic variation of these second level traits was indicated in a two-site and four-year tial of 16 wheat genotypes, in which genetic variability in NUtE rather than NUpE was reported to be of greater significance at low N inputs (Gaju et al., 2011).

Other useful measures of efficiency of N use include the nitrogen harvest index (NHI), which is the fraction of total N taken up by the crop which is partitioned to the grain, and is a refinement of harvest index (HI) which descibes partioning of dry matter alone. However, NHI is independent of yield and uptake efficiency, and a low yielding crop may have a high NHI, but leave substantial unrecovered N in the soil. High grain protein concentration (GPC) is required for end-uses such as flour for breadmaking, however, it is difficult to increase GPC without decreasing yield due to the negative relationship between the two, as high yield usually reflects high carbohydrate content which in turn dilutes N concentration. The desired trait, to increase GPC without reducing yield, can be defined as grain protein deviation (GPD), the deviation from the negative linear relationship between yield and N concentration, and reflects an ability to acquire more N in the grain for a given yield (Bogard et al., 2010; Mosleth et al., 2015). There is some uncertainty of the physiological basis of GPD but it may be related to phenology and post anthesis N uptake (Bogard et al., 2010; Bogard et al., 2011). Both GPC and GPD may be overcome agronomically with higher N-inputs, particularly later in the season when yield has been largely determined, however this inevitably leads to low NUE. Future research may develop techniques for making bread from low protein wheats, which would be a major breakthrough for increasing NUE whilst maintaining end-use suitability, although the reduced protein content may be detrimental for a healthy diet.

Each of these NUE parameters are complex traits involving many underpinning physiological and biochemical reactions and pathways. Genetic studies indicate the multigenic and heritable nature of the major traits and the underpinning processes. However, unravelling the traits and breeding for improved NUE is complex. Genetic variation in many traits is apparent in modern germplasm and to an even greater extent in historic material, landraces and wild relatives, and could be the basis for germplasm selection. Yield is commonly the major commercial target for selection, usually at a constant N input, hence selection for NUE and NUtE is consequentially also selected for. Differentiation between NUpE and NUtE is not made consciously, however higher yielding, high protein genotypes (and hence high GPD types) will have high NUpE also. Efforts have been made to consider management protocols (M) by including selection at different N-inputs (Ortiz-Monasterio et al., 1997), however a common assumption is that ranking of variety performance is independent of N-availability. Growers will also be looking to maximize profitability, which may be different from maximizing NUE, particular if they are aiming for a quality market.

Arguably the greatest genetic improvement (G) has been the introduction of short straw (dwarf) varieties, and as a

consequence, HI and NHI have increased. The immediate effect is that biomass allocation to the grain is favored, maximizing grain yield at the expense of straw biomass. Another direct consequence of utilizing dwarf varieties is that the reduced stature facilitates resistance to lodging, a problem particularly encountered at high levels of N fertilization, particularly when combined with conditions of high wind and rainfall. The ability to exploit higher N-rates has led to a management strategy (M) of increased N-inputs, which promotes greater yields but at lower efficiency. Higher N fertilization can increase disease and weed pressure, requiring additional agrochemical inputs.

The chief environmental factors (E) consider location (and soil type) and local biotic and abiotic stresses. In the latter case heat and drought are the most major impactors limiting yield and decreasing N requirements (Halford, 2009). Long term environmental factors will be global temperature and CO_2 trends, which are affecting yield potentials and can be predicted to have substantial influences in the future by altering timing of phenology or favoring photosynthetic processes determining NUtE (Semenov and Shewry, 2011; Asseng et al., 2019). Climatic changes will also impact on rainfall patterns and influence nutrient availability, requiring optimized root related traits favoring high NUpE.

These genetic, environmental and management interactions in nitrogen fertilizer use and expression of crop NUE traits are amongst the clearest examples of the importance of G x E x M. Fertilizer use underpins crop performance and the interactions between these factors is complex but vital for efficiency. An exemplar dataset is described in the next section.

BROADBALK AS A HISTORIC EXEMPLAR G X E X M EXPERIMENT

The Broadbalk long term experiment, which was initiated in 1843 at Rothamsted Experimental Station, in the United Kingdom, is the world's oldest continuously running agricultural experiment (Johnston and Poulton, 2018). Originally conceived as an investigation into nutritional requirements for wheat growth, the continuous records, varied inputs and the modifications to crop management that have been put in place over the course of the experiment, coupled with a range of varieties grown, each for periods of several years, contribute to making this an exemplar long term G x E x M experiment. The experiment has been recently fully described and datasets are available electronically on request (Johnston and Poulton, 2018; Perryman et al., 2018). Yields from 1852 to 2016 for selected treatments are shown in **Figure 3**. Long term trends in yield responses are clearly seen, and whilst year to year variation is observed, this is not apparent in the figure as the data is presented as multi-year means. Due to multiple factors included over time, these datasets represent a valuable resource for investigating G x E x M, and are all available on request (Perryman et al., 2018).

Progress in wheat breeding (G) is demonstrated as, since the start of the experiment, the variety planted has been changed periodically, and has been usually a variety commonly in use commercially at the time. The major change was the adoption of shorter strawed varieties from Capelle Desprez onwards in 1968. While all varieties have good yield potential, the modern shorter varieties are better adapted for the higher N-inputs, as they are less likely to lodge. The development of plant growth regulators has also enhanced the effect of shorter varieties and further reduced the occurrence of lodging.

The dataset is ideal for examining long term trends due to climatic factors (E) over a considerable period of time, however analysis is complicated by changing agronomic practice, which again, has followed typical commercial practice and, along with improving genetics and changing varieties, has contributed to increasing yields. One recent study focused on datasets from 1968 to 2016 to minimize some the impact of the changing agronomic practice but still enable longer term trends to be evaluated. This study highlighted the strong climatic influence on year to year variability of yield and N-responses in wheat, and also barley in a separate experiment, of particularly temperature and rainfall in specific months (Addy et al., 2020).

Several management interventions (M) are represented in the Broadbalk experiment. Key amongst these are the rotations and specifically the comparison between continuously grown wheat and the first wheat in a 5-year rotation comprising successive wheat crops combined with break crops. A first wheat outperforms the continuous wheat partly due to a lower root disease pressure. Other notable agronomic practices having a positive effect on crop performance are the introduction of herbicides and fungicides. While the former replaced manual weeding or fallowing, the latter became essential with increased canopy disease favored by the greater canopy biomass achieved from the addition of high rates of nitrogen. The key agronomic treatments with respect to NUE are the differential rates of N, with higher N inputs resulting in increased yield, particularly with modern varieties, variations in the patterns of applications (single versus split doses) and forms of applied N (inorganic versus organic sources). The Broadbalk experiment has also been used to investigate, utilizing buried drains, the detrimental effects of N leaching, which occur following excess or inappropriately timed N applications, and will reduce NUpE.

As illustrated above, the Rothamsted "classical" long-term trials are an ideal dataset to examine long term trends due to climatic factors over a considerable period of time, since their inception in 1843. However, for any single year these trials lack the multi-germplasm genetic factor. Therefore many recent trials have sought to introduce genetic variation by working with germplasm panels or multi variety datasets (Foulkes et al., 1998; Gaju et al., 2011; Mackay et al., 2011; Sadras and Lawson, 2013; Guttieri et al., 2017; Laidig et al., 2017). One such study is described below, and early data were reported by Barraclough et al. (2010).

RECENT WHEAT GERMPLASM STUDY IN THE UK FOCUSED ON NUE

The Wheat Genetic Improvement Network (WGIN) germplasm diversity trial is an example of a multi-variety, multi-N treatment series of trials conducted over multiple years. Data from the initial years (2004–2008) of these trials reported variation in yield and N-

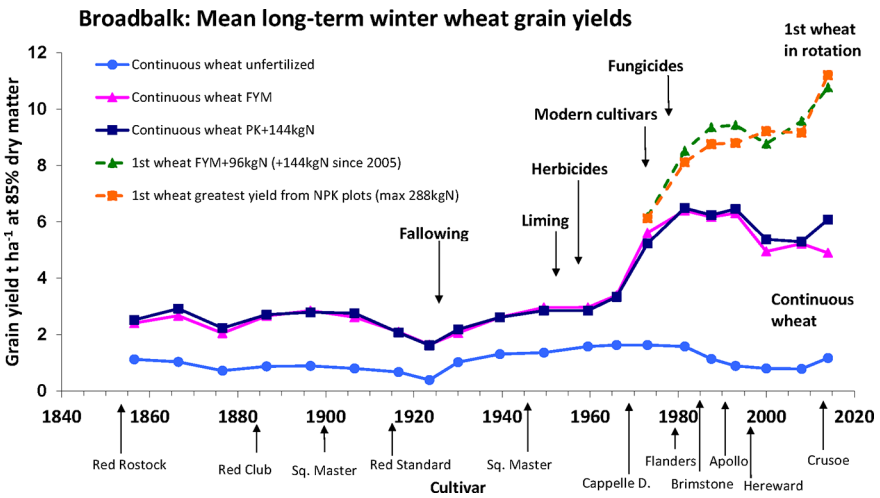

FIGURE 3 | Yield data for selected treatment on the Broadbalk long term experiment at Rothamsted from 1852 to 2016. Taken from 'Broadbalk mean long-term winter wheat grain yields' (Rothamsted-Research, 2017) and used with permission under a creative Commons Attribution 4.0 International Licence.

responses and contributing physiological processes (Barraclough et al., 2010; Barraclough et al., 2014). The trials have continued to the present date and have involved a large panel of modern commercial hexaploid wheats (varieties introduced between 1964 and 2016) and data is summarized here for trials from 2004-2019 (**Figures 4–6**). All data are available on the WGIN website (http://www.wgin.org.uk). In most years there were four N rates, from zero to 350 kg N/ha/yr, which represents no input through to excess applied N. All trials were conducted following local commercial agronomic practice, at the Rothamsted Farm in Hertfordshire in the UK. Whilst more than 60 varieties were examined in total, a smaller subset of 15 core varieties have been grown for most years. The mean grain yield trends of this core set for the 4 N rates over the period of the trial are presented in **Figure 4**. A substantial yield increase in response to fertilizer (N100, N200, and N350) compared to no fertilizer (N0) is seen for all years. A modest increase is seen for rates above 100 kg N/ha (N100), however there was little difference between the two higher rates of 200 and 350 kg N/ha, N200 and N350, respectively. Substantial year to year variation was apparent from 2004 to 2019, with some years having notably low yields (2007, 2010, 2016) and other years having notably higher yields (2008, 2009, 2014, 2015, and 2019). It is likely that the year to year variation was principally due to variations in weather patterns in the individual years. These annual variations have a direct impact on crop growth, and also influence management, for example, wet weather in early spring can delay N applications due to the soil being too wet to drive on with the application machinery, and similarly, wet weather in the autumn can delay drilling; both of these may affect yield and consequently NUE. The same yield variation patterns were apparent for all N levels, with little indication of any year by N interaction. Notably there were no major long-term trends apparent.

An indication of genotypic variation in a high-level nitrogen use trait, NUE, and the interaction with the N fertilizer treatments is illustrated in **Figure 5**. NUE as defined as grain yield per unit of available N (fertilizer and mineral soil N) was determined for the same panel of 15 commercial modern wheat varieties whose mean performances are presented in **Figure 4**. In **Figure 5**, variety data is presented as the means over the period 2006–2017, years for which data at all 4 N-rates was available.

Applied N impacts on yield, however this response is non-linear (see **Figure 4**), with the marginal yield increase decreasing as N rates increase, and therefore NUE progressively decreases as N-inputs increase (**Figure 5**). NUE is highest at the lowest N-rate (N0) but at this rate all varieties also have the widest range of values. There is genetic variation apparent in NUE, which reflects the range of yields, with the highest yielding varieties having the highest NUE. The ranking of the varieties at each of the N-rates is almost identical and therefore appears to be independent of the N-rate.

A more detailed analysis of G, E, M and their interactions for 4 varieties within this dataset is presented in **Figure 6**. These 4 varieties are potential milling quality varieties and are representative of the development of UK wheat over a 40 period; Maris Widgeon was introduced in 1964, Avalon 1980, Hereward 1991 and Solstice 2002. Grain NUtE is plotted against total N taken up by the crop at harvest. In each of the 3 panels the data points are highlighted with color schemes to show the distribution of responses based on variety (**Figure 6A**), year of harvest (**Figure 6B**) and N input level (**Figure 6C**), G, E, and M, respectively. The clearest clustering is due to the 4 N-rates as shown in Fig 6C and these clusters are circled in all three panels to aid visual comparisons. Overall, taking data from all N-inputs, there is a negative relationship between NUtE and N taken up. However, within an N rate, NUtE and N-uptake are poorly correlated, indicative that these are quite distinct physiological processes. **Figure 6A** illustrates that different varieties have different NUtE irrespective of the N-rate, indicative of the intrinsic yield potentials of the separate varieties, with Maris Widgeon (the oldest variety in the panel) generally having the lowest and Solstice the highest NUtE at any given N-uptake. There is no evidence that there is any

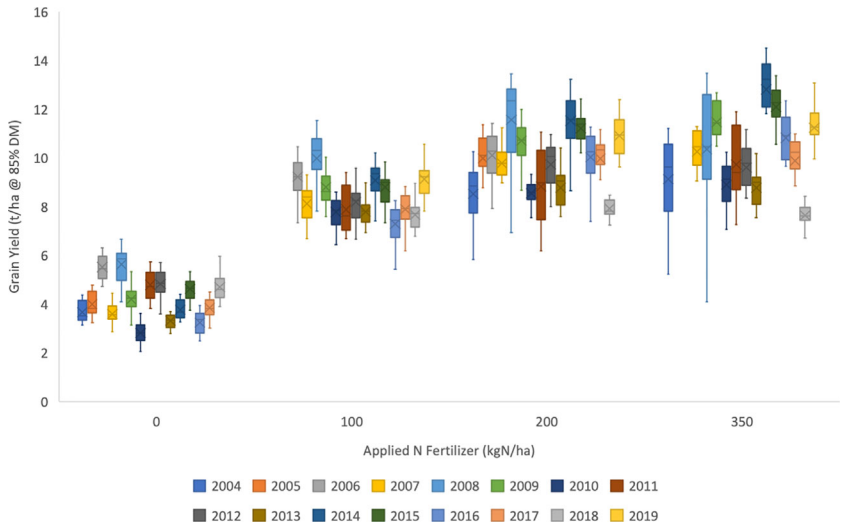

FIGURE 4 | Annual means of 15 wheat varieties (as listed in) for four rates of applied fertiliser-N (0, 100, 200, and 300 kg N/ha), for the duration of the UK Department for Environment, Food and Rural Affairs (Defra)-funded Wheat Genetic Improvement Network (WGIN) trials from 2004 to 2019). The median and upper and lower quartiles are shown for each year at each level of N. There was no N350 treatment in 2005 and 2006; no N100 in 2004 and 2005; and no N0 in 2019. Data available at http://www.wgin.org.uk and is described in (Barraclough et al., 2010). Maris Widgeon, Paragon and Soissons outliers were excluded from the plot.

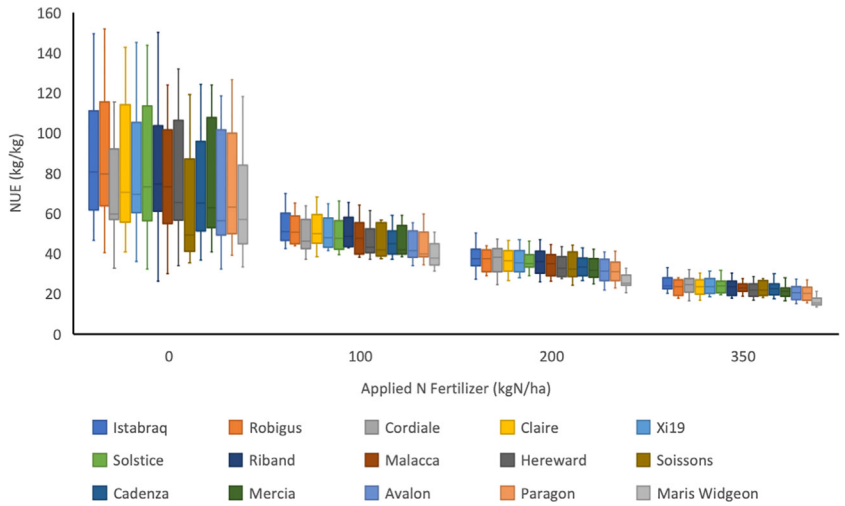

FIGURE 5 | Calculated NUE (kg/kg) for 15 wheat varieties in a UK trial between 2006 and 2017 grown at four levels of nitrogen fertilisation (0, 100, 200 and 350 kg N/ha; N0, N100, N200 and N350, respectively). Soil available N ranged from 25.6 to 115.7. The median and upper and lower quartiles are shown for each cultivar at each level of N. There was no N350 treatment in 2006, and no Soissons data in 2017. The trial was located at Rothamsted Research in the UK and was part of the UK Department for Environment, Food and Rural Affairs (Defra)-funded Wheat Genetic Improvement Network (WGIN) project. Data available at http://www.wgin.org.uk. Malacca and Maris Widgeon outliers were excluded from the plot.

relationship of variety to N-uptake for any given N-rate. Examination of Fig 6B indicates some weak clustering of data points due to year of the trial, reflecting higher or lower yielding years. **Figure 6C** clearly indicates the clustering of data points due to the N-rate. N uptake increases with increasing N-rate. Higher N-availability promotes biomass yield (which will increase NUE), increasing total N-uptake and promotes higher grain N-content (which will decrease NUE) in terms of concentration (data not shown). NUtE is notably higher at the lowest N-rates because of the non-linear relationship between yield and N-rate, as also seen in

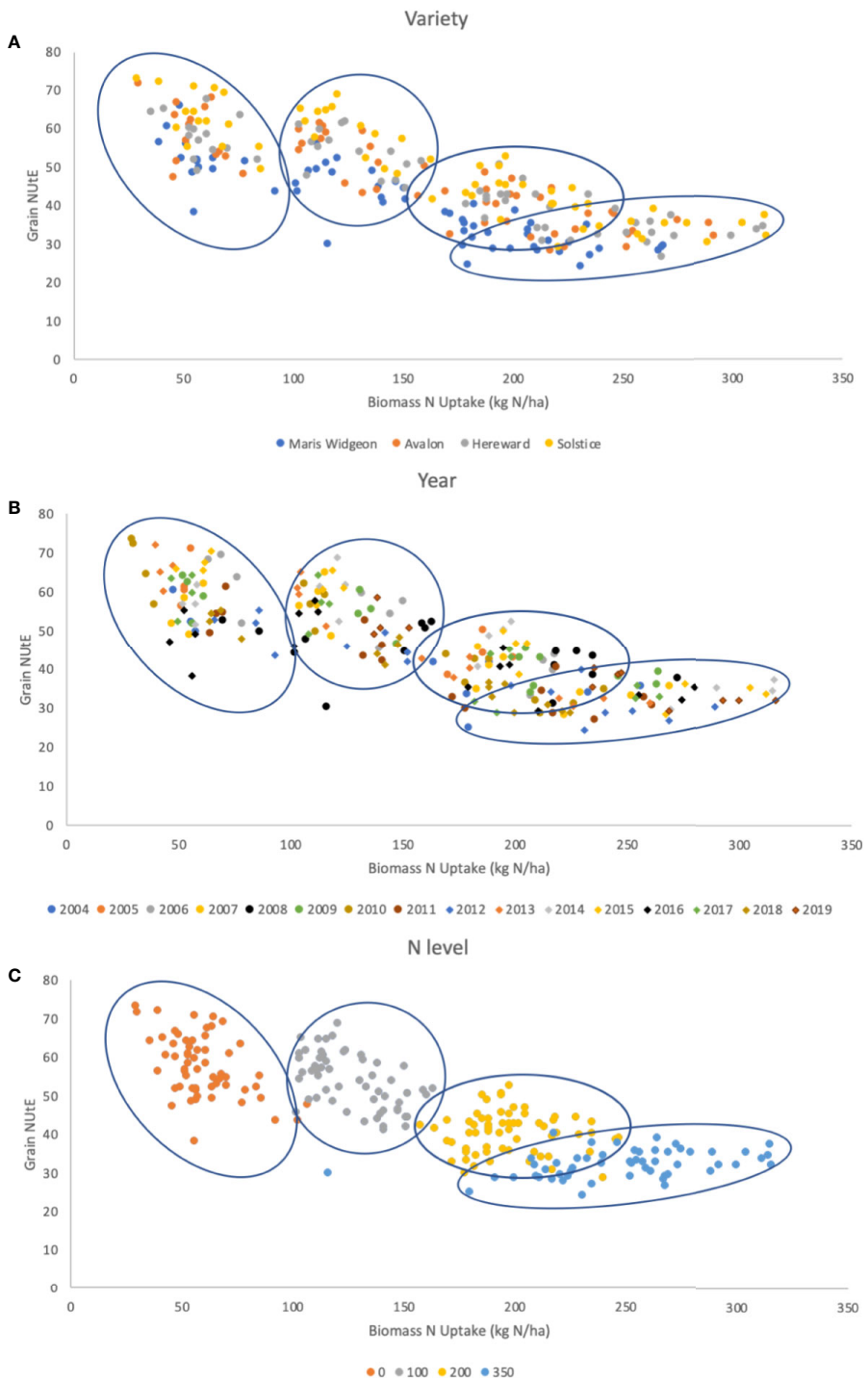

FIGURE 6 | G x E x M for the relationship between grain NUtE and total biomass N uptake. Data are for 4 varieties (G), Maris Wigeon, Avalon, Hereward, and Solstice, for trials harvested from 2004 to 2019 (E), for at 4 different N input rates (M), 0, 100, 200, and 350 kg N/ha. Data points are colored to indicate **(A)** G, **(B)** E, and **(C)** M. The clusters of data points apparent due to the different N-inputs [panel **(C)**] are circled in each of the panes **(A–C)**. Slopes, intercepts and R^2 of data points for **(A)**: overall -0.129, 66.23, 0.666; Maris Widgeon -0.134, 60.374, 0.746; Avalon -0.1322, 67.177, 0.7273; Hereward -0.1243, 66.843, 0.7959; Solstice -0.141, 72.97, 0.8058. Slopes, intercepts and R^2 of data points for **(C)**: overall -0.129, 66.23, 0.666; N0 -0.2532, 72.613, 0.2454; N100 -0.2156, 80.99, 0.2903; N200 -0.0162, 43.367, 0.0038; N350 0.0354, 23.272, 0.1438. There were no significant regressions based on year **(B)**. Data available at http://www.wgin.org.uk.

Figure 4. Within any individual N-rate there is no strong correlation evident between NUtE and N taken up, underling the independent nature of these traits as noted above (see **Figure 2**) and additionally reflecting the year to year variability of performance, shown also in **Figure 4**. At the lower N-rates, and particularly at zero (N0), N-uptakes varied widely with little variation in NUtE; this may at least partially due to NUpE reflecting variations in soil N seen between sites used in individual years of the trial.

In summary, within this germplasm panel, the N-rate, as the major management treatment (M), is the dominant factor. Variety (G), differentiating higher and lower yielding types, and year (E) (higher and lower yielding seasons) also have roles in determining yields, N-uptakes and NUtE. Whilst all three factors and their interactions determine yield and NUE, a clear understanding of the interactions of G x E x M will require larger and more detailed datasets.

FIGURE 7 | Automated phenotyping technology. A field-located automated phenotyping system at Rothamsted Research in the United Kingdom (Virlet et al., 2017). Multiple sensors are located in a platform which can be positioned in 3 dimensions above a growing crop and can record parameters relating to growth and health.

PROSPECTS: RESEARCH GAPS AND USING AUTOMATED PHENOTYPING FOR HIGH RESOLUTION DATA COLLECTION IN FIELD STUDIES

The Broadbalk experiment and similar trials are extremely useful for examining long term trends in (wheat) crop performance and additionally illustrates importance of variety and management. Trials of diversity panels, such as that described here, enable an examination of the genetic components influencing crop performance, however examining the importance of environment and management become a major undertaking in terms of scale and investment of resources. A major gap in effective G x E x M analysis is in having enough contrasting environments with appropriate germplasm and management ranges. An elegant solution is to conduct meta-analyses, bringing together multiple studies. An example is an analysis of 55 individual studies conducted between 1974 and 2014 in multiple global locations, in which a clear non-linear relationship between yield and N uptake was observed and indications of greater opportunities for improved NUtE at higher yielding sites (de Oliveira Silva et al., 2020).

In addition to the challenges of larger trials conducted at multiple sites and in multiple years, there is an increasing demand for higher resolution data, both spatially and temporally. Solutions to this challenge exploit new technologies for automated and high throughput phenotyping, for example using remote sensing and robotics. An example of an automated robotic system is shown in **Figure 7**. This programmable system contains a range of image-based sensors with specific spectral sensitivity mounted in a positionable-platform which can be used for autonomous collection of high-resolution datasets. Plant growth and health parameters are extracted from the collected images (Sadeghi-Tehran et al., 2017; Virlet et al., 2017; Sadeghi-Tehran et al., 2019). Detailed datasets can reveal hitherto unrecognized information concerning the genetic control of performance revealed at different developmental stages (Lyra et al., 2020). Similar datasets can be obtained from drone-based platforms which are able to cover larger trials at multiple sites, but require greater manual inputs for collection (Holman et al., 2016; Holman et al., 2019).

For most high throughput technologies emphasis has been placed on growth and biomass accumulation, both indicators of final performance and yield. Such data may be derived from height measurements or spectral indices, indicative of canopy cover. In addition, spectral parameters, including the growth indices mentioned above, are measures of chlorophyll content and hence the nitrogen status of the canopy. These measurements can be used to assess N uptake and be indicative of NUE parameters. As spectral measurements are non-destructive there is the opportunity to measure in real time, continuous kinetics of N uptake and utilization.

Further applications of these phenotyping approaches will aid pre-breeding and breeding programmes for improved varieties, improved management practices, and better understanding of environmental impacts, and will advance the development of precision farming technologies. Technology, both hardware and interpretive algorithms developed as a result of these platforms can be transferred to less sophisticated and cheaper devices suitable for mass use by growers. Together these advances in accurate and high-resolution monitoring of crop performance will facilitate crop production, best agronomic practice, and minimize environmental impacts on broad field commercial cropping.

AUTHOR CONTRIBUTIONS

MH and AR contributed equally to all aspects of this manuscript.

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