frontiers | Frontiers in Sustainable Food Systems

TYPE Original Research
PUBLISHED 30 January 2026
DOI 10.3389/fsufs.2025.1741810

OPEN ACCESS

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RECEIVED 07 November 2025
REVISED 09 December 2025
ACCEPTED 23 December 2025
PUBLISHED 30 January 2026

CITATION
Silva P, Opazo M and Figueroa-Bustos V (2026) Chilean wheat (*Triticum aestivum* L.) landraces with greater biomass, yield stability, and intrinsic WUE than modern varieties are an opportunity for adaptation to severe drought areas. *Front. Sustain. Food Syst.* 9:1741810. doi: 10.3389/fsufs.2025.1741810

Chilean wheat (*Triticum aestivum* L.) landraces with greater biomass, yield stability, and intrinsic WUE than modern varieties are an opportunity for adaptation to severe drought areas

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In Mediterranean environments, wheat often faces water scarcity during grain filling. The spike growth period may also be affected under severe drought conditions, which are becoming increasingly frequent due to ongoing climate change. Selection for high yield potential has led to yield improvements in wheat under moderate drought conditions, but not under severe drought. Yield stability, biomass, and water-use efficiency (WUE) are important genotypic traits under drought. Under severe drought, landraces represent a valuable source of adaptative traits. In this study, we analyzed yield, stability, biomass and water use efficiency (WUE) in seven Chilean landraces, potentially better adapted to severe drought conditions, and compared them with three modern varieties across 10 contrasting environments, including those affected by severe drought. Chilean landraces analyzed in this study exhibited greater biomass, intrinsic WUE (iWUE), yield stability, and biomass stability than the modern varieties. In one group of landraces, this performance appears to be explained by a longer time to anthesis, while in the other group it would be due to other adaptive traits that warrant further investigation. Yield stability and biomass stability are key traits for adaptation to severe drought, and achieving them requires selection for higher biomass and iWUE. In this context, the Chilean wheat landrace, Furfuya, stands out as a valuable genetic resource for national breeding programs aiming to improve yield and yield stability in Mediterranean environments affected by severe drought.

KEYWORDS

AMMI, discrimination ^{13}C, Mediterranean, above-ground biomass, GGE

1 Introduction

Drought is considered the main environmental factor limiting plant growth and crop yield worldwide, especially in Mediterranean regions (Chaves et al., 2003). These environments commonly experience drought events during spring and summer, and wheat often faces water scarcity during the grain filling period, however under severe drought the spike growth period may also be affected (Acevedo et al., 1999). Blum (2011) suggests that severe drought conditions may also occur in environments with yields below 4000 kg ha^{-1}. The central zone of the Chilean Coastal Mountain Range shares environmental characteristics with the ICARDA E2 mega-environment and frequently experiences severe drought events (Acevedo et al., 1999; Tadesse et al., 2016). In this context, climate change projections indicate that minimum and maximum temperatures in Chile are expected to increase by 2 °C, while precipitation could decrease by more than 40% by the end of the twenty-first century (Araya-Osses et al., 2020). This is expected to have a strong impact on Chile, one of the world's largest countries in per capita bread consumption (Guzmán-Pincheira et al., 2023; Llorca-jaña et al., 2022). The main strategy to address this problem has been irrigation; however, this approach is unsustainable due to a range of environmental, physical, and economic issues, that are further exacerbated by climate change (Araus et al., 2008). A more sustainable solution involves the development of varieties adapted to drought-prone conditions. Although genetic breeding programs have focused on selecting for high yield potential, this strategy is effective under moderate drought conditions but fails under severe drought stress (Foulkes et al., 2009).

In severe drought-prone environments, yield stability is a key criterion for both breeders and farmers, particularly given the increasing frequency of extreme weather events (Bocci et al., 2020; Subira et al., 2015). Under these conditions, crossover interactions between genotypes occurs at an environmental index (defined as the mean genotypic yield) of around 3000 to 4000 Kg ha^{-1} (Blum, 2011). Bellow this threshold, locally adapted germplasm becomes increasingly important (Ceccarelli, 1994).

Landraces perform well in marginal environments and tend to be more resilient than modern varieties (Blum, 2011; Reynolds et al., 2015; Morgounov et al., 2016; Baboev et al., 2021). The characterization of wheat landraces suggests that some exhibit greater yield stability than modern varieties (Migliorini et al., 2016; Bocci et al., 2020) and can achieve relatively higher yields under drought conditions (Blum, 2011). Therefore, landraces could play an important role in advancing the understanding of adaptation mechanisms for drought prone environments and serve as a valuable genetic resource for breeding programs (Lopes et al., 2015; Reynolds et al., 2015; Migliorini et al., 2016; Oumata et al., 2023).

Some wheat breeding programs have focused on targeting specific traits aimed at enhancing water-limited potential yield (Ys) (Richards et al., 2002). Ys refers to the yield of a cereal crop when drought is the sole limiting factor (Passioura, 2006, 1977). It depends on three components: the amount of water transpired (T), the water use efficiency (WUE) for biomass production (i.e., biomass produced per unit of transpired water) and the harvest index (HI).

$$Ys = T \text{ x } WUE \text{ x } HI \tag{1}$$

Improvements in Ys require increased biomass production, which can be achieved through greater T and/or higher WUE. In water limited environments, WUE is closely associated with increased biomass when soil water availability is low (Equation 1) (Reynolds et al., 2015). According to physiological theory, ^{13}C discrimination can serve as a marker for improve WUE in wheat under drought conditions as it has been negatively associated with intrinsic WUE (iWUE) when assessed in plant dry matter (Yasir et al., 2013). Landraces are capable of maintaining higher iWUE as suggested by studies on Spanish landraces with phenology similar to that of modern varieties, which exhibited lower ^{13}C discrimination compared to modern Spanish varieties (Araus et al., 2013). WUE is considered a desirable trait in breeding programs aimed at selecting genotypes with higher yield under drought stress (Reynolds et al., 2015).

In this context, wheat landraces perform better under drought conditions due to their higher biomass production and adaptive physiological traits (Reynolds et al., 2007). Chilean landraces have been cultivated by farmers for centuries in a Mediterranean environment characterized by severe drought, eroded soils and isolated drylands in the central zone of the Chilean Coastal Mountain Range (Riquelme et al., 2004; Silva et al., 2017). We hypothesize that locally adapted Chilean wheat landraces are a valuable source of adaptive traits (stability, biomass, WUE) for severe drought conditions. The characterization of local wheat landraces may therefore help identify adapted germplasm for severe drought conditions. In this study, we analyzed yield, stability, biomass and water use efficiency (WUE) under severe drought conditions for seven Chilean landraces, potentially better adapted to severe drought areas, and compared them with three modern varieties across 10 different environments.

2 Materials and methods

2.1 Environment description

Multi-environment trials (METs) of wheat genotypes were conducted over 2 years in the Metropolitan and Ñuble regions of Chile (Table 1). The Ñuble region accounts for approximately 18% of the 193613 ha sown to wheat annually in Chile (ODEPA, 2024). It represents the Coastal Mountain Range, the oldest wheat producing area in the country (Cortes et al., 2022), and is considered a traditional zone for the cultivation of local wheat varieties (Silva et al., 2017). The trials included two well-watered environments in 2017 and eight rainfed environments over 2 years, 2016 and 2017 (Table 1).

The climate in Antumapu (Metropolitan region) is classified as semi-arid Mediterranean, with a mean maximum temperature of 28.2 °C in January and a mean minimum temperature of 4.4 °C in July. The average annual rainfall is approximately 330 mm (Uribe et al., 2012). The soil is of alluvial origin (Mollisol) characterized by a sandy clay loam texture and shallow depth (CIREN, 1996).

The climate in Antiquereo, San José, San Juan, and Pachagua (Itata valley, Ñuble region) is Mediterranean characterized by hot, dry summers. The mean maximum temperature is 31.3 °C in January, and the mean minimum temperature is 4.6 °C in July. The mean annual rainfall is 641.7 mm (Novoa et al., 1989). The soil is of granitic origin (Alfisols) and is a clay loam soil (Riquelme et al., 2004).

The climate in Santa Rosa (Chillán, Ñuble region) is classified as humid Mediterranean. The mean maximum temperature in January is 28.6 °C, and the mean minimum temperature in July is 3.0 °C. The mean annual rainfall is 1270 mm (Novoa et al., 1989). The soil is a silty loam volcanic ash (Melanoxerands) (del Pozo et al., 2022).

2.2 Plant material and experimental design

Ten genotypes were selected for this study, including seven landraces of the dryland Coastal Mountain Range (Blanco, Cebolla, Chucho, Colorado, Furfuya, Legul and Milufen) and three modern varieties (Kipa INIA, Onda and Pandora INIA). The criteria for

TABLE 1 Characterization of 10 environments.

Location	Year	Environment	Latitude	Longitude	Altitude (masl)	Irrigation	Previous crop	Soil type	Sowing date (dd/mm/yy)
Antiquereo	2016	Aq_16	36°26′57″S	72°30′50″O	101	Dryland	Pasture	Alfisol	17-05-2016
Antumapu	2017	Ar_17	33°34′11″S	70°37′50″O	570	Irrigated	Fallow	Mollisol	21-06-2017
Antumapu	2017	As_17	33°34′11″S	70°37′50″O	570	Dryland	Fallow	Mollisol	15-06-2017
San José	2016	Jo_16	36°24′44″S	72°30′56″O	127	Dryland	Wheat	Alfisol	27-05-2016
San José	2017	Jo_17	36°24′44″S	72°30′56″O	127	Dryland	Faba bean	Alfisol	31-05-2017
San Juan	2016	Ju_16	36°23′23″S	72°29′43″O	119	Dryland	Oat	Alfisol	24-05-2016
San Juan	2017	Ju_17	36°23′23″S	72°29′43″O	119	Dryland	Pea	Alfisol	29-05-2017
Pachagua	2016	Pa_16	36°26′03″S	72°32′06″O	88	Dryland	Pea	Alfisol	27-05-2016
Pachagua	2017	Pa_17	36°26′03″S	72°32′06″O	88	Dryland	Oat	Alfisol	02-06-2017
Santa Rosa	2017	SR_17	36°32′06″S	71°54′59″O	195	Irrigated	Oat	Andisol	06-07-2017

identifying a genotype as a landrace included *in situ* collection and continuous cultivation by local farmers since before the release of the first semi-dwarf variety (Silva et al., 2017). The three modern varieties, Onda, Pandora INIA and Kipa INIA were released by Instituto de Investigación Agropecuaria (INIA) in 1982, 2003 and 2008, respectively (Matus et al., 2011; Mellado and Madariaga, 2003). In this study, 'modern varieties' refers to Chilean wheat varieties released during the post-Green Revolution (post-GR) period. Further details on the genotypes are provided in Table 2.

The experimental design was a completely randomized block design with three replications. Each plot consisted of eight rows of 4 m long and 0.2 m apart.

2.3 Crop management

Wheat seeds were disinfected with Mancozeb and Carbendazim at a rate of 125 g per 100 kg of seeds. Sowing was performed by hand, at a seeding rate of 200 kg ha^{-1}, achieving a target plant density of 380 plants m^{-2} (400 seeds m^{-2}, 95% germination). Every experiment was fertilized at sowing with 50 kg N ha^{-1} and 100 kg P_2O_5 ha^{-1}. Diseases, weeds, and pests were controlled to ensure good crop growth.

2.4 Data collections and measurements

Meteorological data, such as rainfall and average temperature, were collected from INIA Climatological Stations: La Platina for the Metropolitan Region, Ninhue for the Itata valley, and Quilamapu for Chillán. At each site a 60 cm deep soil profile pit was excavated to collect soil samples using cylinders at depths of 20, 40, and 60 cm. These samples were used to measure field capacity, wilting point, soil bulk density and to calculate soil water holding capacity.

Phenological development was regularly monitored using the Zadoks's scale (Zadoks et al., 1974). Flowering date (DA) was recorded when approximately 50% of the plants within each plot had reached the anthesis stage (Z6.5). DA were recorded in seven of the 10 environments and defined as the number of days from planting to flowering. Plant height was measured at harvest from the base of the plant to the top of the main spike (awns not included) in 10 individual plants. At physiological maturity, four central rows (1 m each) were harvested at ground level. Total above-ground biomass was determined, along with grain yield, number of spikes per square meter, and thousand-grain weight (TGW). Harvest index (HI), grains per spike and grains per square meter were calculated based on these measurements. All values are expressed on a dry matter basis.

Samples of 250 grains per experimental unit were collected at harvest for three environments (Pa_16; Ar_17; As_17). Each sample was dried at 70 °C for 48 h in forced air oven (Venticell, MMM Group, Deutschland). The samples were then grounded into a homogeneous powder using a power mill. Two sub-samples were taken from each sample and placed into tin and silver capsules to measure isotopic composition of ^{13}C ($\delta^{13}C$) and ^{18}O ($\delta^{18}O$), respectively. Finally, the samples were sent to the Stable Isotope Facility at the Facultad de Ciencias Agronómicas at Universidad de Chile for analysis. Samples for $\delta^{13}C$ were analyzed using elemental analyzer-isotope-ratio mass spectrometry (EA-IRMS) with an INTEGRA 2 instrument (Sercon Ltd., Crewe, United Kingdom). Samples for $\delta^{18}O$ were measured with a low temperature pyrolysis isotope-ratio mass spectrometry (LTP-IRMS) technique using an INTEGRA 2 instrument (Sercon Ltd., Crewe, United Kingdom). The standards used to measure the $\delta^{13}C$ isotopic composition were SC0465 Wheat Flour Standard OAS, and SC0465, SC0463 (Protein Standard OAS), and SC0467 (Sorghum Flour Standard OAS) as internal checks. Stable carbon isotope ($\delta^{13}C$) measurements were performed in three environments as the high cost of isotope analysis prevented sampling all 10 environments. For the measurement of the $\delta^{18}O$ isotopic composition the international standards were Spruce powder working, and USGS56 (South African Red Ivory Wood Standard), and USGS55 (Mexican Ziricote Standard) as internal checks.

Carbon isotope discrimination ($\Delta^{13}C$) was calculated following the method described by Farquhar et al. (1982):

$$\Delta^{13}C = (\delta\text{air} - \delta\text{plant}) / a\left((1 - \delta\text{plant} / 1000)\right)$$

TABLE 2 Characteristics of the varieties utilized in this study.

Genotype	Constitutor	Origin zone	Color of the wheat spike	Presence of beard	Wheat stalk thickness	Grain productivity	Use
Blanco	Landrace	Ñuble, Quirihue[2]	White	No beard	Thin and soft	Good	Handicraft
Cebolla	Landrace	Ñuble, Ninhue	Red	Beard	Thin and soft	Good	Handicraft and toasted flour
Chucho	Landrace	Ñuble, Trehuaco	Red	Beard	Very thick	Good	Cooking: mote and wheat coffee
Colorado	Landrace	Ñuble, Trehuaco	Red	Beard	Thin and soft	Not good	Handicraft and toasted flour
Furfuya	Landrace	Ñuble, Ninhue	Red	No beard	Thin and soft	Not good	Handicraft and toasted flour
Legul	Landrace	O'Higgins, Paredones	Red	No beard	Thin and soft	Not good	Handicraft
Milufen	Landrace	Ñuble, Quirihue	White	Beard	Thick and soft	Very good	Handicraft
Kipa INIA	INIA[1]		White	Beard	Very thick	Very good	Wheat flour
Onda	INIA		White	Beard	Very thick	Very good	Wheat flour
Pandora INIA	INIA		White	Beard	Very thick	Very good	Wheat flour

Adapted from Silva et al. (2017).
[1]Instituto de Investigación Agropecuaria (Chile).
[2]Region, District.

Carbon isotope discrimination during CO_2 fixation in the leaves of C3 plants is related to the ratio of intercellular to atmospheric CO_2 concentration (Ci/Ca),

$$\Delta^{13}C = a + (b - a)(ci / ca)$$

where a is the discrimination due to slower diffusion of $^{13}CO_2$ through stomata (a = 4.4%) and b is the discrimination by Rubisco against $^{13}CO_2$ (b = 27%) (Farquhar et al., 1989).

Given that leaf conductance to water vapor (gH_2O) is 1.6 times the conductance to CO_2, Δ ^{13}C can be converted to iWUE, defined as Osmond et al. (1980):

$$iWUE = A / gs = \left(1 - \left(1 - \left((\Delta - a)/(b - a)\right)\right)(ca / 1.6)\right)$$

where A is CO_2 assimilation and gs is stomate conductance, which can be simplified to.

$$A / gs = \left((Ca - Ci)\right) / 1.6$$

2.5 Statistical analysis

The analysis of variance was performed using the GLM procedure implemented in InfoStat software with the R interface (Di Rienzo et al., 2017), applying a heteroscedastic model to account for variance heterogeneity among environments. The environment was defined as the combination of location and year. Genotypes and environments were considered as fixed effects, while replicates nested within environments (location × year) were considered as random effects. A DGC test 5% significance level (α = 0.05) was used to compare both overall means and group means. The DGC is a partition test method (no overlap of letters between means) recommended to compare five or more means (Di Rienzo et al., 2002). Hierarchical cluster analysis (using Ward's method and Euclidean distances) was performed to group the genotypes based on height and days to anthesis of all samples (Szentmiklóssy et al., 2020). The cluster analysis was conducted using InfoStat software, version 2020 (Di Rienzo et al., 2020).

Additive main effects and multiplicative interaction model (AMMI) was fitted mathematically as:

$$y = \mu + G_i + A_j + \sum_{n=1}^{r} \lambda_n \xi_{ni} \eta_{nj} + \rho_{ij} + \varepsilon_{ij}$$

where Y is the yield of genotype i in environment j, μ is the grand mean, G is the genotype effect $_i$, A is the environment effect $_j$, $\sum_{n=1}^{r} \lambda_n \xi_{ni} \eta_{nj}$ is the value summatory for interaction principal component (PC), λ_n is its eigenvalue, ξ_{ni} is the eigenvector value for genotype $_i$ and component $_n$, η_{nj} is the eigenvector value for environment $_j$ and component $_n$, ε_{ij} is the error (Gauch, 2013). The model was graphically represented in a GE biplot. The same model was used for biomass. The distance from zero to the point in the PC1 represents the stability of the genotype, lower distances indicate more stable genotypes.

Sites regression model (SREG): The model to build a GGE biplot with the first two principal components (Yan and Hunt, 2001) is:

$$y_{ij} - \bar{y}_j = \lambda_1 \xi_{i1} \eta_{j1} + \lambda_2 \xi_{i2} \eta_{j2} + \varepsilon_{ij}$$

where y_{ij} is the mean yield of genotype i in environment j, $\bar{y}_j$ is the mean of the genotypes in environment j, λ_1 and λ_2 are the eigenvalues for PC1 and PC2, respectively, ξ_{i1} and ξ_{i2} are the values of genotype i in PC1 and PC2 respectively, n_{j1} and n_{j2} are the values of environment j in PC1 and PC2, respectively, and ε_{ij} is the residual term associated to the average observation of genotype i in environment j focused on the effects of environment j. The model is standardized to ensure that PC1 and PC2 are expressed in the same units.

In order to explain the variability of the genotypes and the environments with all variables evaluated, a principal component analysis (PCA) was done. Two PCAs were conducted: the first analysis considered 10 environments and 8 variables (biomass, yield, harvest index, grain per meter square, thousand grain weight, spike per meter square, grains per spike and height). The second analysis considered 10 genotypes and 14 variables (yield stability, biomass stability, days to anthesis, thousand grain weight, biomass, height, $_i$WUE, $\delta^{18}O$, spikes per meter square, plants per meter square, yield, harvest index, grains per meter square, and grains per spike).

The AMMI, SREG and PCA analyses (Figure 1) were conducted using InfoGen software (Balzarini and Rienzo, 2016; Carrera et al., 2011).

To estimate the variance components a GLM was fitted in the R software (R Core Team, 2024) using the lme4 package (Bates et al., 2015). Broad-sense heritability (*H*) was calculated as the proportion of total phenotypic variance explained by genotypic variance.

$$H = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_{ge}^2 \;/ nLoc + \sigma_e^2 / \left(nLoc\ x\ nRep \right)}$$ (Alvarado et al., 2020).

3 Results

3.1 Environment characterization

According to meteorological data, effective precipitation varied across locations from 159.9 mm in Antumapu to 572 mm in Santa Rosa in 2017. In the Itata valley, the effective precipitation increased 65% between 2016 and 2017 (Table 3). The physical soil properties varied across locations (Table 3). The available water holding capacity in the soil ranged from 65 mm in Pachagua to 183 mm in Santa Rosa (Table 3).

Table 4 shows that, across the 10 environments, biomass ranged from 4,970 to 15,367 kg ha^{-1}, while yield ranged from 1061 to 4863 kg ha^{-1}. The HI increased from 0.18 to 0.39. Thousand grain weight varied from 30 to 48 g, and the number of spikes per square meter ranged from 198 to 574 spikes. The lower number of spikes per square meter in San José was mainly attributed to poor plant establishment in this environment (r = 0,63; p-value = 0,0001; data not shown), which was assessed at the second-leaf stage (Z12, Zadoks scale) by counting the number of emerged plants per square meter in each plot.

The first two axes of PCA for environments explained 93.5% of the total variance. All environments in 2017 (except for As_17 and Jo_17) were located on the right side of the PC1; these environments had higher yield and yield components. Yield was positively correlated with biomass ($r = 0.85$, $p = 0.002$), HI ($r = 0.78$, $p = 0.008$), grains per square meter ($r = 0.96$, $p < 0.001$), grains per spike ($r = 0.82$, $p = 0.004$) and height ($r = 0.74$, $p = 0.02$) (Figure 2).

3.2 Agronomic traits and intrinsic water use efficiency in modern varieties and landraces

Given that plant height and growth cycle duration are traits that changed markedly following the Green Revolution, a cluster analysis

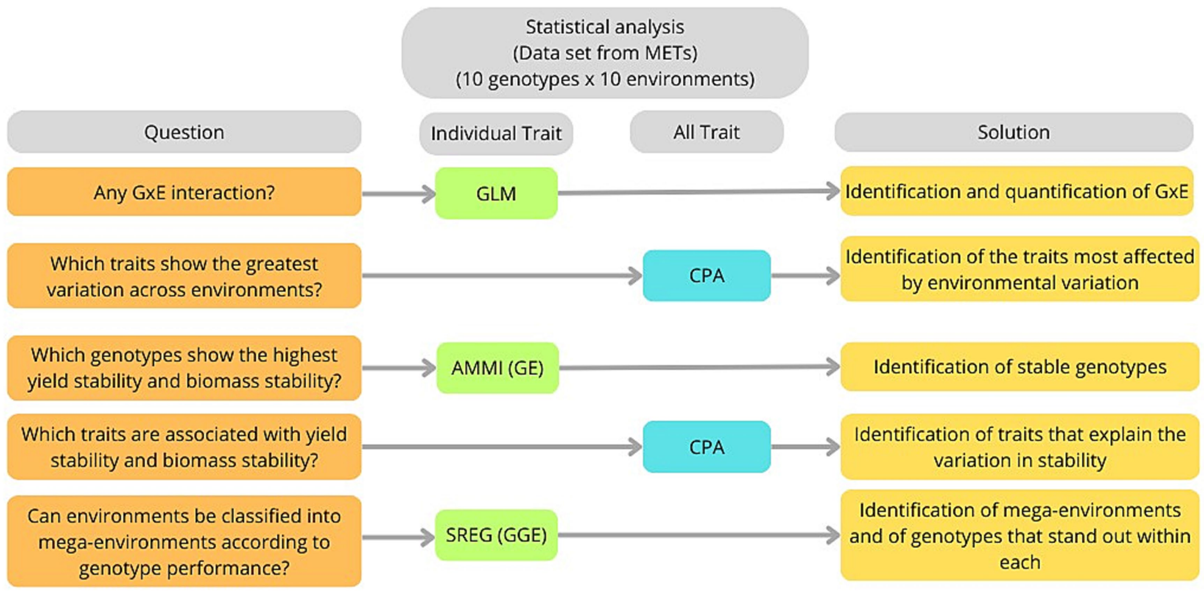

FIGURE 1
Diagram summarizing the statistical analytical framework.

TABLE 3 Climatic and soil characteristics of the 10 environments evaluated, including precipitation (PP), effective precipitation (EP), irrigation (IR), minimum and maximum temperature (T min, T max), solar radiation (RS), soil texture, bulk density (BD), field capacity (FC), permanent wilting point (PWP), available water holding capacity (AWHC) and soil water content at sowing (SWCS).

Environment	Condition	PP	EP[1]	IR	T min	T max	RS	Soil	BD	FC	PWP	AWHC	SWCS
		(mm)	(mm)	(mm)	(°C)		(MJ m^{-2})	Texture[2]	(g cm^{-3})	(%)	(%)	(mm)	(%)
Aq_16	Dryland	401.8	200.9	0	5.5	18.3	2034	Clay loam	1.64	20.9	12.7	81	18.5
Ar_17	Irrigated	159.9	159.9	92	5.8	20.6	2537	Clay loam	1.34	19.9	8.4	92	19.7
As_17	Dryland	209.0	209.0	0	5.5	20.0	2403	Clay loam	1.34	19.9	8.4	92	14.1
Jo_16	Dryland	401.8	200.9	0	5.3	18.3	1953	Sandy clay loam	1.65	22.8	12.4	104	21.6
Jo_17	Dryland	662.6	331.3	0	6.0	18.1	2544	Sandy clay loam	1.65	22.8	12.4	104	22.1
Ju_16	Dryland	401.8	200.9	0	5.4	18.4	2017	Sandy clay loam	1.66	16.8	10.3	66	16.8
Ju_17	Dryland	662.6	331.3	0	5.4	16.9	2114	Sandy clay loam	1.66	16.8	10.3	66	16.7
Pa_16	Dryland	401.8	200.9	0	5.3	18.2	1938	Clay	1.63	19.8	13.2	65	19.7
Pa_17	Dryland	662.6	331.3	0	6.0	18.2	2533	Clay	1.63	19.8	13.2	65	19.7
SR_17	Irrigated	572.0	572.0	35	4.8	17.9	3318	Silty clay loam	0.99	51.0	33.0	183	51.0

[1]Efective precipitation was estimated from Riquelme et al. (2004).
[2]The physical properties of the soil correspond to the average of samples taken at 20, 40, and 60 cm depth.

was performed based on these two variables. The results revealed two main genotype groups (Figure 3): the upper branch included the three modern varieties, while the lower branch grouped the seven landraces. Within the landrace group, two distinct subclusters were identified: Furfuya, Chucho, and Cebolla formed a separate subcluster due to their growth cycle duration being similar to that of the modern genotypes, differing by only 3 days to anthesis (DA), whereas the second subcluster differed from modern varieties by 18 days (Table 5).

All measured traits showed significant differences between landraces and modern varieties, except for spikes m^{-2}. Landraces also exhibited 9% higher total biomass and 11% lower grain yield compared to modern varieties. Biomass ranged from 8,880 to 10,718 kg ha^{-1}, while yield ranged from 2,381 to 3,032 kg ha^{-1}. Harvest index (HI) was 17% lower in landraces, with values ranging from 0.23 to 0.33 (Table 5).

Landraces showed lower $\Delta^{13}C$ and higher $\delta^{18}O$ values than modern varieties, with $\Delta^{13}C$ ranging from 15.9 to 17.7‰ and $\delta^{18}O$ from 29.5 to 33.1‰ (Table 5). Intrinsic water use efficiency (iWUE) varied from 104 to 125 µmol CO_2 mol^{-1} H_2O^{-1}, with landraces displaying a 10% higher iWUE than modern varieties (Table 5).

3.3 Genotype by environment interaction for agronomics and stable isotope traits

Environment (E), genotype (G), and their interaction (G × E) significantly affected all traits, except for $\Delta^{13}C$ and iWUE, where no significant G × E effects were detected (Table 6). Grain yield and biomass exhibited the lowest heritability estimates (0.62 and 0.69, respectively). In contrast, $\Delta^{13}C$, $\delta^{18}O$, and iWUE, which were assessed in only three environments, displayed high heritability values (0.98, 0.94, and 0.94, respectively).

3.4 Stability of yield, biomass and traits association

Based on the genotype yield means plotted against their interaction principal component axis (IPCA) scores (Figure 4), landraces exhibited greater yield stability than modern varieties, while Pandora INIA and Onda were identified as the most unstable genotypes. Regarding biomass, landraces Blanco, Milufen, and Furfuya were distinguished by their higher biomass production and greater stability compared to modern varieties. Pandora INIA and Onda exhibited both the lowest biomass production and the lowest biomass stability (Figure 5).

The first two axes of the PCA for the varieties explained 79.9% of the total variance. Landraces were positioned in the right side of Figure 6 and were associated with higher biomass, thousand grain weight, iWUE, $\delta^{18}O$, yield stability and biomass stability. Modern varieties were located on the left side of the figure and were associated with higher HI, yield, grain per square meter and grains per spike.

Yield stability was positively correlated with biomass stability ($r = 0.93$, $p = 0.0001$), biomass ($r = 0.83$, $p = 0.003$), height ($r = 0.91$, $p = 0.0025$) and iWUE ($r = 0.83$, $p = 0.003$). Biomass showed a significant associations with DA ($r = 0.73$, $p = 0.017$), harvest index (HI) ($r = -0.82$, $p = 0.003$), grains per square meter ($r = -0.68$, $p = 0.031$), height ($r = 0.82$, $p = 0.003$), and intrinsic water use efficiency (iWUE) ($r = 0.89$, $p < 0.001$). iWUE was positively correlated with DA ($r = 0.73$, $p = 0.0168$), height ($r = 0.96$, $p < 0.0001$) and $\delta^{18}O$ ($r = 0.87$, $p = 0.001$).

TABLE 4 Agronomic and physiological traits measured in 10 environments, including biomass, grain yield, harvest index, grain per meter square, thousand grain weight (TGW), spike per meter square, grain per spike, height and days to anthesis (DA), carbon isotope discrimination ($\Delta^{13}C$), oxygen isotope enrichment ($\delta^{18}O$) and intrinsic water use efficiency (iWUE).

Environment	Biomass (kg ha^{-1})	Yield (kg ha^{-1})	HI	Grain m^{-2}	TGW (g)	Spikes m^{-2}	Grain spike^{-1}	Height (cm)	DA days	$\Delta^{13}C$ ‰	$\delta^{18}O$ ‰	$_i$WUE (µmol mol^{-1})
Aq_16	5996 ± 248	1061 ± 74	0.2 ± 0.01	2916 ± 187	36 ± 0.7	320 ± 12	9 ± 0.6	92 ± 2.7	151 ± 2	-	-	-
Ar_17	15367 ± 434	3705 ± 123	0.3 ± 0.01	9821 ± 373	38 ± 0.9	574 ± 27	18 ± 0.8	134 ± 4.7	123 ± 1	18.4 ± 0.1	29.1 ± 0.3	96 ± 1
As_17	10821 ± 235	2195 ± 116	0.2 ± 0.01	7513 ± 423	30 ± 0.6	529 ± 16	15 ± 0.9	113 ± 3.0	127 ± 1	16.5 ± 0.1	29.2 ± 0.3	117 ± 1
Jo_16	5789 ± 334	1240 ± 85	0.2 ± 0.01	3324 ± 199	37 ± 0.9	218 ± 12	15 ± 0.5	98 ± 3.1	136 ± 1	-	-	-
Jo_17	4970 ± 272	1472 ± 83	0.3 ± 0.01	3516 ± 202	42 ± 0.5	198 ± 7	18 ± 0.8	94 ± 4.1	-	-	-	-
Ju_16	8890 ± 221	2099 ± 118	0.2 ± 0.01	5560 ± 337	38 ± 0.3	342 ± 9	16 ± 0.8	103 ± 3.4	140 ± 1	-	-	-
Ju_17	11254 ± 210	4356 ± 126	0.4 ± 0.01	10074 ± 314	43 ± 0.3	317 ± 10	33 ± 1.4	114 ± 4.5	150 ± 1	-	-	-
Pa_16	9055 ± 276	2164 ± 66	0.2 ± 0.01	5644 ± 119	38 ± 0.8	307 ± 8	19 ± 0.7	109 ± 4.0	140 ± 2	15.1 ± 0.1	35.3 ± 0.3	132 ± 1
Pa_17	11532 ± 348	2796 ± 121	0.2 ± 0.01	6708 ± 308	42 ± 0.5	300 ± 9	23 ± 0.9	112 ± 4.2	146 ± 2	-	-	-
SR_17	13646 ± 451	4863 ± 100	0.4 ± 0.01	10229 ± 223	48 ± 0.5	405 ± 12	26 ± 0.9	114 ± 4.1	-	-	-	-

Values are presented as mean ± standard error (SE).

Yield was positive correlated with HI ($r = 0.93$, $p < 0.0001$), grains per square meter ($r = 0.83$, $p < 0.003$) and grains per spike ($r = 0.74$, $p = 0.01$), and was negative correlated with biomass ($r = -0.64$, $p = 0.046$), height ($r = -0.8$, $p = 0.006$), iWUE ($r = -0.79$, $p < 0.007$), yield stability ($r = -0.76$, $p < 0.001$), DA ($r = -0.61$, $p = 0.06$) and biomass stability ($r = -0.76$, $p = 0.011$).

3.5 Water use efficiency and biomass

In all three genotype groups, iWUE was negatively associated with biomass. However, landraces exhibited higher iWUE and biomass than modern varieties, including those with both short and long growth cycles (Figure 7). Additionally, higher iWUE was positively associated with $\delta^{18}O$ across all genotypes, showing a consistent pattern across each of the three environments (Figure 8).

3.6 Mega-environments based on biomass

An SREG analysis of environments revealed the presence of two distinct mega-environments (Figure 9). One of the mega-environments grouped 7 environments, including all those from the year 2017 plus Pa_16. In this mega-environment, the highest biomass was recorded for landrace Blanco, followed by landraces Milufen and Furfuya, the latter having a growth cycle duration similar to that of the modern varieties.

4 Discussion

The Chilean landraces exhibited greater biomass, iWUE, yield stability, and biomass stability, compared to the modern wheat varieties (Table 5 and Figure 6), whereas the latter achieved the highest grain yields. Yield advantages in the modern varieties were associated with specific trait changes such as a higher harvest index, more grains per spike and a greater number of grains per square meter. The substantial improvements in crop yields achieved by modern varieties during the twentieth century have been driven mainly by the increase in HI (Sinclair, 1998) without significant increases in total biomass (Álvaro et al., 2008).

Modern varieties correspond to semi-dwarf genotypes developed Post-GR, and characterized by reduced plant height and shorter growth duration compared to the landraces. Based on these traits and in order to minimize confounding effects, three clusters were identified: one including the modern varieties and two comprising the landraces (Figure 3). The main difference between the two landrace groups was their growth cycle duration. The group composed of Cebolla, Chucho, and Furfuya exhibited a cycle length similar to that of the modern varieties, differing by only 3 days, whereas the group composed of Blanco-Oregón, Colorado, Legul, and Milufen differed from the modern varieties by 18 days (Table 5).

To comprehensively evaluate the performance of Chilean landraces under severe drought, we grew them in 10 environments, 8 of which were rainfed, with average yield ranging from 1,061 to 4,863 kg ha^{-1} (Table 4). The lowest effective precipitation was 159.9 mm, while the highest was 572 mm. The crossover interaction between genotypes and the mean genotypic yield, used as the environmental index, occurs in environments with yields ranging from 3,000 to 4,000 kg ha^{-1}. According

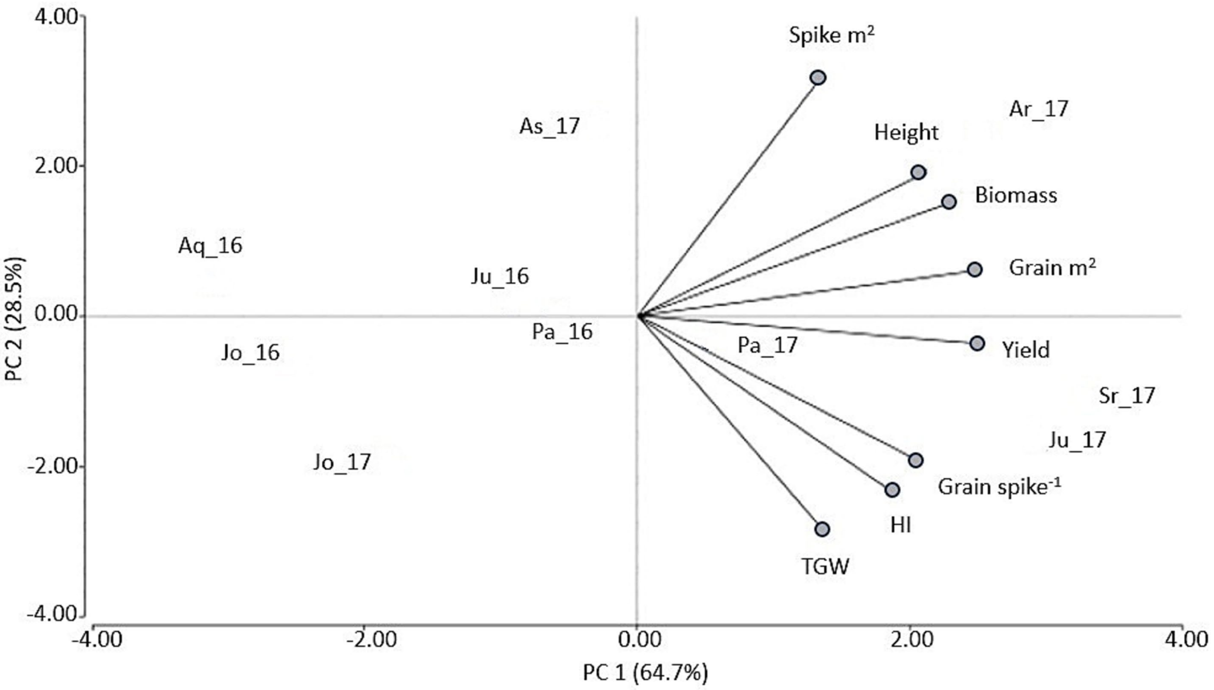

FIGURE 2
Biplot of the first two principal component analysis (PCA) axes showing the relationship among biomass, yield, harvest index (HI), grain per meter square, thousand grain weight (TGW), spike per meter square, grains per spike, and plant height across 10 environments.

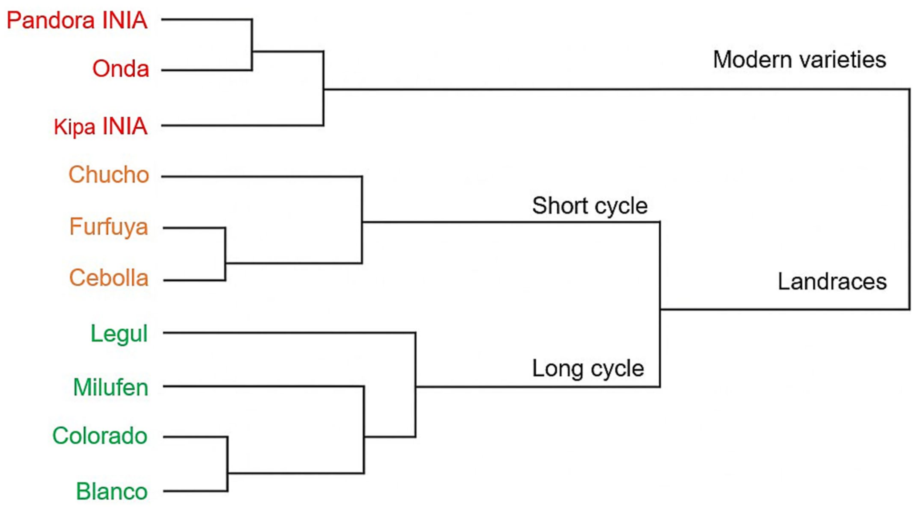

FIGURE 3
Cluster analysis of 10 genotypes based on plant height and days to anthesis, distinguishing modern varieties and landraces. Genotype names in red correspond to modern varieties, those in yellow to short cycle landraces, and those in green to long cycle landraces.

to Blum (2011), yields below this range indicate severe drought. Based on this criterion, seven rainfed environments experienced severe drought, as their average yields were below 3,000 kg ha^{-1}.

Yield stability is an important trait for rainfed systems, such as Mediterranean environments, where rainfall is scarce and yields are unpredictable (Blum, 2011; Ceccarelli et al., 1991; Ceccarelli, 1994; Dawson et al., 2008). The greater yield stability observed in landraces was negatively associated with yield (Figure 6). This has been described by other authors as a compensatory effect between the two traits, which makes the simultaneous improvement of both traits challenging in areas affected by severe drought (Du et al., 2020; Tadesse et al., 2016).

Breeding for higher yield may have inadvertently compromised yield stability. Under low input conditions, plants often allocate more biomass to uptake organs—primarily roots—to maintain access to water and nutrients, potentially reducing investment in reproductive structures (Weiner, 2004; Khateeb et al., 2017).

TABLE 5 Agronomic and physiological traits of seven landraces and three modern varieties, including biomass, grain yield, harvest index (HI), grain per meter square, thousand grain weight (TGW), spike per meter square, grain per spike, height, days to anthesis (DA), carbon isotope discrimination ($\Delta^{13}C$), oxygen isotope enrichment ($\delta^{18}O$) and intrinsic water use efficiency (iWUE).

Genotype	Biomass	Yield	HI	Grain m^{-2}	TGW	Spikes m^{-2}	Grain $spike^{-1}$	Height	DA	$\Delta^{13}C$	$\delta^{18}O$	iWUE
	(kg ha^{-1})	(kg ha^{-1})			(g)			(cm)		‰	‰	(µmol mol^{-1})
Blanco	10718	2493	0.23	5894	41	359	17	128	147	15.9	33.1	125
Cebolla	9608	2483	0.26	5851	42	359	17	119	132	16.6	31.3	117
Chucho	9605	2407	0.24	6039	39	369	17	117	138	16.6	31.1	117
Colorado	9746	2381	0.24	5594	42	348	16	127	149	16.1	31.3	122
Furfuya	10113	2677	0.26	6685	40	348	20	117	134	16.3	32.5	120
Legul	9959	2638	0.25	6473	40	342	19	113	146	16.8	31.7	115
Milufen	10291	2431	0.24	6202	38	346	19	120	152	16.3	32.2	120
Kipa INIA	9510	2541	0.25	7290	34	323	23	85	132	17.2	29.4	110
Onda	8890	2869	0.31	7806	36	399	20	80	131	17.5	30.5	107
Pandora INIA	8880	3032	0.33	7469	40	316	24	76	130	17.7	29.5	104
Long cycle Landraces	10179 A	2486 B	0.24 C	6041 B	40 A	349 A	18 B	122 A	149 A	16.3 B	32.1 A	120 A
Short cycle Landraces	9775 A	2522 B	0.25 B	6192 B	40 A	359 A	18 B	118 B	134 B	16.5 B	35.5 A	118 A
Moderns	9093 B	2814 A	0.30 A	7522 A	37 B	346 A	22 A	80 C	131 C	17.5 A	29.8 B	107 B

Different capital letters vertically indicate that there are significant differences according to DGC multiple comparison test ($p \leq 0.05$).

TABLE 6 Percentage of variance explained by environment, genotype, and genotype by environment interaction (GxE), and broad sense heritability for biomass, grain yield, harvest index (HI), grains per meter square, thousand grain weight (TGW), spike per meter square, grain per spike, height, days to heading (DA), carbon isotope discrimination ($\Delta^{13}C$), oxygen isotope enrichment ($\delta^{18}O$) and intrinsic water use efficiency (iWUE).

V (%)	Biomass	Yield	HI	Grain	TGW	Spikes	Grain	Height	DA	$\Delta^{13}C$	$\delta^{18}O$	iWUE
	(kg ha^{-1})	(kg ha^{-1})		m^{-2}	(g)	m^{-2}	spike	(cm)		‰	‰	(µmol mol^{-1})
Environment	95.73***	99.2***	58.8***	84.9***	71.1***	96.9***	76.1***	14.1***	47.4***	80.5***	53.7***	80.5***
Genotype	2.2***	0.04***	16.7***	6.3***	18.8***	2.8***	10.1***	81.8***	45.3***	19.4***	32.8***	19.4***
G x E	2.05***	0.74***	24.3***	8.8***	10.0***	0.1**	13.7***	4.1***	7.1***	0^{ns}	13.4**	0^{ns}
Heritability	0.69	0.62	0.84	0.85	0.92	0.69	0.83	0.99	0.98	0.98	0.94	0.94

Significance values, **significance $p \leq 0.01$; ***significance $p \leq 0.001$; ns, not significant.

On the other hand, yield stability showed a strong and positive association with biomass stability and was also positively correlated with biomass, iWUE and height (Figure 6). Few studies analyzed yield stability, and virtually no research has specifically addressed biomass stability. Biomass stability has been associated with delayed senescence (stay-green), greater radiation interception and improved water use efficiency (Paul et al., 2016). The greater biomass stability observed in Chilean landraces could be explained by their higher above-ground biomass production and increased iWUE. The positive association between $\delta^{18}O$ and iWUE indicates partial stomatal closure in the evaluated genotypes (Figure 8), as reduced stomatal conductance leads to higher $\delta^{18}O$ enrichment. Because iWUE is defined as the ratio between CO_2 assimilation (A) and stomatal conductance (g), this relationship suggests that the higher iWUE of landraces is mainly driven by reduced g rather than increased A (Eitelberg et al., 2025). Nevertheless, landraces showed higher biomass and iWUE compared to modern varieties (Figure 7). This could be due to a greater photosynthesis, which in certain varieties may be due to a longer cycle length, as is the case of the landraces Blanco, Colorado, Legul and Milufen (Craufurd et al., 1991). In other cases, such as Cebolla, Chucho and Furfuya, which have a similar growth cycle length to modern varieties, the higher biomass and iWUE could result from a higher photosynthetic rate (Farquhar et al., 1989; Eitelberg et al., 2025) or the accumulation of carbohydrates in the stem that can be remobilized during grain filling (Álvaro et al., 2008; Blum, 2011) (Figure 10).

The Chilean wheat breeding program has focused on selecting genotypes with broad adaptation, initially prioritizing high yield potential, and later emphasizing yield stability without directly selecting for biomass or its stability (Matus et al., 2016). In this sense, the Chilean wheat program has been very successful, achieving potential yields of 9,000 Kg ha^{-1} in spring wheat and 20,000 kg ha^{-1} in winter wheat, with genetic gains of 43.5 and 128 kg $ha^{-1}year^{-1}$, respectively (del Pozo et al., 2022; Del Pozo et al., 2014). However, there is no information available on genetic progress under drought

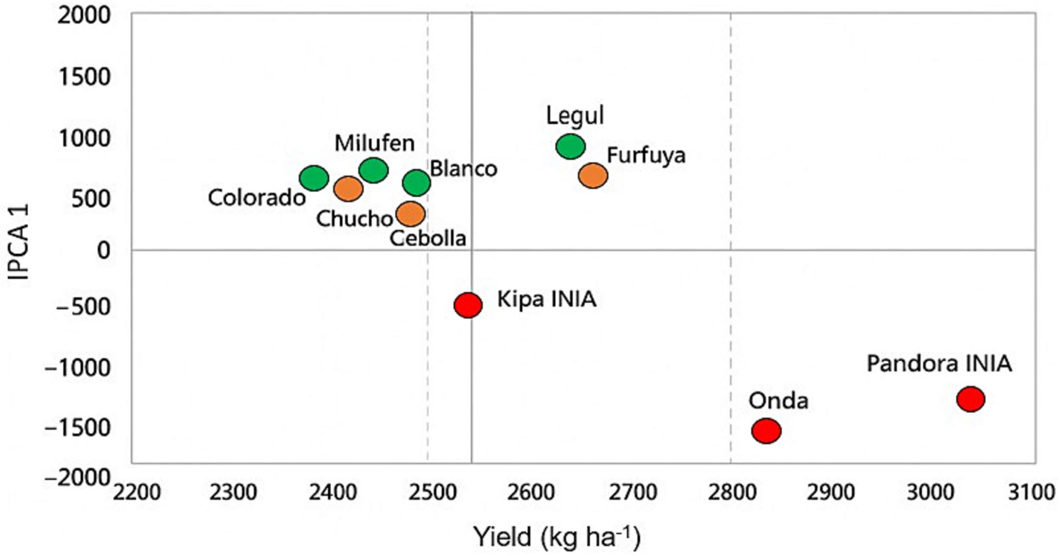

FIGURE 4
AMMI 1 biplot based on IPCA 1 (ordinate) and mean yield data for 10 genotypes (abscissa). The dashed lines indicate the mean yield of landraces (left) and modern varieties (right). Red circles correspond to modern varieties, those in yellow to short cycle landraces, and those in green to long cycle landraces.

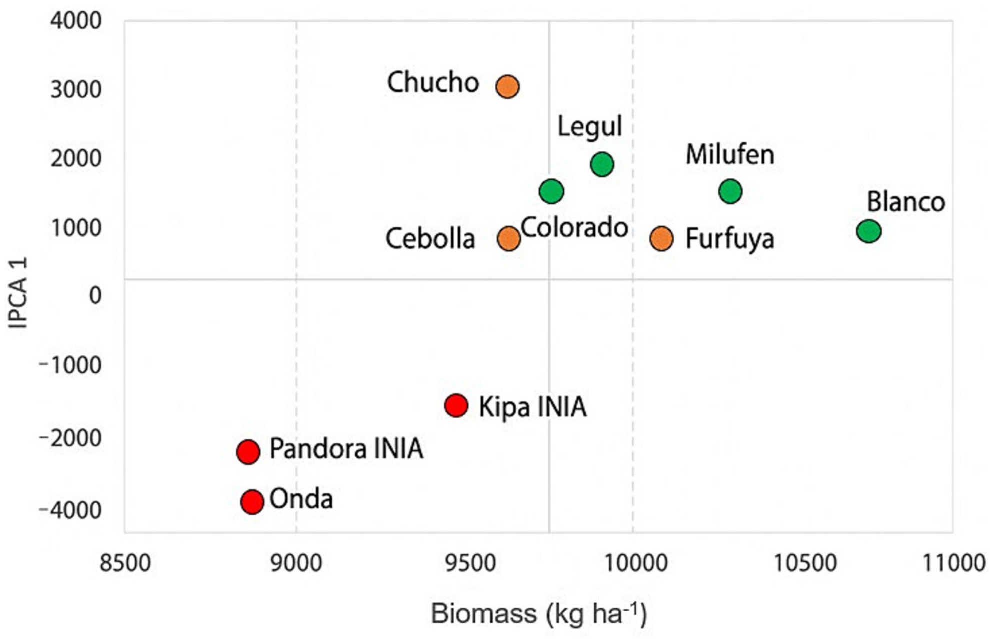

FIGURE 5
AMMI 1 biplot based on IPCA 1 (ordinate) and mean biomass data for 10 genotypes (abscissa). The dashed lines indicate the mean biomass of modern varieties (left) and landraces (right). Red circles correspond to modern varieties, those in yellow to short cycle landraces and those in green to long cycle landraces.

conditions in Chile. In others parts of the world, under stress conditions, genetic gains have been lower than expected (Blum, 2011; Richards et al., 2002), with reported values of 19 Kg ha^{-1} $yr.^{-1}$ (Sadras and Richards, 2014). According to Blum (1996) and Tardieu et al. (2018), one possible explanation for the limited progress in stress environments is that much of the selection for stress tolerance has been conducted under optimal management conditions without exposure to biotic and abiotic stresses. Therefore conclusions and implications derived from irrigated or high rainfall regions may not be applicable to low and variable rainfall environments (Du et al., 2020).

Measuring biomass and biomass stability can be challenging for breeders. However, both variables are closely associated with iWUE, as indicated by correlation coefficients of $r = 0.89$ ($p = 0.0005$) and $r = 0.78$ ($p = 0.0082$), respectively. This suggests that selecting iWUE

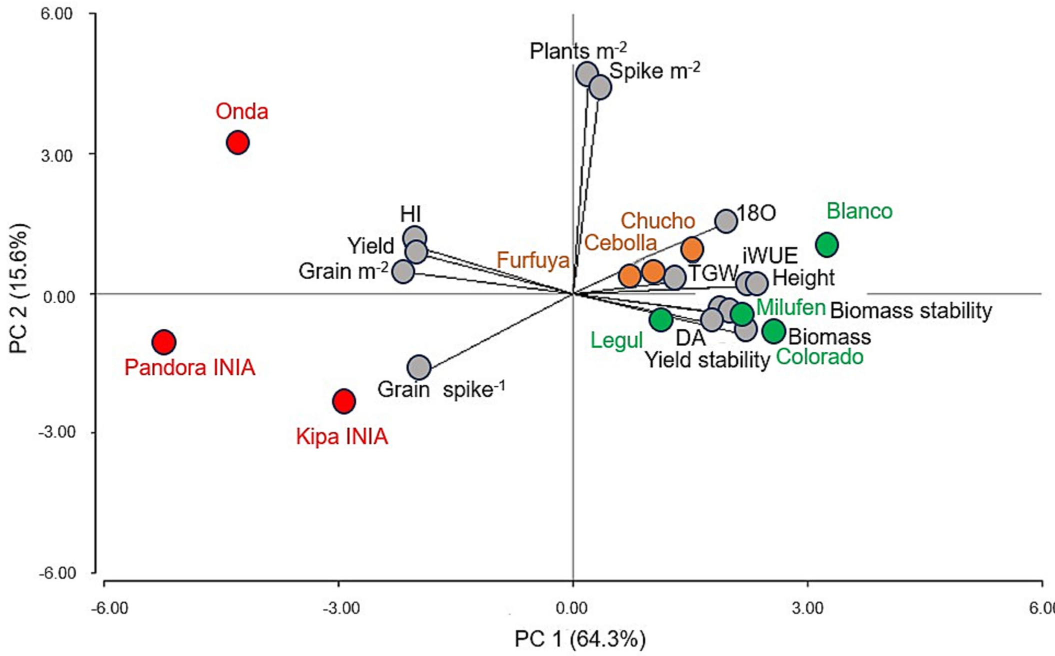

FIGURE 6
Biplot of the first two axes of the principal component analysis showing the relationships among yield stability, biomass stability, days to anthesis (DA), thousand grain weight (TGW), biomass, height, intrinsic water use efficiency (iWUE), oxygen isotope enrichment (^{18}O), spike per meter square, plant per meter square, yield, harvest index (HI), grain per meter square, and grains per spike for the 10 genotypes. Red circles correspond to modern varieties, those in yellow to short cycle landraces, and those in green to long cycle landraces.

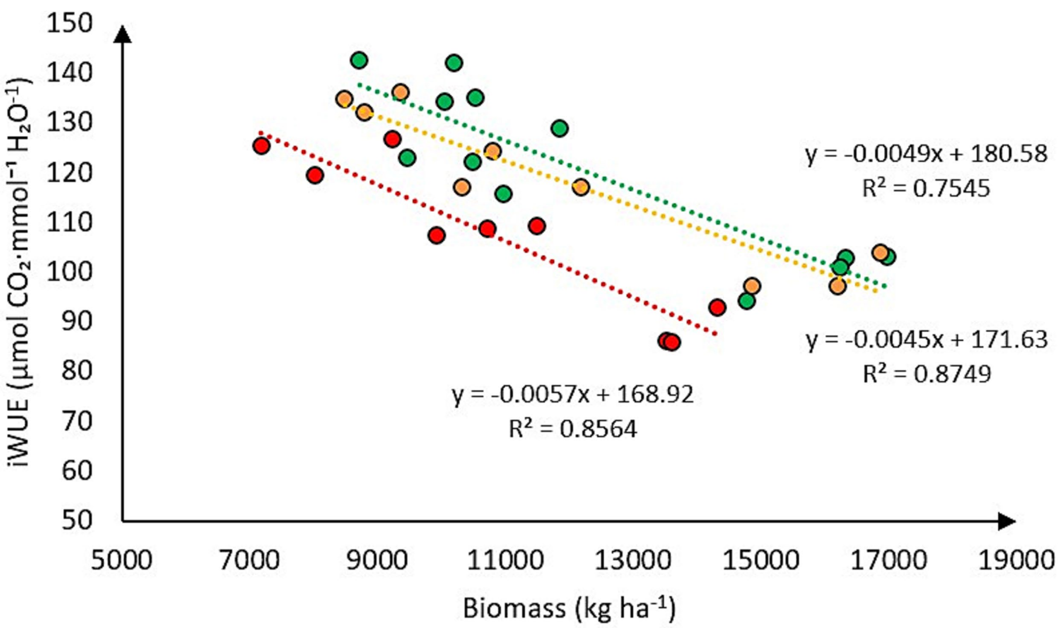

FIGURE 7
Relationship between iWUE and biomass in landraces and modern varieties evaluated in three environments. Red circles correspond to modern varieties, those in yellow to short cycle landraces, and those in green to long cycle landraces.

could be a more practical strategy for breeders, particularly given its high heritability (0.83) (Table 6).

Cebolla and Furfuya are the landraces with the most stable biomass production across environments (Figure 5). Among them, Furfuya stands out for its higher iWUE (Table 5), a trait that did not show a significant G × E interaction. In contrast, biomass production exhibit a significant G × E interaction, as shown in Table 5. There is a mega-environment encompassing 7 of the environments studied

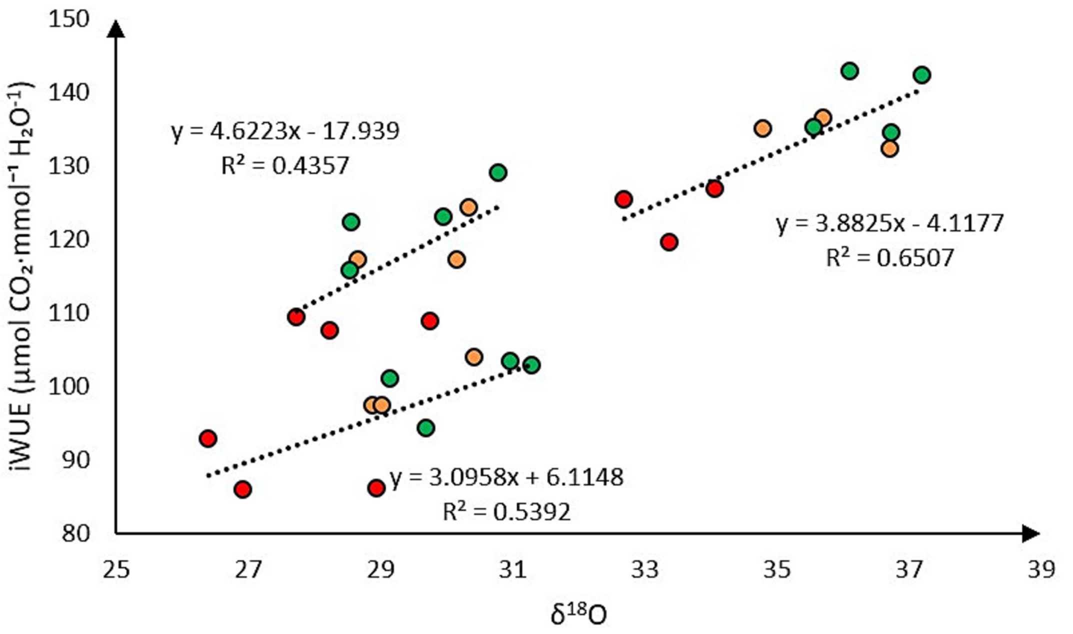

FIGURE 8
Relationship between iWUE and $\delta^{18}O$ in landraces and modern varieties evaluated in three environments. Red circles correspond to modern varieties, those in yellow to short cycle landraces, and those in green to long cycle landraces.

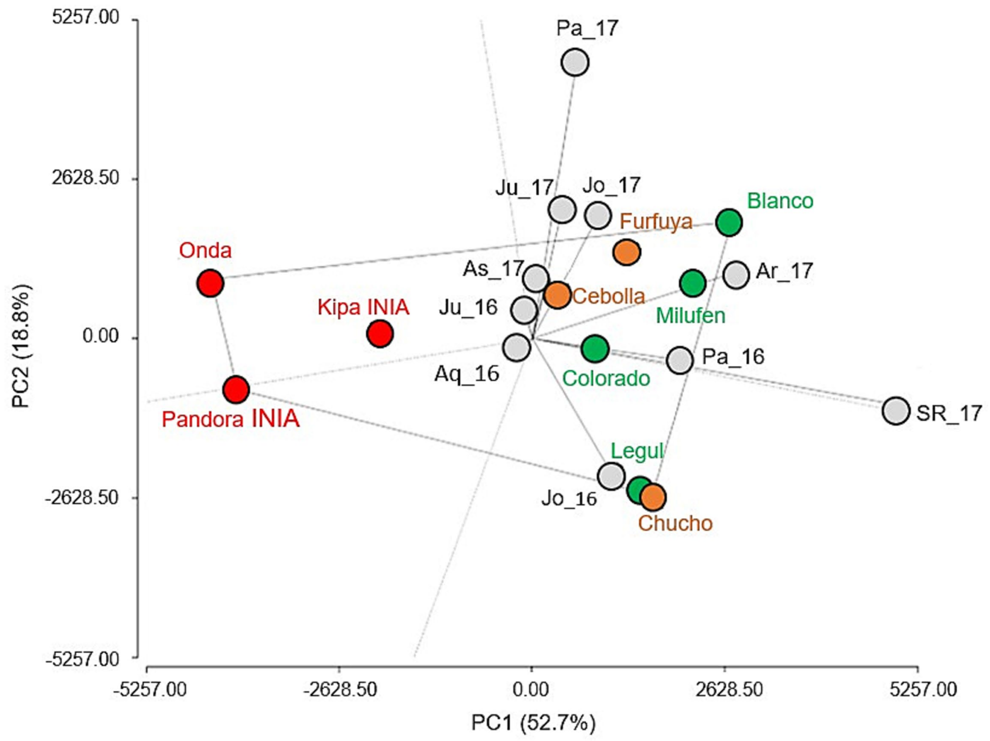

FIGURE 9
SREG biplot using biomass data for genotypes in 10 environments (white circles). Red circles correspond to modern varieties, those in yellow to short cycle landraces, and those in green to long cycle landraces.

(Figure 9), where the highest biomass was recorded for the genotype Blanco, followed by Milufen and Furfuya. Among these, only Furfuya exhibits a shorter time to anthesis, comparable to that of the modern varieties, making it a valuable genetic resource for breeding programs targeting severe drought conditions, such as those increasingly observed in Mediterranean environments.

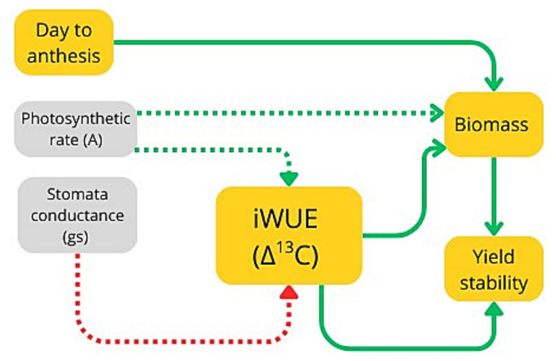

FIGURE 10
Conceptual scheme illustrating relationships among biomass, iWUE, and yield stability under drought conditions for 7 landraces and 3 modern varieties.

Under severe drought conditions, breeding strategies should adopt a new paradigm that explicitly incorporates greater genetic diversity, including locally adapted landraces that have evolved under severe drought environments. This approach is in line with the principles of evolutionary plant breeding (Babalola et al., 2025). Within this new breeding paradigm for severe drought, greater biomass, iWUE and yield stability become key targets despite its association with increased plant height, as in these low-yield environments plants develop shorter stems and lower yields, thereby reducing the risk of lodging.

5 Conclusion

The Chilean landraces analyzed in this study exhibited greater biomass, intrinsic WUE (iWUE), yield stability, and biomass stability than the modern varieties. In one group of landraces, this performance appears to be explained by a longer time to anthesis, while in the other group it would be due to other adaptive traits that need further investigation. Yield stability and biomass stability are key traits for adaptation to severe drought and achieving them requires selection for higher biomass and iWUE. In this context, the Chilean wheat landrace, Furfuya, stands out as a valuable genetic resource for national breeding programs aiming to improve yield and yield stability in Mediterranean environments affected by severe drought.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

PS: Funding acquisition, Conceptualization, Writing – review & editing, Supervision, Investigation, Writing – original draft, Resources, Project administration, Formal analysis, Data curation, Methodology. MO: Writing – original draft, Writing – review & editing, Investigation, Formal analysis. VF-B: Writing – review & editing, Writing – original draft, Investigation, Formal analysis.

Funding

The author(s) declared that financial support was received for this work and/or its publication. This research was funded by Fundación para la Innovación Agraria, grant number FIA PYT-2015-0395 and grant number FIA PYT 2016–0359.

Acknowledgments

We acknowledge Daniela Carvajal, Luis Delgado, Marcelo Becerra and Agustín Fuenzalida for technical assistance. We thank Edmundo Acevedo for reviewing the manuscript. We also acknowledge INIA for providing access to its experimental site.

Conflict of interest

The author(s) declared that this work 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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