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# Functional diversity and ecological niches of C<sub>4</sub> climate-resilient species to guide island ecosystem restoration

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**Introduction:** Arid ecosystems impose particularly harsh conditions on plants. To thrive, many species have evolved a range of adaptive traits, among which those with C<sub>4</sub> photosynthesis are recognised for their high efficiency in hot and dry environments. Therefore, these species are considered crucial for the restoration and management of dry tropical ecosystems. However, their ecological and functional roles remain poorly understood on oceanic islands such as Cabo Verde.

**Methods:** This study, based on herbarium records, GBIF occurrences, and validated field data, presents an analysis of the functional diversity of 162 C<sub>4</sub> species (4,846 occurrences) recorded in the Cabo Verde Islands, representing about 21.6% of the vascular flora of the archipelago. The species were characterised by their functional traits (including life cycle, habit, salinity tolerance, and photosynthetic subtypes NADP-ME, NAD-ME, and PEP-CK), altitudinal distribution, and climatic preferences for temperature and precipitation.

**Results:** The results reveal marked differences in ecological distribution between C<sub>4</sub> eudicots and monocots: eudicots are more frequent in arid and saline habitats at low elevations, whereas monocots occupy a wider ecological range. C<sub>4</sub> halophytes, in particular, show promise for nature-based solutions such as coastal revegetation and soil restoration in degraded areas. The analysis highlights species with strong potential for revegetation and ecosystem management, especially in insular contexts exposed to water scarcity and climate stress. Salinity-adapted annuals and perennials are especially relevant, along with C<sub>4</sub> lineages linked to photosynthetic subtypes that confer enhanced environmental resilience.

**Discussion:** This functional and ecological assessment provides a scientific basis for selecting climate-resilient species to support revegetation and sustainable management of fragile dry tropical island ecosystems. Indeed, understanding the functional differences between C<sub>4</sub> monocots and C<sub>4</sub> eudicots is essential for developing climate-smart revegetation strategies. The approach adopted here promotes the conservation of biodiversity through functional perspectives, offering a model of ecological action in vulnerable regions under climate

change. The findings underscore the ecological preferences of the C<sub>4</sub> species and highlight their potential contributions to ecosystem function, resilience, and restoration.

#### KEYWORDS

C<sub>4</sub> eudicots, C<sub>4</sub> monocots, Cabo Verde, climate-resilient species, ecosystem restoration, halophytes, trait-based ecology, tropical oceanic islands

## 1 Introduction

Plants have developed a variety of adaptive traits to survive and thrive in a wide range of environments, with particularly notable specialised strategies that enable survival in harsh conditions, such as hot and arid environments (Gross et al., 2024). These adaptations enable species to cope with variable water availability (developing, for example, deep root systems to access groundwater in drought-prone areas and leaf modifications to minimise water loss), extreme temperatures, soil nutrient limitations or tolerance to high salinity (Kochhar et al., 2022). The ability to adapt to specific environmental stressors contributes significantly to determining plant ecological fitness and spatial distribution (Gratani, 2014). For example, a key evolutionary innovation was the development of distinct photosynthetic pathways, mainly represented by the C<sub>3</sub>, C<sub>4</sub>, and CAM pathways (Ehleringer and Monson, 1993; Hartzell et al., 2018). For carbon fixation, C<sub>3</sub> plants use the standard Calvin cycle, while C<sub>4</sub> plants rely on a process that improves the effectiveness of CO<sub>2</sub> acquisition under high light and temperature conditions (Arrivault et al., 2019; Sage, 2016). This adaptation is particularly beneficial when water is scarce and salinity levels are high, conditions that typically hinder photosynthesis in C<sub>3</sub> plants (Pearcy and Ehleringer, 1984). The unique efficiency of C<sub>4</sub> plants (Simpson et al., 2020) has received significant attention among the scientific community considering its potential implications for crop productivity and climate change mitigation (Ain et al., 2022; Sage and Zhu, 2011).

The C<sub>4</sub> pathway evolved independently in many different plant lineages; it is most common in monocots and relatively rare in eudicots (Osborne and Beerling, 2006; Sage, 2004; Sage et al., 2018). C<sub>4</sub> monocots and C<sub>4</sub> eudicots have different ecological preferences and adapt to different environmental conditions (Berasategui et al., 2023). The former, mainly those from the Poaceae and Cyperaceae families, are found more frequently in open environments such as savannas, prairies, and deserts; these habitats are characterised by high levels of solar radiation, very high temperatures, and low water availability (Edwards et al., 2010; Sage et al., 2011). Under such conditions, the C<sub>4</sub> metabolic pathway clearly represents a strong competitive advantage and is reflected in extensive parts of dry tropical and subtropical regions, such as African savannas, where C<sub>4</sub> grasses dominate (Edwards and Still, 2008; Edwards et al., 2010). In contrast, C<sub>4</sub> eudicots are fewer but more phylogenetically diverse, represented in 15 families (Berasategui et al., 2023). They present greater anatomical and physiological diversity (Bohley et al., 2015), tending to specialize in more restricted ecological niches (Sage, 2016; Sage et al., 2011; Sage et al., 2018); for example, members of the genera *Amaranthus* (Amaranthaceae) inhabit zones where water is seasonally limiting, such as in semi-arid regions, saline environments, and disturbed or marginal habitats (Pearcy and Ehleringer, 1984; Kadereit et al., 2017). Such a range of

adaptations and ecological niches sustains the wide distribution of C<sub>4</sub> plants across many of the world's ecosystems.

Among C<sub>4</sub> plants there are distinct subtypes, including the NADP-malic enzyme (NADP-ME) and the NAD-malic enzyme (NAD-ME) subtypes, representing additional metabolic specialisations, each suited to specific environmental situations (Sage et al., 2011). NAD-ME species generally occupy hotter and drier habitats, thus upregulating photosynthetic efficiency in the presence of high light and temperature stress, while NADP-ME species are usually more restricted to cooler and more humid sites (Rao and Dixon, 2016; Sage et al., 2011; Sonawane et al., 2018). In eudicots, the NAD-ME and NADP-ME subtypes are represented by a similar number of genera; in monocots, the NADP-ME subtype dominates (Sage et al., 2011). In addition to the two referred subtypes, a third biochemical subtype, phosphoenolpyruvate carboxykinase (PEP-CK), has also been recognized, although its definition and prevalence have historically been debated. Physiological and phylogenetic studies show that PEP-CK does not occur in isolation but is often used in combination with NAD-ME or NADP-ME, resulting in mixed pathways adapted to different environmental conditions (Carmona-Silva et al., 2008; Bräutigam et al., 2014; Rao and Dixon, 2016; Washburn et al., 2021). This subtype occurs among grasses, exclusively in the subfamilies *Panicoideae* and *Chloridoideae* (Sage et al., 1999; Wigley-Coetsee and Staver, 2020). Although the work of Muhaidat and McKown (2013) suggested the presence of PEP-CK in certain C<sub>4</sub> eudicots, Koteyeva et al. (2015) did not corroborate these findings, thereby upholding Poaceae as the sole family in which PEP-CK is known to play a significant role in C<sub>4</sub> photosynthesis.

With growing concern about climate change and ecosystem degradation (Malhi et al., 2020; Vlek et al., 2017), C<sub>4</sub> species are emerging as important allies for ecosystem restoration and mitigation of climate change impacts (Lv et al., 2023; Sage, 2016). Indeed, their ability to thrive under adverse conditions and contribute to ecosystem stability (Sage, 2016) makes them key natural-based players in the search for sustainable solutions (Key et al., 2022), contributing to soil stabilisation, erosion control, and biodiversity enhancement.

C<sub>4</sub> monocots, and especially grasses, are also foundational species, often establishing quickly, providing ground cover and reducing erosion in open, arid, or semi-arid landscapes; their rooting structures stabilise soils and reduce erosion, which is essential for initial recovery in degraded landscapes (Linder et al., 2018) and, at higher altitudes, help promote grassland restoration (Osborne and Sack, 2012). C<sub>4</sub> eudicots, including shrubs and trees, contribute to habitat structural diversity (Edwards and Still, 2008). Particularly in arid regions, woody vegetation also plays an important role in improving soil properties by increasing nutrient levels and facilitating rainwater infiltration, and by

creating microclimates through shading, lowering temperatures, and evaporation rates, aspects that facilitate the establishment of annual species, for example, [Abella and Smith \(2013\)](#) and references cited therein). Well adapted to saline environments ([Berasategui et al., 2023](#); [Sage et al., 2011](#)),  $C_4$  species are especially useful for rehabilitate ecosystems that have been impacted by soil salinisation, a common problem in arid and semi-arid areas ([Chen and Wang, 2024](#)).

Taking into account plant functional traits, such as the photosynthetic pathway, is particularly relevant for restoration practices in arid and semi-arid regions, where resilience under extreme conditions is needed for ecosystem stability ([Gross et al., 2024](#); [Horstmann et al., 2023](#)).

Arid tropical islands, characterised by peculiar climatic conditions and, usually, by geographic isolation, are ideal natural laboratories for studying adaptive responses to drought and climatic stressors ([Whittaker et al., 2017](#)). Many of these islands undergo extended dry seasons, precipitation irregularities, and significant temperature fluctuations, resulting in pronounced selection pressures on native and alien species ([Harter et al., 2015](#)). Such environments have been found to be suitable for testing the relationship between functional traits and ecological resilience ([Schrader et al., 2021](#)), offering great insight into the adaptive strategies used by species while facing climate change.

The Cabo Verde archipelago is faced with environmental issues such as land degradation, including soil salinization ([Baptista et al., 2015](#)), desertification, and water scarcity, impacting biodiversity and food security ([Monteiro et al., 2020](#)). For these reasons, the selection of species with high efficiency of water use and tolerance to drought appears to be a promising strategy for the sustainable revegetation of degraded land in Cabo Verde. Therefore, this study aimed to explore the possible role of certain functional traits, including the  $C_4$  photosynthetic pathway, as criteria to select species for effective restoration of arid ecosystems. As a study area, we used the Cabo Verde archipelago, which is strongly influenced by the climate of the West African Sahel. We aim to: 1) characterise the diversity of  $C_4$  taxa; 2) understand the bioclimatic preferences of  $C_4$  monocots and eudicots, their photosynthetic subtypes, and other functional traits (habit, life cycle, and salt tolerance); and 3) point out a pool of species potentially well suited for ecosystem restoration and climate mitigation in the archipelago, relying on their adaptive functional traits and specific bioclimatic preferences.

## 2 Materials and methods

### 2.1 Study area

The Cabo Verde archipelago belongs to the Macaronesia Region in the North Atlantic Ocean and encompasses ten major islands and some islets ([Figure 1a](#)). Under arid and semi-arid climates influenced by the Sahelian region, the islands are characterised by rainfall scarcity (i.e., irregular and concentrated in a few extreme episodes), recurrent droughts, soil erosion, and desertification ([Florencio et al., 2021](#)). The archipelago's mean annual temperature is 25 °C, its average annual precipitation spans 300–700 mm, and its maximum altitudes range between

387 m (Boavista island) and 2,829 m (Fogo island) ([Duarte and Romeiras, 2009](#)).

The vascular flora of Cabo Verde comprises approximately 750 taxa, including native and naturalised species from more than 100 families, the most prominent being Asteraceae, Cyperaceae, Fabaceae, Malvaceae, and Poaceae ([Duarte et al., 2022](#)). The unique orography and climatic variations create diverse habitats, ranging from xeric communities in arid lowlands to woodlands and shrub vegetation in humid mountainous regions. The highest islands, such as Santo Antão, São Nicolau, Santiago, and Fogo, harbour most of the native species of the archipelago ([Duarte et al., 2008](#)). Grasslands are the dominant plant communities in the landscape and, as suggested by Neto and his collaborators (2020), are physiognomic and floristically related to dry tropical African vegetation. They are predominantly composed of herbaceous species (annual and perennial) of the Poaceae, Asteraceae, Fabaceae and Malvaceae families ([Rivas-Martinez et al., 2017](#)). In some areas, these communities are interspersed with woody elements, adding further complexity to the island's vegetation. The plant communities in Cabo Verde provide important ecosystem services and economic benefits to local people, as sources of food and forage ([Brilhante et al., 2021](#); [Rocha et al., 2021](#)), fuel wood ([Varela et al., 2023](#)) and traditional medicinal plants ([Essoh et al., 2022](#); 2023; [Romeiras et al., 2023](#)). Changes in human population dynamics (e.g., growth and rural exodus) and their implications for food and wellbeing are also important factors strongly affecting plant communities ([Romeiras et al., 2016](#)). Together with geographical isolation, the climatic and environmental factors of Cabo Verde favour a diverse and rich biodiversity, and this poses a critical challenge for resource management and conservation, particularly in the climate change framework ([Duarte et al., 2024a](#)).

### 2.2 Data set

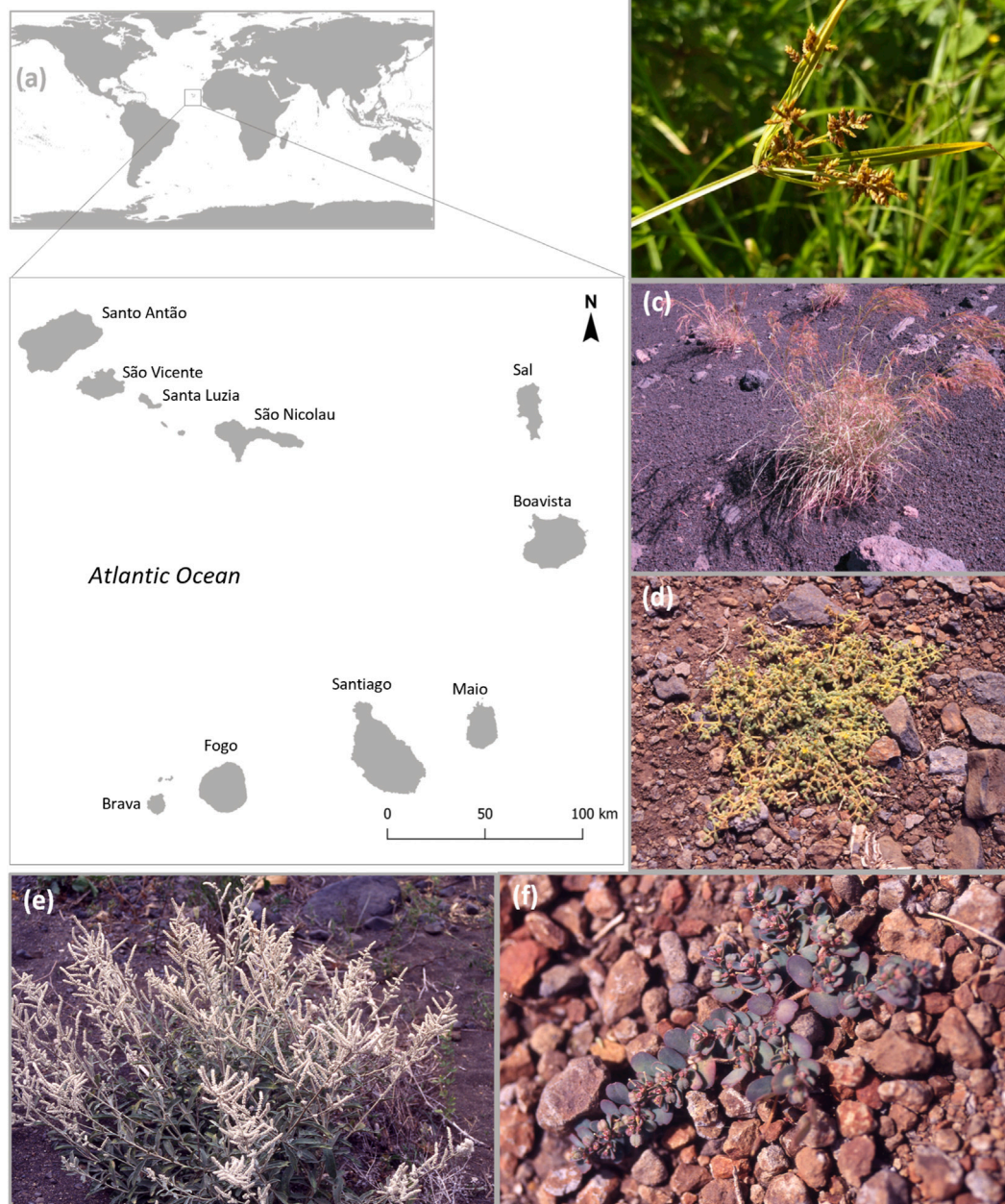
#### 2.2.1 Species and occurrence data

We compile a data set covering all taxa that occur on the Cabo Verde islands and report as  $C_4$  ([Supplementary Appendix S1A](#)). Evidence on  $C_4$  species was collected mainly from [Sage \(2016\)](#) and [Berasategui et al. \(2023\)](#) (additional references are available in). When no clear information was available for  $C_4$  species from the above references, information was retrieved based on phylogenetic trees in [Gallaher et al. \(2022\)](#) and related to ancestral taxa. Taxonomic information, data on distribution status in Cabo Verde islands (native endemic, native non-endemic, non-native), and global native distribution were also included for each taxon. To ensure uniformity in species nomenclature, we standardised the names using Plants of the World Online (POWO 2024; [www.powo.science.kew.org](#)). We considered both native and naturalised  $C_4$  species.

Geographical records were obtained from validated field data or reliable biodiversity databases. The LISC Herbarium (University of Lisbon), which holds the main herbaria collections from Cabo Verde ([Duarte et al., 2024b](#); [Romeiras et al., 2016](#)), and the Global Biodiversity Information Facility (GBIF.org, 2024; [www.gbif.org](#)) were the main sources consulted. GBIF occurrence data come from diverse sources, including museum specimens, human observations through citizen science programs, and DNA barcodes. We



### Cabo Verde Islands and C<sub>4</sub> species



**FIGURE 1**  
Cabo Verde archipelago and representatives of C<sub>4</sub> species. **(a)** Geographic location of Cabo Verde. **(b)** *Cyperus esculentus* (Cyperaceae) and **(c)** *Hyparrhenia caboverdeana* (Poaceae): C<sub>4</sub> NADP-ME subtype, found between 600 and 900 m altitude. **(d)** *Zygodophyllum simplex* (Zygodophyllaceae), C<sub>4</sub> NAD-ME subtype, halophyte, occurring from sea level to 300 m altitude. **(e)** *Aerva javanica* (Amaranthaceae) and **(f)** *Euphorbia granulata* (Euphorbiaceae): C<sub>4</sub> NADP-ME subtype, halophytes, occurring from sea level to 300 m. Author photos.

download the occurrence records for all C<sub>4</sub> taxa reported to Cabo Verde. The occurrence data was meticulously reviewed to exclude duplicate records (i.e., shared between herbaria) due to synonyms. Only individuals with accurate taxonomic identification at the species level, valid geographic information, and information source were considered. Among such records, 975 occurrences (20.1%) presented invalid or inexistent geographical coordinates; however, they contained precise information about the collection/

observation site and, consequently, were georeferenced using the methodology described in Duarte et al. (2024a), Duarte et al. (2024b). After collecting all occurrences with valid geographic information, we cleaned additional data to eliminate outliers. Some of these discrepancies may result from the procedures used in some databases (e.g., GBIF), with occurrences lacking precise location being associated with the centroids of the islands (usually corresponding to high-altitude locations). This underscores the

importance of employing appropriate georeferencing tools and possessing fundamental knowledge of the area and georeferenced species (Chapman and Wieczorek, 2006). We compile 4,846 occurrences (especially from the mid-19th century to 2024) for  $C_4$  taxa on the Cabo Verde islands (Supplementary Appendix S1B).

We extracted bioclimatic variables and digital altitude data from WorldClim 2.1 (Fick and Hijmans, 2017; [www.worldclim.org](http://www.worldclim.org)) at a spatial resolution of 30 arc-seconds (approximately 1 km) for the 4,846 occurrences using tools from QGIS 3.28.5 (QGIS; <http://www.qgis.org>).

## 2.2.2 Species functional traits

The concept of “functional trait” has been widely discussed, and in this study, we have adopted the definition of Volaire et al. (2020) and Sobral (2021), who describe functional traits as traits of organisms that mediate their response to biotic and abiotic conditions and, consequently, directly affect their survival and reproductive success as well as the survival and/or reproduction of its offspring. This interpretation therefore encompasses morphological, physiological, and phenological features.

To examine whether variations in photosynthetic pathways are related with species' adaptability to different environmental conditions,  $C_4$  subtypes were considered. As reported in several studies (Sage, 2004; Bräutigam et al., 2014), PEP-CK rarely occurs as an exclusive subtype and is most frequently associated with either the NADP-ME or NAD-ME  $C_4$  subtypes, primarily participating in mixed pathways or being flexibly regulated by the environment (Koteyeva et al., 2023). In the Poaceae species present in Cabo Verde only the mixed NAD-ME/PEP-CK subtype is present. Henceforth, unless otherwise specified, we consider two main groups: (i) NADP-ME; and (ii) NAD-ME, which includes the mixed NAD-ME/PEP-CK subtype. In cases where a finer distinction within this latter group is made, the respective subgroups are referred to as ‘predominant’ NAD-ME and NAD-ME/PEP-CK (see Figure 2b).

We also consider functional traits such as habit (herb, shrub), life cycle (annual, perennial), and salt tolerance. Concerning the latter, we only considered salt-tolerant species (including obligate and facultative halophytes), as data on non-tolerant taxa are scarce. In fact, there is no information for a large number of species due to a lack of studies on this trait; as a result, only a few taxa have been effectively tested for salinity tolerance. These functional traits were compiled from various sources, including floras, scientific publications, databases, and online sources (further details are provided in Supplementary Appendix S1). To minimise possible data inconsistencies resulting from the use of different criteria or collection methodologies, we chose, whenever possible, to use the same source of information for each trait. In addition, efforts were made to select regional sources, as data obtained at a global scale may not adequately represent the local adaptations of species occurring in Cabo Verde.

Trait selection was guided by expert knowledge of the islands' environments, characterised by high temperatures and limited water availability. As water scarcity strongly constrains plant establishment, the selected traits reflect adaptations to the archipelago's arid and semi-arid conditions. Additional functional traits could be used to aid ecosystem restoration, but existing trait databases suffer from taxonomic, functional, and spatial sampling biases (Merchant et al., 2023) and data for the Western African flora are quite incomplete.

## 2.2.3 Species uses

Documented plant uses were grouped into five categories for each species: environmental (e.g., soil erosion control, revegetation, ornamental), forage/fodder, human food, material (including plants producing essential oils or fibers), and medicinal. To evaluate the economic value of each species, the number of uses (NU) per species was calculated, with a range of 0 (no documented use) to 5 (used in all categories). Data were sourced from Duarte et al. (2022), Duarte et al. (2024c), the Feedipedia database (<https://www.feedipedia.org/>) and the GRIN database (GRIN-Global, <https://npgsweb.ars-grin.gov/gringlobal/>) (further details are provided in Supplementary Appendix S1).

## 2.3 Statistical analyses

### 2.3.1 Ecological preferences of $C_4$ taxa

Taxa occurrence points were pooled into eudicot and monocot groups. Additional information on ecology–altitude, temperature (BIO1) and precipitation (BIO12) –, and functional traits– $C_4$  subtype, life cycle, and salt tolerance – was aggregated to the respective occurrence point.

To analyse the preferences of  $C_4$  eudicots versus  $C_4$  monocots in relation to altitude, annual mean temperature, and annual precipitation, box plots of the occurrences were made, and kernel density estimation (KDE) was used to calculate the density distribution of all the occurrences along these three ecological gradients. KDE was selected due to its ability to reveal concentration areas of species occurrences without predefined class boundaries (Nelson and Boots, 2008). To further identify differences in ecological preferences between eudicots and monocots, box plots were prepared for each of the functional traits studied–life cycle, salt tolerance, and  $C_4$  subtypes; habit was excluded from subsequent analyses because only one  $C_4$  shrub species occurs on the islands. A total of five functional groups – annual, perennial, halophytes, NADP-ME, and NAD-ME (including the mixed NAD-ME/PEP-CK subtype, only present in monocots) – were analysed separately (eudicots vs. monocots) in relation to altitude, temperature, and precipitation, and the Mann-Whitney  $U$  test was used to identify statistically significant differences between the groups.

### 2.3.2 Distribution of $C_4$ taxa on the Cabo Verde Islands

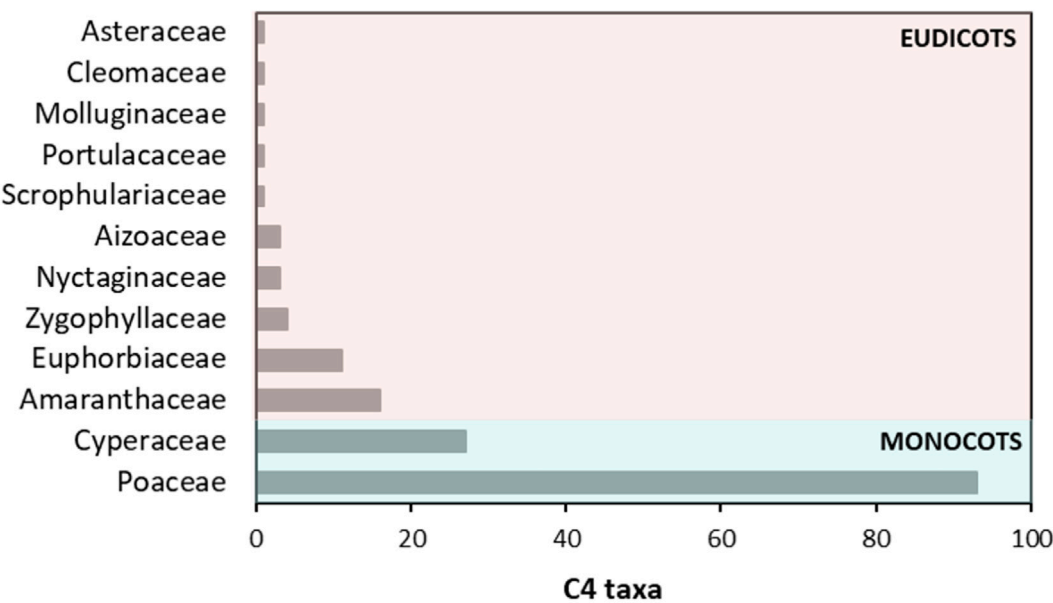
To provide a profile of the ecological preferences of each taxon in the islands, we developed a scatterplot using the median values of annual mean temperature, annual precipitation, and altitude for all its occurrences. These values were calculated on the basis of a minimum threshold of three occurrences per taxon, resulting in 139 taxa for each reliable variable.

## 3 Results

### 3.1 Cabo Verde $C_4$ diversity

A total of 162  $C_4$  taxa belonging to 69 genera and 12 families (ten eudicots and two monocots) have been compiled for the Cabo Verde

(a) Number of taxa per family



(b) Traits

Traits	Eudicots			Monocots		
	Families	Taxa	Occ.	Families	Taxa	Occ.
<b>Habit</b>						
Herb	10	41	1336	2	120	3509
Shrub	1	1	1	0	0	0
<b>Life cycle</b>						
Annual	10	31	919	2	64	2223
Perennial	4	11	418	2	56	1286
<b>Salt tolerance</b>						
Halophyte	6	12	663	2	33	1611
<b>C4 subtype</b>						
NAD-ME	7	18	556	2	48	1572
<i>predominantly NAD-ME</i>				<i>2</i>	<i>27</i>	<i>704</i>
<i>NAD-ME/PEP-CK</i>				<i>1</i>	<i>21</i>	<i>868</i>
NADP-ME	6	23	780	2	70	1934

FIGURE 2  
Characterisation of the C<sub>4</sub> angiosperm taxa (eudicots and monocots) that occur in Cabo Verde. (a) Number of taxa per family; (b) Number of families, taxa, and occurrences according to the functional traits studied.

archipelago (Table 1). A comprehensive list of taxa reported as C<sub>4</sub>, including their taxonomic classifications and functional traits, is presented in Supplementary Appendix S1A.

Most of them (120, corresponding to 74.1%) are monocots, with Poaceae being the most taxa-rich family (93 taxa; Figure 2a). The eudicots include 42 taxa (50% native) from

TABLE 1 List of the C<sub>4</sub> angiosperm genera that occur in Cabo Verde and their respective traits.

Clade Family	Genus	No. Taxa	Distribution status	Life cycle	Salt tolerance	C <sub>4</sub> subtype
EUDICOTS						
Aizoaceae	<i>Sesuvium</i>	1	N	A	Halophyte	NADP-ME
	<i>Trianthema</i>	1	NN	A	Halophyte	NADP-ME
	<i>Zaleya</i>	1	N	P	Halophyte	NAD-ME
Amaranthaceae	<i>Aerva</i>	1	N	P	Halophyte	NADP-ME
	<i>Alternanthera</i>	3	NN	P	n.a	NAD-ME (1), NADP-ME (2)
	<i>Amaranthus</i>	10	N (1), NN (9)	A	n.a	NAD-ME
	<i>Gomphrena</i>	1	N	P	Halophyte	NADP-ME
	<i>Traganum</i>	1	N	P	Halophyte	n.a
Asteraceae	<i>Flaveria</i>	1	NN	A	n.a	NADP-ME
Cleomaceae	<i>Cleome</i>	1	N	A	n.a	NAD-ME
Euphorbiaceae	<i>Euphorbia</i>	11	N (5), NN (6)	A	Halophyte (1), n.a. (10)	NADP-ME
Molluginaceae	<i>Hypertelis</i>	1	N	A	n.a	NAD-ME
Nyctaginaceae	<i>Boerhavia</i>	3	N (2), NN (1)	A (1), P (2)	Halophyte (1), n.a. (2)	NADP-ME (3)
Portulacaceae	<i>Portulaca</i>	1	N	A	Halophyte	NAD-ME
Scrophulariaceae	<i>Anticharis</i>	1	N	A	n.a	NAD-ME
Zygophyllaceae	<i>Tribulus</i>	3	N	A (1), P (2)	Halophyte (2), n.a. (1)	NADP-ME
	<i>Zygophyllum</i>	1	N	A	Halophyte	NAD-ME
MONOCOTS						
Cyperaceae	<i>Bulbostylis</i>	2	N	A	n.a	NADP-ME
	<i>Cyperus</i>	21	N	A (5), P (16)	Halophyte (4), n.a. (17)	NADP-ME
	<i>Eleocharis</i>	2	N	A	n.a	NAD-ME
	<i>Fimbristylis</i>	2	N	A (1), P (1)	Halophyte (1), n.a. (1)	NADP-ME
Poaceae	<i>Acrachne</i>	1	N	A	n.a	NAD-ME
	<i>Andropogon</i>	1	N	P	n.a	NADP-ME
	<i>Antheophora</i>	1	NN	A	n.a	NADP-ME
	<i>Aristida</i>	3	E (1), N (2)	A	Halophyte	NADP-ME
	<i>Arthraxon</i>	1	N	A	n.a	NADP-ME
	<i>Bothriochloa</i>	2	N	P	Halophyte (1), n.a. (1)	NADP-ME
	<i>Cenchrus</i>	7	N (6), NN (1)	A (4), P (3)	Halophyte (1), n.a. (6)	NADP-ME
	<i>Chloris</i>	4	N (3), NN (1)	A (3), P (1)	Halophyte (1), n.a. (3)	NAD-ME/PEP-CK
	<i>Cymbopogon</i>	1	NN	P	Halophyte	NADP-ME
	<i>Cynodon</i>	1	N	P	Halophyte	NAD-ME
	<i>Dactyloctenium</i>	1	N	A	Halophyte	NAD-ME
	<i>Dichanthium</i>	2	N	P	Halophyte (1), n.a. (1)	NADP-ME
	<i>Diectomis</i>	1	N	A	n.a	NADP-ME
	<i>Digitaria</i>	6	N (4), NN (2)	A (4), P (2)	Halophyte (2), n.a. (4)	NADP-ME
	<i>Dinebra</i>	1	NN	A	n.a	NAD-ME

(Continued on following page)



TABLE 1 (Continued) List of the C<sub>4</sub> angiosperm genera that occur in Cabo Verde and their respective traits.

Clade Family	Genus	No. Taxa	Distribution status	Life cycle	Salt tolerance	C <sub>4</sub> subtype
	<i>Echinochloa</i>	1	N	A	Halophyte	NADP-ME
	<i>Eleusine</i>	1	N	A	Halophyte	NAD-ME
	<i>Elionurus</i>	1	N	A	n.a	NADP-ME
	<i>Enneapogon</i>	1	N	P	n.a	NAD-ME
	<i>Enteropogon</i>	2	N	A (1), P (1)	n.a	NAD-ME
	<i>Eragrostis</i>	10	E (1), N (7), NN (2)	A (8), P (2)	Halophyte (2), n.a. (8)	NAD-ME
	<i>Eriochloa</i>	1	N	A	n.a	NAD-ME/PEP-CK
	<i>Hackelochloa</i>	1	N	A	n.a	NADP-ME
	<i>Heteropogon</i>	2	N	A (1), P (1)	n.a	NADP-ME
	<i>Hyparrhenia</i>	1	E	P	n.a	NADP-ME
	<i>Imperata</i>	1	N	P	Halophyte	NADP-ME
	<i>Leptothrium</i>	1	N	P	n.a	n.a
	<i>Megathyrsus</i>	1	N	P	n.a	NAD-ME/PEP-CK
	<i>Melinis</i>	2	N	A (1), P (1)	Halophyte (1), n.a. (1)	NAD-ME/PEP-CK
	<i>Panicum</i>	1	N	A	n.a	NAD-ME
	<i>Paspalum</i>	2	N (1), NN (1)	P	Halophyte (1), n.a. (1)	NADP-ME
	<i>Rottboellia</i>	1	N	A	n.a	NADP-ME
	<i>Schizachyrium</i>	1	N	A	n.a	NADP-ME
	<i>Schmidtia</i>	1	N	P	n.a	NAD-ME/PEP-CK
	<i>Schoenefeldia</i>	1	N	A	n.a	NAD-ME
	<i>Sehima</i>	1	N	A	n.a	NADP-ME
	<i>Setaria</i>	4	N	A (3), P (1)	Halophyte (2), n.a. (2)	NADP-ME
	<i>Sorghum</i>	2	N (1), NN (1)	A (1), P (1)	n.a	NADP-ME
	<i>Sporobolus</i>	6	N (6)	A (2), P (4)	Halophyte (4), n.a. (2)	NAD-ME/PEP-CK
	<i>Stenotaphrum</i>	1	NN	P	Halophyte	NADP-ME
	<i>Stipagrostis</i>	1	N	P	n.a	NAD-ME
	<i>Tetrapogon</i>	2	N	A (1), P (1)	n.a	NAD-ME
	<i>Themeda</i>	1	N	P	n.a	NADP-ME
	<i>Tragus</i>	1	N	A	n.a	NAD-ME
	<i>Tricholaena</i>	1	N	P	n.a	NAD-ME/PEP-CK
	<i>Tripogon</i>	1	N	P	n.a	NAD-ME
	<i>Tripogonella</i>	1	N	P	n.a	n.a
	<i>Urochloa</i>	5	E (1), N (3), NN (1)	A	Halophyte (1), n.a. (4)	NAD-ME/PEP-CK

Distribution status: E, endemic; N, native non-endemic; NN, non-native. Life cycle: A, annual; P, perennial. n.a., information not available. Habit is not included as only one genus (*Traganum*) includes a shrub species. When a given trait varies within the genus, the number of taxa of each kind is indicated in brackets.

10 families, with more representatives in Amaranthaceae and Euphorbiaceae. Five families are represented by a single species (Asteraceae, Cleomaceae, Molluginaceae, Portulacaceae, and Scrophulariaceae). The genera rich in taxa ( $\geq 10$  taxa) are *Amaranthus* (10), *Eragrostis* (10), *Euphorbia* (11), and

*Cyperus* (21) (Table 1). Most C<sub>4</sub> taxa are native (79%), including four endemics belonging to the Poaceae: *Aristida cardosoi*, *Eragrostis conertii*, *Hyparrhenia caboverdeana* (Figure 1c), and *Urochloa caboverdiana*. The 34 non-native taxa belong to five eudicot families (21 taxa) and the Poaceae



family (13 taxa). Except for Asteraceae (with only one species), all  $C_4$  recorded families include native taxa.

Regarding functional traits (Figure 2b; Table 1), most taxa are annual, 95 in total. The 67 perennial taxa belong to six families (Aizoaceae, Amaranthaceae, Cyperaceae, Nyctaginaceae, Poaceae and Zygophyllaceae). Most taxa are herbaceous and only one shrub species (*Traganum moquinii*, Amaranthaceae) occurs on the islands. We found that 27.8% of  $C_4$  taxa (12 eudicots and 33 monocots) are salt tolerant and belong to eight  $C_4$  families (Poaceae – 28; Cyperaceae – 5; Aizoaceae, Amaranthaceae and Zygophyllaceae – three each; and Euphorbiaceae, Nyctaginaceae, and Portulacaceae – one each). The NADP-ME subtype dominates in both eudicots and monocots, with a total of 93 taxa (corresponding to 57.4%). This  $C_4$  subtype occurs in eight families and three of them (Asteraceae, Euphorbiaceae, and Nyctaginaceae) are exclusively NADP-ME in Cabo Verde. The NAD-malic enzyme is used by 66 taxa that belong to nine families, four of which are exclusively NAD-ME (Cleomaceae, Molluginaceae, Portulacaceae, and Scrophulariaceae). Among monocots, the NAD-ME is restricted to three Poaceae subfamilies (Aristidoideae, Chloridoideae, Panicoideae; for details, see Supplementary Appendix S1A).  $C_4$  sedges are generally NADP-ME, whereas *Eleocharis*  $C_4$  species are of the type NAD-ME, the only occurrence (among monocots) of this subtype in Cyperaceae. Mixed NAD-ME/PEP-CK biochemical profiles have been identified in 21 Poaceae species, restricted to the subfamilies Chloridoideae and Panicoideae (see Supplementary Appendix S1A).

## 3.2 Ecological preferences of $C_4$ eudicots and monocots

Taking into account the 4,846 records of  $C_4$  species occurring in Cabo Verde, both eudicots and monocots show very wide altitudinal distribution ranges, from sea level up to 1,813 m for eudicots (median = 118 m) and 2,415 m for monocots (median = 338 m) (Figure 3a). Both groups can occur in environments with maximum annual temperatures reaching approximately 25 °C, with a median temperature of 23.2 °C in the case of eudicots and of 22.4 °C in the case of monocots. The eudicots are distributed in areas that receive between 49 and 505 mm of annual precipitation, with a median value of 259 mm. Monocots occur in areas with values between 49 and 581 mm of annual rainfall, with a median value of 274 mm. Eudicots and monocots differ significantly in median altitude, temperature, and precipitation (Mann–Whitney U Test,  $p < 0.001$ , Supplementary Table S1a).

Comparison between eudicots and monocots by functional trait (annual, perennial, halophyte, NAD-ME, and NADP-ME) shows that their distribution patterns differ significantly with altitude, mean annual temperature, and precipitation (Figure 3b; Supplementary Table S1b–f). Regardless of the functional trait considered, eudicots prefer lower, warmer, and drier regions than their monocot counterparts.

Furthermore, within the same taxonomic group (Supplementary Table S1g,h), significant differences were found in monocots when considering the life cycle, with annuals preferring slightly higher temperatures and higher precipitation than perennials. Regarding photosynthetic subtypes (Supplementary Table S1i,j), the NAD-ME

and NADP-ME eudicots differed in terms of annual precipitation, the former preferring drier areas; NAD-ME monocots were found to occur at lower altitudes, higher temperatures, and lower precipitation ( $p < 0.001$ ) than NADP-ME monocots.

The comparison between predominant NAD-ME and NAD-ME/PEP-CK monocotyledons revealed significant differences ( $p < 0.001$ ), with the mixed biochemical subtype NAD-ME/PEP-CK being associated with higher altitudes and increased precipitation (Supplementary Table S1k).

## 3.3 Distribution and uses of $C_4$ species

To gain a more detailed understanding of the distribution patterns of  $C_4$  species in Cabo Verde, we plotted the temperature and precipitation of each species using median values (Table 2) and considered four groups according to their median altitude values (Figure 4). Species in each altitude class (Table 2) occur preferentially, but not exclusively, in that class.

At altitudes below 300 m (including the driest and hottest areas), eudicots such as *Portulaca oleracea* (Portulacaceae), *Zygophyllum simplex* (see Figure 1d) and *Tribulus cistoides* (Zygophyllaceae), *Aerva javanica* (Amaranthaceae) can be highlighted (see Figure 1e); these species are present in all islands (Table 2). Among monocots, the Poaceae *Cenchrus ciliaris*, *Cynodon dactylon*, *Urochloa ramosa*, *Aristida adscensionis*, *Eragrostis cilianensis*, and several Cyperaceae are notable. At altitudes between 301 and 600 m, the more common species are Poaceae monocots such as *Melinis repens*, *Dactyloctenium aegyptium*, *Heteropogon contortus*, *Setaria verticillata*, *Andropogon gayanus* and *Digitaria nuda*; the only eudicot is *Boerhavia diffusa* (Nyctaginaceae). Above 600 m, the diversity and number of occurrences of  $C_4$  species decrease considerably. Three of the four endemic species (all Poaceae) are quite common: *U. caboverdiana* (0–300 m), *A. cardosoi* (300–600 m) and *H. caboverdeana* (600–900 m). Rarer (only 17 occurrences) is *E. conertii*, found usually in the 600–900 m class. Above 900 m, the number of  $C_4$  species is extremely low and their occurrence is rare. However, the singular high-altitude halophyte *Imperata cylindrica* (only found on one island) can be highlighted; this species and *Eragrostis barrelieri* (occurring on five islands) are the only  $C_4$  species found at the highest altitudes in Cabo Verde.

For both eudicots and monocots, non-native species are generally found in areas with higher precipitation (Figure 5). These species are mainly from Tropical and Subtropical America (Supplementary Appendix S1A).

Taking into account the traditional uses reported worldwide, species such as *A. javanica*, *Amaranthus caudatus*, *Cleome gynandra*, *C. dactylon*, *Cyperus articulatus*, *Cyperus rotundus*, *Cyperus esculentus*, *I. cylindrica*, *Paspalum scrobiculatum* and *Sorghum bicolor* have the highest number of uses (present in four or five of the classes considered) (Table 2). Species used as forage/fodder (80) stand out, most of which belong to the Poaceae; less represented are species used for environmental purposes (34), mostly Poaceae used for soil erosion control, traditional medicine (31) and food (24), namely, vegetables, cereals, and pseudocereals (especially Amaranthaceae and Poaceae species); the material category is the least represented (13) (for detailed information about species uses, see Supplementary Appendix S1A).

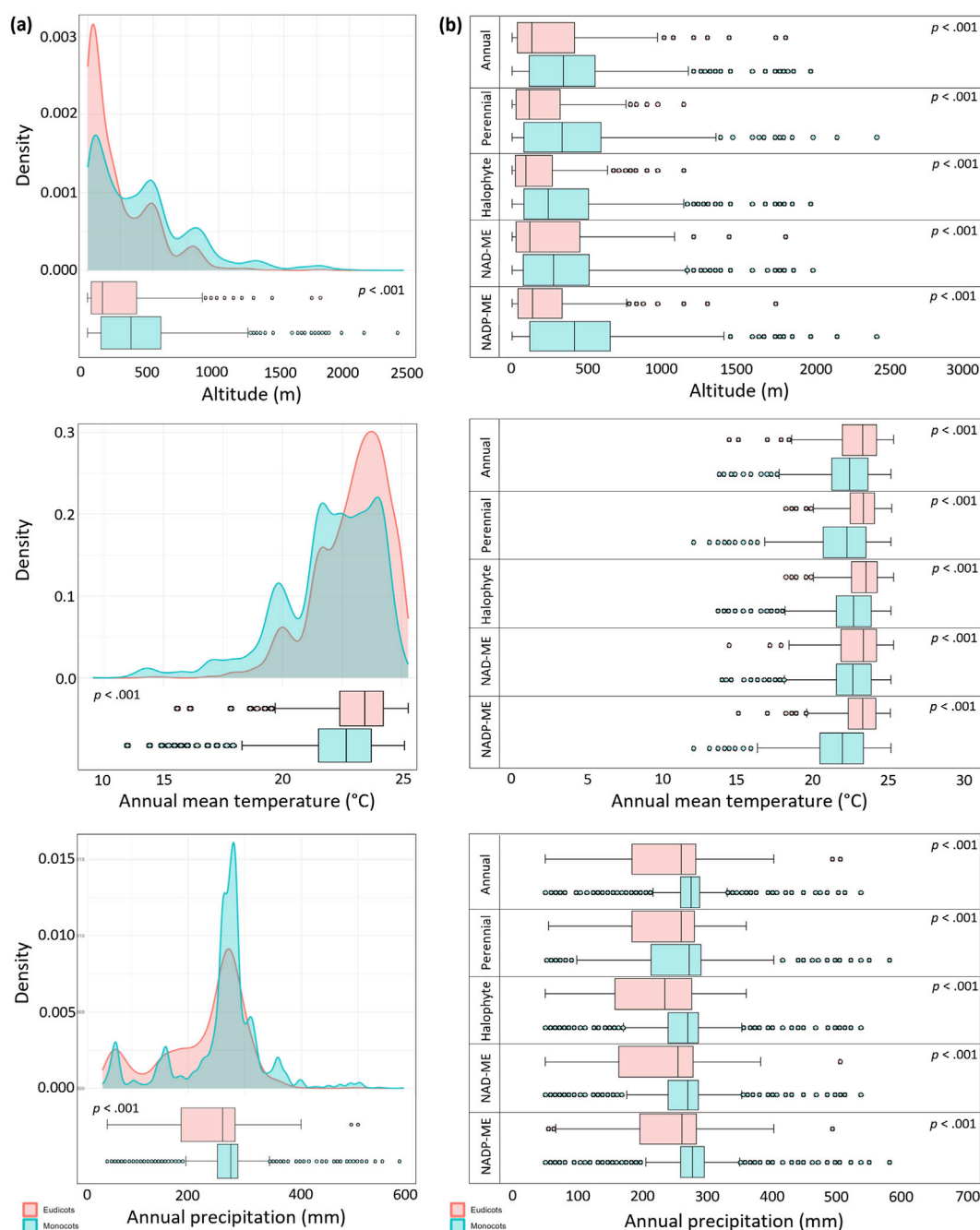


FIGURE 3

Comparison of ecological preferences between  $C_4$  eudicots (pink) and  $C_4$  monocots (blue): (a) total number of taxa occurrences, using kernel density estimation, and box plots of the distribution range of occurrence points as a function of (from top to bottom) altitude (m), annual mean temperature (°C), and annual precipitation (mm); (b) box plots of the distribution range of occurrence points according to the functional traits considered (life cycle, salt tolerance,  $C_4$  pathway subtype) with (from top to bottom) altitude (m), annual mean temperature (°C), and annual precipitation (mm). Box plots: vertical lines within boxes = medians, boxes = 25th and 75th percentiles; horizontal lines = 10th and 90th percentiles; dots = outliers. The Mann–Whitney U test was used to assess the statistical significance between eudicots and monocots in each analysis (significant difference for  $p < 0.05$ ).

## 4 Discussion

### 4.1 Diversity and ecology of $C_4$ eudicots and monocots in Cabo Verde islands

Sage's works (Sage, 2004; 2016; Sage and Zhu, 2011; Sage et al., 2011; 2018) have contributed enormously to our understanding of

$C_4$  photosynthesis, clarifying its evolutionary origins, biochemical mechanisms, and ecological implications. They also highlighted their utility to solve global challenges such as food security and ecosystem restoration, thus setting a useful framework for understanding the ecological and agricultural potential of  $C_4$  species.

Of approximately 18 families including  $C_4$  species (Sage, 2016), 12 occur in the Cabo Verde islands. Gisekiaceae and

TABLE 2 List of C<sub>4</sub> species in Cabo Verde. Taxonomic group (TG): E, Eudicot; M, Monocot. Status: E, endemic; N, native non-endemic; NN, non-native. Life cycle: A, annual; P, perennial. Salt tolerance (halophyte; n.a., information not available). C<sub>4</sub> subtype: NADP-ME; NAD-ME; and mixed NAD-ME/PEP-CK. Median values (Mdn) of altitude (Alt., m), temperature (Temp., °C) and precipitation (Precip., mm), number of islands where the species occurs (No. Isl.) and number and type of uses (NU). Species are organized by altitudinal classes, and in each class by eudicots (E) and monocots (M).

Species	TG	Status	Life cycle	Salt tolerance	C <sub>4</sub> subtype	Mdn alt	Mdn Temp	Mdn Precip	No. Isl	Occ	NU <sup>a</sup>
0–300 m altitude											
<i>Aerva javanica</i>	E	N	P	Halophyte	NADP-ME	54	23.5	189	10	68	4/F M Mt E
<i>Alternanthera caracasana</i>	E	NN	P	n.a	NAD-ME	228	23.0	267	2	10	0
<i>Alternanthera pungens</i>	E	NN	P	n.a	NAD-ME	95	23.6	259	8	77	1/M
<i>Alternanthera sessilis</i>	E	NN	P	n.a	NADP-ME	194	22.4	286	3	7	3/H F M
<i>Amaranthus graecizans</i> subsp. <i>graecizans</i>	E	N	A	n.a	NAD-ME	61	23.5	183	10	27	1/F
<i>Amaranthus viridis</i>	E	NN	A	n.a	NAD-ME	86	23.2	265	5	20	2/H F
<i>Anticharis senegalensis</i>	E	N	A	n.a	NAD-ME	72	23.1	150	4	3	0
<i>Boerhavia coccinea</i>	E	NN	P	n.a	NADP-ME	198	23.3	272	9	60	1/F
<i>Boerhavia repens</i>	E	N	A	n.a	NADP-ME	100	23.6	246	9	39	1/F
<i>Cleome gynandra</i>	E	N	A	n.a	NAD-ME	41	24.4	208	6	11	4/H F M Mt
<i>Euphorbia chamaesyce</i>	E	NN	A	n.a	NADP-ME	108.5	23.5	278	7	12	1/F
<i>Euphorbia forskoolii</i>	E	N	A	n.a	NADP-ME	71	23.6	249	9	33	0
<i>Euphorbia glaucophylla</i>	E	N	A	n.a	NADP-ME	54	24.3	221	4	3	0
<i>Euphorbia granulata</i>	E	N	A	Halophyte	NADP-ME	36	24.1	97	8	9	0
<i>Euphorbia hirta</i>	E	NN	A	n.a	NADP-ME	219	23.0	264	8	169	2/F M
<i>Euphorbia inaequilatera</i>	E	N	A	n.a	NADP-ME	24	22.8	225	6	5	0
<i>Euphorbia prostrata</i>	E	NN	A	n.a	NADP-ME	168	22.8	271	6	45	1/M
<i>Euphorbia scordiifolia</i>	E	N	A	n.a	NADP-ME	11.5	23.0	161	5	4	0
<i>Euphorbia serpens</i>	E	NN	A	n.a	NADP-ME	151	22.7	255	6	26	0
<i>Flaveria bidentis</i>	E	NN	A	n.a	NADP-ME	42	24.2	156	2	6	1/M
<i>Gomphrena vermicularis</i>	E	N	P	Halophyte	NADP-ME	31	24.3	218	5	15	0
<i>Hypertelis cerviana</i>	E	N	A	n.a	NAD-ME	83	23.1	97	4	5	1/M
<i>Portulaca oleracea</i>	E	N	A	Halophyte	NAD-ME	228	22.9	265	10	175	3/H F M
<i>Sesuvium hydaspicum</i>	E	N	A	Halophyte	NADP-ME	7	23.9	118	2	3	0
<i>Trianthema portulacastrum</i>	E	NN	A	Halophyte	NADP-ME	90.5	23.8	252	7	82	1/M
<i>Tribulus cistoides</i>	E	N	P	Halophyte	NADP-ME	86	23.3	226	10	66	1/F
<i>Tribulus pentandrus</i> var. <i>pentandrus</i>	E	N	P	n.a	NADP-ME	12	24.5	85	1	3	0
<i>Tribulus terrestris</i> var. <i>terrestris</i>	E	N	A	Halophyte	NADP-ME	41	24.3	204	7	23	1/M
<i>Zaleya pentandra</i>	E	N	P	Halophyte	NAD-ME	28	23.7	160	8	29	1/F
<i>Zygophyllum simplex</i>	E	N	A	Halophyte	NAD-ME	20.5	23.8	134	10	110	0
<i>Acrachne racemosa</i>	M	N	A	n.a	NAD-ME	189	23.5	246	5	28	0
<i>Aristida adscensionis</i>	M	N	A	Halophyte	NADP-ME	296.5	22.6	274	9	80	2/F E

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**TABLE 2 (Continued)** List of C<sub>4</sub> species in Cabo Verde. Taxonomic group (TG): E, Eudicot; M, Monocot. Status: E, endemic; N, native non-endemic; NN, non-native. Life cycle: A, annual; P, perennial. Salt tolerance (halophyte; n.a., information not available). C<sub>4</sub> subtype: NADP-ME; NAD-ME; and mixed NAD-ME/PEP-CK. Median values (Mdn) of altitude (Alt., m), temperature (Temp., °C) and precipitation (Precip., mm), number of islands where the species occurs (No. Isl.) and number and type of uses (NU). Species are organized by altitudinal classes, and in each class by eudicots (E) and monocots (M).

Species	TG	Status	Life cycle	Salt tolerance	C <sub>4</sub> subtype	Mdn alt	Mdn Temp	Mdn Precip	No. Isl	Occ	NU <sup>a</sup>
<i>Aristida funiculata</i>	M	N	A	Halophyte	NADP-ME	118	23.3	254	9	49	0
<i>Cenchrus biflorus</i>	M	N	A	n.a	NADP-ME	16	24.1	149	4	10	2/F E
<i>Cenchrus ciliaris</i>	M	N	P	Halophyte	NADP-ME	263	22.6	270	10	139	2/F E
<i>Cynodon dactylon</i>	M	N	P	Halophyte	NAD-ME	114.5	23.2	253	9	120	4/H F M E
<i>Cyperus articulatus</i>	M	N	P	n.a	NADP-ME	55	23.2	174	5	14	4/F M Mt E
<i>Cyperus bulbosus</i>	M	N	P	n.a	NADP-ME	10.5	23.6	76	6	28	0
<i>Cyperus capitatus</i>	M	N	P	n.a	NADP-ME	9	23.9	153	4	3	0
<i>Cyperus conglomeratus</i>	M	N	P	Halophyte	NADP-ME	3	23.1	71	2	4	0
<i>Cyperus crassipes</i>	M	N	P	Halophyte	NADP-ME	7	23.4	75	6	22	0
<i>Cyperus jeminicus</i>	M	N	P	n.a	NADP-ME	8	24.0	150	4	10	0
<i>Cyperus laevigatus</i> subsp. <i>laevigatus</i>	M	N	P	n.a	NADP-ME	194	23.1	238	7	29	2/F Mt
<i>Cyperus ligularis</i>	M	N	P	n.a	NADP-ME	133	22.6	274	3	5	0
<i>Cyperus mundii</i>	M	N	P	n.a	NADP-ME	257.5	23.2	266	1	6	0
<i>Cyperus rotundus</i>	M	N	P	Halophyte	NADP-ME	216.5	22.9	265	6	36	5/H F M Mt E
<i>Cyperus squarrosus</i>	M	N	A	n.a	NADP-ME	98	23.0	273	6	12	0
<i>Dichanthium annulatum</i>	M	N	P	Halophyte	NADP-ME	107.5	23.3	163	7	24	3/F Mt E
<i>Dichanthium foveolatum</i>	M	N	P	n.a	NADP-ME	53	23.6	143	9	37	1/F
<i>Digitaria nodosa</i>	M	N	P	n.a	NADP-ME	216.5	22.3	279	5	18	1/F
<i>Dinebra panicea</i>	M	NN	A	n.a	NAD-ME	202	23.8	264	1	11	0
<i>Echinochloa colonum</i>	M	N	A	Halophyte	NADP-ME	107	23.8	277	5	41	1/F
<i>Eleocharis atropurpurea</i>	M	N	A	n.a	NAD-ME	55	23.1	74	1	3	0
<i>Elionurus royleanus</i>	M	N	A	n.a	NADP-ME	54	23.8	159	7	23	0
<i>Enneapogon desvauxii</i>	M	N	P	n.a	NAD-ME	54	23.6	141	8	18	0
<i>Enteropogon prieurii</i>	M	N	A	n.a	NAD-ME	55.5	24.1	278	6	36	0
<i>Enteropogon rupestris</i>	M	N	P	n.a	NAD-ME	134	22.4	286	4	5	0
<i>Eragrostis cilianensis</i>	M	N	A	n.a	NAD-ME	221	23.0	246	9	54	1/F
<i>Eragrostis japonica</i>	M	N	A	n.a	NAD-ME	37	23.8	76	1	5	0
<i>Eragrostis minor</i>	M	N	A	n.a	NAD-ME	31	24.3	159	3	3	1/F
<i>Eragrostis pilosa</i>	M	N	A	Halophyte	NAD-ME	161	22.6	278	3	9	0
<i>Eragrostis viscosa</i>	M	NN	A	n.a	NAD-ME	219	23.1	262	2	6	0
<i>Eriochloa barbatus</i>	M	N	A	n.a	NAD-ME/ PEP-CK	62.5	23.6	278	2	4	0
<i>Fimbristylis ferruginea</i>	M	N	P	Halophyte	NADP-ME	219	22.5	257	3	32	1/F
<i>Fimbristylis microcarya</i>	M	N	A	n.a	NADP-ME	42	23.8	74	1	3	0

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**TABLE 2 (Continued)** List of C<sub>4</sub> species in Cabo Verde. Taxonomic group (TG): E, Eudicot; M, Monocot. Status: E, endemic; N, native non-endemic; NN, non-native. Life cycle: A, annual; P, perennial. Salt tolerance (halophyte; n.a., information not available). C<sub>4</sub> subtype: NADP-ME; NAD-ME; and mixed NAD-ME/PEP-CK. Median values (Mdn) of altitude (Alt., m), temperature (Temp., °C) and precipitation (Precip., mm), number of islands where the species occurs (No. Isl.) and number and type of uses (NU). Species are organized by altitudinal classes, and in each class by eudicots (E) and monocots (M).

Species	TG	Status	Life cycle	Salt tolerance	C <sub>4</sub> subtype	Mdn alt	Mdn Temp	Mdn Precip	No. Isl	Occ	NU <sup>a</sup>
<i>Hackelochloa granularis</i>	M	N	A	n.a	NADP-ME	118	23.1	261	3	6	1/F
<i>Schmidtia pappophoroides</i>	M	N	P	n.a	NAD-ME	65.5	23.8	158	7	16	0
<i>Schoenefeldia gracilis</i>	M	N	A	n.a	NAD-ME	55	23.9	74	2	7	0
<i>Sehima ischaemoides</i>	M	N	A	n.a	NADP-ME	32	23.7	268	5	27	0
<i>Sporobolus minutus</i>	M	N	A	n.a	NAD-ME/ PEP-CK	3	24.2	137	2	4	0
<i>Sporobolus robustus</i>	M	N	P	Halophyte	NAD-ME/ PEP-CK	34.5	23.4	110	7	16	0
<i>Sporobolus spicatus</i>	M	N	P	Halophyte	NAD-ME/ PEP-CK	13	23.4	75	9	31	0
<i>Sporobolus virginicus</i>	M	N	P	Halophyte	NAD-ME/ PEP-CK	8.5	23.5	87	6	12	2/F E
<i>Stipagrostis uniplumis</i>	M	N	P	n.a	NAD-ME	149	24.0	192	4	10	0
<i>Tetrapogon cenchrifolius</i>	M	N	A	n.a	NAD-ME	32	24.2	214	3	11	0
<i>Tragus racemosus</i>	M	N	A	n.a	NAD-ME	60	23.4	162	8	17	0
<i>Urochloa caboverdiana</i>	M	E	A	n.a	NAD-ME/ PEP-CK	283	22.8	264	6	106	2/H F
<i>Urochloa ramosa</i>	M	N	A	Halophyte	NAD-ME/ PEP-CK	117	23.9	269	8	89	2/H F
<i>Urochloa xantholeuca</i>	M	N	A	n.a	NAD-ME/ PEP-CK	118	23.1	249	8	31	1/F
<b>301–600 m altitude</b>											
<i>Amaranthus blitum</i> subsp. <i>emarginatus</i>	E	NN	A	n.a	NAD-ME	462	21.0	273	5	12	1/H
<i>Amaranthus caudatus</i>	E	NN	A	n.a	NAD-ME	420	21.6	293	5	6	4/H F M E
<i>Amaranthus cruentus</i>	E	NN	A	n.a	NAD-ME	503	21.5	275	3	8	3/H F E
<i>Amaranthus spinosus</i>	E	NN	A	n.a	NAD-ME	389.5	22.1	265	8	34	2/H M
<i>Boerhavia diffusa</i>	E	N	P	Halophyte	NADP-ME	322	22.5	271	9	82	2/F M
<i>Euphorbia hypericifolia</i>	E	NN	A	n.a	NADP-ME	321	22.5	264	1	11	1/M
<i>Euphorbia hyssopifolia</i>	E	NN	A	n.a	NADP-ME	438	21.4	274	2	9	2/F M
<i>Andropogon gayanus</i>	M	N	P	n.a	NADP-ME	571	21.2	280	5	91	2/F Mt
<i>Aristida cardosoi</i>	M	E	A	Halophyte	NADP-ME	416	21.7	295	10	50	0
<i>Bothriochloa bladhii</i>	M	N	P	Halophyte	NADP-ME	497	21.4	289	7	23	2/F E
<i>Bothriochloa insculpta</i>	M	N	P	n.a	NADP-ME	481	21.8	276	6	58	2/F E
<i>Bulbostylis barbata</i>	M	N	A	n.a	NADP-ME	416.5	21.7	341	4	10	1/F
<i>Cenchrus echinatus</i>	M	NN	A	n.a	NADP-ME	308	21.6	311	5	10	0
<i>Cenchrus pedicellatus</i> subsp. <i>pedicellatus</i>	M	N	A	n.a	NADP-ME	416	21.9	281	6	35	1/F
<i>Cenchrus pedicellatus</i> subsp. <i>unispiculus</i>	M	N	A	n.a	NADP-ME	429	22.0	281	6	32	1/F

(Continued on following page)

TABLE 2 (Continued) List of C<sub>4</sub> species in Cabo Verde. Taxonomic group (TG): E, Eudicot; M, Monocot. Status: E, endemic; N, native non-endemic; NN, non-native. Life cycle: A, annual; P, perennial. Salt tolerance (halophyte; n.a., information not available). C<sub>4</sub> subtype: NADP-ME; NAD-ME; and mixed NAD-ME/PEP-CK. Median values (Mdn) of altitude (Alt., m), temperature (Temp., °C) and precipitation (Precip., mm), number of islands where the species occurs (No. Isl.) and number and type of uses (NU). Species are organized by altitudinal classes, and in each class by eudicots (E) and monocots (M).

Species	TG	Status	Life cycle	Salt tolerance	C <sub>4</sub> subtype	Mdn alt	Mdn Temp	Mdn Precip	No. Isl	Occ	NU <sup>a</sup>
<i>Cenchrus setosus</i> subsp. <i>setosus</i>	M	N	P	n.a	NADP-ME	568.5	20.5	285	7	52	1/F
<i>Chloris pilosa</i>	M	N	A	n.a	NAD-ME/PEP-CK	438	22.0	274	6	49	1/F
<i>Chloris pycnothrix</i>	M	N	A	n.a	NAD-ME/PEP-CK	511	20.6	287	6	21	1/F
<i>Chloris virgata</i>	M	NN	A	Halophyte	NAD-ME/PEP-CK	323.5	22.5	274	10	122	2/F E
<i>Cyperus alopecuroides</i>	M	N	P	Halophyte	NADP-ME	358	22.0	262	2	6	2/Mt E
<i>Cyperus polystachyos</i>	M	N	P	n.a	NADP-ME	427	21.6	283	6	24	0
<i>Dactyloctenium aegyptium</i>	M	N	A	Halophyte	NAD-ME	316	22.5	271	10	165	3/H F E
<i>Digitaria ciliaris</i>	M	N	A	Halophyte	NADP-ME	356	22.1	279	5	57	2/F E
<i>Digitaria horizontalis</i>	M	N	A	n.a	NADP-ME	321	22.5	274	6	19	1/F
<i>Digitaria nuda</i>	M	N	A	n.a	NADP-ME	362	22.5	275	5	90	0
<i>Eleusine indica</i>	M	N	A	Halophyte	NAD-ME	321	22.3	273	7	76	1/F
<i>Eragrostis ciliaris</i>	M	N	A	Halophyte	NAD-ME	321	22.3	272	9	39	1/F
<i>Heteropogon contortus</i>	M	N	P	n.a	NADP-ME	507.5	21.5	276	8	142	2/F E
<i>Heteropogon melanocarpus</i>	M	N	A	n.a	NADP-ME	571	21.2	296	5	43	1/F
<i>Megathyrsus maximus</i>	M	N	P	n.a	NAD-ME	321	22.4	275	5	40	2/F E
<i>Melinis repens</i>	M	N	A	Halophyte	NAD-ME	464	21.7	276	10	239	2/F E
<i>Paspalum scrobiculatum</i>	M	N	P	n.a	NADP-ME	347.5	21.5	282	4	16	4/H F M E
<i>Rottboellia cochinchinensis</i>	M	N	A	n.a	NADP-ME	499	21.5	276	5	51	1/F
<i>Setaria geminata</i>	M	N	P	Halophyte	NADP-ME	448.5	21.7	257	3	4	1/F
<i>Setaria pumila</i>	M	N	A	n.a	NADP-ME	579	20.8	281	7	61	2/H F
<i>Setaria verticillata</i>	M	N	A	Halophyte	NADP-ME	321	22.4	270	10	115	2/H F
<i>Sorghum bicolor</i>	M	NN	A	n.a	NADP-ME	484	20.7	288	4	7	4/H F M Mt
<i>Tricholaena teneriffae</i>	M	N	P	n.a	NAD-ME/PEP-CK	474	21.5	292	7	46	1/F
<i>Urochloa deflexa</i>	M	N	A	n.a	NAD-ME/PEP-CK	393	22.1	276	6	12	1/H
601–900 m altitude											
<i>Amaranthus hybridus</i> subsp. <i>hybridus</i>	E	NN	A	n.a	NAD-ME	753	19.9	276	4	19	3/H F M
<i>Amaranthus standleyanus</i>	E	NN	A	n.a	NAD-ME	708	20.4	302	2	7	0
<i>Arthraxon lancifolius</i>	M	N	A	n.a	NADP-ME	701.5	20.2	296	6	38	0
<i>Bulbostylis hispidula</i> subsp. <i>hispidula</i>	M	N	A	n.a	NADP-ME	610	20.8	298	3	11	1/M
<i>Cenchrus setosus</i> subsp. <i>hordeoides</i>	M	N	P	n.a	NADP-ME	813	19.8	307	2	3	0

(Continued on following page)

TABLE 2 (Continued) List of  $C_4$  species in Cabo Verde. Taxonomic group (TG): E, Eudicot; M, Monocot. Status: E, endemic; N, native non-endemic; NN, non-native. Life cycle: A, annual; P, perennial. Salt tolerance (halophyte; n.a., information not available).  $C_4$  subtype: NADP-ME; NAD-ME; and mixed NAD-ME/PEP-CK. Median values (Mdn) of altitude (Alt., m), temperature (Temp., °C) and precipitation (Precip., mm), number of islands where the species occurs (No. Isl.) and number and type of uses (NU). Species are organized by altitudinal classes, and in each class by eudicots (E) and monocots (M).

Species	TG	Status	Life cycle	Salt tolerance	$C_4$ subtype	Mdn alt	Mdn Temp	Mdn Precip	No. Isl	Occ	NU <sup>a</sup>
<i>Cyperus amabilis</i>	M	N	A	n.a	NADP-ME	850.5	19.2	366	1	6	0
<i>Cyperus esculentus</i>	M	N	P	n.a	NADP-ME	861.5	19.5	319	6	20	5/H F M Mt E
<i>Cyperus hortensis</i>	M	N	P	n.a	NADP-ME	658.5	20.7	285	1	8	1/F
<i>Cyperus metzii</i>	M	N	A	n.a	NADP-ME	734.5	20.2	320	3	10	0
<i>Diectomis fastigiata</i>	M	N	A	n.a	NADP-ME	727.5	19.5	293	3	8	2/F E
<i>Eragrostis aethiopica</i>	M	NN	A	n.a	NAD-ME	888	19.5	284	1	3	0
<i>Eragrostis conertii</i>	M	E	P	n.a	NAD-ME	652	20.6	293	5	17	0
<i>Hyparrhenia caboverdeana</i>	M	E	P	n.a	NADP-ME	705	19.9	309	8	92	1/F
<i>Melinis minutiflora</i>	M	N	P	n.a	NAD-ME	824	18.9	356	2	13	2/F E
<i>Schizachyrium brevifolium</i>	M	N	A	n.a	NADP-ME	824	19.8	285	2	3	1/F
<i>Setaria barbata</i>	M	N	A	n.a	NADP-ME	698	20.4	281	7	61	2/H F
<i>Sporobolus molleri</i>	M	N	A	n.a	NAD-ME/ PEP-CK	680.5	20.2	315	4	14	0
<i>Tripogon multiflorus</i>	M	N	P	n.a	NAD-ME	705	20.4	280	2	5	0
<i>Tripogonella minima</i>	M	N	P	n.a	n.a	856	19.8	323	2	3	0
> 900 m altitude											
<i>Eragrostis barrelieri</i>	M	N	A	n.a	NAD-ME	1,270	17.2	361	5	51	1/F
<i>Imperata cylindrica</i>	M	N	P	Halophyte	NADP-ME	1,462	15.4	448	1	3	4/F M Mt E

<sup>a</sup>NU, was calculated as the sum of use categories (i.e., H: human food, F: forage/fodder, M: medicinal, Mt: material, E: environmental).

Hydrocharitaceae are absent in the archipelago; the Acanthaceae, Boraginaceae, and Polygonaceae are globally represented by one  $C_4$  lineage each, but these lineages do not occur in Cabo Verde; the  $C_4$  lineage of Caryophyllaceae is *Polycarpaea*, represented in Cabo Verde by the endemic *Polycarpaea gayi*, but there is no information about its photosynthetic pathway. The substantial presence of Poaceae species among  $C_4$  plants in the archipelago (almost a hundred) further emphasises the success of this family in colonising arid and semi-arid environments, with the  $C_4$  pathway representing a significant competitive advantage (Osborne and Freckleton, 2009). The predominance of  $C_4$  monocot species is also consistent with the taxonomic distribution pattern of this taxonomical group in Cabo Verde, where Poaceae and Cyperaceae rank among the most abundant families (Duarte et al., 2024a; Romeiras et al., 2016). The  $C_4$  eudicots have a more diversified taxonomic distribution, with representatives from 10 families.

The NADP-ME subtype is more common than the NAD-ME, representing c. 58% of the total number of  $C_4$  species. The dominant presence of Poaceae (mostly NADP-ME) contributes to this. This pattern reflects the overall distribution of  $C_4$  subtypes, with NADP-ME and NAD-ME presenting similar numbers of lineages in

eudicots and the NADP-ME subtype dominating in monocot lineages (Sage et al., 2011).

Among  $C_4$  plants, the prevalence of herbaceous species is promoted by the edaphic and climatic constraints of the islands, which favour more ephemeral and fast-growing life forms (Sage et al., 2018). The only woody  $C_4$  life form in the archipelago is the shrub species *T. moquinii*. This pattern agrees with the global pattern, since  $C_4$  woody species are few and only known for the Amaranthaceae, Euphorbiaceae, Polygonaceae, and Zygophyllaceae families (about 400 against more than 7,700 herbaceous species) (Sage, 2016).

The substantial proportion of halophyte species (approx. 28%), both eudicots and monocots, mirrors the adaptability of  $C_4$  plants to colonise the saline and marginal environments of the islands.  $C_4$  photosynthesis allows for more efficient use of  $CO_2$ , especially under low water availability and high salinity (Edwards and Smith, 2010; Sage et al., 2018). This characteristic is particularly evident in the arid and coastal regions of Cabo Verde, where salinity and water stress conditions prevail.

In Cabo Verde,  $C_4$  monocots show a wide altitudinal range of distribution and are found in diverse environments, varying from dry habitats in the lowlands to mid- and high-altitude grasslands where they are particularly important as pasture (Duarte et al., 2024a).

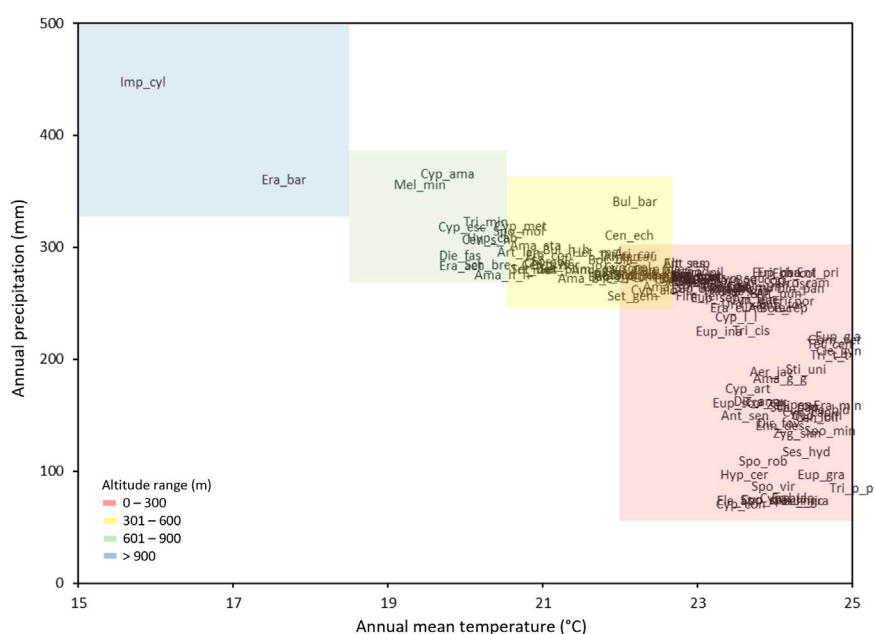


FIGURE 4

Scatterplot of annual mean temperature (°C) and annual precipitation (mm) data (median values) for the C<sub>4</sub> taxa recorded in Cabo Verde. Each taxon is represented by its name acronyms (see Supplementary Appendix S1A). Coloured polygons were defined according to altitude classes using the median value of each taxon: 0–300 m (pink); 301–600 m (yellow); 601–900 m (green); >900 m (blue). The thresholds of the polygons correspond to the minimum and maximum values of the medians for temperature and precipitation (0–300 m: 22.3 °C–24.5 °C temperature, 71–286 mm precipitation; 300–600 m: 20.5 °C–22.5 °C temperature, 257–341 mm precipitation; 600–900 m: 18.9 °C–20.8 °C temperature, 276–366 mm precipitation; >900 m: 15.4 °C–17.2 °C temperature, 361–448 mm precipitation).

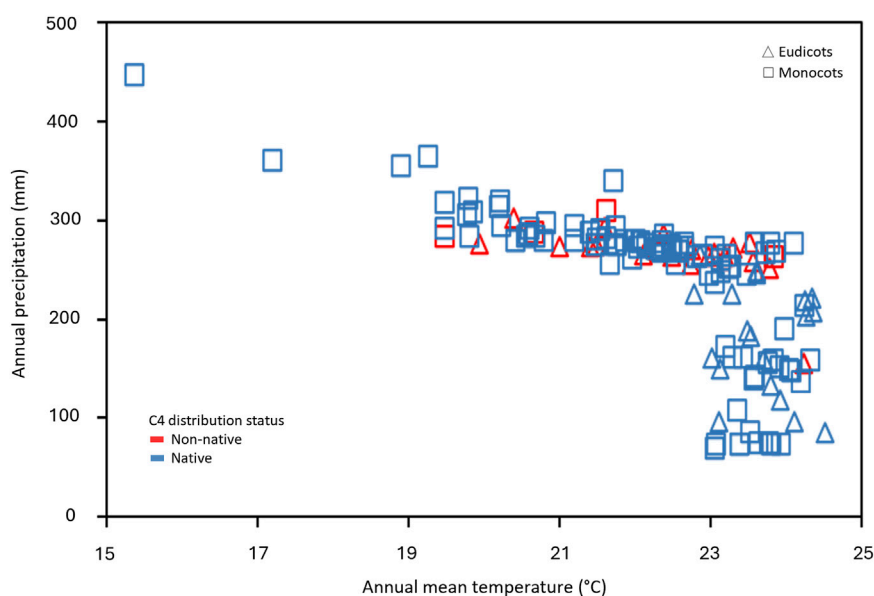


FIGURE 5

Scatterplot of annual mean temperature (°C) and annual precipitation (mm) data (median values) for each C<sub>4</sub> taxon recorded in Cabo Verde, according to status: native (blue symbols) or non-native (red symbols). Triangles represent eudicot taxa, and squares represent monocot taxa.

However, as concluded in the present study, they prefer higher altitudes, where temperatures are milder and precipitations higher.

In contrast, C<sub>4</sub> eudicots are more common in the archipelago lowlands (generally up to approximately 300 m), where the

highest temperatures and the lowest precipitations occur and where saline habitats are more common. Only two species, *Amaranthus hybridus* subsp. *hybridus* and *Amaranthus standleyanus* reach higher altitudes. This confirms the



evolutionary advantage of  $C_4$  eudicots over  $C_4$  monocots in drier areas of low-altitude.

Previous research has also consistently demonstrated that distinct taxonomic groups of  $C_4$  plants exhibit contrasting distribution patterns in response to climatic gradients, supporting that temperature and aridity drive different distribution patterns among  $C_4$  lineages. Across Europe, Pyankov et al. (2010) observed that the distribution of  $C_4$  monocots tends to be associated with regions experiencing higher temperatures (a pattern seemingly opposite to that identified in the present study, yet probably attributable to the markedly lower temperatures characteristic of European latitudes), whereas several  $C_4$  eudicot lineages display a stronger affinity for arid environments. Similarly, in southwestern Asia, Rudov et al. (2020) reported a marked predominance of  $C_4$  eudicots in the Irano-Turanian deserts, emphasising their remarkable adaptation to strongly continental climates with low mean annual precipitation; in contrast, adjacent regions with relatively higher moisture availability were dominated by  $C_4$  Poaceae.

When comparing eudicots with monocots, distinct ecological preferences are also observed regardless of the functional traits analysed (annuals, perennials, halophytes, NAD-ME, and NADP-ME): eudicots are related with significantly lower median values of altitude and precipitation, and higher values of temperature than the corresponding functional groups of monocots. To monocots and eudicots, species of the NAD-ME subtype prefer lowland areas (warmer and drier) to NADP-ME ones. Sage et al. (2018) suggested the biochemical limitations of the NADP-ME subtype at higher temperatures.

At the local scale of the Cabo Verde Islands, these findings align with patterns documented for continental West Africa, where Bocksberger et al. (2016) reported a predominance of Paniceae and Chloridoideae species characterised by the NAD-ME photosynthetic subtype in the Sahelian zone. Comparable patterns have been documented in Neotropical regions, where NAD-ME species become increasingly dominant towards the more arid areas of central Argentina (Cabido et al., 2008), and likewise with decreasing annual precipitation across the United States (Taub, 2000). These observations are further corroborated by recent global biogeographical analyses (Berasategui et al., 2023).

The variation observed between predominant NAD-ME and mixed NAD-ME/PEP-CK monocotyledons in Cabo Verde suggests that the subtypes may respond differently to the archipelago's environmental gradients. While predominantly NAD-ME species occurred mainly in lower-altitude areas with reduced precipitation, mixed NAD-ME/PEP-CK species were primarily associated with relatively higher-altitude regions characterised by higher levels of precipitation.

The same patterns have been observed in other climatic gradients, in which the relative distribution of subtypes may reflect functional adjustments to water availability and temperature, although these patterns are not always linear or universal (Cabido et al., 2008; Taub, 2000). Furthermore, large-scale comparative syntheses have pointed out that environmental factors exert a stronger influence on photosynthetic capacity than the biochemical subtype itself (Fan et al., 2025), which reinforces a cautious interpretation of our results.

Also, the association of grass lineages with annual precipitation, which appears to be as strong as—or even stronger than—that observed for photosynthetic subtypes, suggests that factors other than the decarboxylation pathway may underlie these distributional patterns (Taub, 2000; Cabido et al., 2008; Griffith et al., 2020). Indeed, several studies have demonstrated a clear phylogenetic pattern in the distribution of  $C_4$  grass lineages across broad precipitation gradients (Cabido et al., 2008; Griffith et al., 2020; Taub, 2000). Nevertheless, the mechanisms driving this ecological sorting remain poorly understood (Griffith et al., 2020).

Thus, while our results suggest ecological differentiation between predominant NAD-ME and mixed NAD-ME/PEP-CK in Cabo Verde, additional studies will be needed to clarify the extent to which these differences reflect stabilizing adaptations or plastic responses to contrasting habitats.

Although the set of traits analysed is limited and primarily derived from bibliographic sources, their selection is considered highly pertinent within the ecogeographical framework of Cabo Verde, offering meaningful insights to guide revegetation and restoration efforts. While additional ecological or historical processes may also contribute to the observed distribution patterns, the findings underscore the central role of climate in shaping the spatial variability of these traits. In much the same way that a species may prove successful or competitive under particular conditions but not others, the success of a given trait value likewise depends on the surrounding physical and biotic environment (Westoby, 2025).

## 4.2 The use of $C_4$ species for ecosystem restoration in Cabo Verde

Anthropogenic activities (for example, agricultural practices and exploitation of natural resources), together with climate change, led to the degradation of terrestrial ecosystems globally (Smith et al., 2015; Weiskopf et al., 2020). This degradation presents relevant challenges as it compromises biodiversity integrity, human economic stability, and social wellbeing (Vlek et al., 2017), and ecosystem restoration has been considered a key approach to address these emerging issues. One of the great challenges in this area is finding species that are well suited to effectively restore degraded landscapes (Ostertag et al., 2015; Wang et al., 2021). Among other sustainability and management considerations, such as rural priorities, acceptance by local communities, or policies, species selection supporting nature-based solutions should follow a trait-based approach (Bochet and García-Fayos, 2015; Ostertag et al., 2015).

The results of this study revealed that  $C_4$  species, well adapted to warm and dry environments of Cabo Verde, have various functional characteristics and ecological preferences, which make them good candidates for nature-based solutions and various restoration and management purposes. However, not all  $C_4$  species are equivalent, and restoration success can be enhanced by more accurately matching species traits to their ecological niches (Gann et al., 2019; Sage, 2004). It is therefore essential to understand their specific ecological characteristics in order to select those most suitable for the intended purposes. This knowledge is vital for

planning and implementing restoration actions, as these species contribute differently to habitat structure and resilience (Edwards and Still, 2008; Kadereit et al., 2012). Our study helps to build a scientific basis for ecosystem restoration initiatives in the archipelago.

C<sub>4</sub> monocots, especially grasses, which are essential for the initial recovery of degraded landscapes by stabilizing soils and reducing erosion, are particularly important in Cabo Verde, where desertification and habitat degradation restrict sustainable development (Varela et al., 2020; 2022). Examples of such species are those from the genera *Aristida*, *Bothriochloa*, *Cenchrus*, *Chloris*, *Cynodon*, *Dactyloctenium*, *Heteropogon*, *Melinis*, and *Sporobolus*, present in a considerable number of islands. On the other hand, C<sub>4</sub> eudicots, adapted to more specialised, stress-prone habitats, such as saline environments (Berasategui et al., 2023; Sage et al., 2011), contribute to biodiversity by fulfilling specific roles in plant communities and improving resilience against climate extremes (Osborne and Sack, 2012). Species of the genera *Amaranthus* (NAD-ME), all of which have been introduced, and *Euphorbia* (NADP-ME), including native and non-native species, stand out for their diversity. Incorporating both C<sub>4</sub> eudicots and monocots in restoration projects could enhance the functional diversity and ecological sustainability of restored ecosystems, particularly in regions facing climate-induced stressors (Atkinson and Bonser, 2020).

In Cabo Verde, only one C<sub>4</sub> shrub species occurs, *T. moquinii*; this is a rare but interesting halophyte species restricted to dunes of Sal and Maio islands. It is particularly important because it is the main plant species that generate the foredune on the northwestern coasts of Africa and the Canary Islands (García-Romero et al., 2021). The destruction of the habitat by human activities or, most probably, its use for firewood for cooking, a very limited resource in Cabo Verde (Duarte et al., 2022), may have caused the depletion of *T. moquinii* communities. Recovery of these communities could be an exemplary action to promote. In fact, woody species are particularly important in arid areas, not only for increasing the structural diversity of habitats, but also for improving soil properties by enriching it with nutrients and organic matter, improving soil structure and creating milder microclimates through shading (Abella and Smith, 2013), thus promoting conditions for the establishment of a more diverse flora and fauna.

C<sub>4</sub> halophyte species can function as natural barriers on dunes and shorelines (Hobohm et al., 2021). This highlights their importance in providing a vital ecosystem service and a nature-based solution for coastal protection (Neves et al., 2022), particularly in the islands of Sal, Boavista, Maio, and São Vicente, where halophyte communities (e.g., coastal dunes) are particularly important (Neto et al., 2020). They also offer promising avenues for bioremediation of highly saline soils, halting the deterioration of such degraded land, followed by an improvement in structure and fertility over time (Kafle et al., 2022). In Cabo Verde, differences in niche occupancy between eudicot and monocot halophytes were revealed, with eudicots preferring lower altitudes, higher temperatures, and lower precipitations. Halophytes such as the monocots *A. adscensionis* and *D. aegyptium*, or the eudicot *A. javanica* may be useful for restoration programs in the islands.

In addition to their use in revegetation, they are also interesting as forage species.

Other native forage species worth mentioning include the grasses *A. gyanus*, *Urochloa xantholeuca*, *H. contortus*, and *Bothriochloa bladhii*, the latter two being of particular interest for soil erosion control (Duarte et al., 2022). As far as human food is concerned, several C<sub>4</sub> species also stand out: the eudicots *P. oleracea* and *C. gynandra*, used as vegetables, the sedges *C. esculentus* and *C. rotundus*, with edible tubers, and the grasses *D. aegyptium*, *Setaria barbata* and *Urochloa* species (*U. caboverdiana*, *U. ramosa*, the browntop millet, and *Urochloa deflexa*, the Guinea millet) reported as being used in times of food shortages (e.g., seeds used to make flour) (Duarte et al., 2022). In addition to millets, other valuable small grain crops—*A. caudatus* and *A. cruentus*, of neotropical origin—are also present in Cabo Verde. These species, which are increasingly relevant as alternative crops, could improve food security in dry and semi-dry areas (Duarte et al., 2022).

Species uses can be a criterion for selecting species; however, even species that have no apparent economic use are important for enhancing biodiversity and essential to ensure successful restoration projects.

In species selection, the origin (native versus non-native) also deserves some comments. Cabo Verde is well known for the huge number of introduced species (about 55% of the archipelago's flora, Sánchez-Pinto et al. (2005), many of them important components of plant communities. Our study revealed that naturalised C<sub>4</sub> species found their preferential habitats in regions with higher precipitation values. This may be due to the fact that the species in the more arid areas of the islands originate from the Sahel and tropical Africa (Fernández-Palacios et al., 2024) and, therefore, are clearly adapted to these habitats, while the naturalised species, whether of Neotropical or European origin, prefer wetter habitats. Even if they are already widely spread throughout the archipelago, the impact of introduced species on native ecosystems should be evaluated and warrant further investigation. Specifically, it is essential to explore whether they can enhance ecosystem services synergistically or, conversely, impose competitive pressures that alter the distribution and abundance of native flora (Bonebrake et al., 2018; Jones, 2003). Understanding these dynamics is crucial to effectively managing and restoring ecosystems, as it will clarify whether these species can integrate conservation strategies or threaten native biodiversity and ecosystem balance (Romeiras et al., 2016). In any case, the use of native species in restoration efforts is recommended. However, it should be noted that the difficulties in obtaining native propagules (and in the quantities generally required) and the low germination/establishment rates limit the success of revegetation actions.

Revegetation with native species of Cabo Verde on islands of the archipelago where they do not occur naturally should also be evaluated. For example, of all C<sub>4</sub> species currently found in Cabo Verde, only eleven (*A. javanica*, *Amaranthus graecizans* subsp. *graecizans*, *A. cardosoi*, *C. ciliaris*, *Chloris virgata*, *D. aegyptium*, *M. repens*, *P. oleracea*, *S. verticillata*, *T. cistoides* and *Z. simplex*) are found on all the islands. It should be noted, however, that the climatic and topographical characteristics decisively condition the presence of some species (e.g., the occurrence of species normally found at higher altitudes is unlikely on low islands).

In some cases, the current distribution may result from a reduction in the area of distribution due to anthropogenic factors. However, it cannot be ruled out that these are isolated populations that have established on only a few islands and gone through reproductive isolation; therefore, it might be important to respect their isolation in order to safeguard the unique genetic heritage that these populations have.

In Cabo Verde, arid conditions, soil degradation, and water scarcity represent significant restrictions to ecosystem restoration. In this context, initiatives such as the REFLOR-CV project (<https://reflor.maa.gov.cv/>), or the forthcoming revegetation projects promoted by the Food and Agriculture Organization (FAO), highlight the urgency of selecting resilient plant species. In addition, Cabo Verde's efforts to achieve Land Degradation Neutrality (LDN) emphasize the importance of science-based strategies to restore degraded ecosystems.

## 5 Conclusion

Functional diversity, especially that related to the  $C_4$  photosynthetic pathway, has deserved increased attention in the context of climate resilience and restoration ecology (Sage, 2016; Schrader et al., 2021). This study substantially adds to our understanding of the diversity of  $C_4$  species that occur in Cabo Verde. It provides valuable insights into the functional trait diversity of these species, offering information of direct relevance to the management and ecological restoration of ecosystems across the archipelago. Our findings reveal a clear ecological sorting of  $C_4$  monocots and eudicots along the altitudinal - and consequently climatic - gradients of Cabo Verde.  $C_4$  eudicots are more prevalent in arid, warmer low-elevation habitats, whereas  $C_4$  monocots occupy a broader ecological spectrum. Furthermore,  $C_4$  lineages associated with different photosynthetic subtypes display varying environmental tolerances, with both eudicots and monocots of the NAD-ME subtype showing a marked preference for lowland areas compared with those of the NADP-ME subtype. These fundamental findings provide a direct blueprint for guiding species selection in ecosystem restoration, highlighting the importance of resilient  $C_4$  eudicots such as *A. javanica* for arid lowlands and  $C_4$  monocots such as *B. bladhii* and *H. contortus* for soil stabilisation in mid-altitude grasslands, to name but a few examples.

In the framework of the United Nations Decade on Ecosystem Restoration (2021-2030), strengthening the link between research and management is fundamental to restore ecosystems. This perspective recognizes that social, economic and political factors can significantly impede the advancement of ecosystem restoration efforts even when science can make significant contributions (Meli et al., 2023). By addressing these challenges through collaborative efforts and inclusive practices, we can foster more effective restoration initiatives that benefit both ecosystems and the communities that depend on them.

## Data availability statement

The original contributions presented in the study are included in the article/[Supplementary Material](#), further inquiries can be directed to the corresponding author.

## Author contributions

VR: Data curation, Formal Analysis, Writing – original draft, Conceptualization, Investigation, Methodology, Visualization. MR: Investigation, Supervision, Writing – review and editing, Visualization. MV: Investigation, Supervision, Writing – review and editing. MD: Supervision, Conceptualization, Investigation, Writing – original draft, Methodology.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fenvs.2025.1713396/full#supplementary-material>

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