Morphological, physiological, and biochemical responses of yerba mate (*Ilex paraguariensis*) genotypes to water deficit

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Abstract

Extreme weather events are expected to increase in frequency and intensity in South America, likely causing decreased plant productivity and altering species distributions. Yerba mate (*Ilex paraguariensis*) is a tree species native to South America and has an ecological, social, and economic importance in several countries. Natural forests and cultivated areas of yerba mate will be endangered by climate change because of the expected reduction in water availability. Here we determined how clonal genotypes of yerba mate (BRS BLD Yari, BRS BLD Aupaba, BRS 408, and EC40) respond to four levels of soil water holding capacity (100%, 80%, 60%, and 40% WHC) over 60 days, by evaluating the plants' morphophysiological and biochemical characteristics. We observed a reduction in plant height and biomass accumulation related to the decrease in water availability; physiological and biochemical parameters indicated that water-deficit stress reduced the plants' C assimilation and increased their production of bioactive compounds. BRS BLD Yari had a higher tolerance to low water availability, with greater biomass accumulation and photosynthetic rates that indicate greater water use efficiency. Understanding how different yerba mate genotypes respond to water deficit is essential for species conservation and developing climate-adapted breeding programs.

Keywords Abiotic stress · Climate change · Drought · *Ilex paraguariensis* · Silviculture

Introduction

Climate change is altering forest ecosystems around the world (Seidl et al. 2017; Girona et al. 2023). Recent climate change projections indicate that South America will suffer a greater variability in rainfall patterns and longer and more intense periods of drought (Llopart et al. 2020; Gomes et al. 2022). These unpredictable drought cycles will have potentially devastating effects on forest and agricultural plantations, reducing production capacity, and causing considerable economic losses (Grüter et al. 2022; Jiménez et al. 2023). Production capacity will be reduced mainly because of water deficits that will affect cellular processes, leaf expansion, stomatal conductance, transpiration rates,

foliar abscission, and photosynthetic activities (King and Purcell 2017; Pappas et al. 2022). How plants will respond to these changing conditions is a critical question, and understanding the survival and growth mechanisms of various groups of plants and genotypes will serve to guide future management strategies and breeding programs (Scolforo et al. 2017, 2019).

Yerba mate (*I. paraguariensis* A.St.-Hil.) is a tree species native to the South American humid subtropical forest of Brazil, Paraguay, and Argentina (Carvalho 2003). It is planted in monocultures, in agroforestry systems, semi-hydroponic systems, or exploited in native forests (Aguiar et al. 2022; Tomasi et al. 2024). In 2021, annual yerba mate production in Brazil was 1,060,441 tons (worth approximately US$ 285 million); it is the most important non-timber forest product in Southern Brazil (IBGE 2023a, b a, b). The leaves and young branches of yerba mate are used in South America mainly to produce beverages such as chimarrão, tereré, and tea; it therefore has an important social and cultural aspect related to its consumption (Duarte et al. 2020; Tomasi et al. 2021). Recently, its potential has been explored for use in food, pharmaceutical, cosmetical, and chemical industries because of its bioactive compounds as well as its antioxidant and anti-inflammatory properties. Moreover, the consumption of yerba mate has increased in nontraditional countries, including the United States, Germany, and Syria (Gullón et al. 2018; Vieira et al. 2021; Duarte et al. 2022; Gerber et al. 2023).

The distribution patterns of yerba mate are determined mainly by temperature and rainfall, and climate change will likely negatively affect the productivity of commercial plantations and alter its distribution by reducing its range to higher altitudes and more humid regions (Da Silva et al. 2018). The years of 2019 and 2020, for example, were uncommonly dry in Paraná State, Brazil, with an annual rainfall deficit of more than 600 mm, affecting yerba mate seedlings survival and growth (Aguiar et al. 2023). The latest IPCC report indicates that southern South America will experience significant changes in the regional water regime, and extreme temperature and rainfall events will become more frequent (IPCC 2022).

Climate change affects the morphological, physiological, and anatomical characteristics of plants as well as plant biomass production (Madani et al. 2018; Girona et al. 2023). The magnitude of the water deficit determines the strategy adopted by plants to overcome this stress. Initially, when soil moisture reaches a value lower than the soil water holding capacity, plants maintain turgor to ensure growth continuity; however, after an extended period of water deprivation, photosynthesis decreases, and several mechanisms, e.g., the production of abscisic acid and stomatal closure, are activated to avoid water loss and ensure osmotic adjustment (Tardieu and Simonneau 1998; Brunner et al. 2015).

Recent studies have characterized the molecular mechanisms associated with the drought response in yerba mate, such as leaf osmotic adjustments and alterations of the plant's metabolic profile; the nature of these responses indicate that changes in water regimes may be the most significant factor influencing on yerba mate biomass production in the coming years (Acevedo et al. 2019). Drought resistance and recovery in yerba mate are regulated by gene expression; thus, a marked genetic effect will determine how different genotypes respond to climate change (Acevedo et al. 2016, 2018). Therefore, it is important to identify how genotypes used in breeding programs respond to drought. Such genotype-climate influence studies have not been undertaken for the Brazilian breeding program of yerba mate.

Here we evaluate the response of four yerba mate clonal genotypes to water deficit, as extensive dry periods are projected in South America in the future. We hypothesize that water availability alters plant growth, physiology, and biochemistry and that yerba mate

genotypes differ in their responses to water deficit given that breeding programs select yerba mate genotypes for various non-climate-related purposes and from different regions.

Material and methods

Treatments and experimental design

We used four genotypes of yerba mate propagated via a mini-cutting technique in 110 cm^3 polypropylene tubes; plants were on average 6 months old and 15 ± 3 cm in height. We selected four genotypes from the yerba mate breeding program of the Brazilian agricultural research corporation (Embrapa). Three genotypes (BRS BLD Yari, BRS BLD Aupaba, and BRS 408) are used at a commercial scale and are already registered with the Brazilian ministry of agriculture, livestock, and food supply (MAPA), and one (EC40) is still undergoing tests. The breeding program selects yerba mate genotypes based on leaf biomass productivity and leaf taste (Sturion et al. 2017; Wendling et al. 2018).

Each seedling was transplanted into a 3.8 L pot filled with 3.4 L of a ferralsol, a soil commonly underlying yerba mate plantation (Table S1; IUSS Working Group WRB 2015). The water holding capacity (WHC) of the soil was determined previously according to the methods of Normative Instruction N° 17 (MAPA, 2007). Five days post-transplanting, the plants were subjected to different water availabilities: 100%, 80%, 60%, and 40% WHC of the soil. Three pots filled with soil were randomly placed in the experiment and used as a parameter to replace the water in the treatments. For 60 days, between 8:00 and 9:00 AM, these samples were weighed to define the necessary water amount to reach the established WHC in each treatment.

The study was conducted in Colombo, Paraná, Brazil (25° 19′ 15″ S, 49° 09′ 31″ W; 934 m), at the Brazilian agricultural research corporation (Embrapa Florestas), in a plastic-sided greenhouse. The experiment was established as a randomized block design, in a double factorial arrangement (four genotypes×four water availabilities); the treatments were distributed in four blocks comprising six plants each, resulting in 384 plants.

Morphological analysis

We measured plant height, stem diameter, and dry biomass 60 days after the beginning of water availability treatment, evaluating three plants of each block. For height, we measured plants from the base to the apex with a millimetric-scale ruler, and stem diameter was measured using a digital caliper. For dry biomass, we separated the aerial part and roots; both parts were packed in identified paper packages and dried in an oven with forced ventilation at 60 °C until a constant weight was attained, generally after 72 h. Dry biomass was weighed using a precision balance (0.002 mg Accuris™ Precision Balance, EuroPlug). We used these data to calculate total dry biomass and the shoot:root (SDB:RDB) dry biomass ratio.

Physiological analysis

Gas exchange was evaluated using gas exchange system (LCpro-SD, ADC BioScientific®) at the end of the experiment. Readings were obtained between 9:00 and 11:00

AM on a sunny day (Haworth et al. 2018). We used the environmental CO_2 concentration as a reference, which varied from 380 to 400 μmol CO_2 mol^{-1}; the difference in water vapour pressure was on average 6.54 mbar, the chamber temperature varied from 28 to 30 °C and the leaf temperature from 29 to 32 °C. We used the equipment's LED artificial (869 mol s^{-1} m^{-2}) lighting to avoid interference from external PAR variations. We recorded carbon assimilation (A, μmol CO_2 m^{-2} s^{-1}), transpiration (E, mol H_2O m^{-2} s^{-1}), stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}), and intracellular carbon concentration (C_i, μmol mol^{-1}). From these data, we calculated water use efficiency (WUE, μmol CO_2 mol H_2O^{-1}), and the carboxylation efficiency, determined by the A/C_i ratio. Physiological measurements were carried out in two plants of each block per treatment.

Preparation of plant material and aqueous extracts

After 60 days of water availability treatments, we collected about 50 g of mature leaves from all plants of each block only leaves showing no apparent damage for biochemical analysis and immediately dried the collected material in a microwave for 5 min. The samples were then ground and stored at -4 °C until analysis, following the methodology of Tomasi et al. (2021). We used 0.50 g $\pm$ 0.01 g of ground leaves and 50 mL of boiling water (98 °C) to prepare an aqueous extract. The extract was vortexed for 30 s. The solutions were subjected to ultrasound at 30 °C for 30 min and then filtered through a qualitative filter paper, and the extract was made up to 100 mL by adding distilled water. To correct the mass for chemical analysis, sample moisture was determined by weighing 0.5 g of material, drying it in a forced-air oven at 100 °C for 24 h, and then reweighing the material. All chemical analyses were performed at the Non-Timber Forest Products Laboratory of Embrapa Florestas and in triplicate for each block.

Total phenolic compounds

We quantified the total phenolic compounds using the Folin–Ciocalteau spectrophotometric method (Singleton and Rossi 1965). Briefly, using a 10 mL volumetric flask, we added 0.1 mL of aqueous extract, 6.0 mL of distilled water, and 0.5 mL of Folin–Ciocalteau reagent, followed by 1 min of vortex mixing. We then added 2 mL of 15% aqueous Na_2CO_3 solution, again vortex mixing for 30 s, and we adjusted the final volume to 10 mL by adding distilled water. After two hours of reaction in a dark room at 23 °C, sample absorbance was measured at 760 nm in a Shimadzu-1800 UV/Vis spectrophotometer (Shimadzu®, Japan). We used gallic acid within the range of 0.25–13 mg L^{-1} to produce a reference analytical curve. Our results were expressed in mg gallic acid equivalent per gram of sample (mg GAE g^{-1}) on a dry basis.

Antioxidant activity (ABTS and DPPH free radicals)

Antioxidant activity of the aqueous extracts was determined using the free radicals DPPH (2, 2-diphenyl-1-picrylhydrazyl) and ABTS [2, 2'-azino-bis (3-ethylbenzothiazoline-6-sulfonic acid)] (Brand-Williams et al. 1995; Re et al. 1999). DPPH was determined by adding 0.1 mL of sample to 3.9 mL of DPPH methanolic solution (0.06 mmol L^{-1}). This reaction occurred in a dark room for 30 min, and the absorbance was measured at 515 nm.

Antioxidant activity of ABTS was determined by reacting 10 mL of ABTS (7 mmol L^{-1}) with 176 μL of potassium persulfate (140 mmol L^{-1}) in a dark room at 23 °C for 16 h. An aliquot of 1 mL of ABTS solution was added to 100 mL of sodium acetate buffer (48.5 mmol L^{-1}) pH 4.5, with the absorbance adjusted to 0.7 ± 0.05. Then, 3 mL of ABTS buffered solution was added to 30 μL of extract. The samples were kept in the dark for 2 hours and after the absorbance was measured at 734 nm. All antioxidant activities assays were performed in a spectrophotometer Shimadzu-1800 UV/VIS (Shimadzu®, Japan). Results were compared against a standard curve (Trolox 0–1000 μmol L^{-1} for DPPH and 0–2500 μmol L^{-1} for ABTS) and expressed in μmol Trolox equivalent per gram of sample (TEAC μmol g^{-1}) on a dry basis.

Statistical analysis

To explain the variability in genotype response to water availability and differentiate the morphological, physiological, and biochemical responses of the genotypes, we applied a generalized linear model (GLM) having a Gamma distribution and an identity link function. We set water availability and genotypes as fixed effects. We ran all our analyses in R software version 4.3.3 (R Core Team 2024) using packages dplyr, tibble and ggplot2.

Results

Genotype and water holding capacity (WHC) produced significant differences ($p < 0.05$) in most morphological variables, except for stem diameter and shoot:root biomass ratio (Table 1). Height was the only morphological variable with significant interaction between factors: EC40 genotype had a lower average when subjected to 40% WHC, however, with increasing WHC, it presented higher growth than the others, surpassing BRS408 and similar to Aupaba with 100% WHC (Fig. 1). Yari genotype showed the highest height for all water availability treatments. For shoot, root, and total dry biomass, there was a linear increase with the rise in WHC greater biomass accumulation with higher water availability. The highest biomass values were observed in the Aupaba and Yari genotypes.

There was interaction between genotypes and WHC for almost all physiological variables, except for A, and WUE, $p < 0.05$ (Table 2). Genotype significantly affected all variables; only the g_s, and C_i variables were not impacted by the WHC factor. We observed an increase in the values of A and E variables as the WHC was increasing for all genotypes (Fig. 2); EC40 was superior to other genotypes in all WHC conditions in both

Table 1 ANOVA of GLM (Gamma function) to height (cm), stem diameter (mm), shoot dry biomass (SDB–g), root dry biomass (RDB–g), total dry biomass (TDB–g), and shoot:root ratio (SDB:RDB) of *I. paraguariensis* genotypes subjected to different water availabilities (WHC)

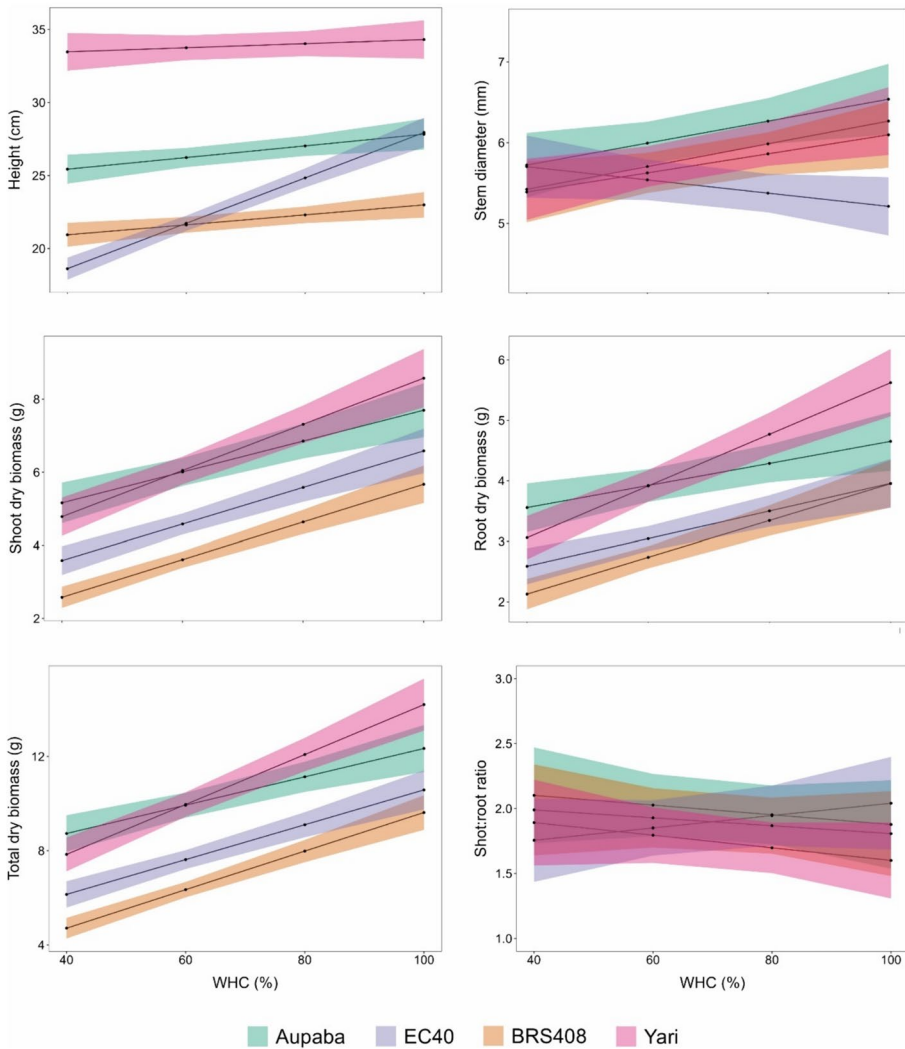| Effect	Pr (> F)					
	Height	Diameter	SDB	RDB	TDB	SDB:RDB
Genotype	$< 2.2 - 16$	0.25	7.2^{-8}	1.5^{-4}	4.2^{-9}	0.86
WHC	8.1^{-8}	0.19	3.3^{-12}	1.6^{-7}	5.2^{-14}	0.77
Genotype:WHC	1.9^{-4}	0.33	0.86	0.47	0.57	0.85

Fig. 1 Height (cm), stem diameter (mm), shoot, root, and total dry biomass (g), and shoot:root ratio (SDB:RDB) of *I. paraguariensis* genotypes (Aupaba, BRS408, EC40, and Yari) subjected to different water availabilities (WHC). 95% confidence interval predicted by GLM (Gamma function)

Table 2 ANOVA of GLM (Gamma function) to carbon assimilation (A, μmol CO_2 m^{-2} s^{-1}), transpiration (E, mol H_2O m^{-2} s^{-1}), stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}), intracellular carbon concentration (C_i, μmol mol^{-1}), water use efficiency (WUE, μmol CO_2 mol H_2O^{-1}), and carboxylation efficiency (A/C_i, mol m^{-2} s^{-1}) of *I. paraguariensis* genotypes subjected to different water availabilities (WHC)

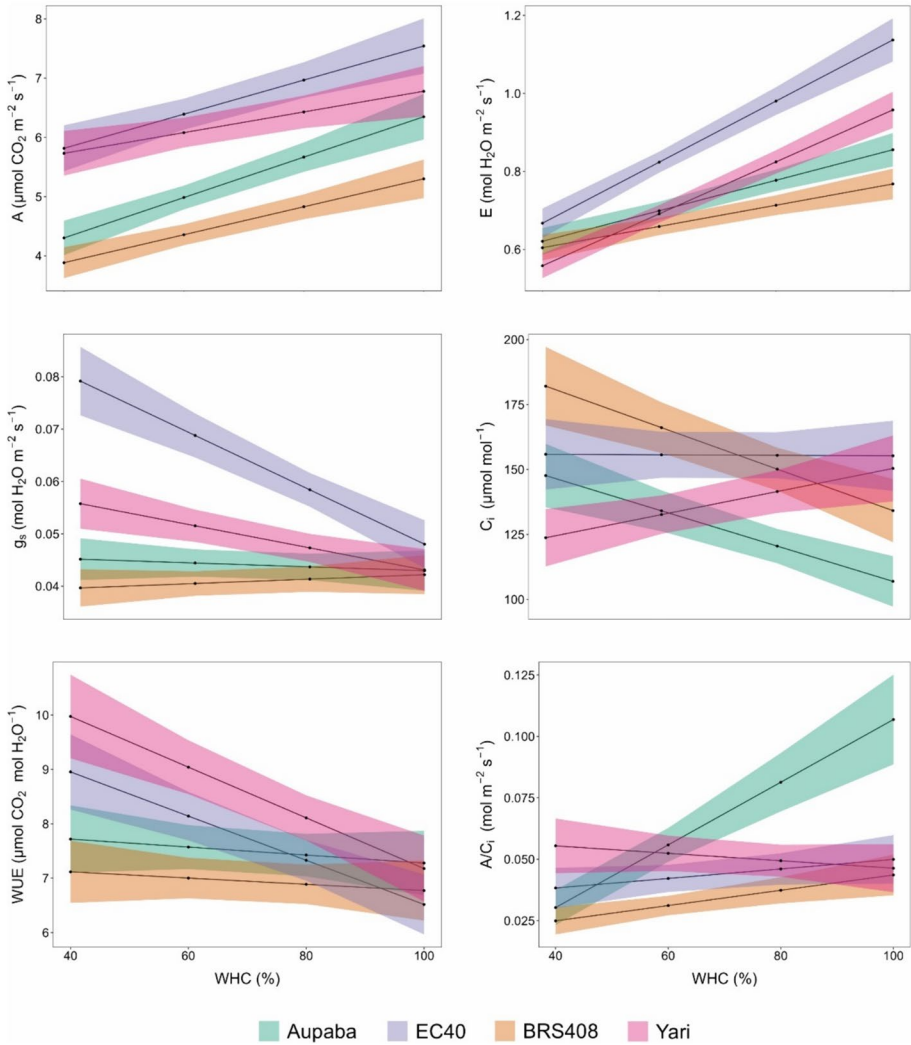| Effect	Pr(> F)					
	A	E	g_s	C_i	WUE	A/C_i
Genotype	4.1^{-10}	9.5^{-8}	1.3^{-7}	9.9^{-3}	0.02	1.5^{-3}
WHC	1.7^{-7}	2.3^{-15}	0.08	0.10	3.5^{-3}	0.03
Genotype:WHC	0.66	4.1^{-3}	0.02	0.02	0.16	0.02

Fig. 2 Physiological variables of *I. paraguariensis* genotypes (Aupaba, BRS408, EC40, and Yari) subjected to different water availabilities (WHC): carbon assimilation (A, $\mu mol\ CO_2\ m^{-2}\ s^{-1}$), transpiration (E, $mol\ H_2O\ m^{-2}\ s^{-1}$), stomatal conductance (g_s, $mol\ H_2O\ m^{-2}\ s^{-1}$), intracellular carbon concentration (C_i, $\mu mol\ mol^{-1}$), water use efficiency (WUE, $\mu mol\ CO_2\ mol\ H_2O^{-1}$), and carboxylation efficiency (A/C_i, $mol\ m^{-2}\ s^{-1}$). 95% confidence interval predicted by GLM (Gamma function)

variables, while BRS408 presented the lowest means. For g_s, EC40 had a sharp decrease with the WCH increase, while other genotypes remained practically stable. For C_i variable, each genotype showed different responses to WHC increase: Aupaba and BRS408 had a decrease, EC40 remained stable, and Yari showed an increase in this physiological parameter.

Regarding WUE, the Yari genotype presented the highest averages, and BRS408 the lowest; for this variable, there was a decreased tendency with increasing WHC (reduction of 52% for the EC40 genotype, comparing 40% and 100% of WHC). For A/C_i, the Aupaba

genotype presented a different response from others, showing a considerable increase in carboxylation efficiency with the increase in WHC, standing out with the highest averages in the conditions of 80% and 100% WHC.

There was an interaction between genotypes and WHC factors for total phenolic compounds and antioxidant capacity (Table 3). Total phenolic compounds content and antioxidant activity decreased 13%–32% for all clones as water availability increased from 40 to 100%; however, interactions between factors indicate that each genotype responded differently to WHC (Table 3 and Fig. 3). When we observed the content of phenolic compounds in 40% WHC, EC40 and Yari genotypes stood out, with the highest values; however, with increasing in WHC, EC40 showed a significant decrease in the content of these compounds. For the free radicals ABTS and DPPH, the results of the genotypes was similar: EC40 and BRS408 had the highest levels at 40% WHC, but BRS408 showed a greater decrease with the highest WHC; regardless of WHC, the Aupaba genotype had the lowest antioxidant capacity. Antioxidant activity varied between 1571.67 and 2048.84 TEAC μmol g^{-1} for ABTS and between 361.23 and 545.11 TEAC μmol g^{-1} for DPPH.

Discussion

Drought resilience is an important property for cultivated plants, particularly in the context of expected future climate change. Studies of various plant species have elucidated the mechanisms related to drought resilience, and genotypes of the same species can differ in their strategies to cope with water deficits (Scolforo et al. 2019; Krzyżak et al. 2023; Toro et al. 2023; Perera-Castro et al. 2023). Using the regulation of leaf water potential by stomata, plants can be classified as having either an isohydric or anisohydric behavior. Isohydric plants have a fast response to water deficits and close their stomata to avoid water loss. Anisohydric plants maintain water potential even under water deficit situations, being insensitive to decreases in soil water potential (Tardieu and Simonneau 1998; Pou et al. 2012; Martínez-Vilalta et al. 2014). Under minimal water deficit conditions, anisohydric plants may have an advantage in terms of biomass production by keeping their stomata open, although more severe and long-lasting water deficits will cause more damage to these plants than to isohydric species (Pou et al. 2012). The selection of genotypes that tend to have an isohydric behavior is therefore highly desirable in breeding programs for species that will likely encounter more severe drought situations in the field.

Yerba mate is a typical isohydric plant, which explains the growth stagnation observed in conditions of less water availability; these plants close their stomata at a relatively high

Table 3 ANOVA of GLM (Gamma function) to content of total phenolic compounds (mg GAE g^{-1}) and antioxidant capacity of the free radicals ABTS and DPPH (TEAC μmol g^{-1}) of *I. paraguariensis* genotypes subjected to different water availabilities (WHC)

Effect	Pr(> F)		
	Phenolic	ABTS	DPPH
Genotype	6.0^{-9}	$<2.2^{-16}$	$<2.2^{-16}$
WHC	$<2.2^{-16}$	$<2.2^{-16}$	$<2.2^{-16}$
Genotype:WHC	2.7^{-3}	9.6^{-11}	1.9^{-14}

Fig. 3 Content of total phenolic compounds (mg GAE g^{-1}) and antioxidant capacity of the free radicals DPPH and ABTS (TEAC μmol g^{-1}) of *I. paraguariensis* genotypes (Aupaba, BRS408, EC40, and Yari) subjected to different water availabilities (WHC). 95% confidence interval predicted by GLM (Gamma function)
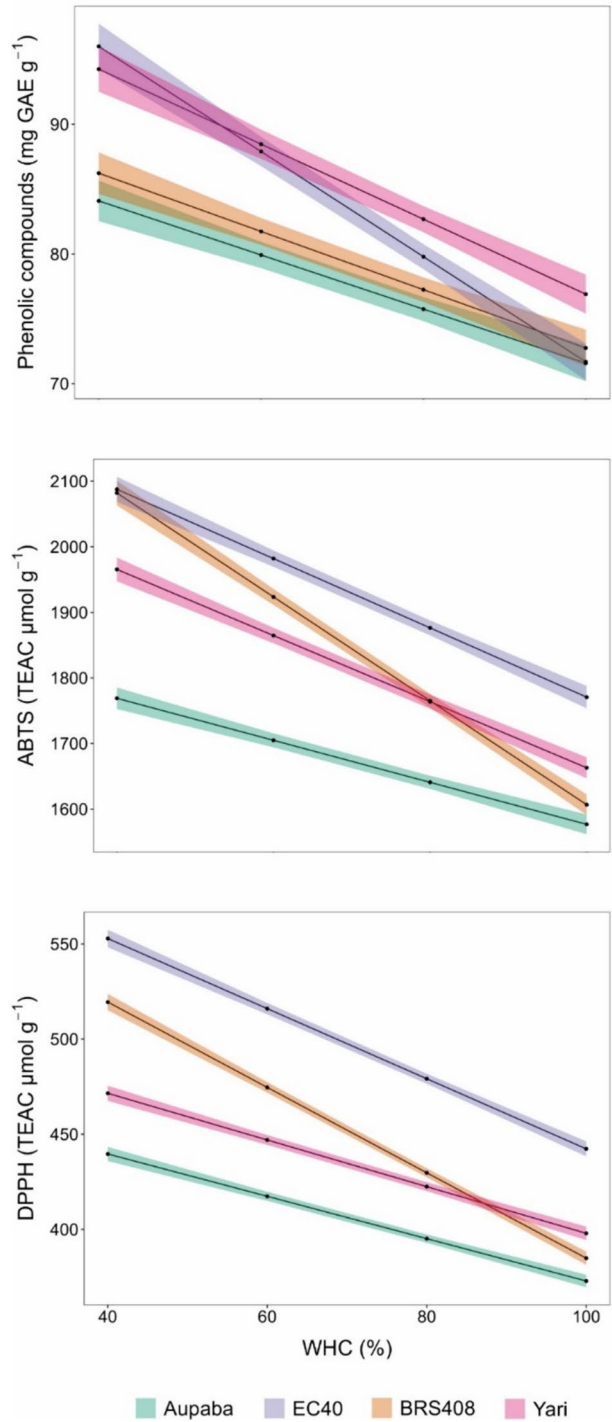
plant water status to avoid dehydration by limiting water loss (Tardieu and Simonneau 1998; Acevedo et al. 2019). This behavior is important for the commercial plantations of yerba mate that use the plant's leaves as the main product, considering that this drought resilience strategy avoids leaf abscission. All genotypes used in our study reduced photosynthesis and transpiration in the low water availability treatments, indicating stomatal closure (Chen et al. 2020). Lower stomatal conductance and photosynthesis rates have also been observed as part of the physiologic and metabolic changes triggered by drought in other yerba mate genotypes (Acevedo et al. 2019). The BRS408 plants presented lower growth rates in any water availability; these results are supported by the physiological variables that indicate a lower C assimilation. Yari and EC40 clones showed a higher water use efficiency when subjected to reduced water availability, indicating a high tolerance of this pair of genotypes to water deficits. Water use efficiency is defined as the quantity of carbon assimilated per unit of water used by the plant; a higher water use efficiency is an advantage to plants subjected to drought (Toro et al. 2023). Hakamada et al. (2020) observed significant differences in the water use efficiency among *Eucalyptus* clones subjected to various planting density and drought treatments, indicating that this physiological characteristic is primarily inherited.

Our results demonstrate that water availability in the substrate significantly affects the morphological, physiological, and biochemical characteristics of yerba mate genotypes. Moreover, we observed that genotypes respond differently to water availability: in general, Yari seedlings had a higher tolerance to low water availability, indicated by the higher biomass accumulation in all WHC treatments and the increased water use efficiency in the lower water availability treatments. Aupaba genotype showed similar growth to Yari but Aupaba had the most pronounced reduction in C assimilation as water availability was reduced. The EC40 genotype presented physiological responses similar to Yari but did not stand out in the morphological variables. Above all, the maximal isohydric behavior of Yari plants among the studied genotypes may be an important characteristic for its use in areas subjected to frequent droughts.

Although we observed a reduced growth and symptoms of water stress in seedlings subjected to a lower water availability, the treatments used in our study and the duration for which seedlings were subjected to this water availability (60 days) were insufficient to cause plant death. It should be noted that the seedlings were not subjected to a constant water level–water availability in the soil was adjusted once a day, and water loss due to evapotranspiration was not controlled. Decreased growth in plants subjected to water deficit has been widely demonstrated for arboreal species and has also been observed in other yerba mate genotypes (Gortari et al. 2020). In the latter study, water deficits reduced plant height, and both seedlings and mini-cuttings responded similarly to water deficit after 50 days.

Biomass accumulation is often the main morphological characteristic affected by water deficit (Amaral et al. 2023; Leite et al. 2023). We observed that all yerba mate genotypes decreased biomass accumulation at a lower water availability. Griebeler et al. (2021) obtained similar responses after subjecting *Cedrella fissilis* and *Eucalyptus saligna* to various irrigation regimes (continuous irrigation and daily irrigation at different intervals). The authors observed increased biomass in both species when the plants had a higher water availability. Griebeler et al. (2021) also noted that the shoot:root ratio differed between species: *E. saligna* experienced a decreased ratio when subjected to water restrictions, whereas the ratio for *C. fissilis* did not differ between treatments. An increase in the root biomass and a stagnation in the aerial part (lower shoot:root ratio) are expected when plants are subjected to a water deficit, as a strategy to reduce water loss and increase water absorption

capacity. In our study, however, we observed that when subjected to a water deficit instead of increased root growth, yerba mate plants stagnated growth in both, shoots and roots, not affecting shoot:root ratio biomass. Similar results were obtained by Gortari et al. (2020) after subjecting yerba mate seedlings and mini-cuttings to simulated drought periods.

Yerba mate is known for its high content of phenolic compounds and its antioxidant activity (Vieira et al. 2021; Duarte et al. 2022). Environmental factors such as temperature, water and nutrient availability, and solar radiation, as well as the plant development stage can influence total phenolic compound levels and antioxidant activity in yerba mate (Croge et al. 2021). We observed that yerba mate subjected to a lower water availability increased phenolic compound contents and antioxidant activity. Phenolic compounds are the largest group of secondary metabolites in plants and have several physiological and metabolic functions. The accumulation of phenolic compounds in plants subjected to abiotic stresses is a known adaptive response to unfavorable conditions (Sharma et al. 2019). The action of phenolic compounds in plants under drought stress is related mainly to inhibiting the production of reactive oxygen species and their accumulation, a phenomenon observed in several plant species (Nina et al. 2023; Shao et al. 2023; Shohani et al. 2023).

The expected increase in the frequency, duration, and severity of drought events requires selecting water deficit-resistant genotypes of yerba mate for both production plantations and genetic conservation purposes (Acevedo et al. 2016, 2019). In Brazil, the yerba mate breeding program focuses primarily on leaf productivity, the main product obtained from yerba mate plantations (Wendling et al. 2016; Sturion et al. 2017); however, as we found, these genotypes do not respond similarly to water deficit. In general, the Yari and Aupaba genotypes presented the best biomass accumulation among the different water availabilities, although Aupaba showed inferior physiological responses. Subjecting different yerba mate genotypes to a controlled water restriction helps predict a genotype's behavior to water deficits in the field and guides future decisions in yerba mate breeding programs. Since yerba mate clones respond differently to water deficit, new studies, and breeding programs must focus on selecting and developing water deficit-resistant genotypes.

Conclusion

Decreased water availability to yerba mate plants reduces plant growth and biomass accumulation, alters physiological activities, and enhances the accumulation of phenolic compounds and antioxidant activity. Among the evaluated genotypes, BRS BLD Yari showed a higher tolerance to low water availability, concerning its morphological and physiological parameters. We recommend the use of drought-resistant genotypes in yerba mate plantations for maintaining commercial production, conserving the species, and adapting to climate change. New research is necessary to detail the yerba mate drought resistance mechanisms.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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