

Physiological mechanisms in *Ficus carica* L. genotypes in response to moisture stress

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Abstract. The genus *Ficus* comprises cultivated and wild species that vary in phenotypic characteristics of both the plant and the fruit. This genus is considered to originate from Mediterranean regions and arid lands of Europe and Africa, known as the Fertile Crescent. *Ficus carica* L. (fig) is a globally emerging fruit crop due to its increasing production trends and capacity to produce in low water availability. Understanding the fig tree's responses to water deficit is essential for adapting to sustainable production and climate change. In this study, we investigated the water deficit tolerance of native *Ficus carica* accession and the Black Mission commercial variety. This research aimed to define the relationship between resistance to water deficit and plant physiological and biochemical markers (physiological and biochemical). Those markers considered relative water content (RWC), photosynthesis (P_N), stomatal conductance (gs), intercellular CO_2 (Ci), transpiration (E), proline (Pro), and soluble sugar content (SSC). The results revealed that fig genotypes exhibit various adaptive mechanisms and physiological responses to water deficit, including osmotic adjustment, stomatal regulation, and proline accumulation. The water deficit condition was confirmed by measuring the soil water potential; the maximum values were in the range of -2.1 to -3.6 MPa. The 'Guadalupe Victoria' accession demonstrated significant water deficit resilience by maintaining higher P_N values in low water availability. Additionally, the study highlighted the role of osmotic adjustments in maintaining water balance and cellular function during stress periods. These findings will provide valuable insights for the selection process of genotypes with enhanced drought tolerance in water-limited environments.

Key words: osmotic response, native accession, photosynthesis, proline.

INTRODUCTION

Moraceae is an angiosperm plant family characterized by milk latex, unisexual flowers, anatropous ovules, and aggregated drupes (Barolo et al., 2014). The *Ficus* genus is an important group to which *Ficus carica* belongs. This family produces a 'fruit' (borne from a complex inflorescence called syconium). According to available data in recent years, fig production has steadily been increasing for 2021; the gross production was about 1,057,349,000 US\$ (FAOSTAT, 2021). The top fig-producing countries from this production are Turkey, Egypt, and Morocco (FAOSTAT, 2021). In addition, the economic value of fig production is reflected in employment opportunities generated throughout the value chain, benefiting farmers, processors, and exporters (Caliskan, 2015). Moreover, fig cultivation supports local economies in many regions, particularly in arid and semi-arid areas where few other crops can thrive. As the importance and consumption of figs continue to grow, it is expected that fig production will remain a vital sector within the global agricultural industry. For producers and consumers, the fig nutrient value is a desirable characteristic (Soni et al., 2014; Caliskan, 2015; Bougiouklis et al., 2020). The levels of nutrients in fig plants are influenced by factors such as absorption, transportation, and internal movement of nutrients (Bougiouklis et al., 2020). All these processes are influenced by various conditions such as genetics, physiology, and climate.

As climate change progresses, there is a growing number of reports indicating water scarcity in agricultural settings (Nikolaou et al., 2020; Tzanakakis et al., 2020). This trend is expected to have ramifications for the availability of food (Paulus et al., 2020). An important focus is the scarcity of water resources because of the efficient use of water in agricultural systems (Kartal et al., 2019). Fig is also grown in different ecologies due to its drought resistance (Gholami et al., 2012). Fig's ability to tolerate water stress and adapt to varying soil conditions allows it to thrive in different ecosystems, contributing to ecosystem stability and biodiversity. This species has evolved several adaptive mechanisms and physiological processes to cope with limited water availability (Ammar et al., 2020, 2023). One of the main strategies employed by figs is drought avoidance, which involves shedding leaves in response to substantial water deficits (Ammar et al., 2023). By reducing leaf surface area, fig trees minimize water loss through transpiration and conserve moisture within their tissues (Akinci & Lösel, 2012). They accomplish this through mechanisms such as adjusting stomatal conductance and regulating gas exchange, reducing water loss while maintaining essential physiological processes (Ammar et al., 2020, 2023).

It is important to highlight the study of the fig for arid and semi-arid zones through the selection of genetic materials that have developed tolerance to water deficiency (Çalışkan & Aytakin Polat, 2011, Ammar et al., 2020). In this context, such knowledge can contribute to the selection of fig trees to explore their full potential and face climate change. Therefore, we hypothesize that native *Ficus carica* genotypes will present differences in their ability to tolerate water deficit in contrast to the Black Mission commercial variety. This research aimed to define the relationship between resistance to water deficit and plant physiological and biochemical markers. The analysis of relative water content (RWC), photosynthesis (P_N), stomatal conductance (g_s), intercellular CO_2 (C_i), transpiration (E), proline (Pro), and soluble sugar content (SSC), as Gholami et al. (2012) suggest, can be used to identify potentially valuable traits in breeding programs.

Moreover, knowing the fig materials' responses under limited and unlimited water availability in deficit and recovery conditions is essential.

MATERIALS AND METHODS

Study site

The experiment was carried out in the experimental areas of the Universidad Autónoma Chapingo, Unidad Regional Universitaria de Zonas Áridas, which is located at 103°36'07" N and 25°53'43" W. Its altitude is 1,109 m above sea level (INEGI, 2014). The climate is a desert with rains during the summer and winter (258 mm of annual rainfall and 2,000 mm of annual evaporation) (Köppen, 1948).

Plant material

Plants were collected in the Comarca Lagunera, which corresponds to a region located between the Durango and Coahuila states in México. The fig materials were obtained from backyards or wild locations by layers. The fig materials were propagated by cutting the layers after 40 days of rotting. The layers in the mother plant presented a rooting rate of 94 %. Those layers were planted in pots and developed for 30 days. For this experiment process, three layers were grown in 10 kg capacity pots filled with 9.5 kg of soil (soil characteristics: organic matter of 2.68 mg kg⁻¹; pH of 8.8, and electric conductivity of 3.61 dS m⁻¹). The used soil presented a field capacity (FC) of 33% and a Permanent Wilting Point (PWP) of 20%. The fig accessions were acclimatized to pot conditions for six months; pots were irrigated according to their water requirements (around 80% of the FC). During the experiment, the daytime mean air temperature was in the range of 29–46 ± 1 °C, the night-time mean air temperature was in the range of 20–24 ± 1 °C, and the daily mean relative humidity was measured in the range of 24–54 ± 3%. Fig. 1 shows the air temperature and relative humidity that were monitored during the experimental period using a high-accuracy humidity and temperature sensor (ORIA OUS-WA62®) (Fig. 1).

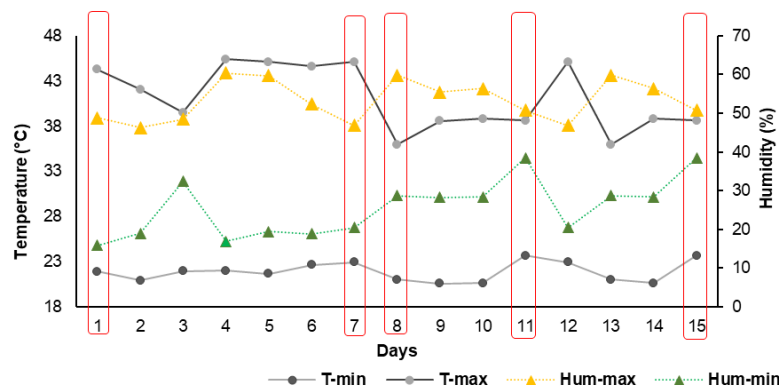


Figure 1. Daily mean minimum and maximum air temperature (T-Min and T-Max, °C) and mean minimum and maximum ambient humidity (Hum-min and Hum-Max, %) at the experimental site. The red rectangles represent the evaluation days of the experimental variables.

Experimental Design

The experiment was established as a randomized block design and arranged into a divided plot layout with three replications in semi-controlled conditions. It was developed using 6-month-old local fig accessions (Arista, Ceballos, Fortuna, Guadalupe Victoria, and San Antonio) and one commercial variety (Black Mission) (Table 1). To group accessions and variety, we call them ‘genotypes’. The plants were divided into two groups the water deficit (WD) and the field capacity (FC). The soil water content was recorded as soil water potential (SWP).

Table 1. Identification and origin of fig accessions of *Ficus carica* L. genotypes

Identification	Origin of fig accessions	Origin
Arista	282°71'73.26" N; 65°74'27.50" E	Backyard
Ceballos	293°36'38.29" N; 58°65'62.21" E	Backyard
Fortuna	293°25'64.71" N; 59°00'43.26" E	Wild
Guadalupe Victoria	282°16'00.44" N; 64°88'06.03" E	Backyard
San Antonio	291°33'54.86" N; 56°05'00.71" E	Wild
Black Mission	NA	Commercial

NA: Not available.

The experiment was conducted from June to July 2022, corresponding to the vegetative plant stage. The experimental process started with all the plants at FC. The WD condition was produced in the plants by interrupting the irrigation. This condition lasted from day 1 to day 7; during this period, we call days after irrigation suspension (DAIS). The WD plants were subjected to a dehydrating period due to evapotranspiration. The pots were weighed all days at the same hour (10:00 h), and the FC pots were rehydrated as needed. Plants were evaluated during this time to determine the daily water loss. The WD condition lasted 7 days; at this time, at least 50% of the plants showed evidence of physical water stress (leaves wilting and turgidity loss). The WD condition was confirmed by measuring the soil water potential at day 7, which was in the range of -2.1 to -3.6 MPa with a mean value of -2.7 MPa, far below PWP (-1.5 MPa).

After the maximum WD was observed, the plants were irrigated. Then, those were evaluated in a recovery period at 8, 11, and 15 days after the experiment was started and the irrigation was recovered (i.e. 1, 4, and 8 days at field capacity moisture). During this recovery period, the plants were maintained at FC. The response variables were measured on day 1 (beginning condition), day 7 (the maximum stress condition), day 8 (24 h recovery), day 11 (medium recovery period), and finally, day 15 (maximum recovery period). All those measures were done in recently matured leaves; the sampling was done between 10:00 and 11:00 h on sunny and clear days.

Relative Water Content (RWC)

A wet chamber was used to collect leaves from each treatment to avoid water loss during transportation to the laboratory. The RWC was determined by considering fresh weight (FW), dry weight (DW), and turgent weight (TW) by the $(FW-DW)/(TW-DW) \times 100$. Foliar sections of 2 cm² were measured (fresh weight), and those were submerged in water at 4 °C for 12 h without light. Passed this time, the weight was determined, and the turgent weight was considered. Those turgent leaf sections were dried at 80 °C for

24 h, and the dry weight (DW) was determined. (U.S. SOLID, model USS-DSS) (Barrs & Weatherley, 1962).

Gas exchange measurements

Leaf samples were used for measuring net photosynthetic assimilation rate (P_N , $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$), stomatal conductance (g_s , $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$), intercellular CO_2 content (C_i , $\mu\text{mol CO}_2 \text{ mol air}^{-1}$), and transpiration rate (E , $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$). All the evaluations were developed on sunny and clear days (10:00 to 11:00 h) using a portable infrared gas exchange analyzer (LI-COR 6400XT, LI-COR Inc., Lincoln, NE, USA). The operative conditions were at 400 ppm CO_2 in the camera and active photosynthetic radiation (PAR) of $750 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at 25°C cuvette temperature. The leaf samples were placed in the cuvette for about one minute for data collection (Evans & Santiago, 2014). Three early mature leaves from each of the three replicants, exposed to sunlight, were measured from each accession and genotype during the evaluation time.

Soluble sugar content (SSC)

The SSC was determined by the method of Dubois et al. (1956). A total of 100 mg of nitrogen-frozen leaf tissue was diluted in distilled water (5 mL). This extract was mixed with phenol and concentrated H_2SO_4 . The mix was measured using a spectrophotometer at A 490 nm (UV-VIS, Model 721, Shanghai Precision and Scientific Instrument Co; Ltd). SSC was calculated using a D-glucose standard curve and expressed as SSC mg g^{-1} FW.

Proline concentration (Pro)

The Pro was determined according to Bates et al. (1973) with minor modifications. The nitrogen-frozen material (500 mg) was mixed with 5 mL of 3% of sulfosalicylic acid solution. The mix was homogenized and centrifuged (6,000 rpm for 30 min at 10°C). The reaction solution was mixed with 1 mL of glacial acid and ninhydrin (previously warmed). The mixture was incubated at 100°C for 1 h, and the reaction was stopped on an ice bath before extraction with 3 mL of toluene. The organic phase (pink-red) was measured at A 530 nm. The proline concentration was determined using L-Proline (Sigma Aldrich) and expressed as $\mu\text{Mol Proline g}^{-1}$ FW.

Statistical Analysis

Factorial variance analysis was done. The mean comparison values were made by T-test of independent samples as well as one-way ANOVA and using Tukey's multiple range test at the $p \leq 0.05$ level. Those procedures were carried out by the software SPSS 18.0 Version (Inc., Chicago IL) and ©2013 Minitab 16.2.4 Inc.

RESULTS AND DISCUSSION

Utilizing breeding programs to choose drought-resistant genetic materials is a strategy to mitigate the impact of drought stress on crop yield. As well, the resilience to drought stress is affected by complex genetic factors and diverse environmental conditions (Arshadi et al., 2018). Additionally, the level of tolerance may be influenced by the severity and duration of drought stress, as well as its interaction with other environmental variables (Anjum et al., 2011; Sachdev et al., 2021). The study provided

twelve treatments, taking into account five accessions and one genotype, and two soil water contents, to understand the responses of young fig plants to drought tolerance. Then, responses were measured using RWC, P_N , gs, Ci, E, Pro, and SSC, as Gholami et al. (2012) suggested. All the means of soil water potential (SWP) were lower than the value of PWP (-1.5 MPa) at 7 Days After Irrigation Suspension (DAIS) under the WD condition. The mean value of SWP was -2.7 MPa. The only statistical difference in SWP among fig plants at 7 DAIS corresponds to the ‘Ceballos’ accession (Fig. 2). In other words, the ‘Ceballos’ accession was submitted to the lowest SWP during the experiment (-3.5 MPa).

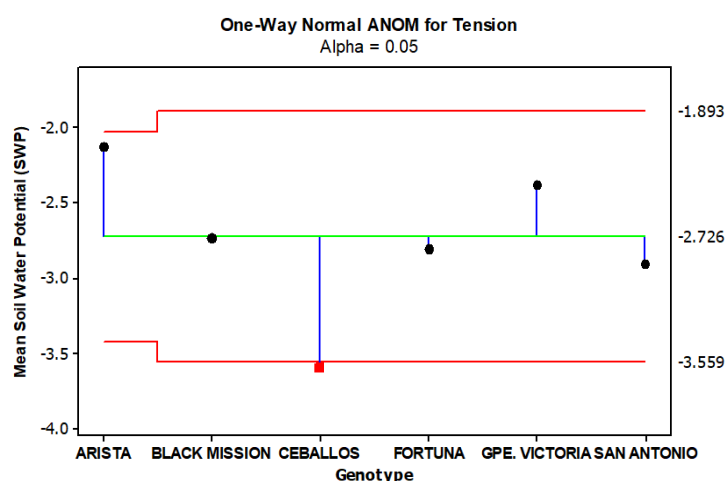


Figure 2. Comparison of means of Soil Water Potential (SWP, MPa) belonging to genotypes at 7 DAIS (Days After Irrigation Suspension) under WD (Water deficit) condition. The green line indicates the mean value, the red line indicates the decision limits, and the blue lines indicate the distance in relation to the mean.

Some water stress adaptive mechanisms and processes are associated with root plasticity, water use efficiency, osmotic adjustment, drought avoidance strategies, and drought resistance traits (Gao et al., 2018). In our study, *Ficus carica* materials could tolerate SWC below the Permanent Wilting Point (PWP) due to various adaptive mechanisms and physiological processes (Fig. 1). One of the main mechanisms of water avoidance strategies in fig is to shed leaves in a substantial water deficit (Ammar et al., 2020); however, all the evaluated fig materials tolerated a mean SWP of -2.7 MPa without shed leaves (Fig. 1). Those fig materials continued their photosynthesis activity even with low soil water potential. In the case of all evaluated fig materials, some plants reduced water loss by a low RWC and recovered their RWC when water became available again.

The evaluated variables were examined by a factorial analysis (FA). The FA presented significant effects of individual factors such as genotypes (G), Soil Water Content (SWC), and Time (T) at Days After Irrigation Suspension (DAIS) and Days at Field Capacity Moisture (DFCM) cases. Moreover, the interaction effect represents the joint influence of factors on the response variable that cannot be explained by the primary effects alone. The interaction effects between GxSWC, GxT, SWCxT, and GxSWCxT presented statistical differences in some of the evaluated variables (Table 2).

Table 2. *P* values of Factorial Analyses of the Genotype (G), Soil Water Content (SWC), and Time (T) and their interactions on physiological (RWC, PN, g_s , Ci, E, Pro, and SSC evaluations in 6 fig genotypes during DAIS (Days after Irrigation Suspension) and DFCM (Days at Field Capacity Moisture) evaluations

	DAIS (Stress period)							DFCM (Recovery period)						
	RWC	P _N	g_s	Ci	E	Pro	SSC	RWC	P _N	g_s	Ci	E	Pro	SSC
Model	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
G	0.339	0.001	0.815	0.786	0.478	0.977	0.494	0.036	0.080	0.117	0.366	0.276	0.923	0.332
SWC	0.001	0.001	0.012	0.001	0.004	0.001	0.001	0.208	0.001	0.555	0.292	0.508	0.001	0.001
T	0.001	0.001	0.001	0.231	0.001	0.001	0.017	0.178	0.996	0.001	0.001	0.001	0.001	0.001
CxSWC	0.050	0.051	0.080	0.045	0.028	0.043	0.038	0.007	0.001	0.018	0.010	0.665	0.017	0.035
CxT	0.331	0.238	0.051	0.232	0.012	0.047	0.776	0.171	0.142	0.002	0.322	0.003	0.457	0.639
SWCxT	0.001	0.001	0.057	0.050	0.022	0.029	0.001	0.098	0.001	0.041	0.001	0.059	0.001	0.054
CxSWCxT	0.329	0.888	0.926	0.221	0.754	0.050	0.952	0.335	0.828	0.068	0.352	0.071	0.018	0.438

Interaction G x SWC

The interaction between G x SWC presented significant effects in all the evaluations, except in g_s in DAIS and E in DFCM cases. In these interactions at the DAIS period in RWC evaluation, we observed that the ‘Arista’ accession exhibited statistical differences between WD and FC conditions (Fig. 3, a). During the DFCM period, the ‘Ceballos’ accession showed statistical differences between the SWC. The ‘Ceballos’ accession exhibited a great recovery capacity in the RWC from the DAIS to the DFCM condition (Fig. 3a). Those changes showed the accessions’ recovery capacity (Fig. 3). The statistical differences in the RWC reflected the metabolic activity in tissues, and it was used as the most meaningful index for dehydration tolerance (Sallam et al., 2019). The RWC in Black Mission (69.85%), Brown Turkey (69.75 %), and Brunswick (68.82%) in stress conditions showed a decrease of around 20% in comparison with the control condition (Rabei Metwali et al., 2016).

When the interaction between factors G x SWC was analyzed in the DAIS context, P_N showed statistical differences for most cases; the only exception was the ‘Ceballos’ accession. The highest P_N in the DAIS period was also observed in the ‘Guadalupe Victoria’ accession in the FC condition (Fig. 3, b). In the DFCM situation, the P_N differences were significant for ‘Arista’ and ‘Ceballos’ accessions.

In the case of g_s evaluation, the interaction C x SWC showed statistical differences in the DFCM case but not in DAIS evaluations (Fig. 3, c). Notably, the ‘Black Mission’ and ‘San Antonio’ genotypes presented statistical variations. Most of the genotypes presented higher g_s in WD condition during the DFCM case, except in ‘Arista’ and ‘San Antonio’ accessions. Moreover, the ‘Guadalupe Victoria’ accession showed the highest g_s under the WD condition and the lowest under the FC condition; the highest g_s belong to ‘Guadalupe Victoria’ (WD) under DFCM (Fig. 3, c).

Notably, significant differences in Ci evaluation belong to the ‘Black Mission’ and ‘Guadalupe Victoria’ genotypes in the DAIS period (Fig. 3, d). Also, it was observed that Ci was not different among genotypes under the two SWC considering DFCM. At the same time, the Ci was markedly low in the ‘Fortune’ accession at FC.

In general, lower E values belonging to ‘Black Mission’, ‘Fortuna’, and ‘Guadalupe Victoria’ genotypes at FC condition at DAIS. However, G x SWC differences were insignificant (Fig. 3, e). In the DAIS case, the E in the WD was higher than the FC

condition in most cases, except in the ‘San Antonio’ accession. All G presented non-significant variation in the DFCM cases.

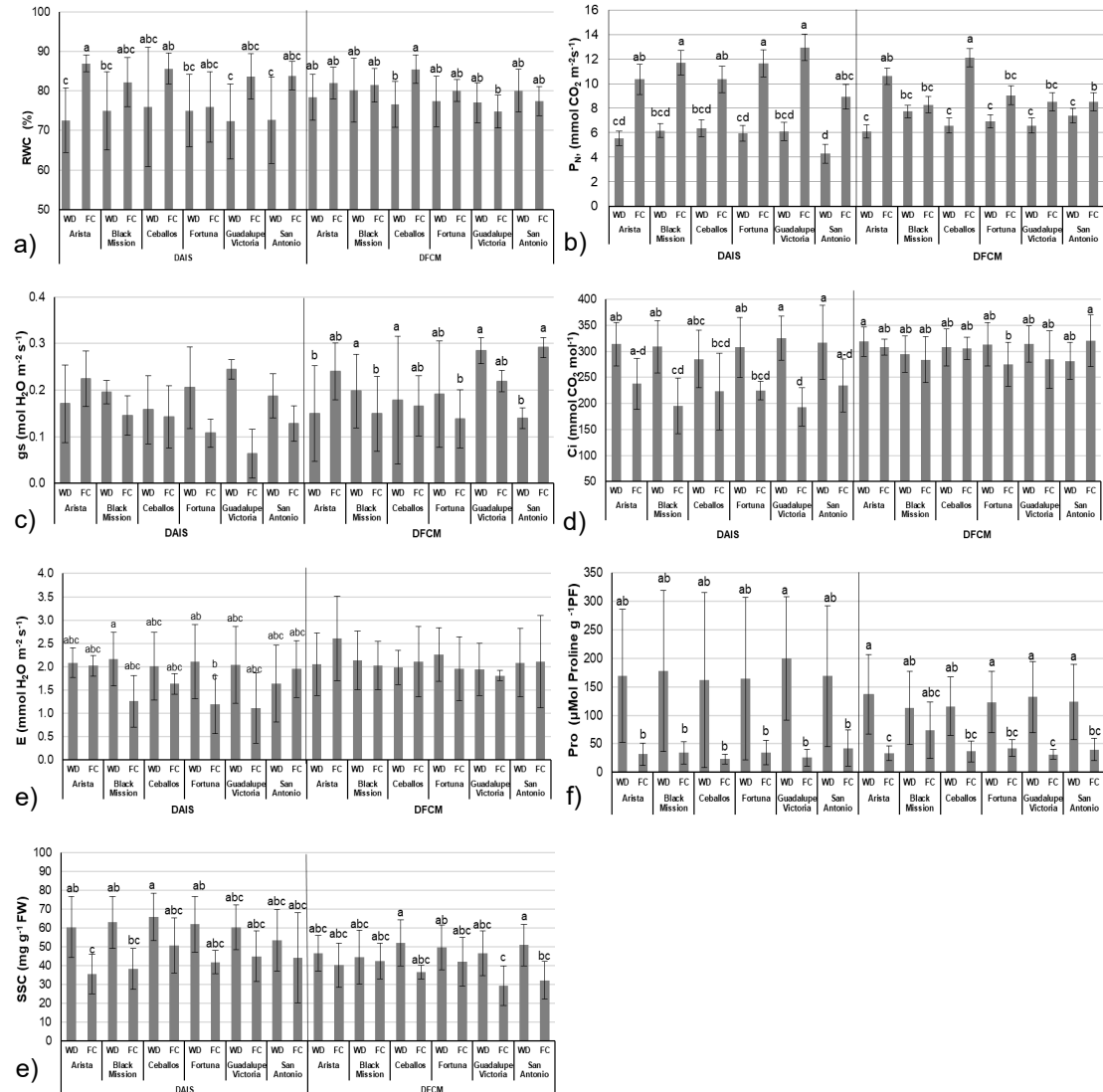


Figure 3. Mean values of the interaction between G x SWC at days after irrigation suspension (DAIS) and at Days at Field Capacity (DFCM) measured in *Ficus carica* mature leaves of six genotypes (Arista, Ceballos, Fortuna, Guadalupe Victoria, and San Antonio, and Black Mission) under two Soil Water Contents (SWC) (Water deficit, WD, i.e. -2.7 MPa; and Field Capacity, FC). a) Relative Water Content (RWC); b) Photosynthetic rate (P_N); c) Stomatal Conductance (gs); d) Intercellular CO_2 concentration (C_i); e) Transpiration rate (E); f) Proline content (Pro); g) Soluble Sugar Content (SSC) in the interaction Bars with different letters indicates statistical differences by Tukey multiple range test at $p \leq 0.05$.

Markedly, the highest increase of the Pro in the WD condition was observed in the ‘Guadalupe Victoria’ accession ($368.1 \mu\text{Mol Proline g}^{-1} \text{FW}$) during the DAIS period (Fig. 3, f). In addition, the Pro content was higher in most of the genotypes in WD evaluations at the DFCM case, except for the ‘Black Mission’ and ‘Ceballos’ genotypes.

Also, statistical differences in the SSC were found in the 'Arista' accession between WD and FC conditions at DAIS (Fig. 3, g). The higher SSC was observed in the WD condition in all genotypes in both DAIS and DFCM cases. Also, the SSC showed statistical differences in the 'San Antonio' accession between SWC conditions in the DFCM case.

The 'Black Mission' and 'Fortuna' genotypes presented the highest RWC in the WD condition (Fig. 3, a). Those RWC can be associated with cuticles, latex, and trichomes, which act as a water loss barrier (Kunjet et al., 2013; Hernandez & Bae Park, 2022). In response to low RWC, plants may produce a thicker cuticle or modulate the deposition of latex (Arya et al., 2017). The fig leaf structure may enhance their leaves' tolerance for water loss.

Plant's osmotic adjustment is activated by distinct mechanisms to maintain cellular turgor and minimize water loss. They accumulate compatible solutes such as sugars, amino acids, and other organic compounds within their cells (Moradi, 2016). These solutes help maintain water potential, preventing excessive water loss and maintaining RWC, cell structure, and function (López-Galiano et al., 2019; Seleiman et al., 2021). In this research, the fig accession presented a high recovery capacity in the RWC, as observed in Fig. 3, a. The quick RWC recovery, together with the increase of Pro, suggests that this amino acid response to WD is in close relation with RWC. The quick RWC recovery permits fig materials to maintain essential physiological processes (Ammar et al., 2020, 2022, 2023).

In contrast, the 'Ceballos' accession did not exhibit a statistical difference in P_N between SWC at the DAIS period (Fig. 3b), even though this accession presented the lowest SWP (-3.6 MPa). This accession may have the ability to acclimate to WD conditions photosynthetically. The acclimation process can be altered or adjusted to optimize resource use efficiency and minimize damage from water deficit (Vincent et al., 2020). Those changes in P_N may be subtle or not immediately apparent. However, that performance can be observed during the DFCM period in the 'Ceballos' accession since P_N did not completely recover from the FC condition.

Physiological resilience can activate stress response pathways and the production of protective compounds, antioxidants, and osmolytes to mitigate the negative impacts of stressors (Sachdev et al., 2021). As we notice, a remarkable recovery was observed in P_N at 'Black Mission', 'Fortuna', 'Guadalupe Victoria', and 'San Antonio' genotypes. This performance is related to the resilience response in fig genotypes (Ammar et al., 2020). This process is also observed with the decrease of Pro in the DFCM period (Fig. 3, f).

Interaction G x T

We observed statistical differences in the interaction G x T in the gs and E variables analysis; however, those differences were not significant in the rest of the evaluations. All the evaluations decreased from 1 DAIS to 7 DAIS (Fig. 4, a). In the case of DFCM evaluations, the gs presented an increased-decreased performance during this recovery period. The gs in the 'Guadalupe Victoria' accession presented a significant increase at 4 DFCM (Fig. 4, a). While water availability decreases, the stress gets progressed by ROS production, and some other responses are active in plants (Ammar et al., 2020). When the stress production and recovery period are evaluated, the physiological functions are also affected. Moreover, the differences in the recovery rate among plat

materials might provide valuable clues to selecting proper plants for periodic droughts in arid and semiarid lands (Rostami & Rahemi, 2013).

In the case of E, we observed that ‘Arista’ and ‘Ceballos’ accessions showed statistical differences from the 1 to 7 DAIS condition (Fig. 4, b). The higher E was observed at 1 DAIS in the stress period, while in the recovery period, the highest was in the 8 DFCM. In the DFCM period, the ‘Guadalupe Victoria’ and ‘San Antonio’ accessions presented a strong recovery at 4 DFCM (Fig. 4, b).

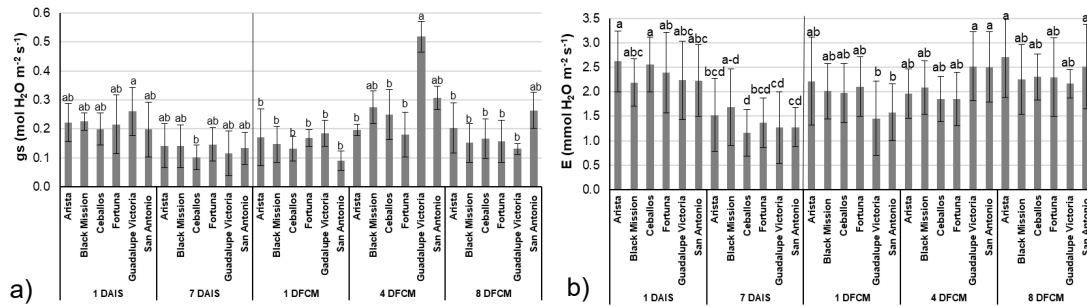


Figure 4. Means of the interaction G x T at 0 and 7 days after irrigation suspension (DAIS) and 1, 4, and 8 Days at Field Capacity Moisture (DFCM) measured in *Ficus carica* mature leaves of six genotypes (Arista, Ceballos, Fortuna, Guadalupe Victoria, San Antonio, and Black Mission). a) Means of stomatal conductance (gs); b) Transpiration rate (E). Bars with different letters indicate statistical differences by Tukey multiple range test at $p \leq 0.05$.

Interaction SWC x T

As a general response, the RWC decreased significantly in the plants under WD conditions (Fig. 5, a). Their RWC decreases 22% in plants at WD in comparison with FC condition at the 7 DAIS. The RWC showed statistical differences between the WD condition from 1 to 7 DAIS; however, the WD and FC evaluations did not differ at the DFCM period in the interaction between SWC x T (Fig. 5, a). In the evaluations of the DFCM period, the genotypes showed a quick recovery at 1 DFCM (Fig. 5, a). Also, fig plants growing in WD reached RWC levels like those growing in FC conditions at 8 DFCM.

Interestingly, P_N was lower in the genotypes growing under the WD condition (Fig. 5, b). In general, P_N decreased 30.3% from 1 to 7 DAIS. Notably, the P_N increased significantly in most genotypes (Fortuna accession was the exception) under the FC condition from 1 to 7 DAIS (Fig. 5, b). At 1 DAIS, WD and FC did not show a significant P_N difference; conversely, the P_N difference belonging to 7 DAIS is significant. In addition, the interaction between SWC x T suggested that P_N differed at 1 and 4 but not at 8 DFCM between the SWC.

The gs showed a general diminishing trend from 1 to 7 DAIS (Fig. 5, c). The gs presented statistical differences in WD condition between 1 and 7 DAIS. The trend increased from 1 to 4 DFCM and then diminished to 8 DFCM in both SWCs.

The C_i was lower in general in the FC than in the WD condition by considering DAIS (Fig. 5, d). The C_i presented statistical differences at 1 and 7 DAIS between SWC. In the case of DFCM, a general pattern of increases from 1 to 4 DFCM and a decrease to 8 DFCM was observed in both SWC (Fig. 5, d). In the DAIS case, the E had essential differences in the WD and FC conditions from 1 to 7 days. Also, the lower E was

observed at 7 DAIS in FC condition (Fig. 5, e). Besides, the E decreased 46% in FC conditions from 1 to 7 DAIS. In addition, the E in the FC condition presented an improvement from 1 to 8 DFCM.

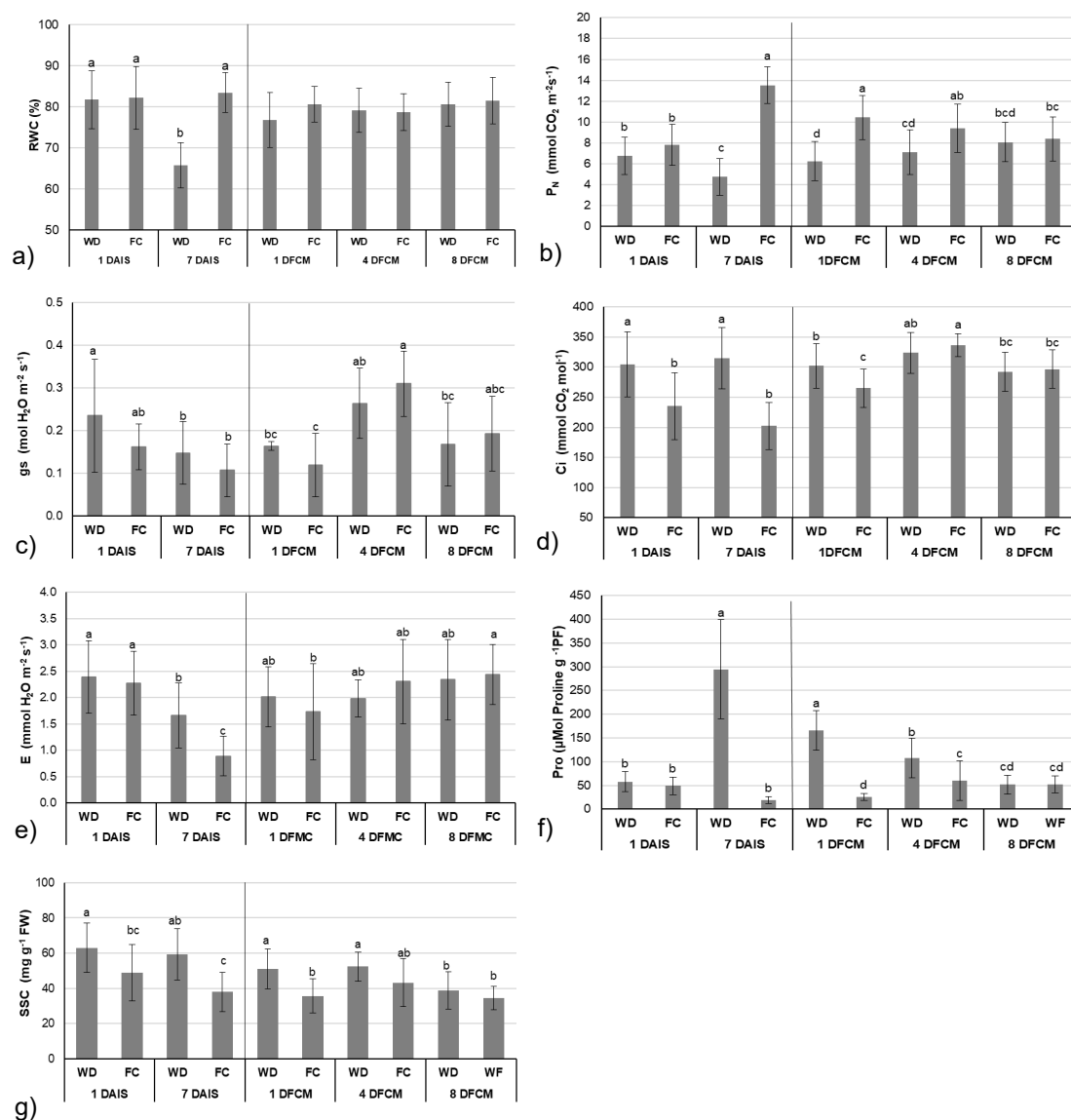


Figure 5. Mean values of the interaction between SWC x T at 0 and 7 days after irrigation suspension (DAIS) and 1, 4, and 8 Days at Field Capacity (DFCM) measured in *Ficus carica* mature leaves of six genotypes (Arista, Ceballos, Fortuna, Guadalupe Victoria, San Antonio, and Black Mission) under two Soil Water Contents (SWC) (Water deficit, WD, i.e. -2.7 MPa; and Field Capacity, FC).

a) Relative Water Content (RWC); b) Photosynthetic rate (P_N); c) Stomatal Conductance (g_s); d) Intercellular CO₂ concentration (C_i); e) Transpiration rate (E); f) Proline content (Pro); g) Soluble Sugar Content (SSC). Bars with different letters indicate statistical differences by Tukey multiple range test at $p \leq 0.05$.

In the interaction between SWC x T, the initial condition did not present statistical differences (Fig. 5, f). The Pro showed that WD at 7 DAIS increased significantly compared to FC condition or the ones at 1 DAIS (Fig. 5, f). In the recovery period, the statistical differences persisted at 1 and 4 DFCM. The Pro content was similar in both SWC at 8 DFCM. Notably, SSC showed statistical differences in the DAIS evaluations between SWC (Fig. 5, g). Lower SSC was observed in the FC condition in both evaluation periods (DAIS and DFCM). Some other fig accessions observed responses such as leaf loss during the stress period as well as the new leaf regeneration after a rewatering period (Rostami & Rahemi, 2013); however, none of those responses were observed in evaluated figgenotypes during this experiment, even substantial water deficit was induced.

The RWC is commonly used for knowing the water status in the plant (Parkash & Singh, 2020). The RWC depends on many factors, such as plant species, growth stage, and environmental conditions; in addition, there are general levels that indicate different stress categories. An RWC above 70% is considered a non-stressful condition; a range of 60 to 70% is associated with mild water stress, moderate stress in the range of 50 to 60%, and severe stress below 50% (Laxa et al., 2019). We observed that the evaluated genotypes presented a mean RWC of 65% in the WD condition at 7 DAIS (Fig. 5, a), corresponding to mild water stress. The 'Ceballos' accession presented the lowest RWC in WD at 7 DAIS (60%). Those values of RWC represent a plant's ability to regulate water balance under a water deficit condition.

Our results showed a decrease of 30% in the P_N in WD at 7 DAIS (Fig. 5, b), which may have some consequences for fig plants. Actually, P_N is closely linked to a plant's ability to withstand and recover from various stressors (Mareri et al., 2022). Besides, when there is a decrease in photosynthesis, it weakens the plant's ability to tolerate and recover from environmental stress, such as drought or heat (Tan et al., 2020; Sherin et al., 2022). In addition, the reduced production of energy and metabolites can compromise the plant's defense mechanisms, making it more susceptible to stress and increasing the risk of damage (dos Santos et al., 2022; Fontanetti-Rodrigues et al., 2019; Sachdev et al., 2021).

The reduction in g_s helps maintain proper gas exchange and temperature regulation and prevent water loss, which can optimize photosynthetic efficiency (Lawson & Blatt, 2014). We could observe that the g_s was lower in the FC condition than WD during the DAIS period (Fig. 5, b). This may be related to the saturation of water uptake, which is detected when the soil moisture is abundant and plant roots can access water easily; the uptake of water by the roots may exceed the plant's immediate transpiration needs (Gavrilescu, 2021; Gul et al., 2023). As a result, the stoma regulates its opening to reduce water loss through transpiration, leading to a decrease in g_s (Taiz & Zeiger, 2002). In addition, under FC conditions, plants can operate at their maximum P_N capacity without experiencing water stress. Our results showed a low g_s and E but a high P_N under FC at the stress period (Fig. 5, b; 5, c, and 5, e).

Feedback regulation in *Ficus carica* has been reported to control the stomatal aperture to regulate gas exchange and water loss (Gholami et al., 2012). Furthermore, the increase and decrease in performance in g_s and C_i evaluations in WD and FC conditions during the DFCM period (Figs 5, c and 5, d) could be associated with feedback regulation. This process in *Ficus carica* material is a dynamic and intricate system that helps the plant maintain equilibrium, adjust its physiological processes, and maximize its chances of survival and reproductive success in a changing environment.

Also, the decrease in C_i is less pronounced or absent because the primary limitation to P_N under water deficit is not the availability of CO_2 (Flexas et al., 2006). In our study, the C_i did not present significant changes in WD condition at DAIS and DFCM periods (Fig. 5, d). Likewise, a limited g_s during the WD condition. Even so, this response of fig genotypes can be related to the reduction of g_s ; the limited diffusion of CO_2 into the leaf can result in a minimal decrease in C_i , which results from a stomatal limitation (Engineer et al., 2016).

In our study, fig plants reduced E in FC condition in DAIS evaluation, probably associated with a partially or entirely stomatal closure (Fig. 5, e). This occurs as part of the plant's natural response to conserve water and avoid problems such as root hypoxia (lack of oxygen to the roots) or waterlogging, which can be detrimental to its survival (Tan & Zwiazek, 2019). In addition, in the DFCM case fig materials presented a recovery performance. This can also be associated with the growth of adventitious roots (Tan & Zwiazek, 2019).

The stomatal closure restricts the entry of external CO_2 into the leaf, resulting in a decrease in C_i (Engineer et al., 2016). Consistently, all evaluated genotypes presented lower C_i at FC than at WD during the DAIS evaluation (Fig. 5, d). The response of fig materials can result from increased stomatal closure in FC conditions. The stomata tend to close partially or wholly when plants experience reduced transpiration rates due to decreased evaporative demand. With reduced E , less CO_2 is drawn into the leaf, leading to a decrease in C_i (Mareri et al., 2022; Sherin et al., 2022). This performance is observed in fig genotypes in the DAIS period (Figs 3, d and 3, e).

Fig genotypes generally presented higher E in WD than in FC at the DAIS period. Also, some plants can adjust their osmotic potential by accumulating solutes (i.e., sugars and amino acids) during WD conditions (Mareri et al., 2022; Seleiman et al., 2021). Higher E can facilitate the removal of excess solutes from the cells, preventing osmotic imbalances and maintaining proper cellular functioning (Lawson & Blatt, 2014). The increase of E in WD conditions at the DAIS period (Fig. 5e) can be correlated with the critical increase of Pro content (Fig. 6a).

Interaction G x SWC x T

Interestingly, Pro increased by $247.5 \mu\text{Mol Proline g}^{-1}\text{FW}$ on average in all genotypes in the WD condition; in contrast, the Pro decreased by $29.3 \mu\text{Mol Proline g}^{-1}\text{FW}$ on average in all genotypes in the FC condition from 1 to 7 DAIS (Fig. 6, a). The Pro decreased 65% from 7 DAIS to 1 DFCM. The subsequent Pro evaluation decreased by 50% from the previous quantification until the 8 DFCM, when the Pro at WD was like the FC condition (Fig. 6, a).

The Pro is an amino acid implicated in response to WD. The Pro in all fig genotypes increased around 550% from 1 to 7 DAIS condition in WD condition. This Pro accumulation is related to osmotic adjustment acting as an osmolyte by accumulating in the cytoplasm and vacuoles, attracting water molecules and counteracting the effects of water stress-induced osmotic imbalance (Laxa et al., 2019; Sachdev et al., 2021). In addition, Pro accumulation during water stress also plays a role in stabilizing subcellular structures and proteins. It can protect enzymes and cellular structures from denaturation or damage caused by dehydration and osmotic stress (Hayat et al., 2012; Meena et al., 2019).

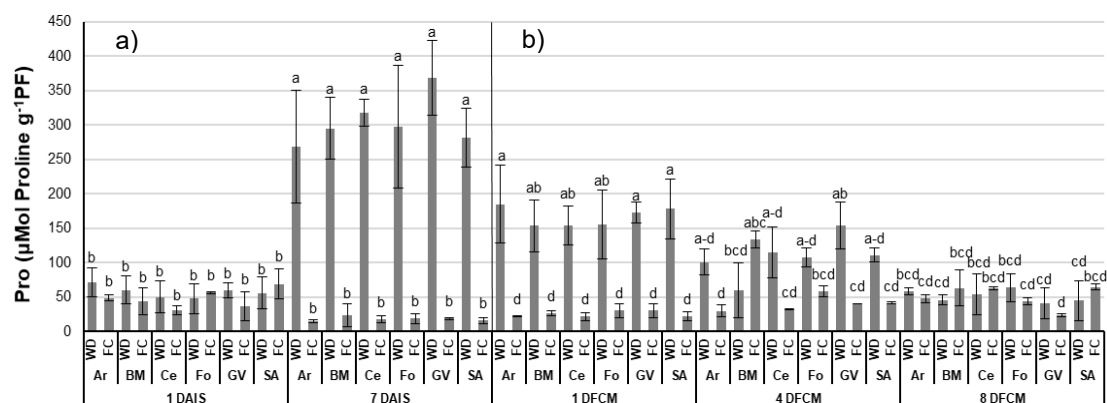


Figure 6. Means of Proline content (Pro) of the interaction between C x SWC x T measured in *Ficus carica* mature leaves of six genotypes (Arista, Ar; Ceballos, Ce; Fortuna, Fo; Guadalupe Victoria, G, San Antonio, SA, and Black Mission, BM) at 0 and 7 days after irrigation suspension (DAIS), and 1, 4, and 8 Days at Field Capacity moisture (DFCM) under two Soil Water Contents (SWC) (Water deficit, WD, i.e. -2.7 MPa; and Field Capacity, FC). Bars with different letters indicate statistical differences by Tukey multiple range test at $p \leq 0.05$.

The fig genotypes could use the enzymes proline dehydrogenase (PDH) and pyrroline-5-carboxylate (P5C) to convert into glutamate, which can be used in various metabolic pathways (Sallam et al., 2019). This conversion allows the reutilization of Pro as a carbon and nitrogen source and facilitates the decrease in Pro levels (Hosseini et al., 2022). This could be the reason for a significant decrease of Pro in the DFCM related to the proline degradation when the stress condition was relieved (Figs 3, f; 5, f, and 6, f). In addition, the Pro in the recovery phase restores osmotic balance by regulating water potential and preventing cellular dehydration (Fig. 3, f). Actually, Pro supports the refolding and reactivation of denatured proteins that may have been damaged during stress (Hosseini et al., 2022).

As part of the osmotic adjustment, SSC increased in the DAIS period (Fig. 3, g). These SSC help lower the water potential in the cell, enabling the plant to retain water and prevent excessive water loss through osmotic regulation (Yang et al., 2021). Also, SSC serves as a readily available energy source for cellular metabolism and respiration. They can be rapidly mobilized and broken down to provide carbon skeletons for essential cellular processes. The lowest SSC in the FC condition in the DAIS and DFCM period could be related to the response of fig plants with no limiting water availability (Fig. 5, g). Generally, plants under FC have less need to accumulate high levels of soluble solids. Consequently, the soluble solids may dilute within the plant tissues, decreasing SSC (Soberanes-Pérez et al., 2020).

CONCLUSIONS

Our study can confirm that the use of young genetic fig materials can express their water deficit tolerance potential. Also, we demonstrated that native *Ficus carica* genotypes present differences in their ability to tolerate water deficit in comparison to the ‘Black Mission’ commercial genotype. The adaptative mechanisms and physiological processes observed in *Ficus carica* genotypes that enable them to tolerate

soil water content below PWP (-2.7 MPa) and recovery to WD conditions were presented in this report. The fig plants' plasticity is a response to water deficit, allowing them to use different mechanisms to use the available water for their physiological processes. For this reason, the P_N response to water deficit diminished by 30% in comparison to FC plants. The 'Guadalupe Victoria' accession presented higher P_N values in WD and FC conditions during the DAIS period; this is an ability to adjust their photosynthetic process under WD to optimize resource use and minimize drought damage. 'Guadalupe Victoria,' 'Black Mission,' and 'Ceballos' genotypes presented necessary stomatal regulations to control gas exchange and water loss, helping them maintain water equilibrium and adjust their physiological process.

'Guadalupe Victoria' and 'Fortuna' accession showed a significant proline accumulation in response to WD, which acts as an osmolyte that attracts water molecules and counteracts the effects of osmotic imbalance. In this context, the 'Ceballos' accession increases SSC under WD conditions to lower water potential in cells and retain water. These mechanisms and processes allow fig plants to cope with mild water stress, maintain RWC, and quickly recover when water becomes available again. They also help the plants optimize their photosynthetic efficiency and physiological functions under varying water availability conditions. This research defines the relationship between resistance to water deficit and plant physiological and biochemical markers in fig materials. Selecting genetic materials tolerant to deficits in juvenile stages is feasible through physiological criteria, such as proline accumulation, soluble solids accumulation, photosynthesis, relative water content, and thereby shortening the time in the selection process.

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