Agronomy Research **23**(3), 1528–1543, 2025
https://doi.org/10.15159/AR.25.059

Variable responses of *Ficus carica* genotypes to water deficit: antioxidant and membrane stability insights

M. del R. Jacobo-Salcedo[1], L.Á. González-Espíndola[2], I. Sánchez Cohen[1], R. Valdez-Cepeda[3], R. Trejo-Calzada[2,*], E. Nava-Reyna[1] and J.G. Arreola-Ávila[2]

[1]Centro Nacional de Investigación Disciplinaria en Relaciones Agua Suelo Planta Atmósfera del Instituto Nacional de Investigaciones Forestales Agrícolas y Pecuarias, km 6.5 Canal Sacramento Zona Industrial, C.P. 35140 Gómez Palacio, Durango, México
[2]Universidad Autónoma Chapingo, Unidad Regional de Zonas Áridas, Carretera Gómez Palacio-Cd. Juárez, km 40. C.P. 35230, Bermejillo, Durango, México
[3]Universidad Autónoma Chapingo, Centro Regional Universitario Centro-Norte, Apdo. Postal 196, C.P. 98001, Zacatecas, México
[*]Correspondence: rtrejo@chapingo.uruza.edu.mx

Received: February 20th, 2025; Accepted: June 16th, 2025; Published: July 1st, 2025

Abstract. Drought stress is a significant challenge to agricultural productivity, particularly for fig plants, which require robust adaptive mechanisms against water-limited environments. This study aims to assess the biochemical responses of six different fig genotypes to varying soil moisture conditions. The measures of electric conductivity (EC), antioxidant activity (AA), total flavonoid (TFC), total phenolic (TPC), tannins (TT), and total protein (TP) were used as markers of stress tolerance in water deficit (WD) and rehydration conditions. Results showed genotype-specific differences in AA and secondary metabolite production. TFC was associated with enhanced oxidative stress tolerance, particularly under WD conditions, as the Arista genotype showed a 40% increase at 7 days after irrigation suspension. TPC levels indicated a general increase in response to WD, with the Arista genotype exhibiting the most pronounced rise. Conversely, TT decreased by nearly 50% in the Ceballos genotype under field capacity (FC) conditions, likely due to dilution effects from increased growth rates. In addition, TP varied significantly among genotypes, with the San Antonio genotype showing a 25% increase under WD. These findings provide insights into physiological mechanisms underpinning fig plant adaptation to water stress, highlighting the potential of specific genotypes for cultivation in arid and semi-arid regions, offering a framework for selecting young drought-resistant fig varieties.

Key words: DPPH, flavonoids, phenols, tannins, native genotypes.

INTRODUCTION

Ficus carica (fig) production holds significant potential as an alternative crop in water-deficit environments due to its promising adaptability to arid and semi-arid conditions (Ammar et al., 2022). This adaptability is particularly significant for

agricultural production because the main factor affecting productivity in these regions is water deficiency (FAO, 2019). While some studies have examined fig productivity, it is influenced by various factors, including ecophysiological, genetic, and biochemical responses (Gholami et al., 2012). Understanding how figs respond to drought periods, insufficient rainfall, shorter irrigation periods, high temperatures, and low ambient humidity is essential for optimizing water use strategies in fig cultivation. However, evaluating fig tree productivity requires long-term observations. Şahin et al. (2001) reported that fig trees achieve optimal yields after seven years. *Ficus carica* has a long evolution; it has developed extensive genetic diversity, resulting in some varieties exhibiting drought tolerance, whereas others do not. Consequently, the identification of early drought-tolerant genotypes is crucial for introducing resilient fig materials to water-deficient areas (Darwish et al., 2015).

Additionally, early-stage screening programs are necessary to select drought-resistant cultivars efficiently (Hssaini et al., 2020). These selection programs should incorporate physiological indicators such as photosynthesis, vegetative growth patterns, and antioxidant activity to facilitate effective selection and acceptable prediction of drought tolerance (Gholami et al., 2012). By studying the response of young fig plants, we can identify potential genotypes to face changes in climatic patterns, mainly water stress conditions.

In this context, we hypothesize that native *Ficus carica* genotypes possess efficient antioxidant mechanisms to tolerate drought conditions in comparison with a commercial variety. The purpose of the research was to evaluate the drought tolerance of native *Ficus carica* genotypes compared to the Black Mission commercial variety by analyzing their eco-physiological and biochemical responses under water deficit and irrigation recovery conditions. This study aims to identify genotypes with efficient antioxidant mechanisms and adaptive traits in early growing stages for cultivation in arid and semi-arid regions.

MATERIAL AND METHODS

Study site and plant material: This study was conducted at the 'Universidad Autonoma Chapingo, Unidad Regional Universitaria de Zonas Aridas', which is in Bermejillo, Durango, Mexico (103.601944° LN and -25.895277° LO, at an altitude of 1,119 m above sea level) (INEGI, 2015). This region has a desert climate with summer and winter rains, an average annual precipitation of 258 mm, and an annual average evaporation of 2,000 mm (Medina et al., 2005).

To identify native plant materials, backyard or wild fig trees were collected during field visits to various zones of the Comarca Lagunera of Durango and Coahuila, Mexico. These fig trees were selected based on specific adaptation characteristics, including low water availability, good-sized figs (over 4 cm in diameter and 5 cm in length), and resistance to environmental conditions. Five accessions were identified, and layers were obtained from those materials. These were named considering the collection site as Arista (282.864794° N; 65.907639° E, backyard), Ceballos (293.610636° N; 58.931169° E, backyard), Fortuna (293.431864° N; 59.011461° E, wild), Guadalupe Victoria (282.266789° N; 64.968342° E, backyard), and San Antonio (291.565239°N; 56.083531° E, wild). In parallel, plants of the Black Mission variety (commercial cultivar) were included in the experiment, which were obtained from the state of Morelos, Mexico.

Experimental Design: The experimental design was a randomized block design in a split-plot arrangement with three replications (blocks). The main plot factor was water regime, consisting of two levels: water deficit (WD) and field capacity (FC). The sub-plot factor was plant genotypes, with six fig material: Arista, Black Mission, Ceballos, Fortuna, Guadalupe Victoria, and San Antonio. Within each block, water treatments were randomly assigned to main plots, and genotypes were randomly assigned to subplots with each water regime. The experimental unit consisted of four six-month-old fig plants grown in a 10 kg capacity pot containing 9.5 kg of soil. Plants were grown under a green shade mesh that reduced light by approximately 40%, ensuring uniform irradiance. Soil used in all pots was characterized by the following properties: sand 38%, clay 32%, and silt 30%, pH of 8.8, electric conductivity of 3.61 dS m^{-1}, organic matter content of 2.68%, bulk density of 1.41 g cm^{-3}, and nitrogen 24.15 mg kg^{-1}. Field capacity (FC) of 33%, and permanent wilting point (PWP) of 20%, FC and PWP were determined based on the pressure plate Apparatus, reported in gravimetric percentage. In addition, the gravimetric percentage of FC and the PWP were transformed according to the soil texture using the software SPAW Version 6.02, from the Natural Resources Conservation Service. To assess evaporation independently of plant transpiration, three additional pots containing bare soil were included and evaluated using the same weighing protocol and supported by an evaporimeter installed in the experimental area.

The young fig trees were subjected to a three-month adaptation period, during which irrigation was adjusted based on their water consumption (pots were measured daily, and water used is registered in rewater as necessary). The control plants (CC) were kept at field capacity (FC), while the plants under water deficit (WD) were subjected to irrigation restriction. This stage was delimited until the loss of turgor, depigmentation of the leaves, and cyanotic apices and petioles pigments (signs of stress) were detected. The period of days after irrigation suppression (DAIS) was delimited from 1 to the 7th day; on the 7th day, plants were rehydrated, and from the 8th to the 15th day, the plants were returned and preserved at field capacity moisture (DFCM) as shown in Fig. 1.

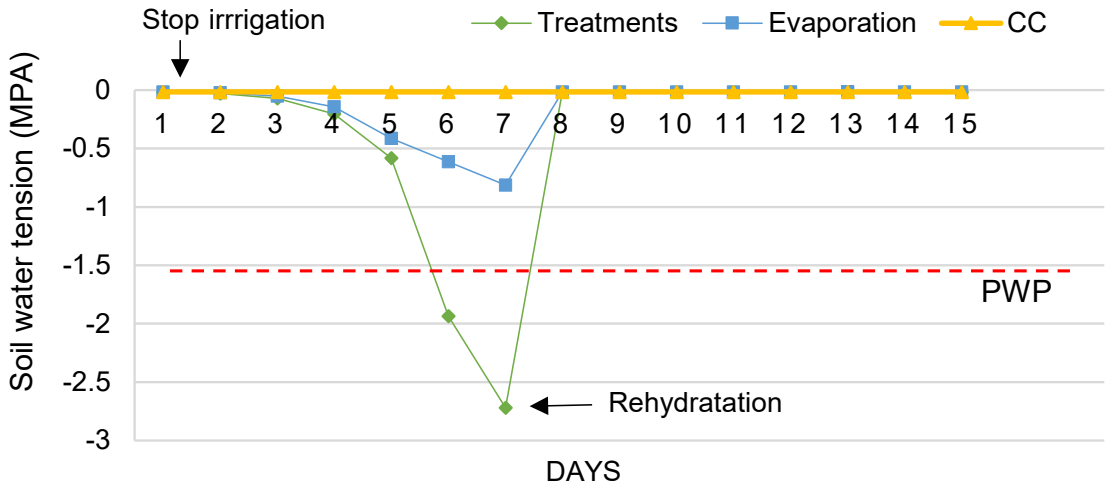

Figure 1. Changes in soil tension (MPa) during the experimental condition in treatments, control plants, and evaporation (water loss in pots without plant water consumption).

The mean soil water tension (SWT) in fig material pots was -2.7 MPa on the seventh day after irrigation suspension (Fig. 1). Notably, in the evaporation pots (without plants), the soil SWT before rehydration was -0.8 MPa. In contrast, control plants (CC) were maintained at field capacity with daily rehydration to preserve soil moisture (0 MPa). The permanent wilting point (PWP, -1.6 MPa) was reached between days 5 and 6 of the irrigation suspension period, even though the plant material did not show physical signs of stress.

Samples from the fig materials were collected for chemical analysis from day one after irrigation suppression until a water deficit was generated. Subsequently, samples were taken on the seventh DAIS, followed by sampling on days one, four, and eight of DFCM. Recently, mature leaves were sampled between 10:00 and 11:00 h on sunny and clear days. The samples were frozen using liquid nitrogen to preserve them before lab measurements were taken. The variables measured were electrical conductivity (EC) in fresh tissue, antioxidant activity (AA, DPPH), total flavonoids (TFL), total phenols (TFE), total tannins (TT), and total proteins (TP).

Electrical conductivity (EC): The changes in EC in the leaf tissue's resuspension medium indirectly quantified the integrity of the membranes. For this purpose, a sample of 4 cm^2 of fresh leaf was taken, weighed (fresh weight), and kept submerged in distilled water for 24 hours. Subsequently, the EC was measured with a conductivity meter (Hanna Instruments) in the tissue resuspension solution (Sánchez-Urdaneta et al., 2003).

Antioxidant activity (AA): The AA was determined by the DPPH method, which is based on the determination of the concentration of 2,2-diphenyl-1-picrylhydrazyl (DPPH, Sigma Aldrich Co., UK). The plant extract (200 µg of sample in 10 mL of acetone-water 7:3) was shaken for 30 min and centrifuged at 5,000 rpm at 4 °C for 15 min. The reaction mixture was incubated in the dark for 60 min and evaluated by spectrometry at 515 nm. Antioxidant activity (AA) was expressed in µM Trolox (6-hydroxy-2,5,7,8-tetramethylchromium-2-carboxylic acid 97%, Sigma Aldrich, Co., UK) equivalent (TE) of fresh matter (TE µM g^{-1}MF) (Parejo et al., 2000).

Secondary metabolites with antioxidant activity: The extract was used to determine total phenols (TPF), total flavonoids (TFL), and total tannins (TT). The plant extract was prepared by mixing 100 mg of the sample in 1 ml of methanol, which was kept under agitation in ice for 24 h before use.

The total phenol content (TPF) was determined using the Folin-Ciocalteu method with modifications. For the reaction mixture, 50 µl of the plant extract, 3 mL of distilled H_2O, and 250 µl of Folin-Ciocalteau (FC) reagent were used. The mixture was allowed to react for 5 min, then 750 µl of 20% Na_2CO_3 was added to the mixture, and it was homogenized in a vortex for 2 min. Once the mixture was homogenized, it was incubated for 30 min at room temperature. Quantification was performed by spectrometry at 760 nm, using gallic acid as a standard at a concentration of 10 mg ml^{-1} in a methanol solution. The TPF was expressed as mg of gallic acid (GA) eq g^{-1} of FW (Lamuela-Raventós, 2018).

The total flavonoids determination was carried out based on the aluminum chloride method (Barnum, 1977), which consisted of preparing the reaction mixture with 100 µl of extract and 1.4 mL of distilled H_2O. Flavonoid reagent (500 µl) was added to the mixture. The mixture was thoroughly shaken and then left undisturbed for 30 min at room temperature in a dark environment. The samples were read at 415 nm in a

spectrometer. The TFL was determined using a calibration curve with Quercetin (QE, Sigma Aldrich, Co. UK.) at a concentration of 1 mg mL^{-1}. The TFL was expressed as eq QE mg 100 g^{-1} FW.

The total tannins TT method (Harborne, 1984) was carried out using 100 µl of the plant extract, 5 mL of distilled H_2O, 500 µl of FC, and 1 ml of 35% Na_2CO_3. The reaction mixture was homogenized at room temperature and left undisturbed for 30 min. After this time, the samples were read at 724 nm in a spectrometer. For quantification in the calibration curve, gallic acid (GA) was used at a concentration of 1 mg mL^{-1}. The TT is expressed as mg GA eq mg^{-1} FW.

The preparation of the plant extract for the quantification of proteins (TP) by the Bradford method (Bradford, 1976) was carried out using 0.5 g of leaf tissue in 5 mL of 100 mm potassium phosphate buffer, pH 7.5. The extract was incubated on ice in a horizontal shaker for one hour and centrifuged for 30 min at 6,000 rpm. For Pro quantification, 200 µl of the protein extract was added with 800 µl of Bradford reagent. The determination was performed in a spectrometer with readings at 590 nm and 450 nm using bovine serum albumin (BSA) at 1.45 mg ml^{-1} as the calibration curve. Pro was expressed as mg of extracted protein g^{-1} FW.

Statistical Analysis: The statistical analyses developed were one-way ANOVA tests and factorial analysis. Statistical differences were determined with a significance of $p \leq 0.05$, according to the Tukey multiple range test. The data were processed in the PASW statistical program version 18.0.0, Chicago, SPSS Inc.

RESULTS AND DISCUSSION

During the experimental period, the maximum observed temperature was 45 °C, and the minimum temperature was 21 °C. These temperatures indicated intense heat and high evaporation rates. The dynamics of the maximum and minimum temperatures and humidity are shown in Fig. 2.

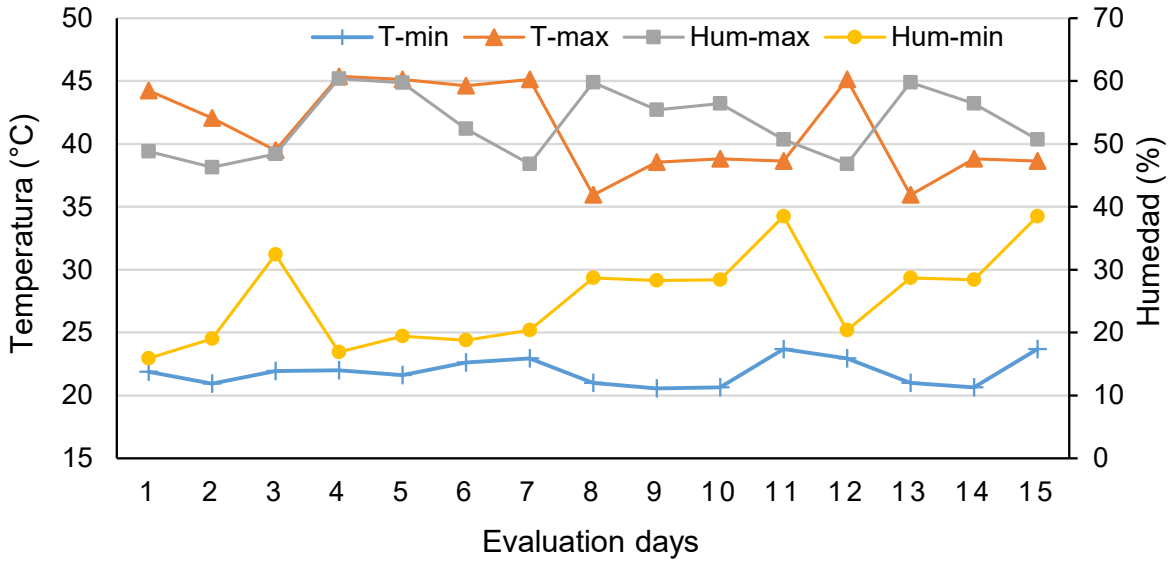

Figure 2. Dynamics of mean minimum and maximum temperature (°C) and mean minimum and maximum relative humidity (%) during the evaluation period.

Table 1 summarizes the evaluated factors (Time (T), Genotypes (G), and Soil Moisture (SM) conditions, and their interactions. The single effects showed significant differences in most of the evaluated variables, leading to interaction responses. Notably, the time and the interaction of T×G were significant for all the evaluated variables. Moreover, all the factors and interactions had important effects on antioxidant activity (AA).

Table 1. Square mean and effects of genotypes (G), time (T), and soil moisture (SM), and their interactions on electric conductivity (EC), and antioxidant parameters (AA, TFC, TPC, TT, and TP) of fig leaves

	Electrical conductivity (EC)	Antioxidant Activity (AA)	Total flavonoids (TFL)	Total phenols (TPF)	Total tannins (TT)	Total protein (TP)
Time (T)	30,633.38***	2,093.58***	42.09***	325.09***	157.36***	1.727***
Genotype (G)	2,923.73^{ns}	2,697.32***	11.63***	189.93**	77.83**	0.044^{ns}
Soil Moisture (SM)	34,311.47**	3,830.80***	15.49***	1,076.56**	445.97***	0.051^{ns}
T×G	5,187.84*	1,005.32***	2.33**	99.76**	66.21***	0.086***
T×SM	12,971.06**	1,719.03***	2.18^{ns}	79.25^{ns}	35.07^{ns}	0.034^{ns}
G×SM	2,279.37^{ns}	298.88**	3.23**	96.40^{ns}	46.18^{ns}	0.097**
T×G×SM	5,169.33^{ns}	504.85***	1.98**	89.63^{ns}	37.20^{ns}	0.051*

Note: Asterisks indicate the level of statistical significance: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; *ns* = not significant.

The electric conductivity (EC) of the leaf tissue incubation solution was evaluated to assess the integrity of cellular membranes in maintaining water and mineral balance. Under normal conditions, apoplast water contains few ions, while symplast water contains a wide variety of ions (Scoffoni et al., 2023). Water deficit disrupts balance, damaging membranes through reactive oxygen species (ROS), leading to ion leakage (Kamanga et al., 2018). The EC evaluation showed significant differences across factors, including T, SM, T×G, and T×SM. This method effectively assessed physiological stress in fig plant tissues under water deficit conditions. The integrity of cellular membranes is essential for maintaining ion gradients and overall cellular function (Abbas et al., 2023). Damage to these membranes causes the leakage of ions, which increases the EC of the surrounding solution (Shcherbakov et al., 2021).

Table 2 presents the dynamics of electric conductivity during the evaluation period for each genotype under WD and FC conditions. The statistical analysis was conducted at each evaluation time among genotypes (horizontal, lowercase), considering the water condition. At the initial condition, the genotype Ceballos showed statistical differences in both water conditions. Although the differences found on the 7th day after irrigation suppression (highest stress stage) were significant, the integrity of the membranes was affected in all genotypes. The electric conductivity showed a significant increase of around 50% compared to the EC of the plants in FC of soil moisture. In optimally irrigated conditions, ions and solutes are diluted, resulting in lower conductivity. During a water deficit, reduced water volumes concentrated ions, increasing EC, an indicator of drought severity (Wu et al., 2022).

Table 2. Interaction T * G mean values of electrical conductivity (EC) in the resuspension of leaf tissue in fig trees subjected to water deficit (WD) and field capacity (FC) during two periods, one of humidity restriction and the second of rehydration

Genotype	SWC	Electrical Conductivity (EC) µs cm^{-1}				
		DAIS		DFCM		
		1	7	8	11	15
Arista	WD	20.65 $^{a-d}$	39.48 ^{a}	30.93 ^{a}	24.58 ^{ab}	17.65 $^{b-e}$
	FC	23.07 ^{ab}	24.15 ^{cde}	25.02 ^{ab}	30.12 ^{a}	14.49 ^{de}
Black Mission	WD	20.16 $^{a-d}$	28.81 ^{bcd}	26.09 ^{ab}	20.99 ^{ab}	15.57 ^{de}
	FC	21.94 ^{abc}	20.98 ^{de}	17.97 ^{b}	22.98 ^{ab}	22.62 $^{a-d}$
Ceballos	WD	21.81 ^{abc}	29.07 ^{bcd}	26.70 ^{ab}	16.56 ^{b}	27.32 ^{a}
	FC	13.66 ^{d}	20.29 ^{de}	18.27 ^{b}	23.50 ^{ab}	12.85 ^{e}
Fortuna	WD	14.39 ^{cd}	30.93 ^{abc}	30.00 ^{ab}	29.48 ^{ab}	18.71 $^{b-e}$
	FC	16.69 ^{bcd}	23.47 ^{cde}	22.29 ^{ab}	27.12 ^{ab}	20.78 $^{a-e}$
Guadalupe	WD	21.74 ^{abc}	37.46 ^{ab}	28.01 ^{ab}	23.92 ^{ab}	17.02 ^{cde}
Victoria	FC	25.98 ^{a}	17.91 ^{e}	22.53 ^{ab}	25.98 ^{ab}	25.48 ^{ab}
San Antonio	WD	20.60 $^{a-d}$	34.19 ^{ab}	29.72 ^{ab}	20.35 ^{ab}	14.92 ^{de}
	FC	23.58 ^{ab}	22.06 ^{cde}	22.63 ^{ab}	20.36 ^{ab}	24.44 ^{abc}

Note: Values are presented as mean EC with standard error, and different letters indicate significant differences between values within each genotype and SWC treatment ($p < 0.05$).

Following rehydration, EC measurements at 24 hours during the days at field capacity moisture (DFCM) stage revealed significant recovery from pick stress conditions. The changes in electric conductivity at 15 days at field capacity moisture showed significant statistical differences between SWC in Ceballos, Guadalupe Victoria, and San Antonio genotypes. Interestingly, a higher EC value was observed for Guadalupe Victoria and San Antonio under FC conditions, possibly associated with waterlogging stress (Wu et al., 2022).

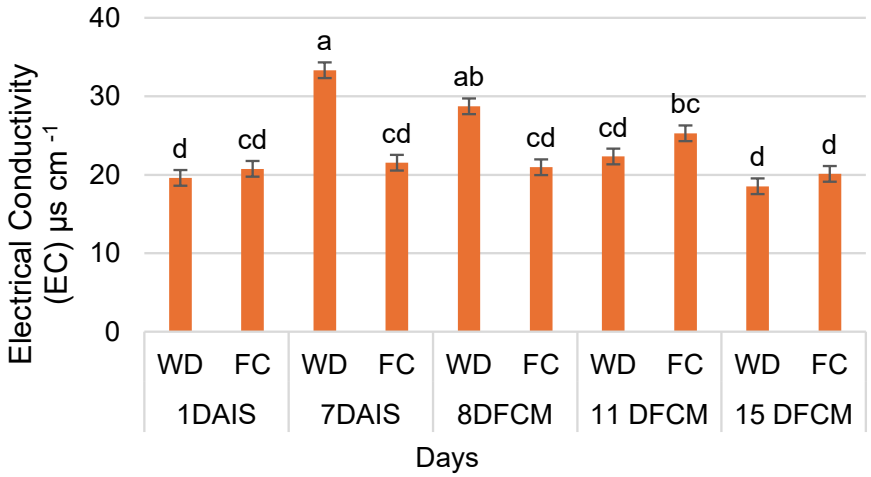

Figure 3. Interaction T and SM mean results of electrical conductivity (EC) in the leaf tissue in fig trees subjected to water deficit (WD) and field capacity (FC) during two periods, one of humidity restriction (DAIS) and the second of rehydration (DFCM).

The interaction between time (T) and soil moisture (SM) showed significant differences at 7 days after irrigation suspension (DAIS) (Fig. 3). Followed by a complete

recovery at 4 days following rehydration to field capacity moisture. By 11 days at field capacity moisture, the EC values were normalized to those of plants under optimal humidity, indicating favorable conditions for selecting materials' tolerance to water deficit. Interestingly, at 11 and 15 days at field capacity moisture, plants in field capacity exhibited higher EC values than those under water deficit. This suggests that plants demonstrated significant osmotic adjustment plasticity, adapting to either water scarcity or abundance. Measurements taken during the experiment revealed that plants experiencing water stress exhibited higher ion concentrations in the solution, leading to increased EC values. Likely, the damage to membrane permeability caused by water stress was not permanent, as recovery was observed in the measurements after 8 days of rehydration.

The assessment of free radical scavenging activity, measured as antioxidant activity (AA), revealed significant differences across factors and their interactions (Table 1). On average, fig genotypes exhibited a 60% increase in AA under water stress as compared to their initial condition. The Black Mission genotype showed the smallest increase in AA. Additionally, the plant's response to oxidative damage was associated with the production of flavonoids (Table 4). Previous research has shown that abiotic stress can enhance the production of secondary metabolites, like antioxidants, which contribute to cellular structural rigidity (Li et al., 2020).

Table 3. Interaction T * G in the Antioxidant Activity (AA) by the DPPH method in leaf tissue of fig trees subjected to water deficit (WD) and field capacity (FC) during two periods, one of humidity restriction and the second of rehydration

Genotype	SWC	AA, DPPH (TE μM g^{-1}FW)				
		DAIS		DFCM		
		1	7	8	11	15
Arista	WD	57.06 ^{a}	91.68 ^{a}	110.35 ^{ab}	82.91 ^{c}	91.18 ^{a}
	FC	57.41 ^{a}	59.00 ^{bc}	54.70 ^{def}	92.91 ^{bc}	80.15 ^{ab}
Black Mission	WD	39.78 ^{a}	55.39 ^{bc}	132.07 ^{a}	103.56 ^{b}	80.56 ^{ab}
	FC	44.25 ^{a}	45.32 ^{cd}	58.80 $^{c-f}$	151.64 ^{a}	85.46 ^{bc}
Ceballos	WD	56.68 ^{a}	48.89 ^{cd}	125.44 ^{a}	96.04 ^{bc}	75.81 ^{b}
	FC	59.84 ^{a}	33.69 ^{d}	72.12 ^{cde}	107.12 ^{b}	75.19 ^{b}
Fortuna	WD	53.45 ^{a}	93.15 ^{a}	88.64 ^{bc}	148.92 ^{a}	83.89 ^{ab}
	FC	52.97 ^{a}	37.93 ^{d}	46.05 ^{ef}	56.87 ^{d}	74.68 ^{b}
Guadalupe Victoria	WD	40.73 ^{a}	68.29 ^{b}	88.64 ^{bc}	37.12 ^{de}	34.05 ^{d}
	FC	43.08 ^{a}	34.19 ^{d}	34.55 ^{f}	48.00 ^{de}	44.63 ^{cd}
San Antonio	WD	59.84 ^{a}	100.53 ^{a}	82.84 ^{bcd}	33.41 ^{e}	35.72 ^{d}
	FC	60.08 ^{a}	36.29 ^{d}	51.94 ^{def}	36.06 ^{e}	54.24 ^{c}

Note: Values are presented as mean AA with standard error, and different letters indicate significant differences between values within each genotype and SWC treatment ($p < 0.05$).

Most genotypes presented an increase in AA from 1 to 7 DAIS in the WD condition, except the Ceballos genotype. The AA increased in different proportions among genotypes, even in the recovery period. Most of the evaluated genotypes had high AA at the final evaluation, except Guadalupe Victoria and San Antonio, which returned to the initial condition. In the Black Mission genotype, the AA increase was detected 24 hours after irrigation was reinstated (Table 3). This suggests that upregulation of AA helps fig plants mitigate the harmful effects of water stress, maintain cellular integrity, and sustain

viability. This response is likely linked to the activation of non-enzymatic antioxidants, including flavonoids, phenolic acids, and other substances (Seleiman et al., 2021).

An intriguing observation was the decrease in AA in the Ceballos genotype at 7 DAIS. This could be attributed to metabolic limitations, as severe water deficit restricts photosynthesis, thereby reducing ATP production and carbon availability due to stomatal closure (Jacobo-Salcedo et al., 2024a & 2024b). As well, the subsequent increase in AA observed at 8 days at field capacity moisture may reflect the plant´s ability to perceive changes in soil and leaf water potential through mechanosensitive proteins and shifts in cell turgor pressure (Osmolovskaya et al., 2018; Sparke & Wünsche, 2020). The gradual activation of AA in response to water stress highlights the enhanced tolerance of these fig plants under challenging conditions.

Reports on AA in fig seed oil range from 17 to 35 mg g^{-1} of oil expressed in Trolox equivalent (Hssaini et al., 2020). These values are lower than those found in the leaf tissue of fig accessions under both soil moisture conditions described in this study, as shown in Fig. 4. When dried figs are considered, reported AA ranges from 387 to 825 mol TE 100g DW^{-1} (Hoxha et al., 2015). Differences may arise due to analytical methods, such as figs being taken as analytical samples in dry matter.

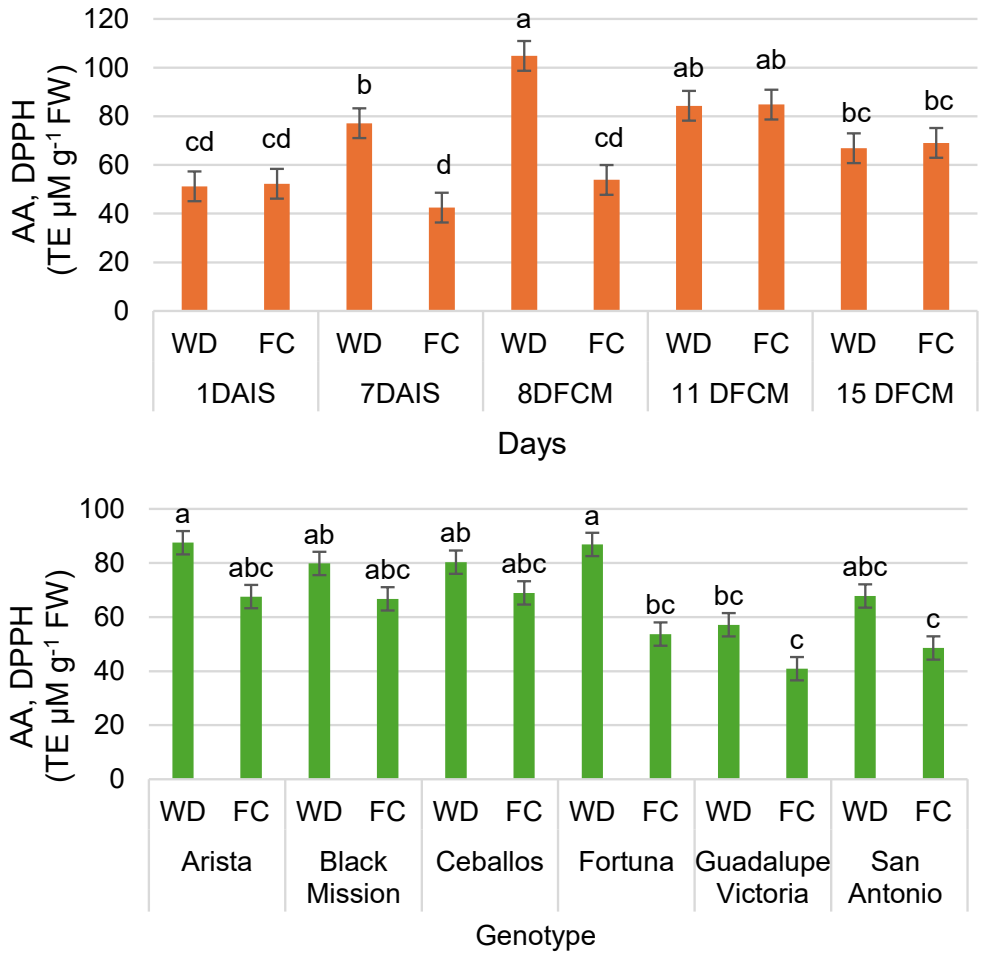

Figure 4. Interaction T*SM and G*SM mean results on antioxidant activity (AA) in leaf tissue in fig trees subjected to water deficit (WD) and field capacity (FC) during two periods, one of humidity restriction (DAIS) and the second of rehydration (DFCM).

The technique employed in this study measures the quantity of free H+ atoms in plant extract that the DPPH radical scavenges. Therefore, the Guadalupe Victoria and San Antonio genotypes exhibited lower AA during the evaluation, in contrast to the fig-evaluated materials. Although these two genotypes presented an increase in AA in both soil moisture conditions, their response was moderate. Our results suggest a relatively low production of free radicals in response to stress. Among the mechanisms by which plants can respond to stress induced by water deficiency, we indicate that these accessions might use other mechanisms. Such characteristics are desirable for these materials in areas with limited water availability.

To better understand the response of the evaluated fig genotype, one of the highlighted antioxidants is total flavonoid content (TFC). TFC acts as an antioxidant by scavenging ROS, thereby protecting the cellular structure. It plays a critical role in plant survival mechanisms by modulating biochemical pathways to adapt to water scarcity, offering valuable insight into the stress tolerance mechanisms of plants. Additionally, TFC accumulation can serve as a biomarker for drought-tolerant plant materials (Shomali et al., 2022).

At 1 DAIS, TFC levels revealed statistical differences among genotypes, which were linked to their origin and the variability among genotypes (Table 4). Plants under field capacity (FC) conditions showed a decrease in TFC from the initial to the final evaluation. A similar performance was observed in Arista and Ceballos genotypes under WD conditions. However, in the Black Mission, Guadalupe Victoria, and San Antonio genotypes, TFC increased significantly under maximum stress conditions at 7 DAIS.

Table 4. Total flavonoid content (TFC) in leaf tissue of fig trees subjected to water deficit (WD) and field capacity (FC) during two periods, one of humidity restriction (DAIS) and the second of rehydration in days at field capacity moisture (DFCM)

Genotype	SWC	Total Flavonoid Content (TFC) (mg EQ g FW^{-1})				
		DAIS		DFCM		
		1	7	8	11	15
Arista	WD	8.61 ^{abc}	7.54 ^{abc}	8.52 ^{a}	5.78 $^{a-e}$	5.19 ^{cd}
	FC	9.08 ^{a}	5.14 ^{d}	6.61 ^{abc}	6.53 ^{ab}	6.45 ^{ab}
Black Mission	WD	5.55 ^{d}	7.54 ^{abc}	6.62 ^{abc}	5.84 $^{a-d}$	3.94 ^{e}
	FC	7.05 $^{a-d}$	6.12 ^{bcd}	4.53 ^{de}	6.21 ^{abc}	5.76 ^{abc}
Ceballos	WD	8.27 ^{abc}	5.52 ^{d}	4.99 $^{b-e}$	5.42 $^{b-e}$	5.81 ^{abc}
	FC	7.50 $^{a-c}$	5.50 ^{d}	6.85 ^{ab}	4.67 ^{cde}	5.21 ^{cd}
Fortuna	WD	7.93 ^{abc}	7.98 ^{ab}	6.10 ^{bcd}	7.41 ^{a}	6.32 ^{ab}
	FC	7.02 $^{a-d}$	5.75 ^{cd}	3.89 ^{e}	4.17 ^{de}	4.76 ^{de}
Guadalupe	WD	6.75 ^{bcd}	9.04 ^{a}	4.76 ^{cde}	4.91 $^{b-e}$	5.23 ^{cd}
Victoria	FC	8.90 ^{ab}	5.75 ^{cd}	4.06 ^{e}	5.77 $^{a-e}$	5.16 ^{cd}
San Antonio	WD	7.95 ^{abc}	9.07 ^{a}	6.13 ^{bcd}	6.31 ^{abc}	6.56 ^{a}
	FC	6.40 ^{cd}	5.77 ^{cd}	5.54 $^{b-e}$	4.02 ^{e}	5.48 ^{bcd}

Note: Values are presented as mean EC with standard error, and different letters indicate significant differences between values within each genotype and SWC treatment ($p < 0.05$).

The results observed in Fig. 5 showed a statistical difference in TFC for the Fortuna genotype between WD and FC conditions throughout the evaluation period. This suggests that TFC plays an important role in the plant´s response to adverse environmental conditions.

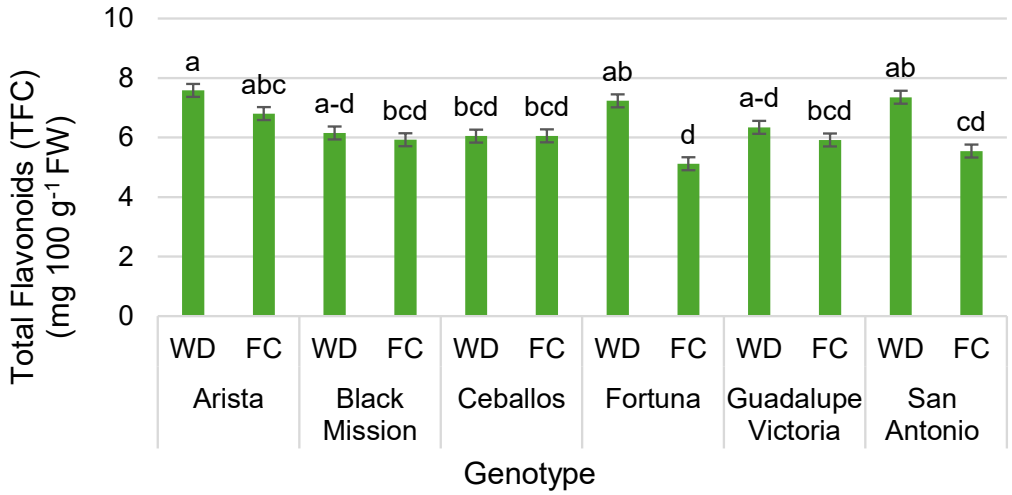

Figure 5. Interaction G*SM mean results of total flavonoid content (TFC) in fig trees subjected to water deficit (WD) and field capacity (FC).

TPC is part of the plant's defense mechanism against oxidative stress caused by drought (Ammar et al., 2015). Under WD conditions, TPC tended to increase in most genotypes (Table 5). TPC responses varied significantly across genotypes and sampling times, indicating genotype-specific reactions to water stress. Measuring TPC provides insight into the plant's capacity to counter oxidative damage caused by stress. Genotypes with higher TPC levels under stress conditions generally exhibit better tolerance to adverse environments. This is the case for the Arista genotype, which presented a significant increase at 7 DAIS from the original condition, even under FC conditions. The performance of TPC in fig genotypes aligns with findings from Stanković (2011) on *Marrubium peregrinum.* Additionally, similar TPC levels have been reported in fig cultivars by Konyalioğlu et al. (2005) and Marrelli et al. (2012).

Table 5. Total Phenolic compounds (TPC) in leaf tissue of fig trees subjected to water deficit (WD) and field capacity (FC) during two periods, one of humidity restriction (DAIS) and the second of rehydration in days at field capacity moisture (DFCM)

Genotype	SWC	Total Phenolic Compounds (TPC) (mg GA g FW^{-1})				
		DAIS		DFCM		
		1	7	8	11	15
Arista	WD	2.646 ^{b}	3.946 ^{a}	3.352 ^{a}	2.382 ^{cd}	3.789 ^{a}
	FC	2.787 ^{b}	2.884 ^{ab}	2.129 ^{a}	3.681 ^{abc}	3.749 ^{a}
Black Mission	WD	2.524 ^{b}	2.616 ^{bc}	3.794 ^{a}	2.526 ^{cd}	1.731 ^{d}
	FC	2.702 ^{b}	2.667 ^{bc}	2.968 ^{a}	33.24 ^{bcd}	3.808 ^{a}
Ceballos	WD	3.655 ^{ab}	2.939 ^{ab}	3.544 ^{a}	3.423 ^{bc}	2.007 ^{cd}
	FC	2.645 ^{a}	3.039 ^{ab}	2.323 ^{a}	2.633 ^{bcd}	1.847 ^{d}
Fortuna	WD	4.174 ^{a}	30.97 ^{ab}	2.755 ^{a}	4.984 ^{a}	1.890 ^{d}
	FC	2.709 ^{b}	2.170 ^{bc}	3.108 ^{a}	2.056 ^{d}	2.013 ^{cd}
Guadalupe	WD	3.284 ^{ab}	1.464 ^{c}	3.520 ^{a}	3.891 ^{ab}	2.792 ^{bc}
Victoria	FC	3.195 ^{ab}	2.952 ^{ab}	3.322 ^{a}	2.483 ^{cd}	1.766 ^{d}
San Antonio	WD	3.486 ^{ab}	2.716 ^{b}	3.355 ^{a}	3.708 ^{abc}	3.593 ^{ab}
	FC	2.984 ^{ab}	3.101 ^{ab}	3.108 ^{a}	2.608 ^{bcd}	1.758 ^{d}

Note: Values are presented as mean EC with standard error, and different letters indicate significant differences between values within each genotype and SWC treatment ($p < 0.05$).

Tannins, which are polyphenolic compounds, interact with proteins, cellulose, and lignin to form hydrophobic complexes. These structures reduce water permeability in plant tissues, enhancing water resistance (Yang et al., 2021). In the initial evaluation, tannin content (TT) was consistent across genotypes (Table 6). However, the Ceballos genotype showed differences at 7 days after irrigation suppression, when the TT was almost half at the FC condition. This genotype maintained consistent performance in subsequent evaluations, suggesting an adaptation response of tannin production to environmental conditions.

Interestingly, most genotypes showed decreased TT levels at 7 days after irrigation suppression under the FC condition, contrary to the expected response. This could be linked to a decrease in ambient humidity and an increase in temperature on the day of evaluation and in the previous days (Fig. 2). Moreover, the fig plants at field capacity had adequate water, leading to faster cell expansion and biomass accumulation due to the increased growth rate, which can dilute the concentration of secondary metabolites like tannins (Table 6).

Table 6. Total tannins (TT) in leaf tissue of fig trees subjected to water deficit (WD) and field capacity (FC) during two periods, one of humidity restriction (DAIS) and the second of rehydration in days at field capacity moisture (DFCM)

Genotype	SWC	Total Tannins (TT) (mg g FW^{-1})				
		DAIS		DFCM		
		1	7	8	11	15
Arista	WD	2.452 ^{a}	2.411 ^{ab}	2.426 ^{bcd}	2.492 ^{c}	3.005 ^{ab}
	FC	2.403 ^{a}	1.865 ^{bc}	2.099 ^{cd}	3.366 ^{abc}	3.457 ^{a}
Black Mission	WD	2.337 ^{a}	2.836 ^{a}	3.867 ^{a}	2.437 ^{c}	1.917 ^{ab}
	FC	2.109 ^{a}	2.238 ^{ab}	3.258 ^{abc}	3.821 ^{ab}	3.049 ^{ab}
Ceballos	WD	2.694 ^{a}	2.544 ^{ab}	3.206 ^{abc}	3.886 ^{ab}	1.978 ^{ab}
	FC	2.575 ^{a}	1.319 ^{c}	3.316 ^{abc}	3.595 ^{abc}	1.696 ^{b}
Fortuna	WD	3.005 ^{a}	2.635 ^{ab}	2.929 $^{a-d}$	4.117 ^{a}	2.376 ^{ab}
	FC	2.245 ^{a}	1.781 ^{bc}	1.961 ^{d}	2.573 ^{c}	1.872 ^{ab}
Guadalupe	WD	2.585 ^{a}	1.859 ^{bc}	2.600 ^{bcd}	3.036 ^{abc}	2.493 ^{ab}
Victoria	FC	2.510 ^{a}	2.170 ^{abc}	1.715 ^{d}	2.733 ^{ab}	2.153 ^{ab}
San Antonio	WD	2.978 ^{a}	2.250 ^{ab}	3.467 ^{ab}	3.367 ^{abc}	3.037 ^{ab}
	FC	3.085 ^{a}	2.339 ^{ab}	2.792 $^{a-d}$	2.954 ^{ab}	1.937 ^{ab}

Note: Values are presented as mean EC with standard error, and different letters indicate significant differences between values within each genotype and SWC treatment ($p < 0.05$).

Total proteins, determined by the Bradford method, reflect the soluble protein content in plant extracts. These proteins generally decrease under water deficit conditions because of ROS, which is associated with high toxicity (Ashraf et al., 2018). TP presented statistical differences among genotypes at 1 day after irrigation suppression (Table 7. This difference in initial condition can be related to the capacity of those materials to use soluble proteins as a mechanism to face water deficit conditions, as it is visible in Fortuna and San Antonio accessions. Moreover, the San Antonio genotype at 7 days after irrigation suppression showed statistical differences in soil water content. This increase in TP was observed at WD, and the condition remained high even in the recovery period. This performance could be related to the plant's response by increasing

the synthesis of antioxidant proteins such as superoxide dismutase, catalase, and peroxidase to mitigate oxidative damage (Hasanuzzaman et al., 2013). Also, the production of enzymes involved in the synthesis of compounds related to osmotic adjustment substances, such as proline (Jacobo-Salcedo et al., 2024b).

Table 7. Total Proteins (TP) in leaf tissue of fig trees subjected to water deficit (FD) and field capacity (FC) during two periods, one of humidity restriction and the second of rehydration

Genotype	SWC	Total Proteins (TP) (mg proteína g FW^{-1})				
		DAIS		DFCM		
		1	7	8	11	15
Arista	WD	0.426 $^{a-d}$	0.361 ^{d}	0.649 ^{cd}	1.213 ^{a}	1.576 ^{a}
	FC	0.508 $^{a-d}$	0.289 ^{d}	0.625 ^{cd}	1.107 ^{abc}	1.026 ^{bc}
Black Mission	WD	0.739 ^{a}	0.424 ^{cd}	0.794 ^{bcd}	1.008 ^{abc}	1.255 ^{ab}
	FC	0.676 ^{ab}	0.422 ^{cd}	0.842 ^{bcd}	1.167 ^{ab}	0.949 ^{bcd}
Ceballos	WD	0.569 ^{abc}	0.398 ^{cd}	0.757 ^{bcd}	1.169 ^{a}	0.954 ^{bcd}
	FC	0.555 ^{abc}	0.552 ^{bcd}	0.677 ^{cd}	0.900 ^{abc}	1.097 ^{bc}
Fortuna	WD	0.290 ^{cd}	0.808 ^{b}	1.376 ^{a}	0.638 ^{bc}	1.067 ^{bc}
	FC	0.225 ^{d}	0.569 ^{bcd}	0.500 ^{d}	0.840 ^{abc}	0.635 ^{cd}
Guadalupe	WD	0.493 $^{a-d}$	0.688 ^{bc}	1.100 ^{ab}	1.045 ^{abc}	0.991 ^{bc}
Victoria	FC	0.390 ^{bcd}	0.821 ^{b}	0.607 ^{cd}	0.715 ^{bc}	0.521 ^{d}
San Antonio	WD	0.395 ^{bcd}	1.547 ^{a}	0.984 ^{abc}	1.009 ^{abc}	1.255 ^{ab}
	FC	0.503 $^{a-d}$	0.771 ^{b}	0.593 ^{cd}	0.634 ^{c}	0.896 ^{bcd}

Note: Values are presented as mean EC with standard error, and different letters indicate significant differences between values within each genotype and SWC treatment ($p < 0.05$).

During the evaluation, the Fortuna genotype presented statistical differences in soil water content (Fig. 6). As previously mentioned, proline (Pro) plays a substantial role in osmotic regulation. Pro exhibited a strong ability to hydrate, which protected cell structures. Pro formed associations with soluble proteins to create hydrophobic skeletons that stabilize and defend biological macromolecules and cell structures (Yang et al., 2021).

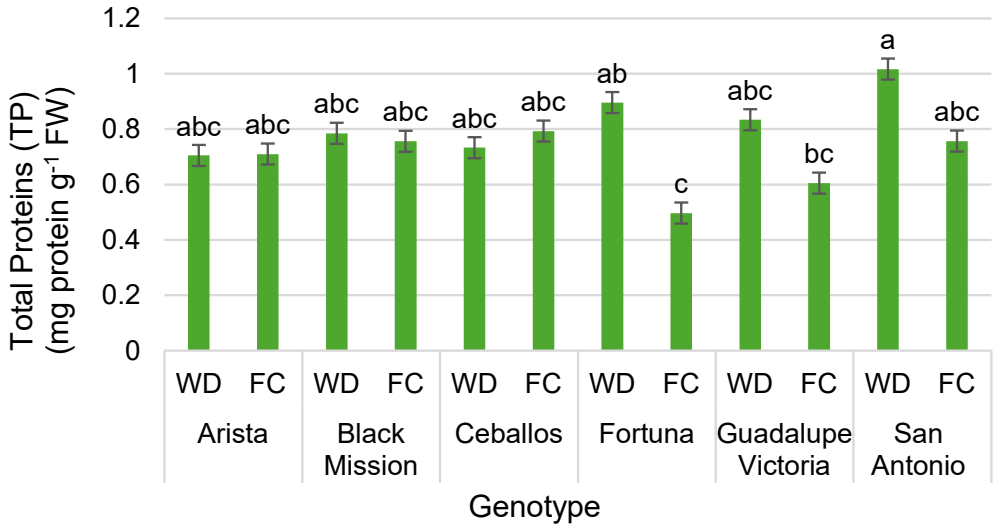

Figure 6. Interaction T*SM and G*SM mean results of total protein (TP) in fig trees subjected to water deficit (WD) and field capacity (FC).

CONCLUSIONS

The PWP reached during 5 to 6 days of the irrigation suspension period presented an absence of physical stress, indicating internal adaptation mechanisms in the evaluated fig genotypes. However, the EC measure revealed an increase in days at the irrigation suspension period evaluation related to membrane damage. This response demonstrates the fig-evaluated genotypes' plasticity. The 60% increase in the AA under drought stress indicates that non-enzymatic antioxidant pathways involving flavonoid and phenolic compounds were activated in young plants. Genotypes demonstrated adaptive processes, including protein synthesis and antioxidant activation, as evidenced by the significant interaction among the examined factors (time, genotype, and soil moisture conditions). Guadalupe Victoria and San Antonio accessions presented an important performance in the evaluation of water stress and water recovery because those present AA response as a critical mechanism for dryland production systems. In most genotypes, TFC and TPC markedly increased under drought conditions, demonstrating their function in scavenging ROS and protecting fig plants. The Arista genotype exhibited the most substantial TPC increase, signifying enhanced drought tolerance. The fig genotypes exhibited unexpected patterns of TT under WD and FC conditions. This response suggests a complex relationship between secondary metabolite production and environmental factors. Notably, the San Antonio genotype maintained elevated protein levels even during the days at field capacity moisture, reflecting a robust stress response mechanism. The evaluations at field capacity moisture indicated a substantial recovery in physiological parameters, considering EC, AA, and SWT. Those variables' responses highlight the potential of Guadalupe Victoria, San Antonio, and Arista genotypes for future breeding programs targeting drought-prone regions. The research highlights the potential of specific *Ficus carica* genotypes for drought tolerance, providing a basis for breeding programs and sustainable agricultural practices in water-limited regions.

REFERENCES

Abbas, K., Li, J., Gong, B., Lu, Y., Wu, X., Lü, G. & Gao, H. 2023. Drought Stress Tolerance in Vegetables: The Functional Role of Structural Features, Key Gene Pathways, and Exogenous Hormones. *International Journal of Molecular Sciences* **24**(18), 1–25. https://doi.org/10.3390/ijms241813876

Ammar, A., Ben, I., Gouiaa, M. & Mars, M. 2022. Fig (*Ficus carica* L.) vulnerability to climate change : Combined effects of water stress and high temperature on ecophysiological behavior of different cultivars. *South African Journal of Botany* **147**, 482–492. https://doi.org/10.1016/j.sajb.2022.02.014

Ammar, S., Del Mar Contreras, M., Belguith-Hadrich, O., Segura-Carretero, A. & Bouaziz, M. 2015. Assessment of the distribution of phenolic compounds and contribution to the antioxidant activity in Tunisian fig leaves, fruits, skins, and pulps using mass spectrometry-based analysis. *Food and Function* **6**(12), 3663–3677. https://doi.org/10.1039/c5fo00837a

Ashraf, M.A., Akbar, A., Askari, S.H., Iqbal, M., Rasheed, R. & Hussain, I. 2018. Recent advances in abiotic stress tolerance of plants through chemical priming: An overview. In Advances in Seed Priming (pp. 51–79). https://doi.org/10.1007/978-981-13-0032-5_4

Barnum, D.W. 1977. Spectrophotometric determination of catechol, epinephrine, dopa, dopamine and other aromatic vic-diols. In *Analytica Chimica acta.* Vol. **89**(1), 157–166. Scientific Publishing Company. https://doi.org/10.1016/S0003-2670(01)83081-6

Bradford, M.M. 1976. A Rapid and Sensitive Method for the Quantitation of Microgram Quantities of Protein Utilizing the Principle of Protein-Dye Binding. In *Analytical Biochemistry.* Vol. **72**.

Darwish, D.A., El-Berry, I.M., Mustafa, N.S., Moursy, F.S. & Hagagg, L.F. 2015. Detecting drought tolerance of fig (*Ficus carica* L.) cultivars depending on vegetative growth and peroxidase activity. *International Journal of ChemTech Research* **8**(4), 1520–1532.

FAO. 2019. Proactive approaches to drought preparedness - Where are we now and where do we go from here? http://www.fao.org/3/ca5794en/ca5794en.pdf

Gholami, M., Rahemi, M. & Rastegar, S. 2012. Use of rapid screening methods for detecting drought-tolerant cultivars of fig (*Ficus carica* L.). *Scientia Horticulturae* **143**, 7–14. https://doi.org/10.1016/j.scienta.2012.05.012

Harborne, J.B. 1984. *Phytochemical Methods: A Guide to Modern Techniques of Plant Analysis*. Chapman and Hall, pp. 84–87.

Hasanuzzaman, M., Nahar, K., Alam, M.M., Roychowdhury, R. & Fujita, M. 2013. Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. In *International Journal of Molecular Sciences* **14**(5), (9643–9684). https://doi.org/10.3390/ijms14059643

Hoxha, L., Kongoli, R. & Hoxha, M. 2015. Antioxidant activity of some dried autochthonous Albanian fig (*Ficus carica*) cultivars. *International Journal of Crop Science and Technology* **1**(2), 20–25.

Hssaini, L., Hanine, H., Charafi, J., Razouk, R., Elantari, A., Ennahli, S., Hernández, F. & Ouaabou, R. 2020. First report on fatty acids composition, total phenolics and antioxidant activity in seeds oil of four fig cultivars (*Ficus carica* L.) grown in Morocco. *OCL - Oilseeds and Fats, Crops and Lipids* **27**(8), 1–10. https://doi.org/10.1051/ocl/2020003

Jacobo-Salcedo, M. del R., Valdez-Cepeda, R.D., Sanchez-Cohen, I., Arreola-Ávila, J.G., González -Espíndola, L.A. & Trejo-Calzada, R. 2024a. Ability of fig tree (*Ficus carica* L.) accessions to thrive under limited and unlimited soil water conditions. *Acta Agrobotanica* **77**, 1–10. https://doi.org/10.5586/aa/183916

Jacobo-Salcedo, M. del R., Valdez-Cepeda, R.D., Sánchez-Cohen, I., González-Espíndola, L., Arreola-ávila, J.G. & Trejo-Calzada, R. 2024b. Physiological mechanisms in Ficus carica L. genotypes in response to moisture stress. *Agronomy Research* **22**(Special Issue II), 685–702. https://doi.org/10.15159/AR.24.047

Kamanga, R.M., Mbega, E. & Ndakidemi, P. 2018. Drought Tolerance Mechanisms in Plants: Physiological Responses Associated with Water Deficit Stress in Solanum lycopersicum. *Advances in Crop Science and Technology* **06**(03), 1–8. https://doi.org/10.4172/2329-8863.1000362

Konyalioğlu, S., Sağlam, H. & Kivçak, B. 2005. α-tocopherol, flavonoid, and phenol contents and antioxidant activity of Ficus carica leaves. *Pharmaceutical Biology* **43**(8), 683–686. https://doi.org/10.1080/13880200500383538

Lamuela-Raventós, R.M. 2018. *Folin-Ciocalteu method for the measurement of total phenolic content and antioxidant capacity*.

Li, Z., Cheng, B., Peng, Y. & Zhang, Y. 2020. Adaptability to abiotic stress regulated by γ-aminobutyric acid in relation to alterations of endogenous polyamines and organic metabolites in creeping bentgrass. *Plant Physiology and Biochemistry* **157**(July), 185–194. https://doi.org/10.1016/j.plaphy.2020.10.025

Marrelli, M., Menichini, F., Statti, G.A., Bonesi, M., Duez, P., Menichini, F. & Conforti, F. 2012. Changes in the phenolic and lipophilic composition, in the enzyme inhibition and antiproliferative activity of *Ficus carica* L. cultivar Dottato fruits during maturation. *Food and Chemical Toxicology* **50**(3–4), 726–733. https://doi.org/10.1016/j.fct.2011.12.025

Medina, G.G., Díaz, P.G., H.J., L., C.J.A., R. & Marín S.M. 2005. B*asic climatological statistics for the state of Durango*. (Period 1961–2003). Technical Book No. 1. Guadiana Valley Experimental Field (in Spanish).

National Institute of Statistics and Geography (INEGI). 2015. 'G*lobal Indicator of Economic Activity*'. Press Release No. 18/15, available at In: http://www.inegi.org.mx/inegi/contenidos/espanol/prensa/Boletines/Boletin/Comunicados/Indicador%20global%20de%20la%20actividad%20economica/2015/Enero/comunica.pdf (in Spanish).

Osmolovskaya, N., Shumilina, J., Kim, A., Didio, A., Grishina, T., Bilova, T., Keltsieva, O.A., Zhukov, V., Tikhonovich, I., Tarakhovskaya, E., Frolov, A. & Wessjohann, L.A. 2018. Methodology of drought stress research: Experimental setup and physiological characterization. In *International Journal of Molecular Sciences* (Vol. **19**, Issue 4089, pp. 1–25). MDPI AG. https://doi.org/10.3390/ijms19124089

Parejo, I., Codina, C., Petrakis, C. & Kefalas, P. 2000. Evaluation of scavenging activity assessed by Co(II)/EDTA-induced luminol chemiluminescence and DPPH (2,2-diphenyl-1-picrylhydrazyl) free radical assay. *Journal of Pharmacological and Toxicological Methods* **44**(3), 507–512. https://doi.org/10.1016/S1056-8719(01)00110-1

Şahin, S. 2013. Evaluation of antioxidant properties and phenolic composition of fruit tea infusions. *Antioxidants* **2**(4), 206–215. https://doi.org/10.3390/antiox2040206

Sánchez-Urdaneta, A.B., Peña-Valdivia, C.B., Trejo, C., Aguirre, R., J.R., Cárdenas, E. & Galicia Jiménez, A.B. 2003. Permeability of root membranes of wild and domesticated bean (*Phaseolus vulgaris* L.) seedlings under moisture deficit. *Interciencia* **28**(10), 597–603 (in Spanish).

Scoffoni, C., Albuquerque, C., Buckley, T.N. & Sack, L. 2023. The dynamic multi-functionality of leaf water transport outside the xylem. *New Phytologist* **239**(6), 2099–2107. https://doi.org/10.1111/nph.19069

Seleiman, M.F., Al-Suhaibani, N., Ali, N., Akmal, M., Alotaibi, M., Refay, Y., Dindaroglu, T., Abdul-Wajid, H.H. & Battaglia, M.L. 2021. Drought stress impacts on plants and different approaches to alleviate its adverse effects. *Plants* **10**(2), 1–25. doi: 10.3390/plants10020259

Shcherbakov, V.V., Artemkina, Y.M., Akimova, I.A. & Artemkina, I.M. 2021. Dielectric characteristics, electrical conductivity and solvation of ions in electrolyte solutions. *Materials* **14**(19), 1–26. https://doi.org/10.3390/ma14195617

Shomali, A., Das, S., Arif, N., Sarraf, M., Zahra, N., Yadav, V., Aliniaeifard, S., Chauhan, D.K. & Hasanuzzaman, M. 2022. Diverse Physiological Roles of Flavonoids in Plant Environmental Stress Responses and Tolerance. *Plants* **11**(22). doi: 10.3390/plants11223158

Sparke, M.A. & Wünsche, J.N. 2020. Mechanosensing of plants. In *Horticultural Reviews* (Issue January 2020, pp. 43–83). https://doi.org/10.1002/9781119625407.ch2

Stanković, M.S. 2011. Total phenolic content, flavonoid concentration and antioxidant activity of *Marrubium peregrinum* L. extracts. *Kragujevac J. Sc.* **33**(1), 63–72.

Wu, J., Wang, J., Hui, W., Zhao, F., Wang, P., Su, C. & Gong, W. 2022. Physiology of Plant Responses to Water Stress and Related Genes: A Review. *Forests* **13**(2). https://doi.org/10.3390/f13020324

Yang, X., Lu, M., Wang, Y., Wang, Y., Liu, Z. & Chen, S. 2021. Response mechanism of plants to drought stress. *Horticulturae* **7**(3), 1–36. https://doi.org/10.3390/horticulturae7030050