UNIVERSIDAD AUTÓNOMA CHAPINGO

UNIDAD REGIONAL UNIVERSITARIA DE ZONAS ÁRIDAS

POSGRADO EN CIENCIAS EN RECURSOS NATURALES Y MEDIO AMBIENTE EN ZONAS ÁRIDAS

RESPUESTA DE ECOTIPOS DE *Ficus carica* Lam A LA CONDICIÓN DE ESTRÉS HÍDRICO

RESPONSE OF *Ficus carica Lam.* ECOTYPES TO WATER STRESS CONDITIONS

THESIS

Submitted as a partial requirement to obtain the degree of:

DOCTOR EN CIENCIAS EN RECURSOS NATURALES Y MEDIO AMBIENTE EN ZONAS ÁRIDAS

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Bermejillo Durango, México, April 6th, 2024

RESPONSE OF *Ficus carica Lam.* ECOTYPES TO WATER STRESS CONDITIONS

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DEDICATED TO

This work is dedicated to **my children,** who were active every day and night, working hard and putting in extra effort. Their outings were to water plants and name snakes and lizards. During a global pandemic, these plants were our motivation and opportunity to go out and learn every day.

Frida and Fabricio are a big part of my heart, and I want them to know that I recognize and appreciate their effort and help, and each one contributed a great source of love to all of this. Forever and ever, I love you.

Luis Angel, we know this has been so different from what we expected, but I want to thank you for the opportunity to work by your side and support us in every step we have taken. I know an extraordinary bond will always unite us, but the one that matches our worlds will be forever.

To my parents and siblings, thank you for your support. I love you.

ACKNOWLEDGEMENTS

I thank the Consejo Nacional de Ciencia y Tecnología (CONAHCYT, scholarship number 383083) and Universidad Autónoma Chapingo for the opportunity, support, and financing to complete my postgraduate studies.

To the Instituto Nacional de Investigaciones Forestal Agricola y Pecuaria, Centro Nacional de Investigación Disiplinario in Relación Agua Suelo y Atmosfera (INIFAP-CENID-RASPA) for their support and for allowing the development of this Doctoral program.

To my Advisory Committee, Dr. Ricardo Trejo Calzada, Dr. Ricardo David Valdez Cepeda, Dr. Ignacio Sanchez Cohen, and Dr. Jesus Arreola Ávila for being a vital guide and support during the development of this project.

I thank my colleagues for their friendship and accompaniment during this time: Dra. (C) Perla Ochoa García, Dr. (C) Luis Ángel González Espíndola, M.C. Sandra Maciel Torres.

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RESUMEN GENERAL

Respuesta de ecotipos de *Ficus carica Lam*. a condiciones de estrés hídrico

El valor nutritivo y la capacidad de *Ficus carica* L. (higuera) para mejorar la salud han atraído recientemente la atención científica, posicionando a este cultivo frutal como un cultivo alternativo crucial para las regiones que enfrentan escasez de agua. Entendiendo la importancia global del cultivo de higuera, los mecanismos de adaptación y las respuestas fisiológicas al déficit hídrico son cruciales, particularmente en áreas con escasez de agua. Este estudio tuvo como objetivo identificar respuestas adaptativas que mitiguen los efectos adversos de la sequía en seis genotipos jóvenes de *Ficus carica* nativos de zonas áridas, evaluando su supervivencia en condiciones extremas de déficit hídrico: el objetivo del uso de materiales jóvenes es identificar respuestas tempranas deseables a la escasez de agua. Un experimento en macetas con diferentes condiciones de agua del suelo se realizó y se midieron las variables de respuesta, como el contenido relativo de agua (RWC), el intercambio de gases foliares (Pn, gs, Ci y E), los parámetros de eficiencia del agua (WUE e int-WUE) y el contenido de solutos (SSC y Pro). La exploración a través del análisis de componentes principales, los coeficientes de correlación de Pearson y la regresión revelaron una posible respuesta adaptativa, en particular en una correlación negativa significativa entre Proline (Pro) y RWC. Las accesiones dignas de mención, Guadalupe Victoria y Ceballos, demostraron una resiliencia excepcional en condiciones de déficit hídrico. Este estudio amplía a los marcadores fisiológicos y bioquímicos, revelando diversos mecanismos adaptativos, incluido el ajuste osmótico, la regulación estomática y la acumulación de prolina. La accesión Guadalupe Victoria mostró una notable resiliencia al déficit de agua, enfatizando el papel de los ajustes osmóticos en el mantenimiento del equilibrio hídrico y la función celular. Estos hallazgos proporcionan información valiosa para seleccionar genotipos de higuera tolerantes a la sequía, lo que contribuye a la producción sostenible en entornos con escasez de agua.

Palabras clave: resiliencia, mecanismos adaptativos y respuestas fisiológicas.

Tesis de: Doctorado en Ciencias en Recursos Naturales y Medio Ambiente en Zonas Áridas
UNIVERSIDAD AUTONOMA CHAPINGO, Unidad Regional Universitaria de Zonas Áridas
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GENERAL ABSTRACT

Response of *Ficus carica* Lam. ecotypes to water stress conditions

The nutritive value and health-promoting capacity of *Ficus carica* L. (common fig) have recently drawn scientific attention, positioning this fruit crop as a crucial alternative for regions facing water scarcity. Understanding the global significance of fig cultivation, the adaptation mechanisms, and physiological responses to water deficit are critical, especially in water-scarce areas. This study aimed to identify adaptive responses that mitigate the adverse effects of drought on six young genotypes of *Ficus carica* native to arid zones, assessing their survival under extreme water deficit conditions: the use of young materials aims to identify early desirable responses to water scarcity. A pot experiment with varying soil water conditions was conducted, and response variables were measured, such as relative water content (RWC), leaf gas exchange (Pn, gs, Ci, and E), water efficiency parameters (WUE and int-WUE), and solute content (SSC, and Pro). Exploration through principal component analysis, Pearson correlation coefficients, and regression revealed a possible adaptive response, particularly a significant negative correlation between Proline (Pro) and RWC. Noteworthy accessions, Guadalupe Victoria, and Ceballos, demonstrated exceptional resilience under water deficit conditions. This study expands to physiological and biochemical markers, revealing various adaptive mechanisms, including osmotic adjustment, stomatal regulation, and proline accumulation. The accession Guadalupe Victoria exhibited a remarkable water deficit, emphasizing the role of osmotic adjustments in maintaining water balance and cellular function. These findings provide valuable insights for selecting drought-tolerant fig genotypes, contributing to sustainable production in water-scarce environments.

Keywords: resilience, adaptative mechanisms, physiological responses

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CHAPTER I: GENERAL INTRODUCTION

Alternative crops refer to options offered as alternatives to traditionally established production in farming sites (Neri-Guzman & Medina-Ortega, 2019). Implementing alternative crops can provide advantages such as breaking pest and disease cycles, nutrient fixation, soil fertility improvement, and better utilization of water resources (SAGARPA, 2016). These crops represent an opportunity to enhance agricultural production profitability (Neri-Guzman & Medina-Ortega, 2019).

Though commonly known as a fruit from the fig tree, the fig is technically a syconium (compressed infructescence). It belongs to the *Ficus* genus, specifically *F. carica*, of which approximately 750 species have been identified, but only 46 are widely cultivated worldwide (Flaishman et al., 2008). Commercial fig fruit production relies on varieties like Adriatic, Black Mission, Brown Turkey, Conadria, Kadota, and Sarylop (Flaishman et al., 2008).

Several studies on fig trees report the presence of phytochemical compounds such as alkaloids, tannins, glycosides, flavonoids, saponins, coumarins, sterols, terpenic carbohydrates, phenols, essential oils, volatile oils, proteins, and minerals (Ahmad et al., 2016; Barolo et al., 2014; Giuliano, 2017; Mopuri et al., 2018). These components confer various properties such as antibacterial, antiviral, antiparasitic, antioxidant, anticancer, antimutagenic, antiangiogenic, anti-inflammatory, antipyretic, antidiabetic, antispasmodic, among others (Al-Snafi, 2017; Pachucho Flores, 2012). These pharmacological properties have increased the importance of fig production and consumption beyond traditional uses.

The total area dedicated to fig cultivation is approximately 218,729 hectares (FAO, 2019; FAOSTAT, 2021). Currently, worldwide fig production for fresh and dried consumption has generated around 540 million euros in revenue, with 160,000 tons produced for dried figs and 60,000 tons for fresh figs (Hueso-Martín & Cuevas-González, 2014). While Mexico is not among the leading global producers, the fig cultivation sector has grown significantly, with a 36% increase in cultivated area from 2003 to 2018 (SIAP, 2020).

Fig trees exhibit greater drought tolerance than most fruit trees, making them desirable crops for arid regions (Flaishman et al., 2008). Their physiological nature allows for efficient water productivity, with water requirements for three-year-old plants estimated at 220 mm per year (2200 $m^{-3}ha^{-1}year$) distributed throughout the year with priority during critical stages of growth. These stages usually occur before the first harvest, generally at the beginning of spring, and the second harvest, which takes place during the summer (Flaishman et al., 2008).

The productive response of fig trees under water deficit conditions makes them an exciting crop for establishing improvement programs focused on selecting fig germplasm. Identifying superior fig genotypes is an optimization method for production under environmental stress. Observing phenotypic characteristics such as leaf shape, fruit weight, form, and color aids in selecting (Rabei Metwali et al., 2016).

Water deficit represents a significant constraint to plant growth and development. Plants have developed physiological, cellular, and molecular responses that lead to adaptation and improved growth under drought stress conditions (Chartzoulakis et al., 1999; Kabbadj et al., 2017; Khan et al., 2017; Khatab et al., 2019). Plant responses to environmental stress include alterations in protein synthesis patterns, which can confer survival capabilities under water scarcity through changes in physiological and biochemical processes (Bocchini et al., 2018). Some physiological responses include stomatal closure, osmolyte accumulation, and upregulation of antioxidant systems (Romero et al., 2017).

One of agriculture's main challenges is reducing water usage without compromising productivity (FAOSTAT, 2021). Favoring drought tolerance is a priority due to water scarcity and the distribution of cultivation systems. Drought tolerance can be evaluated through variables such as stem water potential, relative water content, drought damage index, chlorophyll stability index, and leaf mass per area (Gholami et al., 2012). The mentioned background highlights the complexity of evaluating tolerance mechanisms and responses to water deficiency. However, the need to establish feasible production systems for arid

and semi-arid regions drives the objective of assessing different fig ecotypes under water stress conditions.

1.1 Justification

This study lies in the increasing global significance of *Ficus carica* L. (fig) cultivation (Oukabli et al., 2008), particularly in regions facing water scarcity. As water resources become increasingly limited due to climate change and growing population demands, identifying crop species with adaptive responses to drought stress is predominant for sustainable agriculture (Mohamed et al., 2016). Figs offer a promising alternative due to their nutritional value and ability to thrive in arid and semi-arid conditions where few other crops can be effectively cultivated (Ammar et al., 2020).

This research study looks to understand the adaptive responses of fig genotypes to water deficit stress (Gholami et al., 2012). By evaluating the physiological responses of young *Ficus carica* genotypes under extreme drought conditions, we might provide insights into the potential resilience of fig trees to water scarcity. Additionally, the comparison with a commercial variety like the Black Mission further enhances the applicability of the findings to real-world fig production scenarios.

1.2 General Objective

To identify the relationships among accessions of *Ficus carica* L. and their physiological and antioxidant responses under water deficit conditions

1.2.1 Specific Objectives

a) To detect a possible adaptive response to mitigate the adverse effects of drought and enhance the ability of six *Ficus carica* L. genotypes to survive extreme water stress.
b) To identify outstanding fig tree accessions under water deficit conditions.

c) To define the relationship between tolerance to water deficit and fig plant physiological and biochemical using markers such as Relative Water Content (RWC), Photosynthesis (P_N), Stomatal Conductance (gs), intercellular CO_2 content (Ci), Transpiration Rate (E), Proline Content (Pro), and Soluble Sugar Content (SSC).

1.3 Hypothesis

Wild fig trees might have genetic relationships & those might present different physiological and antioxidant responses to water deficit.

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CHAPTER II. THEORETICAL FRAMEWORK

2.1 Origen and geographical fig distribution

The common fig (*Ficus carica* L.) was one of the first plants to be cultivated globally. Its origin was registered in sub-Occidental Asia (CONABIO). However, recent molecular analyses propose that the fig's origin is in Turkey (Karandeniz,

2009). Human migration played a role in spreading the plant beyond its natural environment, initially to regions such as Arabia, Algeria, Egypt, Spain, France, Greece, Italy, Libya, Morocco, Palestine, Portugal, Tunisia, and Syria, and later to worldwide destinations (Condit, 1955; Storey, 1977). Romans dispersed it to the territories they conquered, and it's believed that during colonization, the Spanish introduced the fig plant to the American continent, particularly in California, United States, in the early 18th century. The fig tree was further distributed from California to the southeastern part of the country (Price & White, 1902).

2.2 Taxonomical *Ficus carica* Lam. classification

The genus *Ficus* comprises cultivated and wild species that vary in phenotypic characteristics of both, the plant and the fruit (Condit, 1955; Flaishman et al., 2008). However, all this variation is represented in basic taxonomic units, as shown below:

- Kingdom: Vegetal
- Subkingdom: Tracheobionta
- Division: Magnoliophyta
- Class: Magnoliopsida
- Order: Rosales
- Family: Moraceae
- Subfamily: Ficeae
- Genre: *Ficus*
- Subgenus: *Ficus*
- Species: *F. carica*

2.3 The Fig Tree

The fig tree originates from Mediterranean regions and arid lands of Europe and Africa, known as the Fertile Crescent. The fig is the fig tree's fruit, which belongs to the *Ficus* genus and the species *F. carica*. Approximately 750 species identified from this genus have been identified within this genus, mainly distributed in tropical regions. Among them, around 607 varieties of figs have been described in the literature, but only 46 are widely cultivated worldwide. Commercial fig fruit

production mainly relies on types such as Adriatic, Black Mission, Brown Turkey, Conadria, Kadota, and Sarylop (Flaishman et al., 2008).

The fig tree is a dioecious species, meaning its flowers and fruits are found inside a fleshy receptacle called a syconium. Female fig trees produce dry fruits called achenes and fleshy and sweet perianth, known as brebas and figs, respectively. Both brebas and figs can be consumed fresh, dried, or processed. Their differentiation is based on their ripening period and the type of wood they develop from. Figs represent the main harvest in most varieties and appear on the current year's growth, developing alongside a leaf when the buds have started sprouting in spring. On the other hand, brebas can be considered a secondary harvest and grow on the previous year wood, appearing alone. Brebas can be seen as latent figs that did not initiate their development until the following spring (Hueso-Martín & Cuevas-González, 2014).

Studies conducted on fig trees have reported the presence of phytochemical compounds that contribute to its potential health benefits such as phenolic compounds (flavonoids, phenolic acids, and tannins), flavonoids (quercetin, kaempferol, and rutin), carotenoids (beta-carotene, lutein, and zeaxanthin), phenolic acids (gallic acid, chlorogenic acid, and caffeic acid), terpenoids, vitamins, and minerals (vitamin A, vitamin K, potassium, calcium, and magnesium), fiber, enzymes (ficin) and fatty acids (linoleic and oleic acids) (Ahmad et al., 2016; Barolo et al., 2014; Giuliano, 2017; Mopuri et al., 2018). These compounds have been found in different plant parts, including fruit, leaves, and stems (Figure 1). The phytochemical composition of figs can vary based on factors such as fig variety, ripeness, growing conditions, and processing methods.

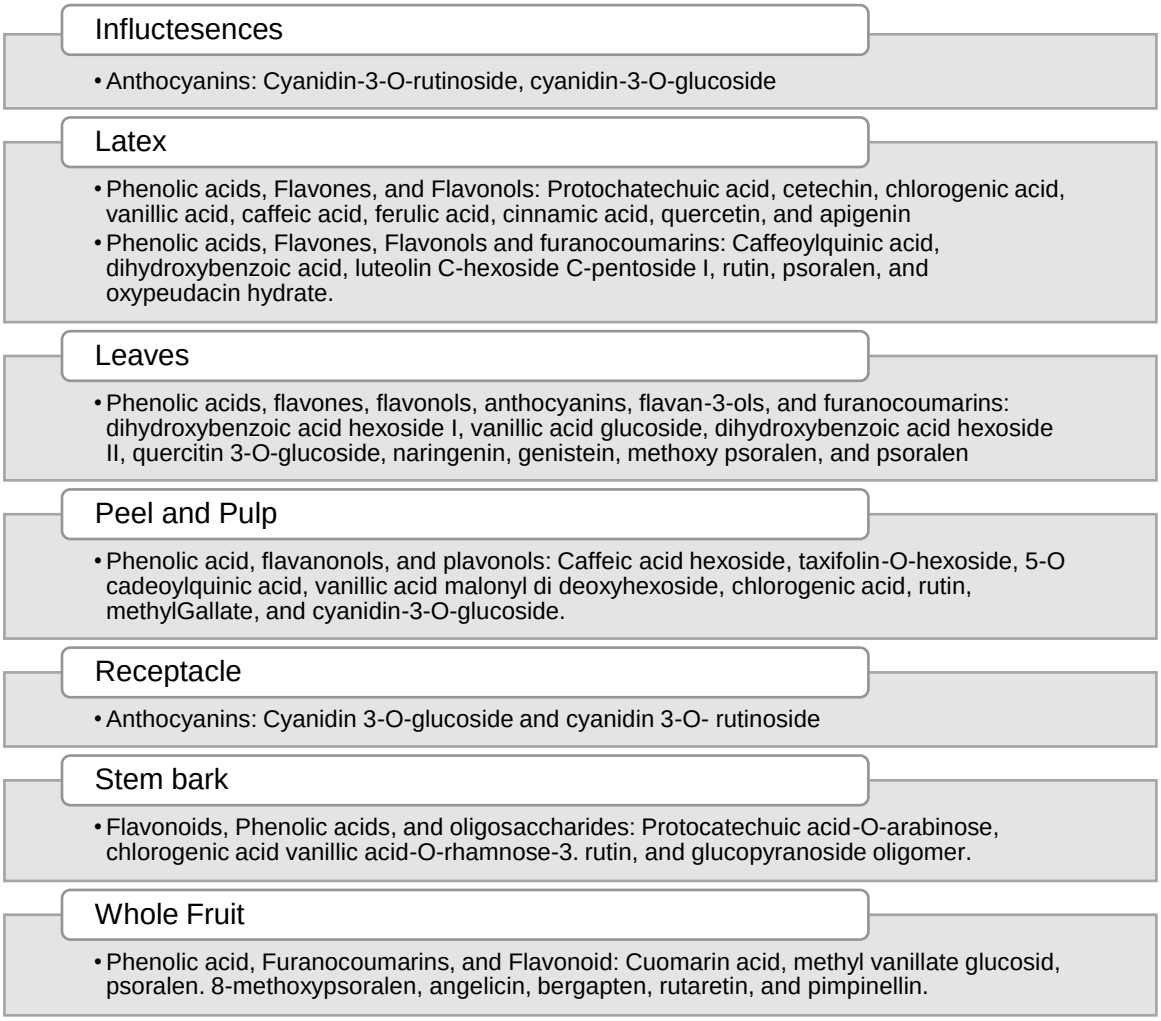

Figure 2. Bioactive compounds from different *F. carica* parts. (Abdel-Aty et al., 2019; Ammar et al., 2015; Backes et al., 2018; Belguith-Hadriche et al., 2017; Irudayaraj et al., 2016; Ladhari et al., 2020; Lama et al., 2020; Marrelli et al., 2012; Oliveira et al., 2010, 2012; Palmeira et al., 2019; Raafat & Wurglics, 2019; Wang et al., 2018; Wang et al., 2017)

The presence of these phytochemical compounds contributes to figs' potential health-promoting properties. Some of these properties include antibacterial, antiviral, antiparasitic, antioxidant, anticancer, antimutagenic, antiangiogenic, anti-inflammatory, antipyretic, antidiabetic, antispasmodic, and more (Al-Snafi, 2017; Fraire Burgos & Carrasco Chinlle, 2015; Martínez-Betancurt, 1995; Pachucho Flores, 2012). These pharmacological properties have elevated the significance of consuming these fruits beyond their traditional uses.

2.4 The economy of fig cultivation

The fig tree originates from Mediterranean regions, and the top fig producers include Turkey, Egypt, Algeria, Iran, Morocco, and Syria, among others. These countries contribute to most of the world's fig production, with statistics from 2013 indicating a total cultivated area of 218,729 hectares (FAO, 2021). Fig production at the global level, both for fresh and dried consumption, generates significant income, reaching approximately 540 million euros. This comes from a worldwide fig production of around 1.2 million metric tons. The primary destination for fresh fig exports is Europe, while the market for dried figs is more widespread (Hueso-Martín & Cuevas-González, 2014).

In Mexico, fig production is a growing market. Records from the SIAP indicate that in 2022, there were 1834 hectares of fig cultivation with a mean yield of 7.11 Ton ha^{-1}. Moreover, the productive value for this year was USD 16,015,918 (SIAP, 2022). The cultivation of figs has become widespread across the country. To improve efficiency, particularly in fresh fruit production, efforts focus on enhancing cultivation techniques. Key factors include pruning, fertilization, and irrigation, contributing to increased productivity and fruit size (Flaishman et al., 2008).

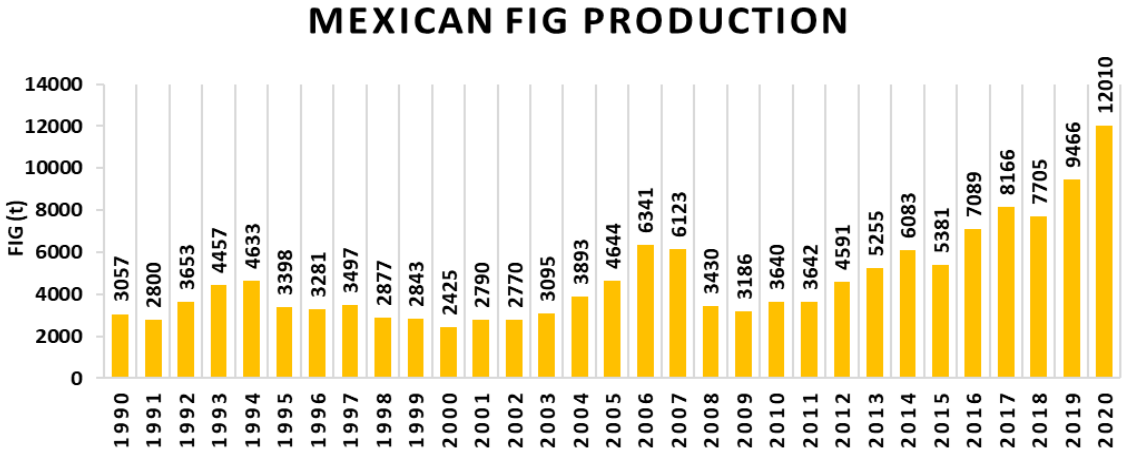

Figure 2. Fig production in Mexico from the last 30 years.

However, one of the main challenges in fig cultivation is the fragility and short shelf life of fresh fruit, which hampers commercialization. The crop is also highly

susceptible to bird attacks and infestation by insects or fruit flies (Balas et al., 2013). Many farmers use protective covers such as shade nets to address this issue, which is considered a step towards protected agriculture. This system offers reduced vulnerability, increased productivity, and efficiency in water and chemical inputs (Lawrence & Ortega, 2018).

Fig trees exhibit greater drought tolerance than most fruit trees, making them an attractive crop for arid regions (Flaishman et al., 2008). The physiological nature of the plant allows for good productivity with relatively low water demand, leading to more efficient water use. Water requirements for three-year-old fig trees are around 220 mm per year (2200 m^3/ha/year), which should be distributed throughout the year, prioritizing critical stages of growth. These stages typically occur before the first harvest, usually at the beginning of spring, and the second harvest during the summer (Flaishman et al., 2008).

Establishing improvement programs aimed at selecting fig germplasm is highly desirable to achieve high yield and quality in drought-stressed environments. Identifying the best genotypes is considered an optimal breeding method for production under environmental stress. This involves observing phenotypic characteristics, such as leaf morphology, fruit weight, shape, and color (Rabei-Metwali et al., 2016).

2.5 Alternative Crops

The advancement of the agricultural sector goes hand in hand with technological developments and innovations in the use of different varieties, planting density, harvesting techniques, and pest and disease control. However, productive development should recognize soil conservation and the rational use of water resources in cultivation conditions. To enhance decision-making and consider alternative options, the production process must consider various risk factors (SAGARPA, 2016). Alternative crops (AC) offer a different choice than traditionally established ones. AC aims to complement or entirely replace a crop with higher demand and better prices locally or internationally. Embracing AC presents an

opportunity to improve farmlands' profitability and agricultural producers' income (Neri-Guzman and Medina-Ortega, 2019).

The implementation of AC comes with various advantages, including breaking pest and disease cycles, promoting nutrient fixation processes, enhancing soil fertility, and optimizing water resource utilization, among other ecological benefits (SAGARPA, 2016). There are also neglected and underutilized species (NUS), which are cultivated, semi-domesticated, or wild plant species, not included in the group of the major staple crops since, in most cases, they still need to meet the global market requirements. However, they often are a source of vitamins, micronutrients, and other phytochemicals (Mavroeidis et al., 2022). Quality is an essential aspect of agricultural production and is directly linked to profitability. The profitability of the farm output is greatly influenced by emerging consumption trends such as organic production and nutraceutical foods.

In dry areas, where water resources are limited, selecting suitable alternative crops becomes crucial for sustainable agricultural practices (Karelakis & Tsantopoulos, 2017). The choice of AC or NUS in such regions depends on their ability to thrive with reduced water availability while providing economic benefits (Elouafi et al., 2020; Marchant, 2019). Some of the most essential alternative crops for dry areas include drought-resistant grains (millet, sorghum, wheat, and barley), pulses, and legumes (lentils, chickpeas, and pigeon peas), oilseeds (safflower and sunflower), fruits and nuts (fig, date palms, olives, almonds, and pistachios), forage crops (clover), medicinal and aromatic plants (lavender, rosemary, and organum), cacti and succulents, halophytes (quinoa and certain salt-tolerant grasses), amaranth, heritage, and indigenous crops (Abdelaziz Hirich et al., 2020). The success of these alternative crops in dry areas depends on factors such as local climate, soil type, available water resources, market demand, and cultural practices (Elouafi et al., 2020; Xiao et al., 2017). Implementing efficient water management techniques, such as drip irrigation and rainwater harvesting, can significantly enhance the viability of cultivating alternative crops in arid regions.

Figs have several characteristics that make them suitable for cultivation as an AC in dry environments. Those properties are drought tolerance, deep rooting, resilience to harsh conditions, fruit production, economic value, cultural significance, biodiversity, and soil improvement (Ammar et al., 2022; Ammar et al., 2020(a), 2020(b); Barolo et al., 2014; Gordon et al., 2022; Vangelisti et al., 2019). While figs are well-suited for dry areas, it's essential to conduct thorough research and possibly seek guidance from local agricultural experts to determine the feasibility of growing figs as an alternative crop in a specific dry region.

2.6 Water Stress in Plants

The agricultural sector faces significant challenges due to environmental conditions resulting from climate change, population growth, and water availability issues. One of the critical challenges of modern agriculture is to sustain increased food production under adverse conditions, including biotic and abiotic stresses. Among these stress factors, water deficit poses a critical restriction to the growth and development of plants. In response to drought stress, plants have developed molecular, osmotic, physiological, and physical reactions that lead to adaptation and improved growth under water scarcity conditions (Chartzoulakis et al., 1999; Kabbadj et al., 2017; Khan et al., 2017; Khatab et al., 2019).

Plants' response to environmental stress involves alterations in protein synthesis patterns. These induced proteins are considered enhancements in survival abilities under water scarcity, achieved through changes in physiological and biochemical processes (Bocchini et al., 2018). The protein synthesis and degradation regulation during the water deficit often leads to a modulation. Some proteins may be synthesized in higher quantities to help the plant cope with stress, while others might be degraded to recycle amino acids to synthesize stress-responsive proteins (Kaur & Asthir, 2017; Moradi, 2016; Rodriguez et al., 2005). Some upregulated proteins are the chaperone proteins, also known as heat shock proteins (HSPs). These proteins help other proteins maintain proper structure and prevent misfolding due to stress conditions. In addition, the dehydrins and late embryogenesis abundant (LEA) proteins are accumulated in response to drought

stress and protect cellular structures and proteins from damage (Goyal et al., 2005; Yang et al., 2021).

Some other proteins involved in water deficit response include antioxidant enzymes, which often scavenge reactive oxygen species (ROS), which can damage cells. Plants respond by increasing the expression of superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) to detoxify ROS (Feng et al., 2013; Janku et al., 2019; Osmolovskaya et al., 2018; Zandalinas et al., 2018). Moreover, signaling proteins as kinases and phosphatases signal the pathways that involve protein phosphorylation and dephosphorylation to activate the downstream responses. Also, the aquaporins are proteins responsible for water transport across cell membranes; however, the expression and activity of those might be altered to regulate water movement and minimize water loss (Kaur & Asthir, 2017; Maurel & Prado, 2017; Tyerman et al., 2002). All those protein responses are regulated by some transcription factors that control the expression of stress-responsive genes that are upregulated under water deficit.

2.8 Tolerance Mechanisms

Plant resistance to drought is a complex process that integrates multiple mechanisms. Many of the molecular events triggered by decreased tissue water potential cannot be attributed solely to avoidance or tolerance strategies. Therefore, a complex regulatory network is needed to recognize the plant's adaptive responses to drought stress. Studies on responses to water deficit, such as stomatal closure, expression of stress-specific genes, accumulation of osmolytes, and upregulation of antioxidant systems, are still under investigation (Romero et al., 2017).

A common characteristic of all drought stress models is the reduction of osmotic potential in the substrate or the surrounding plant roots (Osmolovskaya et al., 2018; Gholami et al., 2012). Developing drought tolerance in different plant varieties and understanding their tolerance mechanisms has become a priority due to water scarcity and the distribution of cropping systems. The challenge lies

in reducing water usage in cultivation without compromising plant growth, development, and productivity (FAO, 2006).

Plants adapting to water stress increase osmotic pressure due to the accumulation of compatible solutes. This osmotic pressure adjustment helps water diffusion in the plant, maintaining turgor, growth, and various physiological processes. Also, during water stress, reactive oxygen species (ROS) levels increase, leading to an increase in malondialdehyde (MDA) levels (Khan et al., 2017).

Plant responses to water stress can be enhanced through inducers, which improve the physiological response of plants to water deficit. One such substance is selenium, which is used as sodium selenate and sodium selenite. Studies show increased photosynthesis and improved water use efficiency in plants subjected to water deficit when selenium is applied to crops like corn, oats, rice, and olive trees (Amato et al., 2018; Bocchini et al., 2018; Nawaz, Ashraf, Ahmad, & Waraich, 2013; Ribeiro Andrade et al., 2018).

2.7 Osmotic Responses

The osmotic response is a crucial mechanism through which plants adapt to water deficit conditions. Plants face difficulty maintaining their cellular water balance when subjected to water scarcity. They employ osmotic adjustments to regulate water movement and minimize water loss. Through the accumulation of osmolytes, such as soluble sugars, amino acids, and compatible solutes like proline, plants decrease their osmotic potential within cells. This elevation in solute concentration encourages water uptake from surrounding tissues or soil, helping to mitigate the effects of water deficit. Additionally, osmotic adjustments reduce the water potential gradient between the plant and its environment, thus lowering the risk of excessive water loss through transpiration. By strategically altering their osmotic balance, plants can endure water scarcity, sustain turgor pressure in cells, and maintain essential metabolic processes even under challenging conditions.

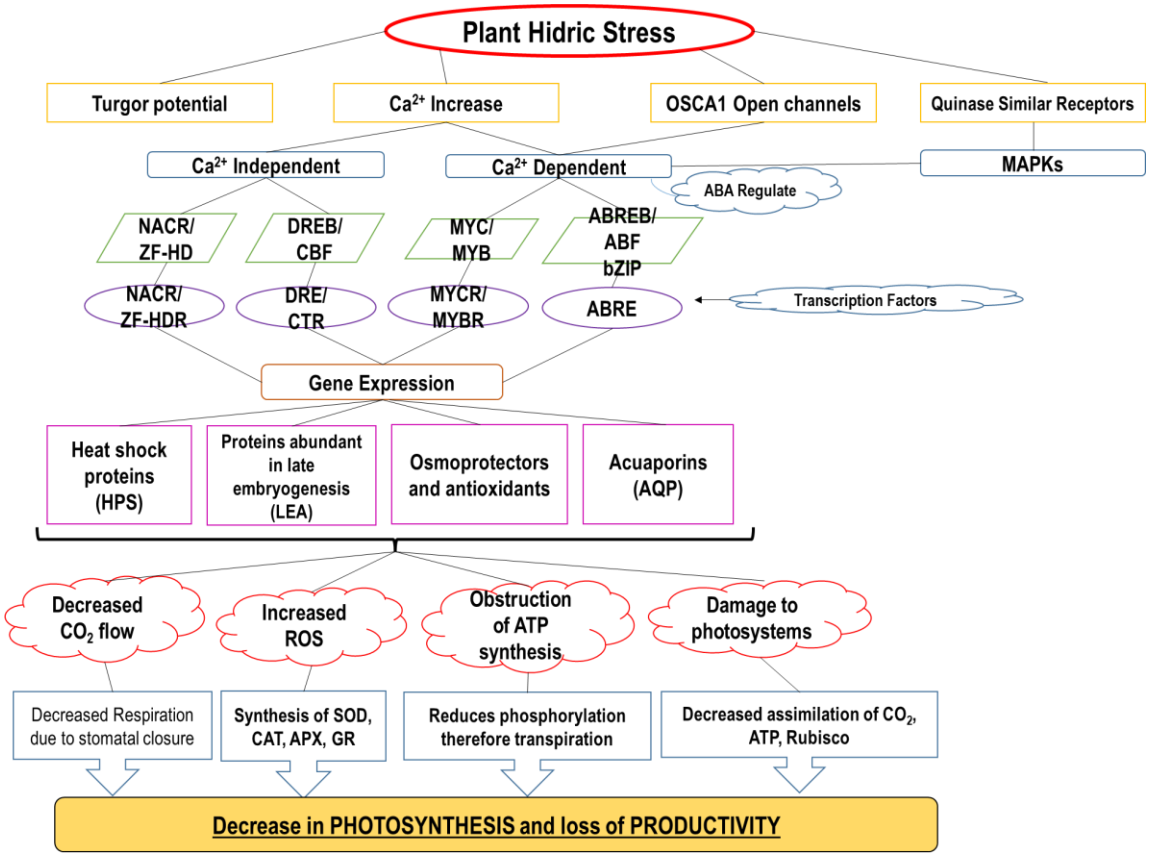

Figure 3. Plant response to hydric stress.

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CHAPTER III.

The ability of fig tree (*Ficus carica* L.) accessions to thrive under limited and unlimited soil-water conditions

3.1 ABSTRACT

The nutritive value of *Ficus carica L.* and the health-promoting capacity of figs have recently gained scientific attention. Its adaptation capacity to climatic variability makes this crop an important production alternative for regions with limited water resources. The aims of this work were i) to identify a possible adaptive response to mitigate the adverse effects of drought, enhance the ability of plants of six *Ficus carica* genotypes, and ii) to identify outstanding fig tree accessions under study to survive once they were subjected to extreme drought. The pot experiment considered two soil water conditions: water deficit and water holding capacity in vase experimental conditions. Relative water content, leaf gas exchange, water efficiency variables, and solute content were measured as response variables. A principal component analysis, Pearson correlation coefficients, and regression analyses were used to analyze the data. Results suggest a possible adaptive response to mitigate the adverse effects of drought; the ability of plants of the six genotypes under study to survive under water deficit conditions was evidenced through a significant negative correlation between Proline (Pro) and relative water content (RWC). In this context, Guadalupe Victoria and Ceballos are outstanding accessions.

Keywords: Native Genetic Materials; Black Mission; Gas Exchanges; Proline; Water efficiency

3.2 INTRODUCTION

Ficus carica L., commonly known as the fig tree, is a deciduous shrub native to the Middle East and Western Asia (Mawa et al., 2013). It is cultivated in 218,729 ha and distributed in 54 countries. Its yearly mean yield is 6.5 t ha^{-1} (FAO- STAT, 2021). The world's total fig production was estimated at approximately 1.4 million t in 2020 (FAO- STAT, 2021).

Ficus carica fruits (figs) are enclosed infructescence with a hollow succulent receptacle (Mawa et al., 2013). The demand for fresh figs has recently attracted much attention due to their potential health-promoting benefits (Ayuso et al., 2022). The increased market is explained because figs are a reliable source of fiber and phenolic compounds, mainly proanthocyanidins, furanocoumarins, and

phenolic acids (Badgujar et al., 2014; Francini et al., 2021; Soni et al., 2014; Z. Wang et al., 2017). Figs are used to develop functional foods and beverages, contributing to a healthier human diet. In addition, figs are eaten by 1,274 bird and mammal species, and many disperse the fig seeds (Shanahan, So, Compton, & Corlett, 2001).

Hitherto, *Ficus carica* is cultivated in many horticultural regions around the world. Also, several studies have been carried out on the behavior of this fruit tree under different environmental conditions, and particularly some of them are focused on dry conditions (Ammar et al., 2020a; Ammar et al., 2020b; Mardinata et al., 2021). Thus, current knowledge of fig trees as photosynthesis rates under different soil water contents indicates that this species exhibits a remarkable ability to adapt to varying moisture levels (Ammar et al., 2020a; Ammar et al., 2020b; Mardinata et al., 2021). Then, fig trees are well adapted to dry and moderate soil moisture conditions (Crisosto et al., 2011; Gholami et al., 2012). Fig trees can display a range of mechanisms through photosynthetic activity (Osakabe et al., 2014).

When soil water availability is unlimited, trees of *Ficus carica* species show well-hydrated root systems that facilitate nutrient uptake, supporting an excellent photosynthetic performance (Fernández-Pavía et al., 2020; Gordon et al., 2022). Thus, fig trees have increased photosynthetic rates due to enhanced stomatal conductance (gs), allowing for higher carbon dioxide (CO_2) uptake and subsequent assimilation under such a soil moisture condition (Mardinata et al., 2021; Xu et al., 2016).

On the other hand, under conditions of limited water availability, fig trees exhibit specific adaptive strategies, such as stomatal regulation and changes in leaf morphology (Ammar et al., 2022; Zafer Can & Aksoy, 2007). These mechanisms help to reduce water loss through transpiration and improve water-use efficiency. As a result, fig trees can maintain relatively high photosynthetic rates even at low soil moisture levels (Ammar et al., 2022); therefore, it appears this species exhibits resilience to drought stress.

In summary, *Ficus carica* species appear to possess adaptive strategies to maintain photosynthetic activity under water-unlimited and water-limited availability conditions. Nonetheless, further research is needed to unravel the intricated molecular, biochemical, and physiological mechanisms underlying these responses and to explore the specific gene networks involved in the fig trees´ ability to thrive under different soil water contents (Lobo et al., 2022). This knowledge can contribute to improved agricultural practices and better management of water resources in fig cultivation, mainly if proper genotypes are identified for each horticultural region. In addition, this crop may be an excellent alternative to drought-prone areas or with low water availability worldwide.

In this context, such knowledge can contribute to developing fig tree drought-resistant varieties in the face of changing climate conditions. So, we hypothesize that *Ficus carica* L. plants will present a crucial negative correlation between proline content and at least a physiological variable. As a consequence, the aims of this work were i) to identify a possible adaptive response to mitigate the adverse effects of drought and enhance the ability of plants of six *Ficus carica* L. genotypes under study to survive once they were subjected to extreme drought and ii) to identify outstanding fig tree accessions under such a situation.

3.3 MATERIAL AND METHODS

3.3.1 Study site and Plant material

The experiment was conducted in the experimental area of the Unidad Regional Universitaria de Zonas Áridas of the Universidad Autónoma Chapingo (Bermejillo, Durango, México), located at 103°36’07” N and 25°53´43” W. Its altitude is 1,119 m above sea level. The average annual rainfall is 258 mm, and the mean annual evaporation is 2000 mm. The regional climate is desert, with rain during the summer and winter (Medina et al., 2005).

The plants were collected in a region known as the Comarca Lagunera, which belongs to Durango and Coahuila states, México. The fig materials were obtained

from backyards or wild sites. The “mother plants” were layering to get vegetative reproduction. The obtained 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 EC of 3.61 dS m^{-1}). The used soil resented a field capacity (FC) of 33 % and a Permanent Wilting Point (PWP) of 20 % (Textual class: clay loam). The fig accessions were adapted to pot conditions for three months; pots were irrigated according to the prescribed soil water depletion (around 0.8 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 field of 20-24 ± 1°C, and the daily mean relative humidity was measured in the range of 24-54 ± 3 %. The air temperature and relative humidity were monitored during the experimental period using a high-accuracy moisture and temperature sensor (ORIA OUS-WA62 ®).

3.3.2 Experimental Design

The experiment was arranged as a randomized block design with divided plot layouts with three replications. The investigation was conducted under semi-controlled conditions using 6-month-old local fig accessions (Arista, Ceballos, Fortuna, Guadalupe Victoria, and San Antonio) and one variety (Black Mission). To group acquisitions and the variety, from now on, we call them “genotypes” (Table 1). The plants were divided into two groups; the first was at field capacity (FC) or water holding capacity (WHC), and the second was on water deficit (WD) conditions. The soil water content was recorded as Soil Water Potential (HSP).

Table 2. Identification and geographical location of F. carica accessions

Identification	Geographical location	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

**** Not available**

The WD condition was generated in the soil pots by preventing irrigation. The experimental process started with all the plants at FC. The experiment was conducted during June and July 2022, corresponding to the vegetative plant stage. The pots were weighed all days at the same hour (10:00 h), and the FC pots were rehydrated as needed. The WD plants were subjected to a dehydrating period due to evaporation. During this time, pots were evaluated 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 measured at day 7 in the range of -2.1 to -3.6 MPa with a mean value of -2.7 MPa when the PWP was -1.5 MPa. Data were recorded daily during the experimental time.

Once 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 (i.e., 1, 4, and 8 days after irrigation was applied). 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.

3.3.3 Relative water content (RWC)

Leaves from each treatment were collected in wet chambers to prevent water loss during the transport time to the laboratory. The RWC was determined by considering fresh weight (FW), dry weight (DW), and turgent weight (TW). Foliar sections of 2 cm^2 were measured (FW) and submerged in water at four °C for 12 h without light. Afterward, the weight was recorded (TW). The turgent leaf sections were dried at 80°C for 24 h, and the DW was determined (U.S. SOLID, model USS-DSS) (Barrs & Weatherley, 1962). In the end, the RWC was calculated using the following formula:

Eq. 1 $$RWC = \frac{(FW-DW)}{(TW-DW)} x\ 100$$

Where *RWC*: Relative Water Content; *FW*: Fresh Weight (g), *DW*: Dry Weight (g); *TW*: Turgent Weight (g)

3.3.4 Gas exchange measurements

Mature leaves were used to measure Photosynthetic rate (Pn, µmol CO_2 $m^{-2}s^{-1}$), Stomatal Conductance (gs, mmol H_2O $m^{-2}s^{-1}$), intercellular CO_2 content (Ci, µmol CO_2 mol air^{-1}), and Transpiration rate (E, mol H_2O m^{-2} s^{-1}). All the determinations were performed on sunny and clear days (10:00 to 11:00 h) using a portable infrared gas exchange analyzer (LI-COR 6400, Lincoln, NE, USA). The operative conditions were at 400 ppm CO_2 in the camera and active photosynthetic radiation (PAR) of 750 µmol $m^{-2}s^{-1}$ at 25 °C cuvette temperature. The leaf samples were placed in the cuvette for about one minute for data collection before physiological parameters (Pn, E, and gs) were stabilized, as indicated by a low coefficient of variation. Three mature leaves from each replicant, exposed to sunlight, were measured from each accession and variety during the evaluation.

3.3.5 Determination of Water-Use Efficiency (WUE) and Intrinsic Water-Use Efficiency (int-WUE)

WUE describes the ratio of Pn to water lost by the plant through transpiration (E) (Eq.2). Photosynthetic water-use efficiency (also known as intrinsic or instantaneous water-use efficiency) was defined as the ratio of Pn to stomatal conductance (gs) (Eq. 3) (Tambussi et al., 2007):

$$\text{Eq. 2} \quad WUE = \frac{Pn}{E} \qquad\qquad Eq. 3 \quad int\,WUE = \frac{Pn}{gs}$$

3.3.6 Solutes content

Soluble sugar content (SSC) was determined by the Dubois *et al.* method (1956). Then, 100 mg of nitrogen frozen leave tissue was diluted using distilled water (5 ml). This extract was mixed with phenol and concentrated H_2SO_4. The mix was tested using a spectrophotometer at A 490nm (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) was determined according to Bates et al. (1973) with minor modifications. The nitrogen-frozen material (500 mg) was mixed with 5 ml of 3% salicylic acid ($C_7H_6O_6S$) solution. The mix was homogenized and centrifuged (6000 rpm for 30 min at 10°C). The reaction solution was mixed with 1 ml of glacial acetic acid and ninhydrin, the mixture was incubated at 100°C for 1 h, and the reaction was stopped in an ice bath before extraction with 3 ml of toluene. The organic phase was read using a spectrophotometer at A530 nm. The Pro concentration was determined using L-Proline (Sigma Aldrich) and expressed as µMol Proline g^{-1} FW.

3.3.7 Statistical Analysis

The Principal Component Analysis (PCA), Pearson correlation coefficients, and Regression analyses were performed using the statistical software ©2013 Minitab 16.2.4 Inc.

3.4 RESULTS

From the Principal Components Analysis (PCA), we considered that the two first principal components were sufficient to explain the variation of the original data (174 observations and 10 variables) (Figure 1). They accounted for 65% of the total variation; PC1 explained 37.9%, and PC2 explained 23.9%. Based on this analysis, we can predict the response of genotypes of *Ficus carica* under water deficit and rehydration process.

The structure of PC1 is composed of Pn, Ci, WUE, int-WUE, and SSC (Figure 1). The first group is positively intercorrelated (Pn, WUE, and int-WUE), and the remaining two (Ci and SSC). However, members of the first group are negatively correlated with members of the other. On the other hand, the structure of PC2 is clearly defined by E, HSP, gs, and RWC. Interestingly, they are positively correlated. Markedly, Pro exhibits similar factor loading's absolute values (0.369) in both principal components: negative in the case of the first principal component and positive in the other.

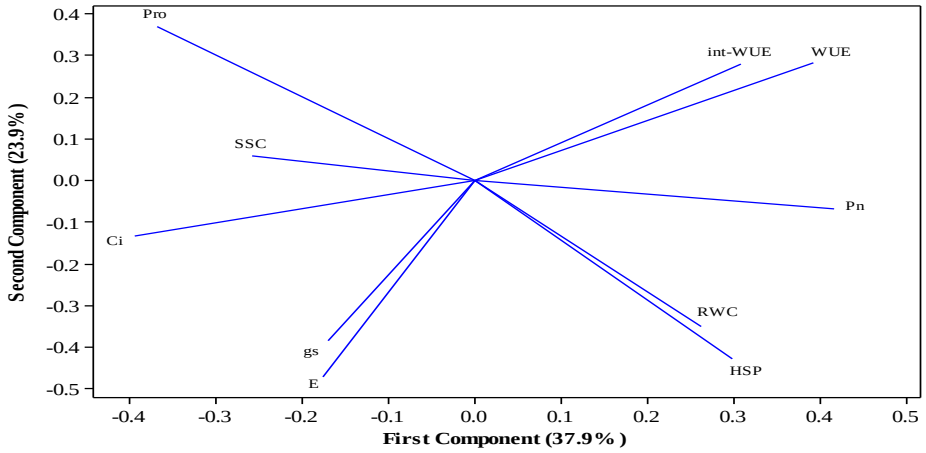

Figure 1. Distribution of the variables Hydric Soil Potential (HSP), Relative Water Content (RWC), Photosynthesis rate (Pn), Stomatal Conductance (gs), Intracellular CO_2 Content (Ci), Transpiration Rate (E), Water Use Efficiency (WUE), intracellular-Water Use Efficiency (int-WUE), Soluble Sugar Content (SSC), and Proline Concentration (Pro) in the orthogonal plane defined by the two first principal components extracted from 174 observations belonging to experimental pots of 6 genotypes of *Ficus carica* L.

In general, the structures of the two first principal components indicate the following meaningful bivariate relationships. WUE, int WUE, and Pn show substantial increases; SSC is augmented as Ci does. When WUE or, int-WUE, or Pn increased, SSC or Pro decreased. Moreover, RWC increased as the HSP did; RWC tended to be higher under unlimited water conditions; and Pro content decreased as each RWC and HSP increased.

Relationships between variables were obtained through Pearson correlations. A general analysis of the matrix of correlations allowed us to appreciate a strong relation between gas interchange variables (Ci, gs, and E) (Table 2). In addition, the correlation between the variables related to the water efficiency used (WUE and int-WUE) and photosynthetic variables (Pn, gs, Ci, and E) is notable. Furthermore, the strongest correlation was observed between HSP and Pro, which is a significant negative correlation.

Table 2. Matrix of Pearson Correlation Coefficients (r) between the variables Hydric Soil Potential (HSP), Relative Water Content (RWC), Net Photosynthesis (Pn), Stomatal Conductance (gs), Intracellular CO_2 Content (Ci), Transpiration Rate (E), Water Use Efficiency (WUE), intracellular-Water Use Efficiency (int-WUE), Soluble Sugar Content (SSC), and Proline Concentration (Pro) from 174 observations belonging to experimental pots of 6 genotypes of *Ficus carica* L.

		RWC	Pn	gs	Ci	E	SSC	Pro	WUE	int-WUE	HPS
RWC	r	1									
	p-value										
Pn	r	0.394	1								
	p-value	0.001									
gs	r	0.024	-0.064								
	p-value	0.754	0.403	1							
Ci	r	-0.272	**-0.555**	0.479	1						
	p-value	0.001	0.001	0.001							
E	r	0.140	-0.132	**0.517**	0.383	1					
	p-value	0.065	0.083	0.001	0.001						
SSC	r	-0.080	-0.434	0.103	0.347	0.096	1				
	p-value	0.292	0.000	0.175	0.001	0.207					
Pro	r	**-0.589**	**-0.565**	-0.036	0.417	-0.118	0.388	1			
	p-value	0.001	0.001	0.640	0.001	0.119	0.001				
WUE	r	0.152	**0.629**	-0.265	**-0.527**	**-0.547**	-0.219	-0.267	1		
	p-value	0.046	0.001	0.001	0.001	0.001	0.004	0.001			
int-WUE	r	0.046	0.389	-0.303	-0.359	-0.312	-0.128	-0.165	**0.805**	1	
	p-value	0.549	0.001	0.001	0.001	0.001	0.093	0.029	0.001		
HPS	r	**0.597**	0.394	0.129	-0.286	0.193	-0.259	**-0.824**	0.134	0.092	1
	p-value	0.001	0.001	0.091	0.001	0.011	0.001	0.000	0.078	0.229	

When the first two PCs account for a high percentage of the total variation, as in the current study case, a plot of PC1 versus PC2 may allow for a cluster of observations that consider the factors involved and their levels. The distribution of the 174 observations in Figure 2 suggests at least three great groups. One cluster contains observations involving the six genotypes under WD condition on day 7 (located at the left-upper part of the graph denoted by red squares). The highest Pro contents mainly characterize this group if the distribution of variables in Figure 1 is considered. In addition, Pro content, Pn, Ci, and SSC were strongly correlated with RWC (r=-0.572, p=0.011), E (r=0.595, p=0.007), E (r=-0.566, p=0.012), and Ci (r=-0.456, p=0.049), respectively. The corresponding dependences were estimated through simple linear regressions analyses, and the results are the following:

Eq. 1 $Pro = 1108.2 - 11.315RWC;\ R^2 = 0.327; p = 0.001$

Eq. 2 $Pn = 0.6131 - 2.434E;\ R^2 = 0.327; p = 0.001$

Eq.3 $Ci = 6.2953 - 0.0139E;\ R^2 = 0.3198; p = 0.011$

Eq. 4 $Ci = 391.11 + 0.784SSC;\ R^2 = 0.207; p = 0.049$

The Pro response depended strongly on RWC (*p=0.001*). The Pn variable varied mainly from E (*p=0.001*). The Ci variable presented an important dependence on E and SSC, as observed in the previous equations.

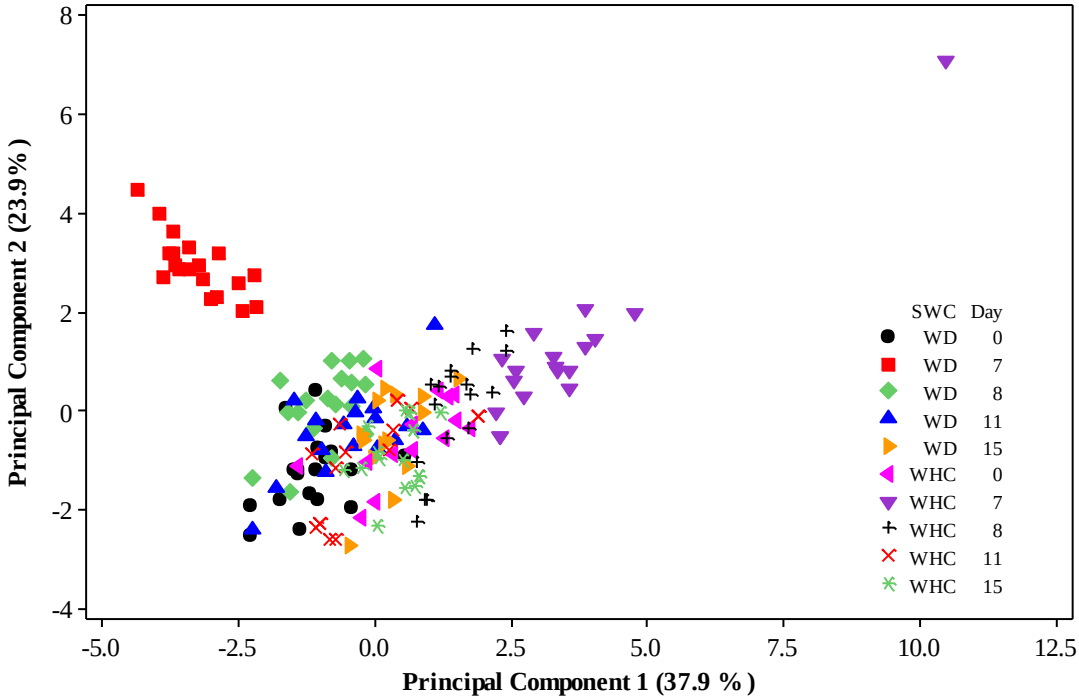

Figure 2. Distribution of 174 observations belonging to experimental pots of 6 genotypes of *Ficus carica* L. in the orthogonal plane defined by the two first principal components. Experimental plants grew for 15 days under two Soil Water Conditions; SWCs (WD refers to Water Deficit conditions due to water being applied once the experiment started (day 1). Still, water application was performed 7 days later, while the Water Holding Capacity (WHC) condition means maintaining such a level during the experimental period).

Another exciting group of observations is readily appreciated in the right-upper region of Figure 2 (purple triangles identify it). These observations are characterized mainly by the highest Pn, WUE, and int-WUE values. They all

correspond to the six genotypes under WHC condition on day 7. Notably, an extreme observation with the highest values of WUE, and int-WUE and low values of gs and E belong to the Guadalupe Victoria accession. In addition, this cluster of cases was characterized by strong correlations between gs and E (r=0.459, p=0.05) and gs and Ci (r=0.507, p=0.032). It implies significant dependences of E and Ci on gs as follows:

Eq. 4 $E = 0.6174 + 2.5627gs;\ R^2 = 0.210; p = 0.05$

Eq. 5 $gs = 170.39 + 300.29Ci;\ R^2 = 0.247; p = 0.032$

A third significant group of observations is located near the origin of the orthogonal plane defined by the two first principal components. This cluster is integrated by observations belonging to the remaining dates, i.e., 1, 8, 11, and 15 days. It means that, in the present group, observations of all six genotypes are involved; interestingly, the observations belonging to the WD condition at 8 and 11 are located in the left-central region. Markedly, observations for the WD condition at 8 and 11 days showed important Pro and SS contents. In addition, the observations linked with the WHC condition are distributed on the right-central region of the graph.

3.5 DISCUSSION

Our working hypothesis proposed that *Ficus carica* plants will present an essential negative correlation between proline content and at least a physiological variable. According to our research outcomes, Pro showed a fascinating negative correlation with RWC and Pn. Therefore, our working scientific hypothesis was confirmed.

It is widely known that many plant species have shown changes in proline concentration. This amino acid serves as an amino acid osmoprotectant in response to varying soil water availability (Szepesi & Sz, 2018). In our study case, *Ficus carica* plants of 6 genotypes under hydric stress showed a high increase in Pro content on day 7 (Figure 2). Thus, such an increase of Pro as a compatible

solute could help the plants to maintain cell turgor and osmotic balance during water stress (Ashraf & Foolad, 2007); it could play an essential role in protecting cellular structures from oxidative damage (Navasona Krishnan et al., 2009). In other words, the accumulation of Pro in *Ficus carica* plants could be considered an adaptive response to mitigate the adverse effects of drought and enhance the ability of plants of the six genotypes under study to survive under WD conditions. The evidence of significant pro dependence on RWC strongly reinforces this idea.

A separate analysis suggested that the six genotypes showed no significant differences in Pro contents under WD conditions on day 7 after the experiment started (data not shown). However, Guadalupe Victoria (368 μ mol Proline g^{-1} FW) and Ceballos (318 μ mol Proline g^{-1} FW) were the accessions with the highest Pro contents, and coincidently, both genetic materials showed the lowest RWC (64% and 60%, respectively). Markedly, the Ceballos accession was subjected to the strongest Hydric Soil Potential (-3.6 MPa), i.e., extreme drought.

The cases characterized by the highest values of WUE, int-WUE, and Pn located at the right-upper part of the graph belong to the WHC condition on day 7 after the experiment started. Then, these fig trees were the individuals with the highest photosynthetic water-use efficiency. In addition, these specimens were characterized by significant dependences of E and Ci on gs.

In general, as HSP absolute values SWT increase (drier soil conditions), *Ficus carica* may experience a decrease in the RWC within its tissues (Zafer Can & Aksoy, 2007). This decrease results from reduced water availability in the soil being absorbed by the plant roots; this response follows similar principles to other species under water stress conditions (Osmolovskaya et al., 2018). *Ficus carica* species regulates gs to minimize water loss by transpiration. The gs reduction also restricts the entry of carbon dioxide (CO_2) into the leaf, increasing intracellular CO_2 within the leaf tissues (Ammar et al., 2020b). It is important to note that *Ficus carica* responses may be influenced by various factors such as the storage of

plant development, the severity and duration of water stress, and the genotype characteristics (Gholami et al., 2012; Hayat et al., 2012).

These Ficus carica plants possibly effectively captured CO_2 from the atmosphere and converted it into organic compounds (Kareya et al., 2020). Then, their efficient carbon assimilation could have led to the rapid consumption of intercellular CO_2. In addition, they could have converted CO_2 into other compounds rather than SS (Liu et al., 2016).

Although the six genotypes showed no significant differences in Pn under WHC conditions on day 7 after the experiment started (data not shown), the link between high Pn, low Ci, and low SSC may suggest an efficient carbon assimilation and utilization system in *Ficus carica* plants. The Guadalupe Victoria accession notably showed the highest Pn (15.48 µmol CO_2 m^{-2} s^{-1}). Such a result indicates that this genetic material might possess an exciting ability to capture and use carbon effectively for growth and metabolic processes rather than storing it as sugars (Dietze et al., 2014; Geigenberger et al., 2005). In other words, the leaves of trees of the Guadalupe Victoria accession might be operating with a higher water use efficiency without a penalty in terms of carbon gain, as Ball & Passioura (1995) pointed out.

It is a complex interpretation of cases located around the origin of the orthogonal plane defined by the two first principal components. Nonetheless, appreciated subgroups allowed us to perform some exciting ideas. For instance, observations of the WD condition at 8 and 11 days showed important Pro and SS contents, possibly because they exerted efforts to express resilience to drought stress. This idea is strongly reinforced by the highest yield of proline on day 7, which is appreciated in Figures 1 and 2. Another idea that could support the fig trees' effort to express resilience to drought stress involves the cases corresponding to WD and WHC conditions on the 15th day because they are clustered nearest the plane's origin (all of them are overlapped).

3.6 CONCLUSIONS

Under conditions of limited soil water content (WD on day 7), fig trees exhibit a controlled reduction in stomatal conductance (gs), transpiration (E), and augmentation in proline (Pro) and soluble sugar (SSC) contents. In addition, a possible adaptive response to mitigate the adverse effects of drought and enhance the ability of plants of the six genotypes under study to survive under WD conditions was evidenced through a significant negative correlation between Pro and relative water content (RWC). In this context, Guadalupe Victoria and Ceballos are outstanding accessions. They were the accessions with the highest Pro contents and the lowest RWC.

The links between high Pn, low Ci, and low SSC in fig trees growing underwater holding capacity (WHC) suggest an efficient carbon assimilation and utilization system. In this context, the Guadalupe Victoria accession shows the highest Pn. In other words, this genetic material can capture and use carbon effectively for growth and metabolic processes rather than storing it as sugars. The relevance of physiological studies for effectively selecting outstanding genotypes of perennial species for tolerance to limited water conditions. In addition, it is necessary to evaluate the yield and fruit quality of superior genotypes.

Author contributions

Conceptualization: M.R.J.-S., R.T.-C., R.D.V.-C., I.S.C., J.G.A.-A., L.A.G.-E. Methodology: M.R.J.-S., R.T.-C., L.A.G.-E. Experiment and Data curation: M.R.J.-S., R.T.-C., R.D.V-.C., L.A.G.-E. Writing - original draft: M.R.J.-S., R.T.-C., R.DV.-C. Writing-review & editing: M.R.J.-S., R.T.-C., R.D.V.-C., I.S.-C., J.G.A.-A., L.A.G.-E. All co-authors reviewed the final version and approved the manuscript before submission.

Financing

Project administration: M.R.J.-S., R.T.-C. Funding acquisition: M.R.J.-S., R.T.-C.

This research was funded by Universidad Autónoma Chapingo (UACh), Unidad Regional Universitaria de Zonas Áridas (URUZA), and Consejo Nacional de

Humanidades, Ciencias y Tecnologías (CONAHCYT), CVU: 383083. Support from the Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias, Centro Nacional Disciplinario Relación Agua-Suelo-Atmosfera (INIFAP-CENID RASPA) is also acknowledged.

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CHAPTER IV.
Adaptative mechanisms and physiological processes in *Ficus carica* genotypes under limited and unlimited water conditions.

4.1 ABSTRACT

Ficus carica L. (fig) is a globally significant fruit crop with increasing production trends, particularly in countries with low water availability. Fig cultivation contributes to the agricultural economy and supports arid and semi-arid regions where few other crops thrive. Understanding the fig tree's responses to water deficit is essential for adaptation to sustainable production and climate change. This study investigated the water deficit tolerance of native *Ficus carica* accessions compared to the Black Mission cultivar. Physiological and biochemical markers, including relative water content (RWC), photosynthesis (P_N), stomatal conductance (gs), Intercellular CO_2 (Ci), Transpiration (E), Proline (Pro), and Soluble Sugar Content (SSC), were analyzed. 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 Guadalupe Victoria accession demonstrated significant water deficit resilience by maintaining higher P_N values. Additionally, the study highlighted the role of osmotic adjustments in maintaining water balance and cellular function during water deficit and recovery periods. These findings provide valuable insights for selecting fig tree genotypes with enhanced drought tolerance for sustainable fig production in water-limited environments.

Key Words: Photosynthesis, Proline, Osmotic Response, Native Accessions

4.2 INTRODUCTION

Fig (*Ficus carica* L.) production statistics indicate the significant global importance of this “fruit” (borne from a complex inflorescence called a syconium, which encloses hundreds of flowers) (Crisosto et al., 2011). According to available data in recent years, fig production has been steadily increasing for 2021; the gross output was about USD 1,057,349,000 (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.

Fig tree exhibits intriguing environmental interactions that make it an ecologically significant species (Gholami et al., 2012). This tree is highly adaptable and capable of growing in diverse habitats. Its 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 specie 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 (Akınci & 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 essential to highlight the study of the fig for arid and semi-arid zones by selecting genetic materials that have developed tolerance to water deficiency. 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* accessions will present differences in their ability to tolerate water deficit in contrast to the Black Mission cultivar. 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 (gs), intercellular CO_2 (Ci), 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, breeding programs need to know the fig materials' responses under limited and unlimited water availability in deficit and recovery conditions.

4.3 MATERIAL AND METHODS

4.3.1 Study site

The experiment was developed 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 yearly evaporation) (Medina et al., 2005).

4.3.2 Experimental conditions

Plants were collected in the Comarca Lagunera, corresponding to a region between the Durango and Coahuila states in México. The fig materials were obtained from backyards or wild locations by layers. The obtained 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 adapted 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 field of 20-24 ± 1°C, and the daily mean relative humidity was measured in the range of 24-54 ± 3 %. Figure 1 shows the air temperature and relative humidity monitored during the experimental period using a high-accuracy moisture and temperature sensor (ORIA OUS-WA62 ®).

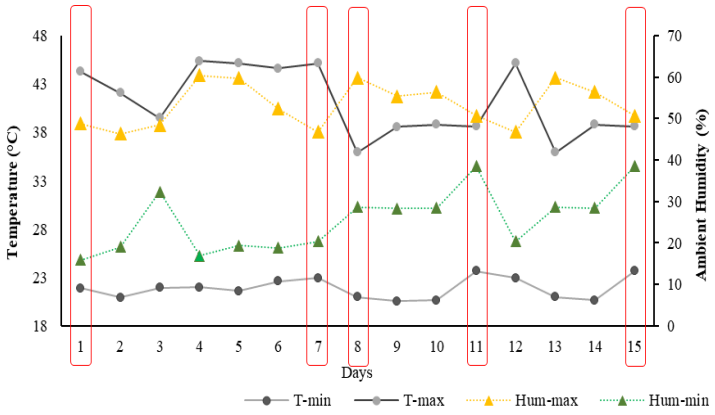


Figure 1. Daily mean minimum and maximum air temperature (T-Min and T-Max, °C) and mean minimum and maximum ambient humidity (Hum-min and Hum-Max, %) at the experimental site. The red rectangles represent the evaluation days of the experimental variables.

4.3.3 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. The investigation

was developed using 6-month-old local fig accessions (Arista, Ceballos, Fortuna, Guadalupe Victoria, and San Antonio) and one cultivar (Black Mission). To group accessions and the cultivar, we call them “genotypes” (Table 1). The genotypes were allocated into two groups for soil water availability, the water deficit (WD), and the field capacity (FC) treatments. The soil water content was recorded as soil water potential (SWP).

Table 1. Identification and geographical location of *Ficus carica* L. accession.

Identification	**Geographical location**	**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

**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, from -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.

4.3.4 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 relative water content (RWC) was determined by considering fresh weight (FW), dry weight (DW), and turgent weight (TW) by the (FW-DW)/(TW-DW) x 100. Foliar sections of 2 cm^2 were measured (fresh weight) and submerged in water at 4°C for 12 h without light. Passed this time, the weight was determined and is considered the turgent weight. 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).

4.3.5 Gas exchange measurements

Leaf samples were used for measuring net photosynthetic assimilation rate (P_N, μmol CO_2 $m^{-2}s^{-1}$), stomatal conductance (gs, mol H_2O m^{-2} s^{-1}), intercellular CO_2 content (Ci, μmol CO_2 mol air^{-1}), and transpiration rate (E, mol H_2O m^{-2} 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 6400, LI-COR Inc., Lincoln, NE, USA). The operative conditions were at 400 ppm CO_2 in the camera and photosynthetically active radiation (PAR) of 750 μmol m^{-2} 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 variety in the evaluation time.

4.3.6 Soluble sugar content (SSC)

Soluble sugar content (SSC) was determined using the Dubois et al. (1956) method. 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 490nm (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.

4.3.7 Proline

Proline concentration (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% sulfosalicylic acid solution. The mix was homogenized and centrifuged (6000 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 µMol Proline g^{-1} FW.

4.3.8 Statistical Analysis

Factorial variance analysis was performed. The mean comparison values were made by the T-test of independent samples, one-way ANOVA, and Tukey´s multiple range test at the $p \leq 0.05$ level. The software SPSS 18.0 Version (Inc., Chicago IL) and ©2013 Minitab 16.2.4 Inc carried out those procedures.

4.4 RESULTS

The experimental design yielded twelve treatments by considering five accessions, one cultivar of fig trees (*Ficus carica* L.), and two soil water contents to understand young fig plants' responses to drought tolerance. Then, responses were measured using RWC, PN, 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 corresponds to the Ceballos accession (Figure 2). In other words, the Ceballos accession was submitted to the lowest SWP during the experiment.

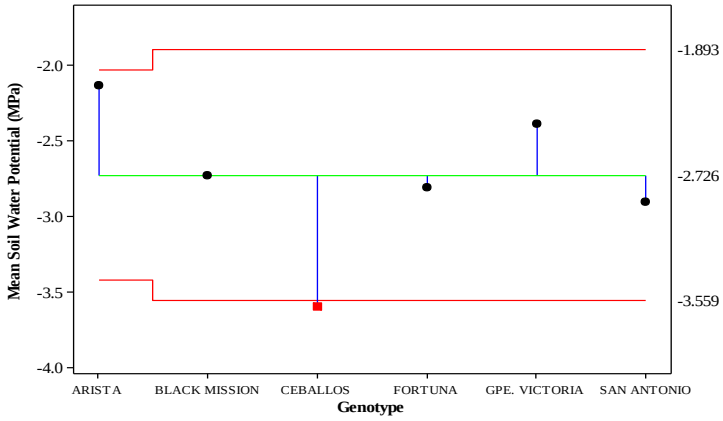


Figure 2. Comparison of means of Soil Water Potential (SWP, MPa) belonging to genotypes at 7 DAIS (Days After Irrigation Suspension) under WD (Water deficit) condition. The green line indicates the mean value, the red line indicates the decision limits, and the blue lines indicate the distance related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

The factorial analysis presented differences during the irrigation suspension and water deficit periods. The effects of individual factors such as genotype (G), soil water content (SWC), and time (T) presented different responses at Days After Irrigation Suspension (DAIS) and Days at Field Capacity Moisture (DFCM). 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 G x SWC, G x T, SWC x T, and G x SWC x T presented statistical differences in different evaluated variables (Table 2). By understanding and interpreting those interactions, we could learn more about fig genotypes' responses under the study conditions.

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, gs, Ci, E, Pro, and SSC evaluations in 6 fig genotypes during DAIS (Days after Irrigation Suspension) and DFCM (Days at Field Capacity Moisture).

	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
G x SWC	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
G x T	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
SWC x T	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
GxSWCxT	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

4.4.1 Interaction G x SWC

The interaction between G x SWC presented significant effects in all the evaluations, except in E in the DFCM case. In this interaction during the DAIS period in the RWC evaluation, we observed that the Arista accession exhibited statistical differences between WD and FC conditions (Figure 3a). 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 (Figure 3a). Those changes showed the genotypes' recovery capacity.

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 Ceballos accession. The highest P_N in the DAIS period was also observed in the Guadalupe Victoria accession in the FC condition (Figure 3b). In the DFCM situation, the P_N differences were significant for Arista and Ceballos accessions.

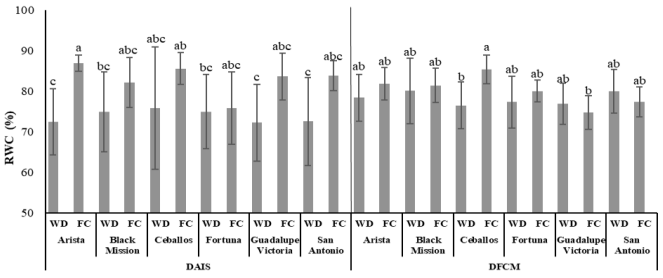
In the case of gs evaluation, the interaction G x SWC showed statistical differences in the DFCM case but not in DAIS evaluations (Figure 3c). Notably, the Black Mission variety and San Antonio accession presented statistical variations. Most genotypes gave higher

gs in WD condition during the DFCM case, except in Arista and San Antonio accessions. Moreover, the Guadalupe Victoria accession showed the highest gs under the WD condition and the lowest under the FC condition; the highest gs belong to Guadalupe Victoria (WD) under DFCM (Figure 3c).

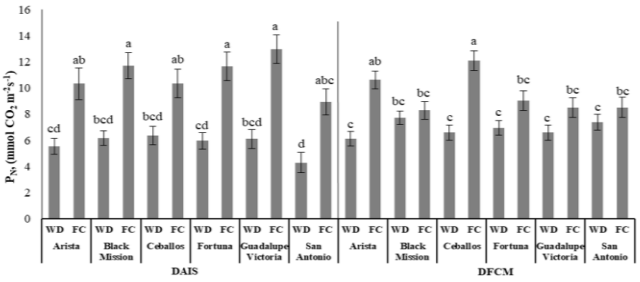
Notably, significant differences in Ci evaluation belong to the Black Mission variety and Guadalupe Victoria accession in the DAIS period (Figure 3d). Also, considering DFCM, Ci was not different among genotypes under the two SWCs. At the same time, Ci was markedly low in the Fortune accession at FC.

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 (Figure 3e). 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.

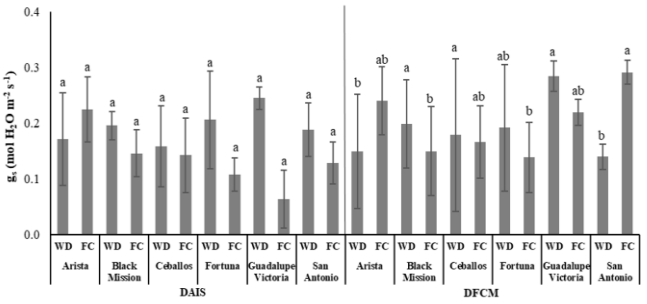
Markedly, the highest increase of the Pro in WD condition was observed in the accession Guadalupe Victoria accession (368.1 µMol Proline g $^{-1}$FW) during the DAIS period (Figure 3f). In addition, the Pro content was higher in most of the genotypes in WD evaluations at the DFCM case, except for the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



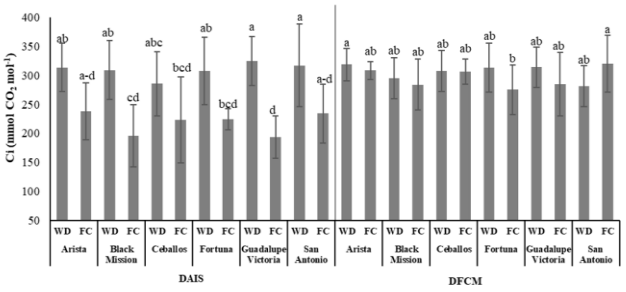
3a.



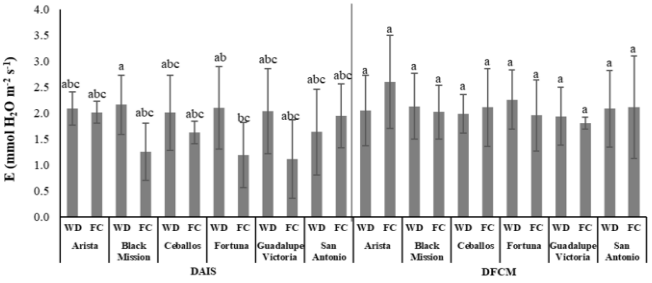
3b.


g$_s$ (mol H$_2$O m^{-2} s^{-1})
0.4
0.3
0.2
0.1
0.0
WD FC
Arista
Black Mission
Ceballos
Fortuna
Guadalupe Victoria
San Antonio
DAIS
DFCM

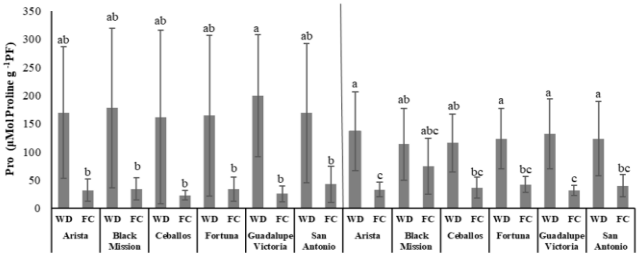
3c.


Ci (mmol CO$_2$ mol^{-1})
400
350
300
250
200
150
100
50
WD FC
Arista
Black Mission
Ceballos
Fortuna
Guadalupe Victoria
San Antonio
DAIS
DFCM

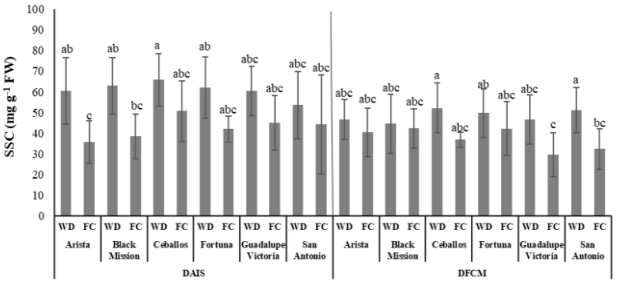
3d.


E (mmol H$_2$O m^{-2} s^{-1})
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
WD FC
Arista
Black Mission
Ceballos
Fortuna
Guadalupe Victoria
San Antonio
DAIS
DFCM

3e.


Pro (µMol Proline g^{-1}PF)
350
300
250
200
150
100
50
0
WD FC
Arista
Black Mission
Ceballos
Fortuna
Guadalupe Victoria
San Antonio

3f.


SSC (mg g^{-1} FW)
100
90
80
70
60
50
40
30
20
10
0
WD FC
Arista
Black Mission
Ceballos
Fortuna
Guadalupe Victoria
San Antonio
DAIS
DFCM

3g.

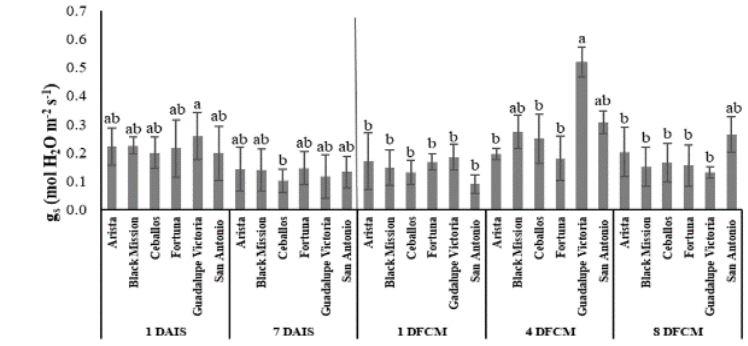
Figures 3a. Means of Relative Water Content (RWC), **3b.** Photosynthetic rate (P_N), **3c.** Stomatal Conductance (gs), **3d.** Intercellular CO_2 concentration (Ci), **3e.** Transpiration rate (E), **3f.** Proline content (Pro), and **3g.** Soluble Sugar Content (SSC) in the interaction between G x SWC at days after irrigation suspension (DAIS) and at Days at Field Capacity (DFCM) measured in *Ficus carica* mature leaves of five accession (Arista, Ceballos, Fortuna, Guadalupe Victoria, and San Antonio), and one variety (Black Mission) 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 $p \leq 0.05$.

Statistical difference in the SSC was found in the Arista accession between WD and FC conditions at DAIS (Figure 3g). A higher SSC was observed in WD conditions in all genotypes in both DAIS and DFCM cases. Also, the SSC showed statistical differences in San Antonio accession between SWC conditions in the DFCM case.

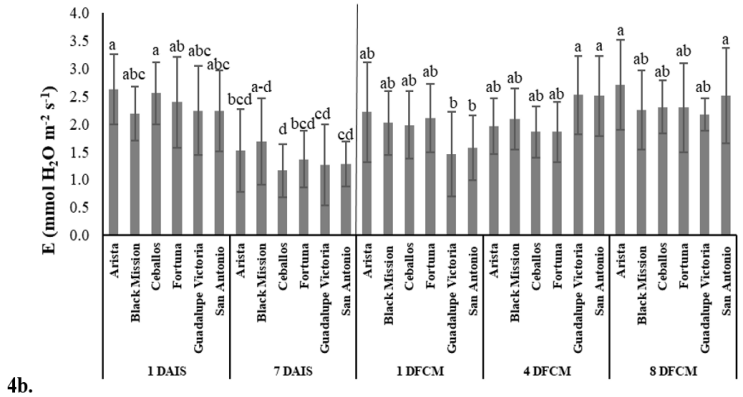
4.4.2 Interaction G x T

We observed statistical differences in the interaction G x T in gs and E variables analysis; however, those differences were not significant in the rest of the evaluations. All the evaluations decrease from 1 DAIS to 7 DAIS(Figure 4a). In the case of DFCM evaluations, the gs presented an increased-decreased performance during this recovery period. The gs in Guadalupe Victoria accession increased significantly at 4 DFCM (Figure 4a).

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



4a.



4b.

Figures 4a. and 4b. Means of stomatal conductance (gs) and Transpiration rate (E) in 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 five accession (Arista, Ceballos, Fortuna, Guadalupe Victoria, and San Antonio) and one variety (Black Mission). Bars with different letters indicate statistical differences by Tukey multiple range test at $p \leq 0.05$.

4.4.3 Interaction SWC x T

As a general response, the RWC decreased significantly in the plants under WD conditions (Figure 5a). Their RWC decreases 22% in plants at WD compared to 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 (Figure 5a). In the assessment of the DFCM period, the genotypes showed a quick recovery at 1 DFCM (Figure 5a). Also, fig plants growing in WD reached RWC levels similar to those growing in FC conditions at 8 DFCM.

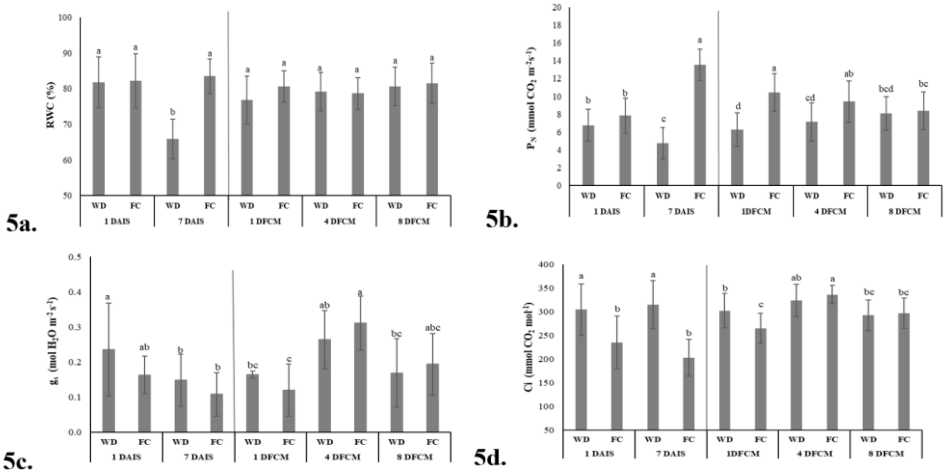
Interestingly, P_N was lower in the genotypes growing under the WD condition (Figure 5b). In general, P_N decreased 30.3 % from 1 to 7 DAIS. Notably, the P_N increased significantly in most genotypes (Fortune accession was the exception) under the FC condition from 1

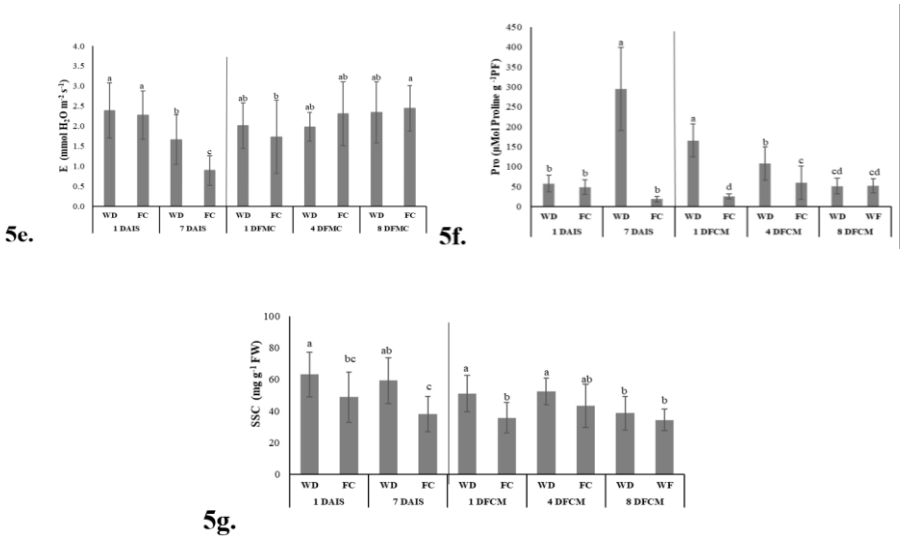
to 7 DAIS (Figure 5b). At 1 DAIS, WD and FC did not show a significant P_N difference; conversely, the P_N difference belonging to 7 DAIS is significant. In addition, the interaction between SWC x T suggested that P_N differed between the SWC at 1 and 4 but not at 8 DFCM.

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

By considering DAIS, the intercellular CO2 concentration (Ci) was generally lower in the FC than in the WD condition (Figure 5d). The Ci presented statistical differences between SWC at 1 and 7 DAIS. In the case of DFCM, a general pattern of increases from 1 to 4 DAIS and a decrease to 8 DFCM was observed in both SWC (Figure 5d). 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 (Figure 5e). 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.

The interaction between SWC x T and the initial condition did not present statistical differences (Figure 5f). The Pro showed that WD at 7 DAIS increased significantly compared to FC condition or the ones at 1 DAIS (Figure 5f). The statistical differences persisted at 1 and 4 DFCM in the recovery period. The Pro content was similar in both SWC at 8 DFCM. Notably, Soluble Sugar Content (SSC) showed statistical differences in the DAIS evaluations between SWC (Figure 5g). Lower SSC was observed in the FC condition in both evaluation periods (DAIS and DFCM).

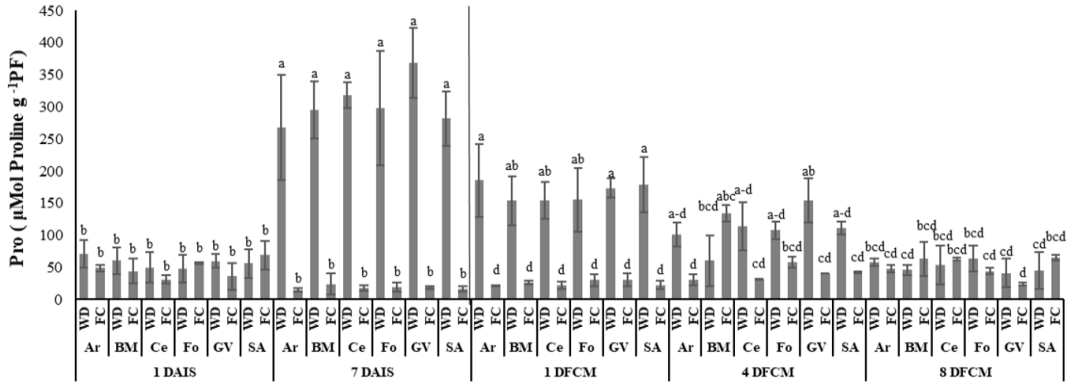




Figures 5a. Means of Relative Water Content (RWC), **5b.** Photosynthetic rate (P_N), **5c.** Stomatal Conductance (gs), **5d.** Intercellular CO_2 concentration (Ci), **5e.** Transpiration rate (E), **5f.** Proline content (Pro), and **5g.** Soluble Sugar Content (SSC) in the interaction between SWC 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 five accession (Arista, Ceballos, Fortuna, Guadalupe Victoria, and San Antonio), and one variety (Black Mission) 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 $p \leq 0.05$.

4.4.4 Interaction G x SWC x T

Interestingly, Proline (Pro) content increased by 247.5 µMol Proline g^{-1}FW on average in all genotypes in the WD condition; in contrast, the Pro decreased by 29.3 µMol Proline g^{-1}FW on average in all genotypes in the FC condition from 1 to 7 DAIS (Figure 6a). Moreover, 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, which showed that the Pro at WD was like the FC condition (Figure 6a).



6a.

Figures 6a. Means of Proline content (Pro) in the interaction between SWC x Gx T and T measured in *Ficus carica* mature leaves of five accession (Arista, Ar; Ceballos, Ce; Fortuna, Fo; Guadalupe Victoria, G, and San Antonio, SA) and one variety (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≤ 0.05.

4.5 DISCUSSION

Some plants' water stress adaptative mechanisms and processes are associated with root plasticity, water use efficiency, osmotic adjustment, drought avoidance strategies, and drought resistance traits (Gao et al., 2018; Valliyodan & Nguyen, 2006). In our study, *Ficus carica* materials could tolerate SWC below the permanent wilting point (PWP) due to various adaptive mechanisms and physiological processes (Figure 1). One of the main mechanisms of water stress avoidance strategies in fig is to shed leaves in a substantial water deficit (Ammar, Ben Aissa, et al., 2020); however, all the evaluated fig materials tolerated a mean SWP of -2.7 MPa without shed leaves (Figure 1). In the case of all considered fig materials, some plants reduced water loss by a low RWC and recovered their RWC when water became available again.

The RWC is commonly used to know the water status of a plant (Parkash & Singh, 2020). The RWC depends on many factors, such as plant species, growth stage, and environmental conditions; general levels 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 field 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 (Figure 5a), corresponding to mild water

stress. The Ceballos accession gave the lowest RWC in WD at 7 DAIS (60 %). Those RWC values represent a plant's ability to regulate water balance under a water deficit condition.

The Arista, Guadalupe Victoria, and San Antonio accessions presented the lowest RWC in the WD condition (Figures 3a and 5a). Those RWCs can be associated with cuticles, latex, trichomes, and water loss barriers. In response to low RWC, plants may produce a thicker cuticle or modulate the deposition of latex (Arya et al., 2017; Kunjet et al., 2013). Also, trichomes act as a protective layer, reducing water loss by creating a microclimate that decreases the water loss (Hernandez & Park, 2022). The fig leaf structure may enhance their leaves' tolerance for water loss.

Plants' 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 genotypes presented a high recovery capacity in the RWC, which is observed in Figure 3a. The quick RWC recovery and the increase of Proline content suggest that this amino acid response to WD is closely related to RWC. The speedy RWC recovery permits fig genotypes to maintain essential physiological processes (Ammar et al., 2022, 2023; Ammar et al., 2020).

Our results showed a decrease of 30 % in the P_N in plants under WD at 7 DAIS (Figure 5b), which may have some consequences for fig plants. P_N is closely linked to a plant's ability to withstand and recover from various stressors (Mareri et al., 2022). Besides, a decrease in photosynthesis weakens the plant's ability to tolerate and recover from environmental stress, such as drought or heat (Sherin et al., 2022; Tan et al., 2020). 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).

In contrast, the Ceballos accession did not exhibit a statistical difference in P_N between SWC at the DAIS period (Figure 3b), even though this accession was growing in soil with 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 recovery period in Ceballos accession since P_N did not completely recover in FC condition.

Physiological resilience can activate stress response pathways, and protective compounds, antioxidants, and osmolytes can be produced to mitigate the negative impacts of stressors (Sachdev et al., 2021; Saharan et al., 2022). 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 (Figures 3f and 5f).

Reducing gs 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 gs was lower in the FC condition than WD during the DAIS period (Figure 5b). 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, decreasing gs (Taiz & Zeiger, 2002). In addition, plants can operate at their maximum PN capacity under FC conditions without experiencing water stress. Our results showed a low gs and E but a high P_N under FC at the stress period (Figure 5b, 5c, and 5e).

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 gs and Ci evaluations in WD and FC conditions during the DFCM period (Figures 5c and 5d) 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 Ci 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

Ci did not present significant changes in WD condition at DAIS and DFCM periods (Figure 5d). Likewise, a limited gs during the WD condition. Even so, this response of fig genotypes can be related to the reduction of gs; the restricted diffusion of CO_2 into the leaf can result in a minimal decrease in Ci, 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 (Figure 5e). 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. Also, this can be associated with growing adventitious roots (Tan & Zwiazek, 2019).

The stomatal closure restricts the entry of external CO_2 into the leaf, resulting in a decrease in Ci (Engineer et al., 2016). Consistently, all evaluated genotypes presented lower Ci at FC than at WD during the DAIS evaluation (Figure 5d). 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, decreasing Ci (Mareri et al., 2022; Sherin et al., 2022). This performance is observed in fig genotypes in the DAIS period (Figures 3d and 3e).

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 (Figure 5e) can be correlated with the critical rise of Pro content (Figure 6a).

Proline (Pro) is an amino acid that is implicated in response to WD. The Pro in all fig genotypes increased 550 % from 1 to 7 DAIS under the 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 networks from denaturation or damage caused by dehydration and osmotic stress (Hayat et al., 2012; Meena et al., 2019).

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 (Hosseinifard et al., 2022). This could be the reason for a significant reduction of Pro in the DFCM related to the proline degradation when the stress condition was relieved (Figures 3f, 5f, and 6f). In addition, the Pro restores osmotic balance in the recovery phase by regulating water potential and preventing cellular dehydration (Figure 3f). Pro supports refolding and reactivating denatured proteins that may have been damaged during stress (Hosseinifard et al., 2022).

As part of the osmotic adjustment, SSC increased in the DAIS period (Figure 3g). These SSCs 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 (Figure 5g). 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).

4.6 CONCLUSIONS

Our study can confirm that young genetic fig materials can express their water deficit tolerance potential. Also, we demonstrated that wild *Ficus carica* accessions present differences in their ability to tolerate water deficit compared to the Black Mission cultivar. The adaptative mechanisms and physiological processes observed in *Ficus carica* genotypes that enable them to tolerate soil water content below PWP (-2.7MPa) and recovery to WD conditions were presented in this study. 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 % compared 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 regulation to control gas exchange and water loss, helping them maintain water equilibrium and adjust their physiological process.

Guadalupe Victoria and Fortuna accessions showed a significant proline accumulation in response to WD and acted as an osmolyte to attract water molecules and counteract 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. 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.

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CHAPTER V. GENERAL CONCLUSIONS

In conclusion, our study provides valuable insights into the adaptive responses of young fig trees under limited soil water conditions. The results exposed a reduction in gs, E, and the augmentation of Pro and SSC, particularly in the Guadalupe Victoria and Ceballos accessions, highlighting their potential for drought tolerance. The significant negative correlation between Pro and RWC further underscores the adaptive nature of these accessions to mitigate the water deficit's adverse effects. The results showed that acquisitions and the Black Mission cultivar response have similar aspects; some genotypes could distinguish specific products and responses to water deficit.

Notably, the Guadalupe Victoria accession exhibited exceptional carbon assimilation and utilization, suggesting its notable ability to capture and use carbon effectively for growth and metabolic processes even in low water availability. This emphasizes the importance of physiological studies in selecting remaining genotypes tolerating limited water conditions. The links between Pn, Ci, and SSC in fig trees under water-holding capacity conditions indicate an efficient carbon assimilation and utilization system.

Furthermore, our findings demonstrate that young genetic fig materials express their potential for water deficit tolerance, showcasing differences between native *Ficus carica* accessions and the Black Mission commercial variety. The adaptative mechanisms and physiological processes observed, such as stomatal regulation, Pro accumulation, and SSC adjustments, contribute to the ability of fig plants to tolerate soil water content below permanent wilting point and recover from water deficit conditions.

The plasticity observed in fig plants' responses to water deficit highlights their capacity to employ various mechanisms to optimize resource use and minimize

drought damage. The study also emphasizes the importance of evaluating the yield and fruit quality of outstanding accessions in addition to physiological studies for effective genotype selection. In conclusion, this research defines the relationship between resistance to water deficit and specific physiological and biochemical markers in fig materials, providing a foundation for further studies on improving drought tolerance in perennial species.