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Botanical Characteristics and Ecological Adaptability of Fig (*Ficus carica* L.)

Nana Zhou [1], Feng Qiao [2]
1 Hainan Tropical Ocean University, Sanya, 572022, Hainan, China
2 Zibo Academy of Agricultural Sciences, Zibo, 255000, Shandong, China
Corresponding author: qiaofeng8804@163.com

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Abstract The fig (*Ficus carica* L.), an ancient fruit tree, is highly valued for its historical, agricultural, and medicinal significance. This study systematically explores the growth characteristics, reproductive mechanisms, and adaptive strategies of fig trees under various environmental conditions. The results indicate that fig trees exhibit remarkable adaptability to drought and nutrient-poor soils, primarily through mechanisms such as leaf abscission, root structure optimization, and symbiotic relationships with mycorrhizal fungi, which enhance drought resistance. Additionally, the morphology of fig fruits is closely related to its unique pollination mechanism, forming a complex mutualistic relationship with fig wasps (*Blastophaga psenes*). The study also reveals that fig trees can promote the growth of surrounding vegetation and enhance biodiversity through root exudates and interactions with soil microorganisms. The multiple ecological adaptations of fig trees make them highly promising for sustainable agricultural practices in arid and semi-arid regions. Further research into the molecular mechanisms underlying the adaptability of fig trees to saline and drought stress will help optimize their cultivation and utilization.

Keywords Fig (*Ficus carica* L.); Ecological adaptability; Drought resistance mechanisms; Mutualistic pollination relationship; Biodiversity; Agroforestry application

1 Introduction

Ficus carica L., commonly known as the fig, is one of the earliest domesticated fruit trees and is highly valued for its historical, agricultural, and medicinal significance (Falistocco, 2020). It is a flowering plants belongs to the *Ficus* genus in the family of Moraceae, recognized for its distinctive fruit, which is botanically classified as a syconium, an enclosed inflorescence (Nair et al., 2021). Native to the Mediterranean region and southwestern Asia, *Ficus carica* has spread widely across the world due to its adaptability and economic value. For centuries, the fig has been cultivated not only for its edible fruit but also for its ecological role and its ability to adapt to various environmental conditions.

The fig (*Ficus carica* L.) tree is a deciduous species that can grow up to 10 meters tall (Hiwale and Hiwale, 2015). It is characterized by its smooth white bark, large palmate leaves, and a unique fruiting mechanism that involves a complex mutualistic relationship with fig wasps. The study found that the reproduction of figs relies on a symbiotic relationship with pollinating wasps (*Blastophaga psenes*). This biological mechanism is highly complex and an integral part of the fig ecosystem (Falistocco, 2020). The tree's adaptability to various climates and soil types has enabled it to thrive in a range of ecological zones, from semi-arid regions to temperate climates. Figs are valued not only for their delicious yet highly perishable fresh fruit but also for their various processed forms, such as dried figs, fig syrup, jams, jellies, spices, or preserved fig paste and fig pulp. Historically, figs have been esteemed for their nutritional and medicinal properties, making them an ancient and important source of food and health benefits (Barolo et al., 2014).

Understanding the botanical characteristics of the fig tree is crucial for optimizing its agricultural production, improving its resistance to environmental stress, and enhancing its ecological contributions. The fig tree's drought tolerance, adaptability to various soil conditions, and ability to grow in diverse climates make it an ideal subject for research, especially in the context of climate change and sustainable agriculture (Liu et al., 2012; Ammar et al., 2020). Figs are rich in nutrients, particularly high in iron and copper, making them a valuable food source (Hiwale and Hiwale, 2015). The historical and ongoing use of figs in traditional medicine highlights their potential as a new and diverse source of bioactive compounds with significant medicinal properties (Barolo et al., 2014). Studying its botanical features can offer insights into its growth patterns, reproductive biology, and cultivation potential in various environments. Furthermore, the fig tree plays a vital role in biodiversity conservation, acting as a keystone species in many ecosystems, providing food and habitat for numerous organisms. Investigating its ecological adaptability can help explore the potential for expanding fig cultivation in regions facing environmental challenges.

This study provides a comprehensive analysis of the botanical characteristics and ecological adaptability of fig (*Ficus carica* L.), covering its morphological structure, growth habits, and reproductive features, with a particular focus on its adaptation mechanisms in drought and nutrient-poor environments. The study integrates current findings on the morphology, physiology, and ecological functions of figs, highlighting their importance in agriculture, ecology, and economics. This study seeks to enhance fig production levels, explore new uses for this ancient and versatile plant, and deepen the understanding of its role in food security, health, and sustainable agriculture.

2 Morphological Characteristics of *Ficus carica*

2.1 Tree structure

Ficus carica L. is a deciduous tree or large shrub that typically grows to a height of 3 to 10 meters. Its trunk is usually short and stout, supporting a broad crown. The bark is smooth and grayish-brown, developing longitudinal fissures as the tree ages. The branches are thick, fleshy, and highly flexible, exuding a milky latex when damaged, which is characteristic of the Moraceae family. The branches can spread extensively, covering a large area. This structural adaptability helps maximize sunlight capture and improve photosynthetic efficiency (Khadivi et al., 2018; Nuzzo et al., 2022).

The leaves of *Ficus carica* L. exhibit significant morphological variability. They are generally large, lobed, and have a rough texture. Leaf length can range from 62.20 mm to 138.00 mm, while leaf width varies from 41.00 mm to 153.00 mm, indicating a high level of phenotypic diversity among different genotypes (Khadivi et al., 2018). This variability in leaf morphology aids in the tree's adaptability to different environmental conditions, enhancing its survival and growth in diverse habitats (Khadivi et al., 2018; Nuzzo et al., 2022).

2.2 Root system

The root system of *Ficus carica* is typically extensive and shallow, consisting of both a primary taproot and a well-developed network of lateral roots. This root architecture provides strong anchorage and efficient nutrient and water uptake from the soil (Hong et al., 2020; Ling et al., 2022). Studies have shown that in well-drained soils, the taproot of *Ficus carica* can penetrate deeply, providing stability to the tree and drawing water from deep underground sources, which is crucial for the survival of fig trees during drought seasons (Ammar et al., 2020). In contrast, the lateral roots spread extensively just below the soil surface, allowing the tree to efficiently utilize water from light rains and absorb nutrients from the upper soil layers.

Additionally, the root system of fig trees is highly adaptable to various soil types and moisture levels, including sandy, loamy, and even rocky soils. A study showed that fig trees exhibited good growth performance in sandy soils (BRIS soil) under the tropical climate of Malaysia (Azmi et al., 2020). Ma et al. (2020) found that in rocky soils with lower moisture levels, the radial expansion of fig tree roots was significantly greater than their depth distribution in deeper soils, ensuring effective resource absorption. This adaptability enables fig trees to thrive in a wide range of environmental conditions, from arid and semi-arid to humid subtropical regions (Hong et al., 2020; Ling et al., 2022).

2.3 Fruit morphology

The fruit of the *Ficus carica*, known as a syconium, is a specialized inflorescence structure that forms an enclosed, fleshy cavity. This enclosed structure protects the developing seeds, facilitating their successful maturation (Khadivi et al., 2018; Ling et al., 2022). At the apex, there is a small opening called the ostiole. Inside the fruit, numerous tiny flowers are housed, which develop into small drupelets upon pollination (Nair et al., 2021).

The shape of the fig fruit can vary from oblong to pear-shaped, with a typical length ranging from 2 to 10 cm. The skin is thin and smooth, displaying colors such as green, purple, or black, depending on the cultivar and ripeness (Khadivi and Mirheidari, 2022). As the fruit matures, the flesh softens and its sweetness increases due to the accumulation of sugars. The ripening process involves complex biochemical changes, including the breakdown of cell walls, the conversion of starches into simple sugars, and the production of aromatic compounds, which attract animals to disperse the fruit. This adaptation enhances the reproductive success of fig trees by encouraging seed dispersal through frugivorous animals (Khadivi et al., 2018; Ling et al., 2022).

2.4 Seed morphology and dispersal mechanisms

The seeds of *Ficus carica* are small and numerous, typically less than 2 mm in length, encased within the tiny drupelets inside the syconium. Each seed contains a small embryo and minimal endosperm, allowing for rapid germination after dispersal (Bougdaoua and Mtili, 2022). The germination rate of fig seeds is high due to their hard outer shell, which protects the embryo and ensures successful germination under suitable conditions. This characteristic is crucial for the reproduction and spread of the species (Khadivi et al., 2018; Ling et al., 2022).

Fig seeds dispersal primarily rely on animals such as birds, bats, and mammals, which consume the mature syconium and excrete the seeds at new locations, often far from the parent tree (Nakabayashi et al., 2019). Additionally, the seeds exhibit some degree of dormancy, enabling them to germinate when conditions become favorable.

3 Growth and Reproductive Traits of *Ficus carica*

3.1 Growth stages: from seedling to maturity

Ficus carica undergoes several distinct growth stages from seedling to maturity. During the seedling stage, the plant exhibits slow growth, primarily developing its primary root system and producing the first true leaves. This stage is crucial for establishing the root structure and overall plant health. The juvenile stage is characterized by rapid vegetative growth, with the formation of lateral branches and an increase in leaf area (Ma et al., 2020). During this period, the tree focuses on building a strong structural framework to support future fruit production.

As the *Ficus carica* plant matures, it enters the vegetative growth phase, during which it develops a more extensive root system and a robust stem structure. This stage is essential for establishing the plant's framework and preparing it for future reproductive activities. The final stage is the reproductive phase, where the fig tree begins to flower and produce fruit. This phase is marked by the development of syconia, a unique inflorescence structure in figs that contains internal flowers (Zolfaghari et al., 2019; Gabibova, 2020). The duration of each growth stage varies depending on environmental conditions and cultivar, with most *Ficus carica* trees reaching reproductive maturity within 3 to 5 years.

3.2 Vegetative propagation methods and advantages

Vegetative propagation is a widely used method for cultivating *Ficus carica* due to its efficiency and reliability. The most common techniques include cutting, grafting, and tissue culture. Cutting involves taking a segment of a mature fig tree and allowing it to root, which is the most commercially viable method due to its simplicity and high success rate (Boliani et al., 2019). Grafting, although not commonly used, can effectively combine the desirable traits of different varieties. Research has shown that grafting can produce plants with ideal characteristics in a relatively short time, which plays a significant role in the conservation of genetic resources and the establishment of high-quality orchards (Teja et al., 2023).

Tissue culture or micropropagation is a more advanced method that allows for the large-scale production of uniform and disease-free seedlings. This technique is particularly successful in producing high-quality seedlings and has a high survival rate during the acclimatization process (Abdolinejad et al., 2020; Hong et al., 2020; Ling et al., 2022). For example, Abdolinejad et al. (2020) employed various tissue culture techniques, including thin cell layer (TCL) technology and somatic embryogenesis. These techniques not only improved the regeneration efficiency of figs but also confirmed the genetic consistency of the regenerated plants through flow cytometry and ISSR markers.

3.3 Seed reproduction: pollination and fruit set

Ficus carica has a unique reproductive strategy that involves a highly specialized mutualistic relationship with the fig wasp *Blastophaga psenes*. This complex interaction is essential for the successful production of seeds and the formation of viable fruits. The fig wasp enters the syconium, a specialized inflorescence structure unique to figs, through a small opening called the ostiole. Inside the syconium, the wasp pollinates the short-styled female flowers while also laying eggs in some of them (Falistocco, 2020). The pollinated flowers develop into seeds, while those in which eggs are laid form galls that provide a habitat for the developing wasp larvae. This intricate pollination process is crucial for the reproductive success of *Ficus carica*, especially for wild-type figs, also known as caprifigs, as they require pollination for seed development (Figure 1) (Proffit et al., 2020). Although many edible fig varieties produce parthenocarpic fruits, which develop without pollination or fertilization, pollination can still enhance the quality and size of the fruit. Pollinated figs tend to be fuller and have a better flavor compared to non-pollinated ones.

The success of pollination is influenced by several factors, including the population of *Blastophaga psene*s, climatic conditions, and the synchronization between the flowering of fig trees and the life cycle of the wasps. Favorable environmental conditions, such as moderate temperatures and stable humidity levels, promote wasp activity and increase the likelihood of successful pollination. In contrast, extreme weather conditions can disrupt this delicate balance, leading to reduced seed set and fruit quality (Boliani et al., 2019; Zolfaghari et al., 2019).

4 Ecological Adaptability of *Ficus carica* in Arid and Barren Environments

4.1 Drought resistance mechanisms

Ficus carica exhibits several structural and physiological adaptations to withstand drought conditions. One key mechanism is leaf abscission, which reduces water loss by shedding leaves during periods of water stress. This was observed in Tunisian fig cultivars, where drought stress led to significant decreases in photosynthesis rate, stomatal conductance, and transpiration rate, along with increased leaf temperature and massive leaf abscission. Upon rehydration, these plants showed recovery in photosynthetic function and vegetative growth, indicating a robust drought avoidance strategy (Ammar et al., 2020).

Additionally, Abdolinejad and Shekafandeh (2022) found that tetraploid figs exhibited superior performance in various physiological and biochemical defense mechanisms compared to diploids. The experiment utilized different concentrations of polyethylene glycol (PEG) to simulate drought stress, revealing that tetraploid genotypes were able to maintain higher relative water content (RWC) and lower ion leakage under high-intensity (15%-25% PEG) stress, whereas diploid genotypes showed a significant decrease in survival rate at 15% PEG stress (Figure 2). These tetraploids maintained higher RWC and enhanced osmotic adjustment by increasing the levels of stress response hormones and osmolytes, such as proline and glycine betaine, thereby sustaining cell turgor and protecting cellular structures under drought conditions (Abdolinejad and Shekafandeh, 2022).

4.2 Water use efficiency

Ficus carica demonstrates efficient water use strategies to survive in low-water environments. Under drought stress, the fig tree adjusts its physiological processes to optimize water use efficiency (WUE). For instance, drought-stressed fig plants show reduced stomatal conductance and transpiration rates, which help in conserving water. Elevated CO_2 levels further enhance WUE by improving photosynthetic rates and reducing water loss through stomata. This dual response to water stress and elevated CO_2 helps *Ficus carica* maintain its physiological and metabolic activities, thereby ensuring survival in arid conditions (Mardinata et al., 2021). Moreover, the ability of tetraploid fig genotypes to maintain higher relative water content and lower ion leakage under water stress conditions also contributes to their improved water use efficiency (Abdolinejad and Shekafandeh, 2022).

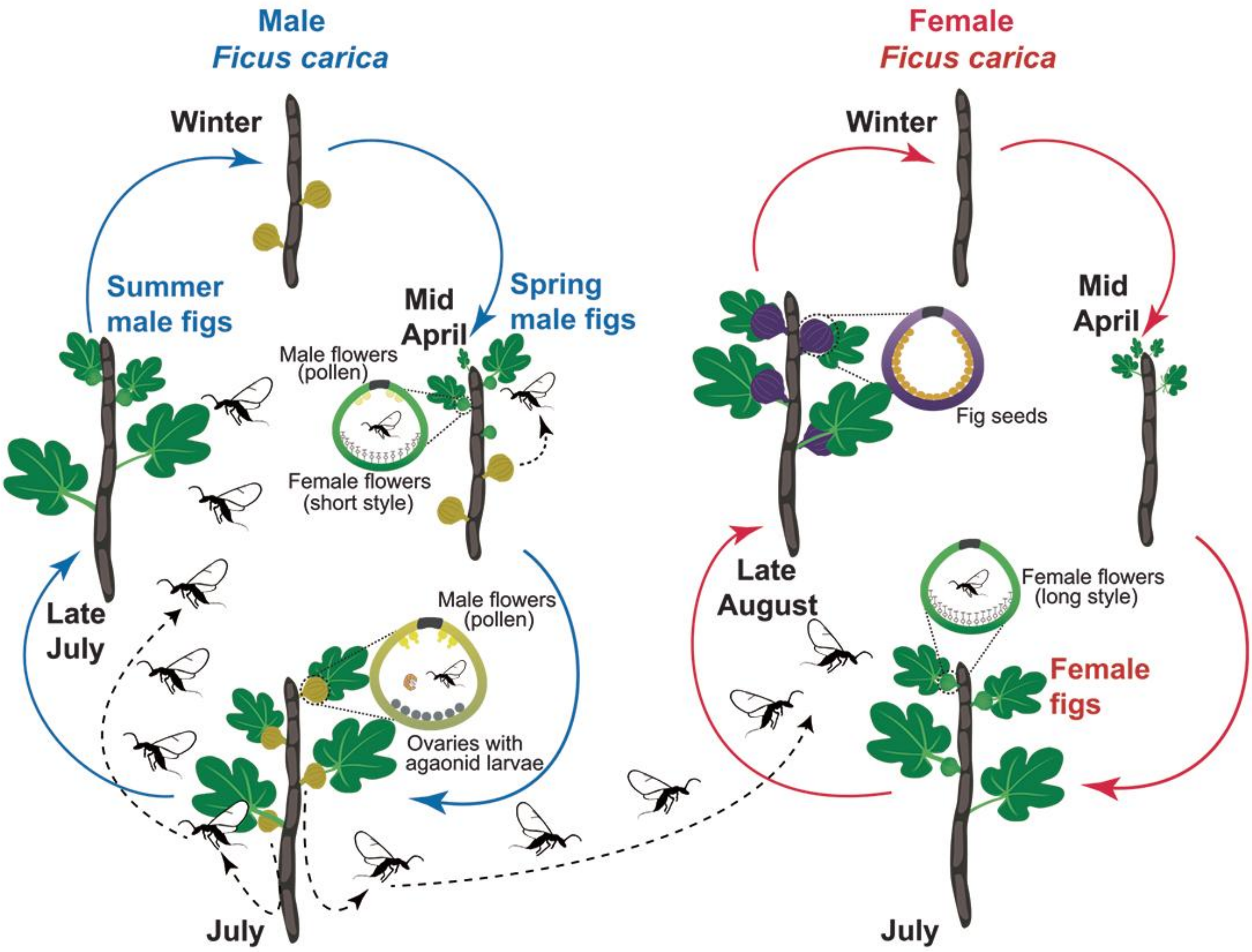

Figure 1 Life cycles of male and female tree of *Ficus carica* (respectively on the left and right side) and *Blastophaga psenes* in southern France (Adopted from Proffit et al., 2020)

Image caption: For each type of fig, receptive (green), ripe male (khaki) and ripe female (purple), a schematic representing wasps and flowers inside the fig is presented. Maturing male figs give rise to wasps (grey) and pollen (yellow), whereas female figs produce only seeds (orange) and contain no male flowers. Females and males of *B. psenes* are also represented in black and brown respectively. *B. psenes* has two generations per year coinciding with the flowering of male trees first in April (spring male figs) and then in July (summer male figs). In contrast, female trees flower only once a year, in July, and thus partially synchronously with summer male figs. The two distinct productions of male figs perform different functions. *B. psenes* larvae survive winter by staying in diapause within summer-produced male figs that will stay on the tree until the following spring. In spring, the overwintering wasps complete their development and male pollinators emerge in the fig cavity and copulate with female wasps before the latter emerge from their galls. After emerging from the gall within the fig cavity, female wasps exit their natal figs to enter the spring male figs, in which they oviposit. In summer, the new generation of adult female wasps, after having been fertilized, exit from their natal figs loaded with pollen grains. At this point in time, figs of male and female trees have reached receptivity, and female wasps face two scenarios: i) penetrate into figs of female trees, pollinate their flowers and then die without laying eggs due to a morphological incompatibility between the wasp ovipositor and the style of the female flowers, or ii) penetrate into figs of male trees and reproduce by laying eggs within the ovaries. Then, the cycle closes when the female offspring that entered male figs exit from them later in summer and find male figs in which they will oviposit, giving rise to the overwintering generation. This figure was prepared with the help of Jennifer McKey (Adopted from Proffit et al., 2020)

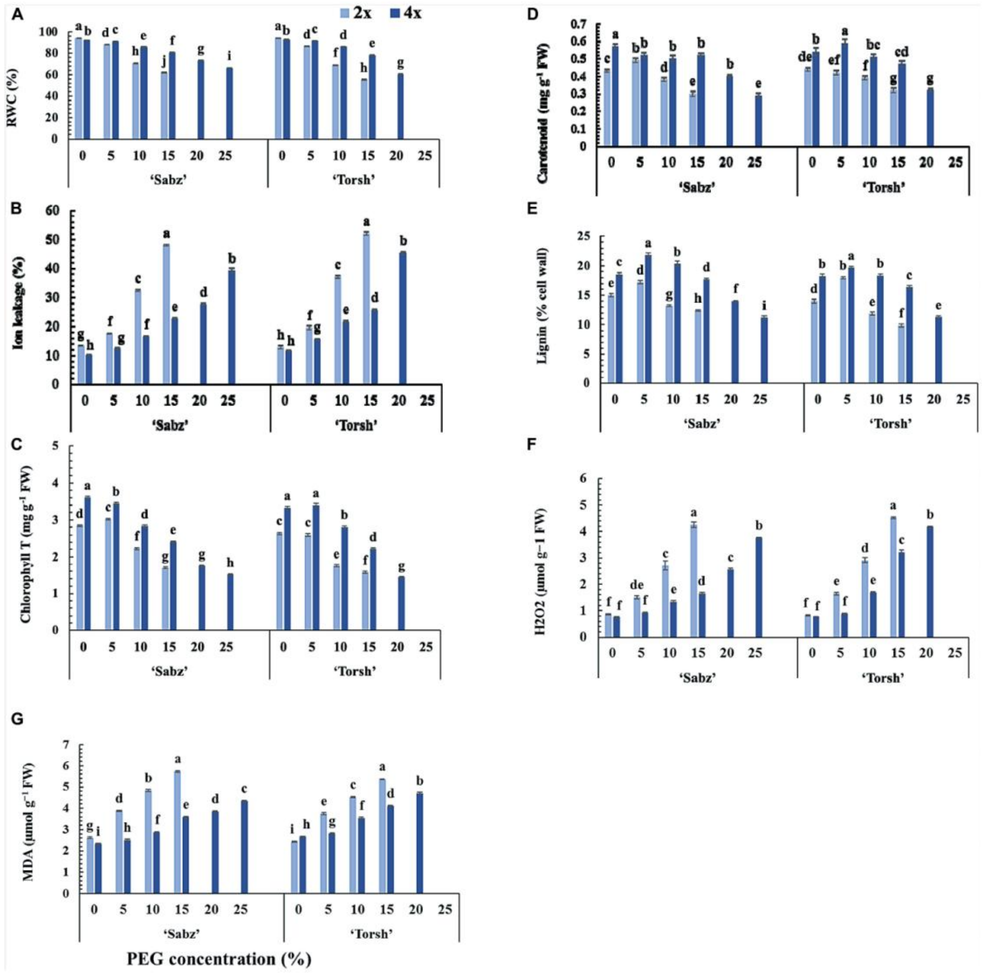

Figure 2 Physiological responses of diploid and tetraploid explants of 'Sabz' and 'Torsh' fig cultivars, 14 days after subjecting to different water stress treatments (Adopted from Abdolinejad and Shekafandeh, 2022)

Image caption: (A) Relative water content, (B) ion leakage, (C) total chlorophyll content, (D) total carotenoid content, (E) lignin, (F) hydrogen peroxide, and (G) malondialdehyde. Means represent the ploidy level and PEG treatment effects tested by two-way ANOVA. Each value represents the means ± SE. Different letters indicate significant differences at $P < 0.05$ using the LSD test. The results showed that with increasing PEG concentrations, tetraploid explants exhibited stronger tolerance across various indicators, such as higher RWC, lower ion leakage, and oxidative stress markers (H_2O_2 and MDA). These data suggest that tetraploid explants have greater antioxidant capacity and cell membrane stability, enabling them to better maintain physiological balance under high-intensity drought stress, confirming the significant physiological advantages of tetraploids under water stress conditions (Adapted from Abdolinejad and Shekafandeh, 2022)

4.3 Adaptation to nutrient-poor soils

In nutrient-poor soils, *Ficus carica* employs several strategies to enhance nutrient uptake and utilization. One significant adaptation is the symbiotic association with arbuscular mycorrhizal fungi (AMF). These fungi enhance the fig tree's ability to absorb water and essential nutrients, such as phosphorus, potassium, and calcium, from the soil. This symbiotic relationship not only improves nutrient acquisition but also boosts the plant's drought tolerance by enhancing its physiological and biochemical responses to water stress (Boutasknit et al., 2020; Madouh and Quoreshi, 2023). The increased levels of osmolytes and antioxidant enzymes in tetraploid fig genotypes under drought conditions also suggest a robust biochemical adaptation that helps in mitigating the adverse effects of nutrient deficiency and water stress (Abdolinejad and Shekafandeh, 2022).

4.4 Interaction with other species in arid environments

Ficus carica interacts with various species in arid environments, which can influence its adaptability and survival. The presence of AMF, for example, plays a crucial role in mediating drought tolerance and recovery in fig trees by regulating stomatal conductance, water relations, and nutrient uptake. These fungi help in maintaining higher water content and reducing oxidative damage during drought stress, thereby enhancing the overall resilience of the fig tree in arid conditions (Boutasknit et al., 2020; Madouh and Quoreshi, 2023).

Study has shown that the interaction with other plant species, such as the invasive *Opuntia ficus*-indica, which also exhibits high phenotypic plasticity and drought tolerance, can impact the ecological dynamics and resource availability in arid ecosystems (Tesfay et al., 2023). Understanding these interactions is essential for developing strategies to manage and conserve *Ficus carica* in its natural habitats.

5 Case Studies

5.1 Impact of climate change and pests on fig yield

Fig cultivation has a long history in the Mediterranean region, providing significant support for local economic and social development. However, in recent years, this region has experienced significant climate changes, particularly rising temperatures and decreasing precipitation, which pose threats to fig yield and health (Mellal et al., 2023). At the same time, the rapid spread of pests has exacerbated this issue, challenging the livelihoods of local farmers and agricultural sustainability.

Mellal et al. (2023) analyzed the combined effects of climate change and pests on fig yield in Bejaïa Province, Algeria. The results showed that, over the past decade, the annual average temperature in the region increased at a rate of 0.057 °C per year, while annual precipitation decreased by 27.1 mm per year. In terms of pests, 11 types were recorded, including the fungi *Diaporthe cinerascens* and *Fusarium* spp., which cause severe damage, as well as the bark beetle *Hypocryphalus scabricollis* (Gaaliche et al., 2018; Bolboli et al., 2024). These pests spread significantly during the study period, with the number of affected communes increasing from 1 in 2011 to 15 in 2022. Yield analysis showed that the yield per fig tree decreased by 25%, closely related to pest infestations and reduced precipitation. This trend reveals the severe impact of the synergistic effects of climate change and pests on fig cultivation (Figure 3). The study suggests adopting sustainable agricultural management strategies, such as enhanced pest monitoring and improved irrigation systems, to mitigate the dual pressures brought by climate change and pests.

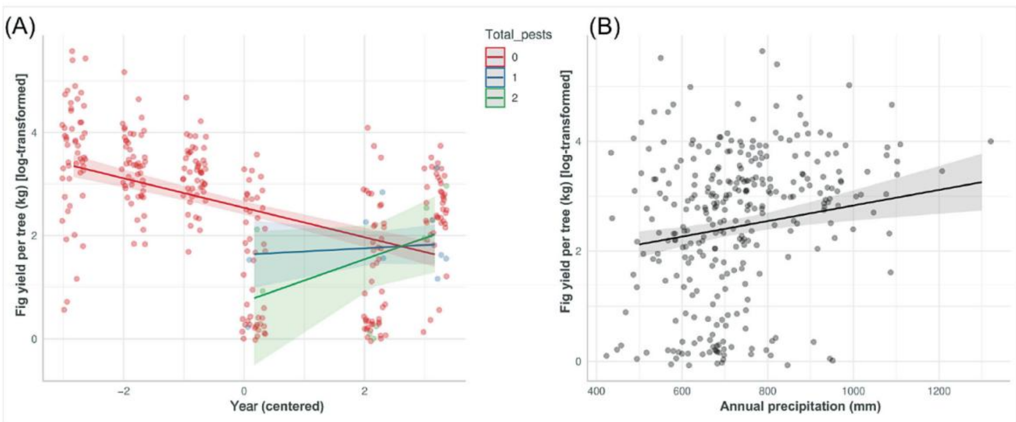

Figure 3 Predicted fig yield per tree across years and total number pests (A) and across annual precipitation (B) in Bejaïa, Northern Algeria (Adopted from Mellal et al., 2023)

Image caption: Figure A shows that as the number of pests increases, the yield per fig tree significantly decreases, with a more pronounced negative impact observed during the early years of the study. Figure B indicates a positive correlation between annual precipitation and fig tree yield, meaning that higher precipitation is associated with higher yields. These two figures validate the dual stress effect of pests and drought conditions on fig yield, highlighting that effective water management and pest control are crucial factors for improving fig yield under the backdrop of climate change and pest invasions (Adapted from Mellal et al., 2023)

5.2 Physiological responses and adaptation mechanisms of fig genotypes under water deficit conditions

With the intensification of global climate change and water scarcity issues, studying the physiological response mechanisms of fig trees under water deficit conditions is crucial for optimizing cultivation management and improving crop yield (Ammar et al., 2020). Especially in arid and semi-arid regions, figs have become an important alternative crop due to their unique drought-resistant mechanisms.

del Rosario Jacobo-Salcedo et al. (2024) analyzed the drought tolerance differences between fig germplasm resources (such as "Guadalupe Victoria") and the commercial variety "Black Mission" under water deficit conditions by measuring physiological and biochemical indicators such as relative water content (RWC), photosynthetic rate (PN), stomatal conductance (gs), intercellular CO_2 concentration (Ci), transpiration rate (E), proline (Pro), and soluble sugar content (SSC). The study showed that "Guadalupe Victoria" maintained a higher photosynthetic rate and relative water content under drought conditions, demonstrating strong drought tolerance. This genotype accumulated more proline under drought stress, which helps regulate cell osmotic pressure and maintain cell function. Additionally, the study found that proper stomatal regulation and the accumulation of soluble sugars also play important roles in the drought tolerance of figs.

The significant physiological response differences among various fig genotypes under water deficit conditions indicate that analyzing these physiological and biochemical markers can effectively identify genotypes with strong drought tolerance, providing a scientific basis for achieving sustainable fig production in water-limited environments. These findings will strongly support future breeding for drought resistance and the formulation of crop management strategies.

5.3 Chemical signaling in the mutualistic relationship between fig trees and *Blastophaga psenes*

The fig tree (*Ficus carica*) and its specific pollinator *Blastophaga psenes* form a complex mutualistic relationship. Fig pollination relies on *B. psenes*, while the larvae of *B. psenes* feed on fig pollen (Falistocco, 2020; Proffit et al., 2020). Researchers have discovered through chemical analysis and behavioral experiments that specific ratios of volatile organic compounds (VOCs) play a critical role in this specialized interaction (Proffit et al., 2020).

Proffit et al. (2020) analyzed 26 VOCs emitted by fig trees and found that only five compounds elicited electrophysiological responses in the antennae of *B. psenes*. These include benzyl alcohol and four monoterpenes, such as (S)-linalool and (Z)-linalool oxide. Behavioral tests indicated that *B. psenes* has a significant preference for a specific blend of these five compounds, and even slight changes in their proportions greatly reduce their attractiveness (Figure 4). This mimicry of chemical signals helps sustain the relationship between fig trees and wasps. The study suggests that fig trees successfully attract their specialized pollinator by adjusting the proportions of VOCs rather than their types, highlighting the importance of chemical signaling in plant-pollinator interactions. This finding provides new insights into understanding other complex plant-pollinator relationships.

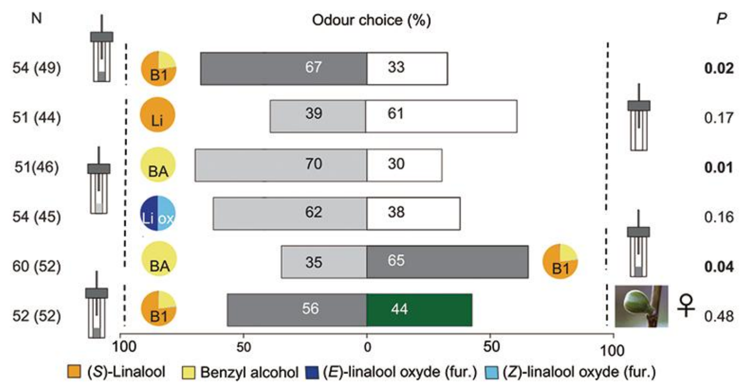

Figure 4 Attraction responses of *Blastophaga psenes* females towards different VOCs alone or in blends (Adopted from Proffit et al., 2020)

Image caption: Tests were conducted in Y-tube olfactometers in which females were allowed to choose between synthetic versions of the four VOCs (alone or in a blend) and control odour. In a second set of tests, female wasps could select between a blend of the four VOCs and benzyl alcohol alone, or, a blend of the four VOCs and odour of female receptive figs. For the four VOCs detected by the pollinator, proportions of each in each odour source are indicated in the pie chart. Number of wasps tested (N), number of individuals that made a choice in parentheses, and P-values (exact binomial test) are indicated for each comparison (Adapted from Proffit et al., 2020)

The figure compares the preference of *B. psenes* in Y-tube olfactometer tests when exposed to single compounds, a specific VOC blend with a fixed ratio (B1), and control conditions. The results show that *B. psenes* exhibits a significant preference for the specific blend of four VOCs, including benzyl alcohol and (S)-linalool (B1), while no significant preference is observed for single compounds or other mixtures with different ratios, which are even less attractive than benzyl alcohol alone (Proffit et al., 2020). This indicates that *B. psenes* requires a specific proportion of VOCs to effectively locate its host plant, highlighting the importance of precise chemical signaling in the mutualistic relationship between plants and pollinators.

6 Ecological Interactions of *Ficus carica* with its Environment

6.1 Role of *Ficus carica* in maintaining biodiversity

Ficus carica plays a significant role in maintaining biodiversity within its ecosystem. The tree supports a diverse community of endophytic fungi, which includes genera such as *Alternaria*, *Cladosporium*, and *Curvularia*. These fungal endophytes exhibit antimicrobial properties and biotransforming abilities, contributing to the ecological balance by inhibiting pathogenic microorganisms and metabolizing plant compounds (Barolo et al., 2023).

Additionally, the presence of mycorrhizal fungi in the root systems of *Ficus carica* enhances nutrient uptake and stress tolerance, which in turn supports the growth and survival of various plant species in the surrounding area (Tedersoo et al., 2020; Caruso et al., 2021). This mutualistic relationship between *Ficus carica* and mycorrhizal fungi fosters a stable and diverse plant community, promoting overall ecosystem health.

6.2 Interactions with soil microorganisms: symbiosis with mycorrhizae

Ficus carica forms symbiotic relationships with mycorrhizal fungi, which are crucial for its nutrient acquisition and stress adaptation. These fungi colonize the roots of *Ficus carica*, facilitating the uptake of essential nutrients such as phosphorus and nitrogen in exchange for photosynthetically derived carbon from the plant (Genre et al., 2020; Shi et al., 2022). The mycorrhizal symbiosis not only enhances the nutrient status of *Ficus carica* but also improves soil structure and ecosystem functionality by influencing soil microbial communities (Mello and Balestrini, 2018). The presence of mycorrhizal fungi, such as arbuscular mycorrhizal fungi (AMF), has been shown to positively affect the root architecture of *Ficus carica*, leading to increased root length and mass, which further enhances the plant's ability to exploit soil resources (Caruso et al., 2021). This intricate interaction between Ficus carica and mycorrhizal fungi underscores the importance of these symbiotic relationships in maintaining soil health and plant productivity.

6.3 Influence on surrounding vegetation and wildlife

Ficus carica exerts a significant influence on the surrounding vegetation and wildlife through its root exudates and interactions with soil microorganisms. Studies have shown that the root extracts of *Ficus carica* can promote the growth of neighboring plants, such as *Taxus cuspidata*, by altering soil microbial diversity and increasing the abundance of growth-promoting bacteria while reducing pathogenic bacteria (Li et al., 2023). This allelopathic effect is primarily mediated by the chemicals secreted by *Ficus carica* roots, which interact with soil microorganisms to create a favorable environment for plant growth. Furthermore, the extensive mycorrhizal networks associated with *Ficus carica* roots facilitate nutrient transfer and communication between plants, thereby enhancing plant community dynamics and stability (Tedersoo et al., 2020). The presence of *Ficus carica* also supports a diverse array of wildlife, including various insect species that rely on the tree for food and habitat, further contributing to the ecological richness of the area.

Ficus carica plays a pivotal role in maintaining biodiversity, fostering symbiotic relationships with mycorrhizal fungi, and influencing the growth and health of surrounding vegetation and wildlife. These ecological interactions highlight the importance of *Ficus carica* in sustaining and enhancing ecosystem functions.

7 Role of *Ficus carica* in Agroforestry and Sustainable Practices

7.1 Contribution to sustainable agricultural practices

Ficus carica also plays a significant role in sustainable agricultural practices, particularly within agroforestry systems. Agroforestry integrates trees with crops and livestock, promoting efficient resource utilization and enhancing soil health. The inclusion of fig trees in agroforestry systems can improve soil fertility, structure, and biodiversity, which are crucial for sustainable agriculture (Kuyah et al., 2019; Udawatta et al., 2019; Fahad et al., 2022). The deep root systems of fig trees help in nutrient cycling and water retention, reducing the need for chemical fertilizers and irrigation (Fahad et al., 2022). Additionally, fig trees provide shade and microclimate regulation, which can protect crops from extreme weather conditions and improve overall farm resilience (Kuyah et al., 2019; Tschora and Cherubini, 2020).

7.2 Potential for use in soil conservation and reforestation projects

Ficus carica is highly effective in soil conservation and reforestation efforts due to its robust root system and adaptability to various soil types. It was reported that the roots of fig trees help in binding soil particles together, thereby reducing soil erosion and runoff (Rafidison et al., 2020; Fahad et al., 2022). This characteristic makes fig trees suitable for planting in degraded lands and areas prone to erosion. Moreover, fig trees can be used in reforestation projects to restore ecological balance and improve soil health. Their ability to thrive in diverse climatic conditions, including arid and semi-arid regions, makes them an excellent choice for reforestation initiatives aimed at combating desertification and land degradation.

7.3 Economic and ecological benefits: food security and biodiversity

The cultivation of *Ficus carica* offers numerous economic and ecological benefits, contributing to food security and biodiversity. Economically, fig trees provide a valuable source of income for farmers through the sale of fresh and dried figs, which are rich in nutrients and have a high market demand (Ighbareyeh et al., 2018; Dalkılıç, 2022; Mellal et al., 2023). The fruit's nutritional value, including vitamins, minerals, and carbohydrates, supports local food security by providing a reliable food source (Dalkılıç, 2022). Ecologically, fig trees support biodiversity by providing habitat and food for various species, including birds and insects, which are essential for pollination and pest control (Udawatta et al., 2019; Rafidison et al., 2020; Castle et al., 2021). The presence of fig trees in agroforestry systems enhances the overall biodiversity of the landscape, promoting a healthier and more resilient ecosystem (Udawatta et al., 2019; Castle et al., 2021).

8 Concluding Remarks

Fig (*Ficus carica* L.), demonstrates remarkable adaptability to various environmental conditions, particularly in arid and saline environments. Studies have shown that certain cultivars exhibit high water-retention capabilities and resilience to drought conditions, making them suitable for cultivation in dry regions. Additionally, the fig's ability to thrive in diverse ecological settings, from the Mediterranean to Northwestern India, underscores its ecological versatility. The fig is also noted for its rich phytochemical composition, which includes bioactive compounds with significant pharmacological properties, such as antioxidant, antimicrobial, and anti-inflammatory activities. These attributes not only enhance its value in traditional medicine but also highlight its potential in modern pharmacological applications.

Despite the extensive research on *Ficus carica*, several gaps remain. There is a need for more comprehensive studies on the molecular mechanisms underlying its adaptability to salinity and drought stress. For instance, while transcriptome analysis has provided insights into the fig's response to salinity, further research is required to identify and characterize the specific genes involved in these stress responses. Additionally, the ecological interactions between Ficus carica and its endophytic fungal communities, which contribute to its resilience and antimicrobial properties, warrant deeper investigation. Future research should also focus on optimizing propagation techniques to ensure the production of high-quality, disease-free seedlings, which is crucial for sustainable fig cultivation.

The adaptability of *Ficus carica* to harsh environmental conditions makes it a valuable crop for arid and semi-arid regions. Cultivars with high drought and salinity tolerance can be promoted for large-scale plantations in these areas, contributing to food security and economic stability. In conservation efforts, the fig's ability to grow in diverse habitats can be leveraged to restore degraded lands and maintain biodiversity, particularly in regions where it is native or naturalized. Moreover, the fig's aesthetic appeal and low maintenance requirements make it an excellent choice for urban greening projects, where it can enhance urban biodiversity and provide ecological benefits such as shade and air purification.

Ficus carica L. stands out as a resilient and versatile species with significant ecological, agricultural, and pharmacological value. Its ability to adapt to various environmental stresses, coupled with its rich phytochemical profile, underscores its potential in multiple domains. However, to fully harness these benefits, continued research and development are essential. By addressing the existing research gaps and exploring new frontiers, we can optimize the cultivation and utilization of this remarkable species, ensuring its contribution to sustainable agriculture, conservation, and urban planning.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Abdolinejad R., and Shekafandeh A., 2022, Tetraploidy confers superior in vitro water-stress tolerance to the fig tree (*Ficus carica*) by reinforcing hormonal, physiological, and biochemical defensive systems, Frontiers in Plant Science, 12: 796215.
https://doi.org/10.3389/fpls.2021.796215

Abdolinejad R., Shekafandeh A., Jowkar A., Gharaghani A., and Alemzadeh A., 2020, Indirect regeneration of *Ficus carica* by the TCL technique and genetic fidelity evaluation of the regenerated plants using flow cytometry and ISSR, Plant Cell, Tissue and Organ Culture (PCTOC), 143: 131-144.
https://doi.org/10.1007/s11240-020-01903-5

Ammar A., Aissa I.B., Mars M., and Gouiaa M., 2020, Comparative physiological behavior of fig (*Ficus carica* L.) cultivars in response to water stress and recovery, Scientia Horticulturae, 260: 108881.
https://doi.org/10.1016/j.scienta.2019.108881

Azmi F.M., Tajudin N.S., Shahari R., and Amri C.N.A.C., 2020, Planted on BRIS soil effected by chicken manure amendments, Journal Clean WAS (JCleanWAS), 4: 61-65.
https://doi.org/10.26480/jcleanwas.02.2020.61.65

Barolo M.I., Castelli M.V., and López S.N., 2023, Antimicrobial properties and biotransforming ability of fungal endophytes from *Ficus carica* L. (Moraceae), Mycology, 14(2): 108-132.
https://doi.org/10.1080/21501203.2023.2175500

Barolo M.I., Mostacero N.R., and López S.N., 2014, *Ficus carica* L. (Moraceae): An ancient source of food and health, Food Chemistry, 164: 119-127.
https://doi.org/10.1016/j.foodchem.2014.04.112

Bolboli Z., Masigol H., and Mostowfizadeh-Ghalamfarsa R., 2024, Genetic diversity assessment of the *Diaporthe cinerascens* causal agent of fig canker using ISSR markers, Mycologia Iranica, 11(1): 29-38.
https://mij.areeo.ac.ir/article_131522.html

Boliani A.C., Ferreira A.F.A., Monteiro L.N.H., Silva M.S.A.C.D., and Rombola A.D., 2019, Advances in propagation of *Ficus carica* L., Revista Brasileira de Fruticultura, 41(3): e-026.
https://doi.org/10.1590/0100-29452019026

Bougdaoua H., and El Mtili N., 2022, Morphological and chemical characteristics of fruits and seeds of two cultivars of *Opuntia ficus-indica* (L.) Miller from northern Morocco, Journal of the Professional Association for Cactus Development, 24: 172-184.
https://doi.org/10.56890/jpacd.v24i.486

Boutasknit A., Baslam M., Ait-El-Mokhtar M., Anli M., Ben-Laouane R., Douira A., Modafar C., Mitsui T., Wahbi S., and Meddich A., 2020, Arbuscular mycorrhizal fungi mediate drought tolerance and recovery in two contrasting carob (*Ceratonia siliqua* L.) ecotypes by regulating stomatal, water relations, and (in)organic adjustments, Plants, 9(1): 80.
https://doi.org/10.3390/plants9010080

Caruso T., Mafrica R., Bruno M., Vescio R., and Sorgonà A., 2021, Root architectural traits of rooted cuttings of two fig cultivars: Treatments with arbuscular mycorrhizal fungi formulation, Scientia Horticulturae, 283: 110083.
https://doi.org/10.1016/J.SCIENTA.2021.110083

Castle S.E., Miller D.C., Ordonez P.J., Baylis K., and Hughes K., 2021, The impacts of agroforestry interventions on agricultural productivity, ecosystem services, and human well-being in low- and middle-income countries: A systematic review, Campbell Systematic Reviews, 17(2): e1167.
https://doi.org/10.1002/CL2.1167

Dalkılıç Z., 2022, Ficus carica: Production, Cultivation and Uses, Ficus carica: Production, Cultivation and Uses.
https://doi.org/10.52305/tpcs5872

del Rosario Jacobo-Salcedo M., David Valdez-Cepeda R., Sánchez-Cohen I., González-Espíndola L.Á., Arreola-Ávila J.G., and Trejo-Calzada R., 2024, Physiological mechanisms in *Ficus carica* L. genotypes in response to moisture stress, Agronomy Research, 22.

Fahad S., Chavan S., Chichaghare A., Uthappa A., Kumar M., Kakade V., Pradhan A., Jinger D., Rawale G., Yadav D., Kumar P., Farooq T., Ali B., Sawant A., Saud S., Chen S., and Poczai P., 2022, Agroforestry systems for soil health improvement and maintenance, Sustainability, 14(22): 14877.
https://doi.org/10.3390/su142214877

Falistocco E., 2020, The millenary history of the fig tree (*Ficus carica* L.), Adv Agric Hortic Entomol, 5: 130.
https://doi.org/10.37722/aahae.202051

Gaaliche B., Ben Abdelaali N., Mouttet R., Ben Halima-Kamel M., and Hajlaoui M.R., 2018, Nouveau signalement de Hypocryphalus scabricollis (Eichhoff, 1878) en Tunisie, un ravageur émergent sur figuier (*Ficus carica* L.), EPPO Bulletin, 48(1): 164-166.

Gabibova A., 2020, Features of ecology of Ficus carica L. in Daghestan, Herald of Daghestan Scientific Center of Russian Academy of Science.
https://doi.org/10.31029/vestdnc78/2

Genre A., Lanfranco L., Perotto S., and Bonfante P., 2020, Unique and common traits in mycorrhizal symbioses, Nature Reviews Microbiology, 18(11): 649-660.
https://doi.org/10.1038/s41579-020-0402-3

Hiwale S., and Hiwale S., 2015, Fig (*Ficus carica*), Sustainable Horticulture in Semiarid Dry Lands, 159-175.
https://doi.org/10.1007/978-81-322-2244-6_11

Hong E.C., Lynn C.B., and Subramaniam S., 2020, Development of plantlet regeneration pathway using in vitro leaf of *Ficus carica* L. cv. Panachee supported with histological analysis, Biocatalysis and Agricultural Biotechnology, 27: 101697.
https://doi.org/10.1016/j.bcab.2020.101697

Ighbareyeh J., Suliemieh A., Ighbareyeh M., Daraweesh A.Q., Ortiz A.C., and Carmona E.C., 2018, Impact of bioclimatic and climatic factors on *Ficus carica* L. yield: Increasing the economy and maintaining the food security of Jerusalem in Palestine, Transylvanian Review, 26(34).

Khadivi A., and Mirheidari F., 2022, Selection of the promising fig (*Ficus carica* L.) accessions using fruit-related characters, Food Science & Nutrition, 10(9): 2911-2921.
https://doi.org/10.1002/fsn3.2886

Khadivi A., Anjam R., and Anjam K., 2018, Morphological and pomological characterization of edible fig (*Ficus carica* L.) to select the superior trees, Scientia Horticulturae, 238: 66-74.
https://doi.org/10.1016/J.SCIENTA.2018.04.031

Kuyah S., Whitney C.W., Jonsson M., Sileshi G.W., Öborn I., Muthuri C.W., and Luedeling E., 2019, Agroforestry delivers a win-win solution for ecosystem services in sub-Saharan Africa: A meta-analysis, Agronomy for Sustainable Development, 39: 1-18.
https://doi.org/10.1007/s13593-019-0589-8

Li Q., Huang J., Yang X., Gul Z., Sun W., Qiao B., Cheng J., Li C., and Zhao C., 2023, Effects of *Ficus carica* L. water extract on *Taxus cuspidata* Sieb. et Zucc. growth, Forests, 14(6): 1213.
https://doi.org/10.3390/f14061213

Ling W.T., Tan L.V., Khor S.P., Sriskanda D., Subramaniam S., and Chew B.L., 2022, Rapid in vitro propagation of fig (*Ficus carica* L.) 'Violette de Solliès' supported by molecular and microscopy analyses, Horticulturae, 8(11): 1025.
https://doi.org/10.3390/horticulturae8111025

Liu J., Fu P., Wang Y., and Cao K., 2012, Different drought-adaptation strategies as characterized by hydraulic and water-relations traits of evergreen and deciduous figs in a tropical karst forest, Plant Science Journal, 30: 484-493.
https://doi.org/10.3724/SP.J.1142.2012.50484

Ma X., Chen H., and Nie Y., 2020, Common species maintain a large root radial extent and a stable resource use status in soil-limited environments: A case study in subtropical China, Frontiers in Plant Science, 11: 1260.
https://doi.org/10.3389/fpls.2020.01260

Madouh T.A., and Quoreshi A.M., 2023, The function of arbuscular mycorrhizal fungi associated with drought stress resistance in native plants of arid desert ecosystems: A review, Diversity, 15(3): 391.
https://doi.org/10.3390/d15030391

Mardinata Z., Edy Sabli T., and Ulpah S., 2021, Biochemical responses and leaf gas exchange of fig (*Ficus carica* L.) to water stress, short-term elevated CO_2 levels and brassinolide application, Horticulturae, 7(4): 73.
https://doi.org/10.3390/HORTICULTURAE7040073

Mellal M.K., Khelifa R., Chelli A., Djouadi N., and Madani K., 2023, Combined effects of climate and pests on fig (*Ficus carica* L.) yield in a Mediterranean region: Implications for sustainable agricultural strategies, Sustainability, 15(7): 5820.
https://doi.org/10.3390/su15075820

Mello A., and Balestrini R., 2018, Recent insights on biological and ecological aspects of ectomycorrhizal fungi and their interactions, Frontiers in Microbiology, 9: 216.
https://doi.org/10.3389/fmicb.2018.00216

Nair S.S., Bachan K.A., and Ebin P.J., 2021, Diversity and phenetic study on syconium of *Ficus* L. (Moraceae) from Kerala, India revealing natural classification along with an identification key, Reinwardtia, 20(1): 27-36.
https://doi.org/10.14203/REINWARDTIA.V20I1.4031

Nakabayashi M., Inoue Y., Ahmad A.H., and Izawa M., 2019, Limited directed seed dispersal in the canopy as one of the determinants of the low hemi-epiphytic figs' recruitments in Bornean rainforests, PLoS One, 14(6): e0217590.
https://doi.org/10.1371/journal.pone.0217590

Nuzzo V., Gatto A., and Montanaro G., 2022, Morphological characterization of some local varieties of fig (*Ficus carica* L.) cultivated in Southern Italy, Sustainability, 14(23): 15970.
https://doi.org/10.3390/su142315970

Proffit M., Lapeyre B., Buatois B., Deng X., Arnal P., Gouzerh F., Carrasco D., and Hossaert-McKey M., 2020, Chemical signal is in the blend: bases of plant-pollinator encounter in a highly specialized interaction, Scientific Reports, 10(1): 10071.
https://doi.org/10.1038/s41598-020-66655-w

Rafidison V.M., Rakouth B., Carrière S.M., Kjellberg F., and Aumeeruddy-Thomas Y., 2020, Multiple values of isolated and clusters of Ficus tree species protected by Betsileo farmers in rural landscapes in Madagascar: implications for biodiversity conservation, Biodiversity and Conservation, 29(3): 1027-1058.
https://doi.org/10.1007/s10531-019-01924-3

Shi J., Wang X., and Wang E., 2023, Mycorrhizal symbiosis in plant growth and stress adaptation: from genes to ecosystems, Annual Review of Plant Biology, 74(1): 569-607.
https://doi.org/10.1146/annurev-arplant-061722-090342

Tedersoo L., Bahram M., and Zobel M., 2020, How mycorrhizal associations drive plant population and community biology, Science, 367(6480): eaba1223.
https://doi.org/10.1126/science.aba1223

Teja T.R., Varma S., Johar V., Singh V., and Rao M.V., 2023, Vegetative propagation of sandalwood (*Santalum album* L.): a review, International Journal of Environment and Climate Change, 13(8): 412-417.
https://doi.org/10.9734/ijecc/2023/v13i81968

Tesfay Y.B., Blaschke A., Ashley N., Portillo L., Scalisi A., Adli B., and Kreyling J., 2023, Increased plasticity in invasive populations of a globally invasive cactus, Plants, 12(18): 3287.
https://doi.org/10.3390/plants12183287

Tschora H., and Cherubini F., 2020, Co-benefits and trade-offs of agroforestry for climate change mitigation and other sustainability goals in West Africa, Global Ecology and Conservation, 22: e00919.
https://doi.org/10.1016/j.gecco.2020.e00919

Udawatta R.P., Rankoth L.M., and Jose S., 2019, Agroforestry and biodiversity, Sustainability, 11(10): 2879.
https://doi.org/10.3390/SU11102879

Zolfaghari M.R., Salimpour F., Sharifnia F., Peyvandi M., and Marandi S.J., 2019, Infraspecific morphological and genetic variations of *Ficus carica* L. from Iran, Biologija, 65(3).
https://doi.org/10.6001/biologija.v65i3.4090