

Review

Not peer-reviewed version

Adaptive Strategies to Biotic Stress in Qatar's Native Flora

Bassam Taha Yasseen *,† and Roda Fahad Al-Thani

Posted Date: 29 September 2025

doi: 10.20944/preprints202509.2325.v1

Keywords: abiotic factors; adaptation; avoidance; biotic stress; chemical constituents; morphology; physical barriers; resistance



Preprints.org is a free multidisciplinary platform providing preprint service that is dedicated to making early versions of research outputs permanently available and citable. Preprints posted at Preprints.org appear in Web of Science, Crossref, Google Scholar, Scilit, Europe PMC.

Copyright: This open access article is published under a Creative Commons CC BY 4.0 license, which permit the free download, distribution, and reuse, provided that the author and preprint are cited in any reuse.

Disclaimer/Publisher's Note: The statements, opinions, and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions, or products referred to in the content.

Review

Adaptive Strategies to Biotic Stress in Qatar's Native Flora

Bassam Taha Yasseen *, t and Roda Fahad Al-Thani

Department of Biological and Environmental Sciences, College of Arts and Sciences, Qatar University, Doha, Qatar

- * Correspondence: bassam_tahaa@yahoo.co.uk
- [†] Current address: 8 James Court, Dunstable Road, Luton, UK, LU4 0HN.

Abstract

Qatar's arid and semi-arid landscapes present extreme environmental conditions where native flora face multiple stressors, and plants must simultaneously combat abiotic pressures, including high salinity, water scarcity, intense solar radiation, and extreme temperatures, alongside biotic threats from herbivory, microbial pathogens, and interspecific competition. However, the integrated mechanisms by which these species coordinate defences against both abiotic and biotic stressors (particularly pathogenic microorganisms) remain insufficiently understood, creating a critical knowledge gap in comprehending plant persistence strategies in harsh desert environments. Therefore, this study investigates the comprehensive defence strategies that facilitate plant survival under dual pressures, examining chemical responses including antimicrobial compounds and phenolic production, structural barriers such as thick cuticles, trichomes, and reinforced cell walls, and functional trade-offs affecting water-use efficiency and gas exchange. The research assesses how abscisic acid accumulation, triggered by abiotic stress, enhances biotic resistance through specific biochemical regulatory processes, while critically evaluating the advantages and costs of structural and biochemical adaptations. These findings demonstrate that native species employ interconnected response systems to sustain themselves under simultaneous abiotic and biotic pressures, thereby supporting biodiversity, ecological resilience, and long-term stability of Qatar's fragile desert habitats through coordinated physiological and morphological strategies.

Keywords: abiotic factors; adaptation; avoidance; biotic stress; chemical constituents; morphology; physical barriers; resistance

1. Introduction

Biotic factors encompass all living components influencing an ecosystem's structure, function, and dynamics. These include plants (such as weeds), animals (including insects, pests, nematodes, and herbivores that consume plants), as well as pathogens like bacteria, fungi, viruses, and other microorganisms. Broadly, biotic factors involve diverse interactions among organisms, including predation, herbivory, competition, symbiosis, parasitism, and decomposition. Although this article does not cover the full range of biotic interactions, it focuses on specific aspects relevant to Qatar's native flora. It examines the methods and strategies adopted by native plant species to develop resistance against herbivory and microbial threats, highlighting how these plants survive and adapt to Qatar's challenging environmental conditions.

Biotic stresses can damage plant tissues, reduce photosynthesis, stunt growth, and ultimately lower crop yield and quality. In response, plants employ various defense mechanisms, such as altering physical structures, producing toxic chemicals, or activating immune responses. Notably, solute accumulation under stress conditions may serve as a preemptive measure, enabling plants to cope with both environmental challenges and opportunistic microbial threats. Microorganisms, including bacteria, fungi, algae, and protozoa, commonly colonize different plant organs [1]. Plants

offer a variety of microhabitats, including the rhizosphere (root-influenced zone), the phyllosphere (aerial parts), and the endosphere (internal transport system). Interactions between microorganisms and plants can be beneficial or detrimental, categorized as neutralism, commensalism, synergism, mutualism, amensalism, competition, or parasitism [2,3].

Additionally, microorganisms possess various means to infiltrate plant tissues, including natural openings such as stomata and lenticels, as well as wounds from external factors like soil particles, pathogenic attacks, or abiotic stresses, such as salinity, drought, and extreme temperatures [4]. Certain small animals within the ecosystem may also act as vectors, directly introducing microbes into plant interiors. Once inside, these microorganisms can colonize and migrate to different plant organs, including flowers, fruits, and seeds. Ultimately, some microbes, notably fungi and bacteria, can be transmitted to the next generation via seeds [5].

The Arabian Gulf exhibits high salinity, extreme temperatures, and primarily arid to semi-arid landscapes, posing significant challenges to both crop cultivation and the survival of native plant species (Figure 1). In Qatar, soils found in sabkhas and coastal regions are particularly saline, with the electrical conductivity (ECe) of saturated soil extracts often surpassing 200 dS/m. The region experiences intense summer heat, with temperatures regularly exceeding 50°C. The climate in Qatar is classified as arid to semi-arid, receiving an average annual precipitation of approximately 80 mm, which rarely surpasses 152 mm [6]. In such a severe environment, few wild plants, and animals can thrive. These native plants have developed various adaptations to endure the extreme conditions. Additional information is provided in a review by Yasseen and Al-Thani [3], who identified several xerophytic and halophytic genera as the primary inhabitants of the Qatari ecosystem.

Many plants along the coastline and throughout Qatar are characterised as xerophytes, including species such as *Cyperus conglomeratus*, *Helianthemum lipii*, *Ochradenus baccatus*, *Oligomeris linifolia*, and *Tetraena qatarensis*. Halophytes, on the other hand, encompass approximately 26 genera reported in various studies and monographs, such as *Anabasis*, *Arthrocnemum*, *Atriplex*, *Avicennia*, *Halocnemum*, *Halopeplis*, *Limonium*, *Salsola*, *Seidlitzia*, and *Suaeda*. These plants employ three primary mechanisms to cope with dry and saline environments: (a) drought-escaping, (b) avoidance, and (c) tolerance mechanisms [3,7–10]. Native plants in these regions may possess integrated mechanisms that coordinate responses to abiotic stresses – including structural modifications, physiological adaptations, and biochemical pathway alterations – with biotic defense strategies, such as resistance to microbial invasion, pathogen attack, and herbivory.

In harsh ecosystems, such as those in the Arabian Gulf region, plants face extreme environmental conditions, including high salinity, drought, and elevated temperatures, as well as biotic pressures from pests and pathogens. These combined stresses require adaptive responses involving structural, physiological, and biochemical modifications. Such adaptations enable plants to maintain functionality and enhance survival under these challenging conditions.

Native plants in Qatar display a range of morphological and anatomical adaptations that enable survival in the country's extreme desert environment. These adaptations encompass specific forms, leaf orientations, and surface structures such as hairs and trichomes. Many desert plants, for example, have reduced leaf sizes or needle-like leaves to minimise water loss through transpiration [9,11]. *Tetraena qatarensis*, a succulent common in Qatar's arid regions, features fleshy leaves that store water and reduce evaporation. Similarly, *Haloxylon salicornicum*, possesses vertically oriented stems, which lessen direct exposure to intense sunlight and conserve moisture.

Trichomes, small hair-like structures on plant surfaces, are prevalent in desert flora and serve multiple protective functions. They can reflect sunlight, reduce leaf temperature, and act as barriers against insects and excessive wind, which can desiccate plant tissues. In Qatar, species such as *Limonium axillare* exhibit these traits, supporting their survival in sandy, saline, and extremely hot conditions.

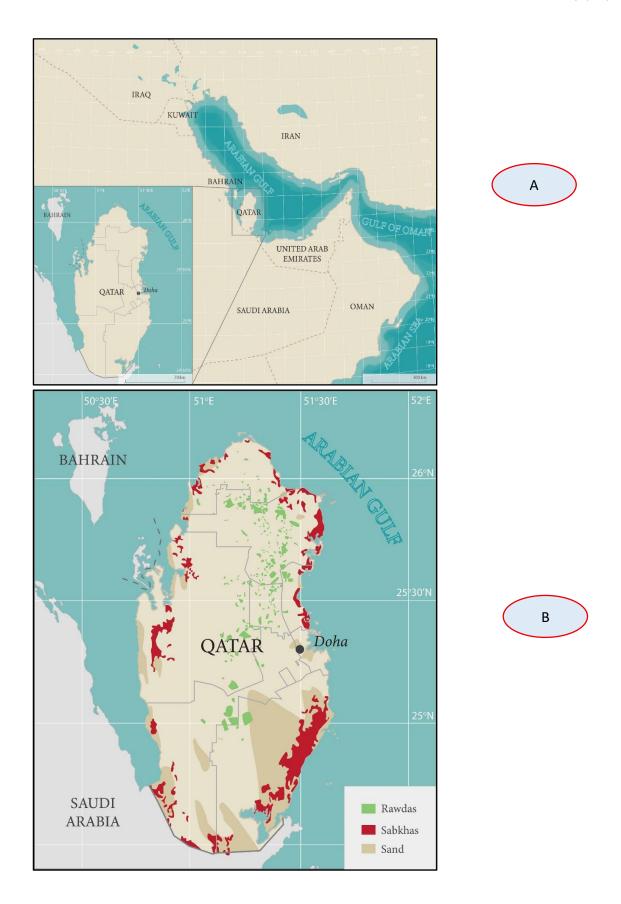


Figure 1. Map of the Arabian Gulf region and Qatar (A), and detailed map of Qatar (B) showing sabkhas (red patches), rawdhas (green patches), desert lands, saline soils (remaining areas), and the surrounding seawater of the Arabian Gulf.

Beyond physical adaptations, many native plants produce specific chemical compounds serving as biochemical defences. These compounds deter herbivores, inhibit pathogen growth, and eliminate invading organisms. *Calligonum comosum*, a desert shrub found in Qatar, produces antimicrobial secondary metabolites that protect against bacterial and fungal infections. Additionally, the presence of phenolic compounds, alkaloids, and essential oils in various species enhances resistance to pests and microbial invasion. These chemical defences are crucial in an ecosystem where biological threats are intensified due to limited resources and competitive pressures. Together, these physical and chemical adaptations allow Qatar's native plants to endure extreme heat, drought, salinity, and biotic stress, making them vital components of the country's unique desert ecosystem [12,13].

This article investigates the physical and chemical defence mechanisms, along with symbiotic relationships, that enable native plants in Qatar to withstand biotic stresses and mitigate potential threats. In addition to these defences, native plants deploy competitive strategies to secure essential resources such as sunlight, water, and nutrients. With approximately 400 native plant species documented in Qatar [14], the region provides a valuable setting for studying desert flora. Notably, about 40% of these species are classified as range plants with high nutritional value. They contain proteins, carbohydrates, fatty acids, essential elements, and potentially other bioactive compounds applicable in pharmaceutical, nutritional, cosmetic, and economic sectors [15]. This article seeks to highlight selected examples from the local flora to demonstrate how these species adapt to and manage biotic stressors, while examining their interactions with both biotic and abiotic factors. Trichomes, small hair-like structures on plant surfaces, are prevalent in desert flora and serve multiple protective functions. They can reflect sunlight, reduce leaf temperature, and act as barriers against insects and excessive wind, which can desiccate plant tissues. In Qatar, species such as Limonium axillare exhibit these traits, supporting their survival in sandy, saline, and extremely hot conditions.

Beyond physical adaptations, many native plants produce specific chemical compounds serving as biochemical defences. These compounds deter herbivores, inhibit pathogen growth, and eliminate invading organisms. *Calligonum comosum*, a desert shrub found in Qatar, produces antimicrobial secondary metabolites that protect against bacterial and fungal infections. Additionally, the presence of phenolic compounds, alkaloids, and essential oils in various species enhances resistance to pests and microbial invasion. These chemical defences are crucial in an ecosystem where biological threats are intensified due to limited resources and competitive pressures.

Together, these physical and chemical adaptations allow Qatar's native plants to endure extreme heat, drought, salinity, and biotic stress, making them vital components of the country's unique desert ecosystem [12,13].

This article investigates the physical and chemical defence mechanisms, along with symbiotic relationships, that enable native plants in Qatar to withstand biotic stresses and mitigate potential threats. In addition to these defences, native plants deploy competitive strategies to secure essential resources such as sunlight, water, and nutrients. With approximately 400 native plant species documented in Qatar [14], the region provides a valuable setting for studying desert flora. Notably, about 40% of these species are classified as range plants with high nutritional value. They contain proteins, carbohydrates, fatty acids, essential elements, and potentially other bioactive compounds applicable in pharmaceutical, nutritional, cosmetic, and economic sectors [15]. This article seeks to highlight selected examples from the local flora to demonstrate how these species adapt to and manage biotic stressors, while examining their interactions with both biotic and abiotic factors.

2. Mechanisms of Resistance Against Biotic Stress

Plants synthesise a diverse array of chemical compounds crucial for defence against various environmental threats. The biosynthesis of these compounds often intensifies when plants face abiotic stresses such as salinity, drought, and extreme temperatures [10]. Early research indicates that these stresses induce structural and biochemical changes at multiple levels, including morphological, anatomical, physiological, and molecular aspects. For example, in salt-affected wheat plants,

mesophyll cells become more compact, intercellular spaces and vascular elements decrease in size, and the cuticle thickens [16]. Additional changes include an increased number of mesophyll layers and lobes within the mesophyll cells [17–19].

Subsequent studies have demonstrated that abiotic stress factors significantly affect structural attributes, such as cell shape and area, ultimately altering overall cell volume [3,20]. Furthermore, stress conditions lead to notable changes in the chemical composition of external protective structures and internal membrane systems [16]. These modifications enhance plant adaptation to adverse environments, improve resistance to microbial pathogens, and strengthen responses to both biotic and abiotic stresses [21]. At the molecular level, these adaptive responses involve altered gene expression, protein modifications, and the restructuring of cellular components. Together, these changes influence plant growth, development, and survival under challenging conditions [22–24].

Native plants, including xerophytes, halophytes, and hydrophytes, have evolved a diverse range of strategies and mechanisms to cope with environmental challenges. These adaptations occur at behavioral, morphological, physiological, and biochemical levels, enabling plants to withstand both abiotic and biotic pressures [1,3,8,10,25]. In Qatar, native flora have developed specialised mechanisms to counteract biotic stressors such as herbivory, pathogen attacks, and competition from neighbouring plants. These adaptations ensure their survival and persistence in the region's harsh, arid ecosystems [26]. These mechanisms can be broadly categorised into (a) physical defences, (b) chemical defences, and (c) symbiotic associations. Concurrently, advancements in biotechnology over recent decades have led to the development of transgenic plants with enhanced resistance to biotic stresses. These advances provide valuable insights and complementary approaches to the natural defence strategies observed in native species [27–29].

2.1. Physical Defences

Physical defences are essential strategies that plants use to mitigate herbivory and pathogen attacks. Many plants produce thorns and spines, which act as mechanical deterrents by injuring or discouraging herbivores from feeding on stems, leaves, or reproductive structures [30]. Trichomes, or leaf hairs, not only serve as barriers that prevent herbivores from easily accessing the plant surface but also impede insect movement and oviposition, thereby reducing herbivore success [31]. Moreover, waxy leaf coatings create a protective layer that minimises water loss and forms a slippery surface, deterring insects from feeding efficiently; these coatings can also obstruct colonisation by microorganisms such as fungi and bacteria [32]. Thick bark and cuticles provide robust physical shields that reduce penetration by pests and pathogens and limit environmental stressors like desiccation and UV damage [33]. These structural adaptations collectively demonstrate the multifaceted methods plants use to employ physical barriers for enhanced survival, a subject that will be explored in greater detail throughout this article.

2.2. Chemical Defences

Plants utilise diverse defensive strategies, such as producing toxins and allelochemicals and releasing volatile compounds, to protect against predators, insects, and microorganisms. These substances deter herbivores and pathogens by rendering the plant unpalatable or harmful or by directly inhibiting or eliminating harmful organisms, such as fungi [31]. For instance, chrysanthemums produce pyrethrin, a natural neurotoxin [34], while mint and witch hazel release antibacterial compounds [35].

Several studies have identified various toxic proteins in plant parts, including roots, tubers, stems, fruits, buds, and foliage. These include ribosome-inactivating proteins, lectins, protease inhibitors, α -amylase inhibitors, canatoxin-like proteins, ureases, arcelins, antimicrobial peptides, and pore-forming toxins. These compounds exhibit significant biological activity and have potential applications in crop protection, drug development, cancer therapy, and genetic engineering. Despite their toxicity, these proteins are valuable bioactive molecules due to their ability to interfere with

specific physiological and cellular processes. However, they can also pose health risks to humans and animals, as detailed by Kocyigit et al. [36].

Advancements in molecular biology and biotechnology have further elucidated the cellular mechanisms of these natural compounds. For example, plant defence responses are activated through complex biochemical pathways often regulated by various transcription factors [37]. Native plants produce toxins through several methods:

- (a) Defence against herbivores: Some plants produce toxins that poison herbivores, while others generate compounds that interfere with growth and digestion. *Phacelia* plants (Family: Boraginaceae), for example, have trichomes containing poisons, insecticides, and allergens.
- (b) Resistance to pathogens: Certain plants produce toxins to combat pathogens such as bacteria and fungi. These toxins disrupt metabolic pathways and damage cell structures, preventing infection.
- (c) Defence against environmental stressors: Some plants produce toxins in response to extreme environmental conditions. These toxins help by reducing water loss and protecting internal structures and organelles from damage by reactive oxygen species (ROS).

Plant toxins include various compounds, such as alkaloids, which are poisonous to animals; glycosides, like cyanogenic glycosides, which release toxins upon tissue damage; resins, which may cause irritation or possess toxic properties; and tannins, which interfere with herbivore digestion.

2.3. Symbiotic Relationships and Ecological Niches

A symbiotic association is a close, long-term interaction between two different organisms, where at least one partner benefits. In plants, such associations may involve fungi, bacteria, other plants, or even animals, and can range from beneficial to neutral or harmful. Interactions with microorganisms are particularly significant, as higher plants are colonised by diverse microbial groups that occupy different ecological niches. These include the rhizosphere, the soil region influenced by roots; the phyllosphere, the aerial surfaces of the plant; and endophytes, which inhabit internal plant tissues without causing disease. Endophytic associations are often considered true symbioses, as they frequently enhance plant stress tolerance, growth, and pathogen resistance, though some may be commensal. Overall, plant-microbe interactions span a spectrum of outcomes and are commonly classified as neutralism, commensalism, synergism, mutualism, amensalism, competition, or parasitism [2]. Among these, parasitism represents a form of association where one organism benefits at the expense of the other. Recent work by Fahmy and Al-Thani [38] illustrates this by showing that the holoparasitic plant *Cynomorium coccineum* effectively exploits its host, *Tetraena qatarensis*, by extracting both water and nutrients.

Plant–microorganism symbioses improve tolerance to salinity and water stress through coordinated physiological, biochemical, and molecular mechanisms. In halophytes, microbes such as *Bacillus* spp. and *Pseudomonas* spp. function as endophytes, facilitating soil desalination and phytoremediation [10]. In the Qatari sabkhas, bacteria and fungi inhabiting both the rhizosphere and endosphere further enhance halophyte resistance to salinity and other stressors, including hydrocarbon pollution. These associations induce the production of bioactive compounds, demonstrating positive biotic interactions that bolster the resilience of native plants in extreme conditions. Recent studies provide additional details [10,39–45]. Leveraging these interactions, especially in saline or degraded soils, represents a promising strategy for sustainable agriculture [46].

The following methods elucidate these relationships: nutrient and water uptake by arbuscular mycorrhizal fungi (AMF) and plant growth-promoting rhizobacteria (PGPR) are key biological methods that enhance plant nutrition and water status. AMF improve nutrient and water uptake by physically extending the root system via hyphal networks, while PGPR contribute through biochemical interactions, such as the production of phytohormones and enzymes. Together, these symbionts strengthen plant stress-tolerance mechanisms. The use of AMF and PGPR as bioinoculants holds significant potential for increasing crop productivity, particularly in challenging environments like saline or nutrient-depleted soils [47].

AMF form symbiotic relationships with the roots of most terrestrial plants. They penetrate the root cortical cells, creating structures such as arbuscules and vesicles that facilitate nutrient exchange. Enhanced nutrient uptake includes phosphorus mobilisation achieved by hyphal networks extending into the soil beyond root zones, thereby aiding the uptake of micronutrients such as copper, iron, and zinc [48]. Additionally, hyphal networks extend the root system, improving water status under conditions of salinity and drought. Furthermore, AMF reduce oxidative stress by enhancing antioxidant enzyme activities in plants and improve osmotic adjustment and root hydraulic conductivity. PGPR are beneficial bacteria that colonise the rhizosphere and promote plant growth through direct and indirect mechanisms [49].

PGPR are beneficial bacteria associated with the root system in the rhizosphere that promote plant growth through both direct and indirect mechanisms. These mechanisms include nitrogen fixation, as certain PGPR fix atmospheric nitrogen [50], while others secrete organic acids and enzymes that solubilise insoluble phosphorus into absorbable forms for plants [51]. Furthermore, these microorganisms produce and modulate phytohormones such as auxins, cytokinins, and gibberellins, which stimulate root growth and enhance nutrient uptake, thereby increasing stress resistance [52]. PGPR also aid in stress alleviation by enhancing antioxidant defences and promoting the accumulation of compatible osmolytes [53]. These solutes, including proline, glycine betaine, and soluble sugars, help maintain cell turgor pressure and protect cellular structures under stress conditions [43,44,54]. Additionally, some strains produce and activate ACC deaminase, which reduces ethylene levels in stressed plants, thus promoting root development [55,56]. Both AMF and PGPR can enhance soil structure and water-holding capacity, which mitigates the effects of salinity on water availability for crops. Importantly, these microbes improve soil health, making it more resilient to salinity stress and more capable of retaining water for plants [57].

Many microbial species, known as endophytes, inhabit plant tissues and can enhance nutrient uptake and stress tolerance. Recent studies have examined the role of endophytes in boosting the remediation potential of halophytes – salt-tolerant plants such as *Halopeplis perfoliata*, *Salicornia europaea*, *Salsola soda*, and *Tetraena qatarensis* – in polluted soils and waters. The microorganisms associated with these halophytes may support the plants' ability to remediate saline and contaminated environments. For further details, refer to Yasseen and Al-Thani [10], Al-Thani and Yasseen [58], and Al-Thani et al. [59].

AMF and PGPR frequently exhibit synergistic effects, enhancing root colonisation and increasing overall plant resilience. These combinations have been effective in remediating polluted soils affected by salt stress, petroleum hydrocarbons, and heavy metals.

2.4. Competition Between Native Plants in Qatar

Biotic interactions among plants for essential resources such as water, nutrients, and, occasionally, sunlight are crucial factors that influence plant growth and development. Al-Thani and Yasseen ([44], Figure 10) reported observations in Qatari sabkhas, where communities of *Halocnemum strobilaceum* display a distinctive pattern. In these communities, plants die in the centre, leaving behind bare patches of dead branches, while green growth persists at the periphery. Over time, this dieback expands outward toward the community's edges. Such patterns underscore how competition and other plant-plant interactions function as biotic factors, shaping the distribution and survival of native species in saline and arid environments.

Plants use various strategies to outcompete neighbouring species, such as rapid growth, efficient resource utilisation, and allelopathy – the release of chemicals that suppress competitors. In Qatar, native plants engage in diverse and complex interactions, including facilitation, allelopathy, and intense competition. Competition is particularly pronounced in arid and saline environments, where water and nutrients are severely limited. Although sunlight is usually abundant, it may become scarce under conditions of shading, dense vegetation, or physiological stress that limits a plant's ability to utilise available light. Species like *Fagonia indica*, *Gisekia pharnacioides*, *Grewia erythraea*, and *Haloxylon salicornicum*, which also serve as important livestock fodder, exemplify the struggle for

survival in such environments. Other species, such as *Cyperus conglomeratus* and *Helianthemum lipii*, have specialised adaptations that allow them to efficiently absorb and retain water. While these traits improve the fitness of individual plants, they also heighten competition for scarce water resources, making water one of the most critical limiting factors in the Qatari desert ecosystem.

2.4.1. Adaptive Strategies to Compete for Sunlight

Plants in Qatar, which thrive in extremely arid, saline, and nutrient-poor environments, have developed diverse adaptive strategies to compete for sunlight – an essential yet intense resource in desert ecosystems. These strategies include:

Growth form and canopy structure: *Haloxylon salicornicum* grows upright with minimal branching, reducing self-shading and allowing greater light penetration. This minimises competition among neighbouring plants. Conversely, *Tetraena qatarensis* exhibits a low-growing form. Additionally, 16 species from 13 genera in Qatar feature rosette leaves [60]. These rosette forms lie close to the ground, capturing early morning and late afternoon light while minimising water loss. Most desert plants also maintain sparse canopy spacing to decrease direct competition for light. However, in microhabitats such as depressions or shaded areas near rocks, competition for light can intensify.

Leaf orientation and morphology: Many Qatari plants possess small or narrow leaves to minimise water loss while efficiently absorbing sunlight. For instance, *Fagonia indica* features small, reduced leaves. Leaves may also orient vertically or at angles, avoiding intense midday sun and preventing overheating. This orientation allows plants to capture light during cooler hours while minimising shading of nearby plants.

Spacing strategies: Some species reduce competition for light through wide spacing, self-thinning, or competitive exclusion. *Haloxylon salicornicum* and *Panicum turgidum*, for example, grow in widely spaced clumps, ensuring unobstructed access to sunlight. This spacing also reduces competition for limited soil moisture and nutrients.

2.4.2. Adaptive Strategies to Compete for Water

Many native plants in Qatar have evolved specific strategies to manage environmental stressors such as drought and soil salinity. Generally – and particularly in Qatar – plants employing these strategies either store water internally or absorb it efficiently from the soil. Several examples illustrate these adaptive strategies. *Tetraena qatarensis*, a xero-halophytic species from the *Chenopodiaceae* family, stores water in its fleshy leaves and is classified as an inducible crassulacean acid metabolism (CAM) plant [10,61]. Other noteworthy members of the same family include *Arthrocnemum macrostachyum*, *Halocnemum strobilaceum*, *Halopeplis perfoliata*, and *Suaeda aegyptiaca*. These species exhibit succulence, a trait that allows them to retain water and tolerate harsh desert and saline conditions [20].

Additionally, competition for limited water resources is a critical survival strategy among native plants in drought- and aridity-affected environments. For instance, *Helianthemum lipii* enhances water uptake by developing a high root-length density in deeper soil layers relative to its leaf area, enabling more effective moisture access. Similarly, *Cyperus conglomeratus* exhibits a high root-to-shoot ratio, increasing the amount of water absorbed per unit of leaf area. This trait supports a drought avoidance mechanism, allowing the plant to survive under prolonged dry conditions [3,20].

2.4.3. Adaptive Strategies to Compete for Nutrients

Soils in Qatar are generally deficient in major nutrients, particularly nitrogen and phosphorus [62,63], leading to intense competition among plants for limited resources. This scarcity, combined with the arid climate, high temperatures, and elevated evaporation rates, presents significant challenges for plant growth. In this context, microorganisms, particularly mycorrhizal fungi, play a crucial role in enhancing plant survival and resilience. AMF, such as *Glomus*, *Rhizophagus*, and *Acaulospora*, are commonly associated with native Qatari plants. They enhance phosphorus uptake,



water absorption, and tolerance to drought and salinity [64]. Other fungi, such as ectomycorrhizal fungi (ECM), including genera like *Pisolithus* and *Laccaria*, assist in nitrogen acquisition from organic sources and support plant growth in nutrient-poor soils [65]. These fungi form symbiotic networks with plant roots, effectively extending the root system and facilitating nutrient exchange, making them essential to plant survival in Qatar's harsh, nutrient-deficient environments. Additionally, these fungi not only improve nutrient and water uptake but also increase plant tolerance to drought and salinity, reduce pathogen infections, and contribute to soil structure and fertility.

3. Native Plants of Qatar and Their Biotic Challenges

As sessile organisms, plants are particularly susceptible to environmental and biotic stressors. To endure these pressures, they have evolved various defence mechanisms that allow either tolerance or avoidance of such challenges. These mechanisms encompass chemical defences and structural modifications that limit pathogen colonisation and deter herbivory [31,66,67]. The native flora of Qatar exhibits diverse adaptive traits that mitigate the effects of herbivory, pathogens, and interspecific competition, while also conferring resilience to the country's extreme abiotic conditions, such as high salinity, prolonged drought, elevated temperatures, and intense solar radiation [3,11,68].

3.1. Qatari Native Plants Resist Herbivores

Livestock such as camels, goats, sheep, and gazelles are unable to consume certain native plants due to the evolution of defensive traits in these plants, such as thorns, tough leaves, bitter sap, and toxic chemicals – including alkaloid compounds [69,70]. Consequently, many Qatari native plants, including *Acacia tortilis*, *Aerva javanica*, *Calotropis procera*, *Cornulaca monocantha*, *Haloxylon salicornicum*, *Leptadenia pyrotechnica*, *Nerium oleander*, *Ricinus communis*, *Salsola imbricata*, and *Tetraena qatarensis*, are inedible to these animals. Conflicting reports exist regarding the edibility of certain native species for domestic livestock. This section outlines selected plant species native to Qatar.

For instance, the ingestion of *Acacia tortilis* by cattle has been associated with undesirable sensory alterations in milk, such as off-odours. *Aerva javanica* has morphological adaptations, including hairy stems and leaves, which reduce its palatability and deter grazing by most livestock. Despite this, it is readily consumed by small ruminants, particularly goats and sheep, while larger herbivores, such as camels and cattle, may also utilise it as forage, especially during drought conditions when alternative feed resources are scarce. *Calotropis procera*, noted for its large leaves and purple flowers, produces a toxic milky latex harmful to humans and livestock. Although toxic, it has long been used in traditional medicine. In contrast, *Acacia tortilis* is protected from over-browsing by its sharp thorns but remains an important forage resource in arid and semi-arid ecosystems, including the Arabian Gulf region. Its pods are particularly high in crude protein, enhancing milk production and providing a significant nutrient source for camels and goats. At the same time, the ingestion of *C. procera* can cause serious effects such as gastrointestinal upset and cardiotoxicity.

Cornulaca monocantha is a resilient shrub characterised by spiny stems and leaves, making it well-adapted to arid environments. It is largely unpalatable due to its bitter taste, which discourages grazing, though it is reported to have certain traditional medicinal applications. *Haloxylon salicornicum*, a hardy shrub with tough stems and low palatability, is common in sandy soils. It resists grazing and remains an important fodder resource in arid regions, staying green during prolonged dry periods and thus providing vital forage when alternative vegetation is scarce.

Leptadenia pyrotechnica features tough stems and adaptations that confer resistance to herbivory, such as the secretion of a bitter, toxic latex rich in diverse chemical constituents, including secondary metabolites as chemical defences. To date, 104 compounds from various phytochemical classes have been identified in this species. Pharmacological studies reveal notable diuretic activity at concentrations ranging from 10 to 300 mg/kg, with doses of 100 and 300 mg/kg producing significant diuretic and saluretic effects comparable to those of furosemide. Leaf extracts have demonstrated diuretic efficacy in both acute and prolonged experimental models, likely mediated through

mechanisms involving carbonic anhydrase inhibition, prostaglandin modulation, and cholinergic pathway activation.

Nerium oleander is a woody evergreen shrub with leathery, lance-shaped leaves and colourful flowers. It is drought-tolerant and frequently cultivated in gardens. All parts of the plant are highly toxic due to cardiac glycosides, posing serious risks to humans and livestock. Traditionally, it has been used medicinally for cancer, uterine stimulation, malaria, dropsy, and skin conditions, but incorrect dosage can cause central nervous system (CNS) depression and other toxic effects. Moreover, the plant demonstrates potential for phytoremediation of pollutants.

Ricinus communis (castor oil plant) is widely cultivated as both an ornamental species and a source of valuable oil, particularly in irrigated fields and garden soils. The plant shows considerable potential for phytoremediation of heavy metals and organic pollutants. R. communis preferentially accumulates heavy metals such as cadmium (Cd), manganese (Mn), nickel (Ni), and lead (Pb) in its leaves, while vanadium (V) concentrates in the roots. These metals can reach toxic levels when their concentrations in the growth medium exceed specific thresholds [74,75]. Additionally, R. communis effectively degrades and removes persistent organic pollutants (POPs), hexachlorocyclohexane (HCH), DDT, heptachlor, and aldrin. Bauddh et al. [76] highlighted R. communis as a promising non-edible phytoremediator, noting its resilience and multipurpose utility as an industrially important, oil-yielding shrub. Recent studies indicate that microorganisms associated with R. communis may significantly enhance both bioremediation and phytoremediation processes [43,44,54].

Salsola imbricata has densely pubescent leaves and salt-accumulating tissues that confer resistance to herbivory. The species exhibits notable antioxidant and antimicrobial activities, mainly due to its complex phytochemical profile. Aerial extracts are rich in secondary metabolites, including phenolic acids, fatty acids, and steroids, all contributing to their bioactivity. In vitro antimicrobial assays reveal significant inhibitory effects against multiple bacterial and fungal strains, with activity levels varying according to extract concentration. These findings highlight the potential of S. imbricata extracts as natural agents in agricultural applications and warrant further investigation into their mechanisms of action and practical efficacy.

Tetraena qatarensis is a halophytic and drought-tolerant plant with leathery leaves that synthesises a diverse array of secondary metabolites both endogenously and through associated endophytic microorganisms. These metabolites include alkaloids, terpenoids, and flavonoids, many of which serve as chemical defences by deterring herbivores or exerting toxicity towards them. Additionally, certain endophytic fungi and bacteria produce bioactive compounds with antifungal and antibacterial properties, potentially impacting herbivores by interfering with their digestive processes. The combined action of plant- and microbe-derived metabolites illustrates the multifaceted chemical defence strategies employed by *T. qatarensis*, underscoring its ecological resilience and potential for bioactive compound exploration.

Over the past four decades, a substantial body of research, including numerous studies and monographs, has been published on the chemical constituents and phytochemistry of various macroalgae, cyanobacteria, and native plants, including rangeland species, poisonous plants, and horticultural varieties. Readers are encouraged to consult these monographs for more detailed information [15,69,77–79].

3.2. Qatari Native Plants Resist Pathogens

Wild plants in Qatar have developed numerous mechanisms to either avoid or tolerate abiotic stressors, as highlighted in several studies [3,9,10]. These strategies may also enhance resistance to biotic factors, including living organisms such as microorganisms and pathogens. This resistance is achieved by inducing changes in the chemical composition of both internal and external plant structures. External structures, such as the cuticle, natural openings like stomata, and wounds, potentially provide pathways for pathogens to access the plants' internal compartments.



3.2.1. The Role of the Cuticle

The epidermis, the outermost cellular layer of plants, is enveloped by a protective cuticle primarily composed of cutin, a waxy and hydrophobic biopolymer. This cuticular layer plays a crucial role in minimising transpirational water loss and acts as a frontline defence against pathogenic invasion. Structurally, cutin is a cross-linked polyester mainly synthesised from C16 and C18 hydroxy fatty acids, which may have up to three hydroxyl functional groups. Representative monomers include 16-hydroxypalmitic acid, 9,16-dihydroxypalmitic acid, and 10,16-dihydroxypalmitic acid in the C16 series. In the C18 group, compounds such as 18-hydroxyoleic acid, 9,10-epoxy-18-hydroxystearic acid, and 9,10,18-trihydroxystearic acid are found. The inherent hydrophobicity and resistance to enzymatic degradation of cutin contribute to its effectiveness as a barrier, promoting water conservation and enhancing the plant's resilience to both abiotic and biotic stressors. Additionally, the cuticle serves as a mechanical barrier, preventing the penetration of microorganisms into internal plant tissues.

Early studies on wheat plants [16] clearly show that plants exposed to salinity have thicker cuticles. This thick cuticle plays a crucial role in several aspects: (1) Xerophytes and halophytes possess thick cuticles as a strategy to protect against water loss through transpiration, thereby conserving water under drought and salinity conditions. (2) The cuticle acts as a physical barrier, protecting the plant from excessive salt entry through the epidermis, which can damage the internal structures of cell organelles. (3) Chemically specialised, the thick cuticle withstands extreme environmental conditions such as intense heat, water scarcity, high radiation - including UV - and microbial attacks, particularly through tissue damage. (4) A thick cuticle generally signifies a high wax load, including long-chain alkanes, fatty alcohols, and esters, and contains higher proportions of triterpenoids and phenolic compounds. (5) These compounds are antimicrobial and enhance the cuticle's hydrophobicity, thereby reducing transpiration. (6) Salt crystals on the leaf surface play vital roles in halophytes, including excess salt removal, leaf surface cooling, maintaining osmotic balance for water flow from the soil to aerial parts, and providing antimicrobial protection. (7) Stomatal behaviour is a critical strategy restricting microbial entry into plant tissues. While the thick cuticle serves as a physical barrier against pathogens, partial or complete stomatal closure adds an additional defence layer by limiting pathogen access through natural openings. However, the internal tissues of desert plants and halophytes often remain vulnerable, as drought and salt stress can impair immune responses by redirecting resources away from defence mechanisms, thus increasing susceptibility to infection. Interestingly, stress-induced modifications like cuticle thickening and stomatal closure, primarily adaptations to abiotic stress, also reduce pathogen entry [80-82]. Consequently, stomatal closure functions not only as a key adaptation to abiotic stresses such as drought and salinity but also as a critical defence against microbial invasion, acting as a "door-closing" strategy that restricts pathogen entry through the pores. Nonetheless, this protective role may be compromised when environmental stresses weaken the plant's immune system, thereby increasing disease susceptibility in desert plants and halophytes [83,84].

In contrast, mesophytic plants typically thrive in temperate, moist environments and have a less chemically fortified cuticle. This group includes most crop species – such as wheat, corn, beans, and tomatoes – as well as various garden and forest plants, including deciduous trees and grasses. These plants generally have a thinner cuticle with lower wax content. The waxes they produce usually exhibit simpler chemical profiles, often composed of shorter-chain hydrocarbons. Mesophytes also contain fewer compounds associated with antimicrobial activity or UV protection, and their overall surface hydrophobicity is lower since water conservation is less critical in their native habitats. Table 1 compares desert plants with mesophytes (non-stressed plants), highlighting key differences in the structural and chemical characteristics of their outer protective layers.

Table 1. Desert plants versus non-stressed plants in terms of some structural and chemical features related to the harsh environments in the Arabian Gulf region.

Features	Desert plants	Mesophytes	Observations
		(non-stressed plants)	
Thickness of cuticle	Thick and waxy	Thin to moderate	Increase in the lipid content of the cuticle, wax biosynthesis by CER1* [85]
Cutin composition	Highly polymerised; includes esters of fatty acids, aliphatic polymers: cutan, stress-adapted	Primarily polyester of hydroxy and/or epoxy fatty acids, less complex and thinner	Less cutan in mesophytes unless under stress [86]
Wax content	High; contains long-chain hydrocarbons	Moderate; composed of simpler compounds	Little information, needs further investigation, more wax per surface area, which reduces non-stomatal water loss under stress conditions [87]
Antimicrobials in the cuticle	Abundant phenolics and terpenoids	Few phenolics and terpenoids (produced mainly during pathogen attack)	Secondary metabolites such as phenolics such as flavonoids, tannins), and the presence of terpenoids, as protective and signaling roles [88]
Salt crystals in cuticle	Present	Absent	Salt crystals might prevent microbial attack, unless adapted [89]
Phenolics	High concentration	Low to moderate level	Play roles as antimicrobials and antioxidants [90]
Stress hormones (Abscisic acid; ABA)	Elevated	Normal physiological levels	The presence of ABA to regulate stomatal movements [91]
Osmo-protectants	Present such as proline and glycine-betaine, etc.	Almost absent	The presence of compatible solutes to prevent water loss [92]
Reactive oxygen species (ROS)	Constitutively Active	Induced only under stress	The scavenging systems include ascorbate and glutathione [93]

^{*}CER1: Agen found in many plants that encodes an enzyme critical for the biosynthesis of cuticular waxes, particularly alkanes, which are major components of the plant cuticle, ** Among desert plants. only halophytes have salt crystals. .

Environmental stress conditions can induce significant physiological and biochemical responses in native wild plants of Qatar, bolstering their defences against both abiotic and biotic factors. Drought and salinity, for instance, create osmotic and ionic imbalances that trigger a cascade of stress responses at cellular and molecular levels. A key adaptation involves enhancing or modifying cutin biosynthesis, the process that forms the cutin polymer contributing to the plant's outer cuticle. These modifications can strengthen the cuticle barrier, reduce water loss, and increase resistance to environmental stresses and pathogen invasion. The potential mechanisms include: (1) an increase in cuticular lipid content, (2) thickening of the cuticle, (3) elevated gene expression related to cutin biosynthesis, (4) negative impacts on photosynthesis, (5) activation of antioxidants, and (6) membrane remodeling.

3.2.2. Key Pathways and Enzymes Involved in Cutin Biosynthesis

Kolattukudy and his colleagues' early work offered foundational insights into the biosynthesis of wax and cutin in plant cuticles [94,95]. Many authors have further elaborated on the biosynthesis of wax components. Scientists and students interested in this topic are encouraged to review relevant studies and monographs for additional details [96–98]. Two primary groups of enzymes play direct roles in cutin biosynthesis, while three other groups, which include enzymes, proteins, and genes, may contribute indirectly, particularly under severe environmental conditions.

(A) Glycerol-3-phosphate acyltransferases (GPATs) are essential enzymes in the synthesis of cutin. They catalyse the acylation of glycerol-3-phosphate (G3P) by esterifying acyl groups at the sn-2-position of G3P.

GPAT

Glycerol-3-phosphate+Acyl-CoA

Lysophosphatidic acid (LPA)+CoA

GPAT (glycerol-3-phosphate acyltransferase) exists in multiple isoforms, some of which are directly involved in cutin biosynthesis. When the GPAT catalysed reaction is followed by dephosphorylation via a phosphatase, it produces sn-2 monoacylglycerol (2-MAG), a key intermediate in this pathway [99]. In *Arabidopsis*, specific isoforms such as GPAT4, GPAT6, and GPAT8 catalyse the acylation of glycerol-3-phosphate or 2-MAG with ω -hydroxy fatty acids, which are precursors for cutin monomers. Sui et al. [100] demonstrated that salt stress induces the expression and activity of GPAT in the halophyte *Suaeda salsa*, a species found in the flora of Qatar. GPAT is crucial in helping the plant adjust its membrane lipid composition to withstand the detrimental effects of salinity. When the gene encoding this enzyme is expressed in *Arabidopsis*, it enhances physiological functions, including membrane stability, water retention, and salt tolerance. These findings confirm the enzyme's significant role in improving plant resilience under saline conditions. Beyond its role in stress responses, GPAT is involved in the biosynthesis of cutin – a polyester forming part of the plant cuticle on aerial surfaces – where it contributes to pathogen defence, environmental stress resistance, and maintenance of organ integrity.

(B) Cytochrome P450 Monooxygenases (CYP86 and CYP77 Families): Environmental stresses, including salinity and water deficit, significantly influence the activity of cytochrome P450 (CYP) monooxygenases. These enzyme families are integral to cutin biosynthesis in plants. Specific members, such as CYP709B3, are also involved in abscisic acid (ABA) biosynthesis, which regulates stomatal movement and facilitates plant responses under salt stress [101]. The role of cytochrome P450 monooxygenases in cutin biosynthesis is crucial for enhancing salt resistance, as cutin forms a protective barrier that reduces water loss. These enzymes participate in various plant growth and developmental processes, helping mitigate a range of stress conditions [102]. The following equations illustrate the initial steps in the biosynthesis of hydroxy fatty acids, which serve as precursors for cutin monomers.

Hydroxylated fatty acids are subsequently polymerised to form cutin, a key structural component of the plant cuticle. Studies have demonstrated that salt stress upregulates the activity and expression of CYP86 and CYP77 family members (Cytochrome P450, families 86 and 77, respectively) as part of the plant's adaptive strategy to enhance barrier properties. These enzymes catalyse the hydroxylation of fatty acids involved in cutin and suberin biosynthesis. This process reinforces the cuticle and suberized tissues, reducing water loss and limiting ion intrusion under salt

stress. The cuticle serves a dual role: acting as a physical barrier against biotic and abiotic stresses and containing bioactive compounds, such as phenolics, with antimicrobial activity. Chakraborty et al. [103] confirmed that CYPs are essential not only for cuticle formation but also for detoxifying xenobiotics in plants, insects, and other organisms, as well as in the biosynthesis of secondary metabolites, antioxidants, and phytohormones in higher plants. Given that plant growth and development are constantly challenged by biotic and abiotic stresses, the contribution of *CYP86* genes is particularly significant. Certain *CYP86* genes, along with their downstream targets, enhance stress tolerance through two main mechanisms: (a) promoting the synthesis of protective lipids and waxes – including cutin, suberin, and wax esters – which strengthen the plant's outer layers and contribute to cuticle formation, and (b) regulating the production of compatible solutes that mitigate the adverse effects of salt stress. These solutes include osmolytes such as proline, glycine betaine, and sugars like trehalose and raffinose, as well as antioxidants such as ascorbic acid (vitamin C), glutathione, carotenoids, flavonoids, and phenolic compounds.

(C) Long-chain acyl-CoA synthetases (LACS) catalyse the activation of long-chain fatty acids into acyl-Co As, providing crucial precursors for various lipid metabolic pathways, including but not limited to cutin biosynthesis. During cutin formation, these acyl-Co As, are integrated into monomers, which are then polymerised to form the cuticle. The cuticle serves as a protective barrier that minimises water loss and limits pathogen invasion. The following equation summarises the reaction catalysed by LACS enzymes.

R-COOH: Long-chain fatty acid (e.g., C16-C20), CoA-SH: Coenzyme A, R-CO-SCoA: The activated long-chain acyl-CoA, and ATP is hydrolysed to AMP + Pyrophosphate (PP_i).

Environmental stresses markedly affect plant survival by altering the activity of LACS in native plants, such as halophytes and xerophytes [104]. These enzymes play a critical role in lipid biosynthesis, including the synthesis of cuticular wax, which serves as a protective barrier against abiotic and biotic stresses [105]. Changes in LACS activity can modify the structure and permeability of the cuticle, thereby influencing plant responses to environmental stresses like drought, salinity, and pathogens [106].

- (D) *Bodyguard* (*BDG*) and *Hothead* (*HTH*) are genes found in *Arabidopsis thaliana*, a well-established model organism for molecular genetic studies. These genes encode distinct proteins involved in cutin biosynthesis. *BDG* encodes an α/β -hydrolase fold protein that plays a role in assembling cutin polymers. In contrast, *HTH* encodes a putative oxidoreductase responsible for modifying cutin precursors. Specifically, *HTH* catalyses the oxidation of ω -hydroxy fatty acids into ω -oxo fatty acids, which are key intermediates in the production of cutin monomers. Both proteins may also help limit pathogen spread by maintaining cuticle integrity.
- (E) GDSL lipase-like proteins, such as cutin synthases, play a significant role in cutin biosynthesis. These enzymes facilitate both the hydrolysis and polymerisation of cutin monomers, thereby contributing to the formation of the initial cutin polymer network. Despite this involvement, many GDSL lipase-like proteins are not directly responsible for the primary synthesis of cutin. Instead, they are believed to aid in cuticle maturation and structural modification, functions that might become especially crucial during stress conditions.

3.2.3. ABA Biosynthesis and Its Role as a Stress Hormone

ABA is a crucial phytohormone with significant developmental and physiological roles [107]. It is primarily recognised as a stress hormone, accumulating in plants under abiotic stress conditions such as drought, salinity, and freezing [108,109]. In desert plants and halophytes, ABA is pivotal in regulating stomatal behaviour [110]. Mechanistically, ABA prompts ion efflux from guard cells,

reducing their turgor pressure and promoting stomatal closure [91]. Under water-deficit conditions, ABA accumulation in leaves leads to partial or complete stomatal closure, thereby reducing transpirational water loss. Although this response is vital for conserving water, it simultaneously limits photosynthesis and can influence the susceptibility to pathogen ingress during stress [80]. Beyond stomatal regulation, extensive research indicates that ABA has diverse and sometimes opposing roles, acting both as a stress hormone and a stress-response regulator. Its accumulation in plant tissues, particularly in mesophyll and guard cells, presents both disadvantages and benefits. The disadvantages – often seen as stress indicators – include stomatal closure, reduced conductance (limiting photosynthesis, respiration, and transpiration), growth inhibition, and premature senescence. In contrast, the benefits of ABA accumulation include enhanced stress tolerance, water conservation, induction of seed and bud dormancy, promotion of senescence, and restriction of pathogen ingress under stress.

ABA biosynthesis shares intermediates with other plant hormones, particularly within the terpenoid pathway, while its catabolism primarily involves oxidation or conjugation reactions. Four main enzyme groups catalyse critical steps in ABA biosynthesis, with their activities significantly influenced by environmental stresses such as drought and salinity. These enzymes include zeaxanthin epoxidase (ZEP) and 9-cis-epoxycarotenoid dioxygenase (NCED), located in plastids, as well as short-chain dehydrogenase/reductase (SDR) and abscisic aldehyde oxidase (AAO), which operate in the cytosol [111].

The stress-induced activation of these enzymes results in increased ABA accumulation, allowing sessile plants to adjust their physiology and improve survival under adverse conditions. A primary example of this is stomatal regulation: ABA-induced ion efflux from guard cells decreases turgor pressure, leading to stomatal closure. This response reduces transpirational water loss but also limits gas exchange, photosynthesis, and transpiration. Although these trade-offs may increase susceptibility to certain biotic stresses, the restricted stomatal aperture can also act as a barrier to pathogen entry. Notably, enhanced ABA synthesis under stress significantly impacts the physiology and biochemistry of native plants, including halophytes and xerophytes [112,113].

Beyond the canonical biosynthetic pathway, other enzyme families may intersect with ABA-mediated stress responses. For instance, members of the CYP77 family, although not directly involved in ABA biosynthesis, contribute to processes such as cuticle and cell wall modifications that may indirectly affect ABA-related signaling. Under certain abiotic stress conditions, both the core ABA biosynthetic enzymes and, in some cases, CYP77 family members show elevated expression levels. While ABA's developmental and adaptive functions are well established, the precise role of CYP77 enzymes in ABA-mediated processes remains unclear. Further studies are necessary to elucidate the relationships between the CYP77 family and the canonical ABA biosynthetic machinery [112,114].

2.2.4. The Chemical Constituents of Native Plants

Several native Qatari plants demonstrate antimicrobial properties that enable them to resist pathogens. Additionally, some of these plants have been traditionally used to treat various ailments, indicating their potential as candidates for pathogen resistance. Table 2 lists some of these plants and their roles in pathogen resistance. However, other species may also possess these properties and warrant further investigation.

Table 2. Selected native plant species from the flora of Qatar [60] exhibiting resistance to pathogens.

Species		General characteristics	Specific features	References
Artemisia	herba-alba,	Medicinal plant	Source of active molecules,	[115,116]
Syn. Artemisia inculta*			extracts may be used to treat breast	
			cancer, antibacterial, and possibly	
			for other uses	

Echium horridium* 67	Madisinal plants might	Fortunate change antiquidant	[117 110]
species	Medicinal plants might contain fatty acids such as	Extracts show antioxidant, analgesic, anxiolytic, anti-	[117–119]
species	palmitic acid	inflammatory, antibacterial, and	
	1	antiviral effects	
Leptadenia pyrotechnica**	Medicinal plant	Produces bioactive compounds with pharmaceutical activities, exhibits antimicrobial properties, extracts can resist certain bacteria	[120,121]
		species like S. aureus, <i>E. coli</i> , and B. subtilis, and some fungi species such as <i>A. flavus</i> , and <i>F. moniliforme</i>	
Leucas urticifolia**	Medicinal plants contain phytochemicals, such as lignans, flavonoids, coumarins, steroids, terpenes, fatty acids, and aliphatic long-chain compounds	The presence of phytochemicals with antimicrobial properties, these constituents play roles in economic, social, cultural, and ecological aspects	[122–125]
Limonium axillare**	A huge number of bacterial isolates were obtained from leaves; many secondary metabolites were found in plant tissues that can play roles in biocontrol of microorganisms and contribute to sustainable agriculture	Antifungal activity, hosts fungal endophytes such as Aspergillus and Cladosporium, a huge number of bacterial isolates were obtained from leaves, while root and bark are sources of antidiabetic compounds	[126–128]
Lycium shawii, Syn. Lycium arabicum**	The most common shrub in Qatar responds phenotypically to water availability, from dried twiggy bare spiny bushes to green leafy plants, medicinal plants, the presence of alkaloids and sterols and terpenes, amino acids, fatty acids, and minerals	It exhibits a wide range of pharmacological properties, including antimicrobial, antioxidant, anti-diabetic, anti-inflammatory, anti-cancer, antitrypanosomal, hepatoprotective, antiplasmodial, and cytotoxic activities, making it a potential candidate for treating malaria through its therapeutic compounds	[129,130]
Rhanterium epapposum*	Medicinal plants and extracts show significant activity against bacteria and fungi, and are used to cure skin infections	Extracts show antimicrobial properties and antileishmanial activity	[131,132]
Ziziphus nummulariais*	Medicinal plants used in traditional folk medicine, rich in phytochemical constituents with pharmacological properties. These components include alkaloids, saponins, glycosides, tannins, and phenolic compounds	Extracts of this plant show a great deal of antibacterial and antifungal activities, exhibit, help to resist pathogens and treat various types of diseases, including cancer, diabetes, and cardiovascular diseases	[133,134]

^{*}Exhibit antimicrobial properties that help them resist pathogens, **Used for various ailments, can be possible candidates for pathogen resistance.

Native plants have evolved distinct morphological, anatomical, physiological, and biochemical traits that allow them to thrive in the harsh environments of Qatar and other areas within the Arabian

Gulf region. An early study by Abulfatih [135] detailed various morphological and anatomical characteristics of native species in Qatar, focusing on xerophytes and halophytes.

The recorded species include Calotropis procera, Cyperus conglomeratus, Fagonia ovalifolia, Glossonema varians (syn. Glossonema edule), Heliotropium bacciferum, Lycium shawii, Ochradenus baccatus, Sporobolus iocladus (syn. Sporobolus arabicus), Tamarix ramosissima, Vachellia flava (syn. Acacia ehrenbergiana), and Ziziphus nummularia (syn. Rhamnus nummularia). These species are morphologically and anatomically well-adapted to Qatar's harsh habitats. Many feature a thick cuticle and well-developed mechanical and supportive tissues, such as vascular bundles, fibres, and sclereids.

The thick cuticle of native plants offers protection against severe environmental stresses, such as excessive water loss under high temperatures and limited water availability. Yasseen and Al-Thani [3] observed that *Cyperus conglomeratus* and *Tetraena qatarensis* possess extensive root systems that facilitate water uptake. Concurrently, their cuticles serve as physical barriers preventing pathogen entry and aiding in water retention. Furthermore, the cuticle may play a role in chemical defence, as some plants produce antimicrobial substances within it that inhibit pathogen growth [29,136,137].

Moreover, when plants face pathogen attacks, they produce various chemical compounds – including phytoalexins, callose, and ROS – as part of their defence mechanisms. These compounds depend on signalling molecules such as salicylic acid, jasmonic acid, and ethylene, which coordinate the overall defence response [28,138]. Many of these signalling molecules are phytohormones essential for plant defence and stress adaptation [139]. In native plants, the cuticle contains additional chemical defences like alkaloids, tannins, and other secondary metabolites, which are toxic to pathogens and bolster the plant's overall immunity.

Considerable attention has been directed toward the internal chemical composition of native plants, which underpins their diverse stress-adaptive strategies. Rizk [77] reported on 301 plant species from 207 genera and 55 families, highlighting the extensive array of chemical constituents crucial to plant physiology and biochemistry in arid and semi-arid conditions. These adaptive strategies often depend on secondary metabolites that play roles in defence, stress signalling, and the accumulation of protective solutes. Notable metabolites include phenolics, such as flavonoids and tannins, which possess antimicrobial and antioxidant properties; alkaloids, primarily associated with anti-herbivory defence; and terpenoids, essential for protection and signalling. Additional metabolite classes comprise steroids, glycosides, coumarins, organic acids, quinones, iridoids, glucosinolates, and cyanogenic glycosides [140].

Several studies have provided detailed insights into these constituents and their roles across different plant groups. For example, Rizk and Al-Nowaihi [78] reported on the phytochemistry of 117 horticultural plant species, while Rizk and El-Ghazaly [69] explored the uses of 184 medicinal and poisonous species. Furthermore, Al-Easa et al. [15] presented comprehensive information on the nutritional values of 162 range plant species. Distinguishing sharply between these groups can be challenging, as some plants serve multiple purposes. For instance, certain range species are edible for livestock but also possess medicinal or toxic properties, posing risks if consumed in excess. *Blepharis* spp., comprising approximately 129 species, is a valuable source of medicinal compounds. Extracts from these plants have demonstrated significant antibacterial, antifungal, anti-ulcer, and cytotoxic activities [141,142], highlighting their therapeutic potential. Interestingly, this plant is grazed by camels but not by sheep or goats [15], a pattern consistently noted in various studies and monographs.

The biosynthesis of these compounds in native plants inhabiting harsh environments likely requires substantial energy and involves numerous intermediate metabolites, highlighting their ecological significance. Furthermore, a wide range of osmolytes, such as proline, glycine betaine, and their derivatives, play critical protective roles under stress conditions. These roles include regulating osmotic balance, maintaining turgor and hydration, stabilising enzymes, and cellular structures, acting as nitrogen and energy reservoirs, and preserving chloroplast integrity to sustain photosynthesis, thereby enhancing tolerance to extreme environmental stress [7,43,54,143–146].

However, the synthesis of such compatible solutes demands considerable energy and metabolic resources, which could otherwise support growth and tissue development, often resulting in reduced productivity under prolonged stress.

ABA biosynthesis under stress relies on two crucial metabolites: farnesyl pyrophosphate (FPP) and violaxanthin (Vx). FPP serves as a central precursor for various isoprenoids, including carotenoids, sterols, and ubiquinones. In contrast, Vx plays a role in the xanthophyll cycle, protecting Photosystem II by dissipating excess light energy and reducing photoinhibition [147]. Since ABA formation utilises the terpenoid pathway, it competes with other hormone biosynthetic routes, such as those for cytokinins, brassinosteroids, gibberellins, and strigolactones. All these pathways ultimately originate from acetyl-CoA, a vital metabolite produced via glycolysis, the TCA cycle, and interconnected metabolic fluxes. Consequently, stress adaptation in plants involves a significant diversion of energy and metabolic intermediates, necessitating a balance between survival and growth [148].

Abiotic stresses, including drought, salinity, and extreme temperatures, can drastically alter chemical composition and disrupt metabolic processes. Maintaining stress-induced pathways requires substantial energy, depletes reserves, and may compromise defence mechanisms, increasing susceptibility to bacterial and fungal pathogens. These physiological adjustments may also diminish the palatability and nutritional value of plants as forage, impacting both ecological interactions and economic utility [149]. Additionally, abiotic stresses reshape metabolic profiles and phytohormone signalling, which can either compromise immunity – thus heightening vulnerability to pathogens – or, in some situations, prime defence responses that enhance resistance [150,151]. Further comprehensive studies are needed to elucidate how stress-induced changes in internal chemical constituents, including the accumulation of compatible solutes, stress hormones, and secondary metabolites, affect plant adaptation and resilience.

4. Concluding Remarks

Most native plants adapted to extreme environments – such as halophytes and xerophytes – employ survival strategies that require substantial energetic and metabolic investments. Rather than focusing on rapid growth, these plants allocate resources to develop protective structures and biochemical defences, enabling them to endure harsh conditions. Features such as thick cuticles, lignified cell walls, compatible solutes, and diverse secondary metabolites protect them from osmotic stress, ion toxicity, dehydration, and pathogen attack. These adaptations emphasise evolutionary persistence and resilience over productivity, ensuring survival in ecosystems where only the most robust traits can sustain life.

While their survival-focused strategy limits direct agricultural value, such plants fulfil critical ecological roles by preventing soil erosion, maintaining biodiversity, and facilitating habitat restoration. Additionally, they serve as reservoirs of stress-tolerance genes with potential applications in breeding resilient crops. Introducing these traits, however, often involves a trade-off, as enhanced stress tolerance can reduce yield – a universal balance between survival and productivity. The accumulation of ABA exemplifies this paradox: while it triggers protective physiological and biochemical responses, it can simultaneously restrict growth. Nonetheless, it also strengthens plant defences against pathogens when immunity is compromised.

The primary challenge moving forward is to achieve a balance between developing crops that can withstand environmental stresses and maintaining acceptable productivity, particularly in regions prone to desertification, salinisation, and pollution. Advances in biotechnology and molecular breeding offer promising approaches to combine the resilience of native stress-adapted plants with the yield potential of conventional cultivars, a crucial step in securing global food supplies under increasing climatic pressures. In this context, an in-depth study of Qatar's native flora – including their morphological traits, ecological functions, and bioactive compounds – could provide a strategic framework for researchers, academic institutions, and students. These plants represent invaluable genetic and biochemical resources with potential contributions to health,

environmental sustainability, and agriculture, positioning them as a cornerstone for innovative solutions to both regional and global challenges.

Author Contributions: These authors contributed equally to this work.

Funding Information: This research received no external funding.

Acknowledgments: The authors thank Qatar University for its continuous support and encouragement of scientific publications. They also express their gratitude to Nada Abbara for designing Figure 1 and the graphical abstract (GA). Editing services were provided by AME (Kevin), USA.

Conflict of Interest: Conflicts of Interest: The authors declare no conflict of interest.

Ethics Statements: No ethical approval was required for this study as it relied solely on publicly available data.

References

- 1. Orcutt, D.M.; Nilsen, E.T. *Physiology of Plants Under Stress: Soil and Biotic Factors*; John Wiley & Sons, Inc.: New York, NY, USA, 2000.
- 2. Montesinos, E. Plant-associated microorganisms: A view from the scope of microbiology. *Int. Microbiol.* **2003**, *6*, 221–223.
- 3. Yasseen, B.T.; Al-Thani, R.F. Ecophysiology of Wild Plants and Conservation Perspectives in the State of Qatar. In *Agricultural Chemistry*; Stoytcheva, M., Zlatev, R., Eds.; InTech: Rijeka, Croatia, 2013; pp. 37–70.
- 4. Lu, H.; Wei, T.; Lou, H.; Shu, X.; Chen, Q. A critical review on communication mechanism within plant-endophytic fungi interactions to cope with biotic and abiotic stresses. *J. Fungi* **2021**, *7*, 719.
- 5. Abdelfattah, A.; Tack, A.; Lobato, C.; Wassermann, B.; Berg, G. From seed to seed: The role of microbial inheritance in the assembly of the plant microbiome. *Trends Microbiol.* **2023**, *31*, 346–358.
- 6. Abulfatih, H.A.; Abdel-Bari, E.M.; Alsubaey, A.; Ibrahim, Y.M. *Vegetation of Qatar*; Scientific and Applied Research Center (SARC), University of Qatar: Doha, Qatar, 2001.
- 7. Levitt, J. Responses of Plants to Environmental Stresses. Vol. II. Water, Radiation, Salt, and Other Stresses; Academic Press: New York, NY, USA; London, UK, 1980.
- 8. Larcher, W. Physiological Plant Ecology. Eco-physiology and Stress Physiology of Functional Groups, 4th ed.; Springer: Berlin, Germany, 2003.
- 9. Abdel-Bari, E.M.; Yasseen, B.T.; Al-Thani, R.F. *Halophytes in the State of Qatar*; Environmental Studies Center, University of Qatar: Doha, Qatar, 2007.
- 10. Yasseen, B.T.; Al-Thani, R.F. Endophytes, and halophytes to remediate industrial wastewater and saline soils: Perspectives from Qatar. *Plants* **2022**, *11*, 1497.
- 11. Batanouny, K.H. Plants in the Deserts of the Middle East; Springer: Berlin, Heidelberg, Germany, 2001.
- 12. Mahasneh, A.M. Screening of some indigenous Qatari medicinal plants for antimicrobial activity. *Phytother. Res.* **2002**, *16*, 751–753.
- 13. Othman, L.; Sleiman, A.; Abdel-Massih, R.M. Antimicrobial activity of polyphenols and alkaloids in Middle Eastern plants. *Front. Microbiol.* **2019**, *10*, 911.
- 14. Norton, J.; Abdul Majid, S.; Allan, D.; Al Safran, M.; Böer, B.; Richer, R. *An Illustrated Checklist of the Flora of Qatar*; UNESCO Office in Doha, Qatar Foundation, MAERSK OIL QATAR AS: Doha, Qatar, 2009.
- 15. Al-Easa, H.S.; Rizk, A.M.; Abdel-Bari, E.M. *Chemical Constituents and Nutritive Values of Range Plants in Qatar*; Scientific and Applied Research Centre, University of Qatar: Doha, Qatar, 2003.
- 16. Yasseen, B.T. An Analysis of the Effects of Salinity on Leaf Growth in Mexican Wheats. Ph.D. Thesis, University of Leeds, Leeds, UK, 1983.
- 17. Chonan, N. Studies on the photosynthetic tissues in the leaves of cereal crops. I. The mesophyll structure of wheat leaves inserted at different levels of the shoot. *Proc. Crop Sci. Soc. Jpn.* **1965**, *33*, 388–393.
- 18. Longstreth, D.J.; Nobel, P.S. Salinity effects on leaf anatomy. Consequences for photosynthesis. *Plant Physiol.* **1979**, *63*, 700–703.
- 19. Yasseen, B.T.; Abu-Al-Basal, M.A.; Alhadi, F.A. An Analysis of leaf growth under osmotic stress. *J. Plant Sci.* **2010**, *5*, 391–401.



- 20. Yasseen, B.T.; Al-Thani, R.F. Wild plants in the Qatari peninsula are hidden gene bank for future research: Perspectives of desirable traits. In *Cutting Edge Research in Biology*; BP International: London, UK, 2023; Volume 8, pp. 207–252.
- Tripathi, G.; Gravit, P.; Stany, B.; Mishra, A.; Basu, S.; Tripathi, S. Stress Determination in Plants: Morphological, Biochemical, and Molecular Parameters. In *Plant-Microbe Interactions for Environmental and Agricultural Sustainability*; Pandey, A., Choure, K., El-Sheekh, M., Yadav, A.N., Eds.; Springer: Cham, Switzerland, 2025; pp. 345–378.
- 22. Neves, J.; Sampaio, M.; Séneca, A.; Pereira, S.; Pissarra, J.; Pereira, C. Abiotic stress triggers the expression of genes involved in protein storage vacuole and exocyst-mediated routes. *Int. J. Mol. Sci.* **2021**, 22, 10644.
- 23. Zhang, Y.; Xu, J.; Li, R.; Ge, Y.; Li, Y.; Li, R. Plants' response to abiotic stress: Mechanisms and strategies. *Int. J. Mol. Sci.* **2023**, 24, 10915.
- 24. Abdulraheem, M.I.; Xiong, Y.; Moshood, A.Y.; Cadenas-Pliego, G.; Zhang, H.; Hu, J. Mechanisms of plant epigenetic regulation in response to plant stress: Recent discoveries and implications. *Plants* **2024**, *13*, 163.
- 25. Nilsen, E.T.; Orcutt, D.M. *The Physiology of Plants Under Stress: Abiotic Factors*, 2nd ed.; John Wiley & Sons, Inc.: New York, NY, USA, 1996; Volume 1.
- 26. Conkey, A.T.; Purchase, C.; Richer, R.; Yamaguchi, N. Terrestrial Biodiversity in Arid Environments: One Global Component of Climate Crisis Resilience. In *Sustainable Qatar. Gulf Studies*; Cochrane, L., Al-Hababi, R., Eds.; Springer: Singapore, 2023; Volume 9, pp. 241–265.
- 27. Andersen, E.J.; Ali, S.; Byamukama, E.; Yen, Y.; Nepal, M.P. Disease resistance mechanisms in plants. *Genes* **2018**, *9*, 339.
- 28. Kaur, S.; Samota, M.K.; Choudhary, M.; Choudhary, M.; Pandey, A.K.; Sharma, A.; Thakur, J. How do plants defend themselves against pathogens-Biochemical mechanisms and genetic interventions. *Physiol. Mol. Biol. Plants* **2022**, *28*, 485–504.
- 29. Jian, Y.; Gong, D.; Wang, Z.; Liu, L.; He, J.; Han, X.; Tsuda, K. How plants manage pathogen infection. *EMBO Rep.* **2024**, 25, 31–44.
- 30. Kariyat, R.R.; Hardison, S.B.; De Moraes, C.M.; Mescher, M.C. Plant spines deter herbivory by restricting caterpillar movement. *Biol. Lett.* **2017**, *13*, 20170176.
- 31. War, A.R.; Paulraj, M.G.; Ahmad, T.; Buhroo, A.A.; Hussain, B.; Ignacimuthu, S.; Sharma, H.C. Mechanisms of plant defense against insect herbivores. *Plant Signal. Behav.* **2012**, *7*, 1306–1320.
- 32. Sevanto, S. Why do plants have waxy leaves? Do we know after all? Tree Physiol. 2020, 40, 823-826.
- 33. Mageroy, M.H.; Nagy, N.E.; Stefenrem, A.; Krokene, P.; Hietala, A.M. Conifer defences against pathogens and pests-mechanisms, breeding, and management. *Curr. For. Rep.* **2023**, *9*, 429–443.
- 34. Xu, H.; Lybrand, D.; Bennewitz, S.; Tissier, A.; Last, R.L.; Pichersky, E. Production of trans-chrysanthemic acid, the monoterpene acid moiety of natural pyrethrin insecticides, in tomato fruit. *Metab. Eng.* **2018**, 47, 271–278.
- 35. Plant Disease-Edexcel, Plant Defense. Available online: https://www.bbc.co.uk/bitesize/guides/z29trwx/revision/3 (accessed on 20 July 2025).
- 36. Kocyigit, E.; Kocaadam-Bozkurt, B.; Bozkurt, O.; Ağagündüz, D.; Capasso, R. Plant toxic proteins: Their biological activities, mechanism of action and removal strategies. *Toxins* **2023**, *15*, 356.
- 37. Jahan, T.; Nurul Huda, M.; Zhang, K.; He, Y.; Lai, D.; Dhami, N.; Quinet, M.; Ali, M.A.; Kreft, I.; Woo, S.-H.; Georgiev, M.I.; Fernie, A.R.; Zhou, M. Plant secondary metabolites against biotic stresses for sustainable crop protection. *Biotechnol. Adv.* **2025**, *79*, 108520.
- 38. Fahmy, G.M.; Al-Thani, R.F. Components of water potential and concentrations of nutrient elements in the holoparasitic angiosperm *Cynomorium coccineum* L. and its host. *Flora* **2025**, *330*, 152786.
- 39. Khare, E.; Mishra, J.; Arora, N.K. Multifaceted interactions between endophytes and plant: Developments and prospects. *Front. Microbiol.* **2018**, *9*, 2732.
- 40. Etemadi, N.; Müller, M.; Etemadi, M.; Brandón, M.G.; Ascher Jenull, J. Salt tolerance of *Cressa cretica* and its rhizosphere microbiota. *Biologia* **2020**, *75*, 355–366.
- 41. Ullah, A.; Mushtaq, H.; Ali, U.; Hakim; Ali, E.; Mubeen, S. Screening, isolation, biochemical and plant growth promoting characterization of endophytic bacteria. *Microbiol. Curr. Res.* **2018**, 2, 62–68.

- 42. Al-Thani, R.F.; Yasseen, B.T. Halo-thermophilic bacteria and heterocyst cyanobacteria found adjacent to halophytes at Sabkhas Qatar: Preliminary study and possible roles. *Afr. J. Microbiol. Res.* **2017**, *11*, 1346–1354.
- 43. Al-Thani, R.F.; Yasseen, B.T. Solutes in native plants in the Arabian Gulf region and the role of microorganisms: Future research. *J. Plant Ecol.* **2018**, *11*, 671–684.
- 44. Al-Thani, R.F.; Yasseen, B.T. Biological soil crusts, and extremophiles adjacent to native plants at Sabkhas and Rawdahs, Qatar: The possible roles. *Front. Environ. Microbiol.* **2018**, *4*, 55–70.
- 45. Al-Thani, R.F.; Yasseen, B.T. Possible future risks of pollution consequent to the expansion of oil and gas operations in Qatar. *Environ. Pollut.* **2023**, *12*, 12–52.
- 46. Singh, M.; Singh, S.K.; Sharma, J.G.; Giri, B. Insights into the multifaceted roles of soil microbes in mitigating abiotic stress in crop plants: A review. *Environ. Exp. Bot.* **2024**, 228, 106010.
- 47. Chatzistathis, T.; Zoukidis, K.; Vasilikiotis, C.; Apostolidis, A.; Giannakoula, A.E.; Bountla, A.; Chatziathanasiadis, A. Plant-growth-promoting rhizobacteria and arbuscular mycorrhizal fungi may improve soil fertility and the growth, nutrient uptake, and physiological performance of batavia lettuce (*Lactuca sativa* L. var. longifolia) plants. *Horticulturae* 2024, 10, 449.
- 48. Ahmed, N.; Li, J.; Li, Y.; Deng, L.; Deng, L.; Chachar, M.; Chachar, Z.; Chachar, S.; Hayat, F.; Raza, A.; Umrani, J.H.; Gong, L.; Tu, P. Symbiotic synergy: How Arbuscular Mycorrhizal Fungi enhance nutrient uptake, stress tolerance, and soil health through molecular mechanisms and hormonal regulation. *IMA Fungus* 2025, 16, 144989.
- 49. Li, J.; Zhou, L.; Chen, G.; Yao, M.; Liu, Z.; Li, X.; Yang, X.; Yang, Y.; Cai, D.; Tuerxun, Z.; Li, B.; Nie, T.; Chen, X. Arbuscular mycorrhizal fungi enhance drought resistance and alter microbial communities in maize rhizosphere soil. *Environ. Technol. Innovation* **2025**, *37*, 103947.
- 50. Timofeeva, A.M.; Galyamova, M.R.; Sedykh, S.E. Plant growth-promoting soil bacteria: Nitrogen fixation, phosphate solubilization, siderophore production, and other biological activities. *Plants* **2023**, *12*, 4074.
- 51. Pan, L.; Cai, B. Phosphate-solubilizing bacteria: Advances in their physiology, molecular mechanisms, and microbial community effects. *Microorganisms* **2023**, *11*, 2904.
- 52. Egamberdieva, D.; Wirth, S.J.; Alqarawi, A.A.; Abd_Allah, E.F.; Hashem, A. Phytohormones and beneficial microbes: Essential components for plants to balance stress and fitness. *Front. Microbiol.* **2017**, *8*, 2104.
- 53. Ahmad, H.M.; Fiaz, S.; Hafeez, S.; Zahra, S.; Shah, A.N.; Gul, B.; Aziz, O.; Mahmood-Ur-Rahman; Fakhar, A.; Rafique, M.; Chen, Y.; Yang, S.H.; Wang, X. Plant growth-promoting rhizobacteria eliminate the effect of drought stress in plants: A review. *Front. Plant Sci.* **2022**, *13*, 875774.
- 54. Yasseen, B.T.; Al-Thani, R.F.; Alhadi, F.A.; Abbas, R.A.A. Soluble sugars in plants under stress at the Arabian Gulf region: Possible roles of microorganisms. *J. Plant Biochem. Physiol.* **2018**, *6*, 224.
- 55. Glick, B.R. Bacteria with ACC deaminase can promote plant growth and help to feed the world. *Microbiol. Res.* **2014**, *169*, 30–39.
- 56. Gamalero, E.; Lingua, G.; Glick, B.R. Ethylene, ACC, and the plant growth-promoting enzyme ACC deaminase. *Biology* **2023**, *12*, 1043.
- 57. Hidri, R.; Metoui Ben Mahmoud, O.; Debez, A.; Zorrig, W.; Abdelly, C.; Zamarreño, A.M.; García Mina, J.M.; Azcon, R.; Aroca, R. Dual PGPR AMF inoculation offsets salinity stress impact on the fodder halophyte *Sulla carnosa* by concomitantly modulating plant ABA content and leaf antioxidant response. *J. Plant Growth Regul.* 2024, https://doi.org/10.1007/s00344-024-11438-0.
- 58. Al-Thani, R.F.; Yasseen, B.T. Phytoremediation of polluted soils and waters by Native Qatari plants: Future perspectives. *Environ. Pollut.* **2020**, 259, 113694.
- 59. Al-Thani, R.F.; Yasseen, B.T.; Balakrishnan, P. Microorganisms and halophytes attracted to the northeast coast of Qatar for potential phytoremediation: A case study and analysis. *Int. J. Curr. Microbiol. Appl. Sci.* **2025**, *14*, 79–102.
- 60. Abdel-Bari, E.M.M. *The Flora of Qatar, The Dicotyledons (Vol. 1), The Monocotyledons (Vol. 2);* Environmental Studies Center, University of Qatar: Doha, Qatar, 2012.
- 61. Mazen, A.M.A. Crassulacean acid metabolism criteria shown by three species from flora of Qatar. *QRS Repository* **2011**, 2011, 2427. Available online: http://www.qscience.com/doi/abs/10.5339/qnrs.2011.2427 (accessed on 28 March 2025).

- 62. Ashore, M.M. Sabkhas in the Peninsula of Qatar– Geomorphologic and Geological and Biological Studies; Centre of Documentation and Humanitarian Studies, University of Qatar: Doha, Qatar, 1991.
- 63. Skariah, S.; Abdul-Majid, S.; Hay, A.G.; Acharya, A.; Kano, N.; Al-Ishaq, R.K.; de Figueiredo, P.; Han, A.; Guzman, A.; Dargham, S.R.; Sameer, S.; Kim, G.E.; Khan, S.; Pillai, P.; Sultan, A.A. Soil properties correlate with microbial community structure in Qatari arid soils. *Microbiol. Spectr.* **2023**, *11*, e0346222.
- 64. Alrajhei, K.; Saleh, I.; Abu-Dieyeh, M.H. Biodiversity of arbuscular mycorrhizal fungi in plant roots and rhizosphere soil from different arid land environment of Qatar. *Plant Direct* **2022**, *6*, e369.
- 65. Umar, A.; Mwaheb, M.A.; Ameen, F.; Almomani, F.; Dufossé, L.; Gancarz, M. Role of ectomycorrhizal colonization in enhancement of nutrients for survival of plants collected from mountainous cold stress areas. *BMC Microbiol.* **2024**, 24, 304.
- 66. Kant, M.R.; Jonckheere, W.; Knegt, B.; Lemos, F.; Liu, J.; Schimmel, B.C.; Villarroel, C.A.; Ataide, L.M.; Dermauw, W.; Glas, J.J.; Egas, M.; Janssen, A.; Van Leeuwen, T.; Schuurink, R.C.; Sabelis, M.W.; Alba, J.M. Mechanisms and ecological consequences of plant defense induction and suppression in herbivore communities. *Ann. Bot.* **2015**, *115*, 1015–1051.
- 67. Nawaz, M.; Sun, J.; Shabbir, S.; Khattak, W.A.; Ren, G.; Nie, X.; Bo, Y.; Javed, Q.; Du, D.; Sonne, C. A review of plants strategies to resist biotic and abiotic environmental stressors. *Sci. Total Environ.* **2023**, *900*, 165832.
- 68. Elgharib, A.; Trigo, M.M.; Moursy, M.M.; Soultan, A. Vegetation analysis and environmental relationships of Qatar's depression habitat. *Plants* **2025**, *14*, 1807.
- 69. Rizk, A.M.; El-Ghazaly, G.A. *Medicinal and Poisonous Plants of Qatar*; Scientific and Applied Research Centre, University of Qatar, The Doha Modern Printing Press, Ltd.: Doha, Qatar, 1995.
- 70. Divekar, P.A.; Narayana, S.; Divekar, B.A.; Kumar, R.; Gadratagi, B.G.; Ray, A.; Singh, A.K.; Rani, V.; Singh, V.; Singh, A.K.; Kumar, A.; Singh, R.P.; Meena, R.S.; Behera, T.K. Plant secondary metabolites as defense tools against herbivores for sustainable crop protection. *Int. J. Mol. Sci.* **2022**, *23*, 2690.
- 71. Vwioko, D.E.; Fashemi, D.S. Growth response of *Ricinus communis* L (Castor Oil) in spent lubricating oil polluted soil. *J. Appl. Sci. Environ. Manage.* **2005**, *9*, 73–79.
- 72. Kvesitadze, E.; Sadunishvili, T.; Kvesitadze, G. Mechanisms of organic contaminants uptake and degradation in plants. *World Acad. Sci. Eng. Technol.* **2009**, *55*, 458–468.
- 73. Yasseen, B.T. Phytoremediation of industrial wastewater from oil and gas fields using native plants: The research perspectives in the State of Qatar. *Cent. Eur. J. Exp. Biol.* **2014**, *3*, 6–23.
- 74. Vwioko, D.E.; Anoliefo, G.O.; Fashemi, S.D. Metal concentration in plant tissues of *Ricinus communis* L. (Castor Oil) grown in soil contaminated with spent lubricating oil. *J. Appl. Sci. Environ. Manage.* **2006**, *10*, 127–134.
- 75. Niu, Z.-X.; Sun, L.-N.; Sun, T.-H.; Li, Y.S.; Wang, H. Evaluation of phytoextracting cadmium and lead by sunflower, ricinus, alfalfa and mustard in hydroponic culture. *J. Environ. Sci.* **2007**, *19*, 961–967.
- 76. Bauddh, K.; Singh, K.; Singh, B.; Singh, R.P. *Ricinus communis*: A robust plant for bio-energy and phytoremediation of toxic metals from contaminated soil. *Ecol. Eng.* **2015**, *84*, 640–652.
- 77. Rizk, A.M. *The Phytochemistry of the Flora of Qatar*; Scientific and Applied Research Centre, University of Qatar, Kingprint: Richmond, UK, 1986.
- 78. Rizk, A.M.; Al-Nowaihi, A.S. *The Phytochemistry of the Horticultural Plants of Qatar*; The Scientific and Applied Research Centre, University of Qatar, The Alden Press: Oxford, UK, 1989.
- 79. Rizk, A.M.; Al-Easa, H.S.; Kornprobst, J.M. *The Phytochemistry of the Macro and Blue-Green Algae of the Arabian Gulf*; Faculty of Science, University of Qatar: Doha, Qatar, 1999.
- 80. Bharath, P.; Gahir, S.; Raghavendra, A.S. Abscisic acid-induced stomatal closure: an important component of plant defense against abiotic and biotic stress. *Front. Plant Sci.* **2021**, *12*, 615114.
- 81. Gahir, S.; Bharath, P.; Raghavendra, A.S. Stomatal closure sets in motion long-term strategies of plant defense against microbial pathogens. *Front. Plant Sci.* **2021**, *12*, 761952.
- 82. Meddya, S.; Meshram, S.; Sarkar, D.; Rakesh, S.; Datta, R.; Singh, S.; Avinash, G.; Kondeti, A.K.; Savani, A.K.; Thulasinathan, T. Plant stomata: An unrealized possibility in plant defense against invading pathogens and stress tolerance. *Plants* **2023**, *12*, 3380.
- 83. Lim, C.W.; Baek, W.; Jung, J.; Kim, J.H.; Lee, S.C. Function of ABA in stomatal defense against biotic and drought stresses. *Int. J. Mol. Sci.* **2015**, *16*, 15251–15270.



- 84. Miller, R.N.; Costa Alves, G.S.; Van Sluys, M.A. Plant immunity: unravelling the complexity of plant responses to biotic stresses. *Ann. Bot.* **2017**, *119*, 681–687.
- 85. Wang, X.; Kong, L.; Zhi, P.; Chang, C. Update on cuticular wax biosynthesis and its roles in plant disease resistance. *Int. J. Mol. Sci.* **2020**, *21*, 5514.
- 86. Devitt, J.K.; Chung, A.; Schenk, J.J. Inferring the genetic responses to acute drought stress across an ecological gradient. *BMC Genomics* **2022**, *23*, 3.
- 87. Seufert, P.; Staiger, S.; Arand, K.; Bueno, A.; Burghardt, M.; Riederer, M. Building a barrier: The influence of different wax fractions on the water transpiration barrier of leaf cuticles. *Front. Plant Sci.* **2022**, *12*, 766602.
- 88. Anjali; Kumar, S.; Korra, T.; Thakur, R.; Arutselvan, R.; Kashyap, A.S.; Nehela, Y.; Chaplygin, V.; Minkina, T.; Keswani, C. Role of plant secondary metabolites in defence and transcriptional regulation in response to biotic stress. *Plant Stress* **2023**, *8*, 100154.
- 89. Dassanayake, M.; Larkin, J.C. Making plants break a sweat: The structure, function, and evolution of plant salt glands. *Front. Plant Sci.* **2017**, *8*, 406.
- 90. Al-Haliem, S.M.; Mohammed, M.J.; Hesarinejad, M.A.; Abedelmaksoud, T.G. Antimicrobial, anti-biofilm activity and antioxidants of phenolic compounds isolated from Hypericum perforatum on periodontal pathogenic oral bacteria. *Food Sci. Nutr.* **2025**, *13*, e70336.
- 91. Hsu, P.K.; Dubeaux, G.; Takahashi, Y.; Schroeder, J.I. Signaling mechanisms in abscisic acid-mediated stomatal closure. *Plant J.* **2021**, *105*, 307–321.
- 92. Zia, R.; Nawaz, M.S.; Siddique, M.J.; Hakim, S.; Imran, A. Plant survival under drought stress: Implications, adaptive responses, and integrated rhizosphere management strategy for stress mitigation. *Microbiol. Res.* **2021**, 242, 126626.
- 93. Mohammed, H.A.; Emwas, A.H.; Khan, R.A. Salt-tolerant plants, halophytes, as renewable natural resources for cancer prevention and treatment: Roles of phenolics and flavonoids in immunomodulation and suppression of oxidative stress towards cancer management. *Int. J. Mol. Sci.* **2023**, *24*, 5171.
- 94. Kolattukudy, P.E. Biopolyester membranes of plants: cutin and suberin. Science 1980, 208, 990-1000.
- 95. Goodwin, T.W.; Mercer, E.I. *Introduction to Plant Biochemistry*, 2nd ed.; Pergamon Press: Oxford, UK, 1990; pp. 312–315.
- 96. Dennis, D.T.; Turpin, D.H. *Plant Physiology, Biochemistry, and Molecular Biology*; Longman Scientific & Technical: Essex, UK, 1993; pp. 339–325.
- 97. Lea, P.J.; Leegood, R.C. *Plant Biochemistry and Molecular Biology*; John Wiley & Sons: Chichester, UK; New York, NY, USA, 1993; p. 312.
- 98. Wang, X.; Chang, C. Exploring and exploiting cuticle biosynthesis for abiotic and biotic stress tolerance in wheat and barley. *Front. Plant Sci.* **2022**, *13*, 1064390.
- 99. Yang, W.; Pollard, M.; Li-Beisson, Y.; Beisson, F.; Feig, M.; Ohlrogge, J. A distinct type of glycerol-3-phosphate acyltransferase with sn-2 preference and phosphatase activity producing 2-monoacylglycerol. *Plant Biol.* **2010**, *107*, 12040–12045.
- 100. Sui, N.; Tian, S.; Wang, W.; Wang, M.; Fan, H. Overexpression of glycerol-3-phosphate acyltransferase from Suaeda salsa improves salt tolerance in Arabidopsis. *Front. Plant Sci.* **2017**, *8*, 1337.
- 101. Mao, G.; Seebeck, T.; Schrenker, D.; Yu, O. CYP709B3, a cytochrome P450 monooxygenase gene involved in salt tolerance in *Arabidopsis thaliana*. *BMC Plant Biol.* **2013**, *13*, 169.
- 102. Pandian, B.A.; Sathishraj, R.; Djanaguiraman, M.; Prasad, P.V.V.; Jugulam, M. Role of cytochrome P450 enzymes in plant stress response. *Antioxidants* **2020**, *9*, 454.
- 103. Chakraborty, P.; Biswas, A.; Dey, S.; Bhattacharjee, T.; Chakrabarty, S. Cytochrome P450 gene families: Role in plant secondary metabolites production and plant defense. *J. Xenobiot.* **2023**, *13*, 402–423.
- 104. Wei, H.; Movahedi, A.; Zhang, Y.; Aghaei-Dargiri, S.; Liu, G.; Zhu, S.; Yu, C.; Chen, Y.; Zhong, F.; Zhang, J. Long-chain acyl-CoA synthetases promote poplar resistance to abiotic stress by regulating long-chain fatty acid biosynthesis. *Int. J. Mol. Sci.* 2022, 23, 8401.
- 105. Zhao, H.; Kosma, D.K.; Lü, S. Functional role of long-chain acyl-CoA synthetases in plant development and stress responses. *Front. Plant Sci.* **2021**, *12*, 640996.
- 106. Zhao, P.; Li, Q.; Lei, Y.; Zou, J.; Li, Q. Adaptation of cuticle metabolism to abiotic stress in plants. *Crop Environ.* **2025**, *4*, 38–44.



- 107. Taiz, L.; Zeiger, E. *Plant Physiology*, 5th ed.; Sinauer Associates, Inc., Publishers: Sunderland, MA, USA, 2010.
- 108. Sah, S.K.; Reddy, K.R.; Li, J. Abscisic acid, and abiotic stress tolerance in crop plants. *Front. Plant Sci.* **2016**, 7, 571.
- 109. Rai, G.K.; Khanday, D.M.; Choudhary, S.M.; Kumar, P.; Kumari, S.; Martínez-Andújar, C.; Martínez-Melgarejo, P.A.; Rai, P.K.; Pérez-Alfocea, F. Unlocking nature's stress buster: Abscisic acid's crucial role in defending plants against abiotic stress. *Plant Stress* **2024**, *11*, 100359.
- 110. Aslam, M.; Waseem, M.; Jakada, B.H.; Okal, E.J.; Lei, Z.; Saqib, H.S.A.; Yuan, W.; Xu, W.; Zhang, Q. Mechanisms of abscisic acid-mediated drought stress responses in plants. *Int. J. Mol. Sci.* **2022**, *23*, 1084.
- 111. Mo, W.; Zheng, X.; Shi, Q.; Zhao, X.; Chen, X.; Yang, Z.; Zuo, Z. Unveiling the crucial roles of abscisic acid in plant physiology: implications for enhancing stress tolerance and productivity. *Front. Plant Sci.* **2024**, *15*, 1437184.
- 112. Kushiro, T.; Okamoto, M.; Nakabayashi, K.; Yamagishi, K.; Kitamura, S.; Asami, T.; Hirai, N.; Koshiba, T.; Kamiya, Y.; Nambara, E. The Arabidopsis cytochrome P450 CYP707A encodes ABA 8'-hydroxylases: key enzymes in ABA catabolism. *EMBO J.* **2004**, 23, 1647–1656.
- 113. Okamoto, M.; Kuwahara, A.; Seo, M.; Kushiro, T.; Asami, T.; Hirai, N.; Kamiya, Y.; Koshiba, T.; Nambara, E. CYP707A1 and CYP707A2, which encode abscisic acid 8'-hydroxylases, are indispensable for proper control of seed dormancy and germination in Arabidopsis. *Plant Physiol.* **2006**, 141, 97–107.
- 114. Saito, S.; Hirai, N.; Matsumoto, C.; Ohigashi, H.; Ohta, D.; Sakata, K.; Mizutani, M. Arabidopsis CYP707As encode (+)-abscisic acid 8'-hydroxylase, a key enzyme in the oxidative catabolism of abscisic acid. *Plant Physiol.* **2004**, *134*, 1439–1449.
- 115. Moussii, I.M.; Nayme, K.; Timinouni, M.; Jamaleddine, J.; Filali, H.; Hakkou, F. Synergistic antibacterial effects of Moroccan Artemisia herba alba, *Lavandula angustifolia* and *Rosmarinus officinalis* essential oils. *Synergy* **2020**, *10*, 100057.
- 116. Mohammed, S.; Alhusseini, L.B. Antibacterial and cytotoxic activities of different solvent extracts from Artemisia herba-alba against MCF-7 human breast cancer cells. *Contemp. Oncol.* **2025**, *29*, 159–164.
- 117. El Sahzly, A.; Abdel-All, M.; Tei, A.; Wink, M. Pyrrolizidine alkaloids from *Echium rauwolfii* and *Echium horridum* (Boraginaceae). Z. *Naturforsch. C* **1999**, *54*, 295–300.
- 118. Dawidar, A.M.; Ghani, A.; El-Shamy, M.; Tawfik, E.; Abdel-Mogib, M. Fatty Acid Pattern and Alkaloids of Echium Rauwolfii. *Int. J. Sci. Eng. Appl.* **2015**, *4*, 208–213.
- 119. Jin, J.; Boersch, M.; Nagarajan, A.; Davey, A.K.; Zunk, M. Antioxidant properties and reported ethnomedicinal use of the genus *Echium* (*Boraginaceae*). *Antioxidants* **2020**, *9*, 722.
- 120. Idrees, S.; Qureshi, R.; Bibi, Y.; Ishfaq, A.; Khalid, N.; Iftikhar, A.; Shabir, A.; Riaz, I.; Ahmad, S.N. Ethnobotanical and biological activities of *Leptadenia pyrotechnica* (Forssk.) Decne.: A Review. *Afr. J. Tradit. Complement. Altern. Med.* **2016**, *13*, 88–96.
- 121. El-Fitiany, R.A.; Khasawneh, M.A. *Leptadenia pyrotechnica* (Forsk) Decne: From edibility to drug discovery (A comparative review). *Food Rev. Int.* **2023**, *39*, 7580–7610.
- 122. Das, S.N.; Patro, V.J.; Dinda, S.C. A review: Ethnobotanical survey of genus *Leucas*. *Pharmacogn*. *Rev*. **2012**, *6*, 100–106.
- 123. Dixit, V.; Irshad, S.; Agnihotri, P.; Paliwal, A.K.; Husain, T. Evaluation of antioxidant and antimicrobial potential of *Leucas urticaefolia* (Lamiaceae). *J. Appl. Pharm. Sci.* **2015**, *5*, 39–45.
- 124. Nutan, R.; Veena, S. Phytochemical analysis of Leucas urticifolia (Vahl) R. Br. Ex Sm.: A traditional medicinal herb. *J. Pharmacogn. Phytochem.* **2019**, *8*, 1752–1756.
- 125. Antil, R.; Singh, L.; Gahlawat, D.K.; Dahiya, P. Antimicrobial, phytochemical, and antioxidant potential of lamiaceae family plant: *L. aspera* (willd.) linn. *Plant Arch.* **2021**, *20*, 616–630.
- 126. Abdel-Sattar, E.; Shams, M.M.; Abd-Rabo, M.M.; Mahmoud, N.; Mahrous, E.A. Chemical and biological investigations of Limonium axillare reveal mechanistic evidence for its antidiabetic activity. *PLoS One* **2021**, *16*, e0255904.
- 127. Alhaddad, F.A.; Bitaar, Z.M.; Abu-Dieyeh, M.H. Diversity, characterization, and potential applications of bacterial endophytes isolated from the halophyte Limonium axillare. *J. Plant Growth Regul.* **2024**, *43*, 2179–2196.

- 128. Alhaddad, F.; Abu-Dieyeh, M.; Jaoua, S.; Al-Ghouti, M.A.; Al-Thani, R.; Ahmed, T. Screening, diversity, and characterization of fungal endophytes isolated from the halophyte Limonium axillare and the potential of biocontrol antagonists against *Fusarium oxysporum*. *Plant Direct* **2025**, *9*, e70026.
- 129. Kaur, N.; Kumar, R.; Alhan, S.; Sharma, H.; Singh, N.; Yogi, R.; Chhokar, V.; Beniwal, V.; Ghosh, M.K.; Chandraker, S.K.; Rustagi, S.; Kumar, A. *Lycium shawii* mediated green synthesis of silver nanoparticles, characterization and assessments of their phytochemical, antioxidant, antimicrobial properties. *Inorg. Chem. Commun.* 2024, 159, 111735.
- 130. Al-Nemi, R.; Akkawi, M.; Sawalha, K.; Kusumastuti, S.A.; Nuralih; Kusumaningrum, S.; Okselni, T.; Situmorang, V.C.; Septama, A.W.; Jaremko, M.; Emwas, A.H. Comprehensive metabolomics profiling and bioactivity study of *Lycium shawii* (Awsaj) extracts with particular emphasis on potential anti-malarial properties. *Metabolites* **2025**, *15*, 84.
- 131. Rajendrasozhan, S.; El Moll, H.; Snoussi, M.; Romeilah, R.M.; Shalaby, E.A.; Younes, K.M.; El-Beltagi, H.S. Phytochemical screening and antimicrobial activity of various extracts of aerial parts of *Rhanterium epapposum*. *Processes* **2021**, *9*, 1351.
- 132. Alanazi, A.D.; Alghabban, A.J. Antileishmanial and synergic effects of *Rhanterium epapposum* essential oil and its main compounds alone and combined with glucantime against Leishmania major infection. *Int. J. Parasitol. Drugs Drug Resist.* **2024**, 26, 100571.
- 133. Mesmar, J.; Abdallah, R.; Badran, A.; Maresca, M.; Shaito, A.; Baydoun, E. *Ziziphus nummularia*: A comprehensive review of its phytochemical constituents and pharmacological properties. *Molecules* **2022**, 27, 4240.
- 134. Poyil, M.M.; Alsharif, M.H.K. Phytocompounds from Saudi medicinal plant *Ziziphus nummularia* against vancomycin-resistant *Staphylococcus aureus* (VRSA) causing atopic dermatitis (AD). *Int. J. Pharmacol.* **2023**, 19, 655–664.
- 135. Abulfatih, H.A. Ecological anatomy of xerophytic leaves from Qatar. J. King Saud Univ. Sci. 2003, 16, 19-29.
- 136. Serrano, M.; Coluccia, F.; Torres, M.; L'Haridon, F.; Métraux, J.P. The cuticle and plant defense to pathogens. *Front. Plant Sci.* **2014**, *5*, 274.
- 137. Ziv, C.; Zhao, Z.; Gao, Y.G.; Xia, Y. Multifunctional roles of plant cuticle during plant-pathogen interactions. *Front. Plant Sci.* **2018**, *9*, 1088.
- 138. Riseh, R.S.; Fathi, F.; Gholizadeh, M.; Vazvani, M.V.; Vatankhah, M.; Kennedy, J.F. Defense-related callose deposition in plants against pathogens: A review. *Int. J. Biol. Macromol.* **2025**, 320, 146005.
- 139. Khan, N. Decoding phytohormone signaling in plant stress physiology: Insights, challenges, and future directions. *Environ. Exp. Bot.* **2025**, 231, 106099.
- 140. Salam, M.A.; Al-Amin, M.Y.; Salam, M.T.; Pawar, J.S.; Akhter, N.; Rabaan, A.A.; Alqumber, M.A.A. Antimicrobial resistance: A growing serious threat for global public health. *Healthcare* **2023**, *11*, 1946.
- 141. Kripa, K.G. Therapeutic uses of plants of genus *Blepharis*: A systematic review. *Int. J. Pharm. Bio. Sci.* **2016**, 7, 236–243.
- 142. Dirar, A.I.; Adhikari-Devkota, A.; Kunwar, R.M.; Paudel, K.R.; Belwal, T.; Gupta, G.; Chellappan, D.K.; Hansbro, P.M.; Dua, K.; Devkota, H.P. Genus *Blepharis* (Acanthaceae): A review of ethnomedicinally used species, and their phytochemistry and pharmacological activities. *J. Ethnopharmacol.* **2021**, 265, 113255.
- 143. Paleg, L.G.; Aspinall, D. *The Physiology and Biochemistry of Drought Resistance in Plants*; Academic Press: Sydney, Australia, 1981.
- 144. Hasegawa, P.M.; Bressan, R.A.; Zhu, J.K.; Bohnert, H.J. Plant cellular and molecular responses to high salinity. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **2000**, *51*, 463–499.
- 145. Kavi Kishor, P.B.; Sangam, S.; Amrutha, R.N.; Sri Laxmi, P.; Naidu, K.R.; Rao, K.R.S.S.; Rao, S.; Reddy, K.J.; Theriappan, P.; Sreenivasulu, N. Regulation of proline biosynthesis, degradation, uptake, and transport in higher plants: its implications in plant growth and abiotic stress tolerance. *Curr. Sci.* **2005**, *88*, 424–438.
- 146. Verbruggen, N.; Hermans, C. Proline accumulation in plants: A review. Amino Acids 2008, 35, 753–759.
- 147. Finkelstein, R.R.; Rock, C.D. Abscisic acid biosynthesis, and response. Arabidopsis Book 2002, 1, e0058.
- 148. Chen, T.H.H.; Murata, N. Enhancement of tolerance of abiotic stress by metabolic engineering of betaines and other compatible solutes. *Curr. Opin. Plant Biol.* **2002**, *5*, 250–257.

- 149. Muhammad, M.; Waheed, A.; Wahab, A.; Majeed, M.; Nazim, M.; Liu, Y.-H.; Li, L.; Li, W.-J. Soil salinity and drought tolerance: An evaluation of plant growth, productivity, microbial diversity, and amelioration strategies. *Plant Stress* **2024**, *11*, 100319.
- 150. Bastías, D.A.; Balestrini, R.; Pollmann, S.; Gundel, P.E. Environmental interference of plant-microbe interactions. *Plant Cell Environ.* **2022**, *45*, 3387–3398.
- 151. Mishra, U.N.; Chauhan, J.; Singhal, R.K.; Anuragi, H.; Dey, P.; Lal, D.; Pandey, S.; Gupta, N.K.; Nayak, J.K.; Tripathi, A.; Singh, M.; Yadav, M.; Sajeevan, R.S. Abiotic stress responses in forage crops and grasses: The role of secondary metabolites and biotechnological interventions. *Front. Plant Sci.* **2025**, *16*, 1542519.

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.