

PLANT STRESS RESPONSES: INTEGRATING MOLECULAR, PHYSIOLOGICAL, AND ECOLOGICAL APPROACHES I

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**Plant Stress Responses Integrating Molecular,
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PREFACE

Plants are constantly exposed to various environmental stressors that can threaten their growth, development and productivity as they cannot move. These stressors which encompass both abiotic factors such as salinity, drought, heat, ultraviolet (UV) radiation, heavy metal pollution and land degradation and biotic factors including pathogens and pests are increasingly exacerbated by global climate change. Shifting in climate, precipitation patterns and the frequency of extreme weather events impose unprecedented pressures on natural and agricultural ecosystems around the world. Understanding how plants perceive, respond to and adapt to these complicated challenges is a key question in plant biology with critical implications for food security, ecosystem sustainability and environmental management.

Over recent decades, advances in molecular biology, physiology, ecology and omics-based technologies have significantly broadened our knowledge about how plants respond to stress. These advances have revealed complicate networks of genes, metabolic pathways and flexible traits which enables plants to survive and to reproduce under challenging conditions. This book compiles a wide range of plant stress biology that examine mechanisms of adaptation and tolerance at different levels of biological organization. They explore how plants cope with drought and salinity, how heat stress affects growth under climate change and how UV-B radiation influences stomatal function and secondary metabolites. Heavy metal stress and the ways plants detoxify or tolerate toxins are discussed along with interactions with pathogens and pests. The book also addresses broader ecological perspectives, such as forest management, litterfall, and ecosystem-level adaptations. Finally, it looks at transcriptional regulation and signalling networks, showing how transcription factors coordinate stress responses.

This book provides a combined framework to researchers, practitioners and students for understanding plant stress biology with the integration of molecular, physiological and ecological scales. Collectively, the chapters demonstrate that plant resilience arises not from isolated gene effects or single physiological responses but from the dynamic coordination of multiple adaptive mechanisms across organizational levels from the molecular to the ecosystem scale.

We hope this book will be a useful tool for advancing applied plant sciences, fundamental research, and sustainable management of agroecosystems and natural landscapes in the light of global environmental change. It aims at stimulating interdisciplinary research and providing insights that can guide breeding programs, conservation strategies and policy decisions to mitigate the impacts of environmental stress on plants and ecosystems. Finally, we express our sincere gratitude to all contributing authors for their expertise, dedication and rigorous scholarship, which have made this volume a timely and comprehensive contribution to the field of plant stress biology.

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Salt Stress in Plants: Mechanisms, Impacts, and Adaptation Strategies

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1. INTRODUCTION

Environmental stress factors that negatively impact plant growth and development are among the leading causes of yield reduction. These factors, considered as abiotic stressors, include salinity, drought, extreme temperatures (both high and low), imbalances in nutrient availability (deficiencies or toxicities), heavy metal contamination, air pollution, and radiation, among others (Takahashi and Shinozaki 2019).

Salt stress accounts for approximately 50% of productivity losses in crop plants. Soil salinity is currently one of the most critical abiotic stressors threatening global agricultural production. Data from the Food and Agriculture Organization (FAO) indicates that around 800 million hectares of land globally are impacted by salinity (Lu and Fricke 2023). The issue is more significant in irrigated agricultural areas, where salt accumulation is more common. This condition markedly diminishes yields in numerous principal crops, particularly cereals, and constitutes a substantial danger to global food security (Fu and Yang 2023). Therefore, enhancing salt stress tolerance in plants is essential for achieving food security and ensuring the sustainability of agriculture (Zhao et al. 2021, Chen et al. 2024).

Plants, subjected to salinity first encounter osmotic stress, which is then succeeded by ionic toxicity and oxidative damage (Mansour and Hassan 2022). These stresses lead to cellular dehydration, diminished turgor pressure, membrane disruption, and impairments in essential metabolic functions, including photosynthesis (Hasanuzzaman and Fujita 2022). Glycophytes typically experience considerable growth inhibition in saline environments, but halophytes can thrive and develop according to their evolved adaptive strategies (Zhao et al. 2021). High salinity affects not only physiological but also developmental processes. Root elongation slows down, necrosis and chlorosis occur in leaves,

flowering is delayed or entirely inhibited, ultimately leading to yield reduction (Liu et al. 2024; Figure 1).

Salt stress interferes with various physiological functions by disrupting water and nutrient uptake due to elevated sodium (Na) concentrations in the soil. While primary stress responses involve osmotic and ionic stress, dehydration, and nutrient imbalance, oxidative stress emerges as a secondary effect, further intensifying cellular damage. Collectively, these physiological and molecular disruptions reduce photosynthetic activity and hinder overall plant development (Van Zelm et al. 2020, Gong 2021, Torun 2023; Figure 1).

To counter these adverse effects, plants employ a range of adaptation strategies, including maintenance of ion homeostasis, osmotic adjustment, activation of antioxidant defense systems, and reprogramming of hormonal signaling pathways (Hao et al. 2021).

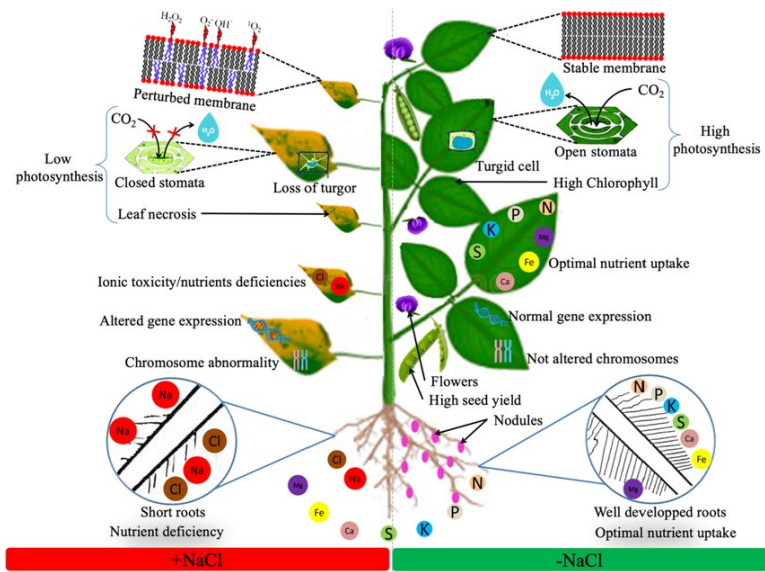


Figure 1. The effects of salt stress on plants (El Moukhtari et al. 2024)

The aim of this chapter is to provide an integrative overview of salt stress in plants by outlining its causes, prevalence, and major impacts on physiological and biochemical processes. It further highlights the key mechanisms of tolerance, including ion regulation, osmotic adjustment, antioxidant defense, and hormonal regulation, while also addressing practical approaches such as biostimulants, plant growth regulators, seed priming, and grafting. Overall, the chapter seeks to enhance understanding of plant responses to salinity and to emphasize strategies that may improve crop resilience under salt stress conditions.

2. CAUSES AND PREVALENCE OF SOIL SALINITY

Soil salinity may arise from both natural and anthropogenic processes. Natural salinization is typically observed in arid and semi-arid regions, where high evaporation rates exceed precipitation, causing salts to accumulate near the soil surface. In contrast, secondary (anthropogenic) salinization is primarily driven by improper irrigation practices, inadequate drainage, and excessive or mismanaged fertilizer application (Liu et al. 2024, Lu and Fricke 2023). Thus, soil salinity is not merely a natural phenomenon but also a serious agricultural management issue (Mansour and Hassan 2022). Soil salinity is commonly assessed through the measurement of electrical conductivity (EC). Soils with an EC value above 4 dS m^{-1} are generally classified as saline (Mansour and Hassan 2022). At this threshold, salt concentrations begin to significantly inhibit the growth of glycophytic (salt-sensitive) plants. In contrast, halophytic (salt-tolerant) species can survive and thrive under much higher salt concentrations.

Salinity can occur not only at the soil surface but also in the root zone as a result of rising groundwater levels, a process referred to as secondary salinity. This is particularly problematic in areas where irrigation water quality is poor (Lu and Fricke 2023). Exposure of plant

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roots to highly saline water reduces their ability to absorb water due to osmotic imbalances, leading to what is termed "physiological drought" (Zhao et al. 2021, Liu et al. 2024).

Anthropogenic factors such as global climate change, improper irrigation practices, inadequate drainage systems, and industrial activities have significantly contributed to the escalation of soil salinity worldwide (Fu and Yang 2023, Liu et al. 2024). In this context, the development of plant species with enhanced salt tolerance is of critical importance for ensuring the sustainability of agricultural production (Mansour and Hassan 2022, Hasanuzzaman and Fujita 2022).

Climate change is another exacerbating factor contributing to salinization. Elevated temperatures increase evaporation rates, promoting salt accumulation at the soil surface. Simultaneously, the depletion of freshwater resources drives excessive irrigation, which—when combined with poor drainage—accelerates salinity buildup (Fu and Yang 2023, Hasanuzzaman and Fujita 2022). Therefore, to ensure the sustainability of agricultural production, it is essential to fully understand the causes of salinity and to develop appropriate breeding programs, soil management practices, and biotechnological solutions.

FAO estimates indicate that over 950 million hectares of land, or about one-third of the global cultivable area, is impacted by salinity (Fu and Yang 2023). Of this, nearly 250 million hectares are irrigated farmlands, and the affected area is expanding by approximately 10% annually (Liu et al. 2024). This problem is especially prevalent in climatically dry regions such as Asia, Africa, and the Middle East (Hasanuzzaman and Fujita 2022).

3. EFFECTS OF SALT STRESS ON PLANTS

3.1. Germination

Germination is a fundamental and dynamic process that determines the subsequent growth and development of plants. In crop production, low germination rates represent a critical limiting factor, often resulting in significant economic losses. The germination process in seeds is generally divided into three distinct phases. The first phase begins with water uptake (imbibition), followed by the second phase, characterized by the activation of enzymatic and metabolic activities. The third phase, referred to as the post-germination stage, involves root elongation and is eventually followed by seedling establishment. Salinity exerts multiple adverse effects on seed germination, either by directly inhibiting the process or by inducing dormancy at low levels. High salinity reduces the osmotic potential of the surrounding environment, so restricting water accessibility to the seed. This reduction in water uptake (imbibition), coupled with salinity-induced toxicity, may disrupt enzymatic activity, impair protein metabolism, alter the balance of plant growth regulators, reduce the utilization of seed reserves, and suppress cell division (Uçarlı 2020, Kurgan 2022, Kesh et al. 2022).

Most major agricultural crops, including tomato, bean, rice, and maize, are classified as glycophytes due to their sensitivity or extreme susceptibility to salinity. Glycophytes constitute approximately 99% of the global plant species and exhibit adverse physiological responses even at low salinity levels ($EC_e < 4 \text{ dS m}^{-1}$). Under moderately saline conditions (EC_e between 4 and 8 dS m^{-1}), the yield of these crops can decline by 50–80%. Salinity stress notably impairs seed germination in glycophytes, primarily due to osmotic imbalance and ionic toxicity. In contrast, halophytes tend to exhibit greater resilience to osmotic stress during the germination phase (Uçarlı 2020). Salt stress alters the metabolic processes associated with seed germination due to the toxic

effects of elevated Na^+ and Cl^- ion concentrations and changes in osmotic pressure. Osmotic stress adversely affects starch synthesis reactions by impairing respiration and ATP (adenosine triphosphate) production, resulting in a diminished germination index and a postponement of germination commencement (Oliveira et al. 2019).

Salt stress is linked to diminished germination rates, postponed seedling emergence, and inhibited root and shoot development in plants. Abdel-Farid et al. (2020) showed a notable prolongation of germination period in cucumber due to elevated salt concentrations, with the most significant impact occurring at 200 mM NaCl treatment.

3.2. Plant Growth and Development

Salt stress negatively impacts the growth and development of numerous plant species. Plant reactions to salt and their tolerance levels significantly differ based on species and cultivars, developmental stage, duration of stress, and intensity (Kuşvuran 2024). Increased levels of sodium and chloride ions impede the absorption of water and nutrients by plant cells, resulting in the accumulation of excessive salt ions within cellular compartments. The elevated osmotic pressure in the root environment hinders essential physiological activities, including water absorption, cell elongation, seed germination, photosynthesis, and nutrient uptake, hence compromising total plant growth. Salt stress can diminish the expression of regulatory genes essential for cell cycle progression, such as cyclins and cyclin-dependent kinases, resulting in a decrease in cell numbers within the meristem, hindering growth, and impairing the plant's ability to effectively absorb water and nutrients (Balasubramaniam et al. 2023). Under stress conditions, osmotic potential decreases in conjunction with water potential, resulting in impaired membrane permeability and integrity (Acosta Matos et al. 2017, Shahzad et al. 2022).

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Balasubramaniam et al. (2023) indicated that upon exposure to salt stress, plant cells undergo immediate shrinkage and dehydration; however, they typically regain turgor over time. Despite this recovery, cellular processes such as elongation—and to a lesser degree, division—remain impaired, leading to a noticeable decline in root and leaf growth rates.

Salinity also disrupts lateral shoot development, resulting in marked differences in overall morphology and visible injury when compared to unstressed plants. These physiological responses are primarily attributed to alterations in the plant–water relationship caused by osmotic imbalances in the rhizosphere. Consequently, the plant's capacity to absorb water is markedly reduced in saline environments. High concentrations of salt in the soil lead to an increase in osmotic pressure, which restricts the plant's ability to absorb water and may even prevent water uptake entirely. The osmotic stress caused by salinity closely resembles the wilting effect induced by drought, and both abiotic stressors trigger partially overlapping metabolic responses in plants (Munns et al. 2002, Läuchli and Grattan 2007). One of the early responses is stomatal closure, which reduces CO₂ diffusion into the leaves, thereby slowing photosynthesis—a key process responsible for carbohydrate production that supports plant growth and development (Atalan and Gökçe 2021). Consequently, reductions in leaf expansion and total photosynthetic capacity ultimately limit overall plant growth. Abiotic stress factors also induce pronounced changes in root anatomy. Under salt stress, root cell walls often exhibit irregular thickening and deformation (Shannon et al. 1994). Additionally, salt accumulation in the soil leads to suberization (corking) of the endodermis, which disrupts the formation of a proper Casparian strip—a critical structure that regulates water flow through the apoplast. As a result, root hydraulic conductivity generally declines, particularly when irrigation with saline water is applied (Atalan and Gökçe 2021).

Plants exposed to salinity also tend to exhibit reductions in both fresh and dry biomass due to a decrease in leaf number (Acosta-Motos et al. 2017). Alterations in leaf anatomy and their subsequent impact on photosynthetic performance are closely linked to the plant's level of salt tolerance. It has been shown that decreases in photosynthetic efficiency under salt stress correlate with changes in anatomical leaf traits (Acosta-Motos et al. 2017, Atalan and Gökçe 2021).

3.3. Ion Homeostasis

Mineral elements, primarily present in ionic form within plant cells, are essential components of cellular structures and play crucial roles in maintaining physiological function. These ions are involved in enzyme and coenzyme complexes, regulating enzymatic activities, and also contribute to essential electrochemical processes such as maintaining osmotic balance, ensuring colloidal stability, and neutralizing electrical charges. Properly controlled ion metabolism is essential for maintaining membrane stability and facilitating plant growth and development. The primary cause of salt-induced damage is the excessive accumulation of sodium and chloride ions, which disturbs the balance of other essential minerals including potassium (K^+) and calcium (Ca^{2+}). Elevated concentrations of Na^+ and Cl^- in the soil inhibit the uptake of these vital ions—particularly K^+ , Ca^{2+} , and nitrate (NO_3^-)—leading to ionic imbalances (Liu et al. 2024). These excess ions may also accumulate in leaf cells, impairing membrane permeability and inducing cytotoxic effects (Hasanuzzaman and Fujita 2022).

High soil sodium levels cause sodium accumulation within plant tissues, which reduces membrane potential and promotes Cl^- uptake through electrochemical gradients. Elevated Na^+ concentrations are harmful to various metabolic activities and key enzymes, leading to osmotic imbalance, membrane dysfunction, and excessive production of reactive oxygen species (ROS). Consequently, cell division and

elongation are negatively affected. Similarly, high Cl^- levels can reduce chlorophyll content and damage membrane systems and organelle structures, further suppressing plant growth (Munns and Tester 2008, Hao et al. 2021).

In addition to its toxic effects, Na^+ competes directly with K^+ due to their similar ionic radius and hydration energy. Most plant cells maintain a high K^+/Na^+ ratio in the cytoplasm to support proper physiological functions. However, excessive Na^+ influx can block K^+ uptake, leading to symptoms of potassium deficiency. Furthermore, Na^+ disrupts the cellular concentration of calcium (Ca^{2+}), a key ion involved in signaling pathways, by competitively inhibiting its absorption. Song et al. (2006) also reported that the uptake of NH_4^+ and NO_3^- is significantly reduced under salt stress conditions. The visible manifestations of ionic toxicity include leaf edge necrosis, chlorosis, and defoliation. Sodium accumulation in leaves also reduces chlorophyll levels, thereby diminishing photosynthetic efficiency (Zhao et al. 2021).

3.4. Photosynthesis

Photosynthesis is an essential biological process for plant development, and variations in photosynthetic capacity directly affect biomass accumulation, yield, and crop quality. Salt stress disrupts the metabolic balance in plants primarily by inhibiting photosynthesis and respiration (Jiang et al. 2021). One of the earliest physiological impacts is the reduction in the synthesis of photosynthetic pigments, leading to a significant decline in photosynthetic efficiency. The activity and stability of Ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), a key enzyme in the Calvin cycle, are particularly sensitive to saline conditions (Hao et al. 2021). Additionally, salt-induced stomatal closure restricts CO_2 uptake, thereby decreasing the net photosynthetic rate (Lu and Fricke 2023). High concentrations of NaCl have been shown to severely impair the photosynthetic electron transport chain in leaves, a

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phenomenon closely associated with structural damage to chloroplasts (Hasanuzzaman and Fujita 2022).

Salinity adversely impacts water absorption, resulting in diminished stomatal opening and reduced transpiration. This consequently impedes electron transport and the function of carbon fixation enzymes, thereby diminishing the overall efficiency of photosynthesis (Zhang et al. 2022). Salt stress adversely affects photosynthesis through direct processes, including modified stomatal conductance and interrupted metabolic pathways, as well as indirect mechanisms, such as oxidative stress from the accumulation of reactive oxygen species (Chaves et al. 2009). Damage to the photosynthetic machinery and pigment degradation diminish photochemical efficiency, hence hindering plant growth and productivity (Jia et al. 2019).

Furthermore, salt stress significantly reduces stomatal conductance (Gs), transpiration rate (Tr), and photochemical quenching coefficient (qP), all of which are critical for effective electron flow in the photosynthetic electron transport chain. These disruptions ultimately limit the photosynthetic rate and the efficacy of light energy conversion. (Tsai et al. 2019). In watermelon seedlings subjected to short-term salt stress, the maximal quantum efficiency of photosystem II (PSII) diminished, and the protein complexes associated with both PSI and PSII reaction centers, along with proteins related to electron transport, were adversely impacted.

Navarro-León et al. (2021) indicated that salt stress markedly diminishes the Fv/Fm ratio, chiefly owing to the suppression of electron transport and modifications in pigment distribution. In cucumber plants, salt stress reduced the number of active reaction centers and the electron transport efficiency between quinone A (QA) and plastoquinone, while increasing the accumulation of reduced centers and thermal energy

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dissipation. These findings indicate that PSII electron transport reactions are partially suppressed under salinity.

The performance index (PI_ABS), which integrates three core aspects of photosynthetic activity—light absorption, excitation energy trapping, and electron transport—through a PSII reaction center complex, is also affected. Parameters derived from fluorescence measurements, such as F_v/F_m , ϕE_o , and Ψ_o , have been shown to decline significantly under salt stress. Specifically, reductions in Ψ_o suggest a disruption in the transfer of electrons beyond QA, highlighting a critical bottleneck in the electron transport system (Toksoy and Doğru 2021).

Beyond the limitations imposed by stomatal closure, salt stress can directly disrupt various components of the photosynthetic process, even in the absence of stomatal involvement. In salt-sensitive species, one of the common effects is the reduction in chlorophyll content, a key pigment essential for light absorption during photosynthesis. Li et al. (2020) demonstrated that in hybrid Pennisetum, prolonged exposure to moderate salinity, as well as short-term drought or their combination, led to a significant decline in foliar pigment content, ranging from 11.4% to 31.5%. Similar reductions in chlorophyll levels have been observed under salt stress conditions in crops such as pepper (Zhang et al. 2014), soybean (Du et al. 2018), and rice (Turan and Tripathy 2015).

Salt stress also induces structural alterations at the subcellular level, particularly in chloroplasts. The thylakoid membrane, the core site of the light-dependent reactions, becomes a primary target of such stress. Under salinity, chloroplasts exhibit disorganized spatial distribution within mesophyll cells, weakened granum interconnections, enlarged thylakoid lumens, damaged chloroplast envelopes, and increased accumulation of lipid droplets (Barhoumi et al. 2007, Hao et al. 2021).

3.5. Membrane Damage

The plasma membrane functions as a crucial structural and functional barrier in plant cells, enabling molecular transport, energy exchange, and intracellular signaling. Its selectively permeable characteristics are crucial for preserving ionic equilibrium and facilitating key physiological processes. Under salt stress conditions, the excessive accumulation of reactive oxygen species (ROS) significantly undermines membrane integrity. This oxidative damage elevates membrane permeability and reduces its fluidity. As a result, ion selectivity, transport efficiency, and flux regulation are negatively impacted. Furthermore, the damaged membrane facilitates substantial electrolyte leakage, exacerbating osmotic stress and further disturbing cellular homeostasis (Ganie et al. 2019, Hao et al. 2021).

3.6. Oxidative Stress and Free Radical Formation

Under stress circumstances, increased levels of reactive oxygen species (ROS) are primarily determined by intracellular ROS metabolism and the interconversion of different ROS products. The rate of these changes and the overall ROS concentration vary depending on the type of cell and the specific organelles involved. Each cell type possesses characteristic ROS species and distinct capacities for ROS scavenging. Maintaining ROS homeostasis is critical for protecting cellular components from oxidative damage. ROS are produced under both standard and stress conditions, predominantly in various organelles such as chloroplasts, mitochondria, peroxisomes, plasma membranes, the endoplasmic reticulum, and the cell wall. Additionally, they may arise as by-products of various metabolic pathways distributed throughout different subcellular compartments (Xie et al. 2019, Hasanuzzaman et al. 2020, Kuşvuran 2021)

ROS are either primary products or by-products of oxygen-containing molecules that exhibit higher reactivity than atmospheric

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molecular oxygen (O_2), often formed through partial reduction or activation of O_2 . These species typically arise when a non-radical atom or molecule loses or gains an electron. In plant systems, the most cellular ROS comprise the superoxide radical ($O_2^{\bullet-}$), singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2), and the hydroxyl radical ($\bullet OH$). Both radical and non-radical kinds of reactive oxygen species are produced within cells. Among them, $O_2^{\bullet-}$, $\bullet OH$, alkoxyl radical ($RO\bullet$), and peroxy radical ($ROO\bullet$) are categorized as free radicals, whereas H_2O_2 and $^1O_2$ are classed as non-radicals. Moreover, certain non-radical reactive oxygen species, including hypochlorous acid ($HOCl$) and excited carbonyl species ($RO\bullet$), are also found in plants. Various acidic chemicals, such as hypochlorous acid ($HOCl$), hypoiodous acid (HOI), and hypobromous acid ($HOBr$), together with radical species like the carbonate radical ($CO_3^{\bullet-}$), are acknowledged as constituents of the extensive spectrum of reactive oxygen species (ROS) derivatives (Maurya 2020, Hasanuzzaman et al. 2020, Kuşvuran 2021).

Under optimal physiological conditions, plants maintain a dynamic equilibrium between the generation and detoxification of ROS, primarily mediated by an intricate antioxidant defense system. In addition to their potentially harmful effects, ROS also function as critical signaling molecules involved in the regulation of various cellular and developmental processes. Notably, ROS serve as early warning signals in response to environmental injuries, triggering defense responses against stress conditions. However, exposure to abiotic stress often leads to excessive ROS accumulation, disturbing the balance between their synthesis and removal, and ultimately causing oxidative damage to cellular structures. Through evolutionary adaptation, plants have developed a sophisticated antioxidant defense network capable of mitigating ROS overproduction under diverse stress conditions. This system consists of two main groups of antioxidants: enzymatic antioxidants, which include superoxide dismutase (SOD), catalase

(CAT), various peroxidases (POD), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), glutathione peroxidase (GPX), and glutathione S-transferase (GST); and non-enzymatic antioxidants, such as ascorbic acid (AsA), glutathione (GSH), carotenoids (CAR), α -tocopherol, and many different of secondary metabolites, including specific alkaloids and flavonoids (Miller et al. 2008, Baxter et al. 2014, Bose et al. 2014, Hao et al. 2021).

4. MECHANISMS OF SALT STRESS TOLERANCE IN PLANTS

4.1. Ion Regulation

The principal cause of salt-induced damage in plants is the disruption of ion control systems. Ion regulation is crucial in establishing a plant's salt tolerance. In settings of elevated salinity, the excessive buildup of sodium (Na^+) and chloride (Cl^-) ions results in ionic imbalance and metabolic impairment within cells. To mitigate these effects, plants have evolved several strategies to maintain ionic homeostasis, including Na^+ exclusion via plasma membrane transporters, intracellular sequestration of Na^+ into vacuoles (compartmentalization), and the regulation of the cytosolic K^+/Na^+ ratio (Fu and Yang 2023, Hao et al. 2021).

Key proteins and transporters involved in these processes include SOS1 (Salt Overly Sensitive 1), NHX-type antiporters (Na^+/H^+ exchangers), HKT1 (High-Affinity K^+ Transporter), and various ATPases (Mansour and Hassan 2022, Zhao et al. 2021). SOS1 functions primarily in root apex cells, actively exporting Na^+ to prevent its toxic accumulation. NHX transporters sequester Na^+ into vacuoles, thereby lowering cytosolic Na^+ levels. Additionally, the enhancement of K^+ uptake is a vital mechanism in counteracting Na^+ toxicity and improving

salt tolerance (Hasanuzzaman and Fujita 2022). Salt-tolerant genotypes exhibit the capacity to accumulate elevated concentrations of K^+ and Ca^{2+} while restricting the absorption of Na^+ and Cl^- . Salt-tolerant plants generally have a greater K^+/Na^+ ratio, which is a crucial indicator of their resistance (Kuşvuran et al. 2021).

Maintaining Na^+/K^+ homeostasis is essential, as excessive Na^+ often induces K^+ deficiency (Park et al. 2016, Van Zelm et al. 2020, Zhao et al. 2021). Increased concentrations of Na^+ and Cl^- in the rhizosphere diminish the absorption of vital nutrients, including potassium (K), calcium (Ca), and nitrate (NO_3^-), resulting in disruptions to cellular ion equilibrium. The buildup of toxic ions to detrimental levels disrupts photosynthesis and protein synthesis, inactivates essential enzymes, and induces structural damage to chloroplasts and other organelles (Atalan and Gökçe 2021).

Potassium uptake is closely associated with Na^+ levels in the root zone. Excess Na^+ , typical of salt-stressed environments, limits K^+ acquisition. Potassium plays a critical role in several stress-related cellular functions, including transpiration, water uptake, stomatal regulation (which ensures CO_2 availability for photosynthesis), cell expansion, and osmoregulation. In a study conducted on melon (*Cucumis melo*), Sheikhalipour et al. (2021) observed a significant decrease in potassium content—up to 54% compared to control plants—corresponding to increased Na^+ accumulation under elevated salt stress. These findings further highlight the essential role of K^+ in maintaining cellular functions under salinity.

4.2. Osmotic Adjustment

Under salt stress, plants experience osmotic stress due to disturbances in ion homeostasis and reduced cellular water content. This condition leads to various temporary biophysical alterations, including decreased turgor pressure, contraction of the plasma membrane, and

structural modifications at the cellular level (Park et al. 2016). Osmotic adjustment refers to the process by which plants increase intracellular solute concentrations to maintain water uptake and cellular turgor under osmotic stress. In saline environments, this adjustment involves the accumulation of various compatible solutes within the cytoplasm and organelles, which not only help in reducing osmotic potential but also play protective roles by stabilizing the structure of macromolecules. Under salt stress, osmolytes such as proline, polyols, and sugars accumulate in plant tissues, contributing to the regulation of cellular osmotic pressure by lowering the cytosolic osmotic potential.

These compounds also function as signaling molecules that stimulate abscisic acid (ABA) synthesis, which is involved in stress-responsive gene expression and growth regulation under abiotic stress conditions (Marusig and Tombesi 2020). Beyond signaling, osmolytes help preserve membrane integrity and enhance the function of antioxidant enzymes, thereby supporting osmotic balance in stressed plants (Hao et al. 2021).

Several research have shown a significant positive link between the creation of organic molecules including glycine betaine and proline, and increased salt tolerance. Proline, a stress-responsive amino acid, not only contributes to osmotic balance under NaCl-induced stress but also supports the regulation of carbon and nitrogen metabolism within the cell. It plays key roles in maintaining cytoplasmic pH, stabilizing protein structure, and modulating enzyme activity. Under stress conditions, decreased NADP⁺ levels lead to the transfer of electrons from ferredoxin to oxygen instead of NADP⁺, resulting in the generation of reactive oxygen species (ROS) that damage cell membranes. Increased proline biosynthesis in chloroplasts helps mitigate this oxidative stress by reducing the NADPH/NADP⁺ ratio and scavenging harmful ROS (Kuşvuran 2024).

Proline accumulation has been widely observed under salt and other abiotic stresses, with more pronounced increases in stress-tolerant genotypes (Bayat et al. 2014). In a study on zucchini, exogenous application of proline (5 and 10 mM) under salt stress (100 mM NaCl) led to increased activity of antioxidant enzymes, particularly in the more salt-tolerant genotype A-19. Similarly, Sheikhalipour et al. (2021) reported that in melon plants subjected to salt stress, total carbohydrate and proline contents increased by 53% and 39%, respectively, suggesting that the accumulation of osmoprotectants such as free proline and soluble sugars is a key mechanism underlying salt tolerance.

Another important osmolyte involved in osmotic adjustment is glycine betaine. This compound is synthesized from choline via choline monooxygenase (CMO) and betaine aldehyde dehydrogenase (BADH). Under saline conditions, glycine betaine has been shown to maintain membrane integrity and enzyme activity, thereby reducing cellular damage and contributing to salt stress tolerance (Hao et al. 2021).

Soluble carbohydrates and polyols are also considered effective osmotic regulators. Non-structural carbohydrates, including glucose, sucrose, fructans, and starch, play significant roles in plant metabolism. Among them, sucrose synthesis, transport, storage, and utilization are closely linked to plant growth and stress resilience (Hao et al. 2021).

4.3. Antioxidant Defense Mechanism

Salt stress triggers a series of morphological, physiological, and biochemical alterations in plants. As with other abiotic stress conditions, plants respond to salinity by closing their stomata to minimize water loss and optimize water use efficiency. However, this stomatal closure also restricts CO₂ uptake, thereby limiting carbon fixation in the Calvin cycle. As a result, excess excitation energy in the chloroplasts is diverted to oxygen reduction pathways, leading to the generation of ROS. These

ROS—including superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH^-)—induce oxidative damage by attacking cellular lipids, proteins, and nucleic acids, ultimately disrupting normal metabolic functions (Figure 2). One of the most damaging consequences of ROS accumulation is lipid peroxidation, a process initiated when oxidants react with polyunsaturated fatty acids in cellular membranes. Lipid peroxidation leads to the formation of secondary byproducts such as malondialdehyde (MDA), a well-established biomarker of oxidative stress. MDA interferes with membrane integrity by disrupting ion exchange processes and promoting cross-linking among membrane-bound compounds. These disruptions alter membrane permeability and compromise enzymatic activities, further exacerbating the detrimental effects of salt stress on plant cells (Kuşvuran 2021).

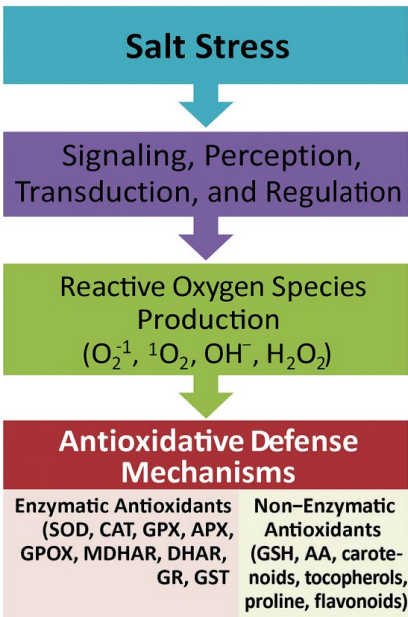


Figure 2. Reactive oxygen species (ROS) generation and the antioxidative defense system in plants under salt stress (Xie et al. 2019, Kuşvuran 2021)

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To counteract the damaging effects of oxidative stress, plants have evolved complex antioxidant defense systems composed of both enzymatic and non-enzymatic components. These defense mechanisms are critical for maintaining redox homeostasis and protecting cellular structures under stress conditions such as salinity. Non-enzymatic antioxidants include a variety of small molecules such as glutathione, cysteine, hydroquinones, ascorbate (vitamin C), α -tocopherol (vitamin E), flavonoids, carotenoids, and alkaloids. These compounds play significant roles in directly scavenging reactive oxygen species (ROS) and stabilizing cellular components. The enzymatic antioxidant system, on the other hand, consists of key enzymes that detoxify specific ROS. Superoxide dismutase (SOD) catalyzes the conversion of superoxide anions ($O_2^{\bullet-}$) into hydrogen peroxide (H_2O_2), which is subsequently broken down by catalase (CAT) and ascorbate peroxidase (APX). Glutathione reductase (GR) is also vital in maintaining the reduced form of glutathione, which supports the regeneration of ascorbate and other antioxidant molecules (Kuşvuran 2021). Together, these antioxidant defenses play a crucial role in mitigating oxidative damage, preserving membrane integrity, and enabling plant survival under salt stress conditions.

Within the plant antioxidant enzyme system, superoxide dismutase (SOD) represents the primary defense mechanism against oxidative stress. This enzyme catalyzes the dismutation of superoxide anions ($O_2^{\bullet-}$) into hydrogen peroxide (H_2O_2), thereby reducing their harmful potential. Based on the type of metal ion cofactor they incorporate, SODs are categorized into three main types: Cu/Zn-SODs, Mn-SODs, and Fe-SODs. Fe-SODs are predominantly localized in chloroplasts, Mn-SODs are confined mainly to mitochondria, while Cu/Zn-SODs are present in chloroplasts, the cytosol, and the apoplastic space (Kim et al. 2017). Catalase (CAT) is a tetrameric hemoprotein enzyme, recognized for its ability to rapidly decompose hydrogen peroxide (H_2O_2). Due to the

presence of a heme group, it is classified as a hemoprotein and is primarily localized in peroxisomes and mitochondria. As one of the key enzymatic antioxidants, CAT plays a critical role in protecting plant cells under stress conditions by catalyzing the conversion of toxic H_2O_2 into water (H_2O) and molecular oxygen (O_2) through a two-electron transfer mechanism. The Halliwell–Asada cycle, also known as the ascorbate–glutathione cycle, is one of the most crucial antioxidant defense systems responsible for the detoxification of hydrogen peroxide (H_2O_2) in plant cells. This pathway utilizes both enzymatic and non-enzymatic components to mitigate the harmful effects of reactive oxygen species (ROS). One of the key functions of this cycle is the inactivation of H_2O_2 while simultaneously safeguarding carbon fixation enzymes from oxidative damage.

Moreover, it plays an essential role in protecting plants from the cytotoxic effects of molecular oxygen (Das and Roychoudhury 2014). Ascorbate peroxidases (APXs) play a key role in the removal of hydrogen peroxide (H_2O_2) within both the water–water cycle and the ascorbate–glutathione (AsA–GSH) cycle, using ascorbate (AsA) as the primary electron donor. By catalyzing the reduction of H_2O_2 to water, APXs contribute significantly to the antioxidant defense system in plants, thus helping to mitigate oxidative damage under stress conditions (Dvorak et al. 2020). Glutathione peroxidase (GPX) reduces hydrogen peroxide (H_2O_2) by utilizing glutathione (GSH) as an electron donor, resulting in the formation of oxidized glutathione (GSSG). In plants, peroxidase enzymes are involved in a wide range of physiological and developmental processes, including cell wall protein cross-linking, regulation of indole-3-acetic acid (IAA) levels, activation of defense responses, seed germination, lignin biosynthesis, and adaptation to oxidative stress (Yalçın 2020).

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Glutathione reductase (GR) is a NADPH-dependent oxidoreductase and a flavoprotein primarily localized in chloroplasts, mitochondria, and the cytosol. Under adverse environmental conditions, GR functions in coordination with other antioxidant enzymes to detoxify hydrogen peroxide (H_2O_2), thereby contributing to the plant's tolerance against oxidative stress. (Kuşvuran 2021). Plants with higher levels of antioxidants have been observed to exhibit greater tolerance to oxidative stress. In this context, the degree of plant stress tolerance is closely linked to the presence and activity of antioxidant enzymes capable of neutralizing ROS. Comparative studies in crops such as melon, squash, pepper, eggplant, and tomato have consistently shown that salt-tolerant cultivars possess significantly higher antioxidant enzyme activity than their sensitive counterparts (Kuşvuran 2021).

Enzymes such as superoxide dismutase (SOD), peroxidase (POX), and catalase (CAT) play a fundamental role in reducing cellular levels of superoxide radicals and hydrogen peroxide, thereby alleviating oxidative stress. Naliwajski and Skłodowska (2021), in their study on cucumber exposed to salt stress (100 and 150 mM NaCl), investigated the dynamic changes in the antioxidative system and proline metabolism. They reported variations in the levels of α -tocopherol, ascorbate peroxidase (APX), glutathione peroxidase (GPX), catalase (CAT), glutathione S-transferase (GST), pyrroline-5-carboxylate synthetase (P5CS), pyrroline-5-carboxylate reductase (P5CR), and proline dehydrogenase at 24 and 72 hours after stress application. The study demonstrated that antioxidant enzyme activities—including APX, GPX, CAT, and GST—as well as α -tocopherol and key enzymes in proline biosynthesis, increased in response to salt stress. Similarly, in melon, rising levels of salt stress were associated with enhanced activities of antioxidative enzymes such as POD, SOD, APX, and CAT. This enzymatic upregulation was accompanied by increased levels of total phenolic compounds and flavonoids, suggesting an integrated biochemical

response contributing to improved stress tolerance (Sheikhalipour et al. 2021).

Ascorbic acid (AsA) is a potent, water-soluble antioxidant that is predominantly found in metabolically active tissues, including meristems, photosynthetically active cells, root apices, floral structures, and developing fruits. Under stress conditions, AsA plays a critical role in mitigating oxidative damage by serving as an electron donor in various redox reactions. Additionally, AsA contributes to the regeneration of α -tocopherol, another key antioxidant molecule involved in maintaining cellular redox balance (Hao et al. 2021). Glutathione (GSH), a low-molecular-weight, non-protein thiol composed of glutamic acid, cysteine, and glycine (γ -glutamylcysteinylglycine), plays a pivotal role in intracellular defense against oxidative damage caused by ROS. Owing to its potent reducing capability, GSH participates in numerous vital biological processes, encompassing cellular growth and division, sulfate transport regulation, signal transduction, metabolite conjugation, enzymatic regulation, protein and nucleic acid synthesis, metal chelation through phytochelatin biosynthesis, and the expression of stress-related genes. Within the ascorbate–glutathione (AsA–GSH) cycle, glutathione is recognized as a key component in maintaining ROS homeostasis and detoxifying reaction products, functioning through multiple pathways as a central antioxidant molecule (Gong et al. 2018).

Carotenoids (CARs) function as accessory pigments in chloroplasts, facilitating light harvesting during photosynthesis. Beyond their photoprotective role, they are also essential in scavenging reactive oxygen species (ROS) generated by the photosynthetic machinery. CARs safeguard the photosystem through multiple mechanisms: they interact with lipid peroxidation products to halt oxidative chain reactions; quench singlet oxygen by converting it into heat; react with triplet-state or excited chlorophyll molecules to prevent singlet oxygen

formation; and dissipate excess excitation energy via the xanthophyll (lutein) cycle (Havaux and Niyogi 1999, Hao et al. 2021). Tocopherols, which are known to play a role in scavenging lipid radicals and reactive oxygen species (ROS), are abundantly localized in biological membranes, particularly in the thylakoid membranes of chloroplasts. They are critically important for maintaining membrane stability under oxidative stress, especially by counteracting singlet oxygen ($^1\text{O}_2$) and hydroxyl radicals ($\bullet\text{OH}$). During stress conditions, tocopherols protect the structural integrity and functional efficiency of photosystem II (PSII) by neutralizing ROS generated within the chloroplast membranes (Kim et al. 2019, Ali et al. 2020).

Phenolic compounds contribute to the neutralization and elimination of reactive oxygen species (ROS) through various mechanisms, including direct scavenging reactions, inhibition of ROS-producing enzymes, and chelation of transition metals involved in ROS-generating reactions such as the Fenton reaction. Additionally, these compounds help stabilize unpaired electrons in free radicals. Among them, flavonoids play a particularly important role in the detoxification of hydrogen peroxide (H_2O_2), thereby enhancing the plant's antioxidative capacity under stress conditions (Dumanovic et al. 2021). Flavonoids have recently been recognized as effective scavengers of reactive oxygen species (ROS); however, their antioxidant activity appears to be spatially restricted to locations proximal to ROS generation sites, such as the vacuole and cell wall. This localization limits their functionality to specific cellular compartments where oxidative stress occurs (Gill and Tuteja 2010, Hao et al. 2021)

4.4. Phytohormone

In response to ever-changing environmental stressors, plants have evolved sophisticated defense strategies largely governed by phytohormones. These signaling molecules are central to coordinating

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plant adaptation to salinity by modulating growth, development, and stress tolerance. Phytohormones play pivotal roles in perceiving salt stress signals and activating downstream defense mechanisms. To date, nine primary plant hormones have been extensively studied and are generally categorized into two main functional groups: those that promote growth and those primarily involved in stress responses. The growth-promoting group includes auxins, gibberellins (GAs), cytokinins (CKs), brassinosteroids (BRs), and strigolactones (SLs), some of which—such as BRs and SLs—also contribute to stress adaptation. Meanwhile, the stress-related group encompasses abscisic acid (ABA), ethylene, salicylic acid (SA), and jasmonic acid (JA). Moreover, the complex interaction (crosstalk) among these hormonal pathways significantly influences the plant's capacity to respond to salt stress (Yu et al. 2020, Zhao et al. 2021).

Among the various plant hormones, abscisic acid (ABA) stands out as the principal regulator of stress-related physiological responses. It acts as a key secondary messenger by initiating kinase signaling cascades and modulating the expression of stress-responsive genes during salt stress episodes. Upon exposure to stress stimuli, plants rapidly enhance ABA biosynthesis, resulting in a swift elevation of its intracellular concentration. Elevated ABA levels trigger kinase pathways that facilitate stress perception and activate protective mechanisms. Under saline conditions, salt-induced water deficiency causes cellular dehydration and disrupts turgor pressure, culminating in osmotic stress. In response, the rise in endogenous ABA promotes stomatal closure, thereby contributing to water conservation and the maintenance of osmotic balance. Consequently, ABA plays a central role in osmoregulatory processes during the plant's adaptation to salt stress (Jia et al. 2002, Zhu et al. 2016, Verma et al. 2016, Zhao et al. 2021).

5. APPROACHES AND METHODS FOR ENHANCING SALT STRESS TOLERANCE IN PLANTS

5.1. Biostimulants

Biostimulants are chemicals that augment nutrient uptake efficiency, enhance plant tolerance to abiotic stress, improve crop quality, and facilitate optimal nutrient usage in the rhizosphere. These substances are primarily classified into two principal categories: microbial and non-microbial biostimulants. Microbial biostimulants comprise advantageous nitrogen-fixing bacteria and arbuscular mycorrhizal fungi, whereas non-microbial biostimulants encompass a diverse array of organic and inorganic compounds or intricate mixtures, including amino acids, humic acids, minerals, seaweed extracts, plant extracts, biopolymers, and protein hydrolysates (Andreotti 2020, Kuşvuran and Kuşvuran 2021).

Amino acids are the most often employed biostimulants, produced from the chemical or enzymatic breakdown of proteins sourced from plants or animals. Essential amino acids, such as leucine, isoleucine, methionine, phenylalanine, arginine, histidine, tryptophan, valine, threonine, and lysine, are solely produced by plants. Conversely, non-essential amino acids including alanine, β -alanine, asparagine, cysteine, glutamine, aspartic acid, glycine, proline, serine, and tyrosine can be synthesized by both plants and humans. These amino acids are effective in enhancing tolerance to stress conditions such as high temperature, drought, frost, insect and hail damage, and flooding—all of which negatively affect plant metabolism and yield (Kuşvuran and Kuşvuran 2021).

Under salt stress, the absorption of macro- and micronutrients is significantly reduced, leading to decreased stomatal aperture and increased transpiration and respiration. This imbalance disturbs carbohydrate metabolism and cellular homeostasis. For example, L-

glutamic acid acts as an osmotic agent within guard cells, promoting stomatal opening. Amino acids also regulate ion flux across membranes and have been shown to reduce the efflux of potassium from cells, especially under NaCl-induced stress (Oosten et al. 2017, Kumar et al. 2017, Kavasoğlu 2018, Popko et al. 2018). Among these, proline plays a central role not only in osmotic adjustment but also in enhancing antioxidant defense, improving nutrient uptake, and maintaining photosynthetic capacity under salinity (Ali et al. 2008, Abdelaal et al. 2020, Hanif et al. 2024).

Seaweeds, comprising green (Chlorophyta), red (Rhodophyta), and brown (Phaeophyta) macroalgae, are another important group of non-microbial biostimulants naturally found in marine environments (Sharma et al. 2014). Their extracts are rich in phytohormones such as cytokinins, auxins, and gibberellins, as well as complex polysaccharides (laminarin, fucoidan, alginates) and essential minerals including nitrogen, iron, aluminum, manganese, and potassium (Battacharyya et al. 2015, Bulgari et al. 2019, Calvo et al. 2014). In a study on zucchini under salt stress (20–60 mM NaCl), seaweed application was found to increase SPAD values, net CO₂ assimilation rate, transpiration rate (E), and leaf contents of P, K, Ca, and Mg, while reducing Na and Cl accumulation. Exogenous seaweed treatment improved yield, growth parameters, dry matter accumulation, and photosynthetic performance compared to untreated salt-stressed plants (Rouphael et al. 2014).

Humic substances—including humic acids, fulvic acids, and humin—have gained significant attention over the last two decades. These compounds improve soil water infiltration, reduce the availability of toxic substances, enhance root development, and improve the uptake of water and nutrients (Canellas et al. 2002, Trevisan et al. 2010). They also contribute to enhanced photosynthesis, respiration, nucleic acid synthesis, and ion absorption. Humic substances increase chlorophyll

content, alleviate symptoms such as chlorosis, and enhance antioxidant activity under stress conditions (Abbas 2013, Drobek et al. 2019). In addition, humic acid-based biostimulants have been shown to improve not only soil structure but also its physical and chemical properties, regulate osmotic potential by improving turgor and water uptake under salinity, and play a protective role under various environmental stresses (Garcia et al. 2012, de Oliveira et al. 2016, de Neta et al. 2018).

Plant Growth-Promoting Rhizobacteria (PGPR) are naturally occurring microorganisms, primarily associated with plant roots, that influence plant health through multiple mechanisms. These include nitrogen fixation, siderophore production, suppression of pathogens, stimulation of resistance mechanisms, modulation of phytohormones, and enhancement of nutrient and water uptake (Aydın et al. 2012, Emilia et al. 2020, Kuşvuran and Kuşvuran 2021). PGPR strains are isolated from extreme environments including saline, alkaline, acidic, and arid soils, and belong to genera such as *Rhizobium*, *Bradyrhizobium*, *Azotobacter*, *Azospirillum*, *Pseudomonas*, and *Bacillus* (Oosten et al. 2017). These microbes improve stress tolerance by altering cell wall composition and accumulating compatible solutes, leading to improved water retention and ionic/osmotic stress mitigation (Upadhyay 2009).

Chitin, a linear polysaccharide composed of N-acetyl-D-glucosamine units, is one of the most abundant and biodegradable biopolymers in nature. Its derivative, chitosan, is known to enhance photosynthetic activity, stimulate antioxidant enzyme systems, increase secondary metabolite production, and upregulate stress-responsive gene expression—thereby promoting plant tolerance to drought, salinity, and heat stress.

5.2. Plant Growth Regulators

Plant growth regulators (PGRs) play a vital role in promoting plant growth and maintaining productivity under salt stress conditions. These

compounds regulate developmental pathways and signal transduction networks, enabling plants to better cope with adverse environmental stimuli. Numerous studies have shown that PGRs function either as signaling molecules or secondary messengers, and can effectively mitigate the detrimental effects of abiotic stress (Yakupoğlu et al. 2021).

Melatonin is a multifunctional molecule in plants that exhibits potent antioxidant properties and is involved in light/dark signal transduction. In addition to its classification as a plant hormone, melatonin also scavenges reactive oxygen and nitrogen species, providing protective effects under both biotic and abiotic stress. The administration of exogenous melatonin has been demonstrated to enhance plant performance under stress by augmenting antioxidant systems. Exogenous melatonin application has been shown to improve plant performance under stress by enhancing antioxidant systems. It does so by upregulating the expression of stress-responsive genes, thus stimulating protective responses at the transcriptional level (Yakupoğlu et al. 2021).

Salicylic acid (SA) is another well-documented plant growth regulator that influences multiple physiological processes. Present in all plant organs and translocated through the phloem, SA is known to regulate protein synthesis and enhance tolerance to various environmental stresses, including salinity, drought, temperature extremes, and heavy metal toxicity (Kuşvuran and Kaya 2019). In melon plants grown under hydroponic conditions, SA was found to alleviate salt-induced damage and improve morphological parameters and yield. However, high concentrations of SA exacerbated the effects of salt stress, negatively impacting gas exchange and fresh biomass (Oliveira et al. 2022). Yan et al. (2023) further reported that SA application under salt stress enhanced the activities of SOD and CAT enzymes, promoted lignin biosynthesis to strengthen cell wall stability, and positively

regulated LOX gene expression, thereby mitigating salt-induced damage.

Jasmonic acid (JA) and its derivatives, such as methyl jasmonate (MeJA), are distributed throughout the plant body and are rapidly activated in response to stress via specific signaling pathways. These compounds are recognized for their role in reducing the negative impacts of abiotic stressors. Parihar et al. (2021) showed that JA applications improved growth in jute plants subjected to NaCl and UV-B stress. Similarly, Wani et al. (2016) found that MeJA and *cis*-(+)-12-oxo-phytodienoic acid (OPDA) enhanced seedling growth by stimulating nitrogen metabolism and photosynthetic capacity.

Brassinosteroids (BRs) are steroidal phytohormones known for their broad-spectrum regulatory effects and are now considered the sixth class of essential plant growth regulators. Among them, 2,4-epibrassinolide (EBR) is a highly active BR homolog widely used in research and agricultural practices. Exogenous application of EBR enhances growth, increases chlorophyll content, improves photosynthetic efficiency, and stimulates antioxidant enzyme activities (Sharma et al. 2016, Sirhindi et al. 2017). BRs have been shown to enhance tolerance to both biotic and abiotic stresses by regulating morphological, physiological, and biochemical traits in various crops. EBR regulates the expression of BR biosynthesis genes and elevates antioxidant capacity, reducing the accumulation of reactive oxygen species (ROS) and malondialdehyde (MDA). As a result, cucumber seedlings treated with EBR demonstrated improved growth under salt stress conditions (Azhar et al. 2017, Anwar et al. 2018). In a study by Nie et al. (2018), exogenous EBR application under NaHCO₃-induced alkali stress significantly increased antioxidant enzyme activities and the antioxidant pool (AsA/DHA and GSH/GSSG ratios) in cucumber leaves and roots. This treatment helped maintain redox balance, reduced ROS

accumulation and lipid peroxidation, preserved root activity, and ultimately improved alkaline stress tolerance in cucumber seedlings.

5.3. Seed Priming

The seed priming technique enhances germination and seedling establishment of crops in saline conditions, as it is posited that crops exhibiting strong germination and seedling development under salt stress may maintain their growth during the adult period under similar conditions (Ashraf and Munns 2022). Seed priming is a pre-sowing, regulated hydration method that enables pre-germination metabolic processes without the emergence of the radicle. This method effectively mitigates salt stress during germination and subsequent growth phases of the crop. Numerous studies have indicated the efficacy of seed priming in mitigating the detrimental impacts of salt on wheat growth (Farooq et al. 2024). Additionally, various seed treatments, including biopriming (utilization of beneficial organisms), matric priming (moistened solid carriers like vermiculite), drum priming (rotation of seeds in a drum with water vapor application), film coating (polymer application to seed surfaces), seed pelleting (application of inert materials for uniform seed shape), and fluid drilling (gel seeding), are utilized to promote early growth stages and subsequent vegetative and adult phases, thereby improving crop yield under both stress and non-stress conditions. They may not safeguard plants against the challenges of salt stress throughout various phenological stages, and different crops may exhibit varying responses to seed priming (Ashraf and Munns 2022).

5.4. Grafting

Grafting, a technique widely employed in vegetative propagation, involves the physical union of two living plant parts that subsequently grow as a single organism. The use of grafting in horticultural production dates back to ancient times. In vegetable cultivation, grafting was first adopted in countries such as Japan and Korea during the early 20th

century, where limited arable land and increasing population density necessitated continuous and intensive agricultural production. The technique later gained popularity in Mediterranean countries as well. Initially, grafting was used primarily to combat biotic stress factors, especially soil-borne diseases. Over time, however, its application expanded to include tolerance to various abiotic stress conditions, becoming a key strategy for improving plant adaptation and productivity. Numerous studies have reported that the use of different rootstocks can significantly enhance plant tolerance to various abiotic stress factors, including drought, salinity, extreme temperatures (both high and low), and flooding (Kubota et al. 2008, Kumar et al. 2015, Meimandi and Kappel 2020). These benefits are largely attributed to the physiological and morphological advantages conferred by the rootstocks. In addition to improved stress tolerance, grafting has been associated with enhanced water and nutrient uptake, earlier maturity, and an extended harvesting period. As a result, grafted plants often exhibit superior fruit quality and increased yield compared to non-grafted plants (Meimandi and Kappel 2020). Moreover, grafting contributes to sustainable production by reducing the need for chemical pesticides and thereby supporting environmental protection. One of the key objectives in the adoption of grafted seedlings is to improve the marketable yield while minimizing agrochemical inputs (Ertok and Padem 2007).

The enhanced tolerance observed in grafted plants is largely attributed to the morphological and physiological characteristics of the rootstock. Rootstocks with robust architecture and well-developed root systems can absorb greater amounts of water and nutrients from the soil compared to non-grafted counterparts, thereby promoting enhanced vegetative growth and development. In situations where a commercially desirable but stress-sensitive cultivar is in high demand and no naturally tolerant alternatives are available, grafting onto a suitable rootstock

offers a viable solution for improving crop performance under suboptimal environmental conditions (Laxman and Bhatt 2017).

The positive effects of grafting on stress tolerance are closely linked to both the inherent traits of the rootstock and the compatibility between scion and rootstock. Through improved root system architecture, increased hydraulic conductivity, and more efficient uptake and transport of water and nutrients, rootstocks can support overall plant vigor. Furthermore, they may facilitate the synthesis and translocation of essential biochemical compounds, including phytohormones, which enhance scion resistance to abiotic stress (Öztekin et al. 2021).

Rootstocks used in vegetable grafting significantly influence earliness, yield, fruit quality, and the plant's tolerance to both biotic and abiotic stress conditions. One of the major benefits of grafting lies in the vigorous root systems of the selected rootstocks, which enhance water and nutrient uptake and contribute to improved plant vigor and overall development (Bekar et al. 2017).

In a study investigating the effect of grafting on salt stress tolerance in melon, several physiological and morphological parameters were measured, including shoot length, leaf chlorophyll index (SPAD), fresh weight of shoots and roots, and root length. Two melon cultivars (Citirex F1 and Kırkağaç) were grafted onto two commercial interspecific rootstocks (*Cucurbita maxima* × *C. moschata*, namely Kardosa and Nun 9075). The experiment was conducted in a hydroponic system under two salinity treatments: 1 dS/m (control) and 8 dS/m (salt stress). Results showed that grafted plants outperformed non-grafted controls under salt stress conditions, exhibiting better growth and development. In a follow-up study involving Citirex and Altınbaş melon cultivars, grafting onto Kardosa and Nun 9075 rootstocks resulted in enhanced plant growth, reduced malondialdehyde (MDA) content, lower ion leakage, and decreased Na⁺ accumulation, while simultaneously increasing K⁺ and

Ca²⁺ uptake. Among all combinations tested, the Citirex/Nun 9075 and Citirex/Kardosa grafts showed the most promising performance in terms of physiological and biochemical responses under salinity stress (Ulaş et al. 2020).

Grafted plants often exhibit distinct phenotypic responses to salinity compared to their ungrafted counterparts, as well as to the original scion and rootstock genotypes. Grafting onto salt-tolerant rootstocks has proven to be an effective approach for enhancing salt tolerance in crops through physiological and biochemical modifications (Kuşvuran et al. 2021). According to Fullana-Pericas et al. (2018), the rootstock can significantly influence the physiological and morphological traits of the scion. This interaction is largely mediated by the grafting-induced disruption of vascular continuity, which alters hydraulic conductivity, nutrient and water transport, and hormonal balance within the grafted plant.

Grafting productive scions onto stress-tolerant rootstocks has become a widely adopted agronomic strategy for improving plant resilience by physical means (Simpson et al. 2015). Talhouni et al. (2017) emphasized that rootstocks can mitigate both biotic and abiotic stress effects by upregulating antioxidant enzyme activity. In solanaceous and cucurbit crops such as tomato and melon, the use of salt-tolerant rootstocks is a commonly employed method for reducing the adverse impacts of salinity (Penella et al. 2015). Grafting has also been shown to enhance plant performance and yield under stress conditions, offering both agronomic and economic benefits (Iseri et al. 2015). However, the effectiveness of this technique depends on the compatibility and specific tolerance mechanisms of the rootstock. For example, tomato plants grafted onto tobacco rootstocks exhibited significantly inhibited growth when exposed to salinity above 0.4 M NaCl. Conversely, in melons, grafting onto tolerant rootstocks improved

growth, biomass accumulation, and physiological performance under saline conditions compared to non-grafted controls (Dasgan et al. 2015). In another study, interspecific-grafted watermelon showed enhanced salt resilience, as indicated by increased biomass and leaf area under salinity (Bohm et al. 2017). Similarly, pumpkins grafted onto melon scions (P/M) had significantly higher root dry weights than ungrafted (M) and self-grafted (M/M) plants under salt stress. Kuşvuran et al. (2021) demonstrated that salt-tolerant rootstocks can alleviate the detrimental effects of salinity by reducing Na^+ and Cl^- uptake while enhancing the absorption of K^+ , Ca^{2+} , and essential micronutrients.

Furthermore, salt-stressed grafted plants exhibited increased activity of antioxidant enzymes such as catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione reductase (GR). These physiological changes contributed to improved growth regulation and stress mitigation in grafted melon plants, likely due to a combination of lower Na^+ and Cl^- accumulation, higher antioxidant responses, and controlled malondialdehyde (MDA) levels. In a separate study focused on eggplant rootstocks, tomato cultivar 'Kashi Aman' was grafted onto two salt-tolerant eggplant accessions (IC-111056 and IC-354557) and evaluated under saline irrigation regimes (ECiw 6 and 9 dS/m) over two growing seasons. The results confirmed that grafting onto eggplant rootstocks enhanced physiological performance and fruit yield under salinity by favorably modulating ion partitioning in the scion (Sanwal et al. 2022).

6. CONCLUSIONS

Salinity represents a major global threat to agricultural productivity among abiotic stressors. Salt stress disrupts normal physiological processes, thereby impairing plant growth and development. Nevertheless, plants have evolved sophisticated regulatory

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systems to cope with such challenges. Plants often actively reduce their growth rate as a strategic adaptation to enhance survival under high-salinity environments. In this context, plant cells undergo substantial structural and functional modifications to mount effective defense responses against salt-induced damage. The use of plant growth-promoting bacteria, phytohormones, and organic acids appears to be a promising strategy for enhancing plant resilience under saline conditions. In addition, modifications and advancements in agricultural management strategies are essential for the effective mitigation of salt-induced stress. Notably, traditional breeding programs aimed at developing salt-tolerant crop and pasture varieties, alongside soil amelioration efforts, contribute significantly to this goal.

Recent advances in agricultural science have introduced novel and innovative approaches, such as microbe–plant interactions and the application of nanotechnology, which have demonstrated considerable potential in mitigating the negative impacts of salt stress. These modern techniques offer promising alternatives to traditional methods and are becoming increasingly relevant in addressing complex agricultural challenges. Moreover, the integration of multidisciplinary solutions—involving not only plant scientists and agri-environmental researchers but also experts in remote sensing, artificial intelligence (AI), machine learning, and big data analytics—has opened new avenues for the detection, monitoring, and management of soil salinization. Such cross-disciplinary collaborations provide powerful tools for early diagnosis, precision intervention, and long-term control of salinity-related stress, ultimately reducing crop damage and improving resilience in agricultural systems.

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Molecular Adaptation in Plants Under Salt Stress Conditions: Gene Expression and Regulation

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1. INTRODUCTION

Soil salinity has become one of the most severe environmental challenges threatening sustainable agriculture across the globe (Negacz et al. 2022). Excess accumulation of salts, particularly sodium (Na^+) and chloride (Cl^-) ions, alters soil osmotic potential and interferes with nutrient uptake, thereby limiting crop productivity. Unlike short-term drought stress, salinity imposes both osmotic pressure and ionic toxicity simultaneously, making it more complex for plants to cope with. In response to this stress, plants activate a wide range of molecular mechanisms, including dynamic changes in gene expression, regulation of ion transport systems, and modifications at the epigenetic level (Acosta-Motos et al. 2017; da Costa et al. 2024).

Understanding these molecular adaptations is essential not only for elucidating the fundamental biology of plant stress responses but also for practical applications in crop improvement. Recent advances in genomics, transcriptomics, and genome editing technologies have opened new avenues to dissect regulatory pathways involved in salt stress adaptation (Singroha et al. 2022). This chapter seeks to offer an in-depth overview of the ways in which plants regulate gene expression and associated regulatory networks under saline stress, with particular focus on transcriptional, post-transcriptional, and epigenetic processes

2. PHYSIOLOGICAL BASIS OF SALT STRESS RESPONSES

The physiological consequences of salinity serve as the foundation for molecular adaptations. When roots encounter saline soils, the osmotic imbalance reduces water absorption, mimicking drought-like conditions. Concurrently, excess Na^+ ions enter plant cells, disturbing potassium (K^+) homeostasis, which is vital for enzymatic activities and protein

synthesis. This ion toxicity is a primary factor behind chlorosis, leaf necrosis, and stunted growth observed in salt-stressed plants (Arzani et al. 2023; Atta et al. 2023).

A characteristic consequence of salt stress is the excessive accumulation of reactive oxygen species (ROS), such as superoxide anions and hydrogen peroxide (Hasanuzzaman and Fujita 2022). While low levels of ROS can act as secondary messengers in signaling, uncontrolled accumulation damages lipids, proteins, and nucleic acids. The impairment of photosynthetic machinery, reduction in chlorophyll content, and decline in stomatal conductance further exacerbate stress effects. These physiological disturbances create the necessity for rapid activation of molecular defense pathways, ensuring survival under prolonged salt exposure (Sachdev et al. 2021; Hannachi et al. 2022).

3. SIGNAL PERCEPTION AND TRANSDUCTION PATHWAYS

The initiation of molecular responses depends on how plants perceive and transduce salt stress signals. Plasma membrane sensors are thought to detect changes in osmotic pressure and ion imbalance, triggering downstream signaling cascades. A pivotal early signaling event is the transient surge in cytosolic Ca^{2+} levels, which is sensed by Ca^{2+} -binding proteins such as calmodulins and calcineurin B-like proteins, thereby initiating the activation of specific downstream kinases within the signaling cascade (Li et al. 2022; Peng et al. 2025).

Among the pivotal intracellular signaling mechanisms, the mitogen-activated protein kinase (MAPK) cascades represent a fundamental route by which plants perceive and transmit salt-induced stress cues; these cascades sequentially activate a series of phosphorylation events that ultimately convey the signals to the nucleus,

where they orchestrate extensive transcriptional reprogramming processes required for stress adaptation and cellular homeostasis (Zhang and Zhang, 2022). Among hormonal signals, abscisic acid (ABA) plays a dominant role by regulating stomatal closure and inducing ABA-responsive transcription factors. However, other hormones including ethylene, jasmonic acid, and salicylic acid also participate, creating a complex network of cross-talk that fine-tunes plant adaptation. This integration ensures that stress responses are balanced with growth and developmental needs, preventing excessive energy allocation solely to defense (Yang et al. 2019; Liu et al. 2024).

4. GENE EXPRESSION REGULATION UNDER SALT STRESS

4.1 Transcriptional Regulation

One of the most critical responses to salinity is the reprogramming of transcriptional networks. A large number of salt-responsive genes are activated or repressed depending on the severity and duration of stress. Transcription factors (TFs) play central roles in this regulation, binding to cis-regulatory elements in promoters and modulating gene expression. Among the key TF families, NAC, DREB/CBF, bZIP, MYB, and WRKY have been extensively studied. For instance, DREB/CBF proteins bind to dehydration-responsive elements (DRE/CRT) and activate genes encoding osmoprotectants and detoxifying enzymes. Similarly, NAC TFs regulate genes involved in ion transport and root architecture remodeling, thereby enhancing plant survival under saline conditions (Zhao et al. 2020; Aizaz et al. 2024).

In *Arabidopsis thaliana*, the *RD29A* gene (Responsive to Desiccation 29A) represents a classical marker for stress-inducible transcription. Its promoter contains both DRE/CRT (Dehydration-

Responsive Element/C-Repeat) and ABRE (ABA-Responsive Element) motifs. These elements allow dual regulation:

- DREB/CBF transcription factors (AP2/ERF family) activate *RD29A* in an ABA-independent pathway.

- ABF/AREB transcription factors (bZIP family) activate the same gene in an ABA-dependent manner. This combinatorial control ensures a robust transcriptional response to salt-induced osmotic stress (Narusaka et al. 2003). The *SOS1* (Salt Overly Sensitive 1) gene, encoding a plasma membrane Na^+/H^+ antiporter, is also transcriptionally induced under salinity. Its promoter is targeted by transcription factors such as WRKY75, enhancing Na^+ extrusion from the cytoplasm and contributing to ionic homeostasis. (Rahmati Ishka 2023).

Rice plants employ a similar strategy with species-specific regulators. *OsHKT1;5*, a transporter responsible for restricting Na^+ accumulation in shoots, shows transcriptional activation in salt-tolerant cultivars. Regulation of this gene involves NAC transcription factors, which bind to NAC recognition sequences in the promoter.

Additionally, *OsDREB2A*, a member of the DREB subfamily, is strongly induced under high salinity and activates downstream stress-protective genes. The *OsbZIP23* transcription factor, functioning in the ABA-dependent pathway, binds ABRE elements and contributes to osmotic adjustment and ion homeostasis (Li et al. 2021).

In wheat, the *TaHKT1;5-D* locus has been directly associated with Na^+ exclusion and enhanced salinity tolerance. This gene exhibits transcriptional upregulation under salt exposure, mediated by cultivar-specific transcription factor activity. The *TaNAC2* transcription factor serves as a regulator of multiple downstream targets, including ion transporters and osmotic balance genes. Similarly, the *TaSOS1* ortholog of Arabidopsis *SOS1* is induced under salinity, reinforcing the conserved

role of SOS pathways across monocots and dicots (Byrt et al. 2014; Wang et al. 2024; Traye et al. 2025).

Cis-elements such as ABA-responsive elements (ABREs) and MYB-binding sites act as molecular switches that integrate hormonal and stress signals. The combinatorial action of different TFs ensures that stress-responsive pathways are selectively activated without completely halting normal metabolic processes (Colinas and Goossens 2018).

4.2 Post-Transcriptional Regulation

Beyond transcriptional control, plants rely on post-transcriptional mechanisms to fine-tune gene expression. Small RNAs, particularly microRNAs (miRNAs), play a pivotal role in regulating mRNA stability and translation. For example, *miR398*, *miR169*, and *miR393* are differentially expressed under salt stress, targeting transcripts related to antioxidant defense, hormone signaling, and transporters. Alternative splicing is a key post-transcriptional mechanism that generates multiple mRNA isoforms from a single gene, thereby expanding proteomic diversity. Splicing is regulated by factors such as SR proteins and hnRNPs, and in plants, isoform switching plays a crucial role under abiotic stress by rapidly adjusting gene expression. mRNA degradation determines transcript stability and abundance, preventing the accumulation of defective RNAs. Major pathways include 5'–3' decay (via *DCP1/DCP2* and *XRN4*), 3'–5' decay (exosome complex), and nonsense-mediated decay (NMD). These mechanisms often act in coordination with translation and help plants reset their transcriptome during stress conditions. Together, alternative splicing and mRNA degradation provide complementary layers of gene regulation, enabling plants to fine-tune gene expression, maintain flexibility, and adapt to environmental challenges (Figure 1) (Schoenberg and Maquat, 2012). This diversification allows plants to adapt their proteome rapidly to fluctuating stress conditions (Zhang et al. 2022; Mandadi et al. 2023).

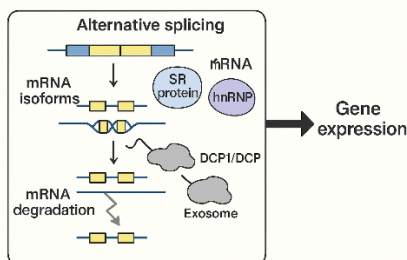


Figure 1. Regulation of gene expression via alternative splicing and mRNA degradation in plants

RNA-binding proteins also contribute by modulating mRNA transport, stability, and localization, ensuring that stress-responsive transcripts are efficiently translated when needed.

4.3 Translational and Post-translational Control

Gene regulation under salinity is further refined at the translational and post-translational levels. Under salinity-induced stress, ribosome function is finely regulated, typically resulting in a widespread attenuation of overall protein biosynthesis, accompanied by the selective enhancement of translational efficiency for specific stress-responsive mRNAs that are crucial for cellular adaptation. Post-translational modifications, including phosphorylation, ubiquitination, and sumoylation, alter protein activity, stability, and localization. For example, stress-activated protein kinases phosphorylate transcription factors, enhancing their DNA-binding capacity. Similarly, ubiquitin-mediated degradation ensures that non-essential or damaged proteins are rapidly removed, preventing cellular toxicity (Chen et al. 2021; Sharma et al. 2023).

5. ION HOMEOSTASIS and TRANSPORTER GENE REGULATION

Maintaining ionic balance is essential for plants under saline conditions. One of the primary molecular responses involves the SOS (Salt Overly Sensitive) signaling pathway, consisting of *SOS1* (a plasma membrane Na^+/H^+ antiporter), *SOS2* (a protein kinase), and *SOS3* (a Ca^{2+} -binding protein). This pathway facilitates the extrusion of Na^+ from the cytoplasm, thereby preventing toxic accumulation (Yang and Guo 2018).

Another key mechanism is mediated by *HKT* transporter genes, which restrict Na^+ entry into the xylem, reducing its transport to shoots. Meanwhile, *NHX* antiporters located at the tonoplast sequester Na^+ into vacuoles, effectively detoxifying the cytoplasm. The expression of these transporter genes is tightly regulated by both TFs and epigenetic modifications (Malakar et al. 2021; Saddhe et al. 2021).

Interestingly, cross-talk between ion transporters and hormonal signaling has been observed. For instance, ABA enhances the expression of certain *HKT* genes, linking stress signaling with ionic adaptation. The coordination of these transporter systems is crucial for maintaining a favorable Na^+/K^+ ratio, which underpins many enzymatic and metabolic functions (Jan et al. 2021).

6. EPIGENETIC REGULATION IN SALT STRESS ADAPTATION

Epigenetic modifications provide plants with a flexible yet stable mechanism to regulate gene expression under salinity. DNA methylation patterns are often altered in salt-stressed plants, leading to the activation or repression of key genes. Hypomethylation of stress-responsive

promoters, for example, can enhance the expression of protective proteins (Sun et al. 2022).

Histone modifications, including acetylation and methylation, also play critical roles (Figure 2). Acetylation of histone H3 at specific lysine residues is generally associated with transcriptional activation of stress-responsive genes, while repressive marks such as H3K9me2 are reduced under stress conditions (Kim 2021).

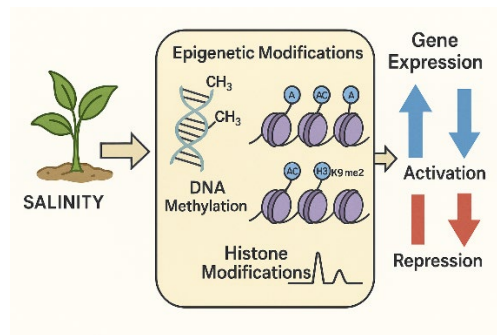


Figure 2. Epigenetic regulation of salinity stress in plants

Non-coding RNAs represent another layer of epigenetic regulation. Long non-coding RNAs (lncRNAs) and miRNAs modulate gene expression post-transcriptionally and also interact with chromatin modifiers to influence gene accessibility. Notably, some of these epigenetic changes can be inherited across generations, providing plants with a form of stress memory that enhances adaptation in progeny (Lagiotis et al. 2023; Zhang et al. 2024a). *miR398* is significantly downregulated under salt stress in *Arabidopsis*. This reduction relieves the repression of its target genes, such as Cu/Zn-superoxide dismutases (*CSD1* and *CSD2*), enhancing the detoxification of reactive oxygen species (ROS). By regulating ROS scavenging enzymes, *miR398* contributes to the cellular balance required for salt tolerance. *miR319* is strongly induced by salinity and negatively regulates TCP transcription

factors, which are involved in leaf growth and developmental processes in *Triticum aestivum*. (Islam et al. 2022; Cheng et al. 2024).

7. INTEGRATIVE OMICS APPROACHES

With the advent of high-throughput technologies, integrative omics has become indispensable in studying salt stress adaptation. Transcriptomic analyses (RNA-seq, microarrays) have identified thousands of salt-responsive genes across different species. Proteomic studies reveal post-translational modifications and protein-protein interaction networks crucial for stress signaling. Metabolomics provides insights into osmolyte accumulation, antioxidant profiles, and energy metabolism under salinity (Dai et al. 2022). Transcriptomic studies in *Oryza sativa* and *Arabidopsis thaliana* have uncovered transcription factors (e.g., DREB, NAC, and bZIP families) and ion transporter genes (e.g., *HKT1;5*, *NHX1*, *SOS1*) that are consistently regulated under salt exposure. These findings provide molecular markers for breeding salt-tolerant varieties (Hualpa-Ramirez et al. 2024).

Systems biology approaches integrate these datasets to construct regulatory networks, revealing hub genes and master regulators (Barua et al. 2022). Moreover, machine learning algorithms are increasingly applied to predict salt-tolerant gene candidates, accelerating breeding programs. Such holistic approaches bridge the gap between molecular mechanisms and practical crop improvement strategies (Zhang et al. 2024b).

8. MOLECULAR BREEDING and GENETIC ENGINEERING PERSPECTIVES

Traditional breeding for salt tolerance has been limited by the polygenic nature of the trait. However, molecular tools have revolutionized this field. Marker-assisted selection (MAS) allows breeders to track favorable alleles associated with salt tolerance. Genome editing technologies, particularly CRISPR/Cas systems, provide unprecedented precision in modifying stress-responsive genes (Aamir et al. 2025).

Transgenic approaches have demonstrated success by overexpressing transcription factors (e.g., DREB, NAC) or transporter genes (e.g., *NHX1*). Transgenic rice expressing *OsDREB1A* gene showed improved growth and yield under saline and drought conditions in *Oryza sativa*. *OsNAC6* gene overexpression strengthened root structure and stress tolerance mechanisms. These engineered plants show improved growth and yield under saline conditions. Additionally, synthetic biology holds promise for designing novel regulatory circuits that enhance plant resilience. Nevertheless, the deployment of genetically modified crops requires careful consideration of biosafety, regulatory, and ecological aspects (Dubouzet et al. 2003; Nakashima et al. 2007; Ullah et al. 2022).

9. FUTURE PROSPECTS and CONCLUSION

The persistence of salinity as a major abiotic stress factor will remain a substantial threat to global food security, most notably in arid and semi-arid zones characterized by fragile agricultural systems. Molecular insights into salt stress adaptation have provided valuable tools for developing tolerant crop varieties. However, the challenge lies

in translating laboratory findings to field conditions, where multiple stresses often interact.

Future research should focus on:

- Unraveling cross-talk between salt stress and other abiotic stresses (drought, heat).
- Expanding studies to non-model and crop species.
- Harnessing epigenetic memory and transgenerational adaptation.
- Applying integrative omics and computational biology for predictive breeding.

In conclusion, understanding gene expression and regulation under salt stress provides a foundation for innovative breeding and biotechnological strategies. By combining classical physiology with cutting-edge molecular approaches, it is possible to engineer crops capable of thriving in saline environments, thereby ensuring agricultural sustainability in the face of global climate change.

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Salt Stress and Its Effects on Volatile Compounds

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1. INTRODUCTION

Plants face various biotic and abiotic stressors in their surroundings, significantly influencing their growth, development, and overall productivity. Nonliving environmental conditions, referred to as abiotic stress factors, encompass drought, salinity, extreme temperatures, and heavy metals. These factors can negatively impact plant metabolism, resulting in diminished crop yield and quality (Zhu 2016; Dey and Raichaudhuri 2022; Suvarna et al. 2024). The agricultural importance of these stressors is particularly pronounced, given that climate change is anticipated to increase their occurrence. This situation points to the urgent need for the development of plant varieties that possess improved stress tolerance to safeguard food security (Teshome et al. 2020; Aloo et al. 2023). Furthermore, the interplay of abiotic and biotic stresses can lead to a compounded negative impact on vegetation and reduce biodiversity, posing significant threats to both forest ecosystems and agricultural landscapes (Dresselhaus and Hückelhoven 2018; Teshome et al. 2020).

Salt stress, as a specific form of abiotic stress, presents considerable challenges in agriculture by disrupting water uptake and ion balance in plants, resulting in physiological and metabolic disturbances. This stress is essential not only for the survival of crops but also for preserving ecological equilibrium, as the buildup of salts can result in desertification and the degradation of arable land (Dresselhaus and Hückelhoven 2018). Therefore, comprehending the mechanisms through which plants withstand salt stress is crucial for advancing agricultural practices and boosting crop resilience (Hasanuzzaman et al. 2020; Quintana et al. 2022).

Moreover, the significance of volatile organic compounds (VOCs), including essential oils and terpenes, is gaining attention in the context of plant metabolism, especially regarding stress responses. These secondary metabolites can alleviate stress effects by functioning as signaling molecules that modulate physiological processes or by offering defensive roles against herbivores and pathogens (Silva et al. 2011; Dutra et al. 2020). For example, the production of essential oils is

frequently initiated by stress conditions and can improve the plant's ability to withstand various pressures (Bonacina et al. 2017; Üner and Cesur Turgut 2024). Investigating the relationship between stress responses and VOC production offers intriguing opportunities to harness these natural compounds for agricultural advantages. It is important to learn how stress conditions affect the biosynthesis of essential oils and other volatile compounds (Vujanović et al. 2021; Quintana et al. 2022; Çetinkol and Cesur Turgut 2024).

2. PHYSIOLOGICAL AND MOLECULAR EFFECTS OF SALT STRESS ON PLANTS

Salt stress presents significant challenges, including osmotic stress, ion toxicity, and the resulting disruptions in metabolic processes, all of which profoundly affect plant physiology and metabolism. Pan et al. (2020) indicate that osmotic stress arises from high salinity, occurring when there is a reduction in the water availability for the plant. This stress obstructs the plant's capacity to take in water, subsequently resulting in a reduction of turgor pressure and cell viability. Furthermore, the buildup of sodium ions (Na^+) and chloride ions (Cl^-) can lead to a disturbance in the cellular ionic balance, subsequently hindering the absorption of vital nutrients such as potassium (K^+) and calcium (Ca^{2+}). (Rengasamy 2018). According to Tavakkoli et al. (2011), this ionic imbalance causes a malfunction in several physiological processes, including the inhibition of growth, the reduction of photosynthesis, and the impairment of nutrient transfer.

The plant will initiate a series of metabolic changes in reaction to salt stress to maintain cellular function and minimize damage incurred. The synthesis of appropriate solutes represents one adaptation technique that can be employed. The presence of these solutes plays a crucial role in stabilizing cellular structures and maintaining osmotic balance. Zhang et al. (2016) and Wu et al. (2013) indicate that organic acids, amino acids like proline, and sugars such as trehalose function as osmoprotectants. Consequently, they allow plants to endure osmotic stress while still preserving the integrity of their cells. Moreover, the alteration of

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standard metabolic pathways could trigger secondary metabolism, serving as a defensive mechanism against oxidative stress induced by salt (Kosar et al. 2022). This outcome leads to an increased synthesis of phenolics and terpenoids.

The activation of antioxidant defense systems is a crucial physiological response that occurs in reaction to salt stress. These systems play a crucial role in addressing reactive oxygen species (ROS). Elevated levels of ROS can lead to oxidative damage, impacting cell membranes, proteins, and nucleic acids (Jiang et al. 2022). The presence of antioxidant enzymes, including superoxide dismutase, catalase, and ascorbate peroxidase, is essential for effectively scavenging these harmful species. This process contributes to sustaining metabolic activity and ensuring the integrity of the cell (Mustafiz et al. 2014). Research by Jiang et al. (2022) and Zhao et al. (2025) indicates that the activation of these antioxidative pathways correlates with enhanced salt tolerance across various plant species.

Moreover, salt stress induces a multifaceted interplay between stress signaling and secondary metabolism in response to its effects. Zhao et al. (2025) indicate that regulating genes associated with the production of secondary metabolites is crucial for enhancing plant resilience under saline conditions. For instance, it has been shown that melatonin can affect secondary metabolic pathways, thereby providing a comprehensive approach to improve salt resistance through β -alanine and glutathione metabolism (Li et al. 2017). The findings indicate a robust connection between antioxidant activity and the generation of secondary metabolites, underscoring the combined importance of these two processes in the context of stress adaptation.

In summary, the physiological and molecular impacts of salt stress encompass a variety of osmotic and ionic challenges, prompting plants to engage in metabolic reprogramming to ensure their survival. This underscores the importance of comprehending these mechanisms for enhancing crop resilience in saline environments. The relationship between antioxidant defenses and the synthesis of secondary metabolites

is crucial for enhancing salt tolerance, making it imperative to comprehend these systems.

3. VOLATILE COMPOUNDS: BIOSYNTHESIS AND FUNCTIONS

VOCs are important secondary metabolites generated by plants, serving vital functions in ecological interactions and plant physiology. The classification of these compounds encompasses various categories, such as monoterpenes, sesquiterpenes, and phenylpropanoids. Monoterpenes, composed of two isoprene units, encompass well-known compounds like limonene, whereas sesquiterpenes, consisting of three isoprene units, feature substances such as β -caryophyllene (Jun et al. 2016). Phenylpropanoids, originating from phenylalanine, include a range of aromatic compounds that contribute to floral scent and bolster plant defense mechanisms (Yang et al. 2023).

The biosynthetic pathways for these VOCs mainly include the mevalonate (MVA) pathway and the methyl-erythritol phosphate (MEP) pathway. The MVA pathway mainly functions in the cytoplasm, enabling the synthesis of sesquiterpenes and sterols, whereas the MEP pathway takes place in plastids and is tasked with producing monoterpenes and various terpenoids. The utilization of sophisticated -omics technologies has greatly enhanced our comprehension of these pathways, delineating the genetic and enzymatic complexities that regulate VOC production (Yu et al. 2020).

VOCs play various roles in ecosystems, especially in how plants protect themselves from herbivores and pathogens. Some terpenes can repel pests or suppress microbial growth, functioning as direct antimicrobial agents. For example, the release of particular sesquiterpenes has been documented to limit pathogen colonization in different plant species, thereby improving overall plant resilience to biotic stress (Chalal et al. 2015). Furthermore, these compounds may function as appealing signals for pollinators. The volatile profiles released by flowers play a vital role in attracting pollinators, thereby

aiding in reproduction. This study highlights the dual function of these compounds in signaling and defense (Lo et al. 2021).

Furthermore, VOCs demonstrate allelopathic effects that can impact the growth of adjacent plants. Plants can enhance their ecological advantage by releasing specific volatile compounds into the environment, which can inhibit seed germination or growth in competing species (Effah et al. 2022). This interaction highlights the importance of VOCs not only in immediate plant defenses but also in influencing the dynamics of plant communities.

In summary, the biosynthesis and functional roles of VOCs in plants are complex and varied. VOCs play a vital role in plant survival and ecological interactions, engaging in diverse biosynthetic pathways and fulfilling essential ecological functions, including defense mechanisms and mediating interactions with pollinators and competitors. Investigating the modulation of these pathways in the future presents opportunities for improving plant resilience in dynamic environments and refining agricultural practices.

4. RELATIONSHIP BETWEEN SALT STRESS AND VOLATILE COMPOUND PRODUCTION IN PLANTS

Salt stress influences plant metabolism, particularly the biosynthesis of VOCs, including monoterpenes and sesquiterpenes. Elevated salinity can enhance the production of secondary metabolites as a stress response mechanism, illustrating the connection between abiotic stress and plant chemistry. Plant hormones, including abscisic acid (ABA) and jasmonates, are crucial in mediating these responses (Tang et al. 2014; Su et al. 2023).

In response to salt stress, *Mentha piperita* demonstrates modified growth patterns and variations in essential oil profiles. Studies show that elevated sodium chloride (NaCl) concentrations can enhance monoterpene production, affecting the plant's defense mechanisms and overall physiology. The accumulation of monoterpenes functions as a protective mechanism against herbivores and pathogens, while also

improving the plant's osmotic balance. Altuntaş et al. (2016) observed that elevated salinity led to significantly increased concentrations of menthol and other monoterpenes in peppermint, which are directly associated with the plant's physiological adaptation to osmotic stress.

The impact of salt stress on rosemary (*Salvia rosmarinus*, formerly *Rosmarinus officinalis*) and sage (*Salvia officinalis*) reveals a relationship between salt concentration and the profiles of volatile compounds. Increased salinity levels correlate with heightened production of aromatic compounds, though the quality of these compounds may differ. *Thymus vulgaris* exhibits variations in its essential oil profile when subjected to salt stress, demonstrating that elevated NaCl concentrations can modify both the quantity and quality of its volatile constituents (Cappellari et al. 2020). The variance influences the quality of the plant's extract and its fragrance, both of which are essential for ecological interactions and human applications.

The modulation of hormones such as ABA and jasmonates induced by stress is significant in driving these changes. ABA is recognized for its involvement in plant stress responses and its regulation of the biosynthetic pathways for terpenoids and phenolic compounds. This connection indicates that increased salt stress elevates ABA levels, potentially activating genes responsible for enzymatic reactions that enhance VOC synthesis (Su et al. 2023).

Adaptive modifications in the biosynthesis of volatile compounds are observed in additional species as well. Salinity induces an increase in the production of phenolic compounds, known for their antioxidant properties. Aromatic compounds play a crucial role in scavenging ROS and enhancing plant defenses against stress (Lim et al. 2012). Furthermore, VOCs released by salt-stressed plants may serve as signaling molecules for adjacent plants, signaling the presence of stress and potentially improving their readiness, a phenomenon referred to as plant priming, as demonstrated in research involving neighboring cotton plants (Tanveer et al. 2019).

5. EXPERIMENTAL RESULTS

Recent studies indicate that salt stress markedly affects the production of VOCs in diverse plant species, especially aromatic and medicinal plants. Experimental findings from laboratory, greenhouse, and field studies illustrate the importance of stress levels, analytical methods such as gas chromatography-mass spectrometry (GC-MS) and headspace-solid phase microextraction (HS-SPME), and the specific alterations in VOC composition resulting from salinity.

Controlled laboratory experiments indicate that specific stress levels of NaCl enhance VOC production across various species. Studies indicate that elevated salinity levels are associated with increased concentrations of desirable monoterpenes and sesquiterpenes in *Rosmarinus officinalis*, resulting in improved aromatic profiles (Al-Fraihat et al. 2023). Field studies have confirmed these findings, demonstrating that aromatic plants thriving in saline soils generate substantial quantities of essential oils, measurable through advanced analytical techniques such as GC-MS and HS-SPME (Stefanakis et al. 2024).

Different NaCl concentrations led to unique VOC profiles in various plants, suggesting that salinity affects both the quantity and quality of oil produced (Khaled and Fawy 2011). This observation was corroborated in a separate field study, where aromatic plants like *Thymus vulgaris* and *Salvia officinalis* demonstrated qualitative alterations in their essential oil composition in response to increased salinity levels, suggesting an adaptive mechanism to endure abiotic stress (Jungklang et al. 2017).

Research by Abdelhamid et al. (2013) indicates that salt stress induces osmotic alterations that impede nutrient absorption, thereby affecting secondary metabolism and the equilibrium of VOCs in plants. Salinity impacts plant physiological processes, including photosynthesis and growth, subsequently affecting the production of secondary metabolites such as terpenes and phenolics, which are essential for plant resilience. The response of *Mentha* species to salt stress is notable, demonstrating increased accumulation of menthol and menthone under

saline conditions, which is ultimately associated with enhanced antioxidant activity and mechanisms of stress tolerance (Pazouki et al. 2015).

Hormonal regulation, particularly involving ABA and jasmonates, plays a crucial role in mediating these responses. In saline conditions, hormones can initiate pathways that enhance VOC synthesis. In an experiment with salt-stressed *Curcuma alismatifolia*, proline accumulation was significantly reduced, indicating differences in stress tolerance associated with hormonal profiles (Jungklang et al. 2017). The application of growth regulators, including amino acids, has demonstrated potential in mitigating the negative impacts of salinity on VOC production (Al-Fraihat et al. 2023).

The combined results of laboratory observations and field data demonstrate the complexities of plant responses to salinity, highlighting the critical relationships among stress levels, VOC production, and plant resilience strategies. With the intensification of environmental stress from climate change, it is necessary to understand these mechanisms to develop salt-tolerant plant cultivars and enhance the agronomic practices of valuable aromatic species.

6. UTILIZATION AND INDUSTRIAL IMPLICATIONS OF VOLATILE COMPOUNDS IN PLANTS UNDER SALT STRESS

In the pursuit of improving the quality of volatile compounds in aromatic and medicinal plants, scientists have concentrated on the strategic application of controlled salt stress as a method for enhancement. This methodology enhances the secondary metabolite profiles of these plants while simultaneously promoting sustainable agricultural practices through the facilitation of species adaptation to saline environments.

Research has shown that particular abiotic stressors, especially salinity, can be utilized to trigger advantageous physiological and biochemical reactions. The introduction of external compounds like salicylic acid (SA) and nitric oxide (NO) has demonstrated the ability to

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mitigate growth reductions and promote the synthesis of essential oils in plants subjected to salt stress, as noted by Ahanger et al. (2019). For example, the engagement of SA with stressed plants has been recognized as a facilitator for metabolic pathways that enhance the production of secondary metabolites, consequently improving the aromatic quality of crops such as *Dianthus superbis* (Zheng et al. 2018). Furthermore, it has been observed that the process of salt acclimation may markedly improve the stability of potassium ions within plant tissues, consequently fostering enhanced plant health and the production of volatile compounds (Zuo et al. 2019).

The identification of halophytic species is essential for enhancing the yield of aromatic and medicinal plants in saline environments. Through the identification and cultivation of cultivars exhibiting inherent salt tolerance, there is potential for substantial enhancement in crop resilience and essential oil yields. The application of genetic engineering presents a significant opportunity to improve salt tolerance and metabolic characteristics across diverse species. For instance, investigations into phytohormones have underscored their involvement in facilitating salt tolerance mechanisms via transcriptomic and metabolomic assessments, illustrating the potential of biotechnological strategies in altering essential stress response pathways (Zhu et al. 2021).

The modulation of plant growth regulators (PGRs) has garnered significant interest for its influence on metabolite production in response to salt stress, alongside advancements in genetic engineering. Hormonal signals, especially those derived from jasmonates and ethylene, have the capacity to modulate the biosynthesis of secondary metabolites, thereby impacting the flavor and aroma characteristics crucial for market competitiveness (Zhu et al. 2021). Moreover, compounds like proline and betaine are recognized for their accumulation in response to saline stress, offering osmoprotection and enhancing the overall resilience of plants (Ahmed et al. 2021).

The findings derived from diverse experimental methodologies, encompassing both laboratory investigations and field assessments,

emphasize the industrial viability of leveraging salt stress to augment the production of volatile compounds in aromatic plants. These strategies enhance the agricultural viability of these plants while simultaneously fostering the advancement of sustainable practices in the face of changing climate conditions. As investigations advance, these integrative methodologies hold the potential to enhance the synthesis of premium essential oils, harmonizing with both economic and ecological goals within agricultural practices.

7. CONCLUSION AND FUTURE PERSPECTIVES

Salinity stress poses a significant risk; however, if managed effectively, it can also create opportunities for agricultural production and plant physiology. High salinity levels inhibit plant growth, whereas low to moderate salinity levels may enhance the biosynthesis of specific volatile compounds. This phenomenon presents opportunities for enhancing the quality and biological activity of aromatic and medicinal plants.

Nonetheless, numerous research gaps are still apparent. Long-term field studies are limited, as the majority of existing data comes from short-term experiments conducted in controlled environments. The specific molecular mechanisms by which salinity stress influences volatile compound biosynthesis remain to be fully clarified.

Future research should incorporate high-resolution methodologies, including metabolomics and transcriptomics, to achieve a comprehensive understanding of the salinity–metabolite relationship. The optimization of controlled stress applications may serve as a strategic tool to improve both the quantity and quality of targeted volatile compounds.

In summary, comprehending the effects of salinity stress on plant metabolism is crucial for agricultural sustainability in the context of climate change and the production of high-value plant-based products. In the future, managing salinity stress will function not only to avert yield

losses but also to develop as a novel production strategy that influences the value chain of plant-derived volatiles.

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Plant Responses to Drought: Physiological Disruptions and Adaptive Mechanisms

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1. INTRODUCTION

Drought stress is a major environmental factor limiting agricultural productivity. With global climate change increasing the frequency and severity of drought events, plant growth and development are increasingly affected, leading to an estimated 70% loss in potential crop yield and productivity (Basu et al. 2016, Bashir et al. 2021). Approximately 41% of the world's land area, 36% of agricultural land (29% of the 536 million hectares of land consists of desert, 44.3% semi-desert, and 26% arid and semi-arid regions) and more than 2 billion people (one-third of the world's population) are affected by drought (Yıldırım et al. 2021). It is believed that current climate scenarios and projected global warming will have a major effect on the moisture timetable, making drought more common and severe globally.

Drought, inadequate light, temperature fluctuations, soil salinity, heat waves, and exposure to heavy metals are just a few of the stresses that plants encounter during growth and development. Dehydration has an effect on plant morphology at every developmental stage that is pertinent to plant metabolism. Crop plants mitigate drought by employing acclimatization and distinct tolerance mechanisms to adapt to unfavorable conditions. The diversity of plant species grown in various climatic regions, including arid areas, shows that plants have evolved morphological, physiological, and biochemical mechanisms to tolerate drought stress (Figure 1). A variety of physiological, biochemical, and molecular processes at both the cellular and entire plant levels are modified in response to water constraint and are crucial for stress alleviation (Basu et al. 2016, Bashir et al. 2021, Jeyasri et al. 2021, Chaudhry and Sidhu 2022). In response to water deprivation, plants employ many stress mechanisms, including the synthesis of reactive oxygen species, the generation of stress hormones like ethylene and abscisic acid, and alterations in root and stem morphology to combat drought (Song et al. 2023).

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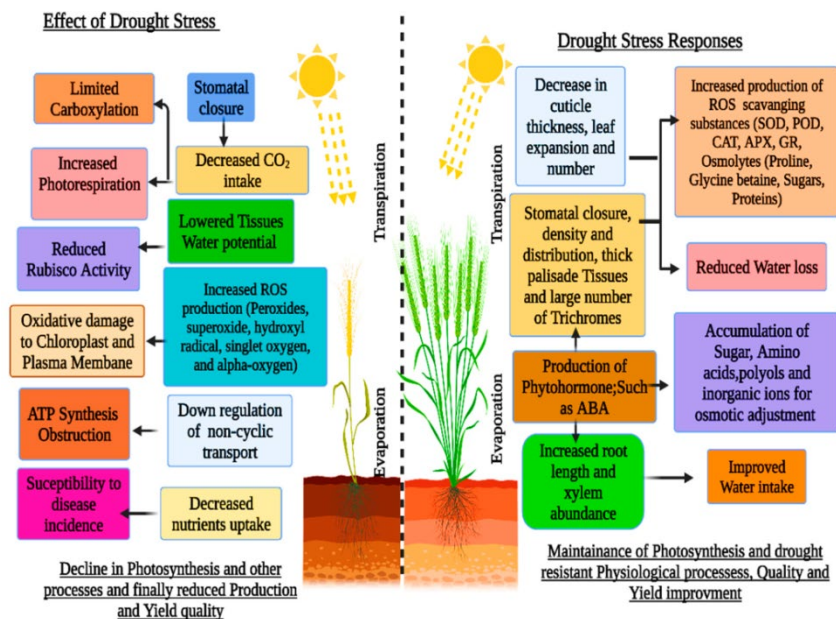


Figure 1. Effects of drought stress on plants (Wahab et al. 2022)

Under drought stress conditions, the plant diminishes its osmotic potential to facilitate water absorption via osmotic accumulation, including soluble carbohydrates. In the process of osmotic control, turgor and related mechanisms persist under times of water scarcity. Consequently, osmotic control facilitates cellular development and promotes plant growth under drought stress (Farooq et al. 2012).

The aim of this chapter is to provide a comprehensive overview of plant responses to drought stress by integrating physiological, biochemical, and molecular perspectives. Specifically, the chapter seeks to elucidate the types and characteristics of drought stress, its disruptive effects on essential physiological processes such as photosynthesis, germination, growth, nutrient uptake, as well as the underlying biochemical and molecular mechanisms involved in osmotic adjustment,

antioxidant defense, and hormonal regulation. Furthermore, the adaptive strategies of drought avoidance, tolerance, and escape, this chapter intends to offer a holistic understanding of how plants cope with water scarcity, thereby contributing to the development of more resilient and sustainable agricultural systems.

2. TYPES AND CHARACTERISTICS OF DROUGHT STRESS

In meteorology, drought is defined as duration characterized by insufficient rainfall. Plants undergo drought stress when soil water availability diminishes, exacerbated by climatic circumstances that lead to increased water loss through evaporation and transpiration (Chaudhry and Sidhu 2022). Researchers have indicated that drought initiates as a meteorological phenomenon, progresses to hydrological and agricultural droughts, and manifests its impacts as a socioeconomic drought (Yıldırım et al. 2021).

Meteorological Drought: Meteorological drought is defined as a significant decrease in rainfall below normal values over a specific period of time (generally a 30-year period) or as a deviation from normal values. Meteorological drought is also defined as the number of days with rainfall below specified threshold values, and it occurs depending on the degree of rainfall deficiency and the length of the dry period (Yıldırım et al. 2021).

Agricultural Drought: Agricultural drought negatively affects plant growth and crop productivity, creating significant pressure on agricultural production. During the growth period, the lack of sufficient soil moisture during a specific critical period when a particular plant needs water causes agricultural drought. In other words, agricultural drought is the inability of a plant to obtain the water it needs, depending on its genetic structure, rainfall amount and distribution, soil water-

holding capacity and physical and chemical properties, and the availability and quality of irrigation water (Yıldırım et al. 2021).

Hydrological Drought: The term refers to the decrease and deficiency in rivers, reservoirs, and groundwater levels resulting from prolonged rainfall deficiency. Although prolonged rainfall deficiency is immediately felt in the agricultural sector, hydrological measurements are not the first indicators of drought due to the time lag between rainfall deficiency and water shortages in rivers and reservoirs (Yıldırım et al. 2021).

Socio-Economic Drought: This transpires when water supply is inadequate to satisfy the requirements of both humans and the ecosystem. This deficiency is attributable to climatic, hydrological, or agricultural dry conditions. The impact on water resources and the industries that rely on these resources—including agriculture, livestock, forestry, fishing, and related sectors—is significant (Kapluhan 2013, Yıldırım et al. 2021, Hirca 2025).

Drought, one of the most important abiotic stress factors, is related to the timing (delays in the onset of the rainy season, the relationship between the crop growing season and the timing of rainfall) and the degree of precipitation impact (intensity and frequency). Other variables, such as high temperatures, strong winds, and low humidity, contribute to drought in many regions (Kusvuran 2010).

Drought can be divided into three categories within general principles: severe (acute), chronic (long-term), and physiological droughts. An elevation in temperature, a swift reduction in humidity, or a desiccated air mass can precipitate rapid and severe water loss in plants. These atmospheric alterations result in elevated transpiration rates. As a result of severe drought, symptoms such as wilting due to insufficient assimilation in young and old leaves, drying of shoot tips, reduced yield, and slowed growth may be observed. The initial indication of drought is

wilting. Provided that the wilting point is not surpassed, withering diminishes when water is provided to the plant (Çırak and Esendal 2006). Chronic drought, on the other hand, occurs due to a decrease in groundwater levels in the soil. In plants continuously exposed to drought, wilting occurs first, followed by drying in later stages. Wilting in plants refers to excessive water loss, which can result in a total disruption of metabolism and cellular structure, finally halting enzyme-catalyzed activities (Eriş 1990, Smirnov 1993, Kalefetoğlu and Ekmekçi 2005, Kusvuran 2010). Even when there is sufficient water in the soil, the inability of the plant to utilize water for various reasons is defined as physiological drought. Even though the soil contains sufficient water, if the soil's water-holding capacity exceeds the plant's suction force, the plants cannot absorb water and enter a state of drought stress (Çırak and Esendal 2006).

3. PHYSIOLOGICAL AND BIOCHEMICAL EFFECTS OF DROUGHT STRESS IN PLANTS

Water stress interferes with various physiological and biochemical functions, thereby limiting plant growth and development. Although plants may tolerate limited water availability, it generally leads to a marked reduce in total biomass and yield. Drought stress conditions disrupt photosynthesis, growth, and other essential physiological and biochemical processes (Wahab et al. 2022).

3.1. Photosynthesis

Drought significantly reduces photosynthesis in plants. Under drought stress, total leaf area decreases and photosynthesis slows down. Under stress conditions, photosynthesis is limited by the closure of stomata, while under prolonged and severe stress, it is inhibited by factors other than stomata. The initial decrease in photosynthesis under drought stress occurs due to the closure of stomata and reduced CO₂

absorption. When the plant occludes its stomata to mitigate water loss, the absorption of CO₂ essential for photosynthesis is concurrently inhibited (Çırak and Esendal 2006). According to Teiz and Zeiger (2003), hydraulic cues (leaf water potential, cell turgor) and chemical signals (abscisic acid) cause plants to shut their stomata. Photosynthesis also decreases due to chloroplastic factors. Photosynthesis generally occurs in chloroplasts. Enzymes such as ribulose biphosphate carboxylase, which accumulate CO₂ in the stoma region and reduce it to organic compounds, have their activity reduced due to water loss, thereby impairing CO₂ fixation. While photosynthesis is initially reduced by stomatal factors, prolonged drought stress and increased intensity lead to depression in chloroplast and enzyme activity, resulting in photosynthesis being reduced by factors apart from stomata. Furthermore, in advanced stages of drought, the diffusion resistance of mesophyll cell walls increases, thereby preventing CO₂ from entering mesophyll cells (Çırak and Esendal 2006).

The limitation of CO₂ transport to carboxylation sites within the chloroplast is recognized as the primary constraint on photosynthesis, particularly during the early stages of stress. The fundamental elements of leaf diffusion, stomatal conductance (gs), and mesophyll conductance (gm) contribute significantly to limitations in photosynthesis under drought conditions and are directly affected by the severity of water scarcity. Therefore, the ability to rapidly adjust gs and gm values is critical for plants to adapt to drought stress at the photosynthetic level and subsequently recover. Indeed, it is known that drought stress negatively affects photosynthesis by reducing both leaf area and photosynthetic rate per unit of leaf area. This decrease is primarily associated with stomatal closure or metabolic dysfunction. Studies on wheat have shown that gas exchange parameters such as photosynthetic rate (Pn), gs, and transpiration rate are significantly reduced under drought stress compared to well-watered conditions (Wasaya et al.

2021). Despite the limited intercellular CO₂ concentration during drought stress, photosynthetic light reactions continue, leading to the accumulation of photosynthetic electron transport components, a decrease in molecular oxygen levels, and ultimately the formation of reactive oxygen species (ROS). ROS can cause serious damage to photosynthetic structures; in response, plants attempt to limit this damage through adaptive mechanisms such as thermal dissipation of light energy, the xanthophyll cycle, the water-water cycle, and the separation of reaction centers from light-harvesting complexes. Additionally, it has been reported that metabolic dysfunction in photosynthesis during drought stress is largely attributed to changes in carbon metabolism, with the metabolic efficiency of photosynthesis during this process being dependent on ribulose-1,5-bisphosphate (RuBP) regeneration and ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) activity (Basu et al. 2016). Water-limited plants exhibited a lower RuBisCO activation state than well-watered plants; at the same time, high temperatures also block RuBisCO under the dry-hot circumstances of semi-arid environments. Both RuBisCO deactivation and CO₂ limitation are responsible for the limiting of photosynthesis (Hasanuzzaman et al. 2013).

3.2. Germination, Growth, and Development

If the amount of water in the soil reaches the “permanent wilting point” (i.e., the soil contains significantly less water than what the plant loses, making it impossible for the plant to maintain the turgor pressure of its cells), wilting occurs in the plant. At this constant wilting point, the soil's water potential typically ranges from -1 MPa (megapascals, which is a unit of water potential) to -2 MPa, with an average value of -1.5 MPa. A reduction in soil water potential is the primary factor responsible for inducing drought stress in plants. When soil water is inadequate and the plant is unable to activate its tolerance mechanisms while simultaneously losing water through transpiration, water stress begins. As the soil's

water potential reaches the permanent wilting point (-1.5 megapascals), the water potential of the leaves falls below that of the roots and the surrounding soil. Despite this difference in water potential, the plant is unable to absorb water and starts to wilt. If this situation persists for an extended period, the plant will eventually dry out and die. When soil water is severely depleted, soil colloids absorb more water, preventing the roots' suction power from overcoming the colloids' suction power, which leads to a lack of water uptake. Therefore, at the permanent wilting point, wilting occurs in both the leaves and the roots (Kusvuran 2010).

When significant water loss occurs in plant cells, it manifests as a loss of turgor pressure in the plant. This water loss increases the concentration of cell sap, leading to greater dehydration of the protoplasm. In cases of osmotic water loss, the protoplast can separate from the cell wall. The collapse of the plasma membrane under stress can cause tears, which release hydrolytic enzymes that are attached to the membranes, ultimately resulting in the autolysis of the cytoplasm. This type of damage typically disrupts normal cellular metabolism permanently. Consequently, growth slows, and turgor pressure decreases. Furthermore, excessive water loss in the cell can result in metabolic disturbances in the plant due to disruptions in cellular metabolism. In this scenario, ion accumulation caused by water loss may harm the cell by compromising membrane integrity and altering protein structure (Kuşvuran 2010).

Drought is a significant environmental condition that influences the success or failure of plant establishment, as water availability is a crucial prerequisite for germination. The evaluation of drought tolerance in plants growth stages of germination is of great importance in determining the drought thresholds specific to each stage of development. Drought stress negatively affects germination and seedling development, leading to losses in plant growth and yield in later stages.

This stress manifests itself not only through the complete inhibition of germination but also through increased rates of abnormal germination and irregularities in seedling development. Additionally, a reduction in osmotic potential leads to an extension of the average germination period and a delay in seedling emergence (Hasanuzzaman et al. 2013). A study investigating the seed germination of eight wheat genotypes under polyethylene glycol (PEG)-induced drought stress (0, -0.6, and -1.2 MPa) observed a decline in seed germination, varying from 32.83% to 53.50%. The study indicated that heightened negative osmotic potential impairs enzyme function, hence diminishing the seeds' germination ability. A significant factor contributing to reduced seed germination is insufficient water absorption and the inability to satisfy the moisture needs necessary for germination. The present investigation established that reduced seed germination under elevated negative osmotic potential was associated with diminished water absorption and a consequent decline in the enzymatic activities essential for seed germination (Mahpara et al. 2022). Similar results were determined in Quinoa (Gholami et al. 2022) and canola (Mazhar et al. 2022), while the germination rate decreased due to drought stress, the germination time increased.

One of the most important limitations in the early phases of plant development and establishment is water stress. Both expansion growth and elongation are impacted (Jaleel et al. 2009). Growth involves cell division, elongation, and differentiation and is defined as an irreversible increase in volume, size, or mass. Drought compromises both cell division and cell expansion due to diminished enzyme activity, reduced turgor pressure, and reduced energy availability. During drought conditions, there is a reduced accumulation of dry matter in all plant organs, although the extent of reduction varies among various organs (Farooq et al. 2012). Mubashir et al. (2023) reported that drought stress applied under 60% water deficit conditions negatively affected the

growth characteristics of tomato plants, leading to gradual and significant decreases in both fresh and dry biomass. In this context, reducing field capacity (%FC) resulted in a 19.4% decrease in leaf number, a 13.6% decrease in flower number, an 11.1% decrease in shoot length, a 10.7% decrease in root length, and an 18.3% decrease in fruit weight per plant. Additionally, shoot fresh weight decreased by 31.8% and root fresh weight decreased by 14.6% compared to control plants. A comparable decline in growth characteristics under drought stress has been noted in various plants, including lettuce (Shin et al. 2021), wheat (Wasaya et al. 2021), eggplant (Alabdallah et al. 2021), and strawberry (Şener et al. 2023).

Reduction in leaf size, suppression of leaf expansion and tillering, decrease in the number of stomata and reduction in stoma size, thickening of the cell wall, cutinization of the leaf surface, increase in the number of large veins, and curling of leaves are morphological and anatomical changes observed in plants subjected to drought. These variables lead to reduced dry matter buildup and grain yield during drought conditions (Farooq et al. 2012, Yıldırım et al. 2021). Drought stress in numerous agriculturally significant crops is initially detected by the root system, which persists in growth beneath the soil despite the suppression of shoot development under such conditions. The core root's growth remains unaffected by drought stress; however, the growth of lateral roots is markedly diminished, mostly due to the inhibition of lateral root meristem activation (Basu et al. 2016).

3.3. Nutrient Elements

Under water stress circumstances, inadequate root functioning and diminished water diffusion rates render roots ineffectual in nutrient absorption from the soil. Water deficiency conditions result in stomatal closure, reduced transpiration, and restricted nutrient transfer from the roots to the aerial regions of plants. Consequently, water scarcity leads

to diminished soil nutrient availability and inconsistent nutrient translocation in plants. All these factors significantly influence plant growth, affecting various physiological processes (Bashir et al. 2021). Changes in nutrient absorption by the roots and its transport to the shoots represent a major effect of water scarcity in plants. Drought stress generally leads to increased nitrogen levels, reduced phosphorus concentration, and no definitive effect on potassium concentration in plants (Salehi-Lisar and Bakhshayeshan-Agdam 2016).

Furthermore, data demonstrate a reduction in the concentrations of Ca, Mg, Na, and K in plants exposed to drought stress conditions (Yıldırım et al. 2021). Research indicates that the levels of N, P, K, Mg, B, Fe, and Zn in cabbage diminish during drought stress (Sahin et al. 2018). It has been noted that the concentrations of vital plant nutrients, such as N, P, K, Ca, Mg, and Zn, markedly diminish in tomatoes cultivated under drought conditions (Ors et al. 2021). The integrity of root membranes is essential for proper mineral feeding in plants. Cell membranes are among the first structures exposed to several types of stress, including water stress. Therefore, proper membrane stability management is necessary for plants to withstand drought. One important mechanism that upsets the ion homeostasis in plants is the degradation of cell membranes during drought stress. Roots are unable to absorb nutrients from the soil while under drought stress due to decreased water diffusion rates and compromised root function. Stomatal closure, reduced transpiration, and restricted nutrient movement from the roots to the top portions of plants are all consequences of water shortage. Numerous physiological processes are impacted by the way these components interact, which has a significant influence on plant growth (Salehi-Lisar and Bakhshayeshan-Agdam 2016, Bashir et al. 2021).

3.4. Oxidative Stress

In usual or unstressed settings, most cellular compartments of plants sustain a decreasing environment and uphold a stable homeostatic state (Hasanuzzaman et al. 2020). Stress exposure typically results in elevated levels of reactive oxygen species (ROS) (Cruz de Carvalho et al. 2008). Excessive synthesis of ROS beyond the plant's scavenging capacity affects redox signaling and regulation, resulting in oxidative stress (Das and Roychoudhury 2014). These processes can oxidatively damage proteins, membrane lipids, photosynthetic pigments, and nucleic acids, and drought stress greatly intensifies this harm (Sachdev et al., 2021). Drought modifies and impairs the photosynthetic pigments and apparatus. A water deficit increases the viscosity of cellular contents, leading to protein denaturation, which subsequently affects the membranes of both the photosynthetic apparatus and the cell. Concurrently, the enzymes involved in the Calvin cycle become inactivated, diminishing the efficiency of the carboxylation reaction and CO₂ fixation by RuBisCO. This ultimately results in heightened photorespiration, a significant contributor to reactive oxygen species (ROS) production.

The process involves the formation of free radicals, particularly active oxygen species such as the superoxide molecule (O₂⁻), singlet oxygen, hydrogen peroxide (H₂O₂), and hydroxyl radicals (OH). Free radicals are highly reactive molecules that contain unpaired electrons. These radicals can also form in plasma membranes, mitochondria, and endoplasmic reticulum (ER) membranes. However, during periods of water scarcity, the primary cause of oxidative stress in vegetative plant tissues is the light-chlorophyll interaction that occurs in chloroplasts. When water becomes limited, plants typically close their stomata to prevent further water loss. This action restricts the uptake of CO₂, which is necessary for photosynthetic fixation. Consequently, there is an excess of energy in the photosynthetic reaction centers. As a result, NADP⁺ (the

electron acceptor in photosynthesis) becomes limited, leading ferredoxin to reduce oxygen instead of NADP⁺. This transfer of electrons from photosystem I (PSI) to O₂ results in the production of reactive O₂ radicals, a process known as the Mehler reaction. In many species, increased O₂ formation rates under water stress lead to lipid peroxidation, fatty acid saturation, and ultimately complete membrane damage. Superoxide itself is not highly reactive; it mainly acts by forming H₂O₂ and subsequently OH. Hydrogen peroxide inactivates many enzymes in the Calvin cycle (Dietz et al. 2016, Foyer 2018, Samanta et al. 2024). During the reaction between superoxide and hydrogen peroxide to form the OH radical (Haber-Weiss reaction), elevated levels of other transition metals, such as iron or copper, can accelerate these reactions, further increasing oxidative damage (Fenton reaction). Additionally, free radicals can also form in the water-splitting region of photosystem II (PS II). Reactive oxygen species (ROS), which are by-products of aerobic metabolism, are naturally produced in plants. However, when plants are subjected to abiotic or biotic stress, excessive ROS production can disrupt the balance between accumulation and scavenging (elimination). This disruption leads to oxidative damage to biomolecules, resulting in cellular damage and/or death. In other words, when the level of ROS accumulation surpasses the capacity of defense mechanisms to manage it, the cell enters a state of “oxidative stress.” During oxidative stress, biomolecules such as lipids, proteins, DNA, carbohydrates, and polynucleic acids may undergo either reversible or irreversible changes (Kuşvuran 2021).

However, under water deficiency plants have developed several mechanisms to overcome this scarcity. In plants, to address the harmful effects of oxidative damage, various types of antioxidants are employed. These include fat-soluble and membrane-bound antioxidants, as well as water-soluble antioxidants like glutathione and ascorbate, which help in detoxifying reactive oxygen species such as superoxide (O₂⁻) and

hydrogen peroxide (H_2O_2). Additionally, enzymatic antioxidants are involved, including superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), ascorbate peroxidase (APX), and glutathione reductase (GR).

4. BIOCHEMICAL AND MOLECULAR RESPONSES TO DROUGHT

In conditions of water scarcity, plants have developed various strategies to cope with this deficiency. Two important defensive systems that improve crop tolerance in water stress situations are the antioxidant system and osmotic regulation (Basir et al. 2021).

4.1. Osmotic Regulation

Osmotic regulation is a crucial mechanism by which plants diminish osmotic potential and withstand adverse conditions during water scarcity. During drought stress, plants can achieve osmotic management through three mechanisms: reduction of intracellular water, decrease in cell volume, and augmentation of cellular contents. These three mechanisms coexist in plants; however, not all plants possess osmotic control. Osmotic control is typically regarded as the active management of cells to diminish their osmotic potential through the augmentation of solute concentration (Yang et al. 2021).

Water deficiency leads to a decrease in osmotic potential and a loss of turgor in plants. This condition, which occurs as a response to water scarcity, results in the accumulation of various soluble substances within the plant. Additionally, there is an observed increase in the transport of osmotic substances from the vacuoles to the leaves, along with water. We refer to this process as osmotic adaptation or osmoregulation, which operates within the context of osmotic potential and water uptake mechanisms in the root region. Osmotic adaptation is essential for plants

to maintain vital functions in response to drought, water, and salt stress. These critical functions include stomatal and photosynthetic adaptations, as well as plant growth, yield, and the continuity of cell development (Kuşvuran 2010).

Osmotic regulation is described as the buildup of solutes in proliferating cells in response to lowered water potential; hence, it aids in the maintenance of turgor pressure. Water availability significantly influences cell expansion and growth in plants, which is essential for maintaining turgor pressure. Turgor measurement in the growth areas of plants, particularly in leaves and stems, exhibits minimal or no decline; nonetheless, cell enlargement is impeded during drought stress, which is thought to be attributable to osmotic regulation. During drought stress, osmotic regulation has been associated with sustaining stomatal conductance, photosynthesis, leaf water content, and growth. During periods of water stress, alongside the decrease in water content, there are other concomitant alterations, including elevated salt concentration and increased mechanical impedance. Plants primarily utilize organic osmotic regulators and inorganic ions sourced from the external environment for osmotic regulation. Organic osmotic regulators, including amine compounds (glycine betaine and polyamines), amino acids (proline), trehalose, fructans, mannitol, and other chemicals, significantly influence the osmotic properties of the cytoplasm. These compounds typically possess low molecular weight, exhibit adequate solubility, and demonstrate minimal cytotoxicity. In response to water stress, inorganic cations, organic acids, carbohydrates, and free amino acids are the primary solutes that accumulate. By promoting osmotic adjustment, detoxifying ROS, preserving membrane integrity, and stabilizing enzymes or proteins, the buildup of appropriate solutes, such as proline and glycine betaine, shields plants against the harmful consequences of drought stress (Basu et al. 2016, Yang et al. 2021).

Proline is synthesized and accumulates in plants under stress conditions. Proline is crucial for regulating osmotic pressure in plants, and its concentration markedly rises during stress conditions, such as drought stress (Franzoni et al. 2021). Shin et al. (2021) documented in their research on lettuce that drought stress resulted in elevated proline levels, attributed to reduced stomatal conductance, which subsequently enhanced ABA accumulation and induced the up-regulation of P5CS ($\Delta 1$ -pyrroline-5-carboxylate synthetase). Proline can mitigate oxygen damage induced by stress by chelating singlet oxygen and hydroxyl radicals. Another method to eliminate ROS is to enhance the activity of peroxidase (POD), catalase (CAT), superoxide dismutase (SOD), polyphenol oxidase (PPO), and other enzymatic systems in plants. In response to stress, proline can attach to proteins, creating a protective layer with water molecules on their surfaces. The establishment of a protective barrier restricts the efflux of water from the cell and reduces water loss. Moreover, the protective barrier efficiently shields proteins and other biological macromolecules, maintaining their structural integrity and functionality. Proline can enhance the hydrophilicity of denatured proteins subjected to stress when it binds with them. It maintains the dissolved state of denatured proteins to prevent their agglutination from disrupting cellular metabolic functions (Yang et al. 2021).

Glycine betaine (GB) is crucial for improving plant stress resilience, facilitating enzyme activities, preserving membrane integrity, detoxifying reactive oxygen species, and controlling osmotic equilibrium. GB is predominantly located in chloroplasts, where it is essential for safeguarding thylakoid membranes and other crucial elements of the photosynthetic apparatus, including ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) and the oxygen-evolving complex. This protection aids in averting stress-induced inactivation and dissociation, thereby maintaining photosynthetic efficiency. For plants

that naturally accumulate moderate levels of GB, the exogenous application of this compound may be an effective approach to alleviate the harmful effects of environmental stressors (Ahanger et al. 2013). By improving osmotic control, stomatal conductance, and the carboxylation efficiency of CO₂ absorption, glycine betaine can significantly aid photosynthesis. In conclusion, glycine betaine can stabilize the structure and characteristics of biological macromolecules under drought stress, such as terminal oxidases, dicarboxylic acid cycle essential enzymes, and photosystem components, all of which are critical for maintaining regular physiological processes (Yang et al. 2021). Glycine betaine applied externally has been demonstrated to increase drought stress tolerance in wheat (Shemi et al., 2021) and lettuce (Ibrahim et al. 2023).

Polyamines are cationic compounds that contain two or more amine groups. Due to their diversity in the number and position of amino groups, they are low-molecular-weight organic molecules found in many organisms and serve various functions. Examples comprise diaminoputrescine (Put), triaminospermidine (Spd), and tetraaminospermine (Spm). Moreover, polyamines may function as signaling molecules that facilitate the expression of plants' responses to drought stress (Yıldırım et al. 2021). Polyamines, owing to their hydrophilic characteristics, have a role in pH regulation and the scavenging of reactive oxygen species; therefore, they serve as mediators in protective responses to various stimuli. Polyamines safeguard membranes from disintegration and mitigate oxidative stress by facilitating the detoxification of reactive oxygen species buildup during stress (Ahanger et al. 2013).

Soluble sugar (SS) is a crucial energy and carbon source for organisms and is involved in numerous metabolic processes in plant life. Soluble sugar (SS) serves as a crucial energy and carbon source for organisms and is involved in numerous metabolic processes in plant life.

Soluble sugars in plants encompass glucose, fructose, sucrose, and various other carbohydrates. Plants are better able to absorb and retain water when soluble sugars build up because they lower the water potential of cells. Moreover, the majority of osmotic regulators are ineffective in safeguarding proteins and biofilms from additional water loss during extreme dry conditions. Only soluble sugars can substitute for water molecules and establish hydrogen bonds with proteins to preserve their unique structure and function. Furthermore, the augmentation of soluble carbohydrates among biofilms can prevent the immediate disintegration of the biofilm system (Afzal et al. 2021, Haghpanah et al. 2024). Nemati et al. (2018) and Yıldırım et al. (2021) shown that drought-resistant plants enhance sucrose production at both metabolic and gene expression levels to optimize energy conservation and control cellular metabolism. Plants subjected to drought stress exhibit an augmentation in soluble carbohydrate storage in both their shoot and root regions.

4.2. Antioxidant Defense Systems

Under normal conditions, a perfect balance exists between the formation and clearance of reactive oxygen species (ROS). However, various adverse environmental factors, such as drought, can disrupt this balance, resulting in increased levels of intracellular ROS production. Antioxidants are vital for eliminating reactive oxygen species (ROS) and are crucial in mitigating abiotic stressors. Plants have established an extensive antioxidant defense network to mitigate excessive reactive oxygen species (ROS) production under diverse abiotic stressors. The primary cellular response to oxidative stress seeks to mitigate damage and to eliminate or rectify any compromised cellular components via antioxidant defenses and repair mechanisms. Antioxidants are substances that can undergo oxidation at low concentrations and can reduce or inhibit the oxidation of other substrates through electron transfer, thereby helping to combat oxidation (Kuşvuran 2021). To help

protect plants from reactive oxygen species (ROS) damage, there exist intrinsic antioxidant defense mechanisms, comprising non-enzymatic antioxidants and antioxidant enzymes. The synergistic interaction between antioxidants and antioxidant enzymes establishes a dynamic equilibrium in the formation and neutralization of reactive oxygen species (ROS) *in vivo*, thereby relieving stress damage and enabling plant adaptation to dry conditions. The non-enzymatic ROS scavenging systems in plants mostly consist of ascorbate, reduced glutathione (GSH), vitamin E, mannitol, carotenoids, and flavonoids. These chemicals may directly interact with reactive oxygen species (ROS) or serve as substrates for enzymes in the ROS scavenging process. Moreover, certain tiny molecules, including vitamins, participate in the scavenging of oxygen free radicals and the prevention of lipid peroxidation. It is an essential component of the body's antioxidant defense mechanism. The enzymes primarily responsible for antioxidant protection in plants are SOD, CAT, APX, DHAR, MDHAR, GR, and POD (Yang et al. 2021).

Cu/Zn-SOD, Fe-SOD, and Mn-SOD are the three metalloenzyme forms of superoxide dismutase (SOD), a vital antioxidant defense enzyme. The cytosol, mitochondria, peroxisomes, and chloroplasts are among the several cellular compartments where these isoenzymes can be found. Ascorbate peroxidase (APX), glutathione reductase (GR), and catalase (CAT) combine to transform hydrogen peroxide (H_2O_2) into molecules of oxygen and water. Although APX is also present in the cytosol, chloroplasts, microbodies, and peroxisomal/glyoxysomal isoforms, CAT and APX are metalloenzymes that are mostly located in peroxisomes and mitochondria. Ascorbate serves as an electron donor, while APX, one of the main antioxidant enzymes in plants, reduces H_2O_2 to offer detoxification.

In chloroplasts, APX is an essential element of the ascorbate–glutathione pathway, facilitating the production of

monodehydroascorbate (MDHA) and necessitating ascorbate as an electron donor. The Foyer–Halliwell–Asada pathway encompasses both enzymatic (APX, DHAR, GPX, MDHAR) and non-enzymatic antioxidants (ascorbic acid and glutathione) that play a critical role in regulating hydrogen peroxide (H_2O_2) concentrations in different cell organelles. MDHAR, an NADPH-dependent flavoprotein, mediates the resynthesis of ascorbate from monodehydroascorbate (MDHA) via a thiol-mediated mechanism. The spontaneous disproportionation of MDHA leads to the formation of dehydroascorbate (DHA). DHA is reduced back to ascorbate via DHAR, which uses glutathione (GSH) as an electron donor. This reaction results in the formation of oxidized glutathione (GSSG), which is reduced back to GSH by NADPH-dependent glutathione reductase (GR), contributing to the maintenance of cellular redox balance. Thus, while DHAR catalyzes the conversion of GSH to GSSG, GR completes this cycle, ensuring the continuity of redox homeostasis.

APX activity necessitating the regeneration of ascorbic acid suggests that a simultaneous enhancement of numerous components within the antioxidative defense system is required to augment the defensive mechanisms of plants as needed. POD, CAT, and APX appear to play a vital protective role in the scavenging process when they work in conjunction with SOD activity. They utilize H_2O_2 produced predominantly by SOD activity (Kusvuran et al. 2016).

Nonenzymatic antioxidants come in two primary varieties. They are water-soluble reductants (like glutathione, phenolics, and ascorbate) and lipid-soluble, membrane-associated antioxidants (like α -tocopherol and β -carotene). By halting chain reactions, non-enzymatic antioxidants are crucial for the detoxification of reactive oxygen species. Ascorbic acid (AsA), glutathione (GSH), appropriate solutes, phenolics, α -tocopherol, carotenoids, flavonoids, anthocyanins, and proline are

among the many vital substances that work together to reduce the accumulation of reactive oxygen species (ROS) brought on by stress (Rao et al. 2025).

Ascorbic acid is the most abundant, powerful, and water-soluble antioxidant that neutralizes damage caused by reactive oxygen species (ROS) in plants. It is synthesized in plant mitochondria and transported to various parts of the plant, including chloroplasts, cytosol, vacuoles, apoplast, and peroxisomes, through proton movement or diffusion. Ascorbic acid functions in dual capacities: as an electron donor for ascorbate peroxidase (APX) and as a cofactor for peroxidase enzymes. Additionally, ascorbic acid (AsA) aids in the regeneration of tocopherol and the synthesis of xanthophyll, which contributes to energy dissipation. Although present in all plant tissues, it is especially abundant in meristematic regions, photosynthetic cells, and certain fruits, often found in higher concentrations than glutathione (GSH), particularly in leaves. AsA is recognized as an effective scavenger of reactive oxygen species due to its ability to donate electrons through both enzymatic and non-enzymatic reactions. It directly scavenges superoxide (O_2^-), hydroxyl (OH^-), and hydrogen peroxide (H_2O_2) radicals, while also reducing oxidized α -tocopherol radicals, allowing α -tocopherol to continue functioning as a free radical scavenging antioxidant (Kuşvuran 2021, Rao et al. 2025).

Glutathione is a key cellular antioxidant that contributes to the reduction of hydrogen peroxide and other reactive oxygen species (ROS). Glutathione (GSH), an essential thiol tripeptide, promotes the breakdown of hydrogen peroxide (H_2O_2) through processes mediated by glutathione peroxidase (GPX). It operates within the AsA-GSH pathway as a reducing agent for dehydroascorbate reductase (DHAR) and also contributes to the removal of H_2O_2 and lipid peroxides via GPX and glutathione S-transferase (GST) conjugation processes. GSH is crucial

in mediating ABA signaling and in controlling seed dormancy and drought adaptation in plants (Haghpanah et al. 2024, Rao et al., 2025).

Carotenoids are generally classified into four groups: carotenes, xanthophylls, carotenoid ketones, and carotenoid acids. Carotenoids are unique pigments that absorb light and, under high light levels, dissipate thermal energy to lessen oxidative stress. By efficiently quenching single chlorophyll, triple chlorophyll, and single oxygen species in thylakoid membranes, these substances also shield photosystem II. Carotenoids protect against oxidative damage from reactive oxygen species, including superoxide radicals ($O_2^{\bullet-}$), hydroxyl ($OH^{\bullet}$), and peroxy ($ROO^{\bullet}$). In addition to controlling root development by influencing cell division and elongation, they may also enhance drought resistance without stomatal closure (Kuşvuran 2021, Haghpanah et al. 2024, Rao et al. 2025).

Phenolics, which are abundant in plant tissues, are secondary metabolites with antioxidant properties (flavonoids, tannins, hydroxycinnamic esters, and lignin). Phenolic chemicals exhibit several molecular and physiological roles within the plant kingdom, including antioxidant activity, free radical scavenging, signaling, facilitation of auxin transport, and plant defense mechanisms. The role of phenolic compounds in plant adaptation to drought stress is extensively studied because of its essential function in regulating plant growth and processes of stress tolerance. Flavonoids significantly enhance plants' drought resistance. Numerous studies have demonstrated the beneficial effects of flavonoids on plant development and stress tolerance. As antioxidants, they perform three distinct functions during both abiotic and biotic stress. These functions include neutralizing and eliminating reactive oxygen species (ROS) through various reactions, chelating metals that are involved in ROS production and processes such as the Fenton reaction—which can lead to ROS formation—and managing the unpaired electrons

of radicals. Furthermore, flavonoids contribute to the detoxification of hydrogen peroxide (H_2O_2). The antioxidant efficacy of flavonoids tends to increase with the degree of hydroxylation; however, this efficacy may decrease depending on the type of sugar attached to their structure (Kuşvuran 2021, Haghpanah et al. 2024).

4.3. Hormonal Regulation

Phytohormones are critical regulators of plant growth and developmental processes, significantly influencing responses to both biotic and abiotic stresses throughout their life cycles. These hormones are required in minute amounts to effectively regulate plant growth. The most comprehensive researched phytohormones in higher plants include auxins, gibberellins, cytokinins, ethylene, and abscisic acid. Among these hormones, gibberellins and cytokinins act as growth promoters, while ethylene and ABA function as growth inhibitors (Farooq et al. 2012). Drought stress stimulates the production of various plant hormones, which modulate processes associated with drought resistance mechanisms. Numerous plant species, such as tomato, radish, strawberry, eggplant, and carrot, have shown improved tolerance to abiotic stress through the action of phytohormones. According to Huang and Jin (2025), the use of these hormones has been shown to control the accumulation of mineral nutrients, preserve osmotic adjustment, balance the water potential of leaves, reduce oxidative damage, and increase the activity of antioxidant enzymes in plants. One of the biggest environmental stresses impacting agricultural production and growth is drought. Phytohormone homeostasis and interactions determine a plant's ability to withstand or respond to drought (Aliniaiefard et al. 2023).

Cell division, elongation, cellular tissue differentiation, embryogenesis, root development, apical dominance, phyllotaxis, and tropic responses are among processes in which auxins are involved. Auxin genes serve as significant biotechnological targets for altering

plant dimensions and morphology, as well as enhancing agricultural productivity. Consequently, they are essential for cellular and growth development (Iqbal et al. 2022). A correlation between auxin levels and antioxidant capacity was proposed when several grass species exhibited enhanced tolerance to abiotic stress after exogenous application of humic acids with auxin-like properties. In fact, it has been noted that wild-type plants treated with exogenous IAA or transgenic *Arabidopsis* with a higher endogenous IAA content are more drought tolerant due to their enhanced ROS reduction through SOD, CAT, POD, and GR activity. Auxin has been associated with modifying hydrogen peroxide dynamics, which subsequently influences stomatal mobility and root shape, both of which are critical factors in overall plant drought tolerance (Burgess and Huang 2016).

Cytokinins are recognized for their impact on various biological functions within the plant system, particularly as prominent positive regulators of senescence, evidenced by exogenous applications or endogenous modifications that inhibit the rate of natural or stress-induced leaf senescence (Burgess and Huang 2016). During drought conditions, cytokinins modulate plant responses through root-to-shoot signaling. Increased ABA levels in plant organs during drought stress induce many physiological alterations to regulate plant growth. Increased ABA accumulation in roots during water scarcity prompts leaves to initiate stomatal closure, hence preventing water loss through transpiration (Farooq et al. 2012). These hormones are crucial for plant growth regulation and adaptation to drought stress (Huang and Jin 2025). Aktaş and Aydın (2021) reported that cytokines, which change under stress conditions, play a role in the balance of other hormones such as ABA. Indeed, under water stress, decreased CK content and ABA accumulation cause an increase in the ABA/CK ratio, and low CK levels, together with ABA regulation of stomatal aperture, increase apical dominance, which helps adaptation to drought stress.

Gibberellins (GAs) represent an important class of diterpenoid plant hormones with hundreds of unique chemical structures; but only a select few exhibit biological activity and influence various plant growth and development processes such as seed germination, stem and root elongation, leaf expansion, transition from juvenile to adult stages, sex determination, and the onset of flowering (Burgess and Huang 2016). Growth inhibitors provided drought resistance to plants by reducing the production of endogenous gibberellins, and in plants that were growth-retarded or GA-deficient, gibberellin therapy improved dwarf growth and stress tolerance responses (Whab et al. 2022). Alongside lateral roots, the existence of diminutive roots is regarded as an adaptation technique to enhance water absorption by offering a greater absorptive surface area. The hormonal interaction involving auxin, cytokinins, gibberellins, and abscisic acid has been identified as a possible chemical signal that modulates root system architecture in response to water stress (Basu et al. 2016). Under drought conditions, changes in hormonal balance, such as a decrease in cytokinin (CK) and gibberellic acid (GA3) and an increase in abscisic acid (ABA), lead to a decrease in membrane permeability and water uptake, which in turn results in reduced growth because of the changes caused by drought (Akter et al., 2014). Based on this approach, exogenous hormone applications are used to mitigate stress in plants. Foliar applications of GA3 and CK have alleviated the adverse effects of drought on maize during the vegetative phase (Akter et al. 2014, Yildirim et al. 2021).

Salicylic acid (SA) is a secondary metabolite that accumulates in plants under drought stress, facilitating drought tolerance by modulating many physiological processes via signaling mechanisms. It is crucial for developing drought resistance in various biological processes, such as CO₂ absorption, antioxidation, stomatal control, and photosynthesis. Water-stressed perennial plants' leaves undergo accelerated leaf senescence when methyl salicylic acid is applied exogenously; in

drought-stressed plants, this programmed senescence promotes nutrient remobilization, allowing the rest of the plant to use the nutrients that have been stored throughout the leaf's life (Farooq et al. 2012, Wahab et al. 2022). Salicylic acid augments chlorophyll levels and promotes photosynthetic efficiency, hence significantly boosting crop productivity and other yield-related physiological metrics in drought-stressed conditions. In response to drought stress, salicylic acid treatment improved ion homeostasis, maintained the integrity of cellular membranes, and controlled the antioxidant defense system. Additionally, salicylic acid protects photosynthesis in plants by encouraging the growth of lateral roots, assisting with osmotic management, and stimulating the action of antioxidant enzymes. Foliar applications of salicylic acid have been demonstrated to promote development in key horticultural crops, including tomato, potato, strawberry, and cucumber, under conditions of drought stress (Huang and Jin 2025). Silva et al. (2023) have shown that watermelon seedlings subjected to drought stress due to water deprivation exhibit accelerated growth, since salicylic acid enhances the production of secondary metabolites, increases osmolyte accumulation, and decreases electrolyte leakage in the seedlings. Salicylic acid administration in melon under drought stress circumstances enhanced yield characteristics, leaf water content, proline accumulation, flavonoid levels, soluble solid concentration, and membrane stability (Alam et al. 2022).

Jasmonic acid (JA) is a plant phytohormone, with its active derivatives referred to as jasmonates. It is crucial in combating many biotic and abiotic stresses. Moreover, JA is associated with enhanced root architecture, increased pollen generation, tendril coiling, and fruit maturation across several species. Exogenously administered jasmonic acid has enhanced plant performance and regulated stomatal dynamics in arid conditions. The JA signaling pathway and its synthesis have been thoroughly investigated (Wahab et al. 2022). JA enhances drought

tolerance in plants through mechanisms such as facilitating reactive oxygen species elimination and boosting root growth. Like ABA, numerous investigations have demonstrated that JA also plays a role in stomatal closure and control in response to drought stress. JA application has reduced oxidative stress and regulated physiological adaptation in Brassica species under drought stress (Alam et al. 2014, Yıldırım et al. 2021). The exogenous treatment of jasmonic acid (JA) or kinetin (K) in wheat effectively imparted drought tolerance to a sensitive cultivar, enabling it to endure severe circumstances in the early stages and perform comparably to tolerant varieties. Through the redistribution of photoassimilates to vegetative sinks, administered hormones caused a definitive shift from downregulation to upregulation of all drought tolerance traits. This improved growth, increased the accumulation of specific osmoregulatory compounds, increased tissue vigor, and regulated the activity of antioxidant enzymes, in addition to morphological adjustments made by restoring the shoot/root ratio. (Abeed et al. 2021). The exogenous administration of jasmonic acid during drought stress enhanced antioxidant activity, leading to a reduction in malondialdehyde levels. This subsequently enhanced photosynthetic efficiency, thereby promoting the growth of *Grewia asiatica* under drought conditions (Waheed et al. 2022).

Absciscic acid (ABA) participates in various biological activities, including germination, gravitropism, and the regulation of stomatal opening by guard cells. It plays a crucial role in helping plants adapt to external stressors. ABA is recognized for its role in regulating water balance and osmotic stress tolerance. Under stress conditions, absciscic acid (ABA) not only promotes stomatal closure but also increases ion flow across root cell membranes and contributes to osmotic regulation by supporting the synthesis and accumulation of osmotically active compounds such as proline and trehalose. ABA functions as a critical regulator in maintaining water balance and regulating growth in plants.

Additionally, increased expression levels of genes encoding various enzymes and proteins associated with drought tolerance have been directly linked to high ABA accumulation. Under stress, abscisic acid (ABA) synthesized in the roots is translocated to the shoots to modulate stomatal dynamics and foliar development. The pH and ionic conditions within the xylem are crucial for this transfer (Ahanger et al. 2013). Exogenous ABA can reduce ROS and enhance cell membrane stability (CMS) to facilitate plant recovery following stress exposure. Application of ABA has been demonstrated in several studies to enhance stress tolerance in various crop species. Exogenous applications of plant growth regulators are utilized to mitigate these stressful situations. Phytohormones were utilized to enhance drought tolerance in various plants and to augment growth, development, and output. Phytohormones significantly influence the plant's response to stress at minimal concentrations, functioning as chemical messengers synthesized in one region and disseminated throughout the plant (Fahad et al. 2015, Aktaş et al. 2021, EL Sabagh et al. 2022).

Melatonin (N-acetyl-5-methoxytryptamine) is a low molecular weight indole derivative that significantly enhances plant tolerance to abiotic stresses (Khattak et al. 2023). Increased melatonin levels may substantially reduce ROS in cells, consequently affecting ROS-dependent signaling pathways and hindering cellular proliferation. Melatonin modulates ROS levels and bolsters molecular defenses, thus augmenting plant tolerance to drought stress. Melatonin is a powerful antioxidant and primary growth regulator that safeguards plants against oxidative damage and regulates many responses to environmental disturbances, including water stress. Melatonin functions as a signaling molecule at the cellular level and augments the expression of many antioxidant enzymes; hence, it enhances its efficacy as an antioxidant. The administration of melatonin significantly improved drought stress tolerance in carrot, radish, pepper, sweet potato, and cucumber (Huang

and Jin 2025). Melatonin has been reported to play a direct antioxidant role in balancing biological membranes such as mitochondria, chloroplasts, and plasma, as well as being effective in combating membrane fluidity and lipid peroxidation. It has been stated that melatonin reduces electron leakage from the inner mitochondrial membrane and stimulates the electron transport chain by limiting reactive O₂ formation in plants under stress. Additionally, it has been reported that POX promotes the activities of glutathione reductase (GR), SOD, and CAT enzymes (Yakupoglu et al. 2021). Melatonin facilitates the buildup of osmolytes, including proline, glycine betaine, and sugars, which serve as osmoprotectants, preserving cellular hydration and osmotic equilibrium under dry circumstances (Dzinyela et al. 2024). The use of melatonin enhanced endogenous plant hormone levels and antioxidant enzyme activity; hence, it improved drought tolerance in soybean seedlings (Imran et al. 2021). Moreover, melatonin enhanced the development and photosynthetic pigment concentration of the three *Capsicum* species under drought stress (Okunlola et al. 2023).

5. DROUGHT AVOIDANCE, TOLERANCE AND ESCAPE MECHANISMS

Plants employ many ways to mitigate drought stress. The employed methods encompass escape, evasion, and tolerance (Salehi-Lisar and Bakhshayeshan-Agdam 2016).

Escaping drought is feasible due to a truncated life cycle or seasonal growth, enabling plants to reproduce prior to environmental desiccation. A brief life cycle can facilitate drought escape through early flowering, regarded as an adaptive strategy for drought via stress avoidance. Drought escape transpires when phenological development aligns with intervals of accessible soil moisture. Consequently, early maturity and subsequent early flowering enable plants to evade drought

stress, albeit with an overall reduction in yield (Ahanger et al. 2013; Salehi-Lisar and Bakhshayeshan-Agdam 2016; Yıldırım et al. 2021).

The main objective of this method is to maintain elevated water potential in plants. In an avoidance strategy, plants mitigate the effects of stress factors despite their presence in the environment. The primary feature of this method is minimizing water loss from plants through stomatal regulation of transpiration and ensuring water absorption from the soil via a vast and prolific root system. An extensive and robust root system is advantageous for accessing water from significant soil depths and great distances from the plant. Root growth rate, root volume, root depth, and root dry weight are characteristics associated with this strategy. The avoidance strategy typically leads to the preservation of optimal internal water content, achieved either by conserving water through mechanisms like stomatal closure, leaf rolling, and dense pubescence, or by enhancing water absorption by the development of deep root systems and water-efficient structures. The creation of these structures results in diminished plant yield owing to the energy expended in their production. Consequently, plants employing the avoidance approach to sustain a comparatively elevated water potential are typically diminutive in stature. Additional avoidance techniques used by plants in dry environments include leaf curling, reducing the angle between the leaf and the stem, diminishing leaf size, lowering leaf placement, developing a waxy coating on the leaf, and abscising older leaves. (Ahanger et al. 2013, Salehi-Lisar and Bakhshayeshan-Agdam 2016, Yıldırım et al. 2021).

Osmotic and stomatal regulation, together with the inhibition and/or removal of reactive oxygen species (ROS), aid in the process of drought stress tolerance. In response to water constraint, plants that use a tolerance strategy to withstand drought limit the number and surface area of their leaves; nonetheless, this strategy leads to reduced yield.

While transpiration increases light reflection and reduces water loss by strengthening the boundary layer's resistance to water vapor diffusion from the leaf surface, foliar hairiness decreases leaf temperature. It is possible to see both intracellular and intercellular changes in leaves. Size, density, proliferation, and rate of root development are important factors influencing how plants react to drought stress. Osmotic adaptation, the buildup of suitable solutes, the activation of an antioxidant system, and changes in metabolic. Other strategies that help plants withstand drought include the buildup of suitable solutes and osmotic adaptation, the activation of an antioxidant system, changes in metabolic pathways, an increased root/shoot ratio, and stomatal closure (Ahanger et al. 2013, Salehi-Lisar and Bakhshayeshan-Agdam 2016, Yildirim et al. 2021).

6. CONCLUSION

Drought remains one of the most critical abiotic stresses limiting plant growth, productivity, and ultimately global food security. As a multifaceted phenomenon, it imposes morphological, physiological, and biochemical constraints on plants, significantly affecting their growth and metabolism. Generally categorized as avoidance and tolerance tactics, plants have evolved a variety of defense mechanisms against drought conditions. To withstand such stress, plants develop complex adaptive mechanisms at cellular, organellar, and whole-plant levels, including morphological modifications, osmotic adjustment, antioxidant defense, and regulation of growth hormones. Despite these adaptive responses, improving drought tolerance in crop species remains a formidable challenge, as it is governed by multiple genes and pathways that vary across species and environments. Therefore, successful development of drought-tolerant cultivars requires an integrative breeding approach that combines phenotypic selection with advanced molecular tools to pyramid favorable traits and genetic determinants.

Ultimately, while some plants escape drought at the cost of reduced productivity, others rely on physiological adjustments such as osmotic regulation and accumulation of osmoprotectants (e.g., proline, glycine betaine, amino acids, and sugars) to sustain metabolic activity under low water potential. Collectively, these underscore the necessity of multidisciplinary approaches that integrate plant physiology, molecular biology, and breeding strategies to secure crop yield stability under increasingly frequent drought episodes.

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Plant Adaptation to Drought Stress: From Morphology to Omics-Based Technologies

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1. INTRODUCTION

Global population is anticipated to reach 9,7 billion in 2050 and 10,4 billion in 2100, according to the United Nations' most probable scenario (Christian et al. 2023). While this requires doubling production in arable land by 2050, projected increases in climatic variability due to global climate change will negatively impact the expansion of arable land and the intensification of agricultural activities required to meet demand in the coming years (Goodfray et al. 2010; Seager et al. 2012; Thornton et al. 2014). Drought is a dangerous and complex environmental event that occurs as a result of unregulated agriculture, misuse of water resources and human disinformation, as well as below-average rainfall and reduced water availability (Patel and Patel 2024). Of the many types of drought hydrological drought has recently received increased attention due to its link with water resource quantity and preservation. Decreases in crop and livestock productivity resulting from hydrological drought also have negative socioeconomic impacts. Furthermore, prolonged hydrological drought can lead to heatwaves, increasing the risk of forest fires and killing established vegetation (Figure 1) (Gu et al. 2023).

The productivity and quality of plants are negatively affected in arid environments, as are their biochemical, physiological, morphological and ecological characteristics. To maintain water potential in plants exposed to drought stress, the stomata first close due to an imbalance of K^+ , Cl^- and H^+ . In this way, plants minimize water loss through evaporation or transpiration. However, this survival strategy ultimately results in reduced productivity due to the decreased uptake of CO_2 and consequently slower photosynthesis rates when the stomata close (Ortiz et al. 2015). Plants naturally generate reactive oxygen species (ROS) during physiological processes such as photosynthesis. Under drought stress, ROS production increases beyond basal levels,

potentially leading to cellular damage (Mittler 2017; Sharma et al. 2020). Oxidative damage to vital macromolecules occurs due to an increase in the production of potentially toxic reactive species and decreased stomatal conductance with reduced CO₂ uptake (Farooq et al. 2009; Hasanuzzaman et al. 2013). In addition, drought stress leads to excessive reduction of the electron transport system and carbon starvation of cellular organelles, which further enhances oxidative stress (Noctor and Foyer 1998; Miller et al. 2010).

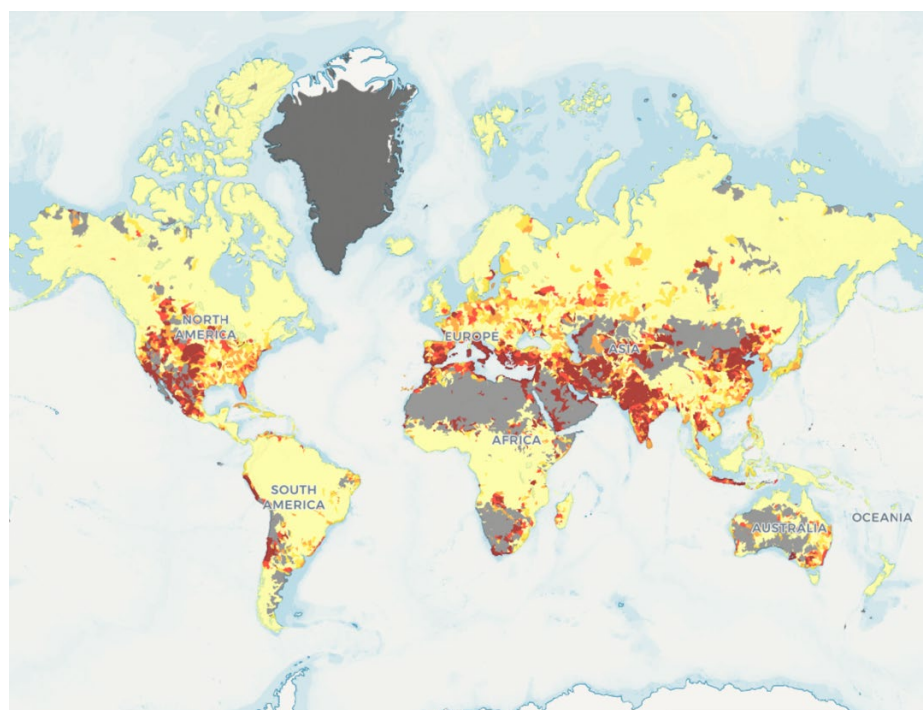


Figure 1. Summary of drought stress effects on plants (Water Risk Atlas 2025)

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Table 1. Effects of Drought Stress on Plants

Effects of Drought Stress on Plants	
Morphological Effects	The leaf surface area decreases. The number of leaves decreases. Leaves curl and close. The cuticle thickens. The stomata narrow or close. Stem growth slows and the plant becomes shorter. The root system develops more deeply. Lateral root formation decreases. Flowering and fruit formation decrease. Premature senescence accelerates.
Physiological Effects	Cell turgor decreases. Water potential decreases. Stomata close, reducing transpiration. The photosynthetic rate decreases. CO₂ uptake is restricted. The respiration rate changes (often increasing). Soluble substances accumulate for osmotic regulation. Hormonal balance is disrupted (ABA increases, while levels of the hormone auxin decrease).
Molecular Effects	ABA signalling pathways are activated. The expression of stress-related genes (LEA, DREB, HSP, etc.) increases. Antioxidant enzyme genes are induced. Osmoprotectant synthesis genes are activated. DNA damage repair mechanisms are activated. Protein synthesis slows and stress proteins increase. Regulation of transcription factors (NAC, MYB and WRKY) is also observed.
Biochemical Effects	Production of reactive oxygen species (ROS) increases. Antioxidant enzyme activities (SOD, CAT, POD and APX) increase. Proline, glycine betaine and trehalose accumulate. Soluble sugar and protein levels change. Lipid peroxidation increases (MDA accumulation). Membrane integrity is impaired. Starch degradation accelerates. Photosynthetic pigments (chlorophyll and carotenoids) decrease.

Drought stress is one of the most important factors limiting plant growth and development, and when plants encounter drought stress, they create various responses by causing the factors listed in Table 1 to emerge. One of the most important ways plants cope with drought stress is adaptation, and they do this through three mechanisms called escape, avoidance and tolerance (Rini et al. 2020; Pamungkas et al. 2022). Plants use drought escape strategies to speed up the generative phase. This results in a pause in the vegetative phase, which allows the plant to produce seeds before the stress of the drought terminates its life. In order to reduce water loss, wheat plants stop vegetative growth and speed up the generative phase (Shavrukov et al. 2017). Plants often use this tactic to complete their life cycle while environmental conditions permit, before experiencing drought. In *Arabidopsis* plants, this tactic is implemented through the effective use of water for growth (Monroe et al. 2018). Drought avoidance is defined as a plant adaptation strategy that sustains cellular water status under water-limited conditions by maintaining a relatively high-water potential. Among the most prominent morphological manifestations of this strategy is root elongation (Rini et al. 2020). In potato, drought avoidance is typically characterized by increased root extension accompanied by alterations in shoot number (Gouveia et al. 2019). In *Arabidopsis*, modifications in root architecture are employed to enhance water acquisition and to preserve tissue water balance (Bouzid et al. 2019). From a physiological perspective, this adaptation is often associated with a reduction in transpiration rate and leaf area, together with the development of fewer and smaller leaves (Moradi 2016). Conversely, drought tolerance represents a distinct adaptive mechanism that enables plants to endure and survive prolonged periods of water deficit.

2. MORPHOLOGICAL EFFECTS IN DROUGHT STRESS

For agricultural production to sustain population growth, it is essential that farming strategies be grounded in a thorough knowledge of crop physiology and developmental processes. The extent to which the plant's vegetative and reproductive development patterns can be managed will determine its optimal performance and sustainability under changing environmental stress circumstances (Anjum et al. 2011). Plant development is determined by the complicated interplay of the resources and water retention limits of the two basic plant organs—the root system and the shoot—to maintain functional equilibrium. Water deficiencies, whether permanent or temporary, exert the most profound influence on plant growth and development, with poor germination and impaired seedling establishment being the earliest and most evident consequences (Harris et al. 2002). Plant growth, which fundamentally depends on meristematic cell division followed by subsequent cell elongation, is highly sensitive to drought due to reductions in turgor pressure. Severe water deficiency disrupts the supply of water from the xylem to elongating cells, thereby inhibiting cell expansion, limiting cell division, and ultimately suppressing overall plant growth (Zia et al. 2021). Drought stress disrupts mitosis as well as cell elongation and expansion, leading to reduced plant growth and yield. Water scarcity lowers soil water potential, thereby affecting leaf number, size, and longevity. Since leaf area expansion depends on turgor, temperature, and water uptake during development, drought-induced reductions in leaf area are primarily attributed to limited leaf growth resulting from decreased photosynthetic activity (Oguz et al. 2022). Drought stress inhibits plant growth and development and has a detrimental influence on critical characteristics such as plant elongation, expansion, and growth (Shao et al. 2008). Numerous studies on various plants, including rice, barley, soybeans, potatoes, and parsley, have repeatedly shown that drought stress affects plant height, root and shoot length, and plant growth (Heuer

and Nadler 1995; Specht et al. 2001; Petropoulos et al. 2008; Jaleel et al. 2009; Ozmen et al. 2023). The growth of a well-branched root system under dry circumstances is crucial for maintaining aboveground biomass, and there is significant variety in root production capability among plant species and even cultivars of the same species. The importance of root systems in water acquisition has long been recognized. A robust and widespread root system, in particular, provides a considerable benefit by promoting fast growth during the early phases of crop development and allowing legumes to use water from shallow soil layers that would otherwise be lost due to evaporation (Jaleel et al. 2009). Changes in root lengths under drought stress in date palm, sunflower, populus, maize, barley, and wheat plants have been linked to stress-induced ABA and proline buildup (Sacks et al. 1997; Tahir et al. 2002; Wullschleger et al. 2005; Mannivanan et al. 2007).

3. CYTOGENETIC CHANGES IN DROUGHT STRESS

While drought stress primarily manifests through visible morphological and physiological changes such as reduced leaf area, shortened stems, and altered root architecture, these effects are ultimately rooted in cellular and genetic alterations. Beyond growth reduction, drought stress interferes with cell division and chromosomal stability, leading to disruptions at the cytogenetic level (Shao et al. 2008; Kwasniewska and Bara 2022). Cytogenetic analyses have shown that water deficit can reduce the mitotic index, increase chromosomal aberrations, and impair proper segregation of genetic material, thereby compromising plant development and stress resilience (Tabur et al. 2024a). Thus, understanding the cytogenetic consequences of drought stress provides a critical link between visible phenotypic responses and underlying genetic mechanisms.

Many studies have found that drought stress has a detrimental cytogenetic impact on plants that rely on soil for survival (Setter and Flannigan 2001; Schuppler et al. 1998; Özmen et al. 2022; Tabur et al. 2024a; Tabur et al. 2024b). The common result obtained from cytogenetic studies conducted under drought stress in plants such as barley, wheat and corn is that the mitotic index decreases and chromosome abnormalities increase. Chromosomal abnormalities, which develop spontaneously or as a result of the harmful impacts of environmental stress, show the negative effects of a toxic chemical on plant cells (Nag et al. 2013). As can be understood from the studies, drought stress causes many abnormalities such as micronuclei (MN), irregular prophase and metaphase, sticky and fragmented chromosomes, irregular anaphase, pole shifts, chromosome circularizations bridge formation in anaphase and telophase. MN refers to structural chromosomal abnormalities that arise during interphase in cells that are not dividing. The MN test may be used to evaluate both physical and chemical genotoxic effects in plants (Kwasniewska and Bara 2022). Drought-induced MNs produce fractures in cell chromosomal structures, which have a negative impact on plant structures. It has been reported that the occurrence of big MNs compared to the size of the MNs created is due to chromosomal loss, whereas tiny MNs are caused by chromosome breakage (Kontek et al. 2007). Chromatin regulation factors—including histone-modifying enzymes, linker histone H1, HMG proteins, and ATP-dependent remodeling complexes—are recognized as key contributors to plant abiotic stress responses (Kim et al. 2010; Fabado et al. 2017). Chromatin granulation in interphase is generally attributed to nuclear material deformation under toxic stress, which may impair proper condensation and lead to abnormalities in subsequent mitosis. Sticky chromosomes are considered to result from faulty DNA condensation, irregular chromatin folding, or axis inactivation, and are often viewed as irreversible markers of chromatin toxicity (Klasterska et

al. 1976; Fiskesjo and Levan 1993; Türkoğlu 2007; Asita and Mokhobo 2013). Structural aberrations such as bridges and breaks are linked to clastogenic effects, whereas chromosome loss, laggards, stickiness, multipolarity, and C-metaphase are associated with aneugenic disturbances (Silveira et al. 2017). Errors in kinetochore attachment further contribute to misorientation (Banerjee et al. 2020). Mitotic anomalies—including bridges, multipolar anaphase, nucleoplasmic bridges, and lagging or vagrant chromosomes—have been proposed to arise from inversions, dicentric formations, chromatid breaks, or spindle dysfunction (Patil and Bhat 1992; Fiskesjö 1997; Tabur and Demir 2010; Bonciu et al. 2018). In addition, irregular chromosomal contractions may cause premature uncoiling in prophase and metaphase, further disrupting cell division.

4. BIOCHEMICAL EFFECTS

Drought tolerance is a complicated process that involves the synchronization of several stress-responsive mechanisms (Ahmad et al. 2015). Under dry and semiarid environments, plants produce more ROS, which causes oxidative damage at the cellular level. Aside from their harmful effects, ROS operate as signaling molecules, activating a cascade of molecular, physiological, and morphological responses to stress (Zou et al. 2021; Sharma et al. 2021). Absciscic acid (ABA), a key mediator in stress signaling, is produced in response to high ROS levels (Sah et al. 2016). ABA modulates the expression of stress-related genes, including those that encode antioxidant enzymes like superoxide dismutase (SOD) and catalase (CAT), peroxidase (POX), glutathione reductase (GR), ascorbate peroxidase (APX), glutathione peroxidase (GPX), thereby contributing to the biochemical defense system (Oguz et al. 2022). The amount of damage induced by ROS is determined by the balance of ROS generation and antioxidant scavenging. Superoxide

dismutase (SOD) is the initial line of defense against ROS, converting O_2^- radicals to H_2O_2 and O_2 (Carvalho 2008). CAT and APX detoxify and inhibit H_2O_2 buildup. Non-enzymatic antioxidants such as flavonoids, tannins, and lignin precursors help to detoxify ROS and decrease oxidative stress (Kumar et al. 2020). These antioxidants work together to activate various redox processes.

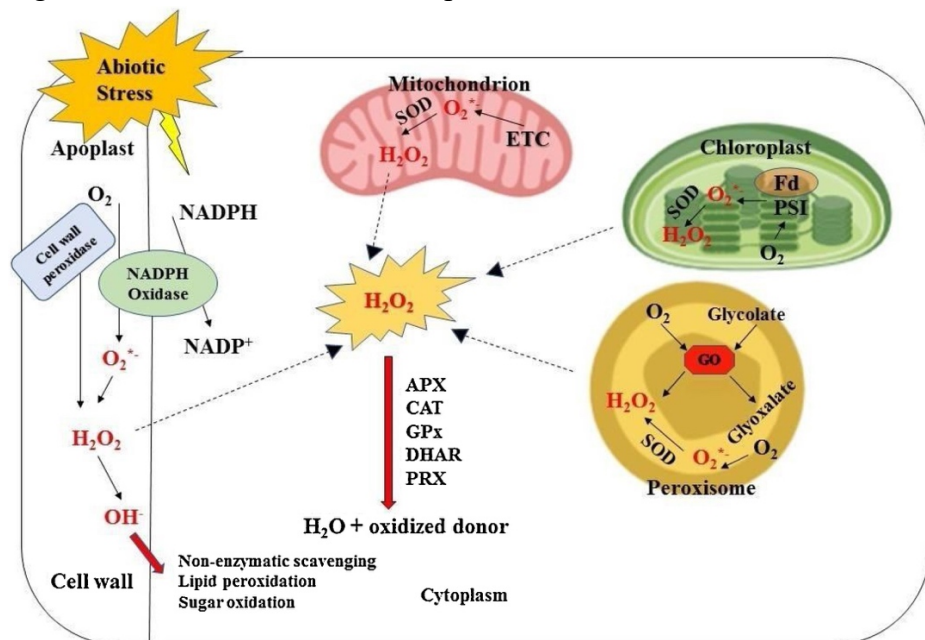


Figure 2. Schematic representation of ROS formation in various plant organelles under abiotic stress and their regulation through enzymatic antioxidants (Zia et al. 2021).

One of the principal effects of drought stress is lipid peroxidation, which results in the formation of malondialdehyde (MDA) as a byproduct. Tomato (Ben Ammar et al. 2007), wheat (Dugasa et al. 2019), barley (Skowron and Trojak 2021), mustard (Harinasut et al. 2003), thyme (Mohammadi et al. 2018), and cotton (Shallan et al. 2012) have all shown elevated MDA levels in response to drought stress. In the

antioxidant defense system, SOD converts superoxide radicals into hydrogen peroxide, while CAT detoxifies H_2O_2 into water and oxygen, protecting cells from oxidative damage under stress. Similar studies have shown that drought stress enhances SOD activity in mulberry, thyme, tomato, barley and chickpea (Gapinska et al. 2007; Buyuk et al. 2012; Mohammadi et al. 2018; Özmen et al. 2023; Tabur et al. 2024). However, CAT activity under drought conditions has been reported to decrease in thyme, wheat, and cotton, while it increases in barley (Shallan et al. 2012; Mohammadi et al. 2018; Hassan et al. 2020; Skowron and Trojak 2021). APX, another critical component of the ROS scavenging system, functions in the ascorbate–glutathione cycle to detoxify hydrogen peroxide generated under stressful conditions (Miller et al. 2007). Consistent with this, previous research has demonstrated enhanced APX activity in plants such as maize (Sun et al. 2020), wheat (Dugasa et al. 2019), and cypress (Aalipour et al. 2020) under drought stress.

5. INTEGRATING MULTI-OMICS AND HIGH-THROUGHPUT PHENOTYPING FOR DROUGHT-RESILIENT CROP DEVELOPMENT

Over the past decade, substantial advances have been made in deciphering plant responses to drought stress, primarily driven by the integration of multi-omics technologies. Omics data alone can reveal how gene expression is altered under drought stress or how metabolite accumulation patterns shift, but such information does not always translate directly to improved agronomic performance in the field. The combined application of transcriptomics, proteomics, metabolomics, and epigenomics provides a comprehensive, systems-level understanding of drought response mechanisms (Araus et al. 2018; Gupta et al. 2020). These integrative approaches have facilitated the identification of key

regulatory genes, molecular pathways, and networks that regulate plant adaptation under water-deficient conditions. Among these advancements, CRISPR/Cas-based genome editing has emerged as a powerful and precise tool for crop improvement. By enabling targeted modifications of stress-responsive genes, genome editing significantly enhances the ability to develop drought-tolerant cultivars with high specificity and efficiency (Chen et al. 2024). However, translating these molecular insights into agronomic traits remains a critical bottleneck one that can be addressed through high-throughput phenotyping (HTP).

Multi-omics data are invaluable for revealing candidate genes and regulatory elements, yet they must be contextualized with phenotypic performance under real-world conditions. This is where high-throughput phenotyping platforms serve as a crucial link. HTP technologies-ranging from drone-based imaging and hyperspectral sensors to thermal and chlorophyll fluorescence cameras enable the non-invasive, real-time monitoring of key physiological and morphological traits, such as canopy temperature, stomatal conductance, and biomass accumulation (Chang et al. 2020; Araus and Kefauver 2022).

When integrated with omics data, high-throughput phenotyping (HTP) enables researchers to validate gene function under field-relevant drought scenarios, effectively bridging the gap between genotype and phenotype. For instance, transcriptomic or epigenomic changes identified under drought stress can be directly correlated with dynamic physiological traits, such as transpiration efficiency or photosynthetic rate, captured via automated imaging systems (Wu et al. 2021; Liang et al. 2025). This multi-layered approach enhances the resolution and reliability of genotype-to-phenotype associations, which are essential for precise trait selection in breeding programs (Araus and Kefauver 2022; Zhang et al. 2024). Moreover, the massive datasets generated by both omics and HTP require sophisticated computational tools for integration.

Looking ahead, integrating these advanced approaches into breeding programs and sustainable agricultural practices will be essential to mitigate the adverse impacts of climate change on crop productivity. The convergence of omics technologies, precision phenotyping, and data-driven modeling holds great potential to accelerate the development of climate-resilient cultivars and ensure global food security in the coming decades.

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Responses of Plants to Heat Stress in Climate Changes

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1. INTRODUCTION

In the coming years, global warming is expected to bring about serious challenges for plant development, growth, reproduction, and productivity. To mitigate the adverse effects of rising temperatures, plants have evolved various mechanisms that influence their molecular processes, physiological functions, and biochemical responses. However, these adaptations often have detrimental impacts on agricultural production. Plants typically experience heat stress under specific conditions: (i) when elevated air temperatures lead to energy absorption via sensitive heat transfer; (ii) when soil surfaces heated by sunlight exceed the air temperature; and (iii) when leaves are unable to effectively dissipate solar radiation and heat, causing rapid heating that can reach up to 15°C above air temperature especially in leaves with low transpiration rates, which are more susceptible to extreme temperatures.

2. PHYSIOLOGICAL RESPONSES of PLANTS to HEAT

2.1. Water Relations

The amphoteric quaternary amine glycine betaine (GB) acts as an important adaptogen, helping plants cope with stress conditions such as salinity and high temperatures. Production capacity under stress varies among species. Similarly, proline is another adaptable solute widely found in higher plants that accumulates significantly in response to environmental stress. Both GB and proline have been shown to play a role in maintaining cellular redox balance under heat and other stress scenarios, highlighting their important roles in stress mitigation. Plants adapt to heat stress through various morphological and physiological mechanisms. These include strengthening their root systems, reducing stomatal number and conductance, curling or folding their leaves to minimize surface area, and thinning their leaf structures to limit water loss through evaporation. Studies by Sicher et al. (2012) and Goufo et al. (2017) highlight such adaptive changes.

Lima et al. (2013) proved that heat effects disrupt photosynthesis in coffee plants by causing cell membrane irregularity, reduction of starch granules, and cell shrinkage in the palisade parenchyma.

2.2. Photosynthesis

High temperatures have a more pronounced impact on the photosynthetic capacity of C3 plants compared to C4 plants. These elevated temperatures disrupt energy distribution, impair enzyme functions critical to carbon metabolism especially rubisco and affect the regeneration of RuBP. This disruption occurs via alterations in electron transfer processes and the inactivation of oxygen-evolving enzymes in PSII as noted by Salvucci and Crafts-Brandner (2004). Heat stress also diminishes the levels of photosynthetic pigments (Todorov et al. 2003), soluble proteins, rubisco-binding proteins (RBP), and both the large (LS) and small (SS) rubisco subunits during dark conditions. Conversely, these components increase under light exposure, suggesting their dual role as chaperones and heat shock proteins (HSPs) according to findings from Demirevska-Kepova et al. (2005). Additionally, heat stress induces considerable shifts in starch and sucrose production, where enzyme activities—such as those of sucrose phosphate synthase (Chaitanya et al. 2001), ADP-glucose pyrophosphorylase, and invertase are reduced (Vu et al. 2001). For plant species, the ability to sustain leaf gas exchange under high-temperature conditions is closely tied to heat tolerance. Elevated daytime temperatures during the vegetative phase impair CO₂ assimilation by restricting compensatory leaf photosynthesis (Hall 1992). Rising temperatures generally reduce photosynthetic efficiency while enhancing the transfer of CO₂ between intercellular spaces and carboxylation zones. Moreover, stomatal conductance (gs) and net photosynthesis (Pn) in many species decline under moderate heat stress due to reduced rubisco activation (Crafts-Brandner and Salvucci 2002; Morales et al. 2003). Although rubisco's catalytic activity increases with temperature, its low affinity for CO₂ and tendency toward oxygenase activity impose limitations on Pn enhancement. For example, in maize, photosynthesis becomes inhibited when leaf temperatures exceed 38 °C, a phenomenon that intensifies when temperature rises abruptly yet remains unaffected by stomatal behavior under heat stress (Crafts-

Brander and Salvucci 2002). Despite these challenges, rising atmospheric CO₂ levels are expected to elevate the optimal temperature range for leaf photosynthesis. Under heat stress, the overall function of the photosynthetic system deteriorates. Stomatal closure reduces transpiration, CO₂ uptake diminishes, enzymatic processes including those of ATP synthase are disrupted, leaf growth rates slow down, and plant senescence accelerates, impeding overall development (Wahid 2007). As an adaptive mechanism to counteract heat-induced damage, plants modify carbon assimilation pathways. During stressful periods, they reactivate starch reserves stored in chloroplasts to release essential energy, sugars, and other metabolites required for survival (Raza 2022).

The enzyme ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco), essential for carbon fixation, achieves optimal activity at temperatures ranging from 20 to 30 C°. Beyond this range, photosynthesis rates generally decline, as documented by Yamori et al. (2014). Over time, plants have evolved various metabolic pathways to adapt to challenging environmental conditions. The C₄ and CAM photosynthetic mechanisms are particularly notable, as they enhance CO₂ concentrations within cells, thereby improving the efficiency of Rubisco under extreme temperature conditions. This adaptive advantage is absent in C₃ plants, which lack systems optimized for high CO₂ concentrations, resulting in reduced carbon fixation at elevated temperatures (Betti et al. 2016). Additionally, heat stress can disrupt the cellular redox balance, leading to the accumulation of reactive oxygen species (ROS). This buildup impairs cellular systems responsible for eliminating these harmful oxygen derivatives, causing oxidative stress. Elevated ROS levels contribute to molecular oxidation, damage to cell membranes, enzyme inactivation, and alterations in gene expression patterns (Singh et al. 2019).

2.3. Biochemical Responses

Approximately 5% of the plant transcriptome shows a twofold or greater upregulation in gene expression upon exposure to heat stress (Rizhsky et al. 2004; Qin et al. 2008). Interestingly, only a small subset of these transcripts encodes heat-induced chaperones; for instance,

among 1,780 transcripts in *Arabidopsis thaliana*, only 88 falls into this category, while in wheat, merely 117 out of 1,509 transcripts belong to the same group (Rizhsky et al. 2004; Qin et al. 2008).

Notwithstanding their limited presence, the importance of these chaperones is underscored by the reduced survival rates observed in mutants deficient in specific heat-induced chaperones (Queitsch et al. 2000; Dafny-Yelin et al. 2008). Heat-induced chaperones are part of the broader molecular chaperone family, which is either continuously expressed or developmentally regulated under normal conditions and may also be activated in response to various stressors. The regulation of chaperones is regulated by the heat shock transcription factor (HSF) network consisting of 21 members in *Arabidopsis thaliana* (von Koskull-Döring et al. 2007). Functional activation of HSFs facilitates oligomerization, nuclear transport, binding to promoters of heat stress-responsive genes (Li et al. 2010), and removal of inhibitory histones from gene promoters by the histone acetyltransferase HAC1 (von Koskull-Döring et al. 2007). These transient disruptions enable macromolecules to function as thermosensors, detecting thermal fluctuations through temporary loss of structural or functional integrity (Saidi et al. 2010). Rising temperatures due to climate change have been reported to have reduced yields in corn and wheat, two of their main food sources, over the past three decades. Furthermore, because plants cannot escape heat during these rising temperatures, they resort to metabolic changes to protect themselves from heat damage by expending their resources (Lobell 2011).

A membrane protein can sense heat through temperature-dependent changes in the fluidity of the membrane. In addition, changes in metabolic flux, accumulation of reactive oxygen species (ROS), ATP release, or decreasing energy levels, which are triggered by heat in metabolism, can also activate the sensor molecule. For example, in plants such as *Arabidopsis thaliana*, energy depletion can be detected via the SNF1-related protein kinase (SnRK1) pathway (Baena-Gonzalez and Sheen 2008).

Heat stress disrupts metabolic balance by adversely affecting the stability of proteins, membrane structures, RNA species, and the cytoskeleton, thereby altering the efficiency of enzymatic reactions (McClung and Davis 2010; Suzuki et al. 2011). As cellular reactions are interdependent, the steady-state flow of metabolites can pave the way for the accumulation of toxic by-products, particularly ROS. Furthermore, just as there is a close relationship between ROS and oxidative stress, oxidative stress and HSR are also closely linked in many organisms (McClung and Davis 2010; Miller et al. 2009). To manage the destabilising effects of heat stress on cellular metabolism, plants and other organisms reprogramme their transcriptomes, proteomes, metabolomes, and lipidomes in response to changes in ambient temperatures. Within this reprogramming framework, they re-establish the balance of metabolic processes by altering the quantity and composition of various transcripts, proteins, and metabolites. Changes are also observed in physical properties such as membrane fluidity, lipid release, or Ca^{2+} release through ion channel activation. Although the regulatory networks and pathways developed in plants to respond to heat have been identified, many questions remain unanswered. The most well-known pathways developed by plants for HSR include the creation of plasma membrane channels that initiate inward calcium influx, a histone sensor in the nucleus, and two unfolded protein sensors in the endoplasmic reticulum and cytosol (Mittler et al. 2012).

Plants transmit these signals through mechanisms involving calcium signalling pathways, kinases, phosphatases, ROS release, transcription factors (TF) or hormone production. During adaptation processes, transcriptomes, proteomes and metabolomes are restructured. While ensuring protein stability, processes such as the exposure of hydrophobic residues and the regulation of translation or degradation are considered. As the cell's skeletal structure breaks down, chromatin modifications can range from DNA-protein interactions to histone translocations. Furthermore, changes in the unbound states of compounds such as ATP, NADPH, or ROS and redox balance play fundamental roles in enzymatic activities. Additionally, processes such as RNA unfolding, miRNA kinetics, and spliceosome functions become

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active in RNA mechanisms. Alternatively, plants can adapt by activating programmed cell death through specific signalling pathways.

The effect of heat-induced chaperones is noteworthy; although these molecules are generally activated during heat stress, they constitute only a small part of HSR. Nevertheless, it has been found that mutants lacking heat-induced chaperones have significantly reduced resistance to heat stress (Queitsch et al. 2000; Dafny-Yelin et al. 2008). Heat-induced chaperones belong to a broader family of molecular chaperones that are continuously produced in cells or induced during developmental stages or because of environmental stress conditions. Under normal physiological conditions, they play a role in controlling protein folding, translocation, degradation, and cellular signalling, while under heat stress, they can prevent protein misfolding and aggregation and maintain membrane integrity (Banti et al. 2010).

Plant growth, productivity, and survival are greatly affected by the increasing intensity and frequency of abiotic stresses such as drought, extreme temperatures, and flooding caused by global warming and climate change. This often leads to the emergence of multiple stress combinations (Steg 2018; Masson-Delmotte et al. 2021; Rivero et al. 2022). Plants produce a variety of metabolites, such as carbohydrates, amino acids, phenolics, polyols, polyamines, and lipids, depending on environmental conditions (Fang et al. 2019), and recent studies suggest that these secondary metabolites are potent regulators of plant growth and development and play a role in defense against pathogens. Environmental responses can be regulated by flavinoids, and it has been suggested that these molecules (Erb and Kliebenstein 2020) function not only as targets of stress response signaling pathways but also as stress signals themselves. In this context, metabolic responses resulting from specific abiotic stresses experienced by plants can trigger adaptation mechanisms to subsequent environmental stresses (Schwachtje et al. 2019).

Higher growth temperatures can directly affect photosynthesis, and these temperatures can transform the ecosystem carbon cycle and carbon uptake by increasing photosynthesis rates or, if optimum temperature

thresholds are exceeded, causing a decrease in photosynthesis. While adaptation to rising temperatures in Arctic plants is important for the development of stress tolerance, there are also studies reporting that exceeding threshold values causes a decrease in photosynthesis (Marchand et al. 2005; Simin 2021). The study suggests that heatwaves may positively affect plant photosynthesis and vegetation growth. However, when plants were returned to normal growth temperatures, increased stress was observed, indicating that adaptation to high temperatures is critical for stress tolerance. It is also known that increasing growth temperatures alter emission rates and the mixture of volatile organic compounds (VOCs) not only through photosynthesis but also in connection with stress events. These changes are associated with reactive hydrocarbon groups that significantly affect the oxidation capacity of the atmosphere and contribute to processes such as the formation of secondary organic aerosols and ozone concentration. Researchers have reportedly detailed the effects of these mechanisms on atmospheric chemistry and, consequently, climate. Models suggest that Arctic plants exhibit thermal adaptation to higher growth temperatures, showing a marked increase in VOC emissions during heat waves. This indicates that thermal adaptation may lead to a stronger VOC emission response to high temperatures. However, there is limited information on the quantitative level of understanding of the responses developed by Arctic shrubs to increasing growth temperatures and how these responses interact with stress conditions (Peñuelas and Staudt 2010; Valolahti et al. 2015; Rieksta et al. 2021).

Studies examining leaf phenology, photosynthesis, and VOC emissions in three widely distributed Arctic shrub species as a function of heatwaves and temperature highlight this. In this context, understanding the carbon cycle requires such studies. Studies generally conclude that increasing temperatures will increase spring phenology and net photosynthesis, which in turn will increase VOC emissions. Net photosynthesis rates will decrease due to drought, thus reducing VOC emissions.

Chaperones are important in maintaining protein folding and membrane structures during heat adaptation (Wahid et al. 2007). These

include pre-treating plants to resist heat stress and applying osmoprotectants or plant growth regulators to seeds or entire plants. Further research based on the results obtained from these applications is crucial for determining the cultivation conditions for species that are resilient and adaptable to climate change.

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**Heat Stress and Climate Change in
Agriculture: Integrated National and
International Adaptation Strategies and Socio-
Economic Dimensions**

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1. INTRODUCTION

Heat is one of the primary abiotic stress factors affecting plants. Among various stress factors, it is known to have a particularly strong negative impact on crop productivity. In the context of global climate change, the increasing frequency and severity of heat waves have made this problem more urgent. As agricultural systems struggle to cope with high temperatures, the threat to global food security becomes even more pronounced.

While this condition is known as abiotic stress in the literature, this type of stress has been shown to disrupt plant physiology and alter vital cellular processes. Zhang et al. (2022) suggest that changes in membrane fluidity and protein structure, particularly under hot or cold conditions, can be detrimental. However, some of these responses may also contribute to stress adaptation and tolerance.

The severity of heat stress depends not only on the intensity of heat but also on the duration of exposure and the plant's developmental stage. Generally, threshold levels are defined as the point at which irreversible cellular damage, such as membrane destabilization, can occur. For example, temperatures exceeding 35°C are considered heat stress in tropical and subtropical crops, while temperatures above 25°C can cause stress in winter (rabi) crops (Wahid et al. 2007; Ahmad et al. 2021). These physiological thresholds are crucial for identifying sensitive growing periods and designing appropriate mitigation strategies.

Given these risks, national and international efforts to mitigate the effects of heat stress in agriculture are becoming increasingly important. These include the development of heat-tolerant crop varieties, improvements in water management, farmer training, technological innovations, and global collaboration through climate agreements and research networks.

This book examines this stress from various perspectives. In this chapter, we focus on examining existing strategies and policy measures

(both national and international) designed to address heat stress in the context of climate change. Our objectives include addressing not only the biological and technological aspects but also the social, economic, and institutional dimensions of resilience. These focus points are even more urgent given recent evidence that extreme heat events (rather than simply increases in average temperature) can have disproportionately detrimental impacts on crop yields. As the Adenäuer et al. (2023) note, integrating extreme heat scenarios into agricultural projections significantly worsens expected outcomes. Therefore, the importance of highlighting the need for targeted and clear mitigation strategies is undeniable.

2. INTEGRATED STRATEGIES FOR ADAPTATION TO HEAT STRESS: NATIONAL AND INTERNATIONAL RESEARCH PROJECTS ON HEAT STRESS IN AGRICULTURE

As the risks posed by heat stress intensify under changing climate conditions, both international institutions and national governments have increased their efforts to support agricultural adaptation. It is increasingly recognized that extreme temperatures now pose one of the most urgent and complex threats to global food systems. Efforts by institutions and organizations support the need for advances in science and technology, while also influencing changes in relevant policies. Recent initiatives prioritize not only the development of heat-tolerant crop varieties but also increasing farmer capacity, reducing climate-induced yield variability, and promoting system stability and equity.

In this section, we look at how targeted research efforts are beginning to produce tangible results. One example is the HOT-AND-COLD project (Grant Agreement No. 101042198) (CORDIS 2025), part of the EU's Horizon Europe programme and coordinated by the Swedish University of Agricultural Sciences. The project, which runs from September 2022 to August 2027, examines how plants react to heat stress at both molecular and cellular levels.

Rather than taking a broad approach, the team focuses on auxin transport and signalling, areas known to play a central role in plant growth under temperature extremes. Using advanced imaging tools and root-specific molecular probes, they have identified transporters and regulatory proteins that respond to heat. They have also observed changes in cell membrane fluidity, which appear to alter auxin gradients and influence root development. These findings are expected to help in breeding crop varieties with greater resilience to both heat and cold. The €1.38 million budget reflects not only the scope of the research but also the economic value that such innovations could deliver for climate-resilient agriculture (CORDIS 2025).

Another initiative worth noting is the CRISPiT project (Grant Agreement ID: 101086293) (CORDIS 2023), part of the Marie Skłodowska-Curie Actions and coordinated by the University of Porto in Portugal. Running from January 2023 to December 2026, it brings together fundamental genetic research and genome-editing tools to improve heat tolerance in rice, a crop central to global food security. The team's work zeroes in on the reproductive stage of plant growth, a period particularly vulnerable to high temperatures. In practice, this means identifying and modifying genes that control ovule and seed development under stress. To achieve this, the researchers are working with both *Arabidopsis thaliana* as a model plant and conducting transcriptomic analyses across multiple rice genotypes. So far, they have produced CRISPR-edited rice lines targeting critical reproductive genes. The project, developed in collaboration with the National Institute of Genetics (Japan), reflects the global nature of heat stress research. It also brings to light the policy debates in Europe about the place of genome-edited crops in agricultural systems.

The PLANTEX project (Grant Agreement ID: 101126019) (CORDIS 2024) takes a different angle. Launched in June 2024 under the European Research Council and led by the Hellas Foundation for Research and Technology in Greece, this five-year study looks at proteolysis and its role in plant adaptation to changing temperatures. The researchers are particularly interested in protein–RNA networks within cellular condensates, and how these networks regulate stress responses. At the heart of their concept is the idea of “core nucleons” groups of interconnected proteins and RNAs stored in condensates which may help plants coordinate their reactions to environmental

shifts. Through proteomic mapping, genetic engineering, and cell biology techniques, the project aims to strengthen heat tolerance in crops such as tomato and Arabidopsis. The long-term goal is to develop methods and tools that can be applied to a broader range of breeding programmes.

In addition to international projects, significant progress has been made at the national level in strengthening the resilience of agricultural systems to extreme temperatures. While various projects specifically for Türkiye have focused on heat stress, this section has attempted to include projects directly addressing this issue. As part of the TÜBİTAK Support Programs, several research projects have been initiated to develop crop varieties with increased heat and cold tolerance. One of these projects, supported by TÜBİTAK, focuses on evaluating heat and drought tolerance in selected *Capsicum chinense* (pepper) lines (Ondokuz Mayıs University 2024a). The project is evaluating morphological, physiological, and biochemical traits through controlled field trials in collaboration with a private seed company in Antalya. The results are expected to contribute to future rootstock development programs. This project is also seen as a good example of public–industry collaboration.

A second project, also supported by TÜBİTAK, focuses on identifying cold-tolerant radish genotypes native to Türkiye (TÜBİTAK 2022). Leveraging the countrys extensive local gene pool, the study aims to develop resistant parental lines for hybrid seed production and evaluates physiological and biochemical responses to low temperatures.

Another TÜBİTAK-funded initiative investigates miRNAs regulating drought and heat tolerance in potato (TÜBİTAK 2019). Using next-generation sequencing and transgenic approaches, the project identified candidate miRNAs and validated their roles under stress conditions, resulting in promising transgenic lines with reduced yield loss in high-temperature and drought environments.

A further initiative, recently accepted under the TÜBİTAK 1002-A Rapid Grant Program, focuses on the identification of genes and miRNAs associated with flowering under high-temperature stress in bean plants (Ondokuz Mayıs University 2024b). This study is based on the findings of a previously completed TÜBİTAK 1001 project (No. 219O301) (TÜBİTAK 2023) and utilizes genome engineering in *Arabidopsis thaliana* to better

understand the mechanisms of flowering under heat stress. Additional projects are also being conducted under TÜBİTAK and COST programs, focusing on enhancing heat resistance in tomatoes using CRISPR/Cas9 and genotype characterization in flax. These initiatives demonstrate Türkiye-s growing institutional capacity and strategic alignment in combating climate-induced stress using molecular approaches.

These international and national efforts constitute a multifaceted response to the growing threat of heat stress in agriculture. By integrating molecular biology, field experiments, and interdisciplinary collaboration, they are accelerating the development of resilient crops. They also contribute to a broader vision for sustainable and adaptable food systems by aligning scientific innovation with policy and practice.

3. ECONOMIC AND SOCIAL DIMENSIONS OF HEAT STRESS IN AGRICULTURE

In addition to academic projects, various international organizations are also contributing to the topic of heat stress. Of course, as seen in the project objectives above, heat stress poses a threat to species and jeopardizes food security. Therefore, the risk of encountering social and economic problems is undeniable. Recent international assessments emphasize the importance of focusing not only on average temperature trends but also on extreme heat events. While many climate impact studies emphasize average climate changes, extreme weather conditions (especially heat waves) can have more severe and sudden impacts on agricultural productivity (Adenäuer et al. 2023). Simulation studies combining climate and crop models have shown that extreme heat during sensitive crop development stages leads to significantly worse yield outcomes compared to scenarios based solely on average warming. It is not hard to conclude that the reduced yields will not be sufficient to offset the increased costs, and therefore, access to food will become more difficult, or even impossible, for many segments of

society. Deryng et al. (2014) found that incorporating extreme heat stress into projections could double globally corn yield losses and significantly reduce projected gains for spring wheat and soybeans by 2080. These findings highlight the need for targeted adaptation strategies that specifically address heat stress as a prominent and growing challenge in climate-resilient agriculture. Global food security remains a pressing concern, with more than 850 million people undernourished and over 2 billion facing critical micronutrient deficiencies (Pérez-Escamilla 2017). Therefore, it remains a pressing concern (Pérez-Escamilla 2017; Zhang et al. 2022).

Despite global commitments such as the Sustainable Development Goals (SDGs), progress in reducing hunger has been extremely limited since the 1990s. Climate-related stressors (particularly water scarcity and extreme heat) further threaten these goals.

A recent simulation study commissioned by the OECD projects that under global warming scenarios, the proportion of individuals experiencing food insecurity will increase compared to 2020 baseline values in many countries (Kompas et al. 2023). These findings demonstrate that heat stress is not merely a physiological or agricultural problem. They also highlight that it is a driver of deepening inequality and nutritional insecurity, particularly in low-income and climate-vulnerable regions.

Beyond impacts on food production and nutrition, climate-related stressors such as heat and drought also have measurable impacts on economic growth. Damania et al. (2020) show that rainfall shocks, often coinciding with periods of extreme heat, significantly impact GDP growth at the national level. Using high-resolution data, they showed that a one standard deviation decrease in annual precipitation could almost halve GDP growth, from 2.14% to 1.11%, while a positive rainfall shock of the same magnitude could increase growth by 0.7%.

As highlighted in the OECD report *The Costs of Droughts* (Tikoudis et al. 2025) national-level averages can mask these effects due to spatial clustering. This makes local-level data critical for accurately assessing economic vulnerability. These findings demonstrate that heat and water stress are not only agricultural concerns but also require regionally tailored interventions. Critical macroeconomic risks are also unavoidable.

The adverse effects of heat stress are further intensified when combined with drought conditions. According to the OECD's *Global Drought Outlook* (OECD 2025), under extreme drought conditions, an additional degree of warmth could reduce maize and wheat yields by more than 9% (Matiu et al. 2017). As we have previously emphasized, heat stress does not affect all regions equally. For example, croplands in Northern Europe appear to be more vulnerable to temperatures exceeding 32°C than those in Southern Europe due to differences in crop species and natural heat tolerance (Matiu et al. 2017). This information highlights the need for regionally differentiated policies that consider the interactions between multiple climate stressors.

The increasing frequency of extreme heat events due to climate change also raises concerns about the resilience of food markets. According to OECD scenario analyses (Adenäuer et al. 2023), trade liberalization plays a stabilizing role by spreading risk and cushioning the negative impacts of weather-induced yield losses. In more integrated trade systems, food prices and availability are less volatile during climate shocks. Conversely, countries that restrict trade may face heightened food security risks due to reduced market flexibility. While liberalization alone is not sufficient, the OECD emphasizes that it should form part of a broader, coherent food security strategy that includes domestic support and long-term planning. These insights underscore the need for international coordination not only in climate adaptation but also in agricultural trade policy.

4. CONCLUSION

It is clear that heat stress affects agriculture in many ways. These effects are also interconnected. The resulting problems are not just biological; they also underline environmental and socioeconomic problems. Problems that begin with microscopic changes in plant cells (e.g., membrane instability or changes in protein structure) can reduce production efficiency over time. They can alter land use on a national scale, ultimately destabilizing agricultural markets in food sectors, and can put pressure on systems, particularly hunger and social injustice.

The OECD states that extreme heat events tend to cause much larger declines in productivity than gradual temperature increases (Kompas et al. 2023). The OECD/FAO (2024) also warns that global malnutrition and micronutrient deficiencies remain unresolved and that climate change will likely make addressing them even more difficult..

The analysis in this chapter points to several areas where targeted action can make a difference. In plant science, molecular innovations and selective breeding offer ways to improve heat tolerance. Landscape management benefits from integrating resilient varieties into diverse cropping systems, which can strengthen ecological balance. From a socio-economic perspective, stabilising yields can help protect rural incomes, moderate price volatility, and limit widening inequality. OECD projections Kompas et al. (2023) suggest that without such measures, climate-related yield losses could push food insecurity to even higher levels.

As summarized in Table 1, it is crucial to align actions in these areas, particularly by adapting strategies to regional contexts and maintaining international cooperation. Furthermore, in an era of accelerating climate change, it is possible to maintain agricultural productivity, sustain rural livelihoods, and secure ecosystems.

Summary of six interconnected economic and financial strategies are given in Figure 1, which are designed to make agricultural systems

less vulnerable to heat stress. Some of these actions, such as yield stabilization measures and direct financial support, will help farmers maintain their incomes and purchasing power during adverse seasons.

Table 1. Summary of focus areas, key actions, and expected outcomes

Focus Area	Key Actions	Expected Outcomes
Plant Science	Apply molecular innovations, targeted breeding, and genomic tools to improve heat tolerance	Higher crop resilience and stable yields under high temperatures
Landscape Management	Integrate heat-resilient varieties into diversified agroecosystems	Stronger ecological stability and improved adaptive capacity
Agricultural Policy	Link scientific advances to agricultural support programs and climate adaptation plans	Faster adoption of climate-resilient practices through aligned policy frameworks
Socio-Economic Measures	Stabilise yields, protect farmer incomes, and manage price volatility	Reduced inequalities and improved food affordability
Trade & Market Resilience	Design trade policies that buffer climate shocks, supported by domestic safety nets	More stable food markets and reduced vulnerability during extreme events
Cross-Sector Collaboration	Foster cooperation between scientists, planners, economists, and policymakers	Coherent, multi-level adaptation strategies bridging research, practice, and governance

Long-term recommendations include targeted investments in innovation and the development of crop varieties that can withstand higher temperatures, aiming to increase long-term productivity. Another important strategy should be to integrate insurance plans and hedging measures into the production process. Risk management tools will provide protection against sudden losses. Awareness meetings are particularly necessary for farmers. Trade facilitation will improve access to markets and keep supply chains moving, cushioning the impact of regional shocks. Finally, sustained research funding will bring these elements together and provide the scientific basis needed for sound policies and practical adaptation. These measures will support both

emergency responses and the long-term sustainability of agricultural systems by combining economic stability with climate resilience.



Figure 1. Building heat stress resilience: An economic and financial perspective

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Climate Change, Oxidative Stress, and Seed

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1. INTRODUCTION

Seeds constitute not only the starting point of plant development but also a critical component in ensuring ecosystem resilience and sustaining genetic diversity. They are essential for species persistence and the inheritance of genetic traits, thereby playing a pivotal role in the preservation of biodiversity and the assurance of global food security. (Mishra and Singh 2022; FAO 2022). Seed formation, which begins with fertilization, occurs when male and female reproductive cells combine to form the smallest unit capable of forming a new plant. However, the direct and indirect impacts of climate change on seed development, viability, and quality have become a growing concern on a global scale, reshaping research priorities in seed science (Lalani et al. 2021; Chen et al. 2023).

Today, climate change triggered by anthropogenic carbon emissions is one of our planet's most urgent and high-risk threats. The complex impacts of factors such as increasing CO₂ concentrations, rising temperatures, and changing precipitation regimes on the quality, physiology, and ecology of seeds are a significant focus of scientific research (IPCC 2021; Davis and Lee 2023). Previous studies have shown that climate change reduces key qualitative attributes of seeds, such as weight, germination ability and viability (Hampton et al. 2013). However, a recent research suggests that these effects include indirect factors such as phenological events, pollination dynamics and pest/disease cycles, which significantly influence seed formation and quality (Garcia et al. 2022). The negative impact of climate change on the reproductive mechanisms of trees puts severe pressure on the natural regeneration capacity of forest ecosystems by reducing the distribution range of species (Zhang and Wang 2023).

In this context, to eliminate the adverse effects of climate change on seeds and ensure the continuity of natural regeneration processes of

forest tree species, it has become a fundamental requirement to protect the genetic diversity of forest reproductive material and identify climate-resilient seed sources. This is because the quality and adaptation potential of reproductive material directly determines the establishment of new forest areas and natural regeneration processes. The long-term health and resilience of future forests will largely depend on these actions and decisions undertaken today (Bradshaw et al. 2014).

The main determinants of seed quality include physical integrity, genetic homogeneity, high viability and resistance to abiotic stresses. These traits are influenced by parameters such as the physiological state of the parent plant, harvest phenology, post-harvest biotic interactions, mechanical damage and storage conditions. Both pre- and post-harvest treatments are critical for maintaining seed viability, enhancing germination capacity and extending the longevity of stored seed. The interactions of these factors on seed quality under increasing environmental stress conditions are more complex than previously thought (Kumar and Singh 2023).

Seed vigor and stress tolerance are significantly related to seed biochemical composition, metabolite concentrations, and genetic makeup. Primary components such as carbohydrates, lipids and proteins as well as secondary metabolites such as hormones, alkaloids and especially antioxidants play important roles in maintaining seed quality. The role of antioxidant mechanisms in seed senescence and resistance to environmental stresses has recently been better understood (Zhou et al. 2024). Although the chemical profile of seed is determined by genetic factors, environmental factors (climatic variations, soil properties, harvesting and storage protocols) and cultural practices can also modulate this profile. Suboptimal environmental conditions, such as extreme weather events and temperature fluctuations resulting from climate change, have been shown to degrade the chemical integrity of

seed, reducing its quality and reducing germination rates (Gornall et al. 2020; Patel et al. 2022). This again demonstrates why seed quality is vital for sustainability and biodiversity management.

In the light of all this detailed and up-to-date information, oxidative stress and oxidative balance mechanisms occurring in seeds and the senescence effects induced by this stress will be elaborately investigated in this chapter, emphasizing its critical importance in the context of current scientific findings and climate change. This study can potentially guide the sustainability of seed quality and the adaptive capacity of species.

In this section, the molecular mechanisms of seed viability and defense against storage stress have been focused on. A thorough examination of the molecular mechanisms of seed aging and oxidative stress was initiated, followed by a detailed discussion of the defense mechanisms that seeds have developed against storage stress and aging. In this context, the critical roles of both enzymatic and non-enzymatic antioxidants have been examined. Finally, the biochemical effects of aging and stress in seeds and their underlying mechanisms have been discussed, and potential methods to mitigate these adverse effects have been explored.

2. SEED VIABILITY AND DEFENSE MECHANISMS AGAINST STORAGE STRESS

The importance of seed storage is increasing within the framework of efficient use of natural resources and sustainable environmental understanding. The basic condition for obtaining quality material in afforestation and sapling production is to use morphologically, physiologically and genetically superior seeds. It is essential to manage seed, critical in ensuring species continuity and genetic diversity,

through proper planning and appropriate storage methods from harvest to end use.

Seed quality refers to a seed lot's performance, genetic purity and viability potential. Post-harvest storage conditions directly affect this quality. However, even under ideal temperature and humidity conditions, seeds experience deterioration and loss of viability over time due to oxidative stress, lipid peroxidation, nutrient reserve and protein structure deterioration, genetic changes in enzymatic activities and chromosome structure, and increased respiration rate. Recent research has detailed the interactions of these degradation mechanisms at the molecular level, particularly the central role of DNA damage and epigenetic changes in seed senescence (Bewley et al. 2013; Sharma and Kaur 2021). Even under low-temperature storage conditions, seed viability cannot be preserved indefinitely. Therefore, it is of great scientific and practical importance to slow seed deterioration, increase viability and improve resilience, especially to the additional stresses of climate change (Probert et al. 2009; Walters et al. 2013).

Seeds, like other plant organs, show a natural aging tendency. The leading causes of seed senescence include free radical-induced lipid peroxidation, enzyme inactivation or protein degradation, disruption of cell membrane integrity and damage to genetic material (nucleic acids) (McDonald, 1999; Zhao et al., 2023). Enzymatic systems that scavenge reactive oxygen species (ROS), such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), as well as non-enzymatic antioxidants such as β -carotene, ascorbic acid, α -tocopherol, and reduced glutathione, can counteract the harmful effects of ROS in plant tissues. The activity of these metabolites and antioxidant enzymes ensures high seed resistance to oxidative damage and minimizes cell damage (Alscher 1989; Tabatabaei 2015). Recent research have provided a better understanding at the molecular level of how antioxidant defense systems

in seeds respond to environmental stressors (e.g., extreme temperature, drought) and the decisive role of these responses on seed viability (Song et al. 2024; Wang and Li 2024). However, the aging process inevitably reduces the germination ability of seeds. The decline in germination ability may vary under the influence of intrinsic factors such as genetic traits, species, and origin, and extrinsic factors such as storage conditions, such as temperature and humidity (Agrawal and Kharlukhi 1985; Tilki and Alptekin 2005). Increasing temperatures and unpredictable moisture changes, especially those caused by climate change, further complicate efforts to optimize seed storage conditions (Walters et al. 2013). These external stressors can accelerate the aging process by challenging the intrinsic defense mechanisms of seeds and may necessitate more advanced storage strategies or updating seed banking techniques to preserve seed gene pools (Pukacka and Ratajczak 2007; Kulac et al. 2013; Colmer et al. 2023).

Biochemical alterations associated with the seed aging process during storage play a critical role in determining seed longevity and overall viability. Degradation of the membrane structure is one of the leading causes of seed deterioration; this loss of integrity leads to the inability of seed cells to fulfill their normal functions. Significant membrane degradation factors include elevated levels of free fatty acids, lipid peroxidation, and the generation of free radicals. (Ghassemi-Golezani et al. 2010; El-Maarouf-Bouteau and Bailly 2008). Recent findings have revealed that this membrane damage is not only a physiological consequence but also affects signaling pathways in seeds, negatively affecting germination processes (Kurek et al. 2019).

Reactive oxygen species are generally recognized as the primary source of seed deterioration due to reduced seed viability and senescence. In humid environments, increased respiratory activity triggers electron leakage from the mitochondrial electron transport chain

and subsequent superoxide anion production during hydrogen peroxide formation (Kumar et al. 2015). This poses additional risks to seed and germplasm banks, especially in the current climate where storage conditions are becoming more variable with climatic fluctuations (Walters et al. 2013).

Seed deterioration due to oxidative stress may increase with exposure of the seed to adverse environmental conditions, reducing its survival potential (Shelar et al. 2008; Ren and Chen 2023). Increases in ROS causing oxidative stress can be observed depending on factors such as seed age, sampling time, harvest and post-harvest conditions (Bailly 2004; Güney et al. 2013). In this context, seed degradation has been described as a cumulative, irreversible and degenerative process (Kapoor et al. 2011; Bewley et al. 2013).

Biochemical changes associated with structural deterioration in the seed are manifested by increased leakage of biomolecules from the cells and decreased total soluble sugar and protein content. Amino acids and protease activity increase with seed deterioration, while some studies have also found a decrease in α -amylase activity (Mitra et al. 1974; Agrawal and Kharlukhi 1987; Kalpana and Madhava 1997). However, recent research suggests that these biochemical changes are not only a consequence of aging, but may also reflect the stress adaptation mechanisms of seeds and the role of epigenetic factors in these processes (Bewley et al. 2013; Sharma and Kaur 2021). According to Harman's (2006) "Free Radical Theory", aging is a progressive accumulation of oxidative damage caused by oxidative stress sources. This theory, supported by recent molecular and genetic studies in seed physiology, emphasizes the critical role of antioxidant defense systems in maintaining seed viability (Song et al. 2024).

Hydrogen peroxide (H_2O_2) is a reactive molecule with a dual role in plant physiology, developmental processes and stress resistance. The

balance between its positive (signaling) and negative (damaging) effects in biological systems depends on the physiological conditions and the characteristics of the processes affected. High concentrations can cause oxidative stress, leading to seed senescence, loss of vigor and morphological and biochemical deterioration (Vianello et al. 2007; Hampton et al. 2009; Sharma et al. 2012). However, recent research shows that it also acts as an important signaling molecule for stress tolerance of seeds and can trigger the expression of antioxidant genes at low concentrations (Wojtyla et al. 2016). It is not only difficult to make a clear distinction between their beneficial and deleterious roles, but it is also important to distinguish their roles in the cell from those of other ROS, such as superoxide anion and hydroxyl radical, which are formed spontaneously or through catalysis (Wojtyla et al. 2016). Recent studies reveal that the balance of these ROS generates critical signals for dormancy breaking and germination of seeds, but their excessive accumulation leads to cellular damage. These complex and sensitive interactions are vital for understanding how seeds respond to the increasing environmental stresses brought about by climate change (Soderman et al. 2015; Tiwari and Tripathi 2022).

3. MOLECULAR MECHANISMS OF SEED SENESCENCE AND OXIDATIVE STRESS

Post-harvest storage conditions exert a critical impact on maintaining seed quality and viability over time. However, even when seeds are stored under ideal temperature and humidity conditions, they deteriorate and lose their viability over time due to oxidative stress, lipid peroxidation, degradation of nutrient and protein structures, genetic changes in enzyme activities and chromosome structure, and increased respiration rate. Recent studies have elaborated the interactions of these degradation processes at the molecular level, especially the key role of

DNA damage and epigenetic changes in seed aging (Bewley et al. 2013; Sharma and Kaur 2021). Even under low-temperature storage conditions, seed viability cannot be preserved indefinitely. Therefore, slowing seed deterioration, increasing viability and enhancing resilience, especially to the additional stresses of climate change, are of great scientific and practical importance. Innovative approaches in this field open new horizons for seed conservation and restoration ecology (Walters et al. 2013; Probert et al. 2009).

Seeds also undergo a natural aging process. This deterioration is primarily caused by free radical-induced lipid peroxidation, inactivation or degradation of enzymes and proteins, loss of cell membrane integrity, and damage to genetic material like DNA (McDonald 1999; Zhao et al. 2023). In the process of senescence-related cellular degeneration, mechanisms involving free radical-scavenging antioxidative enzyme activities such as superoxide dismutase (SOD), peroxidase (POX), catalase (CAT) and glutathione reductase (GR) play a critical role in maintaining cellular integrity. It has been reported that such enzymatic activities reduce reactive oxygen/hydroxyl radical formation and that loss of seed viability is directly related to decreased antioxidant enzyme activities (Hosamani et al. 2013).

Extensive studies have shown that enzyme activities such as SOD, CAT, ascorbate peroxidase (APX) and glutathione peroxidase (GPX) can be used as important and reliable biochemical markers for determining seed quality and especially for predicting the long-term storage potential of seeds (Vertucci and Roos 1990; McDonald 1998; Corbineau 2012). Optimizing or genetically enhancing the activity of these enzyme systems offers promising strategies to increase seed resilience to climate change-induced stresses (Mittler 2002; Sharma and Kaur 2021). Non-enzymatic antioxidants such as β -carotene, ascorbic acid, α -tocopherol and reduced glutathione can also counteract the

harmful effects of ROS in plant tissues. The activity of these metabolites and antioxidant enzymes ensures high seed resistance to oxidative damage and minimizes cell damage (Alscher 1989; Tabatabaei 2015).

The aging process leads to an inevitable decrease in the germination capacity of seeds. This reduction may vary depending on intrinsic factors such as genetic structure, species and origin, and extrinsic storage conditions such as temperature and humidity (Agrawal and Kharlukhi 1985; Tilki and Alptekin 2005).

Temperature increases and unexpected humidity fluctuations caused by climate change further complicate efforts to optimize seed storage conditions (Walters et al. 2013). These external stressors can accelerate the aging process of seeds by challenging their intrinsic defense mechanisms. Therefore, updating more advanced storage strategies or seed banking techniques is imperative to conserve seed gene pools (Pukacka and Ratajczak 2007; Kulac et al. 2013; Colmer et al. 2023).

Exposure of the seed to adverse environmental influences can lead to increased oxidative stress-related degradation, which reduces the survival capacity of the seed (Shelar et al. 2008; Ren and Chen 2023). ROS causing oxidative stress increases can be observed depending on factors such as seed age, sampling time, harvest and post-harvest conditions (Bailly 2004; Güney et al. 2013). In this context, seed deterioration is a cumulative, irreversible and degenerative process (Kapoor et al. 2011; Bewley et al. 2013).

The biochemical changes accompanying structural deterioration of the seed include increased leakage of biomolecules from the cells and a decrease in the total amount of soluble sugars and proteins. While amino acid levels and protease activity increase during seed deterioration, some studies have also shown a decrease in α -amylase activity (Mitra et al.

1974; Agrawal and Kharlukhi 1987; Kalpana and Madhava 1997). However, recent studies have shown that these biochemical changes are not only due to the aging process. However, they may also result from the mechanisms by which seeds adapt to stress conditions and the influence of epigenetic factors in these processes (Bewley et al. 2013; Sharma and Kaur 2021).

As seeds age, due to the progressive increase in ROS, ROS attack polyunsaturated fatty acids in membrane phospholipids, causing fragmentation of long-chain fatty acids into smaller components. This alters membrane permeability, destroying membranes (Ratajczak et al. 2019). This membrane damage is a critical threshold that directly affects the storage capacity of the seed and significantly reduces its germination potential (McDonald 1999; Walters et al. 2013).

Lipid peroxidation is an autooxidation process. Final products of lipid peroxidation include a variety of relatively lipid-soluble compounds such as aldehydes, ketones, alkanes, carboxylic acids and polymerization products. Among the reactive aldehydes, malondialdehyde (MDA) causes peroxidation of organelles and plasma membranes as a result of oxidative stress (El-Maarouf-Bouteau and Bailly 2008; Cakmak et al. 2010) and is often used as a biomarker of lipid peroxidation (Ebene et al. 2019). In a study conducted by Pukacka and Ratajczak (2007) on European beech (*Fagus sylvatica* L.) seeds, ROS effects occurring in seeds due to senescence were examined; it was reported that oxidative reactions and membrane damage occurred in beech seeds during storage, increasing lipid peroxidation and MDA content. Such lipid peroxidation products cause membrane damage and further reduce seed viability by disrupting signal transduction pathways and inhibiting enzyme activities (Pukacka and Ratajczak 2007; Bewley et al. 2013).

Some of the increased levels of ROS during seed senescence are irreversible, leading to protein damage, aggregation and degradation, and disrupting protein structures. The most intensively investigated irreversible protein oxidation during seed degradation is carbonylation (Möller 2001). Recent research confirms that the level of protein carbonylation in seeds is an important aging biomarker directly related to storage duration and loss of viability.

Oxidative modifications of proteins irreversibly affect their catalytic activity and structural integrity, reducing the functional competence of the seed (Walters et al. 2013; Nguyen and Van Hung 2021). Free radicals, such as hydroxyls, react with carbohydrates to remove a hydrogen atom from carbon atoms by abstraction and produce carbon-centered radicals. This causes chain breaks in critical molecules such as hyaluronic acid (Devasagayam et al. 2004). Such carbohydrate damage can negatively affect germination energy by reducing the availability of energy reserves stored in the seed (Corbineau 2012; Bewley et al. 2013).

3.1. Enzymatic Antioxidants

3.1.1. Superoxide dismutase (SOD)

Superoxide dismutase (SOD) is a family of metal-containing enzymes found in all aerobic organisms. Under environmental stress conditions, SOD forms the first line of defense against ROS-induced damage. The enzyme neutralizes the superoxide radical by converting it into oxygen (O_2) and hydrogen peroxide (H_2O_2). This reaction, known as the Haber-Weiss reaction, eliminates the possibility of hydroxyl radical ($-OH$) formation, which is highly harmful in cells (Boguszewska et al. 2010). This detoxification process is vital against oxidative stress to which seeds are exposed during storage and at the beginning of germination (Bailly et al. 2008; El-Maarouf-Bouteau and Bailly 2008).

SODs are classified into three different isoenzymes according to the metal ion in their structure: Mn-SOD in mitochondria, Fe-SOD in chloroplasts and Cu/Zn-SOD in cytosol, peroxisomes and chloroplasts (Mittler 2002). The cellular localization of these isoenzymes allows them to play specialized roles in maintaining ROS balance in different cellular compartments. In a study on maize plants, an increase in the amount of SOD was observed in the deficiency of some essential plant nutrients (K, P, Mg, Ca, S or N) and new isoforms were identified (Tewari et al. 2004). There is also evidence that SODs have positive effects on root growth, germination, flowering and especially chloroplast development (Morgan et al. 2008; Myouga et al. 2008; Dvořák et al. 2020).

Recent research suggests that SOD activity is a critical marker and intervention target for slowing the loss of viability in the aging process of seeds and improving germination performance, especially under drought or heat stress caused by climate change. Studies on the manipulation of SOD genes for the conservation of seed gene pools and the development of stress tolerant varieties have also gained momentum (Song et al. 2024; Gill and Tuteja 2010).

3.1.2. Catalase (CAT)

Catalase (CAT), an iron-containing enzyme composed of four subunits, is found mainly in peroxisomes. It is responsible for the degradation of both H_2O_2 overproduced in peroxisomes, H_2O_2 formed during β -oxidation of fatty acids in glioxisomes, and H_2O_2 produced by Superoxide Dismutase (SOD) (Jaleel et al. 2009; Tuzet et al. 2019). Peroxisomes are the sites where CAT activity is concentrated against H_2O_2 generated by oxidative stress, purine catabolism, photosynthesis and β -oxidation of fatty acids (Frugoli et al. 1996). However, recent research has shown that CAT is also present in other subcellular regions such as the cytosol, chloroplast and mitochondria, although specific CAT activity has not yet been detected (Scandalios, 2005; Mhamdi et al.,

2010). Particularly in the context of seed physiology, not only the peroxisomal localization of CAT, but also its presence and activity in other compartments is considered critical for the maintenance of seed viability and the H₂O₂ balance at the onset of germination (Bailly et al. 2008).

CAT is known to be divided into three main groups in plants:

- CAT in the first group is concentrated in photosynthesizing tissues and actively removes H₂O₂ formed during photosynthesis (Willekens et al. 1994). This group is vital for maintaining photosynthetic efficiency, especially under climate change conditions such as intense light and high temperature (Flexas et al. 2004).
- The second group of CAT is produced significantly in vascular tissues and is implicated in lignin formation (Willekens et al. 1994).
- The third group of CAT removes excess H₂O₂ produced during the breakdown of fatty acids in seeds and young plants (Willekens et al. 1994). This third group plays a central role in the defense of seeds against oxidative stress during storage and germination, especially during lipid mobilization. Studies in the last 5 years have revealed that these specific CAT isoforms are key factors in determining the rate of seed senescence and germination success (Bewley et al. 2013; Zarnovican et al. 2019). Increasing temperatures caused by climate change may accelerate lipid metabolism in seeds, increasing H₂O₂ production, in which case the activity of the third group of CATs becomes even more critical for the maintenance of seed viability (Walters et al. 2013; Sharma and Kaur 2021).

3.1.3. Ascorbate peroxidase (APX)

Catalase (CAT) primarily detoxifies H_2O_2 in peroxisomes, whereas Ascorbate Peroxidase (APX) performs this function specifically in the cytosol and chloroplast compartments. APX reduces H_2O_2 to water and dehydroascorbate (DHA) using ascorbic acid (AA) as a reductant (Asada 1992; Gill and Tuteja 2010). This reaction is a key step of the Ascorbate-Glutathione Cycle (Foyer-Halliwel-Asada Cycle) and plays a central role in maintaining oxidative balance in plants (Ayan and Akin 2023).

The APX family consists of heterogeneous (diverse) isoforms such as cytosolic, mitochondrial, peroxisomal and chloroplastid (stromal and thylakoidal) based on different amino acid sequences and subcellular localization (Sharma and Dubey 2004). This wide range of isoforms increases the flexibility and efficiency of APX in maintaining H_2O_2 homeostasis in different cellular environments and under various stress conditions in plants (Mittler and Zilinskas 1999). Moreover, APX is a more efficient H_2O_2 scavenger under stress conditions due to its wider intracellular distribution and higher affinity for H_2O_2 (Das and Roychoudhury 2014).

It is also reported that APX and CAT enzymes minimize the potential damage of oxidative stress by inhibiting H_2O_2 and ROS synthesis (Bailly 2004). APX activity is vital in the detoxification of H_2O_2 accumulated in seeds, especially during drying and storage processes. Recent research has shown that APX is a critical biomarker for increasing seed vigor and longevity (longevity) and is a potential target for genetic engineering strategies. Increasing APX activity in seeds can significantly improve germination success and seedling health, especially under extreme heat and drought caused by climate change (Gill and Tuteja 2010; Walters et al. 2013; Song et al. 2024).

3.1.4. Monodehydroascorbate reductase (MDHAR)

Monodehydroascorbate Reductase (MDHAR) is responsible for the regeneration (renewal) of Ascorbic acid (AA) from short-lived monodehydroascorbate (MDHA) using Nicotinamide Adenine Dinucleotide Phosphate (reduced form of NADPH) as a reducing agent and consequently replenishing the cellular AA pool. During AA regeneration by MDHA, Ascorbate Peroxidase (APX) is co-localized with APX in peroxisomes and mitochondria where it removes H_2O_2 and oxidizes AA. In addition, MDHAR has several spatially restricted isoenzymes in chloroplasts, mitochondria, peroxisomes, cytosol and glioxisomes (Mittler 2002). The presence of these isoenzymes in different cellular compartments offers an effective defense mechanism against various sources of oxidative stress to which seeds are exposed during different stages of development and storage. Recent research suggests that MDHAR activity in seeds plays a critical role in desiccation tolerance and maintenance of long-term vigor (Bewley et al. 2013; Sharma and Kaur 2021).

3.1.5. Dehydroascorbate reductase (DHAR)

Dehydroascorbate reductase (DHAR) reduces dehydroascorbate (DHA) to AA using reduced glutathione (GSH) as an electron donor. This reaction is a vital step in the Ascorbate-Glutathione Cycle for the regeneration of AA (Eltayeb et al. 2007). DHAR is usually found in seeds, roots and shoots lacking chlorophyll (Das and Roychoudhury 2014). For seeds, DHAR plays an important role in repairing oxidative damage and maintaining antioxidant capacity, especially during storage and at the onset of germination. Genetic modification of DHAR activity in seeds can potentially increase seed viability under increasing

environmental stress conditions caused by climate change (Gill and Tuteja 2010; Walters et al. 2013).

3.1.6. Glutathione reductase (GR)

Glutathione Reductase (GR) is a flavoprotein oxidoreductase that uses NADPH as a reducing substrate to reduce oxidized glutathione (GSSG) to reduced glutathione (GSH). Reduced glutathione (GSH) is used to reduce AA from MDHA and DHA, where it is converted to its oxidized form (GSSG). The GR enzyme is primarily localized in chloroplasts, the cytosol, and mitochondria at lower concentrations (Das and Roychoudhury 2014). As a key enzyme of the Ascorbate-Glutathione Cycle, GR plays a critical role in maintaining cellular redox balance and sustaining the glutathione pool. GR activity in seeds is an important indicator of resistance to abiotic stresses, especially long-term storage and drought. Research in the last 5 years has confirmed GR as a potential biomarker and target gene for developing stress tolerant seed varieties (Sharma and Kaur 2021; Song et al. 2024).

3.1.7. Guaiacol Peroxidase (GPX)

Guaiacol Peroxidase (GPX) is a 40-50 kDa monomeric enzyme that detoxifies hydrogen peroxide H_2O_2 , which is overproduced both in normal metabolic processes and under stress conditions. GPX plays a critical role in lignin biosynthesis and supports defense mechanisms against biotic stress by catabolizing indole acetic acid (IAA) and utilizing H_2O_2 . GPX prefers aromatic compounds such as guaiacol and pyragallol as substrates as electron donors. It is also recognized as a key enzyme in the removal of H_2O_2 as it is active in intracellular (intracellular) (cytosol, vacuole), cell wall and extracellular (extracellular) regions (Asada 1999). Recent studies have revealed that the wide cellular distribution and substrate diversity of GPX is a fundamental mechanism for plant

adaptation to various abiotic stresses such as drought, salinity and metal toxicity (Gill and Tuteja 2010; Mittler 2017).

GPX activity in seeds is considered an important indicator in maintaining viability, especially during storage and managing oxidative stress at the onset of germination. Under increasing environmental stresses caused by climate change, the ability of seeds to modulate the activity of defense enzymes such as GPX directly affects their chances of survival and successful germination. In this context, genetic manipulation or enhancement of GPX activity is seen as a promising strategy to develop more resistant and climate-adapted seed varieties (Walters et al. 2013; Song et al. 2024).

3.2. Non-Enzymatic Antioxidants

3.2.1. Ascorbic acid (Vitamin C)

Ascorbic acid (AA) is the most abundant antioxidant in nature and is highly effective in combating oxidative stress. It is a potent antioxidant due to its capacity to donate electrons to a broad spectrum of enzymatic and non-enzymatic reactions (Barnes et al. 2002). Its primary function in plants under stress is to antagonize the harmful effects of H_2O_2 and other toxic oxygen species. It is synthesized in mitochondria and transported to other cells through a facilitated diffusion mechanism (Smirnoff 2000; Foyer and Noctor 2005). Preserving the ascorbic acid pool in seeds, especially during the drying and germination processes, is vital for maintaining redox balance and thus seed viability. Recent research highlights the potential of ascorbic acid supplementation or enhancement of endogenous synthesis to extend the storage life of seeds and improve germination performance under adverse environmental conditions (De Pinto and De Gara 2004; Walters et al. 2013).

3.2.2. Glutathione (GSH)

Glutathione (GSH) is a low molecular weight thiol tripeptide (γ -glutamyl-cysteinyl-glycine) found in high concentrations in almost all cellular compartments such as the cytosol, endoplasmic reticulum, mitochondria, chloroplasts, vacuoles, peroxisomes and even the apoplast. It is involved in a wide range of physiological processes such as cell differentiation, growth/division, programmed cell death (apoptosis) and senescence, regulation of sulfate transport, conjugation of metabolites, modulation of enzymatic activity, protein and nucleotide synthesis, phytochelatin synthesis and expression of stress-sensitive genes (Mullineaux and Rausch 2005).

As an antioxidant, GSH can function as a scavenger of ROS. As a low relative molecular mass antioxidant, GSH can capture H_2O_2 or react non-enzymatically with singlet oxygen superoxide anion and hydroxyl radical ($\cdot\text{OH}$). However, the central role of GSH as an antioxidant is its capacity to regenerate ascorbic acid, another potent hydrophilic antioxidant, through the Ascorbate-Glutathione (Asc-GSH) cycle (Krasnovsky 1998; Sharma et al. 2012). The level of the GSH pool in seeds is an important marker of seed vigor and stress tolerance. Recent studies suggest that GSH plays a critical role in DNA repair mechanisms and maintenance of protein integrity, especially during desiccation and senescence processes (Bailly et al. 2008; Sharma and Kaur 2021). Under environmental stresses caused by climate change, strategies targeting GSH synthesis or recycling in seeds hold promise for developing stress tolerant crop varieties (Gill and Tuteja 2010; Song et al. 2024).

3.2.3. α -Tocopherol

α -Tocopherol belongs to a family of lipophilic antioxidants that are efficient scavengers of ROS and lipid radicals, making them indispensable protectants and essential structural components of biological membranes. α -tocopherol has the highest antioxidant potential among the four isomers (α -, β -, γ -, δ -). Tocopherols are synthesized only by photosynthetic organisms and are therefore found only in the green tissues of plants (Holländer-Czytko et al. 2005).

Tocopherols protect the lipids and other membrane components of chloroplasts by reacting with O_2 and quenching excess excitation energy, characterized by structural and functional protective capacities. Tocopherol also acts as an effective free radical trap by terminating the chain propagation step of the Lipid Peroxidation (LPO) cycle (Igamberdiev et al. 2004). In seeds, especially oilseeds, α -tocopherol protects membranes from oxidative damage and extends storage life. Recent research indicates that tocopherol content in seeds strongly correlates with germination success and seedling development under stress conditions and could be a target for genetic improvement of seed quality (Walters et al. 2013; Zarnovican et al. 2019).

3.2.4. Carotenoids

Carotenoids are a family of lipophilic (oil-loving) antioxidants localized in the plastids of both photosynthetic and non-photosynthetic plant tissues. They are found not only in plants but also in microorganisms. Through their antioxidative activity, carotenoids protect photosynthetic machinery through four mechanisms: a) by reacting with LPO products to terminate chain reactions, b) by scavenging singlet oxygen O_2 and generating heat as a by-product, c) by reacting with triplet chlorophyll preventing singlet oxygen formation, and d) by dissipating excess excitation energy through the xanthophyll

cycle (Das and Roychoudhury 2014). In seeds, carotenoids play important roles, especially in maintaining membrane stability and as precursors of photosynthetic pigments during germination. The role of carotenoids in increasing the resistance of seeds to oxidative stress during drying and storage has been intensively investigated in recent years (Bewley et al. 2013; Sharma and Kaur 2021).

3.2.5. Flavonoids

Flavonoids are commonly found in the plant kingdom's leaves, flowers and pollen grains. According to their structural properties, they are divided into four classes: flavonols, flavones, isoflavones and anthocyanins. They play various physiological roles such as plant reproduction, pollen germination, pigmentation in seeds, flowers and fruits, and defense against plant pathogens. They also play a role in scavenging singlet oxygen and mitigating damage to the chloroplastic membrane's outer envelope (Fini et al. 2011; Agati et al. 2012). In seeds, flavonoids have versatile antioxidant functions such as protection against UV radiation, defense against pathogens and prevention of oxidative damage during aging. Recent findings point to the potential of manipulating (altering) flavonoid biosynthesis pathways to increase the stress tolerance of seeds (Gill and Tuteja 2010; Sharma and Kaur 2021).

3.2.6. Proline

Considered a potent antioxidant and an osmolyte, proline is widely used in different regions as a non-enzymatic antioxidant against the harmful effects of various reactive oxygen species (ROS). It is an effective scavenger of hydroxyl radical ($\cdot\text{OH}$) and singlet oxygen and can prevent damage caused by lipid peroxidation (LPO). Under stress conditions, proline accumulates in high amounts in plants due to increased synthesis or decreased degradation (Verbruggen and Hermans, 2008). Stress factors such as drought (Hare et al. 1998), salinity (Rhodes

et al. 2002; Munns 2002), low temperature (Naidu et al. 1991) and heavy metal exposure (Bassi and Sharma 1993; Sharma and Dietz et al. 2006) lead to proline accumulation.

In addition to acting as an osmolyte for osmotic regulation, proline contributes to the stabilization of subcellular structures (e.g. membranes and proteins) under stress conditions, scavenging free radicals and buffering the cellular redox potential (Ashraf and Foolad 2007). It can also act as a protein-competent hydrotrope, alleviating cytoplasmic acidosis and maintaining appropriate NADP⁺/NADPH ratios compatible with metabolism (Strizhov et al. 1997). Proline accumulation occurs in the cytoplasm, where it functions as molecular chaperones that stabilize the structure of proteins in everyday functioning and maintains the redox state of the cell by buffering cytosolic pH (Hare and Cress 1997). The accumulation of high proline levels in seeds, especially during drying and storage, is recognized as a key mechanism for enhancing seed viability and stress tolerance. Studies in the last 5 years suggest that proline metabolism in seeds plays a central role in seed adaptation strategies to extreme environmental stresses caused by climate change (Walters et al. 2013; Sharma and Kaur 2021).

4. BIOCHEMICAL EFFECTS OF AGING AND STRESS IN SEED: MECHANISMS AND MITIGATION METHODS

Oxidative stress has been associated with loss of strength in plant tissues. Loss of vigor in plant tissues is a fundamental physiological phenomenon observed when exposed to environmental abiotic and biotic stress under suboptimal external conditions. Seed degradation has been associated with electrolyte leakage, changes in the levels of proline, proteins, soluble sugars and phenolic compounds (Mirdad 2006). However, Golovina et al. (1997) reported that seeds of some orthodox

species stored for 20 to 30 years showed no change in protein secondary structure despite loss of membrane integrity. This points to the complex role of structural integrity of proteins in maintaining seed viability and the unique adaptations of some long-lived orthodox species (Walters et al. 2013). effects of oxidative stress are often expressed about the overall growth of the plant, including vigor, yield, biomass accumulation or primary assimilation events, and seed quality (Taiz and Zeiger 2010).

Seed senescence is closely linked to oxidative stress involving ROS, which are highly reactive, toxic and can cause degradative reactions of various bio-molecules over a long storage period (Kurek et al. 2019). In particular, how ROS affect intracellular and extracellular signaling pathways is one of the hottest research topics in seed physiology (Wojtyla et al. 2016; Soderman et al. 2015). Biological molecules, including carbohydrates, lipids, proteins, and polynucleic acids such as DNA and RNA, are the primary ROS targets during oxidative stress (Demidchik 2017; Mittler 2017). Therefore, the physiological lesions caused by ROS-induced seed senescence include loss of membrane integrity through lipid peroxidation, reduced respiration, enzyme inactivation and degradation, and genetic degradation, with particularly detrimental effects on seed viability, vigor and germinability (Mira 2011; Adetunji et al. 2021). The repair mechanisms of these damages and the effects of genetic variation on repair efficiency open new horizons in seed biotechnology (Bailly et al. 2008; Sharma and Kaur 2021). In addition, oxidative DNA damage caused by ROS is responsible for the aging of stock seeds (Akin et al. 2024; Akin and Ayan 2025). This is also responsible for the death of plants of great agricultural importance (Britt 1996). In Pukacka's (1991) study investigating changes in membrane lipid components and cellular antioxidant systems in sycamore-leaved maple (*Acer platanoides* L.) seeds due to aging for 7 years, increased solute leakage was associated with decreased phospholipid content (especially phosphatidylcholine) and increased free fatty acid content.

After one year of storage, a marked decrease in unsaturated fatty acids in the phospholipid fraction was observed. These findings again confirm how critical membrane integrity and lipid composition are for seed viability (Zarnovican et al. 2019).

Ayan et al. (2018), Taurus cedar (*Cedrus libani* A. Rich.) seeds obtained from central and marginal populations; Emphasizing that enzymes such as SOD, CAT, GuPX and APX are antioxidant defense systems that function as protective mechanisms for plants against stress conditions by controlling ROS levels in plant cells, from a practical point of view, they recommend that Adana-Pozanti and Mersin-Anamur population seeds obtained from the transition areas from the Mediterranean Region to Central Anatolia should be preferred due to their higher resistance to stress factors in improving the performance of afforestation in anthropogenic steppe areas in Central Anatolia. This study demonstrates the importance of local adaptations and genetic variation on seed stress tolerance and provides valuable guidance for seed source selection strategies (Ayan et al. 2018; Gill and Tuteja 2010).

Pukacka and Ratajczak (2007) examined the biochemical changes due to aging during long-term storage of European beech seeds. In their study, electrical conductivity, superoxide anion and H₂O₂, lipid peroxidation increased, while total phenolic content and alpha tocopherol content decreased in seeds stored at -10 °C for different periods (2, 5, 7 and 10 years). Therefore, the study demonstrated that ROS and lipid peroxidation products accompanied the loss of vigor and vigor during storage in seeds stored in cold storage at low temperatures. This emphasizes the need for continuous review of optimal conditions and regular monitoring of seed health, even for long-term seed banking (Walters et al. 2013; Pukacka and Ratajczak 2007). In their study, electrical conductivity and MDA increased with aging, while GR, SOD, CAT enzyme activities decreased, and the germination capacity of seeds

decreased after aging. These findings reinforce that the decrease in enzyme activity strongly correlates with the loss of seed viability as an indicator of oxidative stress (Kim et al. 2010; Corbineau 2012).

Seed senescence decreases the biological value of the seed, reducing its resistance to stress conditions and germination rate. However, priming can alleviate the adverse effects of senescence on seeds. Indeed, priming increases the respiratory activity of seeds (Halpin-Ingham and Sundstrom 1992) and the activity of SOD, CAT and GR enzymes is improved when priming is applied to aged seeds (Bailly et al. 1997). On the other hand, priming increases the activity of various antioxidative enzymes and the levels of various antioxidants such as reduced glutathione and ascorbate (Elkoca 2007). Recent studies show that priming treatments can significantly improve post-germination seedling development, especially under harsh environmental conditions (e.g. drought, salinity) by optimizing the redox balance in seeds (Ghassemi-Golezani et al. 2010; Jain et al. 2019).

The repair of DNA, RNA, proteins, cell membranes and the presence of enzymes during water uptake in seeds is the most important evidence of the repair mechanism. Increased moisture content during water uptake activates the repair mechanism. Respiratory activity is a fundamental part of the repair mechanism. Generally, the repair of seed deterioration caused by lipid peroxidation occurs during priming and water uptake. If the seeds are dried after the application, the advantages realized during repair are preserved until the seed germinates (Kaya 2008). The efficiency of these repair mechanisms may vary depending on the seed's genetic makeup and the priming application type (Walters et al. 2013; Sharma and Kaur 2021). Therefore, seeds with typical orthodox traits age more slowly and lose their viability gradually when stored compared to recalcitrant seeds. In this context, while 'priming' applications are in question to improve the aging and especially the low germination

capacity that occurs during storage in orthodox seeds, since the aging effects occur in a faster period during storage in seeds characterized as recalcitrant, 'coating' applications and storage life extension processes come to the fore in these types of seeds (López-Fernández et al. 2018). Advanced preservation techniques such as cryopreservation for recalcitrant seeds are also becoming increasingly important for conserving genetic diversity where traditional storage methods are inadequate (Pritchard et al. 2004; Walters et al. 2013).

5. CONCLUSION

Seeds are essential for life on Earth, serve as a main source of genetic diversity, and are a significant focus of research, particularly in forestry, due to their high nutritional value. Seeds, used as generative propagation material, have species-specific long-term storage needs that are vital for effective forestry management. Seeds can be subjected to natural senescence and oxidative stress induced by pre-harvest biotic stressors and post-harvest storage conditions. These stressors trigger various reversible and irreversible physiological processes in seeds, limiting the storage life of forest tree seeds.

It is important to study in detail the structural changes induced by ROS at the cellular level during the natural aging process of seeds and their effects on seed quality. This book chapter systematically reviews the oxidative stress factors associated with seed senescence, the defense mechanisms (antioxidant systems) that work against this stress, the detrimental effects of oxidative stress on macromolecules and the acceleration of this process by the effects of climate change. Understanding the effective functioning of defense mechanisms with different functions in plant metabolism against the destructive effects of oxidative stress will increase the efficiency and sustainability of forestry

practices such as seedling production, artificial rejuvenation and afforestation based on seed quality. Since quality seed material forms the basis of quality seedling production, seed quality in artificial rejuvenation and afforestation studies will directly affect the phenotypic characteristics of the seedlings to be grown and the success of subsequent forest growth and maintenance processes.

The effects of oxidative stress on seeds can be manifested at various levels such as reduced germination performance, morphological abnormalities, dysregulation of enzymatic activities and activation of antioxidant systems. The complex nature of oxidative stress mechanisms in seeds highlights the potential of research to improve seed tolerance to stress, optimize storage protocols and increase production efficiency. In this context, it is suggested that seed pretreatments (priming, coating, etc.) to be applied before or after storage, specific to the seed type, can regulate and/or ameliorate adverse physiological changes in seeds.

In conclusion, considering the decisive effects of oxidative stress in seeds on forestry practices, it is an inevitable scientific and practical necessity to conduct in-depth and advanced research in this field. By optimizing seed preservation strategies, this field of research supports the sustainable provision of high-quality production material essential for afforestation activities.

Future studies must analyze the molecular mechanisms of oxidative stress in seeds and effectively transfer the knowledge gained to forestry practice (through translational approaches). It is recommended that advances in scientific research be utilized to make plant breeding and forestry programs more efficient, resilient, and sustainable.

In addition, seed orchards, one of the main components of forest tree breeding in terms of forestry practice, should be reconsidered by

considering the transformative effects of climate change on forest ecosystems and genetic resources. In this context, updating the existing seed orchards regarding material diversity (number of clones, families), population representation and contribution to the gene pool is a priority requirement for modern forestry practices. By increasing genetic diversity in seed orchards, it will be possible to establish sustainable forests with high adaptability and resistance to changing environmental conditions. In the process of establishing new orchards in line with this goal, optimal and marginal populations in the natural distribution areas of species should be carefully monitored; genetic migration trends observed, especially at different elevation levels, should be analyzed, and new material selection should be carried out through joint orchard studies based on scientific foundations.

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Effect of UV-B Stress on Stomatal Characteristics on Some Landscape Plants

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1. INTRODUCTION

Due to industrial and technological developments, the increasing need for raw materials has caused underground mines to be extracted and used as raw materials in industry (Şevik et al. 2024; Isinkaralar et al. 2024). As a result, pollutant concentrations in air, water, and soil have increased significantly (Cebi Kilicoglu, 2024a,b; Tokatli et al. 2024; Mutlu et al. 2024; Koç et al. 2025a,b; Yucedag et al. 2025). In addition, using fossil fuels to meet energy needs has caused an increase in the CO₂ concentration in the atmosphere (Ertürk et al. 2024a). Thus, in this century, the structure of the atmosphere has changed for the first time in history due to anthropogenic sources (Çobanoğlu et al. 2023; Aricak et al. 2024). Global climate change is irreversible and can only be slowed down by taking precautions. Various scenarios are being developed to determine the possible changes that may occur in this process (Canturk et al. 2024). This change will affect all living things on Earth, as climate is a factor that directly or indirectly influences them all (Yucedag et al. 2019; Erdem et al. 2024; Koç et al. 2024). The group of organisms most vulnerable to global climate change will be plants, particularly forest ecosystems, due to their limited capacity for movement and migration in response to environmental shifts (Ertürk et al. 2024b). Forest ecosystems are particularly sensitive to environmental shifts, with trees facing some of the most severe consequences.

A key aspect of climate change is the rise in UV-B radiation levels, resulting from the degradation of the ozone layer in the upper atmosphere (10-30 km altitude) (Ozel et al. 2021). Industrial emissions, including chlorofluorocarbons, have significantly contributed to this thinning. Since the ozone layer filters harmful UV rays, its depletion allows more UV-B to penetrate, endangering ecosystems worldwide (Shaukat et al. 2013). Understanding how escalating UV radiation affects organisms is critical for developing mitigation strategies.

Research on the effects of UV-B radiation on vegetation has shown that increased exposure frequently results in reduced growth and developmental abnormalities in plants. Numerous studies have documented reductions in plant height, stem diameter, overall biomass, and foliage density across a wide range of plant species due to UV-B radiation (Liu et al. 2016; Fu and Shen 2017; Skórska et al. 2019). Additionally, shifts in seasonal growth cycles have been observed, indicating that UV-B radiation influences the timing of plant developmental processes (Stromme et al. 2019).

However, studies aiming to determine the effects of UV-B radiation on plants are still not adequate. Because the complex effects of UV-B on plants are not yet fully understood. This study aims to determine the invisible effects of UV-B radiation in some species.

2. MATERIAL AND METHOD

In the study, 10 broad-leaved plant species, most preferred in landscaping in Türkiye were sampled (Table 1).

Table 1. Species sampled in the study

Species label	Latin names
SP1	<i>Cotoneaster franchetti</i> Bois.
SP2	<i>Laurus nobilis</i> L.
SP3	<i>Ginkgo biloba</i> L.
SP4	<i>Betula pendula</i> Roth
SP5	<i>Cornus mas</i> L.
SP6	<i>Prunus laurocerasus</i> L.
SP7	<i>Lagerstromia indica</i> L.
SP8	<i>Hibiscus syriacus</i> L.
SP9	<i>Buddleja davidii</i> Franch.
SP10	<i>Forsythia viridissima</i> L.

The study was conducted using two-year-old seedlings. All treatments in the study were carried out under controlled conditions in the research greenhouse of the Faculty of Forestry in Düzce University. Seedlings were obtained from nurseries of the General Directorate of Forestry at the end of the vegetation season in 2022. The seedlings were taken to the research greenhouse, and the necessary maintenances were performed until the beginning of the treatments.

A cabin with a base area of 3 m x 3 m and a height of 2 m was prepared for UV-B treatment. The inner surfaces of the UV-B treatment cabin were covered with 12-micron aluminium foil to prevent leakage from outside to inside and from inside to outside. 4 Philips 40w/12 RS broadband UV-B lamps were placed inside the cabin for the UV-B source. When the project was in the implementation phase, the treatment period was determined for each dose amount applied within the scope of the study, and five different UV-B treatments were carried out: low ($8 \text{ kJ m}^{-2} \text{ h}^{-1}$), medium ($10 \text{ kJ m}^{-2} \text{ h}^{-1}$), strong ($12 \text{ kJ m}^{-2} \text{ h}^{-1}$), and very strong ($14 \text{ kJ m}^{-2} \text{ h}^{-1}$) with the control group.

Treatments were started in July 2022, and the seedlings were exposed to different doses of UV-B stress every 3 days. At the end of 45 days, 10 leaf samples from each plant were collected for scanning electron microscope (SEM) image analysis and elemental analysis. After the applications were made, the leaves on the branches were harvested.

Using the conventional pressing technique, the collected leaf samples were compressed and dried. The leaf samples were examined to make sure they were as clean as possible and free of mold and other contaminants. After that, they were taken to the lab and inspected using an electron microscope. The leaf samples were carefully removed from the lower surface of the leaf blade and positioned around the center for examination. A file with the extension ".jpeg" was created from the images that were obtained. After these processes were completed, the

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"ImageJ" computer measurement program performed leaf micromorphological measurements. With this program, stomatal length, width, and density (the number of stomata per mm²) were determined on the images from the lower surface of the leaf blade. The SPSS was used to assess the study's data using variance analysis and the Duncan test.

3. RESULTS

Stomatal width differences between species in terms of the treatments are presented in Table 2.

Stomatal width differs statistically significantly between species in all treatments. Within species, it differs statistically significantly ($P \leq 0.05$) in all species except SP8 ($P > 0.05$). While the lowest mean value was obtained in the low UV-B treatment, the highest mean value resulted from the control group.

Table 2. Stomatal width (μm) differences between species

Species	Control	Low	Medium	Severe	Very severe	F-value	Mean
SP1	15.19aB*	13.39aBCD	14.59aCD	27.01bF	13.53aBC	68.640***	16.74C
SP2	28.42bcD	23.87bcEF	31.66cE	14.43aD	28.20bcF	18.292***	25.32D
SP3	15.23bB	29.89cF	29.06cE	13.60abD	8.60aA	26.425***	19.28C
SP4	25.36cBC	12.12aBC	15.89bD	12.93a	24.76cE	42.222***	18.21C
SP5	21.54cB	7.27aA	7.80aA	7.25aA	16.36bCD	17.760***	12.04AB
SP6	27.02bD	16.68aD	17.34aD	18.14aE	18.36aD	13.372***	19.51C
SP7	14.49bB	9.91aAB	7.53aA	8.58aAB	10.28aAB	6.876**	10.16AB
SP8	9.46A	9.94AB	8.09A	10.06B	10.77AB	0.930ns	9.66A
SP9	14.09abAB	12.23abBC	9.55aAB	10.44aBC	16.54bCD	3.483*	12.57AB
SP10	11.80aAB	14.57bCD	12.17aBC	13.59abD	14.35bC	4.216*	13.29B
F-value	18.263***	23.542***	58.882***	40.695***	28.839***		20.081***
Mean	18.26b	14.99a	15.37ab	13.60a	16.17ab	2.910*	

* Uppercase letters indicate vertical groupings, while lowercase letters indicate horizontal groupings resulting from the Duncan test.

Stomatal length differences between species in terms of the treatments are given in Table 3. The changes in stomatal length are statistically significant ($P \leq 0.05$) between the species in all treatments. However, the change of stomatal length depending on the treatments is

not statistically significant in SP1, 8, and 9 ($P > 0.05$). Similarly, stomatal length changes depending on the treatments are not statistically significant ($P > 0.05$) regarding average values.

Table 3. Stomatal length (μm) differences between species

Species	Control	Low	Medium	Severe	Very severe	F-value	Mean
SP1	26.45BCD*	25.80CDE	25.22D	26.00A	24.87CD	0.210ns	25.67DE
SP2	30.32bCD	29.61bE	31.89bE	24.82aA	29.25bDE	9.105***	29.18EF
SP3	24.03bABC	49.08dF	39.97cF	23.80bA	15.97aA	30.701***	30.57F
SP4	30.01bCD	27.24abDE	29.69bE	22.42aA	46.58cF	18.727***	31.20F
SP5	34.45bD	15.02aA	14.92aA	17.13aB	30.14bE	7.362**	22.33BCD
SP6	30.71bCD	22.88aBCD	22.09aCD	25.99aA	23.13aBC	4.156*	24.96CD
SP7	19.83bAB	19.94bABC	16.52abAB	14.35aB	19.16bAB	3.402*	17.96A
SP8	18.17A	21.72BCD	20.79BCD	21.69A	20.09ABC	1.339ns	20.49AB
SP9	23.04ABC	21.67BCD	19.72BC	21.96A	22.95BC	0.554ns	21.87ABCD
SP10	20.17abAB	17.13aAB	21.82bcCD	22.58bcA	24.22cC	5.312**	21.19ABC
F-value	4.625***	20.740***	25.619***	6.478***	29.956***		10.952***
Mean	25.72	25.01	24.26	22.08	25.64	1.764ns	

** Uppercase letters indicate vertical groupings, while lowercase letters indicate horizontal groupings resulting from the Duncan test.

The differences in the stomatal density among species in terms of the treatments are given in Table 4. The differences in the stomatal density statistically significantly among species in terms of all treatments. However, the change depending on the treatments is not statistically significant in SP1, 6, 7, 9, and 10. Similarly, the difference in the stomatal density depending on the treatments is not statistically significant ($P > 0.05$).

Table 4. Differences in the stomatal density among species

4	Control	Low	Medium	Severe	Very severe	F-value	Mean
SP1	180.00B*	160.00AB	220.00BC	313.33C	226.67D	2.230ns	220.00BCD
SP2	260.00aCDE	293.33abCD	293.33abCD	240.00aBC	338.67bE	5.606*	285.07D
SP3	233.33bBCD	46.67aA	83.33aA	240.00bBC	306.67bD	23.149***	182.00AB
SP4	256.67bCDE	186.67bBC	200.00bBC	233.33bBC	53.33aA	12.297**	186.00ABC
SP5	73.33aA	413.33bE	380.00bDE	313.33bC	100.00aAB	9.773**	256.00CD
SP6	250.00BCD	200.00BC	186.67B	240.00BC	200.00CD	1.754ns	215.33BCD
SP7	306.67DE	340.00DE	393.33E	346.67C	373.33E	0.870ns	352.00E
SP8	326.67bE	186.67aBC	240.00abBC	160.00aAB	173.33aBCD	5.137*	217.33BCD
SP9	213.33BC	226.67BCD	66.67A	80.00A	133.33B	3.133ns	144.00A
SP10	260.00CDE	273.33BCD	253.33BC	253.33BC	220.00D	1.611ns	252.00BCD
F-value	9.638***	7.026***	12.899***	4.127**	16.881***		7.023***
Mean	236.00	232.67	231.67	242.00	212.53	0.358ns	

** Uppercase letters indicate vertical groupings, while lowercase letters indicate horizontal groupings resulting from the Duncan test.

When the elemental analyses were evaluated, there were significant differences between the results, and there could be differences exceeding tenfold even between samples taken from the same species. Therefore, the elemental analyses were excluded from the evaluation.

4. DISCUSSION

The study revealed that stomatal traits changed significantly among species. Studies have shown that stomatal characteristics vary depending on the species (Yücedağ et al. 2019). However, contrary to expectations, UV-B applications had no significant effect on stoma characteristics.

Rai and Agrawal (2022) stated that the axial stomatal density in *Wedelia chinensis* plants exposed to UV-B radiation increased. A study stated that stomatal length generally decreased in *Acer negundo* L. under the influence of UV-B, while it increased in Mountain Maple (Cobanoglu, 2023).

Previous studies show that stomatal movements are controlled by ethylene, but this is somewhat inconsistent with its observed effects on stomatal behavior (Tanaka et al. 2005, 2006; Watkins et al. 2014). UV-B radiation has been described in detail in many studies on stomata (Yigit et al. 2018; Sevik et al. 2021). Gitz et al. (2005) suggested that exposure to UV-B radiation may partially reduce drought stress due to changes in epidermal anatomy or wax deposition. Fraser et al. (2009) also stated that reduced water supply increases stomatal density and reduces leaf area.

It is stated that exposure to UV-B radiation damages proteins, DNA, cell membrane, chloroplasts and associated pigment system in plants (Shaukat et al. 2013), can suppress nutrient and water absorption affecting photosynthesis and growth of aboveground parts (Wang et al. 2013; Yu et al. 2014), and can disturb biochemical, morphological, and cellular factors (Kumar and Bhardwaj, 2019). Plant reactions to UV-B radiation are highly species-dependent (Newsham & Robinson, 2009; Li et al. 2010). This variability stems from differences in metabolic processes and physical structure. For instance, plants with thicker leaves or compact growth forms may experience less UV-B penetration compared to those with delicate foliage (Liu et al. 2011; Fu & Shen, 2017).

Beyond a certain threshold, UV-B becomes a significant stressor for plants, though their resilience depends on multiple traits. Factors like leaf dimensions, surface texture, and structural adaptations influence their ability to withstand radiation (Sevik et al. 2017; Özdikmenli et al. 2024). Environmental context also plays a role-studies note that UV-B effects shift with altitude (Watermann et al. 2020) and between ecosystems like forests and grasslands (Fu & Shen, 2017). For alpine species, local climate conditions largely dictate UV-B's impact (Fu & Shen, 2017).

UV-B triggers changes at both visible and microscopic levels in plants. These cellular and subcellular adjustments serve as biomarkers for environmental stress (Sevik et al. 2016; Yigit et al. 2023). One key response is heightened Phenylalanine ammonia-lyase (PAL) enzyme activity, which signals exposure to stressors ranging from UV-B to pathogens or toxins (Chmielowski et al. 2008; Fu & Shen, 2017). UV-B exposure can suppress growth, shrink leaves, thicken cuticles, and impair root development (Kobzar et al. 1998; Ravindran et al. 2008). Interestingly, when compared to other stressors like drought, UV-B often has a secondary effect.

On the other hand, it should not be disregarded that UV-B radiation may also positively affect plants. For example, although UV-B radiation harms plant tissues, it has been specified that it can stimulate the antioxidant accumulation and UV-protective molecules in specific plants used as food (He et al. 2019). Similarly, it has been determined that UV-B radiation can benefit Mediterranean pine species by partially alleviating the unfavorable influences of summer water deficit in *Pinus halepensis* and *Pinus pinea* (Petropoulou et al. 1995).

When the literature is reviewed, it is noticed that the impacts of UV-B strain on plant species' stomatal traits remain ambiguous. It is essential to study in detail whether this status depends on the plant species or varies according to the treatment. Two basic factors shape plant phenotypic characters. The first is genetic structure (Imren et al. 2021; Yücedağ et al. 2021a, b; Kurz et al. 2023), and the second is environmental conditions (Yucedag et al. 2021; Key et al. 2023). Stomatal characters are also shaped depending on these factors. Atmospheric conditions (Sevik et al. 2017; Cetin et al. 2018) and edaphic conditions (Xu and Zhou, 2008) change stomatal morphology. However, there are still many points that remain unclear on the subject.

5. CONCLUSION AND RECOMMENDATIONS

This study revealed that the changes in stomatal length, width and density showed significant differences among species. However, contrary to expectations, UV-B stress had no significant effect on stomatal characteristics. While stomatal size decreased in some species, no significant change was detected in others (SP1, SP6, SP7, SP9 and SP10). This situation suggests that the responses of plants to UV-B may vary depending on species.

The most striking result of the study is that the effect of UV-B radiation on stomatal characters alone is not clear enough. This situation shows that more precise results can be obtained when evaluating other stress factors (drought, temperature, and nutrient deficiency). In addition, considering that UV-B's effects on plants have negative (growth inhibition, DNA damage) and positive (such as increased antioxidant activity) aspects, a more comprehensive approach should be adopted in future studies.

In future studies, stomatal behaviors should be evaluated together with physiological parameters (such as photosynthesis rate and water use efficiency). In addition, the effects of UV-B in combination with other stress factors on plants under climate change scenarios should be examined. As a result, such studies will be an essential phase in understanding how plants can adapt to changing environmental conditions and developing sustainable landscape practices.

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Plant Adaptations and Defense Mechanisms under UV-B Radiation Stress

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1. INTRODUCTION

Ultraviolet (UV) radiation constitutes a significant component of the solar electromagnetic spectrum and is categorized into three main bands according to wavelength: UV-A (320–400 nm), UV-B (280–320 nm), and UV-C (200–280 nm). While the stratospheric ozone layer completely absorbs UV-C and most of the UV-B fraction, the majority of UV-A reaches the Earth's surface. As a result, UV-B radiation is considered the most biologically active and ecologically relevant portion of the UV spectrum, exerting the strongest influence on terrestrial ecosystems (Robson et al. 2019; Yadav and Sharma 2021).

Being sessile organisms, plants are continuously exposed to environmental fluctuations and thus inevitably experience both the harmful and regulatory effects of UV-B radiation. At high doses, UV-B leads to the formation of DNA lesions such as cyclobutane pyrimidine dimers (CPDs) and (6-4) photoproducts (6-4PPs), reduces photosynthetic capacity, promotes membrane lipid peroxidation, and triggers oxidative stress (Kataria and Singh 2023). Conversely, low levels of UV-B can function as adaptive cues, stimulating the accumulation of secondary metabolites such as flavonoids and anthocyanins, inducing photomorphogenic responses, and activating antioxidant defenses (Mansinhos et al. 2024).

At the center of UV-B perception lies the UV RESISTANCE LOCUS 8 (UVR8) photoreceptor. Upon UV-B activation, UVR8 interacts with COP1, leading to stabilization of the transcription factor HY5, which regulates genes involved in flavonoid biosynthesis, DNA repair, and stress tolerance (Binkert et al. 2014; Ulm and Jenkins 2015). Phytohormones including abscisic acid (ABA), jasmonic acid (JA), salicylic acid (SA), and ethylene further modulate UV-B responses through complex cross-talk networks, thereby enhancing the capacity of plants to adapt under multifactorial stress conditions (Rai et al. 2023).

Recent advances highlight that UV-B radiation induces broad-scale reprogramming beyond the cellular level, extending to transcriptomic, proteomic, and metabolomic landscapes. For instance, RNA-seq studies have documented significant upregulation of genes related to flavonoid biosynthesis (CHS, CHI, FLS) and DNA repair (PHR, UVR3) in response to UV-B exposure (Chen et al. 2022). At the ecological scale, UV-B modifies plant–microbe interactions, pollinator activity, and soil nutrient cycling, thereby contributing to shifts in biodiversity patterns (Zhou et al. 2020).

Taken together, UV-B radiation exerts a dual role in plant biology: functioning as a phototoxic stressor at high intensities while serving as an adaptive signaling cue at lower doses. In this context, the present chapter provides a systematic overview of the physiological, biochemical, and molecular effects of UV-B radiation in plants, with particular emphasis on protective and repair mechanisms, hormonal regulation, and broader agricultural and ecological implications.

2. EFFECTS of UV-B on PLANTS

2.1. Cellular and Molecular Effects

Ultraviolet-B (UV-B) radiation influences plant cells both directly and indirectly, leading to significant disruption of biomolecules such as DNA, proteins, and lipids. DNA is particularly sensitive, with photolesions including cyclobutane pyrimidine dimers (CPDs) and (6-4) photoproducts (6-4PPs) altering the three-dimensional structure of the double helix. These lesions obstruct replication and transcription, thereby threatening the fidelity of genetic information transfer. Their accumulation elevates mutation rates and interferes with normal cell-cycle progression (Chen et al. 2022).

Proteins are also adversely affected. Structural impairment of enzymes compromises metabolic processes, while denaturation of structural proteins undermines cellular organization. Membrane lipids, being rich in unsaturated fatty acids, undergo peroxidation, which increases permeability, disrupts ion homeostasis, and reduces membrane fluidity. The buildup of malondialdehyde (MDA), a product of lipid peroxidation, serves as an important biochemical marker of oxidative damage (Shen et al. 2010).

Exposure to UV-B also intensifies the production of reactive oxygen species (ROS) such as superoxide anion ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), and hydroxyl radical ($\bullet OH$). These highly reactive molecules damage DNA, proteins, and lipids, disrupting cellular redox equilibrium and triggering oxidative stress (Singh et al. 2017). Nevertheless, low levels of ROS act not only as damaging agents but also as signaling molecules, with recent studies showing that moderate ROS accumulation regulates gene expression and activates stress defense pathways (Kataria and Singh 2023). Hence, UV-B radiation serves a dual role: a destructive stressor at high levels and a signaling cue for adaptation at lower intensities.

2.2. DNA Damage and Mutations

UV-B radiation is among the most critical stressors threatening genomic stability in plants. Its primary effect on DNA is the formation of CPDs and 6-4PPs, both of which compromise helical integrity. CPDs occur more frequently and are comparatively easier to repair, whereas 6-4PPs are less common but introduce greater structural distortions, rendering them more mutagenic (Kumar et al. 2023). The accumulation of these lesions can inhibit replication and transcription, causing cell-cycle arrest, genomic instability, and the emergence of irreversible mutations. Such mutations include chromosomal breaks,

misrecombination events, and frameshifts, which exacerbate the genotoxic burden of UV-B.

Plants employ two major mechanisms to repair such damage. Photoreactivation uses photolyase enzymes activated by blue/UV-A light to directly reverse CPDs, representing an energy-efficient repair pathway (Jenkins 2009). In contrast, nucleotide excision repair (NER) is light-independent and involves the excision of damaged nucleotides followed by DNA polymerase-mediated replacement. Transcriptomic analyses have demonstrated that UV-B exposure markedly increases the expression of photolyase genes (*PHR1*, *UVR2*, *UVR3*) as well as NER-associated genes (Chen et al. 2022). These findings highlight that DNA repair is not only crucial for maintaining genomic integrity but also constitutes a central adaptive mechanism conferring UV-B tolerance.

Nevertheless, the efficiency of these repair mechanisms is not always sufficient. Prolonged or intense UV-B exposure can overwhelm the repair capacity, leading to the accumulation of irreversible mutations. Such mutations may disrupt protein synthesis and compromise vital physiological processes, including photosynthesis, growth, and reproduction. Therefore, DNA damage and mutation represent some of the most critical and long-term impacts of UV-B radiation on plant development.

2.3. Effects on Photosynthesis and Energy Metabolism

Photosynthesis is one of the most UV-B-sensitive physiological processes, with its impacts concentrated primarily on Photosystem II (PSII). The D1 and D2 proteins of PSII are particularly susceptible to UV-B, and their degradation disrupts electron transport, diminishing ATP and NADPH production (Piccini et al. 2020; Kataria and Singh 2023). As a result, carbon fixation capacity declines, leading to significant disruptions in energy metabolism. Reduced activity of

Rubisco further limits carbon assimilation and lowers photosynthetic efficiency. Meanwhile, chlorophyll and carotenoid degradation reduces light absorption, and structural alterations in thylakoid membranes directly impair electron transport.

UV-B also interferes with gas exchange. In irradiated leaves, elevated ABA induces stomatal closure, restricting CO₂ uptake (Kumari et al. 2023). Thus, photosynthesis is suppressed both by direct photonic injury and stomatal constraints. Additionally, ROS generated under UV-B exacerbate pigment breakdown, protein oxidation, and membrane lipid peroxidation, further aggravating photosynthetic impairment.

Nevertheless, plants activate adaptive mechanisms to mitigate these effects. Flavonoid and anthocyanin accumulation forms a photoprotective barrier, while the induction of heat shock proteins (HSPs) stabilizes thylakoid membranes and protects photosystem proteins (Mansinhos et al. 2024). However, under prolonged or intense exposure, these defenses become inadequate, and photosynthetic performance declines irreversibly.

Overall, UV-B imposes a dual influence: at high intensities it damages photosystems, pigments, and gas exchange, while at moderate levels it can stimulate protective responses that partially preserve photosynthetic activity.

2.4. Cell Membrane and Lipid Peroxidation

The plant cell membrane, due to its high content of unsaturated fatty acids, is highly vulnerable to UV-B-induced oxidative damage. ROS generated under UV-B initiate lipid peroxidation, a chain reaction that reduces membrane fluidity, increases permeability, and disrupts ion balance. Consequences include cellular dehydration, ionic imbalance, and metabolic disruption. The accumulation of MDA, a key product of

lipid peroxidation, serves as a biochemical indicator of oxidative stress (Shen et al. 2010).

Membrane impairment extends beyond structural damage to include disturbances in signal transduction. Dysfunction of plasma membrane receptors restricts intercellular communication, while damage to ion transport proteins destabilizes metabolic networks. Energy-dependent processes such as photosynthesis and respiration are therefore directly impacted by membrane instability. Recent findings emphasize the roles of antioxidant defenses and osmolytes such as proline and glycine betaine in preserving membrane stability under UV-B (Sharma et al. 2020). Furthermore, biostimulants including silicon and melatonin have been shown to protect membrane lipids, reduce MDA accumulation, and enhance UV-B tolerance (Rai et al. 2023).

Therefore, lipid peroxidation in cellular membranes is regarded as one of the earliest and most critical indicators of UV-B-induced stress. Preserving membrane integrity is vital not only for maintaining cellular homeostasis but also for sustaining photosynthetic efficiency and overall plant metabolic performance.

2.5. Secondary Metabolism and Photomorphogenesis

Plants defend themselves against UV-B radiation not only through DNA repair mechanisms and antioxidant defenses but also by enhancing the production of secondary metabolites. Compounds such as flavonoids, anthocyanins, phenolic acids, and tannins accumulate in the leaf epidermis and cuticle, functioning as natural UV filters that absorb incoming radiation. This accumulation reduces the penetration of harmful UV-B into intracellular organelles. In addition, the strong antioxidant properties of these metabolites contribute to the detoxification of UV-B-induced ROS (Binkert et al. 2014).

The biosynthesis of secondary metabolites is primarily regulated by the UVR8–COP1–HY5 signaling axis. Upon UV-B perception, activated UVR8 interacts with COP1, leading to the stabilization of the HY5 transcription factor. HY5 subsequently enhances the expression of genes encoding enzymes in the phenylpropanoid pathway, particularly chalcone synthase (CHS), along with CHI and FLS. This transcriptional activation promotes the accumulation of flavonoids and anthocyanins, which are essential for both photoprotection and the alleviation of oxidative stress (Hayes et al. 2014). From an agricultural perspective, this process has significant implications, as studies in tomato (*Solanum lycopersicum*) and grapevine (*Vitis vinifera*) have shown that UV-B exposure increases the accumulation of phenolic compounds and anthocyanins, thereby improving fruit quality (Martínez-Lüscher et al. 2016).

UV-B also modulates photomorphogenetic responses. Increased leaf thickness, reduced stem elongation, the development of purple/red pigmentation in leaves, and thickening of the cuticle layer are among the most prominent morphological adaptations observed under UV-B stress (Robson et al. 2019). These structural changes facilitate both the absorption of excess radiation and the storage of photoprotective compounds.

Recent findings suggest that secondary metabolite accumulation and photomorphogenetic adaptations extend beyond mere defensive functions, playing a role in plant–pollinator interactions. For example, changes in floral pigmentation can enhance pollinator attraction, indicating that low levels of UV-B may indirectly contribute to plant reproductive success (Zhou et al. 2020).

Thus, secondary metabolite production and photomorphogenesis represent not only defense mechanisms but also adaptive strategies that broaden plant resilience to UV-B.

2.6. Effects on Physiology and Reproductive Biology

UV-B radiation represents a significant environmental stressor that directly influences plant physiological processes and reproductive success. Depending on the exposure conditions, symptoms such as reduced root and shoot growth, smaller leaf surface area, chlorosis, and premature senescence are frequently observed. These physiological alterations reduce photosynthetic capacity and disrupt metabolic equilibrium. Additionally, oxidative stress generated under UV-B exposure perturbs hormonal balance. For instance, elevated ABA levels trigger stomatal closure, whereas JA and salicylic acid (SA) signaling enhance secondary metabolite production; however, these adjustments may simultaneously impose constraints on growth (Rai et al. 2023).

Reproductive biology is particularly sensitive to UV-B stress. Declines in pollen viability, delayed pollen tube elongation, and reduced germination rates lead to significant decreases in seed yield. Furthermore, damage to ovule and embryo development limits fertilization success, thereby reducing overall productivity. High-intensity UV-B can cause cellular impairments in reproductive tissues due to DNA damage and ROS accumulation, while in the long term, it may also threaten genetic diversity within plant populations (Kataria and Singh 2023).

On the other hand, low-dose UV-B exposure can indirectly enhance reproductive performance in some species. Experimental evidence indicates that moderate UV-B can alter flowering phenology, stimulate the accumulation of metabolites responsible for floral pigmentation, and increase pollinator attraction (Zhou et al. 2020). For example, the buildup of anthocyanins and flavonoids not only serves photoprotective functions but also generates visual and chemical cues for pollinators, thereby reinforcing plant–pollinator interactions.

2.7. Ecosystem-Level Effects

UV-B radiation exerts profound effects not only at the level of individual plants but also across entire ecosystems. Species with greater UV-B tolerance may gain competitive advantages over more sensitive species, ultimately reshaping community composition. Such shifts can alter the structure of both natural and agricultural ecosystems (Robson et al. 2019). Over time, this imbalance among species may lead to reductions in biodiversity and disruptions in habitat functioning.

UV-B also influences plant–pollinator interactions. Alterations in floral pigmentation, reductions in pollen production, and changes in nectar composition can negatively impact pollinator behavior. These disruptions reduce pollination success and consequently reproductive efficiency. The foraging preferences of key pollinators such as bees and butterflies are particularly sensitive to UV-B–induced changes in flowering time and floral coloration (Zhou et al. 2020). Thus, UV-B affects not only plant physiology but also the complex interaction networks among species within ecosystems.

Another critical ecosystem-level impact of UV-B is observed in soil processes. UV-B exposure increases the accumulation of phenolic compounds and lignin in leaf litter. These chemical modifications slow microbial decomposition and disrupt carbon and nitrogen cycling (Mansinhos et al. 2024). Reduced decomposition rates limit soil organic matter turnover and nutrient recycling, ultimately diminishing ecosystem productivity. Moreover, microbial diversity and functional capacity in the rhizosphere are also negatively affected by UV-B, weakening plant–microbe symbioses and indirectly impairing nutrient uptake and stress tolerance in plants.

Contemporary climate models suggest that fluctuations in stratospheric ozone may alter regional UV-B distribution, driving long-

term changes in ecosystem dynamics. In this context, UV-B should be regarded as a globally significant environmental factor capable of reshaping ecosystem functioning and interspecies interactions.

3. PLANT DEFENSE MECHANISMS AGAINST UV-B RADIATION

Plants are able to survive in challenging environments through the development of sophisticated defense strategies against diverse stress factors. Among these, UV-B radiation is one of the most pervasive and influential. This high-energy radiation from sunlight not only causes direct damage to DNA, proteins, and lipids but also induces oxidative stress through the excessive generation of ROS. To counteract these detrimental effects and maintain metabolic homeostasis, plants have evolved a multilayered defense system. These protective mechanisms include DNA repair pathways, antioxidant defense systems, the accumulation of secondary metabolites, hormonal regulation, and photoreceptor-mediated signaling networks specific to UV-B (Jenkins 2009; Binkert et al. 2014; Jordan 2017; Kataria and Singh 2023).

Importantly, these systems do not operate in isolation but are often interconnected through cross-signaling networks and genetic reprogramming, ultimately producing an integrated response. Thus, plant defenses against UV-B are not the outcome of a single mechanism; rather, they represent a multidimensional adaptive process involving perception, signal transduction, and the fine-tuning of downstream responses.

3.1. DNA Repair Mechanisms

UV-B radiation most frequently induces DNA lesions in plants in the form of cyclobutane pyrimidine dimers (CPDs) and (6-4)

photoproducts (6-4PPs). If left unrepaired, these lesions can lead to the accumulation of mutations, cell-cycle arrest, and ultimately cell death. To counter such genetic damage, plants have developed two major repair pathways: photoreactivation and nucleotide excision repair (NER). During photoreactivation, photolyase enzymes utilize blue/UV-A light to directly reverse CPDs, making it the most energy-efficient and widely employed DNA repair route in plants (Jenkins 2009; Rai et al. 2023). In contrast, NER is a light-independent process that involves recognition and excision of damaged nucleotides followed by accurate base replacement via DNA polymerase activity.

Recent transcriptomic and genetic studies have demonstrated that genes associated with DNA repair are strongly activated under UV-B exposure. For example, photolyase genes such as *PHR1*, *UVR2*, and *UVR3*, as well as NER-related genes, exhibit significantly elevated expression levels in irradiated leaves (Chen et al. 2022). Proteomic analyses further reveal the rapid synthesis of repair proteins following UV-B treatment. Nevertheless, prolonged or high-intensity UV-B stress can surpass the repair capacity, leading to the accumulation of irreversible mutations. Such genetic instability has broad physiological consequences, including declines in photosynthetic efficiency, stunted growth, and reduced reproductive success.

Therefore, DNA repair pathways represent the first line of defense against UV-B stress and are fundamental for maintaining genomic stability. However, the efficiency of these mechanisms is influenced by the duration and intensity of UV-B exposure as well as species-specific variability.

3.2. Antioxidant Defense Systems

UV-B radiation is a major inducer of oxidative stress in plants by stimulating the excessive generation of ROS such as superoxide anion

($\text{O}_2\bullet^-$), hydrogen peroxide (H_2O_2), and hydroxyl radical ($\bullet\text{OH}$). These molecules attack DNA, proteins, and lipids, thereby threatening cellular integrity. To mitigate such harmful effects, plants have evolved a highly developed antioxidant defense system consisting of both enzymatic and non-enzymatic components.

Among the enzymatic antioxidants, superoxide dismutase (SOD) plays a pivotal role by catalyzing the rapid dismutation of superoxide radicals into H_2O_2 . Subsequently, catalase (CAT) and ascorbate peroxidase (APX) decompose H_2O_2 into water and oxygen, thereby neutralizing its toxicity. Glutathione reductase (GR) contributes to the ascorbate–glutathione cycle, maintaining redox homeostasis (Sharma et al. 2020; Rai et al. 2023). Together, these enzymes cooperate to prevent ROS levels from exceeding critical thresholds.

The non-enzymatic antioxidants include ascorbic acid (vitamin C), glutathione (GSH), tocopherols (vitamin E), carotenoids, and phenolic compounds. These low-molecular-weight antioxidants directly scavenge free radicals, protect cellular structures, and act as cofactors that enhance the efficiency of enzymatic defenses.

Recent research indicates strong activation of these systems under UV-B stress. For instance, experiments in soybean (*Glycine max*) and tomato (*Solanum lycopersicum*) have shown significant increases in SOD and APX activity under UV-B exposure, contributing to chlorophyll preservation and reduced lipid peroxidation (Kumari et al. 2023). Transcriptomic analyses further confirm that antioxidant enzyme genes are regulated through UVR8-mediated signaling, underscoring the integration between photomorphogenic responses and defense pathways (Rai et al. 2023).

Thus, antioxidant defense systems constitute the primary protective barrier against UV-B-induced oxidative stress. By

safeguarding cellular components and enhancing overall stress tolerance, they play a crucial role in strengthening plant adaptive capacity under environmental stress conditions.

3.3. Secondary Metabolites and UV-B-Absorbing Compounds

One of the most important defense mechanisms plants employ against UV-B radiation is the enhanced production of secondary metabolites. Compounds such as flavonoids, anthocyanins, phenolic acids, stilbenes, and tannins play photoprotective roles by accumulating in the leaf epidermis and cuticle, where they act as natural “UV filters” that limit the penetration of harmful radiation into internal organelles. In addition, their strong antioxidant properties contribute to the detoxification of UV-B-induced ROS, thereby alleviating oxidative stress (Binkert et al. 2014).

The production of secondary metabolites is largely regulated through the UVR8–COP1–HY5 signaling axis. Following UV-B perception, UVR8 interacts with COP1 to stabilize the transcription factor HY5. HY5 subsequently upregulates genes encoding enzymes of the phenylpropanoid pathway, including chalcone synthase (CHS), chalcone isomerase (CHI), and flavonol synthase (FLS), thereby stimulating flavonoid and anthocyanin biosynthesis (Hayes et al. 2014). This accumulation not only provides photoprotection but also reinforces ROS detoxification capacity.

Recent research has underscored the agricultural relevance of this mechanism. For example, UV-B exposure in tomato (*Solanum lycopersicum*) fruits increases the levels of phenolic compounds and anthocyanins, enhancing fruit quality (Martínez-Lüscher et al. 2016). Similar effects have been observed in grapevine (*Vitis vinifera*) and broccoli (*Brassica oleracea*), where UV-B treatment enriched the phenolic profile and improved nutritional value. Such findings suggest

that controlled UV-B application could be strategically used to improve crop quality.

From an ecological perspective, increased levels of secondary metabolites also influence plant–pollinator interactions. Modifications in floral pigmentation and scent can enhance pollinator attraction, indicating that low-dose UV-B may indirectly contribute to reproductive success (Zhou et al. 2020).

Thus, secondary metabolites serve a dual role in UV-B defense: on the one hand, they provide biochemical protection to cellular structures, and on the other, they mediate ecological interactions that enhance plant adaptability.

3.4. Hormonal Regulation and Cross-Signaling Networks

UV-B radiation not only activates DNA repair and antioxidant defenses but also exerts profound effects on phytohormonal signaling pathways, which play central regulatory roles in stress perception and adaptation. Key plant hormones, including ABA, JA, salicylic acid (SA), and ethylene, are all integral to the orchestration of UV-B defense responses (Chgen et al. 2022).

UV-B exposure generally enhances ABA accumulation, which induces stomatal closure, helping to reduce water loss and control ROS production. However, this response simultaneously restricts CO₂ uptake, thereby limiting photosynthesis. JA signaling contributes to the biosynthesis of secondary metabolites such as flavonoids and terpenoids and promotes lignin deposition, thereby strengthening cell walls and enhancing photoprotection. SA activates antioxidant enzymes and systemic acquired resistance (SAR), mitigating oxidative damage caused by UV-B. Ethylene, in turn, accelerates leaf senescence and interacts with JA and SA pathways, modulating the balance of defense responses (Rai et al. 2023).

These hormonal pathways do not act independently; instead, they are integrated through cross-signaling networks. For instance, interactions between JA and SA influence both antioxidant defense activation and secondary metabolite biosynthesis, while ABA and ethylene interplay regulates stomatal behavior and senescence. Recent transcriptomic studies have revealed direct links between the UVR8–COP1–HY5 signaling cascade and hormonal pathways, highlighting that UV-B perception is not restricted to photoreceptor activity but is deeply integrated with hormonal regulation to form a multilayered defense network (Hayes et al. 2014; Zhou et al. 2020).

Therefore, hormonal regulation and cross-talk networks constitute a critical mechanism ensuring that UV-B responses are both rapid and coordinated. The efficiency of these networks directly determines the success of plant defense strategies and their long-term capacity to adapt under UV-B stress.

3.5. UV-B Photoreceptors and Signal Transduction Mechanisms

At the core of UV-B perception in plants lies UV Resistance Locus 8 (UVR8), a unique photoreceptor in which tryptophan residues act as natural chromophores that directly absorb UV-B photons. Upon photon absorption, the UVR8 homodimer dissociates into monomers, and the active form rapidly accumulates in the nucleus. There, UVR8 interacts with Constitutively Photomorphogenic 1 (COP1) and its partners, the SPA proteins, forming a complex that prevents the degradation of Elongated Hypocotyl 5 (HY5) and its close paralog HYH. Under normal conditions, HY5/HYH would otherwise be targeted for destruction by COP1. Stabilized HY5/HYH serve as central transcriptional regulators, activating a broad gene network linked to UV-B-specific photomorphogenic and defense responses. These include genes involved in the phenylpropanoid/flavonoid pathway (e.g., *CHS*, *CHI*, *FLS*), DNA

repair (*PHR1*, *UVR3*), antioxidant defense (*SOD*, *APX*), photoprotective proteins, and morphological adaptations. Thus, the perception-to-response cascade ($\text{UVR8} \rightarrow \text{COP1/SPA} \rightarrow \text{HY5}$ -centered transcriptional program) ensures rapid and coordinated responses to UV-B exposure (Binkert et al. 2014; Ulm and Jenkins 2015).

The termination of UVR8 signaling is also tightly regulated. HY5 induces the expression of RUP1 and RUP2 (WD-40 repeat proteins), which promote the re-dimerization of UVR8, thereby silencing the receptor through negative feedback. This cycle prevents excessive or unnecessary activation of photomorphogenic responses under low to moderate UV-B doses and acts as a fine-tuning mechanism responsive to environmental light conditions. Furthermore, the UVR8 pathway operates in integration with other photoreceptors: cryptochromes (blue light) and phytochromes (red/far-red light) influence COP1 accessibility and HY5 stability, ensuring that UV-B responses are synchronized with the broader spectral environment (Podolec and Ulm 2018).

Beyond the core photoreceptor pathway, UV-B signaling also propagates through a second messenger layer involving ROS, Ca^{2+} oscillations, nitric oxide (NO), and MAPK cascades (e.g., MPK3/MPK6). This network cross-talks with the HY5-mediated transcriptional program, allowing precise temporal and spatial regulation of antioxidant genes, enzymes of secondary metabolism, and repair proteins. At the same time, it intersects with hormonal pathways (ABA, JA, SA, ethylene, and in some contexts brassinosteroids and auxin). For instance, HY5 modulates auxin transport and expression of photomorphogenesis-related genes, thereby contributing to the fine balance between growth and defense under UV-B exposure.

A key conceptual distinction is that plant responses to UV-B operate through two interconnected arms:

(i) the UVR8-dependent photomorphogenic branch, which under low to moderate UV-B doses induces protective metabolite accumulation and developmental reprogramming; and

(ii) the damage-sensing branch, which under high doses activates repair and stress responses through CPD/6-4PP formation, oxidative stress signaling, NER/photoreactivation, HSPs, and stress-related transcription factors.

Depending on dose, duration, and tissue context, the outcomes of this dual system may be reinforced by epigenetic regulation (DNA methylation, histone modifications, small RNAs), creating long-lasting adaptive imprints. Thus, UV-B perception is not merely a light-sensing event but a central regulatory system that integrates spectral information, damage signals, hormonal pathways, and redox status into a unified network that optimizes both stress tolerance and plant development.

3.6. Molecular Adaptations and Genetic Regulation

UV-B radiation in plants not only triggers short-term physiological responses but also induces genome-wide adaptive modifications. These adaptations primarily involve the reprogramming of gene expression, the activation of stress-responsive transcription factors, and the engagement of epigenetic mechanisms. Central to this regulation is the UVR8–COP1–HY5 signaling axis, in which HY5 directly controls the transcription of genes associated with flavonoid biosynthesis (*CHS*, *FLS*, *PAL*), DNA repair (*PHR1*, *UVR3*, *RAD1*), and antioxidant defenses (*SOD*, *APX*), thereby providing comprehensive protection against UV-B stress (Chen et al. 2022).

Transcriptomic studies have revealed widespread alterations in gene expression following UV-B exposure. For instance, RNA-seq analyses in *Arabidopsis thaliana* demonstrated strong induction of genes related to both photoprotective metabolite biosynthesis and DNA repair.

Moreover, transcription factors from the WRKY, NAC, MYB, and bZIP families play critical roles in modulating UV-B-specific genetic responses. These regulators accelerate the synthesis of defense metabolites while ensuring that stress signaling remains balanced with growth processes.

Another key layer of molecular adaptation is mediated through epigenetic regulation. DNA methylation, histone modifications, and small RNAs—particularly microRNAs (miRNAs)—have been implicated in the long-term control of UV-B responses. For example, changes in DNA methylation patterns at certain defense-related loci following UV-B exposure have been reported to strengthen and prolong gene activation (Robson et al. 2019). Similarly, specific miRNAs such as miR156 and miR159 are known to regulate genes associated with secondary metabolite biosynthesis and photomorphogenesis under UV-B conditions.

Recent advances in biotechnology have further expanded the understanding and potential applications of these adaptive mechanisms. Tools such as CRISPR/Cas9 genome editing have enabled the targeted modification of UV-B tolerance-related genes, paving the way for the development of more resilient crop varieties (Rai et al. 2023). Hence, molecular adaptations and genetic regulation serve not only as key subjects of fundamental research but also as strategic avenues for achieving agricultural sustainability under the challenges posed by climate change.

4. AGRICULTURAL AND ECOLOGICAL PERSPECTIVES

UV-B radiation exerts both detrimental and beneficial effects on plants, thereby influencing agricultural productivity and ecosystem functioning in multiple ways. High-intensity and prolonged exposure

reduces photosynthetic capacity, suppresses growth, decreases leaf area, and results in substantial yield losses. Studies on cereals, legumes, and vegetable crops have shown that UV-B shortens the grain-filling period, reduces protein and carbohydrate accumulation, and negatively impacts overall crop quality (Kataria and Singh 2023). Conversely, low-dose UV-B exposure has been reported to stimulate the accumulation of secondary metabolites, thereby enhancing nutritional value, antioxidant capacity, and commercial quality in fruits and vegetables. For example, increases in phenolic compounds in tomato, anthocyanins in grapevine, and flavonoids in cabbage represent key adaptive responses that improve crop quality (Martínez-Lüscher et al. 2016).

From an ecological standpoint, UV-B functions as an important environmental signal that reshapes plant community structure and interspecific interactions. More tolerant species often gain a competitive advantage, whereas sensitive species decline, resulting in shifts in species composition and community dynamics (Robson et al. 2019). Changes in floral pigmentation, pollen viability, and nectar composition can directly affect pollinator behavior, potentially disrupting plant–pollinator interactions. Such effects are regarded as significant threats to the stability of natural ecosystems as well as to the productivity of agricultural systems.

The ecological impacts of UV-B extend beyond plant processes to include soil ecology and biogeochemical cycles. Elevated accumulation of phenolic compounds and lignin in leaf litter slows microbial decomposition, thereby disturbing carbon and nitrogen cycling (Mansinhos et al. 2024). These disruptions constrain soil organic matter turnover and nutrient recycling, ultimately lowering ecosystem productivity. Moreover, reductions in the diversity and functional capacity of rhizosphere microorganisms under UV-B exposure weaken

plant–microbe symbioses, indirectly impairing nutrient acquisition and stress tolerance in plants.

In recent years, biotechnological and agronomic approaches have opened new opportunities to mitigate the adverse impacts of UV-B stress. Biostimulants such as silicon, trehalose, ectoine, and melatonin have been shown to reduce UV-B-induced oxidative damage (Sharma et al. 2020). In addition, modern breeding strategies and CRISPR/Cas9-based genome editing technologies enable the development of UV-B-tolerant crop varieties (Rai et al. 2023). These approaches hold strategic importance for supporting agricultural sustainability under the increasing UV-B pressure associated with climate change.

Thus, from both agricultural and ecological perspectives, UV-B should be regarded as a factor that presents both risks and opportunities. On one hand, it can lead to yield losses and ecosystem imbalances; on the other, it may contribute to improved crop quality through secondary metabolite accumulation and targeted biotechnological interventions. Accordingly, future strategies for managing UV-B impacts will require the integration of fundamental research, agronomic practices, and biotechnological innovations.

5. CONCLUSION AND DISCUSSION

The effects of UV-B radiation on plants are multifaceted, encompassing both detrimental damage pathways and adaptive responses. At the cellular level, DNA lesions, protein denaturation, and lipid peroxidation represent the primary threats to tissue integrity. At the same time, ROS perform a dual role: while excessive accumulation induces oxidative stress, moderate levels act as signaling molecules that trigger the activation of defense-related genes (Kataria and Singh 2023). Yield reductions resulting from impaired photosynthesis and disrupted

reproductive biology present significant challenges to agricultural productivity. Conversely, the accumulation of secondary metabolites and photomorphogenic adjustments represent critical adaptive strategies that enhance plant resilience to environmental stress.

An integrated analysis of defense mechanisms reveals that DNA repair systems, antioxidant pathways, secondary metabolites, and hormonal cross-talk collectively produce a coordinated response to UV-B stress. Central to this integration is the UVR8–COP1–HY5 signaling axis, which orchestrates both photomorphogenic adaptations and metabolic regulation (Ulm and Jenkins 2015). Recent multi-omics studies, including transcriptomic, proteomic, and metabolomic analyses, emphasize that these defense pathways do not operate independently but rather as interconnected networks. These findings underscore that plant responses to UV-B are dynamic, continuously reprogrammed in accordance with environmental conditions.

Thus, UV-B radiation functions as both a limiting and a regulatory factor in plant growth, development, and reproduction. High doses predominantly result in DNA damage, photosynthetic impairment, and reduced fertility, while moderate levels can promote flavonoid accumulation, photoprotection, oxidative stress tolerance, and even improved crop quality. This duality highlights that UV-B should be understood not merely as a stress factor but also as a regulatory component of plant adaptation and ecological interactions.

Understanding plant responses to UV-B is critical not only for unraveling fundamental biological mechanisms but also for advancing agricultural strategies. Deeper insights into antioxidant defenses, secondary metabolite accumulation, and UVR8-mediated signaling networks will directly contribute to the development of crop varieties with enhanced UV-B tolerance.

6. FUTURE PERSPECTIVES

Global climate change and fluctuations in stratospheric ozone indicate that agricultural ecosystems will increasingly be subjected to elevated UV-B levels. In this context, future research is expected to focus on three major directions:

- **Omics-based approaches:** The integration of transcriptomic, proteomic, metabolomic, and epigenomic data to generate molecular maps of UV-B-specific adaptive responses.
- **Biotechnological applications:** The use of genome editing tools such as **CRISPR/Cas9** to target genes associated with UV-B tolerance, thereby enabling the development of more resilient crop varieties (Rai et al. 2023).
- **Field practices and biostimulant strategies:** The evaluation of protective compounds such as silicon, melatonin, trehalose, and ectoine under UV-B stress conditions, alongside the agronomic assessment of low-dose UV-B treatments as a potential means of enhancing crop quality (Sharma et al. 2020).

In addition, the impacts of UV-B radiation on plant–pollinator interactions, soil microbial diversity, and biogeochemical cycles remain insufficiently understood. Therefore, future ecosystem-based research should aim to unravel not only individual plant responses but also the cascading ecological consequences of UV-B exposure.

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Chapter 10

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Plant Stress Responses: Integrating Molecular, Physiological and Ecological Approaches I

Chapter 10

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Molecular and Physiological Adaptations to Heavy Metal Stress in Plants

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1. INTRODUCTION

Heavy metals include metal and metalloid groups that have a density greater than 5 g cm^{-3} . They are naturally found in very low concentrations in water and soil, are not biodegradable, and their potential to enter the human food chain and for accumulation in living organisms is quite high (Hawkes 1997; Zhang et al. 2019; Parlak and Dengiz 2025). Therefore, they are toxic or poisonous even at low concentrations. In this regard, the toxic effects of heavy metals pose a significant problem in terms of ecology, evolutionary processes, nutrition, and the environment.

The increasing concentration of heavy metals in soils is attributed to both anthropogenic activities and natural processes (Bayraklı and Dengiz 2020). Volcanic eruptions, weathering of metal-containing rocks, and metal corrosion are natural factors that cause heavy metal pollution. For instance, Kızılkaya et al. (2011) performed research to determine heavy metal concentration of Bafra Plain in Türkiye. They found the Ni concentration exceeded its maximum permissible concentration in the soils of the middle and northern parts of the plain; the soils of the great area in the region studied (85%) contained more than 50 mg/kg. This relatively high Ni concentration level is not a consequence of industrial or other anthropogenic pollution. It appears to be associated with the properties of the parent (volcanic) rock, which was a source of alluvium enriched in nickel. Also, heavy metal contamination caused by the leaching of metal ions from the soil, resuspension of sediments, and leaching of heavy metals causes serious environmental pollution (Shrestha et al. 2021). Non-natural sources of heavy metal pollution include thermal power plants, mines and quarries, the metal processing industry, nuclear power plants, high-voltage lines, fertilizers and pesticides used in agriculture, urban waste, and various industrial activities (plastic, textile, and paper processing) (Öktüren Asri et al. 2007; Seven et al. 2018).

Depending on their concentration levels, heavy metals in the ecosystem cause pollution, particularly in soil and water. This negatively affects all living organisms through the food chain. Heavy metals in soil and water are transferred from the root system of plants to their buds and leaves, particularly in crops, which threatens plant health. Therefore, it is crucial to determine the amount of heavy metals in soil and assess the risk of contamination, not only to avoid serious consequences such as reduced productivity, loss of product quality and plant death in plants at the first level of the food chain, but also to ensure human health and food safety (Hou et al. 2020; Bayraklı and Dengiz 2020).

Plants encounter many stress factors throughout their lives. Stress factors are divided into two groups: biotic and abiotic (Levitt 1972). Biotic stress factors are stress factors that develop as a result of infection by microorganisms such as fungi, bacteria, and viruses, and attacks by harmful animals. Abiotic stress factors are environmental factors such as heat, temperature, water, radiation, and chemical, magnetic, and electrical fields (Lichtenhaler 1996). Because plants, due to their sessile nature, cannot escape stress factors, they directly affect plants. This negatively impacts plant growth and development, disrupts living tissues, and damages plant organs, leading to plant death (Büyük et al. 2012). In this context, one of the most important factors causing abiotic stress in plants in nature is heavy metal pollution.

Zinc (Zn), copper (Cu), manganese (Mn), cobalt (Co), and nickel (Ni) are necessary for plant growth at low concentrations, but at high concentrations they begin to show toxic effects and become harmful to the plant (Fageria et al. 2010). Some of the many heavy metals, such as lead (Pb), arsenic (As), mercury (Hg), cadmium (Cd) or selenium (Se), are not essential for the overall growth of plants. The main reason for this is that these heavy metals do not have a specific physiological capacity in different plant species, so they exhibit toxic effects even at

low concentrations. In general, whether or not they are essential elements for plants, excessive accumulation of heavy metals in plant organs and tissues causes toxic effects. These toxic effects negatively affect many physiological processes in plants related to transpiration, stomatal opening and closing, water uptake, photosynthesis, enzyme function, germination, protein production, membrane integrity, and hormone balance (Öktüren Asri et al. 2007; Kaur 2021).

Human-induced heavy metal toxicity in plants can occur during agricultural production because the unconscious use of fertilizers during plant production can increase heavy metal concentrations in the soil. Different element concentrations were investigated for shoot, soil, root, and fruit samples of various vegetables. Increases in Cu and Zn concentrations in plant shoots were found most in pepper, followed by kale, radish, lettuce, and tomato. Cu and Zn concentrations were significantly accumulated in tomato plants compared with different sampled plants. It has been noted that Zn and Cu increase the uptake of pollutants by combining with different organic acids in root exudates to form different organometallic complexes. The presence of abundant Zn in the growth medium has led to increased toxicity among plants (Davis et al. 2021).

Oxidative stress, which occurs as a result of abiotic stress factors, is one of the most important causes of cellular damage in plants. Due to their sessile structure, plants have developed various regulatory mechanisms to adapt to different environmental stress conditions (Kar 2019). Therefore, plants also develop defense strategies against heavy metal stress through various regulatory mechanisms. Thus, examining the effects of heavy metals on plant metabolism is important to better understand the functioning of these defense strategies.

2. IMPACT OF HEAVY METALS AND METALLOIDS ON PLANTS

2.1. Zinc

Although defined as a heavy metal, Zn is a micronutrient and is crucial for human, animal, and plant health. Acting as a catalyst in some biochemical processes within plants, zinc plays a crucial role in many physiological processes, including nitrogen metabolism, starch formation, seed ripening, and hormone (auxin) production (Kantarci 2000; Gardiner and Miller 2008; McCauley et al. 2009).

There are many factors that affect zinc uptake in soil (pH, moisture, temperature, soil structure, etc.). Therefore, excess zinc-induced toxicity is rarely observed in plants. Among the most important environmental factors, the colloidal components of soil, both organic and inorganic (like clay), play a particularly critical role. The most active soil components in adsorption processes are mineral and organic colloidal particles of the solid soil phase, according to research. Other factors that affect the soil's adsorption capacity include pH, dissolved organic matter, ionic strength, and the kind and quantity of different metals. Bayraklı et al. (2023b) conducted a research in Black Sea Region, and they reported that Zn adsorption is directly impacted by clay and soil organic carbon, while clay is indirectly impacted by cation exchange capacity (CEC). Zinc, a heavy metal, is found in contaminated soil at levels between 150 and 300 mg kg⁻¹ (Nagajyoti et al. 2010). This situation can generally be seen in soils close to mineral deposits, and the zinc content in plants growing in these soils can be quite high. When soil zinc levels exceed threshold levels, plant root and leaf development is significantly reduced. Consequently, phosphorus and iron uptake from the soil decreases, and manganese and copper deficiencies can be observed in plant shoots (Kacar and Katkat 2010). Furthermore, hydrogen peroxide (H₂O₂) levels, MDA (malondialdehyde) content, and electrolyte leakage increase in the plant.

2.2. Copper

Copper (Cu) which is one of the heavy metals, ranks third among the most used metals in the world, and it is a micronutrient element for plants. Copper is an essential element not only for plant health but also for human and animal health (Jyothi 2020). Copper is an essential plant nutrient element for chlorophyll production, respiration, protein synthesis, carbohydrate metabolism, enzyme activation, and electron transfer in plants. It has a role in symbiotic nitrogen fixation (Gardiner and Miller 2008; McCauley et al. 2009). Copper affects the plant's ability to resist diseases and control plant moisture (Plaster 1992).

A copper content of 100 mg kg⁻¹ in soil and 15-30 mg kg⁻¹ in plant dry matter is considered the threshold value for copper toxicity. Toxic effects occur when soil copper content exceeds the threshold value. Copper toxicity, which leads to an imbalance in plant nutrient uptake, leads to increased reactive oxygen species (ROS) levels and inhibits nitrate uptake and upstream translocation (Huo et al. 2020). Toxic levels of copper in the soil make iron uptake difficult, leading to chlorosis symptoms resembling iron deficiency in plants. Other negative effects observed in plants include poor root and shoot development. Furthermore, excess copper negatively impacts molybdenum utilization (Boşgelmez et al. 2001; Kacar and Katkat 2010). For example, Bayraklı et al. (2023a) detected 2% of the soil samples (total 85) taken from hazelnut gardens total Cu concentration (maximum permissible concentration 3 mg.kg⁻¹) was above the tolerable value in cultivated soil for hazelnut fields of Giresun province.

2.3. Manganese

Manganese (Mn) is an essential nutrient for plants (Boşgelmez et al. 2001). It plays an active role in the activation of vital enzymes, water breakdown, chlorophyll formation, nitrogen metabolism, and

germination and fruit ripening processes in plants (Plaster 1992; Boşgelmez et al. 2001; Güzel et al. 2002; Gardiner and Miller 2008; Kacar and Katkat 2010).

In manganese toxicity, brown spots appear on older leaves, chlorosis forms around these spots, and nutrient deficiencies such as iron, magnesium, and calcium are observed. As a result of the toxic effect, auxin hormone formation decreases, photosynthetic processes are negatively affected, ROS accumulation increases, and fatty acid oxidation occurs (Boşgelmez et al. 2001; Kacar and Katkat 2010; Sevgi and Leblebici 2022).

2.4. Cobalt

Cobalt (Co) is an important component of vitamin B12 (cobalamin) and is involved in various biological processes (Simonsen et al. 2012; Paustenbach et al. 2013; Leyssens et al. 2017), and its levels as high as 100 mg kg⁻¹ in soil cause toxic effects in plants. Co toxicity in plants causes cell membrane disruption, growth retardation, and decreases in biomass, photosynthetic rate, chlorophyll, and carotenoid contents. Increases in ROS and MDA content are also observed (Pandey et al. 2009; Ozfidan-Konakci et al. 2020). It is hypothesized that this may indirectly cause apoptotic DNA damage (Gopal et al. 2003). Furthermore, under Co stress, iron metabolism in the plant is disrupted, leading to iron deficiency (Ozfidan-Konakci et al. 2020). Parmaksızoğlu (2022) notes that corn plants exposed to high concentrations of Co stress (300 µM) for 3 days experienced decreased growth and water content, and photosynthesis and nitrogen metabolism have also been impaired.

2.5. Nickel

Nickel (Ni) is a nutrient element needed for plant growth and development (Fageria 2009). It plays a role in nitrogen metabolism and in the structure of enzymes that convert urea to ammonium and carbon

dioxide (CO₂) during the seed germination phase (Gerendás et al. 1999; Gardiner and Miller 2008; Fageria 2009; McCauley et al. 2009; Kacar and Katkat 2010; Havlin et al. 2016).

High concentrations of Ni become toxic, and prolonged exposure to urea can cause serious damage to the environment, plants, humans, and microorganisms. Ni toxicity inhibits seed germination by negatively affecting amylase, protease, and ribonuclease enzymes (Ahmad and Ashraf 2011). It also causes a decrease in chlorophyll content, and thus negatively affects the photosynthetic mechanism (Sreekanth et al. 2013). It also causes oxidative stress in lipids, DNA, and proteins (Kasprzak et al. 2011). Ni inhibits mitotic cell division in root tip plants through the agglomeration reaction (L'Huillier et al. 1996).

2.6. Lead

Lead (Pb) is one of the most toxic heavy metals found in the Earth's crust and is not biodegradable (Sethy and Ghosh 2013). Therefore, it poses a serious global threat due to its toxicity to ecosystems and living organisms (Raj and Das 2023). Pb is considered one of the most hazardous heavy metals, contaminating soil and reducing its fertility, thereby negatively impacting plant life (Ahmad et al. 2021).

Seed germination, plant growth, chlorophyll synthesis, and metabolic activities are affected by Pb toxicity, and this causes a decrease in crop yield (Osman and Fadhllallah 2023). Moreover, due to Pb stress, oxygen radicals (oxygen species), which are responsible for the excessive production of ROS, occur in plants, which causes damage at the cellular level in plants (Berni et al. 2019), and cell division is delayed (Kumar et al. 2017).

2.7. Aluminum

The aluminum (Al) element does not have an important biological role in the growth and development of plants. At acidic pH (~5–5.5), Al^{3+} becomes dangerous for plants (Figure 1) (Emamverdian et al. 2015).

Al toxicity is first detected in the root system, where absorption occurs. Al toxicity reduces root cell division, thereby inhibiting root elongation, and as a result, root tips become deformed. It also inhibits enzymes responsible for sugar accumulation in cell walls, reduces cytokinin formation and transport, negatively affects DNA formation, and alters the structure and function of cell membranes. This restricts water and nutrient uptake and transport, which in turn leads to growth retardation and cell cycle arrest (Foy et al. 1992). Consequently, necrotic spots appear at leaf tips, stem bruising occurs, young leaves curl, stomatal aperture decreases, and petiole death occurs (Wang et al. 2006; Bian et al. 2013). Furthermore, Al toxicity can cause nutrient imbalances (Kochian et al. 2004).

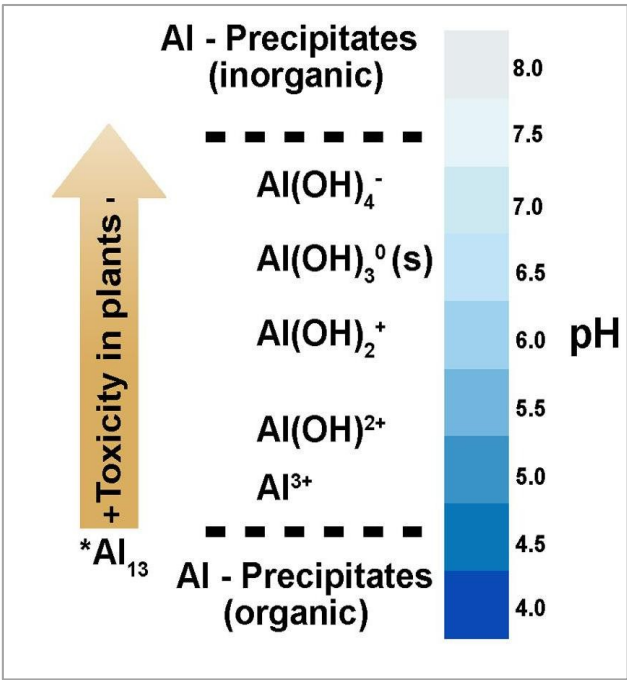


Figure 1. Chemistry of Aluminium with changing soil pH (Quintal et al. 2017)

2.8. Arsenic

Arsenic (As) is a highly toxic and carcinogenic heavy metal that causes environmental pollution. Therefore, toxicity in As is a global environmental, agricultural, and health problem (Abbas et al. 2018). Arsenic not only contaminates groundwater, it also negatively impacts crop productivity in agricultural production and contaminates the entire food chain (Verma et al. 2016). Exposure of plants to As, even at very low concentrations, can cause numerous morphological, physiological, and biochemical changes in the plant (Figure 2) (Abbas et al. 2018).

Trivalent arsenite (AsIII), which is the most toxic form of As, causes DNA cleavage and thus intrachromosomal homologous

recombination (Helleday et al. 2000). As is also responsible for the inhibition of some important respiratory enzymes by binding to neighboring thiols of pyruvate dehydrogenase and 2-oxo-glutarate dehydrogenase (Verma et al. 2016). As toxicity slows down plant growth, while MDA causes an increase in H_2O_2 levels and electrolyte leakage, resulting in necrosis in older leaves and chlorosis in fully developed young leaves (Kaya et al. 2020). Both AsV and AsIII forms lead to ROS formation, which affects antioxidant defense systems and carbon, nitrogen, and sulfur metabolism (Finnegan and Chen 2012).

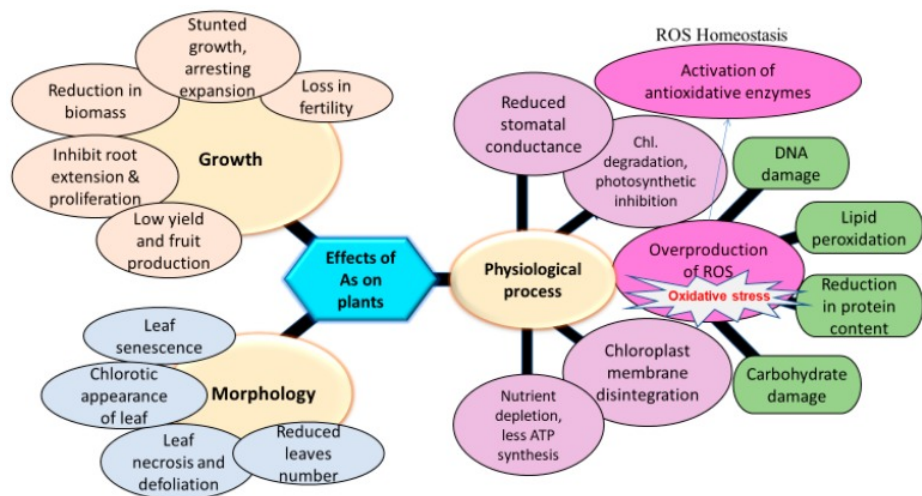


Figure 2. Arsenic toxicity in plants (Abbas et al. 2018).

2.9. Cadmium

Cadmium (Cd) is a highly phytotoxic heavy metal due to its hydrophilic structure, and a Cd concentration of $5\text{--}30\text{ mg kg}^{-1}$ is considered toxic for plants (Haider et al. 2021). Plants can take up Cd from soil or water and enrich it in their roots and shoots (Andresen and Küpper 2012). Even at very low concentrations, Cd can disrupt the

Calvin cycle, inhibiting the utilization of CO₂ and the functioning of some enzymes involved in the processing of carbohydrates and nitrogen (Gill and Tuteja 2011). This causes stunting, leaf curling and warping, and chloroplast structure disruption (Sharma and Dubey 2006). Cd concentration alters basic biochemical reactions, leading to metabolic disorders (Xu and Shi 2000; Epstein and Bloom 2005). Due to its toxic effect, MDA content, H₂O₂ levels, and membrane damage increase (Shaari et al. 2022). Inhibition of DNase (deoxyribonuclease) and RNase (ribonuclease) activities and alteration of nucleolar structure have also been stated in Cd-induced phytotoxicity in plants (Duan and Wang 1992).

2.10. Chromium

Chromium (Cr), which has a wide range of uses in industry, is an important pollutant, and the solubility of Cr (VI) in water is a major threat to biota (Nieboer and Richardson 1980). Cr is not an essential nutrient for plants (Huffman and Allaway 1973). Cr concentrations above 3,8 mg kg⁻¹ are toxic to plants (Ahmad et al. 2020). Cr toxicity negatively affects plant growth and development by reducing biomass production and concentrations of photosynthetic pigments. It can also cause ROS production, electrolyte leakage, and increases in MDA and H₂O₂ levels (Dube et al. 2003). Physiological and biochemical changes, including decreased germination, root growth, seedling growth and development, inhibition of biomass, leaf chlorosis, and necrosis, are among the symptoms of Cr (III, VI) toxicity in plants (Oliveira 2012; Stambulska et al. 2018) (Figure 3). Studies have indicated that Cr (III, VI) toxicity affects plants, including cereals, legumes, vegetables, forage crops, aromatic and medicinal plants and trees (Sanità di Toppi et al. 2002; Jun et al. 2009; Shanker et al. 2009; Barouchas et al. 2014; Park 2020).

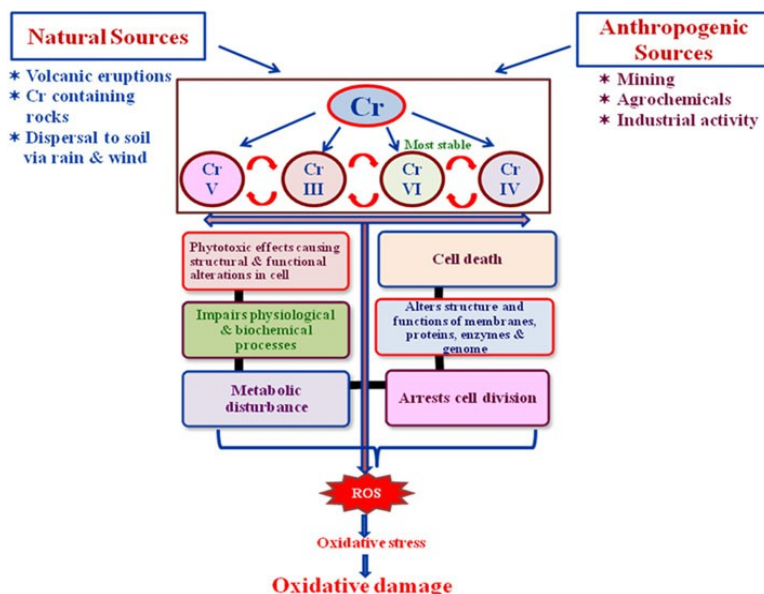


Figure 3. An overview of Cr sources and toxic effects on plant systems (see text for details). ROS (Singh et al. 2013)

2.11. Mercury

Mercury (Hg) is a heavy metal with significant toxicity. Due to its persistent structure and bioaccumulation properties, it poses a major threat to the ecosystem's food chain (Bhattacharya 2018). Hg toxicity negatively affects photosynthesis and inhibits the chloroplast and mitochondrial electron transport chain. Hg has a phytotoxic effect, disrupting water channels in the cell membrane and inhibiting water uptake through the root (Zhou et al. 2009). In plants exposed to Hg stress, free radicals are formed, causing cellular damage and various physiological abnormalities (Zhou et al. 2007).

3. HEAVY METAL TOLERANCE IN PLANTS: PHYSIOLOGICAL AND MOLECULAR ADAPTATIONS

Plants come across many stress factors while obtaining the micronutrients, which are necessary for their growth and development, from the soil throughout their life cycle. It leads to physiological and biochemical damage to plants, particularly when they are exposed to heavy metals. Molecular and cellular levels of heavy metal toxicity are composed of protein and enzyme denaturation, functional group blockage, displacement of essential metals, and membrane disruption (Rascio and Navari-Izzo 2011). All these alterations can result in the inhibition of photosynthesis and negative impacts on respiration (Figure 4) (Ali et al. 2013). Methylglyoxal (MG) is another toxic compound that has recently been found to increase under various stresses (Ali et al. 2013; Sytar et al. 2013). MG production can affect different mechanisms of plants, such as the antioxidant defense system and photosynthesis, and this situation can lead to an intensification of ROS production (Viehweger 2014). Oxidative stress can disrupt macromolecules (such as proteins), membranes, and DNA chains and cause plant death (Figure 4) (Flora et al. 2008; John et al. 2012).

Plants develop defense strategies through physiological and molecular mechanisms to mitigate or inhibit the harmful effects of heavy metal stress (Büyük et al. 2012; Sevgi and Leblebici 2022). Plants use various strategies to struggle against heavy metal stress. They develop avoidance and tolerance strategies. When the plant can restrict heavy metal absorption, it uses the avoidance strategy. In this process, mechanisms such as the formation of metal-ligand complexes in root exudates and changes in pH in the rhizosphere play a significant role in the defense strategy developed by plants. In the avoidance strategy, plants seek to get away from the heavy metal through biosorption onto cell walls, extracellular precipitation, reduced uptake, and increased

efflux. However, when the plant can survive under high heavy metal concentration, it uses the tolerance strategy as a result of the heavy metals penetrating the plant root cells. The plant does this by chelating amino acids, GSH (Glutathione), metallothioneins (MTs), and organic acids or by enhancing compartmentalization with vacuoles, stress-related protein synthesis, and activation of antioxidant defense mechanisms. Thus, the toxic effects of heavy metal ions are reduced and oxidative stress is combated (Hatata and Abdel-Aal 2008; Ali et al. 2013; Bielen et al. 2013; Dalvi and Bhalerao 2013).

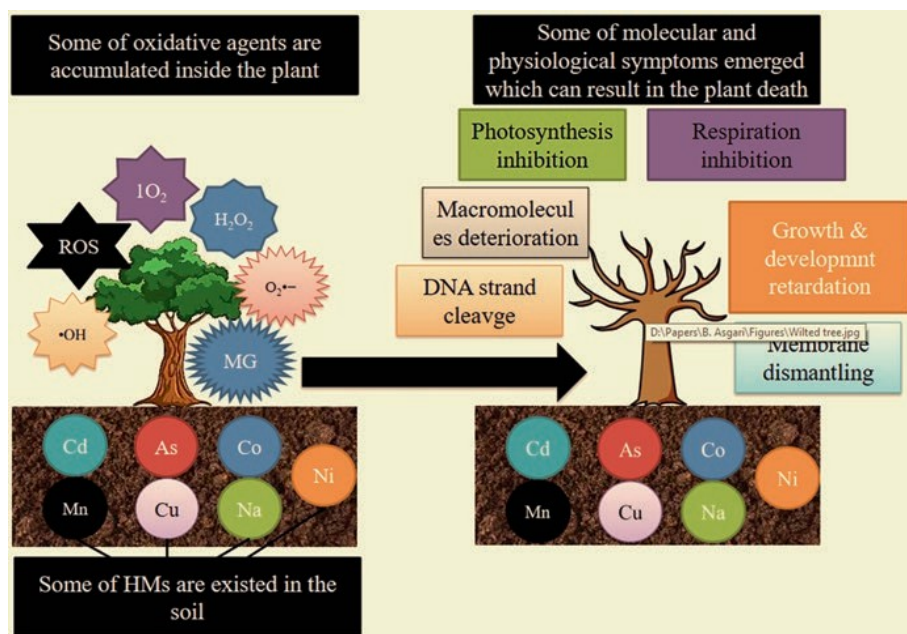


Figure 4. The negative effects of heavy metals on plants (Delangiz et al. 2020).

The perception and response of heavy metals in plants is the result of a physiological and molecular signaling network. Therefore, it is necessary to examine the genetic fundamentals to understand these

signaling pathways and each mechanism (DalCorso et al. 2010). Plants, exposed to heavy metals, can use different mechanisms. Adaptive and constitutive mechanisms are the two main mechanisms used to cope with excessive amounts of heavy metals in the environment (Meharg 1994). In general, signaling pathways are calcium-dependent signaling, ROS signaling, MAPK (Mitogen-Activated Protein Kinase) cascade, and hormone signals. In calcium-dependent signal transduction, in case of exposure to high amounts of heavy metals, heavy metals change the stability of calcium channels, and this situation can cause more calcium to enter the cell. Changes in the calcium level within the cell are detected by calcium-sensing proteins such as CDPK (Ca²⁺ dependent protein kinases), CaM (calmodulins), and CBL (calcineurin B-like proteins), enabling signal transmission. Thus, the expression of stress-related genes increases (Chaturvedi et al. 2020). Recently, it has been determined that heat shock proteins (HSPs) accumulate in plants under heavy metal exposure (Zhao et al. 2011). In the study conducted by Sun et al. (2006), higher proline accumulation was found out in *Solanum nigrum* L. (a Cd hyperaccumulator) compared to *Solanum melongena* L. (a non-Cd accumulator). This may prove the role of proline in the detoxification processes of heavy metals. Some chelating compounds, such as nicotinamine, phytosiderophores, and organic acids, are released by plant roots and can affect the absorption of heavy metals (DalCorso et al. 2010).

MAPKs are one of the highly significant and evolutionarily conserved signaling molecules in response to various abiotic stress responses in plants. The MAPK cascade consists of three kinases (MAPKKKs, MAPKKs, and MAPKs) that regulate sequential phosphorylation reactions, starting from receptors on the cell membrane and extending to target proteins. The MAPK cascade regulates numerous cellular processes by transmitting signals associated with stress. Among various abiotic stress factors, heavy metals can stimulate this signaling

process. MAPKs can be activated directly by a specific metal ligand or indirectly by ROS produced by heavy metals. Several studies have found activation of the MAPK cascade in response to various heavy metals, including Cd, Cu, and As (Jonak et al. 2004; Yeh et al. 2007; Rao et al. 2011; Smeets et al. 2013; Li et al. 2022). For instance, four different MAPKs (MMK2 [Medicago mitogen-activated protein kinase 2], MMK3 [Medicago mitogen-activated protein kinase 3], SAMK [Stress-activated MAP kinase], and SIMK [Salt-induced MAP kinase]) were activated in *Medicago sativa* L. under Cu and Cd stress. Cu stress activated MAPK production faster than Cd stress (Jonak et al. 2004). Membrane exclusion, metal immobilization, limitation of uptake and transport, chelation, activation of stress proteins, and production of polyamines and signaling molecules such as nitric oxide and salicylic acid have also been noted against heavy metal stress in plants (Zhu et al. 2011).

A significant situation observed in plants exposed to heavy metal stress for a long time is oxidative stress, which develops due to the increase in ROS such as H₂O₂ and hydroxyl radical (•OH). Due to ROS activated by heavy metal stress, respiration and photosynthesis processes are negatively affected as a result of the decrease in the amount of chlorophyll in the leaf and the disruption of the electron transport chain. As a result of heavy metal stress, plants slow down root and shoot development by increasing ethylene levels, reduce CO₂ fixation and limit sugar transport (Loureiro et al. 2006; Hu et al. 2007; Gupta et al. 2009; Ghori et al. 2019). Inactivation of enzymes that are important for plant growth and development causes a decrease in the energy production capacity of plants (Buchanan et al. 2000)

This high level of ROS causes oxidative stress in cells, disrupts the structure of biological membranes and macromolecules, and leads to genotoxicity through lipid peroxidation (Mahapatra et al. 2020). The

antioxidative defense system senses these high ROS levels and is thus regulated by antioxidants detoxifying ROS (Huang et al. 2019). Regulation of superoxide dismutase (SOD) enzyme plays an important role in the survival of plants in combating oxidative stress caused by heavy metal stress. SOD converts the O_2^- anion into less reactive O_2 and H_2O_2 , and it is classified into three groups as Fe-SOD, Mn-SOD and Cu/ZnSOD according to the metal cofactors present in its active site (Bowler et al. 1992; Del Río et al. 2018).

The main cause of damage due to oxidative stress is the production of ROS as a product of the electron transport system (ETS) in mitochondria, which can be prevented by an antioxidant system. While the SOD enzyme destroys superoxide radicals in the antioxidant system, the catalase enzyme catalyzes the conversion of H_2O_2 , which is present as ROS in the cells, into water and oxygen (Beyer and Fridovich 1987). Glutathione peroxidase preserves the stability of the cell membrane by scavenging reactive radicals. Ascorbate oxidase takes part in a redox system with ascorbic acid and balances glutathione and Nicotinamide Adenine Dinucleotide Phosphate (NADPH) levels (Lee et al. 2007). Polyphenol oxidase catalyzes the aerobic oxidation of some phenolic compounds to quinones and develops a defense mechanism against water stress via H_2O_2 in chloroplasts (Sarvajeet and Narendra 2010). Although H_2O_2 is not a free radical, it plays a significant role in the formation of free radicals as a reactive type. In the presence of transition metals such as Fe^{+2} and Cu^+ , the Fenton reaction and, in the presence of superoxide radicals, the Haber-Weiss reaction form the $\bullet OH$. The $\bullet OH$ is best described as a radical with oxidizing power and can interact with DNA, proteins, lipids, amino acids, metals, and glucose (Eseryel and Yalçın 2022).

Heavy metal toxicity, which is one of the main factors of oxidative and genotoxic stress, causes lesions in the DNA double helix, and

irreparable damage can disrupt the stability of the genome (Dutta et al. 2018). Heavy metals can also act as premutagenic agents. Heavy metals can reach the nucleus and cause various DNA damages, including DNA strand breaks, rearrangements, and depurination. These chemical reactions are indicators of oxidative DNA attack (Kasprzak 1995). Molecular tools such as RAPD (Random Amplified Polymorphic DNA) and PCR, which are molecular markers, are used for the direct detection of DNA damage at the genomic DNA level caused by heavy metals.

Against heavy metal stress, various plasma membrane transporters have an important role in the uptake and balancing of heavy metals. Proteins such as ABC (ATP-Binding Cassettes) transporters, NRAMP (Natural Resistance-Associated Macrophage), CDF (Cation Diffusion Facilitators), ZIP transporter proteins, Copper Transporters (CTR), Heavy Metal ATPases (HMA), and Oligopeptide Transporters (OPT) contribute to the detoxification of heavy metals through metal transport, chelate formation, and accumulation (Yu et al. 2017). Metal transporters ABC, CDF, and NRAMP transporters contribute to the development of tolerance by reducing the harmful effects of heavy metals in plants by transporting heavy metals to vacuoles. Cytoplasmic export of transition metal ions such as Zn^{2+} , Cd^{2+} , Co^{2+} , Ni^{2+} , or Mn^{2+} in root cells occurs via CDF transporters (previously called MTP or Metal Tolerance Protein) (Yang and Chu 2011). Moreover, Cation/Proton Exchanger (CAX) transporters, which transport heavy metals to the vacuole by direct proton exchange, are proteins that play an important role in the sequestration of heavy metals (Bovet et al. 2005; Koren'kov et al. 2007). Hirschi et al. (2000) transferred a gene, namely CAX2 (calcium vacuolar transporter), from *Arabidopsis thaliana* to tobacco and found that this gene increased the accumulation of Ca, Mn, and Cd in tobacco.

ZIP membrane transporters, another type of transporter, also have an important role in the transport of particularly Zn, Fe, Mn, and Cu and

in balancing metal uptake and homeostasis (Milner et al. 2013). ZIP proteins have eight potential transmembrane domains and a variable domain between TM-3 and TM-4 that contains a rich potential metal-binding domain (Guerinot 2000). HMA transporters belong to the P-type ATPase protein family and actively participate in the transport of heavy metals, especially Cu, Zn, Cd, and Pb, using ATP (Hanikenne and Baurain 2014). The COPT transporter family differs in the number of methionine- and histidine-rich domains; except for COPT4, all its members have an important role in copper transport (Yuan et al. 2011; Andresen et al. 2018).

Some transcription factors increase the resistance of plants to heavy metal stress by controlling the expression of genes (Li et al. 2022). WRKY proteins are one of these factors and carry a specific sequence called “WRKYGQK” (Eulgem et al. 2020). These proteins bind to a domain called the W box, enabling the switching on and off of stress-related genes (Asai et al. 2002). Wei et al. (2008) stated that the expression of the WRKY53 gene in *Thlaspi caerulescens* was significantly increased under Cd stress.

The MYB (Myeloblastosis) gene family constitutes one of the richest groups of transcription factors in plants. Plant MYB proteins are characterized by a highly conserved MYB DNA-binding domain. MYB proteins are divided into four main groups, 1R-MYB, 2R-MYB, 3R-MYB, and 4R-MYB, based on the number and location of MYB repeats. MYB transcription factors play roles in plant development, secondary metabolism, hormone signal transduction, disease resistance, and abiotic stress tolerance (Katiyar et al. 2012). Recent studies have revealed that the transcript of the MYB4 transcription factor, a member of the R2R3 subfamily of the MYB domain protein, is strongly induced in response to heavy metal elements including Cd and Zn in *Arabidopsis* (Oono et al. 2014; van de Mortel et al. 2008).

Members of the Basic Leucine Zipper (bZIP) family, one of the transcription factor superfamilies, play a role as controllers and regulators in many morphological and physiological processes in plant development, balancing energy production and use, and under biotic and abiotic stress conditions (Wang et al. 2015). The bZIP protein can regulate necessary defense genes in heavy metal stress by combining with other bZIPs or different transcription factors and activating gene networks appropriate for stress conditions. These domains, which are 60–80 amino acids long and contain a highly conserved leucine zipper dimerization motif, are responsible for nuclear localization and DNA binding (Wang et al. 2011). While DNA binding and nuclear localization function are carried out by the binding domain, the leucine zipper structure controls the homodimerization or heterodimerization processes of these proteins to direct their gene activities (Jakoby et al. 2002; Nijhawan et al. 2008).

The ACGT sequence motifs found in plant bZIP proteins serve as simple and specific DNA binding sites. Among the DNA binding domains, the amino acid sequences G-box, CACGTG; C-box, GACGTC; and A-box, TACGTA have been identified (Izawa et al. 1993). In vivo transient and transgenic plant studies on bZIP proteins have revealed that the G-box plays a role in the control of gene expression and in responses to stimuli such as light, abscisic acid (ABA), and abiotic stress in plants (Sib  ril et al. 2001).

AP2/ERF transcription factors play an important role in plant resistance processes against stress conditions. AP2/ERF can regulate the stress response by affecting the synthesis of plant hormones. Under abiotic stress conditions such as heavy metal stress, DERF can increase the expression of negative regulatory genes by binding to GCC motifs in their promoters. Overexpression of JERF1, a transcription factor found in plants, can increase stress tolerance and increase ABA levels by

elevating the expression of genes that contribute to ABA synthesis; thus, JERF1 regulates the stress response through ABA (Cheng et al. 2013; Yang et al. 2021). 147 AP2/ERF members have been identified in Arabidopsis, and they have been classified into the AP2, ERF, RAV, and Soloist subfamilies. The DREB and ERF subfamilies were combined into a single ERF subfamily, which was further subdivided into 12 groups based on amino acid motifs. Currently, this classification is the most widely used method in the literature (Nakano et al. 2006; Zhu et al. 2021). The DRE/CRT element can be recognized by ERFs primarily from subgroups 3a, 3d, 3e, 6b, 6e, 7a, and 8b. Despite the previous generalization that ERFs bind to the GCC box and DREBs bind to the DRE/CRT element, an increasing number of studies have found out that some ERFs can also bind to DRE/CRT elements and vice versa (Sun et al. 2008), indicating their potential roles in abiotic stress (Eini et al. 2013; Thirugnanasambantham et al. 2015; Behera et al. 2022). The RAV subfamily contains an AP2 structure and a B3 structure, while the Soloist subfamily contains an AP2 structural domain that differs significantly from that of other ERF transcription factors (Feng et al. 2020).

Phytochelatins (PCs) and MTs are cysteine-rich proteins found in plants and other organisms. PCs are synthesized from reduced GSH via the enzyme phytochelatin synthase (PCS). MTs are polypeptide proteins that are the product of genes. Numerous studies have shown that PCs and MTs, which can bind metal ions via thiol groups on cysteine residues, play important roles in metal and metalloid tolerance and in maintaining intracellular metal homeostasis in plants (Cobbett and Goldsbrough 2002; Iglesia-Turiño et al. 2006; Guo et al. 2008). Identifying genes and proteins such as PCs, MTs, heat shock proteins (HSPs), glutathione-related proteins, and antioxidant enzymes that emerge under the influence of heavy metals and understanding their functions helps to explain how heavy metal tolerance occurs in plants (Cobbett and Goldsbrough 2002; Clemens 2006).

PCs form complexes by binding to heavy metals thanks to the cysteine sulfhydryl groups in their structures, and these complexes are transported to vacuoles (Cobbett and Goldsbrough 2002). PCs have been noted to be involved in the long-distance transport of Cd in phloem conduction tissue (Mendoza-Cozatl et al. 2010) and the retention of Zn within the cell (Tennstedt et al., 2009). PC-Cd complexes transported to vacuoles bind to sulfide (S^{2-}) and free Cd^{2+} ions, forming high molecular weight structures surrounding Cd-sulfur clusters (Ortiz et al. 1995). These phytochelatin-metal complexes are recruited to the vacuole via ABC transporters on the tonoplast (Ortiz et al. 1995; Salt and Rauser 1995). In yeast, the Hmt1 (Heavy Metal Tolerance 1) transporter protein, a half-sized ABC transporter with a broad substrate spectrum, is stated to be the vacuolar PC transporter required for Cd tolerance (Ortiz et al. 1995; Salt and Rauser 1995). In a study conducted by Mendoza-Cózatl et al. (2010) on *Schizosaccharomyces pombe*, it was reported that Hmt1, a half-size ABC transporter, mediates the vacuolar accumulation of GS-bimane conjugates and that this transport is dependent on Hmt1 expression (Figure 5).

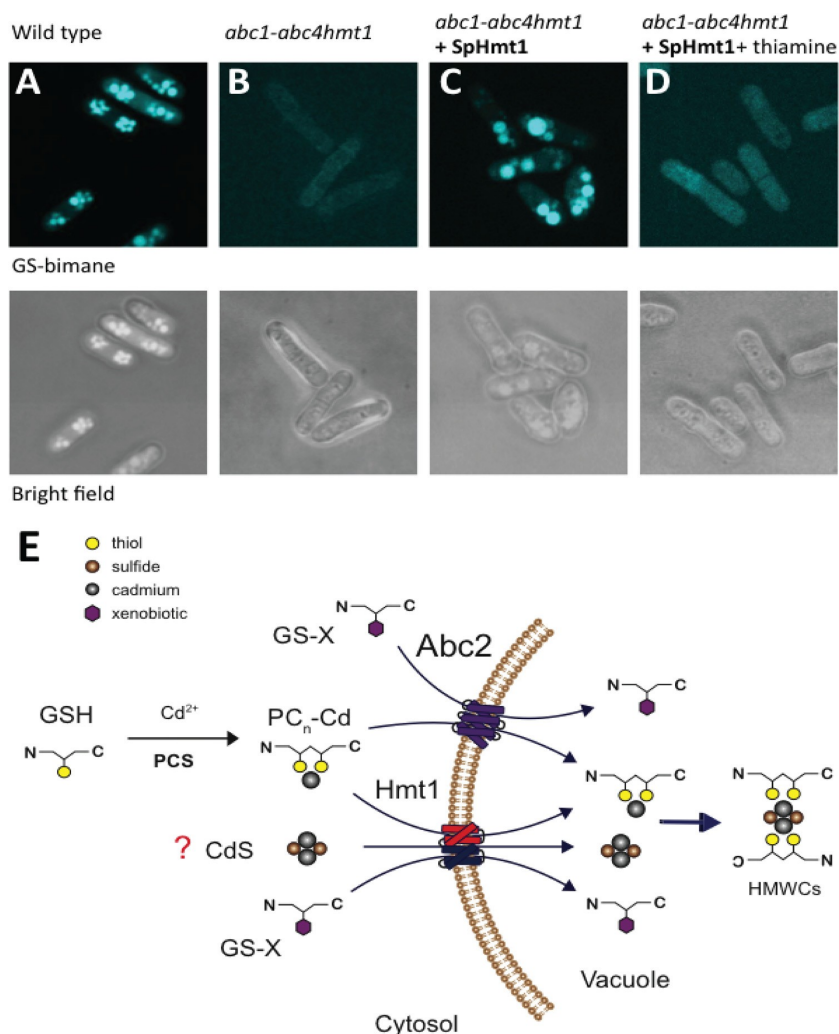


Figure 5. Proposed mechanism of cadmium detoxification in *S. pombe*. (A, B) GS-bimane conjugates accumulated in wild-type vacuoles but not in the *abc1-4hmt1* quintuple mutant. (C) Expression of Hmt1 in the mutant restored GS-bimane accumulation. (D) Addition of thiamine to the culture medium repressed *hmt1* expression and abolished GS-bimane accumulation. (E) The schematic model shows that PC-Cd complexes transported into vacuoles interact with sulfide (S^{2-}) and free Cd^{2+} ions to form high-molecular-weight structures surrounding Cd-sulfur clusters, thereby contributing to cadmium tolerance (Mendoza-Cozatl et al., 2010).

MTs comprise a family of low molecular weight proteins rich in cysteine amino acid (Palacios et al. 2011; Vasak and Meloni 2011). Most plant MTs are divided into four types based on the distribution of the cysteine residues (Usha et al. 2007). It is noted that types 1, 2 and 3 MTs are involved in Cu homeostasis and tolerance (Roosens et al. 2004; Guo et al. 2008), while type 4 MTs are involved in Zn homeostasis (Guo et al. 2008). In addition to their roles in Cu and Zn homeostasis, the functions of MTs include detoxification of nonessential metal ions, neuroprotection, maintenance of intracellular thiol redox potential, and regulation of cell proliferation (Cobbett and Goldsbrough 2002; Guo et al. 2008; Colvin et al. 2010; Maret 2011; Vasak and Meloni 2011).

4. PHYTOREMEDIATION WITH HYPERACCUMULATOR PLANTS

Plants growing in soils contaminated with heavy metals have developed different defense strategies against abiotic stress conditions caused by heavy metals, and accordingly, plants are divided into three classes: metal excluders, indicators, and accumulators. Metal-excluder plants retain heavy metals in the roots and prevent their passage to the shoots by slowing down the absorption of heavy metals or ensuring that the heavy metal concentration in their shoots is kept at low levels. Metal indicators accumulate metals in above-ground tissues, and therefore the metal content in the plant reflects the metal concentration in the soil. Metal accumulators (hyperaccumulators) store 50 to 500 times more metal in their tissues than the heavy metal concentration in the soil and have developed special mechanisms for metal detoxification. Hyperaccumulator plants accumulate 100 to 1000 times more heavy metals in their above-ground organs than other plant species but are not adversely affected by them. Therefore, thanks to these characteristics,

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accumulator plants are frequently used in phytoremediation studies to remove heavy metals from soil (Brooks 1998; Clemens 2006; Özay and Mammadov 2013; Doğru et al. 2021).

Unlike other plant species, hyperaccumulator plants uptake metals at a high rate and effectively transport heavy metals from roots to stems and leaves and detoxify heavy metals in the leaves. The main reason for this difference is the different expression and regulation of some genes found in the structure of non-hyperaccumulator plants. In addition, a large portion of the heavy metals absorbed by hyperaccumulator plants are essential elements for living things (Mitra et al. 2014; Doğru et al. 2021).

Approximately 450 angiosperm plant species (only 0.2% of angiosperms) have been identified as hyperaccumulators for some heavy metals (As, Cd, Co, Cu, Mn, Ni, Pb, Sb, Se, Zn) (Baker and Brooks 1989; Reeves 2006; Milner and Kochian 2008). Moreover, in general, plant species that can accumulate more than 10000 mg kg⁻¹ of Mn and Zn, more than 1000 mg kg⁻¹ of As, Co, Cr, Cu, Ni, Pb, Se, or more than 100 mg kg⁻¹ of Cd in their tissues are considered to be in the group of metal hyperaccumulators (Sytar et al. 2021). The most hyperaccumulator plant species are in the Brassicaceae family (Farraji et al. 2016). However, in recent years, their number has been increasing day by day with the studies on hyperaccumulator plants (Sun et al. 2006). On the other hand, some plant species defined as hyperaccumulators are removed from the hyperaccumulator plant group because of contradictory results obtained from field studies (Macnair 2003). For instance, in some plant species known to be hyperaccumulators of copper and cobalt, heavy metal accumulation has been determined to occur under field conditions due to leaf surface contamination (Faucon 2009). A large proportion of hyperaccumulator plants accumulate Ni, and it is known that plants can also accumulate other heavy metals (Hanikenne and Nouet 2011).

Many hyperaccumulator plant species are endemic species that can only grow in metal-rich soils and are therefore called “complete metallophytes.” However, some species fall into the group of “facultative metallophytes”; although these plants can survive in both metal-rich and metal-free environments, they are often more abundant in metal-rich areas (Assunção et al. 2003). Furthermore, some individuals within the same population can survive in metal-containing soils, while others can survive in metal-poor soils. For instance, in *Zn hyperaccumulators* such as *Arabidopsis halleri* and *T. caerulescens*, hyperaccumulation is a fundamental and distinctive trait at the species level, seen in the entire population (Bert et al. 2000). In contrast, in the *Zn hyperaccumulator* *S. alfredii* and the *Cd hyperaccumulators*, this trait is not species-specific; it occurs only in populations located in metal-rich habitats (Bert 2003).

In phytoremediation, which is the method used by plants and related soil microorganisms to reduce the concentrations or toxic effects of pollutants in the environment, bioconcentration and translocation factors are considered as the basic criteria in the selection of the hyperaccumulator plant (Ali et al. 2013; Sevgi and Leblebici 2022).

Bioconcentration factor (BCF) indicates the efficiency of a plant species to accumulate metals from the environment into its tissues (Ladislav et al. 2012; Wilson and Pyatt 2007). Calculated as shown in Equation 1 (Zhuang et al. 2007). High BCF values indicate that the plant is effective in metal accumulation.

$$\text{Bioconcentration Factor (BCF)} = \frac{C_{\{\text{harvested tissue}\}}}{C_{\{\text{soil}\}}} \quad \text{Equation (1)}$$

$C_{\{\text{harvested tissue}\}}$ → element/metal concentration in the harvested part of the plant (mg kg⁻¹)

$C_{\{\text{soil}\}}$ → soil concentration for the same element/metal (mg kg⁻¹)

Translocation factor (TF) shows the efficiency of the plant to transport the accumulated metal from its roots to its shoots and is calculated as follows (Padmavathiamma and Li 2007).

$$TF = \frac{C_{shoot}}{C_{root}} \quad \text{Equation (2)}$$

C_{shoot} → metal concentration in the plant's shoots

C_{root} → metal concentration in the plant's roots

If the BCF and TF values of plants are greater than 1, they can be used as bioaccumulators in phytoremediation (Takarina and Pin 2017; Sürmen et al. 2019).

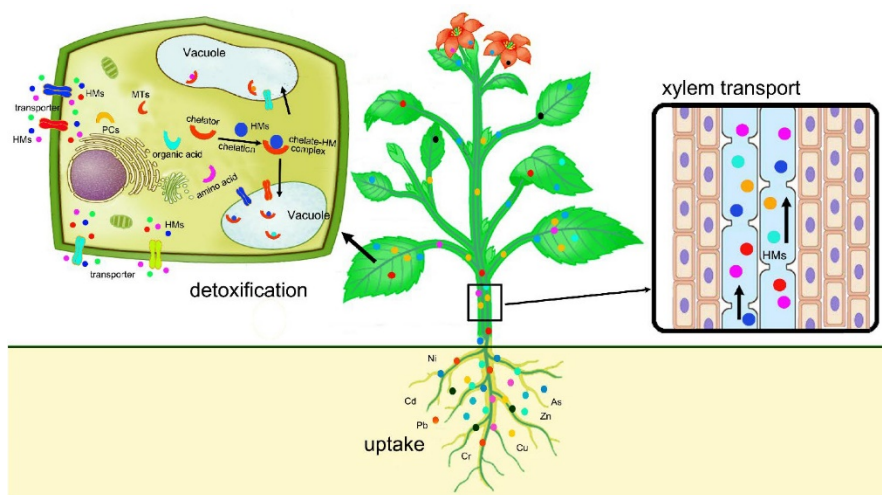


Figure 6. The schematic diagram shows the uptake, transport, and storage of heavy metals in plants (Yan et al. 2020).

In phytoremediation, the selection and development of species that have the capacity to give correct molecular responses to the genes responsible for the tolerance of plants to heavy metals and the processes of taking up, transporting, and storing metals in their tissues are of great importance (Figure 6). These species may exhibit resistance to metal

stress and increase the effectiveness of phytoremediation. Therefore, the development of transgenic strains suitable for phytoremediation is necessary.

5. CONCLUSION

Heavy metals in the ecosystem cause soil and water pollution. This situation threatens the health of all living things, especially plant health, through the food chain. Heavy metal pollution can cause serious consequences such as reduced productivity in plants, which are at the top of the food chain, loss of product quality, and plant death.

Heavy metals cause different biochemical reactions in plants depending on the species and environmental conditions. Plants reduce toxicity by limiting metal ions, chelating them, or accumulating them in vacuoles; in this process, they develop defense mechanisms that prevent damage caused by oxidative stress through antioxidant enzymes. The activation of key genes in response to heavy metal stress indicates the existence of complex cross-communication between the plant and the metal. Therefore, the accurate and precise interpretation of heavy metal stress signaling pathways is of great importance for understanding the stress response network in plants. In this context, knowledge of the physiological and molecular responses in plants exposed to heavy metal stress will contribute significantly to understanding heavy metal tolerance mechanisms and, in particular, to the development of tolerance-resistant transgenic species.

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Abiotic Stress Effects on Secondary Metabolite Composition of Medicinal Plants and Their Significance in Phytomedicine

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1. INTRODUCTION

Medicinal plants have long been revered as rich reservoirs of healing properties, a legacy that weaves through the annals of ancient civilizations. Their virtues extend far beyond mere therapeutic applications; these botanical wonders are celebrated for their profound contributions to beauty, holistic wellness, and the intricate tapestry of traditional practices (Yasser et al. 2018).

However, today, climate change is a serious threat, presenting significant challenges that suggest a future with harsh environmental conditions, which will greatly impact the shape and function of these important plants (Rodrigues et al. 2021). This predicament is primarily driven by escalating water scarcity and searing heat stress (Griesser et al. 2015; Qaderi et al. 2023).

As we grapple with the increasing impacts of climate change, it is becoming increasingly apparent that the rich biodiversity of aromatic and medicinal plants in terms of their complex morphological and physiological processes is on the verge of negative transformation due to stress conditions in the coming decades. Numerous studies have highlighted the fragility of these plants in the face of shifting climate conditions, especially their sensitivity to erratic temperature fluctuations and the harsh realities of drought. Like all flora, medicinal plants are beset by a myriad of challenges arising from both biotic and abiotic stressors (Rahman et al. 2023). Abiotic stressors encompass a range of harsh influences, including debilitating drought, increasing salinity, extreme temperature variations, disruptive ultraviolet radiation, and insidious air pollutants (Talebi 2023).

Under such environmental strains, biosynthesis of secondary metabolites, key biochemical compounds significantly enhancing medicinal efficacy, may fluctuate, either increasing or decreasing depending on the stress encountered. The intensity of these reactions is

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intricately shaped by the specific type of stress and the unique genetic characteristics of each species (Liu et al. 2023).

Looking toward the future, we can foresee escalated soil-related stresses, such as rising salinity, nutrient imbalances, and contamination from heavy metals, all compounding the adversities that future plant ecosystems will contend with (Zandalinas et al. 2022). This complex interplay of multiple stressors demands that these resilient plants adapt through multifaceted responses, refining gene expression and physiological processes while simultaneously adjusting their structural makeup and metabolic pathways. Such remarkable adaptations enable them to endure and flourish in conditions that might otherwise be catastrophic (Balfagón et al. 2022; Mareri et al. 2022).

As climate change reshapes the landscape of these aromatic and medicinal plants, it threatens to disrupt their delicate morphological and physiological functions, which could, in turn, adversely affect the quantity and quality of their secondary metabolites and the nuanced chemical compositions of their essential oils.

In many countries, the age-old tradition of harnessing medicinal plants for therapeutic practices has survived the test of time, interweaving a rich tapestry of cultural heritage and knowledge. Yet, this reliance often lacks the precision afforded by contemporary medical advancements. Despite their enduring legacy and increasing recognition in both developing and developed nations for healing and wellness, it is imperative to acknowledge the potential ramifications of climate change on these cherished plants. To ensure their preservation for future generations, we must prioritize the meticulous monitoring and evaluation of environmental stresses impacting medicinal plants, safeguarding their sustainable use and the rich healing traditions they represent.

Acknowledging the essential role of secondary metabolites in plant biology and human holistic health, this chapter describes the complex

dynamics by which biotic and abiotic factors influence the variations in these compounds. It presents the latest insights into the fluctuations in diverse secondary metabolite levels and explores the vital functions these compounds serve in aiding plants to adapt and respond to environmental stresses. This chapter emphasizes the intricate relationship between plants and their surroundings, offering a deeper understanding of the strategic roles that secondary metabolites (SM) play in ensuring survival and resilience. Many of the insights presented are drawn from a variety of published research studies.

2. THERAPEUTIC ROLES OF SECONDARY METABOLITES IN HUMAN HEALTH

SM represent a fascinating and diverse category of compounds that are crucial not only for the survival and adaptability of plants but also for their intricate mechanisms of action. These metabolites possess a wide array of medicinal properties, capable of significantly enhancing human health and well-being. The concentration and diversity of these compounds can differ dramatically among various plant species, positioning plants as particularly abundant reservoirs of these bioactive substances (Bisson et al. 2016).

Exhibiting remarkable antioxidant activities, secondary metabolites can alleviate a myriad of health concerns while promoting overall vitality. They encompass diverse families, including alkaloids, flavonoids, essential oils, glycosides, tannins, and resins, each contributing unique benefits. These compounds are used in a wide range of applications, including dietary supplements, flavoring agents, and essential pharmaceutical formulations, which emphasizes their central importance in both the health and industrial sectors (Baell et al. 2016).

The therapeutic potential of these metabolites to improve human health is substantial, especially concerning the mitigation of chronic diseases and the aging process. Notably, certain components derived from plants have demonstrated the ability to reduce cancer risk, protect genomic integrity, enhance immune system function, and aid in detoxification processes. Among these metabolites, polyphenols are particularly notable for their prowess as free radical scavengers; they combat oxidative stress and possess anti-mutagenic properties, which contribute significantly to the prevention of cancer and cardiovascular diseases, as well as the progression of atherosclerosis (Li et al. 2015).

The production and composition of secondary metabolites in plants are strongly influenced by a wide array of biotic and abiotic factors, which can either enhance or inhibit their biosynthesis. Strategies to enhance the yield of these essential compounds can be effectively implemented through the application of various elicitors. These elicitors can be classified into biotic factors, such as hormones, proteins, fungi, bacteria, and carbohydrates, as well as abiotic factors, including drought, varying light conditions, exposure to heavy metals, temperature extremes, and salinity. This complex interplay underscores the remarkable resilience and adaptability of plants in response to their environments, ultimately influencing the richness of their secondary metabolite profiles (Mandlekar et al. 2006; Suzuki et al. 2014; Pandey et al. 2017; Jan et al. 2021).

2.1. Phenolic Compounds as Secondary Metabolites in Plants

In the complex biochemical landscape of plants, phenolic compounds stand out as the most extensive and vital group of secondary metabolites, ranging from simpler aromatic structures to more complex formations such as lignin. These compounds play a pivotal physiological role, enabling plants to bolster their resistance and adaptability under various environmental conditions throughout their life cycle (Waterman,

2007; Kabera et al. 2014). They are synthesized under both favorable and stressful conditions, significantly contributing to various developmental processes, including cell division, hormonal balance, photosynthesis, and reproduction, while also facilitating the mineralization of essential nutrients (Sharma et al. 2019).

Phenolic compounds include a wide array of bioactive molecules such as lignins, tannins, flavonoids, isoflavonoids, anthocyanins, and coumarins (Saltveit, 2017). Their production within plants is orchestrated by the phenylpropanoid pathway, with phenylalanine serving as the primary substrate that drives substantial resistance mechanisms against a plethora of environmental stressors (Dong and Lin, 2021). This pathway is highly regulated by both biotic and abiotic factors, such as drought, salt stress, temperature extremes, physical wounding, pathogen attacks, herbicide treatments, nutrient deficiencies, and ultraviolet radiation (Valifard et al. 2015; Sharma et al. 2019). These external stimuli lead to the accumulation of phenolic compounds as a vital protective mechanism for plants living in stressful environments.

These compounds help mitigate stress responses by neutralizing reactive oxygen species (ROS), catalyzing oxygenation reactions, establishing vital metabolic structures, and inhibiting oxidative enzyme processes, thus enhancing evolutionary fitness (Nada et al. 2022). To cope with oxidative stress, plants have developed two distinct biological strategies: escaping ROS production and removing them via enzymatic and non-enzymatic pathways, including the accumulation of low molecular weight antioxidants (Signorelli et al. 2014; Kuluev et al. 2017). This antioxidant activity is supported by key enzymes such as phenylalanine ammonia-lyase (PAL) and chalcone synthase (CHS) (Dehghan et al. 2014).

The physiological processes associated with plant growth and development, such as seed germination, cell division, and the synthesis of photosynthetic pigments, are profoundly influenced by the levels of

phenolic acids and flavonoids, which are crucial for persistence and adaptation under environmental stress (Hernandez et al. 2021; Mencin et al. 2021). Among phenolic compounds, particularly flavonoids, exhibit remarkable tolerance against stressors like temperature extremes, enhancing ROS production (Huihui et al. 2020) and, in turn, facilitating protective mechanisms against oxidative damage through chelation processes (Kohli et al. 2018; Handa et al. 2019).

Abiotic factors such as drought disrupt plant metabolism and alter phenolic profiles. For instance, under drought conditions, ferulic acid levels decline while p-coumaric and caffeic acid concentrations rise in maize xylem sap, potentially aiding cell wall lignification and structural reinforcement (Alvarez et al. 2008). The spatial distribution of cell wall phenolics in *Zea mays* has been shown to play a significant role in restricting wall extensibility and root growth, thereby facilitating drought adaptation (Fan et al. 2006). A myriad of environmental stressors influence the synthesis of flavonoids, isoflavonoids, and anthocyanins. Flavonoids are known to accumulate under water-deficit conditions and have been shown to significantly improve drought tolerance in *Arabidopsis thaliana* (Li et al. 2021).

Similarly, phenolic acids and flavonoids act as antioxidants and protective barriers, underscoring their importance in a plant's response to arid conditions. Research has indicated that polyphenolic compounds are closely linked to gene expression changes in potato plants under drought, with variations largely dependent on the specific cultivar (Nichols et al. 2015). They help maintain osmotic balance, scavenge free radicals, and influence nutrient availability; they often serve as early indicators of deficiency before visible symptoms appear (André et al. 2009; Parida et al. 2007; Rodziewicz et al. 2014).

Stress from drought and waterlogging has been observed to elevate flavonoid levels of quercetin and rutin in *Hypericum brasiliense*,

whereas cold stress elicited a different response altogether (de Abreu and Mazzafera 2005). Flavonoid concentrations show a more severe downward trend in stress-sensitive genotypes, further emphasizing their role in maintaining antioxidant capacity (Rodziewicz et al. 2014; Djoukeng et al. 2008).

Anthocyanins also show significant increases in their concentrations when exposed to drought and cold stress due to their ability to scavenge ROS and protect cellular components (Ancillotti et al. 2015; Xiang et al. 2021). For example, in red-fleshed apple callus cultures, exposure to a low temperature leads to elevated anthocyanin levels, reflecting an adaptive mechanism (Wang et al. 2016). Cold stress also triggers suberin and lignin accumulation in the cell walls of plants, increasing mechanical strength and tolerance (Cabane et al. 2012; Naikoo et al. 2019).

Ultraviolet radiation causes flavonoids to accumulate beneath the epidermis in plants, creating a biochemical shield that protects against cellular damage (Bulotta et al. 2013). Similarly, the flavonolignan silymarin has been observed to accumulate in in-vitro cultures of *Silybum marianum* when subjected to various abiotic stress factors, including sodium chloride, polyethylene glycol, and gamma irradiation (Elateeq et al. 2020).

This accumulation is indicative of the cellular defensive strategies employed to mitigate the impacts of these stressors. As a result, the elicitation of stress responses in plants effectively enhances the production of valuable phytoconstituents in medicinal crops, demonstrating the intricate relationship between environmental stress and phytochemical adaptation (Elateeq et al. 2021; Mujib et al. 2022).

2.2. Terpenoids as Secondary Metabolites in Plants

Plants have developed complex and highly responsive resistance systems, enabling them to rapidly perceive and respond to various environmental stressors within their ecosystems (Andersen et al. 2018). A critical component of this defense is the production of secondary metabolites, among which terpenoids stand out as a diverse and structurally rich group of lipophilic compounds synthesized from isoprene units (C_5H_8) (Toffolatti et al. 2021). These compounds perform essential physiological functions by acting as phytohormones that support plant responses to biotic and abiotic stress factors. For example, the sesquiterpenoid abscisic acid (ABA) and the diterpenoid gibberellic acid (GA) contribute notably to these defense mechanisms. Research has revealed that ABA plays an important role in triggering various defense responses, including changes in membrane properties, especially by strengthening adaptive mechanisms against drought and water stress. (Kumar et al. 2022).

In addition, terpenoids are endowed with powerful antioxidants and antibiotic properties, which assist in maintaining the integrity of lipid membranes and bolster the plant's resilience against herbivorous threats (Al Musayeib et al. 2022). Terpenoids, which function as phytoalexins, low-molecular-weight antimicrobial compounds, are synthesized in plants as part of their defense system in response to environmental threats. Several diterpene phytoalexins have been identified in *Oryza sativa* (rice), highlighting their important role in disease resistance (Gu et al. 2019). Likewise, in cotton, sesquiterpenoid phytoalexins such as gossypol, hemigossypolone, and heliocides accumulate both aerial and underground, serving as vital defensive metabolites against pathogens and herbivores (Yang et al. 2013).

In maize and rice, a variety of diterpene phytoalexins including zealexins, kauralexins, and oryzalexins, are produced in leaves and roots.

These compounds exhibit notable antimicrobial properties, effectively responding to pathogenic threats such as the fungal blast disease caused by *Magnaporthe grisea* (Vaughan et al. 2015; Gu et al. 2019). Recent studies have indicated that UV radiation and trace metal stress can stimulate the accumulation of phytoalexins in rice. Interestingly, Vaughan et al. (2015) reported that under drought conditions, this accumulation is localized specifically to root tissues, without affecting levels in aerial parts.

However, it has also been documented that drought conditions lead to a diminished content of terpenoids in certain cotton species Massacci et al. 2008). In a related finding, Yusuf et al. (2010) observed that higher levels of soluble alcohol tocopherol, a known antioxidant, play a pivotal role in mitigating stress by stabilizing cellular membranes exposed to salinity, trace metals, and osmotic stress in *Brassica juncea*. Additionally, the accumulation of saponins in soybean plants has emerged as a critical secondary metabolite intricately linked to their resistance to salt stress, further underscoring the essential role of terpenoids and related compounds in plant resilience across diverse environmental challenges (Wu et al. 2008).

2.3. Nitrogen Containing Biochemicals as Secondary Metabolites in Plants

Plants have developed effective defense mechanisms to protect themselves from threats such as microbial pathogens, herbivores, and abiotic stress such as drought, waterlogging, and salinity. These stress factors contribute to declines in global crop production (Miyagawa et al. 2009). To counter these stressors, they have developed a sophisticated defense system rooted in secondary metabolism, which includes a variety of nitrogen-containing secondary metabolites such as alkaloids, cyanogenic glycosides, glucosinolates, and non-protein amino acids (Miyagawa et al. 2009; Divekar et al. 2022). Although sometimes

considered as undesirable metabolic byproducts, these nitrogenous compounds are considered essential elements in increasing plant resistance under both biotic and abiotic stress conditions.

Alkaloids, which are among these compounds, attract attention in literature as a structurally diverse group of nitrogen-containing metabolites (Cao et al. 2018). Their synthesis tends to escalate in response to abiotic stress conditions, where they play a crucial role in defending against microbial invaders and herbivorous threats. For instance, poppy plants exhibit increased alkaloid synthesis during periods of drought as well as under salinity stress, showcasing their adaptive response to unfavorable conditions (Davodnia et al. 2017). Similarly, in the case of lupins (*Lupinus termis*), the alkaloid content is significantly influenced by water scarcity and the application of activated yeast extract (Taha et al. 2020).

Glucosinolates and cyanogenic glycosides, which contain nitrogen and sulfur and are derived from glucose and amino acids, are also compounds that contribute significantly to plant defense strategies. Rodziewicz et al. (2014) reported that these natural compounds are essential for plants to withstand various environmental stress conditions. Mewis et al. (2012) reported that in *Arabidopsis thaliana*, drought and waterlogging conditions are associated with a marked increase in the production of aliphatic glucosinolates and flavonoids. Similarly, elevated glucosinolate levels were observed in *Brassica juncea* during its vegetative stage when subjected to water deficit.

Beyond the 20 standard amino acids required for protein synthesis, plants possess over 200 free amino acids that remain unincorporated into proteins, known as non-protein amino acids. These compounds play a critical role in the plant's response to various environmental stresses, further underscoring the complexity and adaptability of plant defense mechanisms (Miyagawa et al. 2009; Divekar et al. 2022).

3. ANALYTICAL INSTRUMENTS IN THE STUDY OF SECONDARY METABOLITES

The classification of the wide range of metabolite classes in plants is predominantly anchored in sophisticated hyphenated mass spectrometric techniques, which are expertly integrated with advanced chromatographic and electrophoretic systems (Piestansky et al. 2021). Selecting the optimal ionization technique and analyzer type is crucial for refining metabolite analysis within mass spectrometry (MS) systems (Chen et al. 2023). This analytical process enables precise measurement of ionized molecules, determining the mass-to-charge ratio (m/z) of the ions produced with exceptional accuracy, often down to four decimal places.

This meticulous evaluation results in the generation of both small and high-resolution mass spectra following the separation of compounds within the MS analyzer. Utilizing a high-resolution mass analyzer allows for the precise determination of the elemental composition of the ions captured in the mass spectra. This foundational step enables researchers to estimate the elemental structure and molecular weight of compounds by carefully analyzing the obtained m/z values, particularly for protonated species denoted as $[M + H]^+$ and their deprotonated counterparts $[M - H]^-$. The clear identification and thorough documentation of compounds heavily depend on the specific mass spectrometry system employed. Mass spectrometers equipped with electrospray ionization (ESI) and matrix-assisted laser desorption/ionization (MALDI) sources provide fruitful pathways for comprehensive analysis. The ionization process facilitated by MALDI can be efficiently coupled with one or two time-of-flight analyzers (TOF or TOF/TOF), while ESI operates proficiently with a variety of configurations, including quadrupole (Q), ion trap (IT), and time-of-flight (TOF) analyzers, or even a combination of these approaches. The

pinnacle of mass resolution is achieved through Fourier Transform Ion Cyclotron Resonance Mass Spectrometry (FT ICR MS) when employing ESI as the ionization method (Rodrigues et al. 2019).

Furthermore, the design of experiments adhering to the Metabolomics Standard Initiative (MSI) is imperative, as it advocates for stringent protocols concerning the preparation of biological materials, methodologies for metabolite extraction, and analytical procedures. Adhering closely to these established guidelines ensures a substantial number of sample replications and clearly defined conditions essential for studying plant development. Equally critical is the rigorous control of MS parameters during the acquisition of mass spectra, cultivating an environment that promotes accurate documentation, reliable quantification of metabolites, and robust study design (Fiehn et al. 2007). When such rigorously implemented methodologies are adopted, a vast array of statistical examinations can be conducted to elucidate the capabilities of diverse metabolites. This facilitates the identification of changes in specific compounds under well-defined conditions (Van den Berg et al. 2006).

The diversity of primary and secondary metabolites within a single organism can exhibit striking variability, with total numbers ranging from hundreds to tens of thousands, and concentrations often showcasing extensive fluctuations. Strategies crafted for metabolite analysis encompass metabolic profiling, metabolic fingerprinting, and targeted analyses (Gholkar et al. 2021). Metabolic profiling seeks to achieve the concurrent measurement of a wide spectrum of metabolites within a single sample.

Techniques such as gas chromatography-mass spectrometry (GC-MS), liquid chromatography-mass spectrometry (LC-MS), and nuclear magnetic resonance (NMR), are widely used. To date, GC-MS has risen to prominence as a leading analytical method for metabolic profiling in

plants, enabling the identification of a plethora of compounds across multiple classes, including sugars, organic acids, amino acids, alcohols, amines, and fatty acids (Shulaev et al. 2008).

LC-MS is more suitable for non-volatile or thermally labile metabolites and has gained prominence, particularly with the advancements in ultra-performance liquid chromatography (UPLC), which has increased separation efficiency and reduced analysis time (Giri et al. 2007).

NMR spectroscopy, on the other hand, introduces an entirely distinct analytical modality when compared to mass spectrometry-based methods. While the sensitivity of NMR is generally lower than that of mass spectrometry techniques, its advantages lie in its ability to elucidate molecular structures, ensure reproducibility, and engage in computational analyses that can sometimes exceed those offered by mass spectrometry (Schripsema 2010). Additionally, NMR's straightforward sample preparation process, ease of use, and potential for non-destructive measurements render it an invaluable tool for identifying metabolites in the context of metabolic profiling (Krishnan et al. 2005).

4. METABOLOMICS-BASED INSIGHTS INTO BIOCHEMICAL RESPONSES TO PLANT STRESS

Biochemicals, including both primary and secondary metabolites, constitute a dynamic and rapidly developing scientific field that focuses on the comprehensive analysis of small molecules involved in metabolic processes within an organism, plant cell, or tissue (Guo et al. 2019). This discipline plays a crucial role in understanding how organisms respond to various forms of stress that can disrupt their growth and developmental equilibrium. Such stressors may include environmental factors that disturb metabolic homeostasis, necessitating adjustments in

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metabolic pathways. This adaptive process is commonly referred to as acclimatization (Shulaev et al. 2008).

Over the past decade, biochemicals have seen remarkable advancements, emerging as a leading technology for studying the impacts of changing climatic conditions. It provides valuable insights into the phenotypic responses of diverse living systems under stress (Guy et al. 2008). By identifying numerous molecules, including byproducts of stress metabolism and compounds involved in stress signal transduction, metabolomics is greatly improving our understanding of how plants and other organisms cope with environmental challenges and adapt their physiological responses (Ghatak et al. 2018).

The applications of metabolomics are extensive and span multiple fields, including medicinal research, synthetic biology, and the analytical profiling of plants, animals, and microscopic organisms. Its versatility enables researchers to explore the intricate relationships between metabolic pathways and stress responses, paving the way for innovations in agricultural practices, therapeutic developments, and ecological conservation (Putri et al. 2013).

In addition to its relevance in various scientific fields, metabolomics has emerged as a powerful tool in the large-scale assessment and selection of plant varieties that exhibit resilience to changing environmental conditions. Numerous studies have highlighted that factors such as drought stress, salinity, extreme temperatures, and soil flooding can lead to significant disruptions within the plant metabolome, revealing essential insights into plant responses to these challenges (Obata and Fernie 2012).

Biochemicals represents the pinnacle of omics technologies, providing a comprehensive view of the biochemical alterations that occur within living organisms and shedding light on modifications in

traits and functions. Current research has focused on how plants respond to various abiotic stress factors at the metabolite level, including heat and cold stress (Cook et al. 2004), salinity and drought (Javed et al. 2022), and excess soil moisture (Ackah et al. 2021). Further studies have examined the impact of a range of metals and metalloids, including sulfur (Chung et al. 2022) and phosphorus (Li et al. 2022), as well as the complexities of oxidative stress (Savchenko and Tikhonov 2021), trace metals (Feng et al. 2021), and the combinatorial stress interactions (Patel et al. 2022).

A visual representation of various environmental factors that can disrupt the delicate balance of homeostasis and impede the growth of plants is illustrated in Figure 1, serving to underscore the myriad challenges faced by these vital organisms in an ever-changing world.

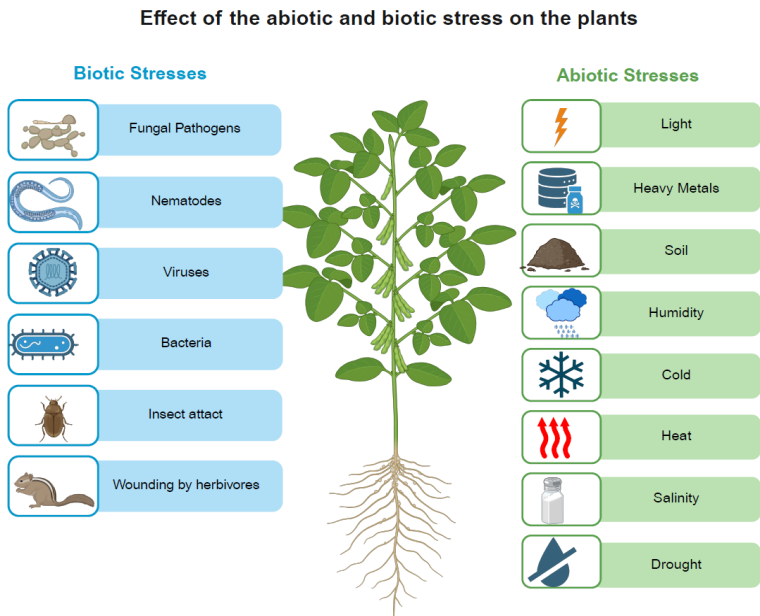


Figure 1. Environmental stresses arising from both biotic and abiotic factors significantly influence the growth and homeostasis of plants. (Created with [BioRender.com](https://www.biorender.com), Accessed on 19 April 2025)

4.1. Effect of Abiotic Stresses on the Primary Metabolites

Plants have evolved a remarkable array of adaptive mechanisms to withstand various abiotic stresses, demonstrating impressive metabolic flexibility to thrive in challenging environmental conditions (Ashapkin et al. 2020). These adaptations are crucial for their survival in the face of adversity, such as salinity, drought, and extreme temperatures. Among the defensive strategies employed, numerous plant metabolites play a vital role in alleviating the harsh impacts of these stresses by functioning as osmolytes and osmoprotectants (Teklić et al. 2021). Prominent examples of such metabolites include dimethylsulfoniopropionate (DMSP) and glycine betaine, along with essential sugars like sucrose, trehalose, and fructan. Additionally, specific amino acids, notably proline and ectoine, contribute to this protective arsenal, complemented by polyol metabolites such as sorbitol and mannitol (Dikilitas et al. 2020; Kebert et al. 2022). These compounds collectively work to maintain osmotic balance, ensuring cellular integrity during periods of water scarcity.

In addition to metabolic osmoprotection, plants are surrounded by epicuticular waxes, which minimize water loss and serve as physical barriers against pathogens. Plants also produce several antioxidants, including ascorbic acid, glutamine, alpha-tocopherol, anthocyanins, and carotenoids, which neutralize ROS generated under oxidative stress (Hüdig et al. 2018; Patel et al. 2022). These antioxidants help prevent damage to cell membranes and biomolecules, thus maintaining cellular homeostasis.

In addition to these protective compounds, the plant defense system intricately involves the synthesis of phytoalexins, which activate the phenylpropanoid pathway and enhance lignin biosynthesis (Kishi-Kaboshi et al. 2010). Essential phytochemicals and hormones such as salicylic acid, methyl salicylate, methyl jasmonate, and jasmonic acid are

important compounds that respond to environmental challenges. (Creelman et al. 1992; Hou et al. 2016; Li et al. 2019). These molecules can also function as signaling agents, triggering the plant's resistance mechanisms and mediating acclimation responses, thereby fortifying their defenses (Sharma et al. 2019).

One of the most pronounced adaptive responses to water scarcity is osmotic regulation, which necessitates the accumulation of compatible solutes such as sugars, amino acids, polyols, and glycine betaine (Rady et al. 2018). These chemical compounds are instrumental in maintaining cell turgor, stabilizing cellular membranes, and ensuring proper protein function. Additionally, research emphasizes the critical role of these metabolites in restoring redox balance by scavenging ROS, which can otherwise disrupt cellular structures and metabolic processes. Through these multifaceted strategies, plants exhibit resilience and adaptability in the face of environmental stresses, underscoring their intricate biochemical landscape (Janská et al. 2010; Dikilitas et al. 2020).

4.2. Effect of Abiotic Stresses on the Secondary Metabolites

Primary metabolites are essential compounds integral to the vital physiological functions of organisms, thus making them ubiquitous across all plant species. These metabolites play a direct role in critical processes such as growth, development, and reproduction (Wink 2010).

In contrast, secondary metabolites possess more specific functions that are not directly tied to these fundamental aspects of plant life. Typically, secondary metabolites are species-specific, and their roles can vary depending on environmental contexts, rendering them seemingly redundant in some scenarios (Böttger et al. 2018).

These compounds are synthesized under conditions and serve specific purposes, most notably in plant defense mechanisms against pathogen infections, enhancing resilience to abiotic stresses, and

providing protection against the damaging effects of ultraviolet radiation (Debona et al. 2017). Moreover, secondary metabolites contribute to a diverse array of substances that are vital for numerous biochemical and biophysical processes occurring within plant cells and tissues. However, they do not participate in the core physiological functions usually associated with plants, such as photosynthesis, respiration, nutrient translocation, solute transportation, nutrient acclimatization, and cellular differentiation (Divekar et al. 2022).

The production of these natural products is unique to specific plant species, and their concentration can be influenced by factors such as growth duration, environmental conditions, and adjustment mechanisms (Ochoa-Villarreal et al. 2016). Notably, certain secondary metabolites also play a role in attracting insects and animals, facilitating processes like pollination and seed dispersal. For instance, the accumulation of phenylamides in beans in response to abiotic factors such as heat suggests an antioxidant role for these secondary metabolites (Edreva et al. 2007).

Contemporary research continues to explore the multifaceted roles that secondary metabolites play in plants, examining their functions as biochemical indicators, antioxidants, and more. Additionally, these compounds have significant importance in human health treatment applications (Pagare et al. 2015). They serve as unique sources of food essences, medicinal compounds, flavorings, and a variety of industrial materials (Elateeq et al. 2022).

The accumulation of specific metabolites often occurs when plants are exposed to various stressors, including phytohormones, elicitors, trace metals, and signaling compounds (Bosila et al. 2016; Ali and Baek 2020; Elshahawy et al. 2022). Some well-known secondary metabolites with medicinal properties include salicin, an anesthetic and antipyretic compound derived from the willow tree (*Salix* sp.), which is a key

ingredient in aspirin (Mahdi et al. 2006). Other notable pharmacological secondary metabolites include taxol, an anticancer agent extracted from the Pacific yew tree (*Taxus brevifolia*), and morphine, a potent analgesic obtained from opium poppy (*Papaver somniferum*). Secondary metabolites can be categorized into three primary groups: phenolics, terpenes, and sulfur and nitrogen-containing compounds, each contributing to the rich tapestry of plant chemistry and its numerous applications (Grace 2005; Yazici 2022).

5. CONCLUSION

Abiotic stress factors have a significant impact on plant development and metabolic regulation by affecting the biosynthesis of secondary metabolites. In addition to their pharmacological importance, these compounds are critical not only for plant survival but also for human health. The strong relationship between changes in environmental influences and agricultural productivity highlights the urgent need to understand how plants biochemically respond to stress conditions.

Climate-related stress factors such as water deficit, salinity, ultraviolet radiation, and soil degradation affect crop yields and the quality of secondary metabolite production. These stress factors also negatively impact vital ecological interactions essential for plant ontogeny, including pollination and symbiotic relationships with soil microflora.

The integration of advanced analytical tools such as MS, NMR, and LC-MS with genetic and biochemical approaches allows for the detailed profiling and control of metabolite biosynthetic pathways. These advanced technologies effectively address the yield and sustainability limitations of traditional plant extraction methods, offering a significant solution for the production of medicinally important phytochemicals.

Furthermore, expanding our molecular understanding of plant responses to both biotic and abiotic factors is crucial for enhancing stress resistance and maximizing secondary metabolite output. This knowledge becomes even more critical in the face of accelerating climate change, which poses a growing threat to global plant biodiversity.

Future research should aim to deepen metabolomics-based understanding, foster interdisciplinary collaboration, and develop sustainable strategies to conserve plant chemical diversity. Such efforts will not only enhance agricultural resilience but also increase access to natural therapeutic resources.

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Ecophysiological Responses and Adaptive Strategies of Plants to Land Degradation and Climatic Stressors

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1. INTRODUCTION

Land degradation, characterized by the decline in land's biological productivity (Eswaran et al. 2019), poses a significant threat to ecosystems globally (Gomiero 2016), exacerbated by the ongoing impacts of climate change, and is one of the most pressing environmental challenges of the twenty-first century. It threatens ecosystem stability, agricultural productivity, and global biodiversity (Lal 2015). This degradation results from a complex interplay of human activities, including unsustainable agricultural practices, deforestation, urban expansion, and improper land use, as well as natural disturbances (Çakır and Bozkuş 2017; Çakır 2020). Local examples illustrate how accessible green infrastructure influences microclimate and ecosystem services in urban planning and green space standards at a neighborhood level (Alkan 2024). Together, these factors contribute to nutrient depletion, soil erosion, and biodiversity loss (Webb et al. 2017; Kawy and Darwish 2019). The effects of climate change, including rising temperatures, changing precipitation patterns, and increased salinity, not only worsen land degradation but also introduce new ecological pressures. This situation boosts the importance of understanding how plants respond and adapt to these environmental stressors (Kumari and Jha 2019; Kalaycı Kadak et al. 2024).

In addition to biological and climatic factors, the sustainability of ecosystems also depends on the degree of environmental responsibility demonstrated by individuals and institutions. Studies show that fostering environmental citizenship behaviour can significantly enhance the effectiveness of ecological policies and restoration initiatives (Candan & Dölarslan, 2023).

In this context, an ecophysiological perspective provides a valuable framework for understanding how plants respond to degrading environments and climatic variability. By focusing on essential

physiological processes, such as photosynthesis, nutrient uptake, and water-use efficiency, in variable and often challenging environmental conditions, ecophysiology enables a mechanistic understanding of plant adaptation (Lewandrowski et al. 2024). These insights go beyond theoretical considerations and have direct implications for practical fields, including conservation biology, reforestation, agroforestry, and the ecological restoration of degraded landscapes. Implementing ecophysiological approaches alongside air corridors and shade/evapotranspiration-based design principles can significantly reduce heat islands (Alkan et al. 2017). This aligns closely with global sustainability agendas (Peprah 2017). Furthermore, identifying plant species with superior resilience traits enhances the effectiveness of rehabilitation strategies, enabling land managers to select ecologically suitable candidates for afforestation and restoration initiatives (Alem and Habrová 2019; Renjana et al. 2024).

Over evolutionary timescales, plants have developed a variety of morphological, physiological, and phenological strategies to cope with environmental stress (Jing et al. 2016; Münzbergová et al. 2017; Kosová et al. 2021). Morphological adaptations, such as changes in leaf structure or root system architecture, improve a plant's ability to access and use water and nutrients in conditions like drought or nutrient-poor soils (Münzbergová et al. 2017; Tang et al. 2019). For instance, deeper root systems enable plants to access water stored in deeper soil layers, thereby helping them maintain physiological functions during prolonged dry periods (Jing et al. 2016). Complementing these traits, phenological plasticity, demonstrated by earlier flowering, adjusted leaf greening, or altered growth cycles, helps synchronize plant developmental stages with changing environmental conditions, ultimately improving survival prospects (Münzbergová et al. 2017; Ribeiro et al. 2022). In Anatolian cities like Siirt and Bitlis, local factors such as topography and fuel use

worsen air pollution, increasing pressure on the health of plants and humans (Alkan 2015; Alkan 2018).

At the physiological level, adaptive mechanisms such as osmotic adjustment, regulation of stomatal conductance, and improvements in photosynthetic efficiency contribute significantly to stress tolerance (Wilson 2012; Buesa et al. 2021). Enhanced water-use efficiency and carbon assimilation capacity are particularly relevant in regions exposed to intensified heat and salinity stress (Egamberdieva et al. 2019; Kumari and Jha 2019). Certain plant groups, such as halophytes, provide striking examples of resilience, having evolved specific biochemical and physiological adaptations that enable them to thrive in saline environments. These species represent promising tools for the ecological rehabilitation of salt-affected lands (Kumari and Jha 2019; Tang et al. 2019).

The relationship between genetic plasticity and environmental conditions further highlights the adaptive potential of plant species. Genetic differentiation enables various strategies to cope with extreme climate events, such as droughts and floods, thereby enhancing resilience at both species and community levels (Münzbergová et al. 2017; Kosová et al. 2022; Çakır and Çakır 2024). Additionally, integrating biotechnological and ecological approaches, such as the use of plant growth-promoting rhizobacteria alongside salt-tolerant species, has emerged as a promising method for restoring productivity and ecosystem function in degraded landscapes (Egamberdieva et al. 2019).

Land management practices also play a crucial role in shaping plant responses to stressors. Effective planting techniques can enhance soil water retention and reduce erosion. At the same time, reforestation programs that utilize native species adapted to local conditions significantly contribute to ecological recovery, improve soil health, and promote biodiversity conservation (Bayen et al. 2020; Renjana et al.

2024). When combined with ecophysiological insights, such practices provide a pathway towards sustainable ecosystem rehabilitation.

This chapter, therefore, aims to provide a comprehensive overview of how plants respond ecophysiologicaly and adapt to land degradation and stressors caused by climate change. The primary goal is to elucidate the mechanisms that enable plants to withstand environmental challenges, thereby informing restoration practices, enhancing agricultural resilience, and promoting biodiversity. By incorporating findings from recent research, the chapter underscores the crucial role of plant ecophysiology in developing sustainable land management strategies that foster ecological stability, resilience, and long-term sustainability in a changing global climate. Nevertheless, significant research gaps remain in linking specific adaptive mechanisms with large-scale restoration outcomes. Addressing these gaps will be essential for advancing both scientific understanding and practical applications in the years ahead.

2. LAND DEGRADATION PROCESSES AND THEIR IMPACT ON PLANT FUNCTIONING

Land degradation is a complex environmental challenge primarily characterized by the deterioration of soil quality and its ability to support plant life (Lal 2015). The major mechanisms driving soil degradation include erosion, salinization, and nutrient depletion. Each of these processes significantly alters soil properties and the relationships between soil, water, and plants. The consequences of these changes are profound, particularly regarding plant physiological performance in terms of water uptake, nutrient assimilation, and overall growth.

2.1. Soil Degradation Mechanisms

Erosion is one of the primary processes leading to land degradation and poses a significant threat to soil integrity. It occurs when wind or water removes topsoil, which is essential for plant growth due to its rich nutrient content and organic matter (Haskevych et al. 2022). The removal of this top layer not only reduces soil fertility but also disrupts soil structure, leading to increased runoff and subsequent erosion, a vicious cycle undermining plant establishment and long-term productivity. Notably, agricultural practices that expose bare soil surfaces intensify the risk of erosion, progressively diminishing the land's productive potential (Wang et al. 2023).

In addition to erosion, salinization is another major mechanism of degradation, particularly in arid and semi-arid regions. Salinization occurs when salts accumulate in the soil, often due to excessive irrigation or inadequate drainage systems. The resulting increase in salinity inhibits plant growth by restricting water uptake, inducing osmotic stress, and causing toxic ion accumulation within plant tissues (Zhang et al. 2023). The effects of salinization extend beyond individual plants, influencing vegetation diversity and altering community structures. While certain halophytic species may tolerate or thrive under saline conditions, many others experience severe decline, thereby disrupting ecological balance (Gavrilescu 2021).

Nutrient depletion is another critical outcome of soil degradation. As soil loses organic matter and essential macro- and micronutrients through erosion and leaching, their capacity to support plant growth diminishes (Hao et al. 2022). This reduction in soil fertility compromises plant health, lowers crop yields, and increases vulnerability to pests and diseases (Yang et al. 2021). Although fertilization practices are often used to counteract nutrient loss, they can introduce additional ecological challenges, such as water pollution and imbalances in soil microbial

communities (Song et al. 2018). Ultimately, this degradation pathway represents not only a soil management challenge but also a direct constraint on plant ecophysiological functioning.

2.2.Changes in Soil–Plant–Water Relations

The interaction between soil degradation and water availability is crucial in determining plant health and productivity. Degraded soils typically have a reduced capacity to retain water due to the breakdown of soil structure and organic matter. This leads to higher evaporation rates and lower moisture availability for plants (Long et al. 2024). As a result, these changes affect root system development; in degraded soils, shallow root systems may become more prevalent as plant species adapt to limited moisture, thereby reshaping competition dynamics among coexisting species (Yang et al. 2021).

Alterations in soil–water relations hinder root penetration and reduce the efficiency of water uptake (Sriskandarajah et al. 2024). In response to reduced water availability, plants frequently decrease stomatal conductance, reduce transpiration, and limit nutrient uptake efficiency (Kim et al. 2020). For instance, water-stressed plants often shift their resource allocation from aboveground growth to root development, resulting in increased root-to-shoot ratios as a survival strategy (Long et al. 2024). However, these adjustments come at a significant cost: reduced photosynthetic performance, lower carbon assimilation, and diminished biomass production.

2.3. Effects on Plant Physiological Performance

The physiological performance of plants is closely linked to the modifications in soil structure and water dynamics induced by degradation. Water uptake efficiency significantly declines in degraded soils due to moisture loss and disrupted root systems (Zhang et al. 2023). This decline undermines the plant's ability to maintain turgor pressure, which is critical for cell expansion, nutrient transport, and metabolic

activity. Therefore, many plants show stress symptoms, including wilting, slowed growth rates, and increased susceptibility to herbivory and disease (Kim et al. 2020).

At the same time, nutrient assimilation is impeded as essential elements become less accessible in degraded soils. Changes in soil pH and declines in microbial populations, key players in nutrient cycling, further exacerbate this issue (Long et al. 2024). For example, the efficiency of nitrogen-fixing bacteria may decline in nutrient-depleted soils, limiting the availability of nitrogen, a vital nutrient for plant productivity (Breidenbach et al. 2022). Moreover, degradation-driven shifts in microbial communities often result in nutrient immobilization, further restricting plant access to essential resources. Taken together, these processes create a feedback loop where poor soil health and impaired plant performance reinforce one another, accelerating ecosystem decline.

Drawing together the above mechanisms, it becomes evident that soil degradation, through erosion, salinization, and nutrient depletion, induces profound alterations in soil structure and function, with cascading effects on soil–plant–water relations and plant physiological performance. These dynamics compromise plants' ability to maintain water balance, assimilate nutrients, and sustain growth, ultimately reducing ecosystem productivity and resilience. Understanding these mechanisms is therefore critical for designing ecological restoration strategies and enhancing plant resistance to stress. Importantly, such degradation-induced changes seldom occur in isolation; they often interact synergistically with climatic stressors such as heat and drought. The following section explores how climatic extremes further compound the impacts of soil degradation and shape plant ecophysiological responses.

3. CLIMATIC STRESSORS AND PLANT ECOPHYSIOLOGY

Climatic stressors, such as extreme temperatures and changes in precipitation patterns, significantly impact plant ecophysiology, altering metabolic processes, growth, and survival (Acarer 2024; Acarer and Mert 2025; Kaya et al. 2025;). As climate change intensifies, it is increasingly important to understand how these stressors interact with existing challenges such as soil degradation, and the adaptive mechanisms that plants employ to cope with these combined pressures.

3.1. Temperature Extremes and Heat Stress Effects on Plant Metabolism

Extreme temperatures, including both excessive heat and severe cold, can disrupt metabolic pathways in plants. High temperatures in particular cause heat stress, triggering a variety of physiological responses aimed at reducing damage. For example, plants experiencing heat stress often increase transpiration rates as a cooling mechanism, helping to regulate leaf temperature and reduce oxidative stress, which can otherwise damage cellular components and inhibit growth (Wei et al. 2024).

At the molecular level, heat stress activates signaling pathways associated with the transcription of heat shock factors (HSFs) and heat shock proteins (HSPs). These proteins are essential for protecting other proteins and facilitating recovery from heat-induced damage. Simultaneously, oxidative metabolism is activated alongside the expression of antioxidant enzyme genes, which enhance tolerance to heat stress (Wei et al. 2024). Prolonged exposure to high temperatures, however, disrupts chloroplast functions, leading to reduced photochemical efficiency and impaired CO₂ assimilation (Hu et al. 2020). Thus, extended heat waves can jeopardize not only plant productivity but also overall ecosystem stability. Beyond temperature

stress, altered precipitation regimes introduce another major challenge to plant ecophysiology.

3.2. Altered Precipitation Patterns and Drought Stress Responses

Changing precipitation patterns, particularly the increasing frequency and severity of droughts, directly affect plant physiology. Drought conditions reduce soil moisture, limiting water availability and forcing plants to adopt strategies such as stomatal closure, root system adjustments, and altered growth patterns (Raza et al. 2023). These responses reduce transpiration and conserve water but also restrict photosynthesis and nutrient transport, ultimately decreasing biomass production (Manna et al. 2020).

During drought, plants frequently accumulate osmolytes such as proline, which help maintain cell turgor, stabilize proteins, and protect cellular structures (Raza et al. 2023). Such adaptations improve water retention and sustain metabolic activity under stress. In addition, some species respond by altering phenology, for instance, delaying flowering until conditions become more favorable (Wagg et al. 2014). These strategies increase survival probability but often come at the expense of growth and reproductive success.

The interaction between drought stress and soil degradation further complicates plant responses. The loss of organic matter and nutrients in degraded soils reduces water retention, amplifying the effects of drought (Zhou et al. 2016). As a result, prolonged dry periods not only impair plant performance but also reshape vegetation composition, favoring drought-tolerant species while threatening more sensitive ones.

3.3. Interaction of Climate Stressors with Soil Degradation Processes

The interplay of climatic stressors with soil degradation processes presents a compounded challenge for plant health and ecosystem sustainability. Soil degradation through erosion, salinization, and nutrient depletion already weakens essential soil functions; under climatic stress, these effects are magnified. For instance, higher temperatures and variable rainfall accelerate soil erosion, further deplete nutrients, and degrade soil structure, thereby heightening vulnerability across plant communities (Guild et al. 2024).

Moreover, the biochemical processes governing soil respiration, critical for nutrient cycling and plant growth, are also sensitive to the combined effects of climate and soil stressors. Elevated temperatures can enhance microbial respiration rates, altering soil carbon balance and nutrient availability. Such disruptions reduce soil biodiversity and weaken the soil–plant feedback necessary for ecosystem stability. The decline of microbial diversity under these combined pressures can diminish nutrient cycling efficiency, undermining both plant productivity and long-term soil health (Wagg et al. 2014).

Understanding these complex interactions requires a holistic perspective on plant ecophysiology under climate change. By recognizing the synergies between climatic stressors and soil degradation, researchers and land managers can better anticipate risks and design strategies to strengthen resilience. Adaptive approaches may include the use of cultivars with inherent stress tolerance, alongside land management practices that restore soil health and buffer ecosystems against climatic extremes (McDowell and Hess 2012, Kalaycı Kadak 2025).

Overall, these insights underscore the importance of an integrated understanding of climate–soil–plant interactions. Such knowledge not

only advances ecological theory but also provides practical guidance for conservation and restoration efforts. The subsequent section therefore examines the ecophysiological adaptation strategies plants employ to withstand these intertwined stressors.

4. ECOPHYSIOLOGICAL ADAPTATION STRATEGIES OF PLANTS IN DEGRADED ENVIRONMENTS

In response to land degradation and climatic stressors, plants have developed a variety of ecophysiological adaptation strategies encompassing morphological, physiological, and biochemical responses. These adaptations optimize plant functioning and survival in challenging environments, while also contributing to the stability of entire ecosystems. Understanding these mechanisms is essential for guiding conservation efforts and enhancing resilience in landscapes affected by human activities (Çakır and Çakır 2024).

4.1. Morphological Adaptations

Morphological adaptations are primary strategies that plants employ to cope with environmental stress in degraded areas. Key adaptations include modifications in root structure and leaf traits. Deep and extensive root systems allow plants to access water stored deeper in the soil during droughts, thereby sustaining hydration under water-scarce conditions (Cheema et al. 2015). Conversely, shallow-rooted plants may enhance lateral root development to capture surface moisture during brief rainfall events (Pelak et al. 2016).

Leaf morphology also plays a central role in minimizing water loss. Traits such as thicker leaves, smaller surface areas, waxy cuticles, or trichomes reduce transpiration and improve drought tolerance (Hamman and Hawkes 2012). Adjustments in leaf orientation further reduce sun exposure and water loss, demonstrating the plasticity of plants in

adapting to aridity and heat. Thus, root and leaf modifications are not only survival traits but also determinants of long-term plant competitiveness in degraded landscapes. Beyond structural modifications, plants also rely on physiological mechanisms to withstand stress at the cellular level.

4.2. Physiological Mechanisms

Physiological processes underpin plant capacity to function under abiotic stress. One key adjustment is osmotic regulation, whereby plants accumulate inorganic ions or compatible solutes such as proline and glycine betaine to maintain turgor pressure during osmotic. This adjustment preserves cellular integrity and metabolic activity under limited water availability.

Another crucial trait is water-use efficiency (WUE). Plants with enhanced WUE maintain higher rates of photosynthesis while reducing water loss through transpiration, an attribute particularly important in drought-prone regions. High-WUE species demonstrate improved resilience during prolonged dry periods, increasing their chances of survival in degraded environments (Sameera Hassan et al. 2015). These physiological strategies provide the foundation for stress tolerance but are complemented by additional biochemical defenses.

4.3. Biochemical Responses

Biochemical responses provide an additional layer of protection against climatic and soil stressors. Antioxidant systems play a pivotal role in reducing oxidative damage caused by heat, drought, and salinity. The accumulation of antioxidants mitigates the harmful effects of reactive oxygen species (ROS), safeguarding proteins, membranes, and other cellular components. Plants also produce Osmo protectants that stabilize macromolecules, thereby maintaining cellular function under stress.

Secondary metabolites contribute further to adaptation by deterring herbivores, protecting against pathogens, and mediating plant–soil interactions (Bever et al. 2010). In the rhizosphere, these compounds influence microbial community structure and soil chemistry, indirectly enhancing nutrient availability and stress resilience. Such biochemical responses highlight the remarkable metabolic flexibility of plants in coping with complex environmental challenges. Complementing these biochemical adjustments, plants also benefit from dynamic soil–plant feedback mechanisms.

4.4. Role of Soil–Plant Feedback Mechanisms

Soil–plant feedback forms a complex web of interactions that influence plant performance in degraded environments. This feedback can be positive or negative. For instance, plants may improve soil fertility through root exudates that enhance nutrient availability and foster symbioses with mycorrhizal fungi and beneficial bacteria (Mascagni et al. 2018). Such interactions significantly improve nutrient and water uptake, reinforcing plant growth under degraded conditions.

By contrast, negative feedback can occur when plants alter soil properties in ways that reduce their own performance, such as pathogen buildup or nutrient depletion (Hendriks et al. 2013). The balance of this feedback often determines the success of plant communities in degraded landscapes. Consequently, selecting plant species that stimulate beneficial microbial activity can facilitate soil rehabilitation and increase ecosystem resilience (Xiao et al. 2019; Huberty et al. 2022).

In conclusion, the ecophysiological strategies that plants employ in degraded environments encompass morphological, physiological, and biochemical adjustments, along with intricate soil–plant feedback. These adaptations not only support individual plant survival but also underpin ecosystem functions such as nutrient cycling, biodiversity maintenance, and productivity. Ongoing research into these mechanisms provides

valuable insights into developing sustainable land management and restoration practices capable of withstanding the pressures of climate change and land degradation. The following section illustrates these adaptation strategies through case examples, highlighting how specific plant groups thrive under degraded and climate-stressed ecosystems.

5. EXAMPLES OF PLANT ADAPTATION IN DEGRADED AND CLIMATE-STRESSED ECOSYSTEMS

Plants exhibit remarkable adaptability in response to environmental stresses, especially in degraded ecosystems affected by climate change. This section highlights two significant examples: halophytes that thrive in saline soil and xerophytes that flourish in desertified regions. These species demonstrate exceptional resilience and specialized mechanisms that enable them to thrive under challenging conditions.

5.1. Example 1: Halophytes in Saline Soils

Halophytes are a group of salt-tolerant plants that have evolved specialized mechanisms to survive and thrive in saline environments, where high salt concentrations often hinder the growth of conventional crops. Their adaptations include a variety of morphological and physiological traits that enable them to manage saline soil effectively.

One important adaptation observed in halophytes is the development of complex root structures that enhance their ability to extract water from deeper soil layers while simultaneously facilitating salt exclusion. For example, species like *Atriplex* and *Suaeda* develop extensive root systems that can access groundwater, thereby reducing their exposure to saline surface soils (Wang et al. 2021; Gao et al. 2022). Additionally, some halophytes have evolved salt glands that excrete

excess salts, helping to maintain osmotic balance within their tissues (Ashilenje et al. 2022).

On a physiological level, halophytes demonstrate osmotic adjustment mechanisms, which include the accumulation of compatible solutes such as proline and glycine betaine. These compounds are crucial for maintaining turgor pressure and protecting cellular structures from osmotic stress (Uzilday et al. 2014; Ruppel et al. 2013). Furthermore, halophytes often establish symbiotic relationships with arbuscular mycorrhizal fungi (AMF) and plant growth-promoting rhizobacteria (PGPR), which enhance nutrient uptake and improve salinity tolerance by influencing the microbial community in the rhizosphere (Jia et al., 2019; Pan et al. 2020). These mutualistic interactions not only strengthen plant health under saline conditions but also contribute to soil fertility and ecological restoration.

Research conducted by Wang et al. (2021) demonstrated that planting halophytes can effectively improve the physical and chemical properties of saline-alkali soils, while also reshaping microbial communities in ways that enhance soil health. Therefore, halophytes do not merely survive; they actively contribute to the rehabilitation of saline soils, making them key candidates for ecological restoration projects.

5.2. Example 2: Xerophytes in Desertified Regions

While halophytes thrive in saline conditions, xerophytes represent a remarkable group of plants that have developed survival strategies to endure the harsh environments of desertified regions. These adaptations are essential in areas characterized by high temperatures, limited rainfall, and extreme fluctuations in temperature and moisture availability.

Xerophytes typically exhibit morphological adaptations, such as reduced leaf areas, thickened cuticles, and specialized structures like spines or modified leaves. These features minimize water loss through

transpiration (Wang et al. 2007; Zhao et al. 2023). For example, plants from the Agave and Cactaceae families are well-known for their ability to store water in specialized tissues, allowing them to survive prolonged droughts. Additionally, many xerophytes possess deep and extensive root systems that enable them to access groundwater, buffering against the impacts of aridity (Hu et al. 2022; Anburaj et al. 2011).

Physiologically, xerophytes optimize water-use efficiency through specialized metabolic pathways. Many of these plants utilize Crassulacean Acid Metabolism (CAM), a process that allows them to fix carbon during the cooler nighttime hours. This adaptation reduces water loss that typically occurs from transpiration during the hotter daytime (Wang et al. 2007). Such strategies provide a significant advantage in desert ecosystems, where high temperatures can lead to rapid moisture loss.

Beyond their individual survival, xerophytes play essential ecological roles. They aid in soil stabilization and erosion control by maintaining vegetative cover, while also enhancing soil organic matter in desertified areas (Wang et al. 2007). Their interactions with soil microorganisms further improve soil fertility and resilience against climatic stressors, positioning xerophytes as keystone species within arid ecosystems. These traits allow xerophytes to act as not only survivors but also as ecological engineers in desert environments.

In conclusion, both halophytes and xerophytes exemplify the resilience of plant species in the face of severe environmental stress caused by land degradation and climate change. Their adaptive traits not only ensure individual plant survival but also contribute to broader ecosystem services, such as soil fertility, erosion control, and support for biodiversity. Understanding these mechanisms is vital for developing effective conservation strategies and restoring degraded lands. Building on these examples, the next section examines how ecophysiological

insights can be applied to land restoration and sustainable management practices.

5.3. Example 3: Adaptation Strategies of Winter Wheat to Drought Stress in Türkiye

Cultivated crops, like wild plant species, have developed remarkable strategies to adapt to environmental stressors. A significant example is winter wheat (*Triticum aestivum*) in Türkiye, a staple food crop that has been bred and managed to endure recurrent drought stress—one of the region's most pressing agricultural challenges.

The International Winter Wheat Improvement Program (IWWIP) has played a critical role in developing drought-tolerant wheat germplasm suitable for the climate in Central and West Asia. Established in 1986 through a collaboration between the Turkish government and the International Maize and Wheat Improvement Center (CIMMYT), the program focuses on breeding cultivars that are more resilient to water scarcity (Morgounov et al. 2019).

Morphological and Physiological Adaptations

Research shows that several winter wheat cultivars developed under the IWWIP exhibit modified root structures, featuring deeper and more extensive root systems that allow them to access subsoil moisture, thus increasing drought tolerance (Kaya 2021). These cultivars also have leaves with reduced surface areas and thicker cuticles, which minimize water loss through transpiration and enhance water-use efficiency. These traits not only improve plant survival but also contribute to greater grain yield stability in drought conditions.

Biochemical Responses

At the biochemical level, winter wheat adapts by accumulating Osmo protectants, such as proline, which helps maintain cell turgor,

stabilize proteins and membranes, and reduce the damaging effects of water deficit (Aktoprakligil and Memon 2023). Moreover, treatments like salicylic acid application have been shown to regulate stress-related microRNAs, thereby enhancing the drought resilience of specific cultivars (Tüfekçi and İnal 2020). These responses illustrate the biochemical flexibility of wheat cultivars, offering valuable targets for crop improvement.

Soil–Plant Feedback Mechanisms

In drought-prone areas of Türkiye, arbuscular mycorrhizal fungi (AMF) play a crucial role. The symbiotic relationships between winter wheat and AMF enhance nutrient acquisition, improve water-use efficiency, and contribute to soil health (Kaya 2021). By strengthening soil–plant feedback, AMF not only improve wheat performance during droughts but also enhance long-term soil fertility and ecosystem resilience.

Implications for Agricultural Practices

The effective adaptation strategies of winter wheat in Türkiye highlight the need for integrating breeding programs with ecological insights. By developing cultivars with advanced morphological, physiological, and biochemical traits and promoting AMF symbiosis, Turkish agricultural systems can maintain productivity in the face of climate stress. Türkiye's integrated approach demonstrates how ecophysiological knowledge can be effectively transformed into resilient agricultural practices and food security policies.

In summary, the adaptation strategies of winter wheat in Türkiye exemplify how targeted breeding, ecological management, and beneficial soil interactions can mitigate the impacts of drought. This case study, along with previous examples of halophytes and xerophytes, emphasizes how ecophysiological insights can inform restoration and

management practices, a topic that will be further explored in the following section.

6. ECOPHYSIOLOGICAL IMPLICATIONS FOR LAND RESTORATION AND MANAGEMENT

Integrating ecophysiological knowledge into land restoration and management practices is crucial for achieving sustainable ecosystem resilience, especially in the face of climate change and land degradation. This section explores the importance of selecting stress-resilient species, enhancing soil–plant interactions, and incorporating ecophysiological insights into adaptive land management frameworks.

6.1. Selection of Stress-Resilient Species for Rehabilitation

Selecting stress-resilient species is essential for the successful rehabilitation of degraded landscapes. Plants that demonstrate high resistance to abiotic stresses such as drought, salinity, or nutrient limitations, are better equipped to establish themselves in challenging environments and facilitate ecosystem recovery. For example, *Pinus brutia* and several native leguminous species have shown significant potential in afforestation projects aimed at reclaiming degraded lands (Werden et al. 2017).

Researchers emphasize the importance of ecophysiological traits, including water-use efficiency and stress tolerance mechanisms, when evaluating species for restoration. Plants with deep root systems or strong osmotic adjustment capabilities tend to perform better in arid and saline environments (Malik et al. 2018). Therefore, incorporating ecophysiological traits into species selection enhances both short-term establishment and long-term ecosystem stability. However, species selection alone is not enough; their success heavily depends on how they interact with soils and microbial communities.

6.2. Enhancing Soil-Plant Interactions to Improve Ecosystem Resilience

A crucial aspect of land restoration involves enhancing soil-plant interactions to build resilience. The relationships between plants and soil microorganisms particularly mycorrhizal fungi and rhizobacteria play a vital role in improving nutrient uptake and strengthening stress tolerance (Richardson et al. 2024). For example, arbuscular mycorrhizal fungi can significantly increase phosphorus acquisition, which enhances the health and performance of plants in nutrient-poor soils.

Additionally, soil amendments like organic matter or biochar can improve soil structure, water retention, and microbial activity, thereby creating favorable conditions for plant establishment (Castro et al. 2016). By fostering strong soil-plant interactions, restoration efforts not only rehabilitate degraded soils but also create self-sustaining feedback loops that enhance resilience over time. These improved soil-plant dynamics should be integrated into broader land management frameworks.

6.3. Integrating Ecophysiological Knowledge into Sustainable Land Management Practices

Successful land management based on ecophysiological principles acknowledges the complex interdependence among species, soil, and climate. Integrating this knowledge enables the development of adaptive strategies that respond to the dynamic nature of ecosystems. Monitoring the physiological responses of plant communities under changing conditions provides managers with essential feedback for decision-making (Bateman et al. 2016).

Implementing ecophysiological indicators strengthens monitoring frameworks for evaluating restoration effectiveness. For instance, assessing stomatal conductance and leaf water potential can reveal plant stress responses and provide insights into ecosystem health during

recovery (Valliere et al. 2021). Such indicators allow for timely interventions to ensure the success of restoration efforts.

Overall, combining strategic species selection, enhancing soil-plant interactions, and integrating ecophysiological monitoring into management frameworks offers substantial potential for boosting resilience. These approaches enable the creation of landscapes that are not only restored but also better equipped to withstand future environmental challenges. The final section synthesizes these insights, highlighting key lessons and outlining future research and practice directions.

7. CONCLUSION

Integrating ecophysiological insights into land restoration strategies is crucial for addressing the effects of land degradation, which are intensified by climate change. This chapter highlights several key themes:

- **Adaptive Mechanisms:** Plants utilize morphological, physiological, and biochemical strategies to cope with drought, salinity, and nutrient scarcity. These traits that confer stress tolerance are crucial in degraded areas and should inform the design of rehabilitation efforts.
- **Species Selection:** Prioritizing species that can withstand the predominant local stressors enhances vegetation re-establishment and the recovery of ecosystem functions.
- **Soil–Plant Interactions:** Strengthening beneficial relationships between soil microbes and plants can improve plant vigor, nutrient uptake, and overall soil fertility.
- **Integration of Knowledge:** Incorporating ecophysiological monitoring such as measuring stomatal conductance and water

potential into management practices enables adaptive, evidence-based decision-making.

7.1. Future Directions

Despite significant progress, we still have much to learn about plant ecophysiology in the context of land degradation and climate stress. Future research should focus on the following areas:

- **Long-Term Studies:** We need to conduct extended, field-based experiments to assess the long-term performance and ecological impacts of stress-resilient species in restoration projects.
- **Climate-Specific Research:** There should be a greater emphasis on understanding local-scale variability in climate, topography, and soils. This will help refine restoration practices tailored to different ecosystems.
- **Integrative Approaches:** Developing frameworks that combine ecophysiology with remote sensing technologies, ecological modeling, and big-data analytics is essential for predicting species responses to changing climate scenarios.
- **Policy Development:** We need stronger policy frameworks that incorporate ecophysiological insights into land-use planning and management, enabling more effective scaling of rehabilitation efforts.

Integrating lessons from sustainable forest management frameworks, as discussed in Turkish and European contexts, provides valuable insights for establishing robust policy mechanisms that align ecological restoration with long-term governance principles (Dölarslan, 2007; Dölarslan, 2009).

In conclusion, advancing ecophysiological research and fostering collaboration among scientists, practitioners, and policymakers are vital for creating adaptive, self-sustaining ecosystems. By placing ecophysiological knowledge at the core of restoration science, we can

shift our focus from short-term recovery to achieving lasting resilience in the face of climate change and land degradation.

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Litterfall as an Indicator of Stress in Forest Ecosystems

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1. INTRODUCTION

In forest ecosystems, stress factors affecting the physiological processes of trees can be classified into two groups: biotic (pests, pathogens, competition) and abiotic (drought, extreme heat, frost, air pollution, nutrient deficiency, fire, wind, etc.). These stressors limit photosynthesis, transpiration, growth, and carbon storage capacity, thereby impairing ecosystem functioning (Allen et al. 2010; Teskey et al. 2015). In particular, drought stress in semi-arid and arid regions leads to needle shedding in coniferous species, reduced stem increment, and depletion of carbon reserves (McDowell et al. 2008).

Stress can be defined as the combined effect of environmental and biotic drivers that force tree physiological functions beyond their optimal ranges, often leading to shifts in energy allocation among growth, reproduction, and survival through adaptive or avoidance responses. The concept of stress in woody plants spans a continuum from short-term (acute) events (e.g., drought spells) to chronic conditions (e.g., prolonged water deficit, rising temperatures, trophic network pressures) and often manifests as multiple stress interactions (e.g., drought $\times$ ozone; drought $\times$ pathogen). Within this framework, litterfall dynamics serve not only as early indicators of stress but also as key processes reflecting the consequences of stress on ecosystem functioning (Dobbertin 2005; Rowland et al. 2018).

1.1. Patterns of Litterfall

In forest ecosystems, litterfall consists of leaves, branches, bark, and other organic components shed from trees that reach the soil surface. These inputs are fundamental components of carbon and nutrient cycles; they provide substrates for soil respiration, regulate soil organic matter stocks and fertility, and shape the hydrothermal regime and surface properties (e.g., hydraulic conductivity, albedo) of the topsoil (Berg and

McClaugherty 2014; Andivia et al. 2018). The amount and chemical composition of litterfall are determined by species composition, climate, and soil characteristics, as well as the stresses to which trees are exposed. Globally, annual litterfall varies between approximately 3–11 Mg ha⁻¹ yr⁻¹ depending on forest type (Zhang et al. 2014). In Türkiye, values of 3.9–4.5 Mg ha⁻¹ yr⁻¹ have been reported for oak (*Quercus petraea*) and beech (*Fagus orientalis*) stands in the humid Belgrad Forest, whereas in semi-arid black pine (*Pinus nigra*) forests of Eldivan (Çankırı), litterfall values range between 3.5–4.8 Mg ha⁻¹ yr⁻¹ (Çakır and Akburak 2017; Çakır et al. 2019). Similarly, studies from the Western Black Sea mountain ecosystems (Türkiye) also confirm that litterfall dynamics are strongly influenced by stand composition and regional climate (Sarginci et al. 2021). Litterfall fractions leaves, reproductive material (flowers, fruits), and fine woody debris exhibit different sensitivities to climate and stress. For instance, in tropical forests, leaf litter typically accounts for ~70% of the total, whereas the reproductive fraction shows greater variability in response to nutrient availability (Rowland et al. 2018).

1.2. Drought Stress and Litterfall Interactions

The relationship between tree physiological responses under stress and litterfall dynamics is crucial for understanding ecosystem functioning. For example, acute stress factors such as fire or insect outbreaks can trigger large amounts of litterfall in a short time, whereas chronic stress factors such as prolonged drought affect litter quantity and nutrient content more gradually. The effects of drought and heat stress on litterfall vary according to species, biome, and stress intensity. In *P. brutia* forests of Türkiye, litterfall was shown to be closely linked to stand parameters such as crown cover and stem volume, as well as to interannual climatic variability (Erkan et al. 2018). Therefore, litterfall can be regarded as one of the indicators of stress in forest ecosystems (Jandl et al. 2007). In addition, temperature fluctuations and climate

change-induced extreme events disrupt the physiological balance of trees, leading to increased litter production (Bréda et al. 2006). Moreover, drought stress influences litterfall by impairing water transport in trees, increasing the costs of osmotic adjustment, and altering carbon reserves.

1.3. Litterfall, Decomposition and Nutrient Cycling Linkages

Under drought stress, litterfall can exhibit temporal fluctuations. In some tree species, drought conditions trigger early leaf shedding as a water-saving strategy, whereas under extreme drought, leaf shedding may be suppressed and trees tend to retain their leaves (Meir et al. 2009). In addition, leaves shed under stress often contain reduced levels of essential nutrients such as nitrogen (N), phosphorus (P), and potassium (K). This reduction decreases nutrient inputs to the soil, ultimately lowering soil fertility in the long term (Sayer and Banin 2016).

The amount and fractional composition of litterfall directly determine decomposition rates and nutrient cycling. Drought alters litter quality (e.g., C:N ratio, lignin content) and reduces the activity of soil fauna, thereby slowing decomposition. Temperate forest experiments have reported reductions in decomposition rates, while Mediterranean forests highlight that drought $\times$ litter quality interactions diminish the contribution of soil fauna (Andivia et al. 2018; Wilson et al. 2022). Consequently, although drought-induced litterfall provides a rapid input of carbon and nutrients to the soil in the short term, simultaneous slowing of decomposition and mineralization results in complex changes in nutrient availability. This dual effect is particularly critical in ecosystems where water and nutrients (N, P, K) are limited, as it shapes tree stress tolerance and recovery capacity.

1.4. Effects of Climate, Seasonality, and Local Factors on Litterfall

The seasonal pattern of litterfall is an outcome of phenology–climate interactions, determined not only by environmental drivers such as temperature, precipitation, wind, and storm events, but also by stand structure (Zhang et al. 2014; Andivia et al. 2018). In Mediterranean cork oak (*Quercus suber*) forests, nine years of observations showed that litterfall occurs predominantly in spring, with a secondary and smaller peak in some years during autumn, and that the influence of climatic factors such as temperature, rainfall, and wind may be highly localized (Andivia et al. 2018). Similarly, in *P. brutia* forests, climatic factors such as rainfall and temperature were found to be strong drivers of interannual and seasonal variation in litterfall (Erkan et al. 2018). In *P. nigra* forests, litterfall has been reported to show two seasonal peaks: in spring, dominated by the shedding of male flowers and bark, and in autumn, primarily through needle fall (Çakır et al. 2023). These findings highlight that litterfall must be explicitly incorporated into carbon budget and nutrient cycling models under climate change scenarios, as it represents a critical variable shaping ecosystem projections.

1.5. Multiple Stresses, Biotic Interactions, and Indicators

Forest trees are frequently exposed to simultaneous or sequential combinations of drought, nutrient limitation, and pathogen and insect attacks. Within an interactive stress framework, such conditions trigger non-linear responses as well as threshold and feedback processes, reducing growth or weakening defence through hydraulic failure, depletion of carbon reserves, and trade-offs in resource allocation among defence, growth, and reproduction (Niinemets 2010; Bussotti and Pollastrini 2021).

Climate-driven stress is particularly pronounced through increasing vapor pressure deficit (VPD) in summer and declining winter precipitation. The Forest Drought Stress Index (FDSI), derived from tree-ring records, is strongly correlated with productivity loss, bark beetle outbreaks, and rising mortality; models project that, if VPD continues to rise, average drought stress around the 2050s may surpass even the most severe droughts of the past millennium (Park Williams et al. 2013; Gül 2025). This indicates that the combined effects of heat stress and water deficit may also lower the threshold for disturbances such as fire and insect outbreaks.

Drought weakens host trees by impairing xylem integrity, depleting carbon reserves, and suppressing defence metabolism; in most pathogens, this relationship is indirect and explained by the concepts of predisposition and multiple-stress theory (Desprez-Loustau et al. 2006). Herbivore interactions are also context-dependent: in semi-arid *P. edulis* ecosystems, water and nutrient scarcity reduced needle litterfall by ~20%, while the impact of dominant herbivores varied, causing additional losses in some years but remaining negligible in others due to compensatory needle production (Schuster et al. 2005).

Therefore, the monitoring and management of multiple stresses cannot be reduced to a single indicator; tree growth, litterfall, climate-derived indices, and physiological–morphological measurements across scales should be integrated and assessed over the long term. Such a holistic monitoring approach clarifies cause–effect relationships and strengthens management decisions such as thinning intensity and species selection.

2. COMBINED STRESSES: HEAT AND PATHOGENS

Under the current climate regime, forest trees are exposed to simultaneous or sequential stresses whose impacts are often non-linear meaning that they differ from the simple sum of single stress effects and are instead interactive in nature (Niinemets 2010; Bussotti and Pollastrini 2021). This section brings together two main axes: (i) drought driven by rising temperatures and increased vapor pressure deficit (VPD), and (ii) drought $\times$ pathogen interactions.

2.1. Intensification of Heat and Drought Stress

In the context of global climate change, rising temperatures and prolonged droughts represent two of the most critical stress factors in forest ecosystems. Heat waves, particularly during summer, increase vapor pressure deficit (VPD), causing excessive water loss through leaf transpiration. This process disrupts the hydraulic integrity of xylem tissues, leading to impaired water transport (Allen et al. 2010; Teskey et al. 2015). Under chronic drought conditions, trees close their stomata to reduce water loss; however, this response also limits carbon assimilation. Consequently, long-term depletion of carbon reserves occurs, growth slows, and defence capacity declines (McDowell et al. 2008; Gül and Esen 2024).

The effects of drought and heat stress on litterfall vary according to species, biome, and stress intensity. In the short term, water deficit and elevated VPD may shorten leaf lifespan and increase litterfall, although this increase often occurs mainly through reproductive organs (flowers and fruits) (Rowland et al. 2018). When heat and drought are considered together, litterfall is regulated in a dual manner—through both water balance and carbon allocation.

Over prolonged periods of chronic drought, ecosystems may evolve toward a new functional equilibrium. However, this new balance

typically involves a resource shift in favour of reproduction and canopy maintenance at the expense of woody growth (increment). This pattern demonstrates that the combined effects of drought and heat not only alter short-term litterfall dynamics but also permanently reshape long-term carbon stocks, increment, and growth processes.

2.2. Drought × Pathogen Interactions

Interactions between drought and pathogen pressure are of critical importance for understanding forest health and litterfall dynamics. Drought weakens xylem integrity, limits carbon reserves, and suppresses defence metabolism. These physiological impairments make trees more susceptible to pathogens; in the literature, this condition is referred to as predisposition (Desprez-Loustau et al. 2006). For example, in drought-stressed individuals, the reduction of defensive compounds can promote the proliferation of wood-decaying fungi and xylem-blocking pathogens. Similarly, insect pests, particularly bark beetles, can more easily attack drought-weakened hosts, increasing their rates of spread (Anderegg et al. 2013).

The combination of drought with pathogen or insect pressure can also lead to sudden increases in litterfall. In broadleaf forests, abrupt rises in leaf and fine branch litter increase the substrate available for decomposition in the short term; however, when the nutrient quality of this material (e.g., N/P ratio) is low, microbial decomposition rates may be suppressed. In such cases, decomposition and nutrient cycling processes are shaped by both host physiology and the ecosystem-level impacts of pathogens.

Thus, drought–pathogen interactions create ecosystem-specific variations in litterfall patterns. In some ecosystems, drought suppresses defence mechanisms and amplifies pathogen impacts, while in others increased leaf shedding may partially compensate for pathogen damage.

Overall, these interactions make litterfall not only a measure of productivity but also an early indicator of how trees respond to the combined effects of biotic and abiotic stresses.

3. LITTERFALL–DROUGHT INTERACTIONS: SHORT-TERM “SHOCK”, LONG-TERM “NEW EQUILIBRIUM”

Litterfall is one of the primary pathways through which carbon and nutrients are transferred from trees to the soil in forest ecosystems; the shedding of leaves, fine branches, and reproductive organs initiates decomposition and sustains soil nutrient cycling (Kim et al. 2003; Pandey et al. 2007). The amount and fractional composition of litterfall vary significantly with seasonality, extreme climatic events (e.g., drought, shifts in rainfall frequency), and management or disturbance regimes (e.g., fire, afforestation/plantations) (Weber 1987; Ni et al. 2021).

Drought reshapes canopy dynamics in forest ecosystems through both short-term (acute) and long-term (chronic) processes. Litterfall—including leaves, flowers, fruits, and fine branches—serves as both an early warning indicator of such restructuring and a direct flux feeding into carbon and nutrient cycles. The following section synthesizes how drought–litterfall interactions diverge across temporal scales, fractions, and species/biome differences, and outlines the underlying carbon cycling and phenological mechanisms driving these patterns.

3.1. Short-Term “Shock” Responses: Sharp Decline in Reproductive Fractions, Context-Dependent Leaf Fall

In the short term, drought primarily constrains the canopy through impaired water transport and stomatal regulation. The most pronounced outcome of this pressure is a sharp reduction in the production of

reproductive organs such as flowers and fruits. The Amazon rainfall-exclusion experiment—the longest-running tropical throughfall reduction study worldwide—showed that during the first four years total litterfall and leaf-fall declined by only 12–13%, whereas reproductive fractions (flowers and fruits) exhibited a dramatic 54% reduction (Rowland et al. 2018). This initial phase is characterized by a temporary weakening of the linkage between litterfall and seasonal climatic drivers; in other words, the seasonality of litterfall does not mirror climatic fluctuations as expected. Similarly, in a seven-year Amazon throughfall reduction experiment, stem growth decreased by 13% in the first year and up to 62% in subsequent years, while litterfall declined only from the third year onward and by no more than 23% (Brando et al. 2008).

The direction and magnitude of leaf litterfall responses vary across ecosystems. For instance, in New Zealand's *Agathis australis* conifer forests, litterfall in a drought year increased by 72% compared to a wet year, with most of the increase attributable to leaf and fine branch fractions (Macinnis-Ng and Schwendenmann 2015). In contrast, in the subtropical broadleaf forests of the Ailao Mountains in China, extreme drought in 2009–2010 caused a 12% decline in total litterfall; the leaf fraction showed a slight increase, whereas other fractions decreased substantially. Recovery times also varied among fractions, with the sequence reported as branch < leaf < flower–fruit < moss < bark (Xiuwen et al. 2024).

3.2. Long-Term “New Equilibrium”: Reallocation and Return of Seasonality

Over extended periods of chronic drought, ecosystems may evolve toward a new functional equilibrium. In the Amazon experiment, beginning around year 10, flower and fruit production exceeded control levels and stabilized, the relationship between litterfall and climatic drivers was reestablished, and a new balance between litterfall and stem

growth emerged (Rowland et al. 2018). This indicates that under chronic drought, resource allocation may shift in favour of reproduction and canopy maintenance at the expense of woody growth. Modelling studies in eastern Mediterranean conifer forests have further demonstrated that litterfall can be predicted at regional scales using fractional tree cover, highlighting its role in carbon budget assessments under climate change (Taskinsu-Meydan et al. 2010). Indeed, Brando et al. (2008) reported that litterfall recovered rapidly while wood increment improved only gradually; as a result, aboveground live carbon stocks declined significantly ($-32.5 \text{ Mg C ha}^{-1}$), creating a persistent deficit in the system's carbon budget.

This re-equilibration is not confined to tropical moist forests. In subtropical broadleaf forests, post-drought litterfall became more sensitive to climatic variables, with water-related factors playing a dominant role in recovery dynamics (Xiuwen et al. 2024). In kauri (*Agathis australis*) forests, drought years triggered sharp increases in litterfall, substantially elevating C and N fluxes and generating a transient litter pulse that enhanced substrate availability for decomposition and mineralization potential (Macinnis-Ng and Schwendenmann 2015).

Chronic water stress and/or structural shifts can permanently reposition the litterfall–nutrient cycling relationship into a different equilibrium. For example, a 10 year monitoring study in China showed that conversion from natural forest to plantation markedly reduced N, P, K inputs via litterfall, signalling long-term risks for soil fertility and drought sensitivity (Ni et al. 2021). Similarly, in northeastern India, comparisons between natural oak forests and plantations revealed that natural stands provided higher litter inputs and faster decomposition, thereby supporting more efficient nutrient turnover (Pandey et al. 2007). These contrasting equilibrium states determine the buffering capacity of

ecosystems, microbial functioning, and leaf nutrient status under drought years (Kim et al. 2003).

3.3. Synthesis and Implications

Findings on drought–litterfall relationships generally reveal a two-phase process:

(i) Short-term shock: Reproductive components (flowers and fruits) show a rapid and pronounced decline, while leaf and fine branch litterfall may increase contextually or exhibit only limited changes. During this phase, stem growth decreases sharply (Brando et al. 2008; Rowland et al. 2018; Janssen et al. 2021).

(ii) Long-term new equilibrium: Over time, the link between litterfall and climatic variables is reestablished, with reproductive fractions recovering and, in some cases, exceeding control levels. At the same time, a new balance emerges between litterfall and stem growth, accompanied by persistent deficits in the ecosystem’s carbon budget (Brando et al. 2008; Rowland et al. 2018).

These results demonstrate that component-based differentiation of litterfall (leaf, flower–fruit, fine branch) should be routinely incorporated into drought monitoring. Integrating litterfall data with growth and climatic variables is critical both for understanding underlying processes and for improving ecosystem models. From a management and modelling perspective, it is essential to accurately represent component-specific thresholds and recovery times (e.g., branch < leaf < flower–fruit), as well as to account for lags in decomposition–nutrient feedbacks (Brando et al. 2008; Xiuwen et al. 2024).

4. DECOMPOSITION–NUTRIENT CYCLING AND FUNCTION UNDER STRESS

In forest ecosystems, litter decomposition and nutrient cycling are the primary drivers of tree growth and increment. Litterfall represents the major source of organic matter accumulated on the soil surface; through its decomposition, pools of N, P, K, and soluble C are released, providing resources for microorganisms and enhancing aboveground productivity (Macinnis-Ng and Schwendenmann 2015; Paudel et al. 2015). Drought and accompanying stresses simultaneously alter: (i) substrate quality (leaf C:N:P:K ratios, lignin/cellulose content), (ii) climate-related constraints (soil water, temperature, radiation), (iii) the decomposer food web (microorganisms–mesofauna–macrofauna), and (iv) plant nutrient-use strategies. The following section explains how drought and related stresses influence decomposition–nutrient cycling in relation to litter components, trophic groups, and nutrient limitations.

4.1. Litter Quality and Decomposition Rates

Drought alters leaf shedding and the chemical composition of litter, thereby influencing decomposition rates in ways that depend on species traits and phenology it can either accelerate or slow down decomposition. For example, in five deciduous species in northeastern USA, litter produced during drought contained 14% more N but 31% less pectin compared to post-drought cohorts; however, differences in decomposition rates remained species-specific and limited (Wilson et al. 2022). These results indicate that drought affects decomposition via changes in litter chemistry in a species-dependent manner. By contrast, in New Zealand's *Agathis australis* conifer forests, total litterfall increased by 72% during a drought year (2013), with most of the increase derived from leaf and fine branch fractions. This rise elevated carbon and nitrogen fluxes to the soil by ~85% and ~69%, respectively, yet reduced N concentration in leaves (Macinnis-Ng and Schwendenmann 2015).

Thus, under drought conditions the quantity of litter available for decomposition may increase, but its quality (e.g., N content) can decline.

In a long-term rainfall exclusion experiment in Mediterranean-type forests, *Phillyrea latifolia* litter decomposed more rapidly under drought due to its high N content, whereas differences in *Q. ilex* litter remained limited. Moreover, drought reduced soil mesofauna abundance by 38%, thereby lowering their contribution to decomposition; at the same time, increased light penetration to the forest floor due to canopy thinning facilitated photodegradation of lignin and cellulose, providing an opposing pathway (Villazón-Orozco et al. 2025). These findings suggest that decomposition is under dual control: while microbial processes slow under water limitation, photodegradation can partially compensate.

4.2. Decomposer Communities: Microorganisms and Soil Fauna

The decomposition process depends not only on the properties of the organic material shed but also on the structure and functional activity of decomposer communities. Soil fauna and microorganisms play critical roles in maintaining nutrient cycling and mineralizing organic matter. However, under prolonged drought conditions, mesofauna abundance has been reported to decline significantly (-37.9%), thereby reducing their contribution to decomposition (Çakır et al. 2018; Villazón-Orozco et al. 2025). Similarly, drought-induced reductions in canopy density decrease light attenuation, facilitating photochemical breakdown. Thus, decomposition is shaped by the combined effects of biotic activities (fauna and microbial processes) and abiotic drivers such as photodegradation (Austin and Vivanco 2006; King et al. 2012).

At the microbial level, drought alters the composition and function of root-associated bacterial communities. Declines in water availability, diffusion constraints, and changes in root exudates direct microbial

diversity, while plant stress responses (e.g., antioxidant defenses, root morphological changes) further shape microbiome selection (Naylor and Coleman-Derr 2018). Under drought conditions, the selection of desiccation-tolerant taxa, shifts in root exudate composition, and differentiation of initial microbial communities trigger functional changes in enzymatic decomposition processes (Bastida et al. 2017; Schimel 2018). In this way, drought reshapes decomposition pathways through both biotic community dynamics and enzymatic capacity.

4.3. Nutrient Limitations: The Critical Roles of K and P

In dry seasons, increased litterfall and stagnation in productivity represent a fundamental defence mechanism of plants; however, the severity of this response is shaped by nutrient limitations. Studies have shown that leaf litterfall can be particularly constrained by potassium (K) and phosphorus (P). K supplementation during the dry season reduced leaf litterfall (i.e., extended leaf lifespan), while the effect of P emerged only during prolonged drought years. Moreover, K addition delayed the peak timing of litterfall (Manu et al. 2024). Thus, drought-induced increases in litterfall during dry seasons highlight the interactive role of both water scarcity and nutrient limitations within ecosystems.

From a management perspective, fertilization in eucalyptus plantations reduced litter C:N and C:P ratios, enhanced soil enzyme activities (β -glucosidase, urease, polyphenol oxidase), and thereby accelerated decomposition. Seasonal irrigation during dry periods also enhanced decomposition, though nutrient release was influenced particularly through the carbon/potassium (C:K) ratio (Kong et al. 2022). This study indicates that decomposition rates are primarily determined by litter nutrient ratios, followed by enzyme activity, and finally by water availability; in some forest ecosystems, nutrient limitations may therefore exert a stronger influence than water scarcity.

In conclusion, decomposition and nutrient cycling under drought cannot be monitored by a single indicator; litterfall components, nutrient ratios, enzyme activities, and soil fauna must be considered together. Findings demonstrate that drought may either impair litter quality and slow decomposition or, in some cases, partially compensate through enhanced leaf litterfall and photodegradation. Moreover, the availability of K and P strongly shapes the timing and quantity of litterfall, while litter manipulation experiments have shown that soil carbon stocks can shift by approximately $\pm 30\%$. Hence accounting for changes in litter quantity and quality, decomposition processes, and carbon–nutrient feedbacks during drought is critical for ecosystem management.

5. CONCLUSION

The relationships between stress factors and litterfall in forest ecosystems are critically important for tree physiological resilience and ecosystem functioning. Evidence shows that drought and heat stress cause short-term fluctuations in leaf and reproductive litter production, while in the long term they drive a reallocation of carbon. In these processes, litterfall is not merely a by-product of stress but functions as a key mechanism reorganizing carbon and nutrient cycles within ecosystems. When combined with pathogen and insect pressures, drought further complicates litterfall dynamics, influencing both decomposition rates and nutrient return.

In conclusion, litterfall emerges as a crucial variable for detecting both the early warning signals of stress and its long-term impacts on ecosystems. Therefore, stress research must incorporate fraction-based litterfall separation, routine monitoring of nutrient contents, and integration with decomposition processes. From a management perspective, the interactions between water and nutrient limitations,

species-specific responses, and the thresholds of multiple stresses must be considered in adapting practices such as thinning, species selection, and fertilization. In the era of climate change, monitoring litterfall processes and representing them more effectively in models are strategic imperatives for enhancing the resistance and resilience capacity of forests—both scientifically and in applied forestry.

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Chapter 14

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Thinning and Stress in Forest Trees

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1. INTRODUCTION

Climate-driven droughts and heat waves heighten the risk of hydraulic failure and carbon imbalance in forest trees, triggering growth declines and mortality. By lowering stand density, thinning relaxes competition for water–light–nutrients, thereby jointly regulating hydraulic processes, carbon allocation, and microclimate as a core tool of adaptive silviculture. The conceptual framework rests on three pillars: (i) an increase in per-tree water supply in the root zone and a wider hydraulic safety margin along the transport pathway; (ii) stomatal limitation engaged at higher atmospheric demand (vapor pressure deficit, VPD), allowing carbon gain to persist longer; and (iii) management of thermal load through adjustments in above- and below-canopy light and wind regimes. Accordingly, thinning has the potential to enhance both resistance (maintaining performance during disturbance) and resilience (speed of post-disturbance recovery), consistent with syntheses from the past decade (Sohn et al. 2016a; Moreau et al. 2022).

Cumulative evidence across species and climates points to a common pattern: following thinning, per-tree water use and growth may increase, while stand-level total water loss often remains similar or declines due to fewer stems; this alleviates the drought burden at the stand scale during dry periods (Sohn et al. 2016b). Tree-ring and stable-isotope records indicate a delay in the growth-cessation threshold during hot–dry years and faster recovery thereafter—a window of improved growth continuity—observed in both conifers (e.g., *Pinus* spp.) and broadleaves (e.g., Mediterranean evergreen oak coppice) (Sohn et al. 2016b; Moreau et al. 2022). Field measurements and remote-sensing studies likewise support these mechanisms by documenting accompanying shifts in microclimate and canopy energy balance (Sankey and Tatum 2022; Schrader-Patton et al. 2024).

Conversely, over-thinned stands can experience elevated midday VPD, leaf temperature, and wind exposure, introducing short-lived physiological constraints and tissue-damage risks. Therefore, the intensity, timing, and frequency of thinning should be calibrated to local thresholds considering species strategy (iso-/anisohydric tendencies), age/social position, site conditions (climate–soil), and target density metrics (basal area—BA; stand density index—SDI). Long-term evaluations show that such threshold-aware prescriptions can mitigate drought impacts in both the short and long term, particularly in mountainous and water-limited regions (Elkin et al. 2015; Moreau et al. 2022; Gül and Esen 2024).

First, this chapter examines competition and stand density (BA, SDI, LAI) together with crown architecture and social position, and how these relate to physiological stress. It then discusses hydraulic responses and water balance (Ψ_{leaf} , sap flow, soil water) alongside microclimate/VPD effects. Next, we synthesize the carbon economy, growth–climate sensitivity, and water-use efficiency (WUE) to evaluate how thinning influences resistance and recovery. Finally, we outline thinning prescriptions—timing, intensity, frequency, and method—with threshold-based density targets (BA/SDI).

2. COMPETITION AND STAND DENSITY: LINKS TO STRESS INDICATORS

At the core of thinning's stress-mitigating effect lies the reconfiguration of competition. When stand density (e.g., basal area—BA, stand density index—SDI, crown ratio, and leaf area index—LAI) is reduced, the share of soil water and light per tree increases while root and crown competition weakens. Theoretical expectations are that thinning will: (i) attenuate declines in leaf water potential (Ψ_{leaf}), (ii) delay the onset of stomatal limitation (even under high vapor pressure

deficit, VPD), (iii) widen the hydraulic safety margin (the gap between the embolism threshold and the operating point), and (iv) promote a more balanced carbon allocation between growth and defence (Sohn et al. 2016a; Moreau et al. 2022).

2.1. Water Relations: Leaf Water Potential, Soil Moisture, Sap Flow

Following thinning, per-tree water use and transpiration frequently increase, whereas stand-level total water loss often remains similar or declines due to fewer stems; this helps alleviate collective drought stress at the stand scale during dry periods (Sohn et al. 2016a). Thermal and multispectral remote sensing further shows that canopy temperature and thermal-stress signatures weaken in thinned stands (Schrader-Patton et al. 2024). Regarding soil moisture, the configuration of within-stand gaps and vertical stratification is critical: post-thinning structural differences have been shown to markedly shape the spatial pattern of moisture during seasonal drought (Belmonte et al. 2022). In conifers, increases in per-tree water use often coincide with less negative daytime leaf water potential (Ψ_{leaf}); in Korean pine (*Pinus koraiensis* Siebold & Zucc.), varying thinning intensities elevated water use and growth and were accompanied by systematic shifts in water-use efficiency (WUE) (Park et al. 2018).

2.2. Growth–Climate Relationships and Stand Density: Ring-Based Evidence

Stand density markedly modulates the strength of the drought–growth relationship observed in tree-ring records. In Anatolian black pine (*P. nigra* Arn.) plantations, sensitivity to climatic variables decreased after thinning, while water-use efficiency (WUE) increased (Martín-Benito et al. 2010). A multi-species study from the North Temperate region similarly showed that thinning weakens drought

sensitivity and responses to climatic variability, leading to systematic reductions in vulnerability metrics (D'Amato et al. 2013). Long-term observations—especially in Mediterranean pines—indicate that thinning strengthens growth continuity as well as drought resistance and resilience; notably, this effect persists even under non-stationary climate conditions (Sohn et al. 2016b).

2.3. Crown Architecture and Social Position

Competition is asymmetric: dominant trees benefit from superior light access, whereas suppressed individuals are more vulnerable in terms of water and nutrient status. Review evidence shows that tree height and social position are closely linked to drought-related mortality and growth decline, and that thinning reduces these asymmetries (Grote et al. 2016). That said, over-thinning can locally amplify wind exposure, midday VPD, and solar load, temporarily intensifying heat stress. In European beech (*Fagus sylvatica* L.), thinning at appropriate densities reduced growth losses not only under drought but also after late-spring frost (Rubio-Cuadrado et al. 2024). Accordingly, density thresholds (target BA/SDI) should be defined for each species–site combination, while maintaining vertical stratification and managing edges to preserve microclimatic balance.

3. HYDRAULIC RESPONSE AND WATER BALANCE

Thinning's effects on water stress can be read through three coupled components: (i) leaf water potential (Ψ_{leaf}), (ii) per-tree water use/sap flow, and (iii) soil water status (θ , Ψ_{soil}). As stand density declines, per-tree water supply in the rooting zone increases, crown competition and pathway resistance decrease. Together, these changes widen the hydraulic safety margin and allow stomatal limitation to be engaged later on dry days (Sohn et al. 2016a). However, in over-thinned

structures, midday increases in VPD/thermal load can partly offset these gains; hence, responses are sensitive to density thresholds and microclimate management (Sohn et al. 2016b; Schrader-Patton et al. 2024).

3.1. Metrics and Interpretation Guidelines

Ψ_{leaf} (predawn–midday): Predawn Ψ_{pd} reflects the soil–root water status, whereas midday Ψ_{md} captures the response to atmospheric demand (VPD). After thinning, Ψ_{pd} —and in most cases Ψ_{md} —tends to become less negative; under extreme drought, improvements in Ψ_{md} may be limited (Bréda et al. 1995; Sohn et al. 2013).

Sap flow (J_s ; Q_{tree}): Commonly measured with heat-dissipation or heat-ratio methods. Thinning can increase per-tree sap flow, while stand-scale water loss (ET) in many studies remains similar or declines due to fewer trees (Sohn et al. 2016a; Park et al. 2018).

Soil water (θ , Ψ_{soil}): Post-thinning structure (gap size, vertical stratification) markedly reshapes the spatial distribution of moisture during the dry season; sensor arrays reveal clearer under-gap water-availability patterns (Belmonte et al. 2022).

3.2. Ψ_{leaf} : The Hydraulic Signature of Competition

Across multiple species and climates, thinning has repeatedly been shown to make predawn Ψ_{pd} less negative and to moderate midday Ψ_{md} with respect to atmospheric demand (Sohn et al. 2016a). In Norway spruce (*Picea abies* L.), heavy thinning does not necessarily increase relative growth during drought, yet it markedly accelerates post-drought recovery; isotope evidence ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) indicates a reduction in hydraulic load and a rebound in carbon assimilation (Sohn et al. 2013). In a broadleaf forest tree species example, sessile oak (*Quercus petraea* Matt.) showed improved soil–tree water relations and smoother daily

Ψ_{leaf} dynamics after thinning, leading to recovery of transpiration and growth (Bréda et al. 1995).

3.3. Sap Flow and Per-Tree/Stand Water Use

In Korean white pine (*P. koraiensis*), a four-year monitoring across thinning intensities documented higher per-tree sap flow and biomass increment, accompanied by improvements in water-use efficiency (WUE) (Park et al. 2018). Consistently, meta-analysis shows that thinning tends to increase per-tree water use, while stand-level total water loss (ET) in most scenarios declines or remains unchanged because fewer stems transpire (Sohn et al. 2016a). Together, these responses alleviate collective drought stress during dry periods and widen the hydraulic safety margin at the stand scale.

3.4. Soil Moisture: Spatial Pattern and Seasonality

In semi-arid to dry forests, dense sensor networks reveal that post-thinning soil water potential (Ψ_{soil}) develops pronounced spatial heterogeneity through the summer drought; under-gap water-availability pockets can persist (Belmonte et al. 2022). As a result, during the most severe phases of drought, the root-zone water supply is buffered and declines in Ψ_{leaf} are limited. Thermal–multispectral remote sensing likewise confirms that, after thinning, the density of canopy-temperature “hot spots” decreases and stand water balance improves (Schrader-Patton et al. 2024).

3.5. Species Strategies (Isohydic–Anisohydric) and Age/Social Class

In isohydric strategy, trees restrict stomata early under drought to keep leaf water potential (Ψ_{leaf}) within a narrow range; this increases hydraulic safety but constrains carbon uptake sooner. In anisohydric strategy, stomata close later; Ψ_{leaf} is allowed to drop further, so carbon

uptake continues longer but the risk of hydraulic failure rises. In isohydric species e.g., *P. abies* trees keep Ψ_{leaf} tightly controlled; therefore, thinning does not necessarily increase growth during drought but markedly accelerates post-drought recovery (Sohn et al. 2013). By contrast, in anisohydric species e.g., Scots pine (*P. sylvestris*) because Ψ_{leaf} is allowed to fluctuate more widely, frequent and/or heavy thinning can strengthen long-term indicators of drought adaptation (both resistance and recovery) (Sohn et al. 2016b). Thinning also reduces differences among crown classes; in suppressed individuals, Ψ_{leaf} and growth responses become more balanced. Finally, pre-commercial thinning in the juvenile stage lowers future drought sensitivity and enhances hydraulic flexibility (Wotherspoon et al. 2022).

3.6. Density, Timing, and Risk Management

Moderate-intensity thinning maximizes hydraulic benefits. In contrast, over-thinned stands often show higher midday vapor pressure deficit (VPD), thermal load, and wind exposure, which can cause short-lived drops in midday Ψ_{leaf} (Ψ_{md}) and raise tissue-level risks (cambial heating, sunscald). Therefore, targets for basal area (BA) and stand density index (SDI) should be calibrated to species and site conditions, while edge shading and vertical stratification are maintained.

4. CARBON ECONOMY, GROWTH, AND WATER-USE EFFICIENCY

Thinning influences the carbon economy along three planes: (i) source–sink dynamics (photosynthesis, NSC–non-structural carbohydrate reserves, and growth–defense allocation), (ii) growth continuity and climate sensitivity (tree-ring–based resistance–recovery metrics), and (iii) water–carbon efficiency (WUE). As density and competition decline, improved access to resources (water/light) relieves

sink limitations, delays premature growth cessation, and stabilizes the carbon balance during drought years. Conversely, in over-thinned stands, midday increases in vapor pressure deficit (VPD) and thermal load can impose short-lived photosynthetic constraints; thus, the magnitude of benefit is sensitive to target density thresholds.

4.1. Source–Sink Interplay and Growth Continuity

In Mediterranean oak coppices, thinning postponed the phenological threshold at which growth ceases under drought, thereby extending the stem-growth season—evidence that thinning is particularly effective where growth is sink-limited (i.e., by cambial activity) (Cabon et al. 2018). Similarly, in Aleppo pine (*P. halepensis*), high-intensity thinning under prolonged aridity facilitated the recovery of per-tree leaf area and growth metrics; after drought, carbon allocation and the leaf–stem ratio were rebalanced (Calev et al. 2016). Early-life interventions can also yield gains that carry over to later years, constraining drought-period growth losses: in young *P. contorta* stands, juvenile thinning under water limitation increased both stem increment and water use (Wang et al. 2019).

4.2. Growth–Climate Sensitivity and Resilience

In conifers, thinning generally reduces the sensitivity of growth to climatic variability and dampens interannual variability. A tree-ring study in red pine (*Pinus resinosa* Ait.) showed that low thinning from below lowered climate sensitivity while increasing tree size; at intermediate basal areas, it yielded the best compromise among tree size, stand biomass, and low climate sensitivity (Magruder et al. 2013). In *P. halepensis*, thinning across a range of intensities stabilized growth–climate relationships, making responses to short-term climatic fluctuations more muted (Olivar et al. 2014). Long-term observations draw a similar picture: across Alpine forests with differing stand

structures, thinning alleviated the growth impacts of drought in both the short and long term (Elkin et al. 2015).

4.3. Productivity and Leaf Area

Leaf area index (LAI) is a primary determinant of carbon gain, yet the LAI–productivity relationship is strongly modulated by water limitation. Along a water-stress gradient in Chilean Monterey pine (*Pinus radiata*) plantations, thinning reset the LAI–yield relationship in a water-sensitive manner: at appropriate densities, LAI maximized carbon uptake without exacerbating water stress (Ojeda et al. 2018). This underscores a dual objective for thinning: constraining excessive LAI to enhance hydraulic safety while retaining sufficient LAI to sustain photosynthetic capacity.

4.4. Water Use Efficiency

Water use efficiency (WUE) depends on method and scale (e.g., intrinsic WUE, $iWUE = A/gs$; growth-based WUE = biomass increment/transpiration; ecosystem WUE = GPP/ET). In young *P. contorta*, juvenile thinning increased per-tree water use while simultaneously boosting growth; in such cases, reported WUE responses differ with definition and scale (Wang et al. 2019). In rainfall-exclusion $\times$ thinning experiments, above-ground production and allocation shifted; while drought effects on ANPP persisted, thinning rescaled functional relationships (e.g., productivity–transpiration, productivity–leaf production) (Gavinet et al. 2019). Long-term monitoring of commercial thinning indicates that increases in stem diameter/silvicultural vigor and survival at the tree level can co-occur with controlled stand-level water loss, making yield–WUE trade-offs manageable at operational scales (Bose et al. 2018).

4.5. Survival and Long-Term Carbon Gains

In practice, the carbon economy is realized as a combination of sustained growth and low mortality. In four major North American softwood species, commercial thinning spanning a range of densities and timings increased per-tree growth and raised survival over 13–24 years. Transient increases in mortality observed in the early years under some treatment intensities were offset over the long term by appropriate thinning regimes (Bose et al. 2018). This confirms that thinning is effective not only in tree-ring metrics but also for composite carbon outcomes—including stem increment, stand volume, and product yield—even under stochastic drought events.

5. MICROCLIMATE AND EXTREME EVENTS (VPD, THERMAL LOAD, LATE FROST)

Thinning influences microclimate along three axes: (i) the radiation–light regime (loss of shading and increased shortwave radiation), (ii) airflow and heat budget (thinner boundary layers with wind, larger diurnal temperature amplitudes), and (iii) atmospheric water demand (VPD) and the resulting leaf and canopy temperatures. By increasing light and wind penetration below the canopy, thinning can cause short-lived midday rises in vapor pressure deficit (VPD) and leaf temperature. Conversely, it typically increases per-tree soil water availability and the hydraulic safety margin. The balance between these two effects—higher thermal load versus lower water stress—is set by the applied density level and site conditions (climate–soil) (Chase et al. 2016).

5.1. Vapor Pressure Deficit and Thermal Load

In conifers of dry interior regions, pre-commercial thinning increases photosynthetically active radiation (PAR) and wind speed beneath the canopy. This elevates daytime vapor pressure deficit (VPD) and, as the boundary layer thins, promotes faster nocturnal cooling. Although leaf temperature can rise briefly at midday, reduced competition generally diminishes water stress and smooths diurnal Ψ_{leaf} variability; in light-limited individuals, net carbon gain increases (Chase et al. 2016). Remote-sensing studies show that, after thinning, the density of canopy-temperature “hot spots” declines and stand water balance improves—an effect that becomes especially visible as greater drought resilience during extreme heat waves (Sankey & Tatum 2022; Schrader-Patton et al. 2024). That said, heavy thinning can raise VPD and midday thermal load excessively, increasing the risk of needle scorch; this threshold should be managed using appropriate target BA/SDI levels and a mosaic gap pattern.

5.2. Compound “Heat + Drought” Events

In very hot and dry years, thinning diversifies microclimate spatially: arranging gaps alongside narrow “reserve” strips that limit wind, and radiation creates escape pockets for both transpiration and leaf temperature. Observations and modelling indicate that such configurations improve canopy-scale energy balance and delay the threshold of photosynthetic collapse on the hottest days (Sankey & Tatum, 2022; Schrader-Patton et al. 2024).

5.3. Late-Spring Frost: Direction of Risk and Buffering

Thinning can theoretically increase nocturnal radiative cooling and thus frost risk; however, when density and spatial pattern are chosen judiciously, the impact of frost on growth can be attenuated. In *Fagus sylvatica*, thinning at appropriate densities significantly reduced the

negative effect of late-spring frost on stem radial growth (Rubio-Cuadrado et al. 2024). By rebalancing overstory light and competition, suitable density thinning stabilizes budburst phenology, lowering the likelihood of premature flushing coinciding with frost. When frost does occur, reduced competition facilitates rapid mobilization of non-structural carbohydrate reserves and canopy repair; as a result, growth losses are limited and recovery accelerated. In addition, patch–mosaic openings (small gaps with retained overstory continuity) help disperse cold-air pooling, mitigating frost damage.

5.4. Species Strategy and Age/Social Class

In isohydric-leaning species (e.g., *Fagus sylvatica*), thinning makes stomatal restriction under higher heat and VPD less costly and speeds post-frost recovery (Diaconu et al. 2017). In anisohydric or more deeply rooted pines (*P. ponderosa*, *P. halepensis*), microclimatic opening provides an advantage for sustaining carbon uptake during the dry season; however, large single-tree gaps can raise midday VPD and leaf temperature (T_{leaf})—risks that are mitigated by progressive and strip–mosaic layouts (Calev et al. 2016; Skov et al. 2004).

6. SPECIES–AGE–SOCIAL POSITION DIFFERENCES

Thinning’s stress-mitigating effect varies with species-specific physiology, developmental stage (juvenile vs. mature), and social position (dominant/co-dominant/suppressed). Together with traits such as water-use strategy (iso-/anisohydric), rooting depth, crown architecture, shade tolerance, and leaf area (LAI), these axes determine hydraulic safety, carbon allocation, and microclimatic exposure.

6.1. Species Differences

Conifers. In *Pinus* spp. (e.g., red pine, *radiata*, *ponderosa*) and *Picea*, thinning reduces competition, weakens the drought–climate signal in growth, and strengthens growth continuity. In *P. resinosa*, intermediate densities yielded the best compromise among larger tree size, stand biomass, and low climate sensitivity (Magruder et al. 2013). In *P. radiata*, along a water-stress gradient, thinning reset the LAI–yield relationship in a water-sensitive manner—maintaining productivity while limiting hydraulic pressure (Ojeda et al. 2018). In *ponderosa* pine, tree size $\times$ drought interactions after thinning + prescribed fire rendered physiological responses (gs, Tleaf) size-dependent (Skov et al. 2004).

Broadleaves. In Mediterranean evergreen oak coppices, thinning delayed the growth-cessation threshold during dry years and extended the growing period (Cabon et al. 2018). In beech (*Fagus sylvatica*), moderate thinning reduced growth losses due to both drought and late-spring frost, thereby increasing tolerance (Diaconu et al. 2017).

Practical note. In Mediterranean and semi-arid sites, the light–water trade-off is critical: in *P. halepensis* and *Pinus nigra*, somewhat stronger thinning can be beneficial, whereas in isohydric species over-opening may backfire via midday VPD/Tleaf spikes.

6.2. Age Class

Juvenile/pre-commercial thinning: In young stands, pre-commercial and juvenile thinning increases hydraulic flexibility in later drought years. In Black spruce (*Picea mariana*), pre-commercial thinning alleviated drought stress and improved both growth and tree–soil water relations (Wotherspoon et al. 2022). In young *Pinus contorta*, juvenile thinning under water limitation increased stem increment and water use (Wang et al. 2019).

Mature stands: In maturity, thinning can reduce growth–climate sensitivity and enhance tolerance, but over-thinning may raise exposure to wind and midday heat, limiting net benefits (Magruder et al. 2013; Diaconu et al. 2017).

6.3. Social Position and Crown Class

Despite their light advantage, dominant trees can operate near the limits of water–nutrient sharing under high competition, whereas suppressed trees face a dual stress of light limitation and hydraulic limitation. Synthesis work shows that tree height and social position are closely linked to drought-related growth decline and mortality, and that thinning reduces asymmetric competition, thereby dampening these differences (Grote et al. 2016). In young *P. sylvestris*, individual-tree models indicate that thinning response is predictable from tree diameter and local competition; suppressed trees that are locally released exhibit a near-term growth surge (Pukkala et al. 2002). In *Cedrus atlantica* Manetti, the tree size $\times$ thinning intensity interaction governs the stability of ring–climate relationships (Guillemot et al. 2015).

6.4. Size Thresholds and Species-Specific Prescriptions

Small/medium diameters often show stronger relative growth responses and WUE improvements after thinning (Pukkala et al. 2002; Park et al. 2018).

Large diameters trees still benefit hydraulically, but edge effects/thermal load can be more pronounced—favor mosaic gap patterns and graduated (progressive) thinning (Skov et al. 2004; Magruder et al. 2013).

Species-specific examples: In *P. radiata* and *P. resinosa*, intermediate density targets achieve the best compromise between growth and low climate sensitivity (Magruder et al. 2013; Ojeda et al.

2018). In beech and Mediterranean evergreen oak coppices, moderate thinning coupled with phenology/reserve dynamics dampens drought and late-frost impacts (Diaconu et al. 2017; Cabon et al. 2018).

7. THINNING REGIME: TIMING, INTENSITY, FREQUENCY, AND METHOD

The stress-mitigating effect of thinning is not a simple yes/no outcome; it depends on when, how much, how often, and by which method it is applied. Reducing stand density relaxes competition for water and light and widens the hydraulic safety margin, while simultaneously resetting microclimate. Accordingly, regime design must jointly consider phenology and climate windows, target density thresholds, age and social class, and the spatial pattern of interventions (mosaic gaps, shading strips).

Timing is pivotal for managing microclimatic risks. In areas with high frost hazard, heavy thinning should not be clustered in early spring, when enhanced nocturnal radiative cooling can amplify frost damage. Indeed, in *Fagus sylvatica* moderate thinning reduced late-spring frost-related losses in stem growth (Diaconu et al. 2017; Rubio-Cuadrado et al. 2024). Creating very wide openings in early summer can push VPD and leaf temperature to undesired midday peaks and impose short-lived physiological constraints; this effect has been detected following pre-commercial thinning in dry interior regions (Chase et al. 2016). Hence, the guiding principle for timing is a calendar that minimizes overlap with frost windows and heat waves.

Regarding intensity, the literature indicates that, for most species and sites, moderate thinning strikes the best balance between hydraulic benefits and microclimatic costs. In *Pinus resinosa*, low thinning from below at moderate levels reduced over-sensitivity to climate signals

while increasing growth and tree size (Magruder et al. 2013). In *P. halepensis*, thinning stabilized growth–climate relationships and delayed drought-year growth collapse (Olivar et al. 2014; Cabon et al. 2018). Intensity, however, interacts with tree size: in *Cedrus atlantica*, the size $\times$ intensity interaction governed the stability of ring–climate responses; the same intensity can yield different outcomes across size classes (Guillemot et al. 2015). In dry and semi-arid *Pinus* stands, the edge effects and fragmentation induced by over-thinning can further erode the continuity of suitable habitats already projected to contract; therefore, it is essential to remain within a moderate thinning intensity, calibrated to species- and elevation-specific thresholds (Gül 2025).

Frequency and developmental stage shape long-term drought robustness. Pre-commercial/juvenile thinnings act as insurance for future dry years: in *Picea mariana*, pre-commercial thinning mitigated drought sensitivity (Wotherspoon et al. 2022), and in young *Pinus contorta* it raised both stem increment and water use under water limitation (Wang et al. 2019). Multi-species, commercial-thinning follow-ups show durable improvements in per-tree growth and survival over 13–24 years, indicating that appropriate recurrence supports carbon outcomes (Bose et al. 2018).

In method selection (thinning from below/above, crop-tree release), the goal is to reduce asymmetric competition while improving crown and root resource access for vital individuals. Individual-tree models in young *Pinus sylvestris* demonstrate that thinning response is predictable from diameter and local competition, and that locally released suppressed trees show a short-term growth surge (Pukkala et al. 2002). In *P. resinosa*, thinning from below also reduced climate sensitivity (Magruder et al. 2013). Therefore, method should focus not only on how many trees to remove, but which trees to release.

The spatial pattern is the main lever for balancing hydraulic gains with microclimatic costs. *Combining mosaic gaps* with shading strips caps midday $\Psi_{\text{leaf}}/\text{VPD}$ peaks while creating pockets of soil-water availability; sensor networks clearly show increased seasonal and spatial heterogeneity in soil moisture after thinning (Belmonte et al. 2022). Thermal and multispectral imaging likewise reports fewer canopy-temperature hot spots and improved water-balance indicators under suitable density and layout (Schrader-Patton et al. 2024). These findings support fine-tuning (touch-up) thinning: implement the regime, then track with sensors and remote sensing, and make small adjustments when threshold indicators are exceeded.

Finally, integrated treatments can reinforce thinning effects but require careful risk management. Across mountainous European forests, thinning has alleviated drought impacts in both the short and long term; when combined with fuel discontinuity (e.g., prescribed fire), performance can be maintained through multi-year drought–heat sequences (Elkin et al. 2015). In *P. ponderosa*, responses to thinning + prescribed fire interact with tree size and drought; in edge and high-radiation zones, gap sizes should be graduated to limit thermal/wind damage (Skov et al. 2004). Overall, the most robust approach is BACI-style monitoring (Before–After, Control–Impact) to continuously track Ψ_{leaf} , sap flow, ring-based resistance–recovery, and canopy temperature, updating the regime adaptively (Schrader-Patton et al. 2024).

8. CONCLUSION

This chapter shows that thinning influences the genesis and management of tree stress through coupled structural and physiological pathways. By reducing competition and stand density (e.g.,

BA/SDI/LAI), thinning restructures crown architecture and local microclimate, moderating vapor pressure deficit and thermal loads while enlarging hydraulic safety margins (via leaf water potential, sap flow, and soil-water access). These adjustments stabilize the carbon economy, support growth continuity under drought, and often improve water-use efficiency. The magnitude and durability of benefits remain contingent on species traits, age class, initial density, soil–climate context, and the timing–intensity–frequency of interventions. Accordingly, prescriptions should be adaptive and threshold-based, aligning density targets with site-specific risk profiles (heat waves, late frosts, multi-year droughts). Integrated monitoring—combining hydraulic and carbon indicators with canopy metrics, microclimate, and soil moisture—should explicitly quantify near-term yield gains against long-term resistance and resilience. In sum, well-timed, context-aware thinning is not merely a growth tool; it is a core climate adaptation strategy that safeguards functional integrity and ecosystem services in increasingly heat- and drought-prone forests.

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Plant Stress Responses: Integrating Molecular, Physiological and Ecological Approaches I

Chapter 15

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Biotic Stressors in Forest Ecosystems

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1. INTRODUCTION

Biotic stressors are important in tree health, stand dynamics and overall ecosystem integrity. Unlike abiotic stressors such as drought or extreme temperatures, biotic stressors originate from living organisms; these include pathogens (fungi, bacteria, viruses), insects, parasitic plants, and vertebrate herbivores. These biological agents can cause a wide range of damage, from localized lesions to adverse growth, widespread defoliation, disease outbreaks, and tree mortality. This can profoundly alter forest structure and function.

In recent years, the impact of biotic stressors has become a growing concern, with global climate crises becoming more pronounced. These changes often amplify the effects of biotic stressors. There are indications that the threat posed by forest pests and diseases has been steadily increasing in recent years. In particular, the accelerating effects of climate change play a critical role in this increase by increasing the susceptibility of host plants to stress and altering pests' geographical distribution and reproductive cycles. This leads to new outbreaks in previously stabilized ecosystems and a global deterioration of forest health (FAO 2022; Pautasso et al. 2022; Asaro et al. 2023). Furthermore, climate change is associated with changes in host sensitivity, pest distribution, and pathogen virulence (Desprez-Loustau et al. 2020; Pautasso et al. 2022; Turlure et al. 2024).

Recent research are increasingly focusing on the complex interactions between biotic and abiotic stressors, as it is recognized that combined stresses can lead to synergistic adverse effects, pushing forest ecosystems beyond loss of resilience (Jactel et al. 2021). It also highlights the role that global trade and human mobility play in the geographical spread of new pathogens and pest species, and the vulnerability of forests to invasive species poses a significant threat (Seidl et al. 2017).

Climate change is thought to amplify the effect between wildfires and insect outbreaks. Drought and high temperatures make trees more vulnerable to bark beetle and pathogen attacks. In this context, tree mortality caused by pests also increases the amount of flammable material in forests, leading to more severe and frequent fires (Biedermann et al. 2023). This, combined with the amount of dead trees following drought and fires, creates ideal breeding grounds for bark beetles, leading to devastating effects. Understanding these complex biological interactions and how they are modulated by environmental change is vital for developing effective forest management and conservation strategies in a changing world.

Recent scientific studies provide a better understanding of how plants cope with the stresses they experience, namely the cellular and molecular processes underlying their defense mechanisms. Each cell of the plant responds differently when faced with stress. Thanks to advanced methods such as single-cell RNA sequencing, we can see in great detail which genes work differently in plant cells under stress. These innovative studies reveal how cells in different parts of the plant (tissues and cell types) use their limited resources wisely in sensing and responding to stress, i.e., how they apply the principle of "resource efficiency" at the cellular level (Li et al. 2024). This suggests that when a plant encounters even a single type of stress, different cells apply different strategies and that this diversity enhances the adaptive ability of the plant in general. It suggests that plants not only distinguish between stressors but also adopt flexible and complementary adaptive strategies when faced with multiple threats, thus maximizing their chances of survival and reproduction.

In forestry, silvicultural treatments, growing environment conditions, and the genetic potential of forest trees directly affect the quality and quantity of wood and other forest products. Given that climate and existing soil conditions cannot be altered by man, efforts to

increase the productivity and resilience of forests focus on silvicultural interventions and tree breeding. Especially under the increasing influence of biotic stressors, classical breeding techniques play a critical role in securing the health and sustainability of forest ecosystems. Recent research have shown that classical breeding methods (such as selection breeding, hybridization breeding, and resistant breeding) still have great potential in identifying origins/populations, genotypes, or clones with high adaptability to different environments, strong biological adaptability, and high increments in forestry important traits such as wood yield (Yücedağ et al. 2021; Jansson et al. 2022; Gailing et al. 2023). For example, selecting and breeding individuals with natural resistance to pests or crossbreeding parents carrying these resistance genes can lead to forest populations that are more resilient to pathogen outbreaks and insect infestations (Snieszko and Cohen 2020; Porth and Rweyongeza 2022).

These traditional approaches, supported by genomic tools, accelerate breeding processes and allow for more precise identification of adaptive genotypes. Therefore, identifying and optimizing genetic potential and integrating it with appropriate silvicultural techniques remains an indispensable strategy for the future of our forests under changing climatic conditions and increasing biotic threats.

This section aims to comprehensively address the biotic stress factors that forest ecosystems face and the defense strategies that plants have developed against these threats. First, the impacts of increasing insect populations on forests and the fundamental roles of insects within these ecosystems are discussed. Then, attention is directed to the species that cause the greatest damage to woody taxa in Turkey. In addition, emphasis has been placed on the foundations of sustainable management strategies aimed at preserving forest health.

2. PLANT DEFENSE STRATEGIES AGAINST BIOTIC STRESSES

Trees can be subjected to different herbivore and pathogen pressures, and protection from these adverse conditions requires different conservation modes. While information from herbaceous species is mostly utilized, the findings from these models are not always applicable to forest trees (Hammerschmidt 2006). Three defense strategies generally define resistance traits in plants. These are direct defense, indirect defense, and tolerance (Karban and Baldwin 1997). For plants, mechanical protection, growth strategies (repair of damaged parts in perennial plants), spines, trichomes, hairs, resins, and waxes function as physical barriers to protect plants against pathogens and herbivores (Fürstenberg-Hägg et al. 2013), chemical protection is provided by the cell wall (presence of lignin), the synthesis of inhibitory proteins or enzymes capable of degrading microbial cell walls and other microbial components, or peroxidase and phenoloxidase that can help inactivate phytotoxins of microbial origin, and additionally proteins that can also be considered an anti-herbivore strategy (Wink 1984; Boller and Wiemken 1986).

During their lifetime, conifers are exposed to many herbivorous insects (e.g. bark beetles, beetles, budworms) with different feeding strategies and preferences. To protect themselves against insect attacks, trees have a wide range of adequate protection mechanisms, including producing specialized compounds that exert repellent anti-nutritive or toxic effects on herbivores (Franceschi et al. 2005; Howe and Jander 2008). While physical and chemical defenses are considered 'direct defenses,' 'indirect defenses' of plants include volatile compounds (e.g., terpenes) that attract predators and parasitoids of herbivorous insects (Dicke et al. 2003).

Plant secondary metabolites play important functions in plant defense and ecological roles. These secondary compounds can be

divided into three main categories: alkaloids, terpenoids, and phenolics (Bernards 2010a, 2010b). When herbivores attack plants, they try to reduce herbivore damage by reducing nutrient quality. Studies have shown that herbivore damage decreases as plants grow and develop (Haukioja and Koricheva 2000; Warner and Cushman 2002). For this reason, the youth period for plants is the most important period to fight against pathogens (Stowe et al. 2000).

Many insect species survive in forest habitats. It is evident that these insect species damage trees. According to the type of damage caused by insects on plants, insects are divided into five groups. These are leaf-damaging insects, i.e., leaf-feeders, borers (bark and tree pests), sucking insects, gall-formers (abnormal growth of tissues), and root-feeding insects (harmful to plant roots) (Glavendekić and Medarević 2010).

The defense mechanisms developed by plants against damaging insects are minimal compared to those developed by host plants against pathogens. When a herbivorous insect damages the plant, its response is often modified by insect-specific elicitors, allowing plants to optimize their defenses. Insects that differ in this respect trigger different but overlapping gene expression patterns. The specific plant response may depend on differences in mechanical damage to the tissue. This is related to the type of mouthparts, feeding method, compounds entering a plant, and insect saliva, i.e., oral and digestive tract secretions (Howe and Jander 2008). Elicitors are defined as signals that plants are close to being attacked or substances that trigger the production of bioactive compounds when they are incorporated into plant cells, even in tiny amounts (Naik and Al-Khayri 2016). This is because elicitors are compounds that activate plant chemical defenses (Holopainen et al. 2009).

Plant resistance to biotic stress depends on structural and induced mechanisms. Depending on the damage caused to plant tissues by

herbivorous insects, stimuli, including salivary gland secretions and gastrointestinal secretions, trigger signals that generate plant defenses. Moreover, the type of damage and elicitor activate specific signaling pathways and the biosynthesis of secondary metabolites. At the same time, plants can recognize compounds that are oral secretions of insects (Felton and Tumlinson 2008; Fürstenberg-Hägg et al. 2013).

The ability of plants to sense insect attacks and initiate specific defense responses is vital. This sensing occurs through specialized molecular patterns (Herbivore-Associated Molecular Patterns, HAMPs) found in insect saliva or footprints. When plants perceive these signals, they directly produce toxic or deterrent secondary metabolites and activate indirect defense mechanisms. For example, releasing volatile organic compounds (VOCs) that attract insects' natural enemies (predatory insects or parasitoids) is one of these strategies (Kaiser et al. 2023). These VOCs act as a "distress signal," creating a warning system against insects attacking the plant.

Furthermore, the role of the microbiome in plant defense is increasingly understood. Some microorganisms associated with roots or leaves have been found to increase plant resistance to biotic stress by enhancing plant defense responses or producing compounds that directly affect insects (Durán et al. 2024). At this point, the effects of climate change, which have been frequently discussed in recent years, are the primary focus. Increasing CO₂ levels or changing temperature regimes can alter the chemical defense profile of plants. This, in turn, may cause insects to become more harmful to plants or, conversely, make their defenses more effective (Rasul et al. 2024). These complex interactions emphasize the importance of developing holistic approaches to biotic stress management that consider not only the plant's defenses but also environmental factors and other living organisms in the ecosystem.

Plants use specific receptor proteins to recognize pathogens as "threats." These receptors recognize pathogen-associated molecular

patterns (PAMPs - Pathogen-Associated Molecular Patterns) such as cell wall components or secreted toxins. This recognition triggers a series of signaling mechanisms that spread rapidly within the plant. For example, calcium signaling and reactive oxygen species (ROS) production is one of the first and most rapid steps of the plant's defense response (Meng et al. 2024). ROS both directly inhibit the growth of the pathogen and initiate further defense mechanisms by altering gene expression in the plant. Research on ROS signaling has also gained new dimensions. ROS are not only a harmful by-product but also function as critical signaling molecules that coordinate stress responses in the plant. The delicate balance between the production and scavenging of ROS is essential for the plant to activate its defense mechanisms effectively and simultaneously prevent oxidative damage (Meng et al. 2024). Disruption of this balance may cause the plant to be vulnerable to stress. Also noteworthy are studies focusing on the genetic manipulation of the production pathways of PR (pathogen-associated) proteins and phytoalexins in plant immunity. PR proteins are a diverse group of defense proteins that plants produce in response to pathogen attacks and may have direct antimicrobial activity or play an important role in plant immune signaling. Phytoalexins are low molecular weight compounds with broad-spectrum antimicrobial properties synthesized by plants after infection or stress. These substances accumulate in plant cells and inhibit the growth of pathogens or kill them. Developing plants that increase the production of these defense molecules or synthesize more effective forms of them through genetic manipulation will aim to protect plant health in an environmentally friendly approach by reducing the use of chemical pesticides. For example, transferring genes that increase phytoalexin production in tomatoes significantly increases the plant's resistance to fungal diseases (Shiratake et al. 2005; He et al. 2020), while overexpression of specific PR proteins in tobacco plants can provide a

stronger immune response against virus infections (Datta et al. 1999; Liu et al. 2007).

While classical breeding techniques still play a fundamental role in forestry, recent research shows that genomic breeding and gene editing technologies such as CRISPR-Cas9 offer revolutionary potentials in enhancing resistance to biotic stresses. These modern approaches overcome the constraints faced by traditional breeding processes, such as long timelines and limited genetic variation (Liu et al. 2023). Genomic breeding utilizes information in the genetic code of trees to identify disease or pest-resistant genotypes early and accurately. This accelerates the selection of individuals with desired traits and shortens breeding cycles (Borthakur et al. 2022; Chen et al. 2024).

In particular, precision gene editing tools such as CRISPR-Cas9 can directly manipulate resistance mechanisms by targeting specific genes that interact with plant pathogens or insects. For example, it is possible to activate genes that initiate or enhance plant defense responses or to deactivate susceptibility genes that facilitate pathogen entry (Kim and Kim 2021; Bhat et al. 2023). This is particularly advantageous for developing fast and effective solutions to emerging or rapidly spreading disease and insect threats. However, issues such as the potential long-term impacts of gene-edited trees on the ecosystem, public acceptance, and regulatory considerations remain important areas of research and debate ahead of the widespread application of these technologies (Mullins et al. 2023; Van Deynze et al. 2024).

Silencing or modifying disease susceptibility genes (S-genes), which are the cornerstones of the plant immune system, has also become possible with CRISPR-Cas9. Using gene editing technologies such as CRISPR-Cas9, the potential to increase the resistance of plants against diseases by targeting genes that increase the production of these defense components or make them more efficient is being investigated (Li et al. 2022; Bhat et al. 2023).

Recent studies show that plants respond not only to the direct attack of the pathogen but also to the damage caused by the pathogen in plant tissues. Damage-associated molecular patterns (DAMPs), which are generated by the plant cell wall breakdown, further strengthen the plant's defense system. These DAMPs lead to the activation of specific genes that help the plant to repair itself and prevent the spread of infection (Duran et al. 2023).

In plant defense strategies, the complex interplay of phytohormones (especially salicylic acid and jasmonic acid) defense pathways plays a key role in generating pathogen-type-specific responses. Against bacterial or bio-trophic (feeding on living cells) pathogens, the salicylic acid pathway usually predominates, whereas, against necro-trophic (feeding on dead cells) pathogens or insects, the jasmonic acid pathway may be more dominant. The delicate balance between these two pathways allows the plant to utilize its limited resources most efficiently (Zou et al. 2024). Current research also explores the potential to increase plant resistance to stress through genetic manipulation of these hormonal networks (Shigenaga et al. 2021).

Changes in plant metabolism in response to herbivore or pathogen attacks are likely governed by complex transcriptional activities involving genes encoding both primary and secondary metabolism. Procedures performed by researchers such as microarrays, subtractive libraries, AFLP-cDNA display, and DDRT-PCR are important to study the differences in the transcriptome that occur in plants exposed to herbivore attack and also to recognize differences in gene expression between genotypes that vary in resistance. These methods are new techniques that have recently been applied in plant-insect interactions. The data obtained showed that changes due to herbivore and pathogen attacks are comparable (Schenk et al. 2000; Maleck et al. 2000).

Studies investigating how plants establish stress-specific patterns of gene expression and how these patterns are affected by a single stressor (e.g., drought) or multiple stressors (e.g., combination of drought and heat) are critical to our understanding of plant adaptation mechanisms. Epigenetic mechanisms (such as DNA methylation and histone modifications) have been identified to play an important role in how plant genes "turn on and off" or modulate the stress response and, in turn, in the formation of stress memory (Miryeganeh 2024). This means that by "remembering" previous stress experiences, plants can develop faster and more effective responses to similar stresses in the future.

3. IMPACTS OF INCREASING INSECT POPULATIONS ON FORESTS

The impact of increasing insect populations on forests has become a global problem, especially nowadays, when the effects of climate change are increasing. These increases can cause significant disturbances in forest ecosystems, accelerating tree mortality, altering forest structure, and affecting the carbon cycle. Recent research suggests that changing temperature and precipitation regimes associated with climate change are critical in increasing the severity and frequency of insect outbreaks (Bentz et al. 2022; Gámez-Rodríguez et al. 2024). For example, shorter life cycles of pests such as bark beetles and their ability to produce multiple offspring per year, combined with warmer winters and reduced defensive capacity of trees weakened by drought, are causing large-scale tree mortality (Fettig et al. 2021; Singh et al. 2024). Increasing populations of leaf-eating insects (defoliators) slow tree growth, reduce photosynthetic capacity, and make trees more vulnerable to secondary stressors (Raffa et al. 2015). Furthermore, the spread of invasive insect species into new regions through global trade and travel causes severe imbalances in local ecosystems, allowing species without natural

enemies to spread rapidly and damage new forest areas (Seidl et al. 2017; Lázaro-Lobo and Ervin 2021). This has long-term negative impacts on forest health, biodiversity, and ecosystem services, making it imperative that future forest management strategies consider these threats.

Karolewski et al. (2007) examined the effects of temperature on the survival rate and development time of *Lymantria monachal* L. and *L. dispar* L. larvae. The study used *Pinus sylvestris* L. and *Quercus robur* L. leaves to provide food for the larvae. They explored to address the following questions: (1) How does temperature affect larval survival of *L. monacha* and *L. dispar* (2) Do both species respond similarly to changes in temperature? The study's results suggest that due to the high tolerance of *L. dispar* to high temperatures in terms of larval survival, this beetle species can be expected to pose a greater potential threat to forests than *L. monacha* in warmer years or under global warming conditions. Confirming the higher survival rate of *L. dispar* than *L. monacha* at higher temperatures if global warming scenarios materialize, this study suggests that the natural range of these species may shift to the temperate zone. As a result, the distribution ranges of both species may overlap to a large extent.

Many studies evaluating the effects of temperature increase or global warming on insect survival and development have used tropical plants (Wilf and Labandeira 1999; Walther 2003; Andrew and Hughes 2004; Hallam and Read 2006). However, it is also important to investigate the effect of temperature increases on insects that survive on plant species in the high latitudes of the northern hemisphere. Most scientific predictions suggest that global warming will stimulate the rate and range of spread of forest insect pests (Fritz and Simms, 1992; Ayres and Lombardero 2000; Hódar and Zamora 2004). Therefore, in the study by Karolewski et al. (2007), the tree species used are important species that contribute to forest regeneration in a significant part of Europe. With its current effects, global warming is expected to cause significant

damage to forest ecosystems that have not previously been affected by severe outbreaks. The damage caused by *Dendroctonus rufipennis* (Kirby 1837), *D. ponderosa* Hopkins, 1902, and *Ips confusus* Wood & Bright, 1992 confirms this. The biotic damage is most likely linked to the complex interactions between the direct effects of warming and the indirect effects of climate change, such as changes in bark beetle development and survival rates and reductions in tree resistance (Aukema et al. 2008; Raffa et al. 2008). In addition, studies have shown that *I. typographus* has recently developed in a shorter period in Europe, even at high altitudes during mild and dry spring months, and that it is bivoltine, i.e. gives two offspring per year (Baier et al. 2007).

There is a consensus among scientists that global warming and climate change have and will have an impact on herbivorous insects. It is an undeniable fact that alpine and boreal forests will be adversely affected by this negative situation, especially by particular pest species such as leafhoppers and bark beetles. This is because the developmental success of a herbivorous insect is indirectly linked to climate, as environmental factors affect plant metabolism. It is well known that the state of plant fitness and stress affect secondary metabolites, insect infestation, and plant nutrient quality (Netherer and Schopf 2010).

4. THE ROLE OF INSECTS IN FOREST ECOSYSTEMS

While it is widely accepted that herbivorous insects harm trees, recent research has taken a more holistic view of insect-plant interactions at the ecosystem level. This approach, initiated by Schowalter (1981) who asked "can ecosystem nutrient cycling be biotically regulated through ecological succession in host-host relationships?", emphasizes the critical importance of plant-insect interactions for the effective management of ecosystem resources. Recent studies reveal the complex roles of insect activities in key functions such as nutrient cycling, carbon storage, and biodiversity in forest ecosystems (Ayres and Lombardero

2000; Moreira et al. 2022). For example, some herbivorous insects can contribute to forest health by eliminating weak or diseased trees or accelerating the return of nutrients to the soil by increasing organic matter debris (Gandhi et al. 2020; Starr et al. 2023). However, insect outbreaks triggered by climate change lead to large-scale degradation of forests, negatively affecting ecosystem structure and function (Hart et al. 2022; Senf et al. 2020; Gámez-Rodríguez et al. 2024). In this context, insects need to be understood not only as pests but also as part of ecosystem dynamics for the intelligent management of ecosystems. As pioneers such as Bormann and Likens (1979) and Odum et al. (1979) emphasized, analyzing the causes of ecosystem disturbance is essential for understanding ecosystem structure and function. Despite this, herbivorous insects are often the target of control measures in managed ecosystems. Future forest management strategies should better integrate the multifaceted role of insects in ecosystems.

Herbivorous insects will accelerate the transitions from plant communities with smaller biomass and higher nutrient/light requirements to plant communities with larger biomass and lower nutrient/light requirements. In this context, Schowalter's (1981) research suggests that herbivorous insects can thus regulate ecological succession and nutrient cycling by altering plant competition relationships so that nutrient demand more closely matches nutrient availability. Because they are herbivorous insects;

- Supporting primary productivity and promoting nutrient uptake,
- Increased transport of nutrients from plant reserves to areas where insects feed,
- By Increasing leaching of foliar nutrients from chewed leaves, it stimulates nitrification, nitrogen fixation, litter-sediment decomposition, and/or plant root growth rates within the sediment-sediment/soil complex,

- It benefits nutrient flow by altering long- and short-term nutrient cycling pathways through changes in the relative biomass of shade-tolerant plant species (Springett 1978; Owen 1980; Petelle 1980; Schowalter et al. 1981a; 1981b).

5. THE MOST DAMAGING SPECIES OF WOODY TAXA IN TURKEY

Although many insects have a harmful effect on forest areas, Coleoptera, Lepidoptera, and Hemiptera are the most important orders to which these insects belong. On a species basis, *Thaumetopoea pityocampa* (Schiff), *Ips typographus* (Linnaeus 1758), *I. sexdentatus* (Börner 1776), *Dendroctonus micans* (Kugelann 1794) and *Leptoglossus occidentalis* are the prominent pests (Ertuğrul 2002). Bark beetles such as *D. micans*, *I. sexdentatus*, *I. typographus* become primary forest pests and cause significant damage in forests when favorable conditions occur, mainly when they reproduce en masse (Göktürk and Eldemir 2005). For this reason; in order to protect and improve existing forest assets, forest pests should be studied very well and studies should support existing information.

I. edentates (Börner 1767) (Coleoptera: Curculionidae, Scolytinae), one of the most common bark beetle species in Turkey, is a *Paelearctic* species capable of breeding in many coniferous tree species, including *Pinus* L., *Picea* A. Dietr., *Larix* Mill. and *Abies* Mill. (*Pinaceae*) (Lopez and Goldarazena 2012). This beetle species is distributed throughout the coniferous forests of Turkey, except in Southeastern Anatolia *I. typographus*, which entered Turkey from Georgia in 1984 and started to be seen in Artvin, caused damage to 1,000,000 m³ of eastern spruce trees between 1998 and 2005 (Yüksel et al. 2003). Lepidoptera causing damage to forest trees are of particular importance for forestry. In general, although adults do not cause any damage, larvae cause damage by destroying plant parts. The damage

occurs in the physiological characteristics of the plant (Çanakçı and Mol 2000). In their study on seed and cone pests in coniferous forest trees, Yılmaz et al. (2022) reported that 33 species belonging to the order *Lepidoptera* caused damage to seeds and cones.

Despite all these results, when the availability of herbivorous insects and the forest cover of Turkey are evaluated, it can be stated that Turkish forests are threatened by many harmful herbivorous insects. In their research, Çanakçıoğlu and Mol (2000) stated that the *Coleoptera* order constitutes 40% of all known insect species and emphasized that most insect species belonging to this order, which has more than 350 thousand species, also damage forest trees. Bark beetles (*Coleoptera: Curculionidae, Scolytinae*), one of the secondary forest pests, are recognized as one of the most famous biotic agents causing extensive damage to conifer forests. Most bark beetles infest dead or weakened trees. However, aggressive species can also damage healthy trees during outbreaks (Jurc et al. 2006; Rossi et al. 2009). Population density and attack intensity of bark beetles in a forest vary depending on many biotic and abiotic factors such as inappropriate forest management, stand structure, edge effect, wind, and long-term drought (Ünal et al. 2009; Akkuzu and Güzel 2015).

6. CONCLUSION

Accurately identifying the threats and impacts on forest ecosystems is crucial for anticipating, minimizing, and preventing potential damage to biodiversity and ecosystem functions. This understanding is vital for effective forest management. By comprehending and predicting disturbance patterns, we can deepen our knowledge of the mechanisms that generate and sustain biodiversity. Despite what is known about global climate change, there are still significant gaps in our understanding of how these changes will affect natural ecosystems, particularly the intricate interactions between living

organisms. Plant-insect relationships are significant, as they involve nearly half of the world's species and play key roles in most ecosystems. Recent research highlights that climate change alters these interactions, leading to more frequent and severe insect outbreaks and modifying plant defense responses.

In research on plant responses to biotic factors, there is a notable lack of quantitative data, which can be attributed to the difficulty in characterizing the importance of biotic stress and the presence of confounding factors such as genetic differences, a plant's physiological state, and environmental interactions. Given that plants in nature are constantly exposed to varying levels of biotic stress, the lack of studies on plant responses to different stress doses is a significant knowledge gap. Current efforts are focused on integrating high-resolution phenotyping with "omics" approaches (like genomics and transcriptomics) to improve the predictability of plant-stress responses. These combined methods allow us to more accurately model the molecular and physiological reactions of plants to different levels of stress.

It is certain that global warming and climate change, which are widely accepted by scientists today, will impact forest ecosystems. Since it is impossible to eliminate the problems caused by this situation, protecting and managing forest ecosystems is necessary to minimize damage. In this context, the fact that abiotic stressors can increase the severity of biotic stress should not be ignored. To maintain forest health, it is essential to accelerate research on tree resistance mechanisms. This includes integrating traditional breeding methods with genomic tools (such as gene editing with CRISPR-Cas9) and conducting advanced molecular and ecological studies on how trees respond to stressors. These efforts will form the foundation for future forest management strategies and strengthen our forests' ability to adapt.

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Biotic and Abiotic Stress in Common Bean
(*Phaseolus vulgaris* L.)

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1. INTRODUCTION

Over the past few years, the food chain has grown and changed quickly. Also, it has become easier to get refined, high-fat foods. This is primarily because of improvements in industrial processing and the ability to move goods over long distances (Albuquerque et al. 2022). Because of this, people eat less local and seasonal foods, especially those high in fiber, and more heavily processed foods high in refined starch, sugar, saturated fat, and salt (Monteiro et al. 2019; Albuquerque et al. 2022). As food production practices intensify, people in high-income countries are eating more high-calorie, animal-based foods. This is worsening the environment and using natural resources faster (Swinburn et al. 2011; Westhoek et al. 2014). By 2050, the world's population is expected to double, which raises serious concerns about food security. Even though much food is made for the world's population, serious and harmful nutritional deficiencies exist worldwide. Certain parts of the world are starting to see high rates of obesity, overeating, and nutritional deficiencies caused by diseases that can't be spread from person to person. On the other hand, in some areas, the number of people without enough food is increasing, which could lead to big problems (Clapp 2018; Rahut et al. 2022). Many people worldwide suffer from 'hidden hunger', a type of nutritional deficiency that keeps them from living a healthy life because they don't get enough micronutrients (von Grebmer et al. 2014; Temba et al. 2016). People think a sustainable diet is a meaningful way to make the world's food system healthier. This could be one of people's most important and urgent problems (Springmann et al. 2018; Willett et al. 2019; Pörtner et al. 2023).

Beans are known for feeding more than 300 million people and being important to agricultural economies worldwide (Uebersax et al. 2023). Beans are legumes that are generally consumed dried but are also consumed fresh in small amounts in their shells (Rawal and Navarro 2019). The amount of dry beans grown has gone up by about 60% since

the early 1990s, and the amount of land used to produce them has gone up by 36% in the same time (Rawal and Navarro 2019; Uebersax et al. 2023). Asia is the world's largest producer of dry beans, making up about 43% of the total. Next, the Americas comprise about 29% of the total, and Africa constitutes 26% (Uebersax et al. 2023). All common plants grown on different continents have a long history of breeding and evolution. They can be traced back to wild plants like *Phaseolus vulgaris* var. *aborgines* and *Phaseolus vulgaris* var. *mexicanus*, native to the Americas (Rodiño and Drevon 2004). Beans are a valuable global resource for biodiversity because they have landraces grown in different ways in different cultures, which adds to genetic diversity (Uebersax et al. 2023). In this book chapter, information is given about the bean plant's biochemical, physiological, morphological, and molecular response mechanisms under biotic and abiotic stress conditions.

2. ABIOTIC STRESSES in COMMON BEAN

2.1. Drought Stress

Drought stress has become a significant problem in recent years, significantly affecting the global food supply (Budak et al. 2013). Legume-producing regions worldwide, such as common beans, experience moderate to severe drought conditions. It is thought that drought stress caused by drier weather conditions following climate change will increasingly affect bean production (Mohammed and Feleke 2022). It is predicted that drought will be a significant problem in the coming years, and crops may experience prolonged and severe drought. However, increasing drought tolerance in bean varieties can significantly increase production levels and yields (Broughton et al. 2003; Ghanbari et al. 2013; Asfaw et al. 2014). Research indicates that bean yields experiencing drought stress during the flowering and post-flowering

stages are diminished by 60-99% (Manjeru et al. 2007; Ambachew et al. 2015). Drought stress can often lead to reduced osmotic pressure and storage of water potential in the plant's capacity. This condition mainly causes oxidative stress and cellular damage, affecting photosynthesis, carbon fixation, and primary metabolism. As a result, crop yields and survival rates decrease significantly. Current breeding efforts concentrate on identifying physiological markers that correlate with enhanced phenotypic traits in plants subjected to drought conditions (Lizana et al. 2006; Mladenov et al. 2023).

Drought stress significantly affects hormones, the movement of stored substances, and the structure of proteins. This, in turn, makes it harder for seeds to germinate and plants to grow (Basal et al. 2020). When plants are stressed by drought, reactive oxygen species (ROS) build up in their cells. This buildup causes oxidative damage, which can change the shape of proteins and break down cell membranes (Bahadur et al. 2019). This process can severely disrupt the structural integrity of membranes, proteins, and DNA (Qari et al. 2022; Rehman et al. 2022). Working on making plants more drought-resistant in safe and cost-effective ways is very important. There are now many ways to deal with the problems that drought stress causes, such as utilizing superabsorbent moisture, adding mycorrhizal fungi, applying nanoparticles, and breeding plants that can handle drought (Fadiji et al. 2022).

Mycorrhizal fungi play an important role in the ecosystems as they can colonize the roots of approximately 80% of plant species. This partnership has several benefits, such as better plant growth, more nutrients, stronger roots, more flowers, and more resistance to stress (Pozo et al. 2015). More research on common bean and other legumes shows that mycorrhizal symbiosis is important in making plants more resistant to drought (Recchia et al. 2018; Hashem et al. 2019).

Nanofertilizer is an important part of farming that has caught the attention of both soil and environmental scientists. It can boost crop yields, make soil more fertile, reduce pollution, and improve the environment for microorganisms (Ahmadian et al. 2021). Utilizing chemical fertilizers can be very expensive for farmers and bad for people's health and the environment. So, nanofertilizers might help plants deal with abiotic stress better (Astaneh et al. 2021; Márquez-Prieto et al. 2022; Salama et al. 2022).

Seed priming is an effective and cost-efficient method that enhances drought stress tolerance by facilitating better seed germination (Sadeghipour et al. 2018; Marthandan et al. 2020). When hydrogen peroxide (H_2O_2) is in low concentrations, it acts as a secondary messenger and helps plants deal with stress (You and Chan 2015; Farooq et al. 2017).

Gene activation and regulation of gene expression control the many changes in shape, function, and chemistry that happen when there is a drought. *MYB*, *WRKY*, *DREB*, and *NAC* are transcription factors that are very important in shaping these responses (Recchia et al. 2013; Wu et al. 2016; Wu et al. 2017; López et al. 2020). In general, osmoprotection means coordinating the transcription of genes, which is important for controlling hormones and stomata (Liu et al. 2020).

Aquaporins (*AQPs*) are a group of genes that are very important because aquaporin proteins help move water across cell membranes. In drought-stressed beans, higher expression levels of *AQP* genes in the roots and leaves have been shown to help the plants hold onto water and lose less water through transpiration (Aroca and Ruiz-Lozano 2012; Zupin et al. 2017). The results show how important aquaporins are in keeping cells hydrated, especially when there isn't much water. Researchers also found important proteins for taking in and moving water and ions. These include aquaporins, RING-type E3 ubiquitin

transferases, and antioxidant enzymes such as glutathione S-transferase (GSTs) and Cytochrome P450 (CYPs), and thioredoxins (TRX) (Ponce et al. 2024).

2.2. Salinity Stress

Salt stress is the second most important abiotic stress after drought stress. It greatly affects how well crops grow (Mosa et al. 2017). Soil salinity is caused by high salt levels in the soil, which can impair crop growth and even kill plants. Salt buildup in farm soil can change how plants work in many ways. Soil salinity can affect everything from seed germination to growth, flowering, and fruit set. This can then affect productivity (Mbarki et al. 2020).

Biostimulants, nature's subtle but powerful helpers, are essential to modern farming, especially when reducing salt stress's destructive effects on legumes. These resources encompass diverse substances, including compounds from biological origins, seaweed extracts, humic acids, and microbial inoculants. Each has biochemical properties that help plants grow, develop, and fight off disease (Johnson et al. 2024). Biostimulants are crucial in managing osmotic imbalance, ion toxicity, and oxidative damage from salt stress in plants. Their participation in osmotic regulation is vital because they regulate the accumulation of compatible solutes such as proline and glycine betaine. For example, these solutes are essential for maintaining cellular turgor and facilitating water uptake in mung bean (Kumawat et al. 2021). Biostimulants also make the plant's antioxidant defenses stronger, which helps it fight off reactive oxygen species. This neutralization stops oxidative damage to cell structures (Hasanuzzaman et al. 2021). When legumes are under stress, they use biostimulants to improve their relationship with nitrogen-fixing root bacteria. This support helps with nodulation, fixes nitrogen, and helps plants absorb nutrients (Dubey et al. 2020). Biostimulants

work in complex ways to boost the plant's natural defense systems, which makes it better able to handle and adapt to salt stress.

Microbial biostimulants, like nitrogen-fixing bacteria (NFB), are essential for controlling the levels of ethylene, cytokinin, ABA (abscisic acid), and GA (gibberellic acid). These levels help maintain many physiological activities (Sofy et al. 2021). Recent studies indicate that NFB may enhance the activity of ROS-scavenging enzymes, such as catalase (CAT), superoxide dismutase (SOD), and peroxidases (POD). This rise strengthens the faba bean's antioxidant defense system (Hafez et al. 2021).

The presence of varying salt concentrations has led to reduced growth in legumes. Salt stress negatively affects nodulation in legume plants by disrupting initial symbiotic interactions. Legume plants co-inoculated with bacterial biostimulant strains of *Rhizobium* and *Pseudomonas* exhibited a reduction in salt stress, which in turn increased colonization of root tips (Egamberdieva et al. 2013). Plant growth-promoting bacterial biostimulants bind to legume roots and promote root elongation by reducing ethylene levels. (Shaharoona et al. 2006). Another study highlighted the role of the plant growth-promoting bacterial biostimulant *Bacillus cereus*, known for its production of ACC-deaminase, siderophores, and IAA (indole-3-acetic acid), and its ability to solubilize phosphate. This biostimulant has reduced high ethylene levels under salinity stress conditions (Kothari and Manuel 2015). Developing salt-tolerant symbiosis is essential to enhance crop growth in saline soils. Inoculation of soybean plants with plant growth-promoting bacterial biostimulants, particularly *Bradyrhizobium japonicum* strains, has been observed to enhance plant growth, photosynthesis, and nutrient uptake, particularly under salt stress conditions (Han and Lee 2005).

2.3. Molecular Mechanisms Developed Against Stress in Beans

Plants possess sophisticated response mechanisms against pathogens. These response mechanisms are closely linked to the evolution of the centuries-long plant-pathogen association. Key molecular responses include the production of phenolic compounds, changes in peroxidase metabolism, Type III secretion, blockage of vascular tissues, lignin production, and the restriction of pathogen-infected tissues, as well as mechanisms such as apoptosis. Phenolic compounds are the names given to certain compounds that are produced primarily as secondary metabolites in plants. Phenolic compounds rapidly increase at the tissue level during pathogen spread. Similarly, peroxidase enzymes can also play a role in polymerization, promoting cell wall thickening. Bacterial and viral infections, particularly, activate plants' Type III secretion system. This secretion system also causes hormonal changes, activating plant defense systems. Oligomers called NOD-like receptors (NLRs) have been identified in some bean genotypes. It has been determined that these receptors, upon recognition of the infectious agent, activate the caspases responsible for infection, causing a hypersensitive response (HR) (Franchi et al. 2009). As a result of this hypersensitive response, necrotic lesions, senescence, and even apoptosis can occur in plant leaves.

In addition to all this, plant infection elicits several tissue-level responses. These responses are generally observed in the leaves and stems. However, if the plant fails in this control, these responses can also be seen in the roots and flowers. The most obvious examples of tissue-level responses include the plant limiting the spread of the pathogen by killing the infected area through programmed cell death and deliberately blocking the vascular tissues, preventing the pathogen from spreading into the plant through interstitial fluids. These are accompanied by the detachment of the entire leaf from the plant, a phenomenon particularly

seen in fungal infections. In fact, increasing peroxide levels following Type III secretion cause immediate tissue-level responses. Concomitantly, increases in salicylic acid levels have been recorded (Duncan et al. 2011; Chen et al. 2021). This activates MAPK signaling pathways, and the plant attempts to interrupt the pathogen's interaction with its nutrient sources and environment.

In addition, Makhumbila et al. (2025) investigated the responses to bean rust using a resistant (Teebus-RR-1) and a susceptible (Golden Gate Wax) bean cultivar. A total of 3175 differentially expressed genes (DEGs) were identified in this study. The resistant cultivar (Teebus-RR-1) contained 88% of these genes (2806), while the susceptible cultivar contained only 369 DEGs. In plants, early and late responses were obtained through RNA-seq analyses performed on days 14 and 21. The studies revealed that heat shock proteins, receptor-like kinases (CRK29), cytochrome P450 enzymes, and terpene synthesis enzymes were activated in the early stage, initiating defense. In the late stage (day 21), a stronger stress response and enhanced photosynthetic cultivar were observed, while increased secondary metabolite levels and activation of general defense pathways were observed in the susceptible cultivar. However, insufficient defense success was noted in susceptible cultivars. This study revealed that the defense proteins of RPS2, CAR1, and DM2H are associated with this disease. Its agriculturally significant contribution is the discovery of new biomarkers using RNA-seq for marker-assisted breeding. The primary contribution of such studies is the development of durable resistance to specific diseases (Makhumbila et al. 2025).

Specific transcription factors, such as MYB, bZIP, bHLH, WRKY, NAC, ERF, and DREB, have been shown to function as key regulators of signal transduction pathways in plant drought tolerance (Singh et al. 2015). Furthermore, various functional proteins, such as aquaporin (Wu

et al. 2022), late embryogenesis abundant (LEA) proteins (Jia et al. 2022), and heat shock proteins (ALH) (Zhou et al. 2016), have also attracted attention. New research suggests that ncRNAs and protein-coding RNAs may play important regulatory roles in plant responses to drought stress (Gelaw and Sanan-Mishra 2021; Thanmalagan et al. 2022). Earlier research has demonstrated that miR159, miR160, miR167, miR169, and miR393 influence the drought resistance of tomatoes by regulating hormone signaling, stomatal closure, and auxin-responsive genes (Rao et al. 2020; Zhou et al. 2020b). In common bean (*Phaseolus vulgaris*), legume-specific miR1514a, miR2119, and a conserved miR2118 were upregulated with a concomitant decrease of their targets, such as superoxide dismutase (MnSOD) and cysteine protease, ADH1, and APS reductase, respectively (Arenas-Huertero et al. 2009; Chatterjee et al. 2025).

Recent improvements in high-throughput methods for analyzing gene expression profiles have made it easier to understand how plants react to abiotic and biotic stressors (Qing et al. 2009; Xu et al. 2013). There has been a notable increase in research employing RNA sequencing data and expression profiling in model plants and essential crops to identify the genes involved in stress responses (Ge et al. 2010; Postnikova et al. 2013). Next-generation RNA sequencing analyses will use continuously generated reference genome sequences for different legume species to help find and clone stress tolerance genes and make new varieties with better tolerance mechanisms (Schmutz et al. 2010; Young et al. 2011; Goodstein et al. 2012; Varshney et al. 2013).

2.4. Heavy Metal Stress

Heavy metals (HMs) are used for metals with a specific gravity greater than 5 g/cm³ (Järup 2003; Bothe 2011). HMs are among the most dangerous and polluting elements for all living organisms. Excessive accumulation of HMs such as cadmium (Cd), lead (Pb), and mercury (Hg) causes permanent damage to plants. In response, plants try to show tolerance by providing intracellular and extracellular sequestration (Kosakivska et al. 2021). HM stress is one of the most damaging abiotic factors affecting plant quality and yield, resulting in death. Adverse effects such as oxidative stress, damage to cell membrane permeability, and disruption of the photosynthetic mechanism may occur due to increased production of reactive oxygen radicals in plants exposed to HMs (Feng et al. 2021). HMs are released into soil as a result of natural processes or industrial activities, excessive fertilization, use of wastewater for irrigation, and other anthropogenic activities and cause adverse effects on plants due to their solubility in water and lack of biodegradability (Başdinç and Çirka 2021; Khatun et al. 2022; Kiran et al. 2022; Sharma et al. 2022).

P. vulgaris is one of the primary food sources preferred for good nutrition due to its high fiber, protein, and low-fat content (He et al. 2018). However, it has been observed that *P. vulgaris* metabolizes HMs and negatively affects plant growth stages, disrupting growth and development processes (Çelik and Nadaroglu 2018; Silva-Gigante et al. 2023). It has been found that HMs inhibit water and element uptake and nitrogenase activity in beans and reduce the number of nodules by disrupting the nodule structure (Hammami et al. 2022).

Changes such as chlorophyll content, enzyme production, growth and development rate, and leaf and root area are examined as indicators of plant responses to HM stress (Farid et al. 2013). HMs are transported into plants via roots, and heavy metal concentrations in roots are often

higher than in shoots (Małkowski et al. 2019). As a result of Cd and Pb treatment, heavy metal content in *P. vulgaris* roots was higher than in other plant organs (Cannata et al. 2015). Copper (Cu) and zinc (Zn) treatments also resulted in greater accumulation of heavy metals in *P. vulgaris* roots than in shoots (Urwat et al. 2021; Younis et al. 2018a). As a result, when the morphological effects of HMs are examined, more damaging effects occur on the roots. In common bean treated with 200 mg/kg Cd, a decrease of 53.07% and 54.35% in root fresh and dry weights, respectively, occurred compared to the control, and this decrease was found to have the highest reduction rate compared to other parts of the plant (Dadasoglu et al. 2022). Cd, which enters plants through carriers such as Ca^{2+} , Fe^{2+} , Mn^{2+} , and Zn^{2+} , negatively affects plant development (Verbruggen et al. 2009; Liu et al. 2025). More Cd accumulation occurred in *P. vulgaris* roots exposed to Cd stress compared to shoots (Bahmani et al. 2020). Similarly, increasing Cd doses decreased leaf number and leaf area (Yildirim et al. 2023). When examining plant physiological responses to HMs, one of the critical indicators is photosynthetic performance (Chen et al. 2019). It is known that Fe (III) reductase is inhibited in plants exposed to Cd, and Fe (II) deficiency occurs, causing photosynthesis to be negatively affected (Alcántara et al. 1994). The decrease in photosynthetic pigment contents in *P. vulgaris* under Cd stress at 0.25 μM , 0.5 μM , and one μM concentrations also occurred as a result of these effects (Beatriz Gutiérrez-Martínez et al. 2024). Another effect is that HMs affect water intake, causing water imbalance (AbdElgawad et al. 2020). It was observed that the water content decreased as the application dose increased in common beans exposed to Pb stress (Kul et al. 2019). In addition, HMs disrupt protein homeostasis by interfering with protein folding processes and lead to loss of cell viability (Hasan et al. 2017). While the arsenate [As (V): AsO_4^{3-}] form enters plants with the help of phosphate carriers, it disrupts phosphate metabolism, the As (III) form

binds to sulfhydryl groups and causes degradation of the protein structure (Su et al. 2010; Silva-Gigante et al. 2023). It was determined that the soluble protein content in *P. vulgaris* decreased after 2 and 5 mg As application compared to the control group (Stoeva et al. 2005). Similarly, it was determined that the total protein content in *P. vulgaris* exposed to Pb stress for 1 week decreased due to increasing heavy metal concentration (Hamid et al. 2010). One of the biochemical responses that plants give when exposed to HM stress is lipid peroxidation (MDA) due to membrane damage. It was determined that MDA content in *P. vulgaris* under Cu and Cd stresses increased as a response to HM (Younis et al. 2018b). Another biochemical change is the production of reactive oxygen species (ROS). Enzymatic antioxidants such as SOD, POD, CAT, APX, DHAR, and MDHAR, as well as non-enzymatic antioxidants such as ASA, GSH, carotenoids, and tocopherols, are involved in the detoxification of these ROS (Arif et al. 2016; Raza et al. 2021). Both enzymatic and non-enzymatic antioxidants increased *P. vulgaris* growth with wastewater and exposed to heavy metals such as Cd, Co, Ni, and Pb (Nowwar et al. 2023).

Phytohormones such as abscisic acid (ABA) and indole acetic acid (IAA) act as signal molecules in the removal of ROS and trigger the production of antioxidant enzyme system elements (Emamverdian et al. 2020). In common bean under Cd stress, the expression of *ABA 8'-hydroxylase* and *IAA* genes, which regulate ABA degradation, increased due to stress (Ekinici et al. 2023). In addition, plants can control events such as the uptake and detoxification of HMs by regulating gene expression through transcription factors such as heat shock protein (HSF) and basic leucine zipper (bZIP) (Li et al. 2022b). It was determined that the expression of *HSF* gene family members changed due to Cd and Hg treatment, and the expression of bZIP gene family members changed due to Zn treatment (Astudillo et al. 2013; Zhang et al. 2022). In addition, transporters such as natural resistance-associated

macrophage protein (NRAMP) in HM transport are one of the critical genes responsible for the accumulation of HMs in plants (Kanwal et al. 2024). The increase in *NRAMP* gene expression after 300 μ M Zn treatment in common bean confirms that it plays a role in this transport (Urwat et al. 2021). Moreover, microRNAs (miRNAs) and their targets that regulate gene expression in plant tolerance to HM stress should not be ignored (Noman and Aqeel 2017). It was found that overexpressed miR1511 in aluminum (Al) treated common bean suppressed its target, aluminum-responsive 3 protein (ALS3). As a result, the plant became more sensitive to Al stress (Ángel Martín-Rodríguez et al. 2021). These results indicate that the plant tries to gain tolerance to stress by regulating gene expressions for resistance to HM stress.

Various strategies have been developed to mitigate the damaging effects of HM on plants. One of these strategies is using exogenous applications of phytohormones (Saini et al. 2021). One of these phytohormones is gibberellic acid (GA3). GA3 applied exogenously to common beans under Cd and Pb stress was found to have a healing effect by reducing HM toxicity (Dilek Tepe 2022). Exogenous application of salicylic acid (SA), another phytohormone, increased antioxidant and proline activities in common bean under Cd, Ni, and Pb stress (Hediji et al. 2021; Khalil et al. 2021). Similar effects were observed after applying jasmonic acid (JA) (Hashem and El-Sherif 2019). Another strategy is using polyamines as antioxidant enzyme activators (Malik et al. 2022). Exogenous application of spermine, a polyamine used to alleviate the adverse effects of As (III) and As (V) forms on common bean, increased the expression of antioxidant enzyme activity and zinc finger protein-related genes involved in stress responses (Shah et al. 2022). Another strategy is nanoparticles (NPs), which are preferred due to their ability to penetrate a large area of plants and their contribution to ROS scavenging and plant growth and development stages (Zhou et al. 2020a; Faizan et al. 2023). For this purpose, biological silicon NPs used for

common beans in HM soil were found to affect protecting plant health against stress by increasing antioxidant enzyme activity (El-Saadony et al. 2021). Similarly, iron oxide NP (IONP), zinc oxide NP (ZnO NP), and copper oxide NP (CuO NP) applications also increased the stress tolerance of common bean under Cd stress (Hidouri et al. 2022; Koleva et al. 2022).

HMs are one of the abiotic stress factors that negatively affect common bean development and yield. HMs such as As, Cd, Ni, and Pb, which mix with the soil through anthropogenic and non-anthropogenic means, enter the plant through the roots and cause permanent damage to the morphological and physiological systems. Plants try to provide tolerance to stress by responding to these damages through various defense mechanisms. This tolerance is achieved through antioxidant enzyme systems, the synthesis of metal transporters, and their regulation by compounds such as phytohormones, transcription factors, and miRNA. The elucidation of HM stress responses and tolerant mechanisms of common beans will facilitate the selection of varieties that are resistant to this stress. In addition to the plant's own tolerance, exogenous phytohormone, polyamine, and nanoparticle applications are also used to help the plant's tolerance. Different applications applied to common beans and the determination of the underlying mechanism of these applications will contribute to the development of common bean varieties resistant to HM stress in the future.

2.5. Cold and Heat Stress

Due to extreme weather events and global climate change, plants are increasingly exposed to temperature changes. This causes temperature stress, which includes both cold and heat stress. From a food security perspective, heat stress reduces plant production and impacts crop yields. Furthermore, temperature changes negatively impact the distribution of plants worldwide (Ding and Yang 2022).

Heat stress is categorized into three classes based on stressors: high, chilling, and freezing temperatures. High heat stress refers to temperatures above 27°C. Chilling temperatures are between 0°C and 15°C, and freezing temperatures are below 0°C. Because temperature is a physical signal, it is quickly sensed by the nucleus or cell membrane in the plant cell. Plants respond soon to heat stress by developing molecular strategies such as proteins, metabolites, antioxidants, membrane lipids, and regulatory factors (Kai and Iba 2014; Ding and Yang 2022; Yang et al. 2023). On the other hand, cold stress can inhibit growth because it affects enzyme activity (Zhang et al. 2020). In addition, plants inhibit photosynthesis, and cell membranes undergo lipid peroxidation (Ali et al. 2025; Cheng et al. 2025). Therefore, elucidating the molecular mechanisms that play a role in plant adaptation to heat and cold stress is essential and helps agricultural production.

Recently, attempts have been made to elucidate the molecular mechanisms underlying heat stress. When plants perceive heat stress, heat-responsive genes are activated, and these genes are regulated at both the transcriptional and post-transcriptional levels. Expression of cold-responsive (COR) and heat-responsive genes is activated by transcriptional factors such as CBF/DREB1 (C-repeat binding factor/Dehydration responsive element binding 1) and HsfA1 (heat shock factor A1), respectively (Li et al. 2022a; Wang et al. 2022).

Cold and heat signal perception occurs through Ca^{2+} and ROS signals and regulation of gene expression, protein activities, and protein homeostasis (Wang et al. 2022). The cell membrane is the first line of defense against heat stress. Another important organelle is the nucleus (Ding et al. 2019). Both cold and heat stresses can cause changes in the fluidity of cellular phospholipid membranes (Dutta et al. 2025; Su et al. 2025). This change is sensed by channels, various transporters, and integral membrane proteins such as membrane-anchored receptor-like

kinases (RLKs). Heat stress is sensed by molecular chaperones (Zhu 2016). Histidine kinases such as Ethylene Response 1 (ETR1), Arabidopsis Histidine Kinase 2 (AHK2), and AHK3 are associated with cold stress (Nongpiur et al. 2012; Zhang et al. 2025).

Various ion channels are located in the plasma membrane as heat sensors. COLD1 (Chilling-tolerance divergence 1), a protein located in the plasma membrane and endoplasmic reticulum in plants, forms a complex with RGA1 (G-protein α -subunit 1) in the plasma membrane, which promotes Ca^{2+} entry into the cell for cold sensing in rice (Zhu 2016). The role of COD1 in heat stress, however, is not fully elucidated (Ding and Yang 2022).

Several nuclear proteins, such as UVR (UV resistance locus 8), PHOTS (phototropins), CRYs (cryptochromes), and phytochromes (photoreceptors), along with members of the ZEITLUPE family (ZTL, FKF1, and LKP2), play essential roles in heat sensing. These proteins are responsible for the reception of UV-A, UV-B, red, and blue light (Bian et al. 2022). phyB, a thermosensor, is found in the cytosol and nucleus. Depending on temperature, phyB transitions from an active to an inactive state. phyB releases the inhibition of the transcription factor PIF4 (phytochrome-interacting factor 4). High ambient temperatures cause thermomorphogenesis, which leads to rapid plant growth and morphological changes (Fan et al. 2025). Similarly, phyB increases plant freezing tolerance through the PIF3-CBF interaction (Das et al. 2025; Xu et al. 2025). PIF1, PIF4, and PIF5, negative regulators of cold stress, are degraded by phyB, which is stabilized by cold treatment. Thus, plants improve their tolerance to cold (Bian et al. 2022). UVR8 responds to cold stress by converting from an inactive dimer to an active monomer, contrary to UV-B, resulting in a decreased thermomorphogenic response (Hwang et al. 2025).

Low and high temperature stresses are important abiotic stresses for bean plants (Srivastava et al. 2015; Vargas et al. 2021). Studies on beans under heat stress were evaluated with molecular, biochemical, morphological, and physiological parameters. In their study investigating the effect of cold stress occurring during the flowering period on reproduction, Gobatto et al. (2025) determined that cold stress had an adverse impact on yield components by extending the growth cycle of bean genotypes in the field and caused a decrease in yield. Also, low superoxide dismutase enzyme activity was reported to be associated with greater cold tolerance. On the other hand, in a study in which both transcriptomic and metabolomic methods determined the effects of cold stress on common bean, it was defined that the genes induced under chilling stress were involved in lipid, amino acid, and flavonoid metabolisms. Malondialdehyde (MDA) content, amino acid concentration, methionine accumulation, and flavonoid content differed between cold-tolerant and susceptible genotypes. It was also suggested that flavonoids, MDA, and methionine could be biomarkers for plant chilling injury. According to the transcriptomic analysis of hormone metabolism, it has been determined that the expression levels of genes responsible for gibberellin (GA), abscisic acid (ABA), and jasmonic acid (JA) synthesis differ among genotypes during chilling stress (Yang et al. 2023). A study investigating the effects of exogenous acetylsalicylic acid (ASA) on cold stress found that ASA treatment positively improved physiological and biochemical parameters such as carotenoid concentrations, total soluble proteins, electrical conductivity, photosynthesis, antioxidant enzyme activity, and malondialdehyde. A positive correlation was identified between antioxidant enzymes and photosynthetic activity. Additionally, it was reported that expression levels of antioxidant genes such as *APX1*, *POD1*, and *SODC*, and photosynthesis genes such as *RbcS1*, *PsbS*, and *POR* were increased, suggesting that these genes may be important in reducing cold-induced

oxidative stress and preserving chloroplast functions (Ali et al. 2025). Sheikhi Didani and Dumlupinar (2022) also investigated the effects of progesterone (Pro), B-estradiol (ES), abscisic acid (ABA), and salicylic acid (SA) treatments on cold stress in bean seedlings. Antioxidant and nitrate assimilation enzyme activities, plant growth, chlorophyll, MDA, and hydrogen peroxide measurements were taken. According to the study results, plant growth decreased under cold stress, while MDA and H₂O₂ contents increased. Compared to the control, cold stress decreased nitrate reductase, nitrite reductase, and glutamate synthase enzyme activities, while they increased in Pro, ES, ABA, and SA treatments.

Kabay and Şensoy (2017) explored the effects of high temperature stress on tolerant and susceptible genotypes during five different growth stages. Biochemical, physiological, and elemental analyses were conducted in the study. Among the parameters examined, chlorophyll A, B, and A-B decreased compared to the control group in the treated and susceptible genotypes on the days examined. Except for MDA and APX enzymes, levels of CAT and SOD enzymes consistently increased across the treatment groups. While K and Ca levels in roots and shoots decreased, Na levels increased.

The effects of nitric oxide and trehalose treatment on managing heat stress in bean plants were explored. The results showed that nitric oxide and trehalose application improved the examined agronomic traits (Ahmed 2023). Da Silva et al. (2020) investigated the effects of high temperature stress on the reproductive biology of bean plants. Significant effects of high temperature stress were found on parameters such as 100-seed weight, seed yield, number of viable seeds, total pollen grains, number of flowers, pod set, and pods. Increasing temperature was found to decrease all parameters except the percentage of pod set, while it also caused increases in meiotic irregularities. Vargas et al. (2021) physiologically and genetically characterized the effects of heat stress on

the bean RIL population. Yields decreased under non-stress conditions. Furthermore, heat stress affected many traits throughout the reproductive phase under field conditions. In susceptible lines, the reproductive phase was prolonged, and defects that reduced seed filling, seed formation, and grain quality were detected. Higher yields under heat stress were associated with earlier flowering, effective seed filling, and high pollen viability.

3. BIOTIC STRESSES in COMMON BEAN

Biotic stress refers to the difficulties organisms experience due to their interactions with other living organisms, such as infections, pests, parasites, and competing organisms. It is known that biotic stress significantly affects crop yields and food security globally. Biotic stress causes a variety of physiological, biochemical, and molecular responses that significantly affect plant growth, development, and productivity. The mechanisms by which plants respond to biotic stress are complex. This complexity encompasses the host's resistance genes, the pathogen's virulence factors, and various environmental conditions.

Common bean is one of the most important legumes globally and a significant source of protein, carbohydrates, and nutrients (Hayat et al. 2014). However, numerous stress factors can affect bean growth and yield. Viruses, bacteria, and pests can cause severe yield losses. Biotic stress usually occurs in environments where disease management is poor and pathogens can proliferate. Plant-stress interactions in common bean have evolved over centuries, as in other plants. Understanding these complex dynamics, which result in infection developing in the pathogen and increased resistance and defense mechanisms in the plant, is very important for studies and breeding programs to develop resistance in common bean varieties.

3.1. Fungal Diseases

Fungal pathogens are widespread worldwide and major biotic stress factors affect production and yield. These pathogens can seriously affect the entire plant, from the shoot to the root, and from the seed to the stem. These organisms, which affect plants throughout the growth period, can also spread quickly and extensively, possibly affecting a large portion of the planting area in a short period.

Rust disease caused by *Uromyces appendiculatus* (Pers.:Pers.) Unger, an obligate biotrophic fungal pathogen, is one of the most damaging diseases affecting common beans. It causes significant worldwide losses in common bean production (Makhumbila et al. 2025). This pathogen has evolved alongside common beans, allowing it to overcome specific resistance genes easily. The leaves of infected plants are covered with distinct rust-colored pustules filled with urediniospores. This exposes the plant to biotic stress and initiates a different form of abiotic stress as the spreading disease inhibits light absorption by the plant's leaves. This reduces photosynthesis in the plant, causing it to weaken, become less productive, and in severe cases, die (Bassanezi et al. 2001; Yahya et al. 2020).

Another disease caused by *Colletotrichum lindemuthianum* is anthracnose. It represents the oldest and most extensively studied plant-pathogen system in plant pathology. This disease and pathogen have illuminated the molecular interactions between *P. vulgaris* and *C. lindemuthianum* (Nabi et al. 2022). The pathogen forms salmon-colored spore masses in the presence of moisture in the environment and causes collapsed lesions on the stem and leaves. Like rust disease, infected plants showed reduced photosynthetic activity (Bassanezi et al. 2001). There are a large number of identified isolates of this pathogen worldwide. This is another important consideration in the development of resistant varieties/cultivars.

The white mold disease is a plant disease that mainly strikes plants in humid and cool weather conditions. The fungus responsible for this infection is named *Sclerotinia sclerotiorum*. This necrotrophic pathogen produces sclerotia, named after itself, which makes disease management much more challenging. These sclerotia mycelia can persist in the soil for long planting/cropping seasons. Studies have shown that some common bean varieties exhibit physiological resistance to *S. sclerotiorum* (Robison et al. 2018). This pathogen generally produces enzymes that lyse the plant cell walls, causing foliage lesions and damage. It then proceeds to proliferate and grow in these necrotic lesions.

Fusarium, *Rhizoctonia*, *Pythium*, *Rhizoctonia*, *Pythium*, and *Phytophthora* are widespread, soil-borne root rot pathogens in beans. In most cases, these fungi can persist in dry soils for extended periods and usually infect plants in moist or wet soil conditions. In particular, *Pythium* species such as *P. debaryanum* and *P. ultimum* create significant difficulties in disease control because of their ability to remain in the soil for long periods, up to years (Schwartz et al. 2005). An interaction between waterlogging, an abiotic stress factor, and *Pythium* infection, a biotic stress, has been determined. Root rot pathogens often interact with other stressors and create complex scenarios to manage with a single approach (Li et al. 2014).

Due to investigations on seed-borne fungal pathogens in *P. vulgaris*, many pathogen species responsible for significant damage have been revealed (Marcenaro and Valkonen 2016; Dell’Olmo et al. 2023). Many seed-borne fungal species have been identified in bean-growing areas and fields. Among them are various genera such as *Colletotrichum*, *Macrophomina*, and *Alternaria*. These pathogens can also remain dormant in the seed for extended periods. Under optimal conditions, they become reactivated and infect the plants. This situation may lead to seed

rot, shoot failure, or infections that may not appear until later in the growth period. To prevent the transmission of fungal infections, it is essential to carry out seed-borne fungal pathogen diagnostics (Dell'Olmo et al. 2023).

3.2. Bacterial Diseases

Common Bacterial Blight (CBB) is the most significant bacterial disease affecting beans globally. *Xanthomonas citri* pv. *fuscans* (Xcf) and *Xanthomonas phaseoli* pv. *phaseoli* (Xpp) species are responsible for this disease. The disease is characterized by moisture-absorbing, browning of the leaves, often accompanied by a yellow halo, and usually results in mortality. Conditions that negatively affect plant growth also led to the development of the bacterium. As a result, all the leaves are subjected to blight. This disease can also spread in low doses throughout the entire plant, affecting pods and seeds, resulting in severe yield losses (Chen et al. 2021).

CBB can be transmitted through seeds. This brings a critical challenge for the global seed market. The bacteria remaining dormant in seeds for long periods can be the primary source of the following infection. Some Quantitative Trait Locus (QTL) studies have shown the existence of loci associated with CBB resistance in plants. However, many different factors are involved in the occurrence of this disease. This situation makes it challenging to develop resistant plant cultivars (Duncan et al. 2011). It is possible to manage CBB effectively. However, this requires multifaceted approaches such as pathogen-free seed, crop rotation, sterilization, and the development of resistant lines. Furthermore, to reduce the risk of disease, carefully selecting planting fields is also essential, as the bacteria can remain in the soil for long periods.

3.3. Viral Diseases

One of the essential biotic stress factors affecting *P. vulgaris* is viral infections. Viruses generally affect an organism's yield, and in plants, they significantly impact growth, development, and yield. The Bean common mosaic virus (BCMV) is a global viral threat to common beans. There are no pharmaceutical methods to combat viral infections. This makes genetic resistance the primary strategy for disease management (Expósito-Goás et al. 2024).

Symptoms of viral infections in common beans include mosaic patterns, damaged leaves, dwarfed growth, and low yields. Insects, machinery, or contaminated seeds can spread viral diseases. This transmission diversity makes it difficult to combat and control viral diseases. Combining conventional breeding and modern molecular biological techniques to develop virus/viral disease-resistant varieties is the most effective strategy for managing infections (Expósito-Goás et al. 2024).

3.4. Insecticide Diseases

Insects damage common beans in two main ways. The first is by feeding directly on the plant, and the second is indirectly transmitting plant pathogens during feeding or foraging. Sap-sucking whiteflies (*Bemisia tabaci*) are an important case study. Feeding by these insects reduces the vitality of plants, but more importantly, they cause greater damage by infecting plants with specific pathogens such as *Begomovirus* (eg, Bean golden mosaic virus). Regular insecticide applications are not preferred as they cause the development of resistance in insects and pose a risk of environmental pollution. Developing resistance to vectors or viruses through innovative strategies is one of the most important and powerful steps that can be taken in this regard (Ferreira et al. 2024). Pests that chew and feed on plant sap activate plant defense mechanisms

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(Jasmonic Acid/Salicylic Acid) and cause responses and changes in secondary metabolites.

Covering the field border with flowering plants increased the natural enemies of aphids, thereby protecting bean plants from insects without using insecticides. This experiment is a highly innovative and impressive approach to pest management on small farms (Ndakidemi et al. 2022). The common bean aphid (*Acanthoscelides obtectus*) is a major threat to stored grain. Laboratory studies have shown that spinetoram (an insecticide mixture derived from *Saccharopolyspora spinosa*) rapidly kills adult aphids on storage surfaces. However, since the efficacy of this pesticide varies depending on surface shape, surface structure, and exposure time, it is crucial to conduct real-world trials and develop innovative strategies (Sağlam et al. 2022).

It is essential to develop integrated approaches that use multiple methods to effectively manage biotic stress-induced diseases in common bean. Crop rotation, maintaining cleanliness, providing suitable field conditions, and using sterile seeds are important steps in disease management and prevention (Schwartz et al. 2005).

Using chemicals such as fungicides and antibacterials is an effective and quick method for protecting plants in the short term. However, this can lead to developing resistance in pathogens, so these applications must be carefully considered (Duncan et al. 2011). Preventive applications are more effective than therapeutic approaches. Developing disease-resistant varieties is the most effective approach to combating biotic stress in common bean. In addition, control strategies include beneficial approaches such as particular species of *Trichoderma* fungi and plant growth-promoting rhizobacteria. These organisms can inhibit pathogen growth through competitive and resistance-induced mechanisms. This could be a promising approach for reducing disease stress and improving plant health.

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The Effects of Abiotic and Biotic Stress Factors on Plant Protection Strategies

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1. INTRODUCTION

Living organisms has a continuous interaction with surrounding environment. Changes in the environment exceed the adaptive capacity of organisms, stress conditions arise. In plant science, stress is the set of physiological and biochemical responses that emerge when environmental external factors change to a level that adversely affects plant growth and developmental processes (Bolaji Umar et al. 2022).

Plant responses to stress are observed in various forms, such as alterations in gene expression, disruptions in metabolic activities and reductions in growth and yield. Prolonged or severe stress conditions may result in growth inhibition or plant death. Stress tolerant species can gradually develop resistance mechanisms over time. Stress factors are divided into two main groups:

- **Abiotic factors:** Non living environmental elements, such as drought, high/low temperatures, salinity and heavy metals (He et al. 2018; Munghwar and Zaman 2024).
- **Biotic factors:** Living agents, such as fungi, bacteria, viruses, nematodes, insects and weeds (Gull et al. 2019).

2. ABIOTIC STRESS FACTORS

Abiotic stress factors are non living environmental conditions that negatively affect plant growth and productivity. These include drought, salinity, extreme temperatures, and heavy metal toxicity, which disrupt physiological and biochemical processes such as photosynthesis and nutrient uptake. To survive, plants develop defense mechanisms like antioxidant production, osmotic adjustment, and expression of stress responsive genes.

2.1. The Effects of Temperature Stress on Plant Development

Plant growth and developmental processes occur most efficiently within specific temperature ranges. Within these optimal thresholds, cellular metabolism, photosynthetic activity and nutrient uptake operate at maximum levels. When temperature falls below the optimal range, cellular functions slow down and the catalytic efficiency of enzymes decreases. Consequently, roots are unable to absorb sufficient water and minerals, which leads to nutrient deficiencies (Jones et al. 2021).

2.1.1. Under Low Temperature Conditions

- Seed germination is adversely affected, resulting in reduced root length and thinner root structures (Yu et al. 2025).
- Photoinhibition develops, stomatal conductance decreases and photosystem activities are reduced. This disrupts chloroplast membrane structures, causing the accumulation of reactive oxygen species (ROS) and a loss of photosynthetic efficiency (Xu et al. 2022).
- Reproductive development is critically impaired; pollen viability is declined, pollen tube growth is inhibited, and fertilization success is reduced. In rice, low temperature during anther dehiscence causes sterility, thereby lowering seed set and yield (Jiang et al. 2010). Similarly, in cereals such as wheat and barley, spikelet formation is disrupted (Frederiks et al. 2015).
- Thus, cold stress during the flowering stage is a critical limiting factor for both the productivity and quality of crops.

2.1.2. High Temperature Effects and Global Climate Change

One of the most critical outcomes of global climate change is the increase in heat waves and prolonged periods of high temperature. This

phenomenon severely affects the growth and developmental processes of many crops, particularly cereals, leading to substantial yield losses (Resentini et al. 2023). Studies have shown that drought and heat waves cause about 9-10% yield reduction in cereal production, while every 1 °C increase results in approximately 10% yield loss in rice and 3-4% yield loss in wheat (Lesk et al. 2016). Reported impacts include:

- In maize and barley, each day with temperatures above 30 °C reduces yield by about 1%.
- Heat waves in sunflower can lead to 40% yield reduction.
- Yield reductions of 42% in maize and 50% in rice have been documented (Badu-Apraku et al. 1983; Peng et al. 2004; Balla et al. 2011; Xu et al. 2020; Wang et al. 2020).

At the physiological level, high temperature stress induces the following disruptions:

- Decline in photosynthetic rate, reduced pollen viability, and shortened grain filling duration.
- Increased water loss, degradation of photosynthetic pigments, and induction of oxidative stress (Rezaei et al. 2015).
- Leaf and shoot scorching, sunburn, premature leaf senescence, and stunted growth.
- Poor seed germination and reduced seedling establishment.
- Damage to cell membranes, disruption of ion homeostasis, protein denaturation, and restricted enzyme activity (Mishra et al. 2023).

The most heat sensitive organs are pollen and anthers, where high temperatures commonly cause floral sterility. This is manifested by reduced spikelet and flower numbers in cereals, lower seed set in sorghum, and decreased growth, biomass accumulation, and net

assimilation rates in crops such as maize and sugarcane (Fahad et al. 2017).

2.2. Drouht Stress

Drought stress is recognized as one of the most detrimental environmental factors impairing plant productivity. Given that water comprises 80–95% of the fresh biomass of plant tissues, its pivotal role in growth, developmental processes, and metabolic regulation is undeniable. Therefore, some researchers consider drought to be the primary environmental stress factor for many crops, particularly in regions highly sensitive to water scarcity (Seleiman et al. 2021).

Water deficiency suppresses fundamental processes such as photosynthesis, respiration, cell division, and cell expansion. In addition, stomatal closure, while limiting water loss, also reduces carbon assimilation, thereby leading to a decline in photosynthetic efficiency (Zhao et al. 2020).

Drought stress significantly affects root and shoot growth. Root hairs, branching, and density are critical for efficient water uptake. In cotton, seedling growth is suppressed, the lifespan of fine roots is shortened, and root hairs elongate rapidly but die prematurely. In maize, root systems develop deeper and more vertically, enhancing their ability to access water; whereas in soybean, pea, and chickpea, shoot biomass is reduced more severely than root biomass, leading to an increased root to shoot ratio. In sugarcane, drought stress increases internode length and disrupts the structural integrity of the root system. Overall, drought reduces root and shoot biomass, plant height, leaf size, and stem thickness (Yang et al. 2021).

Plants exhibit various morphological adaptations to cope with drought stress. For instance, in tea plants, drought induces anatomical changes such as cuticle thickening, increased wax deposition on leaves,

proliferation of palisade parenchyma, and reduction of spongy mesophyll tissue (Chen et al. 2020). Stomatal traits also vary among species: in *Leymus chinensis*, water deficiency results in reduced stomatal size but increased stomatal density on the abaxial epidermis (Xu and Zhou 2008), whereas in *Populus balsamifera*, water stress is associated with a lower stomatal index (Hamanishi et al. 2012).

Drought stress severely reduces seed germination and seedling emergence. In chickpea, both germination and early seedling growth are suppressed; in alfalfa, drought decreases germination potential, hypocotyl length, and fresh/dry shoot and root biomass, while increasing root length. In rice, drought during the vegetative stage drastically limits growth (Farooq et al. 2009). This inhibition is mainly due to loss of turgor and insufficient water movement from the xylem to surrounding cells, which restricts cell division and elongation. As a result, leaf expansion and photosynthetic rate decline. Ultimately, drought stress leads to reductions in leaf number, leaf size, plant height, stem thickness, and significant decreases in both fresh and dry biomass (Fahad et al. 2017).

The most striking impact of drought stress is yield loss. Numerous studies across different crops have clearly demonstrated this effect. Reported reductions include:

- ✓ Maize: 63–87%
- ✓ Wheat: 57%
- ✓ Rice: 53–92%
- ✓ Chickpea: 45–69%
- ✓ Soybean: 46–71%

- ✓ Sunflower: up to 60% (Kamara et al. 2003; Mazahery-Laghab et al. 2003; Nayyar et al. 2006; Lafitte et al. 2007).

2.3. Salinity Stress

Salinity is a major abiotic stress factor in agriculture that significantly restricts crop productivity. Elevated levels of soluble salts in the soil, especially sodium chloride (NaCl), negatively influence plant growth and developmental processes. Soils are considered saline when their electrical conductivity (ECe) reaches 4 dS m⁻¹ or higher (Yıldız et al. 2021).

Salinity stress exerts its effects on plants through two primary mechanisms:

- ✓ **Osmotic stress:** High salt concentrations in the rhizosphere restrict water uptake, leading to physiological drought.
- ✓ **Ion toxicity:** Excessive accumulation of Na⁺ and Cl⁻ disrupts the uptake of essential nutrients such as K⁺, Ca²⁺, and Mg²⁺, causing nutrient imbalances (Botella et al. 2007). This condition limits cell division, slows root and shoot growth, and reduces both leaf size and leaf number.

At the cellular and organelle levels, salinity stress causes severe damage. Lipid peroxidation increases in the cell membrane, membrane permeability is disrupted, the Na⁺/K⁺ balance is disturbed, and Ca²⁺ metabolism is impaired. These processes trigger oxidative stress and lead to the accumulation of ROS.

Reported structural damages include:

- ✓ **Chloroplasts:** thylakoid swelling, disruption of grana structure, and starch accumulation.

- ✓ **Mitochondria:** structural deformations and impairments in energy metabolism (Çulha and Çakırlar 2011; Önal Aşçı and Altun 2021).

Salinity stress also imposes major restrictions during the germination stage:

- ✓ It reduces gibberellic acid (GA) levels while increasing abscisic acid (ABA), thereby altering seed metabolism.
- ✓ Changes in seed coat permeability restrict water uptake during imbibition.
- ✓ Decreased α -amylase activity slows starch hydrolysis and sugar transport, suppressing embryo development (Atta et al. 2023).
- ✓ Accumulated Na^+ and Cl^- ions reduce embryo viability, while increased ROS levels cause oxidative damage to DNA and proteins.

As a result:

- ✓ Germination rate decreases,
- ✓ Germination duration is prolonged,
- ✓ Seedling establishment is weakened.

At the morphological level, salinity stress results in reductions in plant height, leaf and root length, root volume, leaf area, leaf number, and stem thickness. In some species, adaptive responses such as thickening of the waxy cuticle or modifications in mesophyll tissue structure may occur. However, the general trend under salt stress is the suppression of biomass production, seedling growth, and flowering.

At the physiological level, salinity stress induces a wide range of detrimental effects:

- ✓ It causes stomatal closure, restricting CO₂ uptake and leading to a reduction in chlorophyll content.
- ✓ In Photosystem II (PSII), the D1 protein becomes damaged, resulting in photoinhibition and increased accumulation of reROS.
- ✓ Elevated ROS levels cause oxidative damage to proteins, membrane structures and DNA.
- ✓ Salinity alters the balance of plant hormones: gibberellins, auxins and cytokinins decline, while ABA and ethylene increase. This triggers leaf yellowing and premature senescence.
- ✓ Signal molecules such as jasmonates and salicylic acid play a positive role in enhancing salinity tolerance (Pandit et al. 2024).

2.3.1. Species and genotype specific differences

Plant responses to salinity stress vary considerably among species, as well as among different genotypes within the same species. Reported yield reductions include:

- ✓ Tomato: 10% yield loss at 1.5 dS m⁻¹ salinity.
- ✓ Wheat: 50% yield loss at 13.0 dS m⁻¹ salinity.
- ✓ Legumes: yield reductions of 69% in chickpea, 88% in lentil, and 50% in faba bean.
- ✓ Soybean genotypes: yield losses ranging between 46–67%.
- ✓ Mung bean varieties: yield losses between 62–68%.

- ✓ Pinto bean: 86% yield reduction under 12 dS m⁻¹ salinity (Mushtag et al. 2000).

These findings highlight that salinity tolerance is closely linked to genetic variation, indicating that breeding and selection of tolerant genotypes is a critical strategy for sustaining crop productivity in saline environments.

2.4. Heavy Metal Stress

Heavy metals are recognized as major environmental pollutants, accumulating in ecosystems through both natural processes and anthropogenic activities. Agricultural soils across the world are frequently contaminated with elements such as cadmium (Cd), cobalt (Co), copper (Cu), chromium (Cr), zinc (Zn), nickel (Ni), lead (Pb), and arsenic (As). The principal sources of this contamination include prolonged phosphate fertilizer use, sewage sludge application, industrial dust emissions, discharge of industrial effluents onto farmlands, and unsustainable irrigation practices (Yadav 2010).

The initial response of plants to heavy metal stress is the production of ROS. While some metals directly induce ROS formation, others increase ROS indirectly by impairing the antioxidant defense system, damaging the electron transport chain, or disrupting the metabolism of essential nutrients (Mithöfer et al. 2004).

A critical mechanism by which heavy metal toxicity exerts its harmful effects is lipid peroxidation. This process involves the breakdown of polyunsaturated fatty acids within cellular membranes and leads to the accumulation of malondialdehyde (MDA), a compound widely used as a biomarker of oxidative stress (Demiral and Türkan 2005).

2.4.1. Heavy Metals and Their Effects on Plants

2.4.1.1. Cadmium

Cadmium reduces photosynthesis, water, and nutrient uptake in plants. Characteristic symptoms include chlorosis, browning at root tips, and stunted growth. Cd exposure also suppresses protein synthesis and enzyme activities.

2.4.1.2. Zinc

Although Zn is an essential micronutrient, excessive levels become phytotoxic. Zinc toxicity restricts root and shoots development, induces chlorosis in leaves, and causes purple red discoloration due to phosphorus deficiency.

2.4.1.3. Copper

Copper is another essential micronutrient; however, when accumulated in excess, it generates oxidative stress, leading to growth retardation and leaf yellowing (Yadav 2010).

2.4.1.4. Mercury

Particularly in its ionic form (Hg^{2+}), mercury accumulates in soils and exerts strong phytotoxic effects. It disrupts water balance, mitochondrial activity, and cellular metabolism (Yadav 2010).

2.4.1.5. Chromium

Primarily released from the tanning industry, chromium causes chlorosis in young leaves, root damage, nutrient imbalance, and photosynthetic losses. In barley, 100 μM Cr exposure was reported to cause a 40% reduction in growth (Skeffington et al. 1976; Shanker et al. 2005).

2.4.1.6. Lead

As one of the most widespread pollutants, Pb at high levels inhibits plant growth, enzyme activity, water balance, and nutrient metabolism (Sharma and Dubey 2005).

2.4.1.7. Arsenic

Due to its chemical similarity to phosphate, arsenic competes with phosphate transporters and causes toxicity at elevated levels. Some plants can metabolize arsenic into less toxic forms at low concentrations (Li et al. 2009).

2.4.1.8. Cobalt and Nickel

These metals can accumulate in soil and, at high concentrations, cause growth retardation, chlorophyll loss, nutrient imbalance, oxidative stress, reduced water content, and membrane damage (Yadav 2010). For example, in cauliflower, excessive cobalt accumulation reduced biomass production and decreased Fe, chlorophyll, protein, and catalase activity in leaves. It also inhibited the translocation of P, S, Mn, Zn, and Cu from roots to shoots. Unlike excess copper or chromium, cobalt toxicity lowered leaf water potential and transpiration rate but increased relative water content (Chatterjee and Chatterjee 2000).

3. BIOTIC STRESS FACTORS

Throughout their life cycle, plants are exposed to a wide range of biotic stress factors caused by surrounding living organisms. These include fungi, viruses, bacteria, nematodes, weeds, and insects, all of which contribute to significant yield losses in agricultural production systems. Biotic stress agents lead to the development of various plant diseases, infections, and physiological disorders, ultimately resulting in

severe reductions in plant growth, development, and productivity (Bolaji Umar et al. 2022).

3.1. Viruses

Plant viruses alter the physiological and biochemical processes of their host plants, causing pathological disruptions throughout all stages of the plant life cycle. Most viral diseases appear as systemic infections, spreading from the initial inoculation site to other plant parts. These infections are typically chronic, leading to plant death, severe yield losses, and stress induction.

Plant viruses are responsible for nearly half of all pathogen induced plant diseases, posing a serious threat to global food security and the economy. To date, at least 2,026 plant viruses have been reported, classified into 73 genera and 49 families (ICTV 2025). As obligate intracellular parasites, viruses cannot replicate independently and depend entirely on host cell metabolism.

Structurally, plant viruses are composed of a nucleic acid core (either DNA or RNA) surrounded by a protective protein coat called the capsid. Around 75% of all known plant viruses contain a single stranded RNA (ssRNA) genome, of which approximately 65% are positive sense and 10% are negative sense. Negative sense ssRNA viruses must first be transcribed into positive sense RNA before protein synthesis can proceed. About 5% of plant viruses carry a double stranded RNA (dsRNA) genome, 17% possess a single stranded DNA (ssDNA) genome, and only a very small fraction have double stranded DNA (dsDNA) genomes (Raikhy and Tripathi 2017).

Because the plant cell wall restricts viral movement between cells, viruses spread through two major pathways:

- ✓ **Horizontal transmission:** via insect vectors, nematodes, plasmodiophorid protists, seeds, or pollen.
- ✓ **Vertical transmission:** from parent to progeny through seeds or vegetative propagation (Escalante et al. 2024).

Infected plants exhibit a wide range of symptoms, including mosaic patterns, streaks, ring spots, leaf curling, deformations, necrosis, stem pitting, and fruit or tuber malformations (Jiang and Zhou 2023). Additionally, virus infections reduce photosynthetic activity, cause chloroplast deformation, and disrupt carbon and nitrogen metabolism. Alterations in phloem tissue hinder starch transport, leading to leaf thickening, brittleness, necrosis, and disturbances in water balance (Ananthu and Umamaheswaran 2019).

3.2. Fungal Plant Pathogens

Due to their ecological diversity and high adaptive capacity, plant pathogenic fungi is considered as one of the most harmful threats to agricultural production. The most of the plant pathogenic fungi belong to the Ascomycetes and Basidiomycetes classes, and they exhibit three main lifestyles: biotrophic, necrotrophic, and hemibiotrophic (Sharma 2021).

- ✓ **Biotrophic fungi:** feed on living host cells without killing them.
- ✓ **Necrotrophic fungi:** induce host cell death through toxins and cell wall-degrading enzymes.
- ✓ **Hemibiotrophic fungi:** initially behave as biotrophs but switch to a necrotrophic phase later in infection (Doehlemann et al. 2017).

These pathogens suppress host defense mechanisms using effector proteins, oxalic acid, fumonisins, mycotoxins, and cell wall-degrading

enzymes. Structurally, fungi consist of septate or aseptate hyphae, surrounded by a plasmalemma containing ergosterol, and enclosed by a cell wall composed primarily of chitin and glucans. Their spores are dispersed by wind, raindrops, soil, and insects (Golan and Pringle, 2017). Pathogenic fungi can infect host plants by entering through natural openings (e.g., stomata) or wounds; in biotrophic fungi, specialized structures called haustoria function as feeding organs (De Wit et al. 2016).

Approximately 20,000 fungal species are parasitic and capable of causing diseases in crop plants (Mahmood et al. 2017). The most common fungal diseases include leaf spots, rusts, wilts, blights, root rots, downy mildews, and molds, all of which result in severe yield and quality losses, posing a major threat to global food security (Jain et al. 2019).

Scientifically and economically important phytopathogenic fungi include *Magnaporthe oryzae*, *Botrytis cinerea*, *Puccinia* spp., *Fusarium graminearum*, *Colletotrichum* spp., *Fusarium oxysporum*, *Blumeria graminis*, *Melampsora lini*, *Mycosphaerella graminicola*, and *Ustilago maydis*. Additionally, *Phakopsora pachyrhizi* and *Rhizoctonia solani* are recognized as highly destructive pathogens (Dean et al. 2012). These fungi are notable for their wide host ranges, high adaptability, and strong potential to develop resistance to fungicides.

3.3. Bacteria

Bacteria are microscopic organisms capable of surviving in almost every environment on Earth. Their primary habitats include soil, water, and the bodies of plants and animals. Typically measuring 1–2 μm , these unicellular organisms are invisible to the naked eye but can be observed as aggregates in liquids, biofilms on plant surfaces, plugs in vascular tissues, or as colonies on culture media when they reach high population densities.

Plant associated bacteria may exist as epiphytes on plant surfaces or as endophytes within plant tissues. While some are beneficial, others are pathogenic. As plants mature, bacterial colonization increases, and for both effective biological control activity and disease development, bacterial populations usually need to reach 10^6 CFU/mL or higher.

Although plant pathogenic bacteria generally cause fewer economic losses compared with fungi and viruses, they still result in significant yield and quality reductions in agriculture. Most plant species possess a degree of natural resistance to bacterial pathogens, but some can act as symptomless carriers, contributing to the dissemination of diseases (Vidaver and Lambrecht 2004).

Out of approximately 7,100 classified bacterial species, only about 150 are known to cause plant diseases (Rajesh-Kannan et al. 2016). Plant pathogenic bacteria are primarily grouped into three main families:

- ✓ Xanthomonadaceae
- ✓ Pseudomonadaceae
- ✓ Enterobacteriaceae

Within these families, the major pathogenic genera include: *Liberibacter*, *Clavibacter*, *Erwinia*, *Pectobacterium*, *Candidatus*, *Pantoea*, *Agrobacterium*, *Pseudomonas*, *Streptomyces*, *Ralstonia*, *Burkholderia*, *Acidovorax*, *Xanthomonas*, *Spiroplasma*, *Phytoplasma*, and *Xylophilus* (Agrios 2005).

In field crops, the main disease symptoms caused by bacterial pathogens include: abnormal growth in roots and stems, leaf and fruit spots, cankers and tumors, leaf and stem blights, tissue necrosis, and rotting of roots and tubers (Vidaver and Lambrecht 2004).

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Morphologically, bacteria may appear in rod shaped (bacilli), spherical (cocci), spiral, or pleomorphic forms, with the majority being bacilli. Modern biochemical and molecular analyses confirm that plant pathogenic bacteria constitute a highly heterogeneous group.

Plant associated bacteria possess several key cellular components and traits that influence both pathogenicity and ecological roles.

- ✓ **Intracellular structures:** These include DNA chromosomes, plasmids that may encode virulence factors or biocontrol traits, and storage granules.
- ✓ **Motility and adhesion:** Flagella and fimbriae play critical roles in bacterial motility and attachment to host surfaces.
- ✓ **Colonization:** Pathogenic bacteria may establish themselves by forming biofilms on plant surfaces or by blocking vascular tissues. However, even bacteria lacking prominent appendages can act as effective pathogens (Vidaver and Lambrecht 2004).

Bacteria reproduce asexually, most commonly by binary fission:

- ✓ The cell replicates its genetic material.
- ✓ The cytoplasm and membrane constrict, forming two daughter cells.
- ✓ These daughter cells are genetically similar to the parent cell.
- ✓ Under favorable conditions, some bacterial populations may double every 20 minutes.

In addition to clonal reproduction, bacteria enhance genetic diversity through three major mechanisms:

- ✓ **Conjugation:** transfer of plasmids or other DNA fragments via a pilus.
- ✓ **Transformation:** uptake of free DNA fragments from the environment.
- ✓ **Transduction:** gene transfer mediated by bacteriophages.

These processes do not directly increase population size but significantly enhance adaptive capacity.

Under adverse conditions, some bacteria restrict their metabolic activity and form spores, which confer resistance against heat, drought, nutrient scarcity, and chemical stress. Once favorable conditions return, spores germinate and resume active division.

Soil dwelling bacteria are essential for ecosystem functioning, contributing to:

- ✓ Nitrogen fixation,
- ✓ Nutrient cycling,
- ✓ Organic matter decomposition,
- ✓ Soil formation.

It is estimated that 1 gram of soil contains 10^{10} - 10^{11} bacterial cells and thousands of species. Autotrophic bacteria convert nutrients into plant available forms, whereas heterotrophs decompose organic matter. Their rapid adaptability allows them to survive even in extreme ecosystems worldwide (FAO 2025).

3.4. Nematodes

With approximately 30,000 described species worldwide, nematodes represent the most abundant group among invertebrates and

are notable for their functional diversity in ecosystems. Based on their feeding habits, nematodes are classified into five major groups: bacterivores (feeding on bacteria), fungivores (feeding on fungal hyphae), predators (feeding on other nematodes and invertebrates), omnivores (utilizing diverse food sources), and herbivores (feeding on various plant organs) (Kennedy and Luna 2005). Among these, herbivorous nematodes are the most economically damaging group in agriculture. About 250 species from 43 genera are considered high risk pests, and 126 species from 33 genera are included on quarantine lists in multiple countries (Singh et al. 2013).

Plant parasitic nematodes feed on roots, stems, leaves, or flowers and are grouped according to their feeding strategies into ectoparasites, endoparasites, and semi endoparasites:

- ✓ Ectoparasites (e.g., *Longidorus*, *Criconeema*, *Xiphinema*) remain outside the root and insert their stylets to withdraw cell contents.
- ✓ Endoparasites (e.g., *Meloidogyne*, *Pratylenchus*) penetrate root tissues, feeding directly on cells. They may either complete their entire life cycle within roots or migrate between tissues.
- ✓ Semi endoparasites partially embed the anterior part of their body into root tissues while the posterior remains outside (Decraemer and Hunt 2006).

The use of a stylet to extract cellular contents can lead to direct cell death, while some nematodes induce abnormal cell growth and differentiation, forming giant cells that serve as metabolically active feeding sites (Lambert and Bekal 2002).

The most harmful nematode species in crop plants were as follows;

***Tylenchulus semipenetrans* → citrus orchards**

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Hirschmaniella oryzae → rice fields

Meloidogyne javanica, *M. incognita* → vegetable production

Meloidogyne chitwoodi, *Globodera pallida*, *G. rostochiensis* → potato cultivation

Heterodera avenae, *H. latipons*, *H. filipjevi* → wheat and barley fields

Ditylenchus dipsaci → onion and garlic

Pratylenchus neglectus, *P. thornei* → cereals, fruit orchards, and vineyards

Longidorus elongatus, *Xiphinema index* → fruit orchards and vineyards (Brown 1984; Smiley 2009; Janati et al. 2018).

By feeding on root tissues, these nematodes directly impair water and nutrient uptake, resulting in wilting, stunting, nutrient deficiencies, and reduced plant vigor (Granett et al. 2003). Yield losses may range from moderate reductions to complete crop failure in severe infestations.

The damage caused by plant parasitic nematodes is not limited to direct feeding. They also play a crucial role in the transmission and facilitation of other plant pathogens:

- ✓ **Virus transmission:** Members of the families Longidoridae and Trichodoridae are among the most important vectors of plant viruses. Species such as *Xiphinema index*, *X. italiae*, *X. diversicaudatum*, *X. rivesi*, *X. americanum*, *Longidorus elongatus*, *L. attenuatus*, *Paralongidorus maximus*, *Trichodorus similis*, and *Paratrachodorus minor* are known to transmit 23 nepoviruses and 2 tobnaviruses (Macfarlane and Robinson 2004).
- ✓ **Fungal facilitation:** Feeding wounds caused by nematodes enable the entry of soilborne fungi. For example, *Rhizoctonia*

solani and *Thielaviopsis basicola* spread more rapidly in nematode damaged roots, intensifying root rot disease (Manzanilla-López and Starr 2009).

Thus, nematodes are not only independent pests but also critical initiators and enhancers of disease complexes, significantly contributing to plant disease epidemics.

3.5. Pests

Pests create biotic stress in plants either by directly damaging plant tissues or by triggering the plant's defense mechanisms.

Sap sucking pests (aphids, whiteflies, thrips) extract plant sap, leading to chlorophyll loss, leaf yellowing, wilting, and a reduction in photosynthesis.

Chewing pests, such as leaf miners and caterpillars, cause tissue loss on leaf surfaces, thereby reducing carbon assimilation.

Soil dwelling pests (wireworms, root knot nematodes, larvae) damage root tissues, restricting water and nutrient uptake and resulting in physiological drought within the plant.

Virus transmitting pests (especially aphids and whiteflies) cause systemic stress through secondary infections. This leads to the accumulation of reactive oxygen species (ROS) and triggers oxidative stress in plant tissues.

3.6. Weeds

Weeds compete with crop plants for essential resources such as water, nutrients, and light. In general, an increase of 1 kg in weed dry matter corresponds to a 1 kg decrease in crop dry matter. The intensity of competition depends on several factors, including time of emergence, species differences, growth rate, and allelopathic effects. The first 3–8

weeks after sowing are considered the “critical period” for weed control; failure to manage weeds during this time leads to significant yield losses.

Weeds often gain an advantage in light competition due to their broad leaves and rapid height growth. For instance, studies in soybean fields have shown that 44–56% shading by weeds can reduce yields by 19–25%. In nutrient competition, nitrogen (N), phosphorus (P), and potassium (K) are especially critical. *Amaranthus* species, for example, can accumulate over 3% N in their dry matter, while *Chenopodium* and *Portulaca* species may store more than 1.3% K.

In terms of water competition, weeds often have deep root systems and high transpiration capacity, enabling them to outcompete crops. Many weed species also utilize the C4 photosynthetic pathway, allowing them to use water and nitrogen more efficiently than C3 crops (Başaran 2022).

In newly established orchards, where young trees have shallow and weak root systems, weed infestation causes even more severe damage. Deep rooted weeds deplete nutrients and water from deeper soil layers, while shading reduces light interception for seedlings (Wisler and Norris 2005). Globally, failure to control weeds can result in yield losses of up to 43% (Abouzienna and Haggag 2016).

Weeds also act as alternative hosts for numerous pathogens, nematodes, and insects. Viral, bacterial, and fungal agents may overwinter in weed species, maintaining their viability in the absence of crop plants. Furthermore, some weeds such as *Datura stramonium*, *Conium maculatum*, *Cirsium arvense*, and *Cuscuta* spp. contain toxic compounds such as alkaloids, glycosides, and saponins, which can exert phytotoxic effects on crops (Rich et al. 2008; Marinov-Serafimov et al. 2017).

Weeds are classified according to their life span (Rao 2000):

- ✓ **Annuals:** reproduce only by seeds.
- ✓ **Biennials:** complete their life cycle in two years.
- ✓ **Perennials:** reproduce both by seeds and vegetative structures such as rhizomes, stolons, tubers, and bulbs.

The soil seed bank serves as the primary source of new infestations, ranging from 0 to over 1 million seeds/m². Of this, 70–90% is contributed by a few dominant species, 10–20% by adaptive but less dominant species, while the remainder consists of long lived resistant species from previous years (Talaka and Rajab 2013).

Due to their high seed production, dormancy, and vegetative propagation abilities, weeds cannot be completely eradicated from agricultural fields despite intensive management practices. For this reason, they are regarded as one of the most critical biotic stress factors in crop production.

4. INTERACTIONS BETWEEN ABIOTIC AND BIOTIC STRESSES

Plants are inherently immobile organisms and are therefore directly exposed to sudden or prolonged changes in environmental conditions. These conditions often act not in isolation but in combination, resulting in “dual” or “multiple stress” scenarios. The interaction between abiotic and biotic stresses triggers distinct physiological, biochemical, and molecular responses in plants. Compared to individual stress conditions, combined stresses generally cause much more severe losses in yield and crop quality.

When drought and pathogen attack occur simultaneously, water deficiency weakens plant cellular defense capacity, while the virulence

factors of certain pathogens become more effective, thereby intensifying infection severity. However, in some cases, plants such as tobacco and tomato grown under drought conditions exhibit enhanced resistance against fungal and bacterial pathogens. This tolerance is often associated with the regulation of ROS balance, ABA accumulation, phytoalexin synthesis, and the activation of pathogenesis related (PR) genes. Similarly, salinity or heavy metal accumulation may suppress the growth of certain pathogens, thereby indirectly contributing to plant resistance.

Conversely, biotic stressors can also influence abiotic stress tolerance. Beneficial microorganisms, including plant growth-promoting rhizobacteria (PGPR), mycorrhizal fungi, and endophytes, enhance plant resistance not only to pathogens but also to abiotic stresses such as drought, salinity, and heat. This resistance is linked to mechanisms such as antioxidant production, osmolyte accumulation, and ABA and salicylic acid (SA) signaling. Furthermore, some viral infections have been reported to increase tolerance to drought or cold by limiting water loss.

Common signaling networks play a central role in plant responses to both abiotic and biotic stresses. For instance, ABA, which regulates water balance under abiotic stress, also contributes to pathogen defense. ROS act as both signaling molecules and toxic agents: at low concentrations they activate defense responses, while at high concentrations they cause cellular damage. Additionally, salicylic acid (SA), jasmonic acid (JA), and ethylene are key hormones that mediate plant responses to both biotic and abiotic stresses. The convergence of these signaling pathways enables plants to adapt to multiple stress factors simultaneously.

5. STRESS MECHANISMS IN PLANTS

Plants have developed multilayered defense strategies to cope with abiotic and biotic stresses. These mechanisms can be grouped into five major categories:

5.1. Apoplastic Mechanisms (Extracellular Defense)

Molecules such as ascorbate (ASC), glutathione (GSH), defensins, phenolic compounds, and lignin function in the apoplast to restrict oxidative stress and prevent pathogen entry (Podgorska et al. 2017).

A key feature of plant stress tolerance is the maintenance of intracellular redox homeostasis, largely mediated by antioxidant enzymes:

- ✓ **Ascorbate–glutathione (ASC–GSH) cycle:** A central ROS detoxification system. Ascorbate peroxidase (APx) neutralizes superoxide and hydrogen peroxide using ASC. Dehydroascorbate (DHA) is then reduced back to ASC by GSH, maintaining redox balance.
- ✓ **Superoxide dismutase (SOD):** Converts the highly toxic superoxide radical into hydrogen peroxide.
- ✓ **Catalase (CAT):** Predominantly active in peroxisomes, decomposing H_2O_2 into water and oxygen.
- ✓ **Glutathione peroxidase (GPx):** Reduces lipid peroxides and H_2O_2 using GSH, protecting membranes from oxidative injury.

Several stress responsive proteins provide additional protection:

- ✓ **Heat shock proteins (HSPs):** Prevent protein misfolding and assist in refolding damaged proteins, thereby maintaining protein homeostasis (Ul Hag et al. 2019).

- ✓ **Late embryogenesis abundant (LEA) proteins:** Preserve water balance and stabilize proteins and membranes under drought and salinity stress (Hand et al. 2011).
- ✓ **Osmotins:** Maintain membrane integrity under osmotic stress and exhibit antifungal properties (Bashir et al. 2020).
- ✓ **Lectins:** Carbohydrate binding proteins involved in cell–cell interactions and pathogen defense activation (De Hoff et al. 2009).

Secondary metabolites also play an important role (Upadhyay et al. 2025):

- ✓ **Flavonoids:** Provide protection against UV radiation, pathogens, and oxidative stress through antioxidant activity.
- ✓ **Alkaloids:** Exhibit toxicity against herbivores and pathogens.
- ✓ **Phenolic compounds:** Reinforce cell walls, enhance lignification, and scavenge ROS.
- ✓ **Defensins and small peptides:** Defensins are cysteine rich antimicrobial proteins that disrupt microbial membranes, while small peptides can chelate heavy metals and contribute to detoxification, in addition to antimicrobial activity.

5.2. Symplastic Mechanisms (Intracellular Defense)

Key antioxidant enzymes including the ASC–GSH cycle, SOD, CAT, and GPx mediate ROS detoxification within the cytoplasm. Proteins such as HSPs, LEA proteins, and osmotins protect protein stability and mitigate osmotic stress.

5.3. Organ and Whole Plant Level Mechanisms

- ✓ **Stomatal regulation:** ABA mediated stomatal closure reduces water loss and pathogen entry but prolonged closure restricts photosynthesis, imposing growth costs.
- ✓ **Hypersensitive response (HR):** Characterized by ROS and NO accumulation, protease activation, and localized programmed cell death, effectively restricting pathogen spread.
- ✓ **Systemic responses:** Stress induced signaling molecules are transported via the phloem and xylem, triggering systemic acquired resistance (SAR) throughout the plant (Du et al. 2024).
- ✓ **Key signaling molecules:** ROS and NO function in defense signaling; salicylic acid (SA) is crucial against biotrophic pathogens; jasmonic acid (JA) and ethylene act synergistically against necrotrophs and herbivores; ABA plays dual roles in drought and pathogen defense.

5.4. Ecosystem Level Mechanisms

Plants enhance their resilience not only through internal physiology but also via interactions with their environment:

- ✓ **Root exudates:** Sugars, amino acids, organic acids, and phenolics attract beneficial rhizosphere microbes and suppress pathogen development.
- ✓ **Phytoalexins and phytoanticipins:** Antimicrobial secondary metabolites that restrict pathogen spread—phytoalexins are induced upon attack, whereas phytoanticipins are constitutively present.

- ✓ **Volatile organic compounds (VOCs):** Act as interplant signals, deter herbivores, attract natural enemies, and provide protection against atmospheric pollutants (War et al. 2012).

5.5. Molecular and Epigenetic Mechanisms

Long term adaptation to stress involves hormone signaling, small RNAs, and epigenetic memory mechanisms:

- ✓ **ABA:** Regulates stomatal closure during drought and salinity stress, and also contributes to pathogen defense (Lim et al. 2015).
- ✓ **SA:** Central to defense against biotrophic pathogens and activation of SAR (Klessig et al. 2018).
- ✓ **JA and ethylene:** Cooperatively regulate defenses against necrotrophic pathogens and herbivores (Zhang et al. 2017).
- ✓ **Epigenetic regulation (stress memory):** DNA methylation, histone modifications, and small RNAs enable plants to “remember” past stress exposure, leading to faster and stronger responses upon re exposure (Sun et al. 2021).

6. CURRENT APPROACHES IN PLANT PROTECTION STRATEGIES

In modern agriculture, both classical methods and innovative approaches are being employed to combat abiotic and biotic stress factors. Recent advancements focus on enhancing plant resilience and achieving sustainable crop protection:

- ✓ **Development of resistant varieties:** In addition to traditional breeding techniques, molecular markers and genomic selection

are widely applied to develop plant cultivars with high levels of stress tolerance.

- ✓ **Molecular biology and genetic approaches:** CRISPR/Cas9 based genome editing enables precise targeting of stress related genes. Transgenic plants have been developed to improve resistance not only against abiotic stresses such as drought and salinity but also against biotic stresses caused by pathogens.
- ✓ **Biological control and microbial biotechnology:** Plant growth–promoting rhizobacteria (PGPR), mycorrhizal fungi, and endophytic microorganisms enhance plant stress tolerance while also serving as effective biocontrol agents against pathogens.
- ✓ **Precision agriculture and digital applications:** The use of sensors, satellite imaging, drone technologies, and AI driven decision support systems enables early detection and effective management of stress factors. These approaches contribute to reduced chemical inputs and promote long term agricultural sustainability.

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Role of Transcription Factors in Regulating Abiotic Stress Tolerance in Plants

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1. INTRODUCTION

Abiotic stresses represent a major constraint on global crop production, leading to severe reductions in both yield and quality. Environmental challenges such as drought, salinity, heat waves, chilling, heavy metal toxicity, and oxidative stress interfere with plant growth, metabolism, and reproduction, ultimately endangering food security and sustainable agriculture (Lesk et al. 2016). Unlike mobile organisms, plants are sessile and thus cannot avoid unfavourable conditions. Instead, they rely on intricate physiological, biochemical, and molecular mechanisms to withstand stress throughout their life cycle (Zhu, 2016). These strategies include preserving cellular water balance and ion homeostasis, detoxifying reactive oxygen species (ROS), synthesizing compatible solutes, maintaining membrane stability, and producing stress-associated proteins (Liu et al. 2014).

Central to these adaptive responses are transcription factors (TFs)—DNA-binding regulatory proteins that modulate the transcription of downstream genes by recognizing specific motifs in promoter regions. In plants, TFs play pivotal roles in coordinating defense responses through both ABA-dependent and ABA-independent signaling pathways. Families such as NAC, MYB, bZIP, WRKY, and AP2/ERF (including DREB and AREB/ABF subgroups) have been extensively characterized for their contribution to stress resilience (Singh et al. 2002). These TFs function at multiple levels of the signaling cascade, orchestrating protective protein synthesis, activation of antioxidant machinery, and metabolic adjustments required for survival under stress (Baillo et al. 2019).

The present chapter highlights the molecular and functional roles of plant TFs in abiotic stress regulation. It focuses on their structural features, mechanisms of action, stress-specific responses, and potential

applications in crop biotechnology aimed at improving resilience and productivity under adverse environmental conditions.

2. ABIOTIC STRESS and RESPONSE MECHANISMS in PLANTS

Throughout their life span, plants encounter diverse abiotic stresses including drought, salinity, extreme temperatures, heavy metal accumulation, and oxidative damage. These stresses impair normal physiology and gene expression, leading to substantial yield penalties (Lesk et al. 2016). To counteract such conditions, plants deploy multifaceted adaptations ranging from morphological and biochemical adjustments to transcriptional reprogramming.

Drought stress reduces water potential, causing turgor loss, decreased photosynthesis, and slowed metabolism. Plants mitigate these effects by accumulating osmoprotectants such as proline, trehalose, and glycine betaine, while also adjusting morphology through stomatal closure, leaf abscission, and enhanced root-to-shoot ratios. At the molecular level, the ABA pathway induces the expression of stress-responsive genes like *RD29A*, *NCED3*, and *LEA*. For instance, root-specific overexpression of *OsNAC10* in rice enhanced drought resistance and improved water use efficiency (Jeong et al. 2018).

Salt stress exerts both osmotic and ionic toxicity, primarily via excess NaCl. To maintain ion balance, plants activate Na^+/H^+ antiporters and components of the Salt Overly Sensitive (SOS) pathway. Osmotic balance is supported through proline and mannitol biosynthesis. Experimental data show that overexpression of *GhWRKY34* in cotton improves salt tolerance by modulating ion transport and redox homeostasis (Li et al. 2019).

Heat stress destabilizes cellular proteins, disrupts membrane fluidity, and inactivates photosynthetic enzymes. To minimize these damages, plants synthesize heat shock proteins (HSPs: HSP70, HSP90, HSP101) under the regulation of heat shock transcription factors (HSFs). *Arabidopsis thaliana* mutants lacking *AtHSFA1* exhibit high temperature sensitivity, underlining the crucial role of HSFs (Ohama et al. 2017).

Cold stress leads to ice crystal formation and membrane disruption. Plants maintain membrane fluidity by increasing unsaturated fatty acids and accumulate cryoprotective proteins and sugars. CBF/DREB1 TFs regulate downstream cold-inducible genes such as *COR15A* and *KIN1*. Overexpression of *BnCBF17* in *Brassica napus* notably improved frost resistance (Shi et al. 2018).

Heavy metal toxicity, arising from lead, cadmium, or arsenic accumulation, triggers excessive ROS generation. Plants counter this through phytochelatins and metallothioneins that chelate toxic ions. For example, *OsMT1e* overexpression in rice enhanced cadmium detoxification (Li et al. 2020). In addition, oxidative stress, common across all stress types, is mitigated by antioxidant enzymes such as SOD, CAT, and APX. Tomato plants with *SLAPX2* overexpression exhibited reduced oxidative injury under stress (Wang et al. 2021a). Together, these adaptive strategies demonstrate how plants utilize complex molecular networks, including transcriptional regulators, to maintain growth and reproduction under hostile environments.

2.1. Transcription Factors in Plants: Structure and Function

Transcription factors are fundamental components that translate environmental cues into gene expression changes, thereby enabling plants to adjust development and stress responses (Wang et al. 2021b). They typically consist of three core domains: a DNA-binding domain, a transcriptional activation or repression domain, and a nuclear

localization signal (NLS). The DNA-binding domain allows recognition of specific cis-elements in promoters; the activation/repression domain interacts with RNA polymerase II and cofactors to regulate transcription; and the NLS ensures proper transport of TFs into the nucleus (Nakashima et al. 2018; Jin et al. 2021).

The regulation of TF activity occurs at multiple levels. At the transcriptional level, expression patterns of TF genes shift in response to stress signals, while alternative splicing may generate functionally distinct isoforms. At the post-transcriptional level, microRNAs contribute to TF regulation—for example, miR164 targets NAC1 mRNA, modulating both lateral root formation and drought tolerance (Zhao et al. 2020). Post-translational modifications such as phosphorylation, acetylation, or ubiquitination further modulate TF activity, stability, and localization. Notably, SnRK2 kinases phosphorylate AREB/ABF-type bZIP TFs under ABA signaling, enabling them to activate downstream genes (Nakashima et al. 2018).

In terms of signaling pathways, TFs operate in both ABA-dependent and ABA-independent networks. In the ABA-dependent system, elevated ABA during drought or salinity stress is sensed by PYR/PYL/RCAR receptors, leading to inhibition of PP2C phosphatases and activation of SnRK2 kinases. These kinases phosphorylate AREB/ABF TFs, which subsequently activate ABA-responsive genes (Nakashima et al. 2018). Conversely, ABA-independent mechanisms often involve DREB/CBF TFs activated through MAPK cascades and calcium signaling, binding to DRE/CRT motifs of genes such as *RD29A*, *COR15A*, and *KIN1*.

TFs also integrate signals across pathways, contributing to multi-stress tolerance. For instance, NAC and WRKY proteins participate in both ABA-dependent and ABA-independent responses (Wang et al. 2021). Moreover, TFs frequently act in complexes with other proteins.

A prominent example is the MBW complex, composed of MYB and bHLH TFs along with WD40 proteins, which regulates flavonoid biosynthesis (Jin et al. 2021). Such interactions illustrate how TFs control broad genetic networks, thereby fine-tuning plant responses to dynamic environments.

2.2. The Role of Transcription Factors in Abiotic Stress Responses in Plants

Plant TFs are grouped into diverse families, each defined by specific structural motifs, DNA-binding domains, and regulatory functions. Among these, NAC, MYB, bZIP, WRKY, and AP2/ERF are the most thoroughly studied due to their wide-ranging influence on abiotic stress adaptation.

The NAC family, named after NAM, ATAF, and CUC genes, regulates development, senescence, and stress tolerance. These TFs act through both ABA-dependent and ABA-independent signaling. For example, root-specific expression of *OsNAC10* in rice enhanced root growth and minimized yield loss during drought (Jeong et al. 2018). Similarly, *GhNAC79* expression in cotton improved tolerance to salinity and drought (Shang et al. 2020).

The MYB family, characterized by MYB DNA-binding repeats, is central to secondary metabolism, cell cycle control, and stress defense. MYB TFs regulate pathways such as flavonoid biosynthesis and osmolyte accumulation. *AtMYB44* enhances drought and salt tolerance by modulating ABA-related genes, whereas *OsMYB2* boosts osmotic stress tolerance by promoting proline and sugar alcohol accumulation (Yang et al. 2019).

The bZIP family contains a basic region for DNA binding and a leucine zipper for dimerization. Members such as AREB/ABF function mainly in ABA-mediated stress signaling. For instance, *ABF3* and *ABF4*

overexpression in Arabidopsis improved water deficit tolerance and seed germination efficiency (Yoshida et al. 2019).

The WRKY family, defined by the WRKYGQK motif, was first linked to pathogen responses but is now recognized as crucial for abiotic stress tolerance as well. WRKY TFs govern ROS detoxification, ion balance, and osmolyte synthesis. Overexpression of *TaWRKY46* in wheat improved salinity tolerance by regulating ion transport genes (Niu et al. 2020).

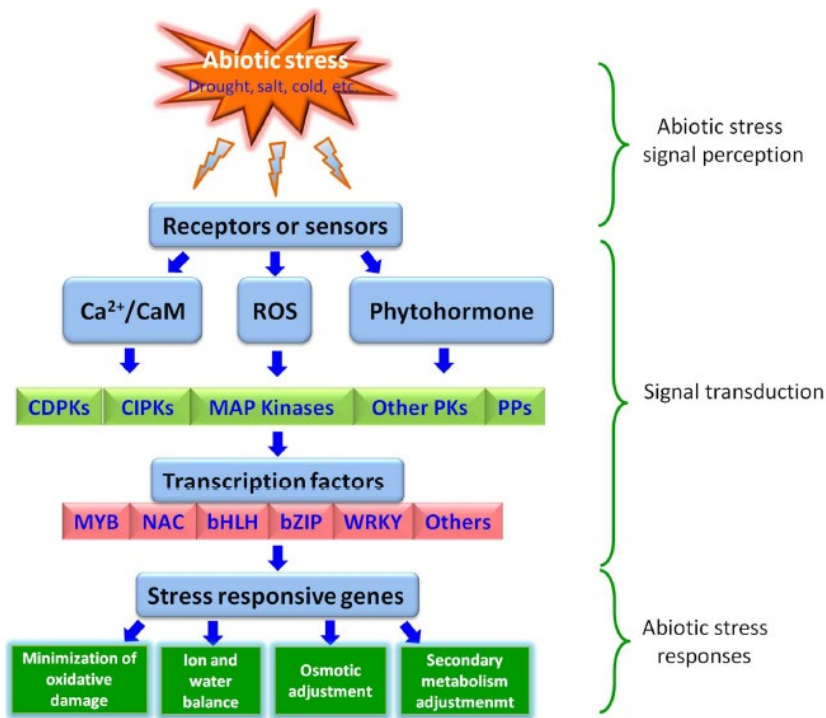


Figure 1. Transcription factors regulating abiotic stress signalling pathways (Khan et al. 2018)

The AP2/ERF family, particularly the DREB subgroup, is vital for drought, salinity, and cold responses. DREB proteins bind DRE/CRT promoter elements in an ABA-independent manner. For example, *AtDREB1A* expression across multiple plant species conferred enhanced drought and freezing tolerance (Kasuga et al. 2019a). Similarly, regulated activation of *OsDREB2A* in rice improved resilience to both drought and heat (Mallikarjuna et al. 2021). Collectively, these TF families form interconnected regulatory networks that integrate various signaling pathways.

NAC and WRKY proteins often act as cross-talk mediators, while MYB and bZIP factors coordinate metabolic adjustments with stress signaling. Understanding these interactions provides valuable insight into plant resilience and offers molecular targets for engineering stress-tolerant crops.

3. GENETIC ENGINEERING APPROACHES

Due to their central roles in regulating stress responses, TFs are prime targets in genetic engineering to increase abiotic stress tolerance. Strategies include overexpression, gene silencing, promoter engineering, and genome editing.

Overexpression of TFs ensures constitutive activation of protective pathways. For instance, driving *OsNAC10* expression under a root-specific promoter in rice improved root structure, drought tolerance, and yield stability (Jeong et al. 2018). Similarly, *AtDREB1A* overexpression in *Arabidopsis* enhanced both drought and cold tolerance (Kasuga et al. 2019b).

Gene silencing or knockout approaches are applied when certain TFs negatively affect stress resilience. RNA interference (RNAi) or

CRISPR/Cas9-mediated knockouts can eliminate detrimental functions. For example, suppression of *OsWRKY45* in rice optimized energy use and minimized yield loss under stress (Tao et al. 2021).

Table 1. Transcription factors involved in plant abiotic stress responses

Transcription Factor	Plant Species	Stress Type	Function/Mechanism	Reference
<i>OsNAC10</i>	<i>Oryza sativa</i>	Drought	Root-specific expression improves drought tolerance and increases grain yield.	Jeong et al. 2018
<i>DREB1A</i>	<i>Multiple species</i>	Drought, salt, freezing	Stress-inducible TF; enhances tolerance by activating multiple stress-responsive genes.	Kasuga et al. 2019
<i>GhNAC42</i>	<i>Gossypium hirsutum</i>	Salt	CRISPR/Cas9 mutagenesis improves salt tolerance through stress-responsive gene regulation.	Li et al. 2022
<i>OsWRKY45</i>	<i>Oryza sativa</i>	Multiple stresses	Regulates ABA-dependent and ABA-independent pathways for stress adaptation.	Tao et al. 2021
<i>GhWRKY34</i>	<i>Gossypium hirsutum</i>	Salt	Overexpression enhances salt tolerance by regulating ion homeostasis and antioxidant enzymes.	Li et al. 2019
<i>BnCBF17</i>	<i>Brassica napus</i>	Freezing	Overexpression enhances freezing tolerance by regulating COR genes.	Shi et al. 2018
<i>SIAPX2</i>	<i>Solanum lycopersicum</i>	Oxidative stress	Overexpression improves oxidative stress tolerance by enhancing ROS-scavenging capacity.	Wang et al. 2021
<i>OsMYB2</i>	<i>Oryza sativa</i>	Salt, drought	Overexpression increases tolerance through osmolyte accumulation and stress gene regulation.	Yang et al. 2019
<i>ABF3/ABF4</i>	<i>Arabidopsis thaliana</i>	Drought	ABA-dependent TFs activating drought-responsive genes via ABRE elements.	Yoshida et al. 2019

Promoter engineering enables spatial- and stress-specific regulation of TFs, avoiding unnecessary metabolic cost under normal conditions. The rd29A promoter, when coupled with DREB1A, induced expression only under stress, preventing growth penalties (Kasuga et al. 2019). Genome editing technologies, particularly CRISPR/Cas9, allow precise modifications in TF coding or regulatory regions. Editing of *GhNAC42* regulatory sequences in cotton significantly enhanced salt tolerance (Li et al. 2022). Furthermore, stacking multiple TF modifications or combining them with metabolic engineering approaches can generate broad-spectrum tolerance, such as enhanced osmolyte accumulation or improved antioxidant defenses. While these approaches hold promise, challenges remain regarding pleiotropic effects, growth penalties, and biosafety considerations. Future applications will benefit from controlled TF regulation using inducible promoters, systems biology models, and multi-gene editing strategies to develop stress-resilient crops with minimal trade-offs.

4. CONCLUSION

TFs are pivotal regulators that coordinate genetic and physiological processes underlying plant adaptation to abiotic stresses. Prominent TF families, including NAC, MYB, bZIP, WRKY, and AP2/ERF, contribute to tolerance against drought, salinity, temperature fluctuations, heavy metals, and oxidative stress by modulating both ABA-dependent and ABA-independent signaling cascades. Elucidating the molecular functions of these families is therefore crucial, not only for advancing our knowledge of plant biology but also for designing crop varieties with enhanced stress resilience.

In recent years, advances in genome-wide identification, transcriptomic profiling, and systems biology analyses have

substantially expanded our understanding of TF networks and their regulatory roles. These studies have uncovered key TFs responsive to specific stressors and their associated gene targets. Nonetheless, altering the expression of a single TF often provides limited protection under complex, multi-stress conditions. This underscores the need for future strategies that combine multi-gene manipulation, metabolic engineering, and upstream signal perception mechanisms, offering more comprehensive and sustainable improvements in stress tolerance.

New-generation gene editing technologies, particularly CRISPR/Cas-based systems, enable targeted mutations and promoter optimizations in TF genes, opening the door to more precise and predictable stress tolerance improvements. Additionally, the use of tissue- and developmental stage-specific promoters can ensure that TFs are active only under necessary conditions, thereby minimizing potential negative effects on pleiotropic effects and growth-yield balance.

Future studies should investigate not only the direct roles of TFs in stress tolerance but also their relationships with plant-microbe interactions, epigenetic regulatory mechanisms, and small RNAs. In particular, considering that abiotic stress tolerance is regulated through common regulatory networks with biotic stresses, elucidating the role of TFs in these crosstalk processes will contribute to the design of holistic resistance mechanisms.

In conclusion, TFs, as the molecular architects of adaptation to abiotic stresses in plants, are indispensable regulatory elements for both basic science and applied agriculture. In the coming years, the combined use of multidisciplinary approaches, high-throughput functional screening methods, and advanced biotechnological tools will enable the development of new generations of stress-tolerant plant varieties that will safeguard food security under global climate change conditions.

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Plant Responses to Heavy Metal Pollution: Stress Mechanisms and Adaptation

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1. INTRODUCTION

In recent years, human-induced activities such as industrialization, mining, agricultural activities, and rapid urbanization have caused environmental pollution to increase significantly (Ozturk Pulatoglu et al. 2025). In particular, mixing heavy metals into air, soil, and water environments seriously threatens ecosystems (Cebi Kilicoglu 2024; Mutlu and Aydın Uncumusaoglu 2024; Koç et al. 2025a). Heavy metals, which are naturally found on Earth and have high molecular weight/density compared to water, are metallic elements that can cause their environmental concentrations to increase to harmful levels with anthropogenic effects (Tchounwou et al. 2012). Metals such as cadmium (Cd), lead (Pb), mercury (Hg), arsenic (As), nickel (Ni), and chromium (Cr) are not biodegradable and accumulate in the environment, causing toxic effects on living organisms (Rahman and Singh 2019).

Plants are the source of life, and all living things on Earth depend on plants (Yigit et al. 2021). Plants, which do not have effective mobility, have developed various defense mechanisms against environmental stress because they have to survive in a fixed position. Plants exhibit multi-level responses to heavy metal stress, including morphological, physiological, biochemical, and molecular adaptations (Sharma and Dubey 2005). These adaptive responses both increase the survival chances of plants and allow the use of these plants for phytoremediation purposes (Shourie et al. 2024).

This study synthesizes current knowledge on plant responses to heavy metal pollution, encompassing the physiological, biochemical, and molecular mechanisms underlying their tolerance and adaptation. We critically assess the potential of phytoremediation as a sustainable, plant-based strategy for mitigating heavy metal-contaminated environments, highlighting recent advances, challenges, and future directions in the field.

2. DEFINITION AND SOURCES OF HEAVY METALS

2.1. General Properties of Heavy Metals

Heavy metals are generally defined as metals with a density greater than 5 g/cm³ and have toxic effects on biological systems (Duffus 2002). Most of these metals are found in nature as trace elements, while some (e.g., Fe, Zn, Mn, Cu) are among the micronutrients necessary for plant growth. However, exceeding the threshold of these elements causes toxicity (Nagajyoti et al. 2010). International organizations such as ATSDR (Agency for Toxic Substances and Disease Registry) and EPA (Environmental Protection Agency) categorize heavy metals according to their hazard classes. Ag, Hg, As, Pb, Pd, Zn, Be, Al, Ba, Sb, Cd, Sr, Cr, U, Pu, Se, Tl, Cu, Th, and V are on the priority pollutant list of ATSDR, which has a broader pollutant list than EPA (Sahin et al. 2025).

Heavy metal toxicity varies depending on their redox properties, binding affinities, interactions with biological membranes, and triggering of reactive oxygen species (ROS) production (Halliwell and Gutteridge 2015). When exposed to heavy metals, plants produce ROS, which they scavenge by activating their antioxidant defense mechanism. While enzymatic antioxidants include catalase (CAT), glutathione peroxidase (GPX), superoxide dismutase (SOD), and peroxidase (POX), non-enzymatic antioxidants include glutathione, carotenoids, ascorbate, etc. Low molecular weight polypeptides called phytochelatins (PCs) carry harmful metals to vacuoles for detoxification (Ghuge et al. 2023). It has been determined that metals, especially Cd, Cu, Fe, Pb, As, Hg, and Ni, can generate reactive radicals, which lead to cellular damage such as decreased enzyme activities, damage to the lipid bilayer and DNA (Bhaduri and Fulekar 2012).

2.2. Natural and Anthropogenic Sources

The presence of heavy metals in the environment is a result of both natural processes and human actions. Natural sources include volcanic activities, geological erosions, sea salt aerosols, and biological processes (Alloway et al. 2013). However, anthropogenic activities are the main source of heavy metal pollution. These sources are:

- Industrial activities: Mining, metal processing, battery and accumulator production, textile dyes, petrochemicals, and the automotive sector (Giacomin et al. 2019).

- Mining activities: extraction and exploitation of mineral resources, including minerals, rocks, natural fuels, and metals (Kuzmina et al. 2023; Ergül and Kravkaz Kuşçu 2025)

- Agricultural practices: Phosphate fertilizers, pesticides, animal manure, and heavy metals enter the soil (Golia 2023).

- Domestic and urban waste: Wastewater discharges, solid waste landfills, and vehicle emissions (Wuana and Okieimen 2011; Kaya et al. 2024).

- Traffic emissions: Brake pads, tire wear, engine wear, and exhaust emissions (Isinkaralar et al. 2022; Canturk et al. 2024).

After these pollutants mix with the soil, water, and atmosphere, they are taken into the plant body by the roots from the soil and water and by the leaves or stem parts from the air (Cobanoglu et al. 2023). Thus, the risk of bioaccumulation along the food chain increases (Yadav 2010). One of the concerns about heavy metals is that the number of heavy metals released into nature due to anthropogenic sources is much higher than natural release (Ozturk Pulatoglu et al. 2025).

3. EFFECTS OF HEAVY METALS ON PLANTS

Heavy metal effects on plants are multi-layered and generally vary depending on concentration, exposure time, plant species, and environmental conditions. These metals affect plant metabolism at various levels, adversely impacting growth, development, and yield (Yadav 2010).

Toxicity caused by heavy metals begins primarily with the root system. When metal ions are taken from the soil, they accumulate in root cells and can prevent water and nutrient uptake. Metals, such as Cd and Pb, disrupt ion homeostasis by changing cell wall permeability (Lux et al. 2011). In addition, basic physiological processes, such as photosynthesis, respiration, protein synthesis, and hormonal balance, are also damaged by the effects of these metals (Benavides et al. 2005).

In particular, chlorophyll synthesis and the activity of photosynthetic enzymes decrease in the presence of metals. This situation manifests itself with symptoms such as yellowing (chlorosis), necrosis, and early senescence in leaves. In addition, lipid peroxidation increases, and cellular membrane structures are damaged in plants exposed to metal stress (Rai et al. 2016).

4. RESPONSES TO HEAVY METAL STRESS IN PLANTS

4.1. Morphological Responses

One of the first observed changes to heavy metal stress occurs at the morphological level. Reduction in root and shoot growth, decreased leaf area, and stunted plant height are typical symptoms (Sharma and Dubey 2005). Such changes may be defense responses developed to ensure that the plant is less exposed to toxic elements.

For instance, in some plant species, the root system may exhibit orientation behavior to move away from soil areas with high metal concentration. In addition, cell wall thickening can be observed in the epidermis and cortex tissue (Martinka et al. 2014). The root system is a vital plant tissue that absorbs water and mineral nutrients. Under abiotic strain situations, the plant root structure is the first tissue to undergo strain. Plant roots have a certain developmental flexibility, and plants can adjust the morphology and dispersal of their roots to adapt to environmental strain. Therefore, toxicity symptoms are first seen in plant roots. Root length is a sign of the potential of plants to absorb water and nutrients. Root zone indicates root absorption efficiency (Hu et al. 2023). The shortening or shrinkage observed in roots due to heavy metal stress directly affects plant development, leading to a decline in plant growth (Sharma et al. 2024).

4.2. Physiological And Biochemical Changes

The physiological effects of heavy metals are mostly observed in water uptake, ion transport, photosynthesis, respiration, and enzyme activities. Metals such as Cd, which create an effect like water stress, reduce water uptake in roots. During the transport of metal ions, essential nutrients, such as Ca, Mg, and K, can also be inhibited (Clemens 2006).

Biochemically, the most striking response is the excessive production of ROS. ROS species such as hydrogen peroxide (H_2O_2), superoxide anion (O_2^-), and hydroxyl radical ($\text{OH}\cdot$) interact with proteins, lipids, and nucleic acids, causing cellular damage. Therefore, antioxidant defense systems (enzymes such as CAT, SOD, GR, and APX) are activated (Madkour 2019)

4.3. Molecular Responses

Plants also show notable changes in gene expression against heavy metal stress. Metal transporter proteins (ABC, NRAMP, HMA

transporters), antioxidant enzymes, and metal chelator genes (metallothionein, phytochelatin synthase) are up regulated during stress (Hall 2002).

It is also known that regulatory proteins such as transcription factors (MYB, bZIP, WRKY) are involved in this process. Studies in recent years have revealed that some microRNAs (miR398, miR397, etc.) play a role in gene regulation against metal stress (Ghosh et al. 2022).

5. TOLERANCE MECHANISMS AND ADAPTATION

Heavy metal toxicity triggers root discoloration (browning), leaf chlorosis, inhibited growth, and lethal effects in plants. Heavy metals inhibit several metabolic activities that are necessary for plant development and survival. However, hyperaccumulator plant species and certain halophytes can resist metal toxicity by limiting their uptake, arranging them into vacuoles, and producing enzymatic and non-enzymatic antioxidants, phytochelatins, hormones, metallothioneins, etc. Advances in omics technologies, including metabolomics, miRNAomics, transcriptomics, proteomics, and genomics, have shed light on the molecular and metabolic regulators of metal tolerance in plants. Specific genes have been recognized as critical regulators of plant metal tolerance pathways (Ghuge et al. 2023). Plants develop metal chelation mechanisms at the cellular level to protect themselves from the adverse effects of heavy metal toxicity. These mechanisms mainly aim to bind free metal ions and inactivate their biologically active forms. Phytochelatins and metallothioneins are the most important compounds that serve this purpose (Clemens 2001).

Phytochelatins are short peptides derived from glutathione and form complexes with metals, such as Cd, Pb, As, and Hg, enabling the

transport of these ions to vacuoles. Metallothioneins are low molecular weight proteins rich in cysteine and limit the harmful effects of metal ions by binding them while maintaining intracellular redox balance (Tripathi and Poluri 2021).

6. PHYTOREMEDIATION

Phytoremediation is a biotechnological method based on the ability of plants to reduce pollution in soil, water, and air by taking up, accumulating, decomposing, or fixing environmental pollutants (heavy metals, pesticides, organic pollutants). This environmentally friendly and low-cost method offers sustainable solutions, especially against heavy metal pollution (Salt et al. 1998). Phytoremediation can occur through different mechanisms:

- **Phytostabilization:** Plants fix heavy metals in the soil by holding them in the root zone.
- **Phytoextraction:** Plants take metal ions from the soil and accumulate them in their stems and leaves.
- **Phytovolatilization:** Metals are converted into volatile compounds due to plant metabolism and release into the atmosphere.
- **Rhizofiltration:** Metal ions in the water environment are adsorbed by plant roots (Sharma et al. 2023).

The success of these methods depends on the characteristics of the plant species used. Hyperaccumulator plants, especially *Alyssum*, *Thlaspi*, and *Brassica* species, are preferred due to their high metal uptake and accumulation capacities. Hyperaccumulator plants can take metal ions from the soil and accumulate them in high concentrations in their stem tissues. This feature provides a remarkable advantage in plant

applications for soil cleaning. Plants that accumulate more than 1000 μg metal g^{-1} dry mass are called “hyperaccumulator” plants (Visoottiviseth et al. 2002). However, the total volume of the plant and the organ in which it can accumulate heavy metals are also extremely critical in terms of phytoremediation potential. The number of heavy metals that trees with long life cycles can accumulate in their wood is especially important. Because the wood part is the largest plant organ, the elements accumulated in the wood part remain away from nature for tens or even hundreds of years. Therefore, for effective use in phytoremediation studies, it is tried to determine the species that accumulate the most harmful heavy metals in their wood part (Sevik et al. 2024; Koç et al. 2025a,b). Studies on woody species have revealed that heavy metals accumulate more in wood than in other organs (Sevik et al. 2024; Isinkaralar et al. 2025).

In recent years, genetic engineering applications have also played a significant role in increasing the phytoremediation potential. More effective phytoremediation is possible, especially with modifying genes related to metal transporter proteins, chelator synthesis enzymes, and antioxidant enzymes (Chaney et al. 2007).

7. CONCLUSION AND FUTURE PERSPECTIVES

In the future, multidisciplinary approaches in this field will create innovations in both environmental protection and plant biotechnology. In this context, sustainable ecosystem management and developing environmentally sensitive agricultural practices will play a key role in protecting human health and natural resources.

Heavy metal pollution has become a serious concern for all living things and ecosystems, especially humans. Plant growth and human health are adversely affected by the accumulation of heavy metals in the

environment because of their harmful effects. In conclusion, chemical and physical remedies can be suggested to eliminate pollutants. However, the active use of these methods is not yet possible. For this reason, using plants that are resistant to heavy metal pollution and that accumulate heavy metals in large amounts and remove them from the environment, i.e., phytoremediation studies, is seen as an effective and promising strategy to clean environments polluted with heavy metals.

In the future, multidisciplinary approaches in this field will create innovations in both environmental protection and plant biotechnology. In this context, sustainable ecosystem management and developing environmentally sensitive agricultural practices will play a key role in protecting human health and natural resources.

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Chapter 20

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Plant Stress Responses: Integrating Molecular, Physiological and Ecological Approaches I

Chapter 20

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**Elevated UV-B Radiation Under Climate
Change: Physiological Stress Responses in
Plants**

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1. UV-B RADIATION AND GLOBAL CLIMATE CHANGE

It is now widely accepted that global climate change (GCC) has evolved into an irreversible concern worldwide (Ozturk Pulatoglu et al. 2025). The most apparent effects of climate shift are forecasted to occur in the form of drought, increasing temperatures, and higher levels of ultraviolet-B (UV-B) radiation (Araújo et al. 2016). Based on the 2021 Climate Change Atlas report, most global regions are heating faster than the worldwide average, and this warming is stated to have increased by at least 0.1°C per decade since 1960. The report emphasized that the northern, eastern, and southwestern parts of the African continent, Australia, Central America, the Amazon, and West Antarctica experience temperature changes of 0.2°C-0.3°C, the Europe, East and Central Asia, and Arabian Peninsula experience temperature changes of 0.3°C-0.5°C and the Arctic and land areas close to the North Pole experience temperature changes of up to 1°C per decade (Gutiérrez et al. 2021). Scientific reports indicate that more droughts will occur in the next 30 years and that the yield of agricultural crops will be adversely affected (Zargar et al. 2017).

It is estimated that these rapid changes in climate change will cause species and population losses due to plants' limited mobility and ability to adapt to these effects (Cantürk et al. 2023). It is not yet fully known how plants will respond to stress elements that will happen in a shorter period than the span required for plants to adapt (Mishra and Singh 2011). Plants are frequently exposed to biotic and abiotic stress in their natural life cycles (Koç 2021; Yaşar İsmail et al. 2025). UV-B stress is also a source of stress that plants are actually exposed to at various levels throughout their lives. The worrying concern is that UV-B stress is predicted to exceed its normal course due to GCC (Ozel et al. 2021; Çobanoğlu et al. 2023).

In recent times, the intensity of UV-B radiation (280-320 nm) in the atmosphere continues to increase due to the depletion of the

stratospheric ozone layer due to anthropogenic causes (Gitz et al. 2005; Hectors et al. 2007). Scientists cannot fully determine the level of UV-B increase due to ozone layer depletion. Nonetheless, most experts agree that UV-B rays hasten the ozone layer's depletion process. Since the second part of the 20th century, it has been found that increases in UV-B radiation have outpaced natural changes. These modifications are believed to have both positive and negative effects. As stated differently, it is hypothesized that ozone layer changes could impact the climate and influence climate shift (McKenzie et al. 2007).

Time of day, latitude, altitude, season, shade, and numerous other environmental elements all impact the UV-B levels that reach the Earth's surface. It is yet unclear how plants adjust to these fluctuating UV-B levels and how they synchronize their development and UV-B-induced stress reactions (Liang et al. 2020). The development of many plant species will be significantly impacted by drought and increased UV-B radiation, two of the significant effects of GCC. A more profound comprehension of the mechanisms by which plants gain tolerance to UV-B radiation and the interplay among UV-B and other environmental strain parameters is required to properly assess the potential effects of changes in solar radiation (Teramura and Sullivan 1994).

2. UV-B STRESS AND ITS EFFECTS

UV-B rays are a signal and a possible abiotic stressor that helps plants survive and acclimate to UV light (Heijde and Ulm 2012; Liang et al. 2020; Shi and Liu 2021). While the atmospheric ozone layer absorbs most UV-B radiation, about 5% of solar UV-B energy spreads the Earth's surface. This energy is possibly unsafe to living organisms exposed to sunlight. Excessive UV-B rays not only lead to cell death in plants but also cause skin cancers in people. These adverse effects are manifested by wilting, yellowing, or bleaching of leaves in plants (Chen et al. 2022).

Due to their sunlight requirements, high-intensity UV-B radiation is particularly detrimental to sessile autotrophs. Because plants cannot escape high-intensity UV-B radiation. UV-B radiation has several direct and indirect effects on plant species, including damage to transpiration, pollination (Booij-James et al. 2000), deoxyribonucleic acid (DNA), membranes, and proteins, alterations in photosynthesis, growth, development, and morphology (Hectors et al. 2007). While UV-B stress raises the quantities of reactive oxygen species (ROS), a class of molecules derived from molecular oxygen (O_2), which cause oxidative strain and oxidize DNA, RNA, lipids, proteins, and several small molecules in plant cells. UV-B pressure or stress can also directly cause damage at the DNA level, resulting in DNA lesions that affect DNA transcription and replication, thereby impeding plant expansion and metabolism. UV-B radiation directly damages photosynthesis and slows down photosynthesis by reducing chlorophyll content (Chen et al. 2022).

Furthermore, UV-B radiation can decrease PAR (photosynthetic activity radiation) penetration, accessory and photosynthetic pigments, harm stomatal function, change canopy morphology, and thus indirectly delay photosynthetic carbon assimilation (Teramura and Sullivan 1994). It is known that the net CO_2 uptake of a leaf is reduced in plants when exposed to mild desiccation due to stomatal closure. In short, CO_2 concentration in chloroplasts is reduced in plants exposed to water deficit (Cornic and Massacci 1996). It has been found that accumulation of polyphenolic UV-B in epidermal cells causes reduced UV-B penetration and thus damages the underlying photosynthetically active mesophyll cells (Mazza et al. 2000).

In contrast, UV-B exposure may partially alleviate drought strain due to alterations in epidermal anatomy or wax deposition (Gitz et al. 2005). This situation is critical because studies have shown that UV-B stress effects combined with drought significantly affect plants and slow

their growth. In addition, these effects vary from plant to plant (Çobanoğlu 2024).

Petropoulou et al. (1995) investigated the effects of UV-B radiation on *Pinus halepensis* Mill. and *P. pinea* L. and noted that UV-B radiation may benefit pine trees from Mediterranean regions by partially alleviating the negative outcomes of summer water scarcity. Nogués and Baker (2000) reported that drought significantly decreased leaf area in *Olea europea* L., *Rosmarinus officinalis* L., *Lavandula stoechas* L. species, and that UV-B exposure to high UV-B radiation (0.47 W m^{-2}) before and during water stress had no noteworthy effect on plant development or photosynthetic activities. Sullivan and Teramura (1990) reported that UV-B radiation and drought together caused combined and interactive effects on photosynthetic gas changes. High doses of UV-B radiation can act as genetic stressors by causing various physiological and molecular disorders on plants, such as decreased growth and photosynthetic capacity, direct DNA injury, formation of ROS, cell membrane disruptions and changes in pigment and hormone synthesis (Frohnmeier and Staiger 2003).

3. PLANT PROTECTION MECHANISMS AGAINST UV-B RADIATION

There are some mechanisms that plant species have developed to reduce the effects of stress factors related to UV-B radiation. The best approach to deal with light stress is to escape it. Chloroplasts can alter their position to minimize high light absorption, thus avoiding damage (Chen et al. 2022). One of the most effective UV protection strategies is reducing UV-B penetration into plant tissues (Hectors et al. 2007). UV-B tolerant plants mitigate these effects by using UV-screening pigments that diminish the penetration of UV-B into the mesophyll tissue (Booij-James et al. 2000). Despite UV-B stress, a noteworthy reduction in

growing rate and biomass production has been observed in plants (Doupis et al. 2011). It has been discovered that certain plant species, including *Deschampsia antarctica* Desv. (Poaceae), *Carex arenaria* L., *Batrachium trichophyllum* (Chaix) FW Schultz, *Vicia faba* L., *Calamagrostis epigejos* L., *Potamogeton alpinus* Balb., and *Deschampsia borealis* (Poaceae) use flavonoids as UV screens to stop UV-B induction (Rozema et al. 2002). They are used by certain plants to build up extreme levels of UV-absorbing polyphenolic flavonoids in the epidermis (Booij-James et al. 2000).

4. STUDIES ON THE EFFECTS OF UV-B STRESS ON PLANTS

UV-B exposure generally has detrimental effects on plants' growth, morphology, and development processes. Increases in leaf thickness, leaf curling, and changes in leaf width and shape are the most common UV-B-induced morphological changes (Liaqat et al. 2024). UV-B stress in nature is highly variable. It can change significantly in a short time depending on the effects of numerous factors, from the time of day to the season, from weather conditions to the plant's location. Therefore, studies should be conducted in controlled environments to determine the effects of UV-B stress on plants. Due to the importance of the subject, many studies have been conducted in recent years. Some of these studies are summarized below.

Chen et al. (2016) applied increased UV-B radiation to one-year-old *Morus alba* L. seedlings. As a result, the total leaf area, shoot height, and basal diameter were significantly reduced compared to the control group. However, it did not significantly affect the number of leaves. They also emphasized that UV-B radiation significantly reduced relative chlorophyll content, leaf petiole length, leaf length, and leaf length.

According to Hock et al. (2020), UV-B radiation reduced leaf length, rosette area, and leaf number. Nevertheless, under greenhouse conditions, artificial UV-B application appeared to mitigate these effects, possibly due to the exclusion of photosynthetically active radiation, which might have otherwise activated drought tolerance responses. Therefore, they suppose that drought-tolerant plant species may be more resistant to higher levels of UV-B radiation. Photosystem II (PSII) activity was increased similarly by UV-B and drought, whether applied separately or together. This situation indicates a similar and non-additive effect size of both abiotic strains at the physiological level. Unexpectedly, the minimum chlorophyll fluorescence appeared to be more sensitive in response to UV-B radiation in the second harvest and in the repeated measurement analysis, which could only explain the decrease in chlorophyll fluorescence due to the greater number of intact PSII reaction centers, which the activation of efficient photoprotection and healing mechanisms could provide.

Qi et al. (2010) determined that the commonly used plant species absorb UV-B radiation to a large extent, reflecting about 5-10% and transmitting less than 1% of the UV-B radiation in 30 broadleaf tree species. They determined that there was a cumulative increase in the total concentration of UV-B absorbing compounds, leaf thickness, and chlorophyll content during the plants' leaf growth and development periods due to the increase in UV-B radiation. They also suggested that this situation may help protect the plants against increased UV-B radiation.

Ren et al. (2007) investigated the effects of UV-B radiation and drought on greenhouse-grown cuttings of poplars (*Populus kangdigensis* and *P. cathayana*). The study pointed out that seedlings of both species cultivated under water deficit conditions gathered more abscisic acid (ABA) and demonstrated slower growth than seedlings growing in well-watered conditions. Additionally, elevated UV-B light greatly reduced

plant development, but it had no noticeable effect on the ABA accumulation. They declared that there were some variances between the two species' responses to strain. The effects of water deficiency and UV-B radiation on poplar cuttings (*P. kangdigensis* and *P. cathayana*) growing in greenhouses were examined by Ren et al. (2007). As a result, both species' cuttings grown under water shortage conditions showed less development and accumulated more ABA than well-watered cuttings. In addition, UV-B radiation treatment significantly reduced plant growth, and UV-B radiation did not affect ABA accumulation much. They specified that there were partial differences in the responses of both species to stress.

Cantürk (2023) indicated that increased UV-B radiation and drought triggered plant stress mechanisms, significantly affected plant development, reduced net photosynthesis and stomatal conductance, and caused leaf size reduction in drought stress and UV-B stress applications on *Tilia platyphyllos* Scop., *T. cordata* Mill., and *T. tomentosa* Moench. species.

Carvalho et al. (2023) examined the parameters determining wood density change, the maximum water content in wood, and their possible outcomes on the hydraulic functioning of plants in tropical semiarid climates. They stated that libriform fibers contribute to wood density. Very few studies can explain the relationship between libriform fibers and climate parameters (drought and UV-B stress).

Ren et al. (2007) stated that plants showed low growth under drought conditions in two contrasting species (*Populus kangdigensis* and *P. cathayana*) and that UV-B radiation application reduced plant growth. However, there was an increase in the amount of UV-B absorbed compounds in plants when only UV-B radiation was applied, and drought stress and UV-B were applied together in *P. kangdigensis*. They

said that *P. cathayana* showed a certain rise in the combination of UV-B absorption compounds during drought and UV-B radiation.

It was shown that the plant's stem length increased when drought treatments and UV-B radiation were administered concurrently (Zhang et al. 2020). According to Wu et al. (2008), drought stress reduced citrus seedling heights by as much as 25%. Examining the studies, it can be concluded that UV-B radiation may lessen the effects of drought stress on plants and that plants may have a greater tolerance to stress when exposed to both UV-B and drought stress. Nonetheless, it is well-recognized that UV-B radiation can shorten plant height, slow down physiological processes, and reduce leaf area and biomass (Kataria et al. 2019).

Çobanoğlu (2024) reported that the number of leaves and leaflets reduced in all treatments where drought was applied to the *Acer negundo* species. In contrast, when only UV-B radiation was applied, the number of leaves and leaflets was generally not significantly affected and even increased at low doses of UV-B radiation. Chen et al. (2016) stated that the number of leaves was not affected by UV-B strain in the increased UV-B radiation applied to the *M. alba* plant.

Qi et al. (2010) stated that broad-leaved species absorb 91-95% of UV-B radiation, reflect 5-9%, and transmit <1% of UV-B radiation. Developing optimum leaf area is critical for photosynthesis and dry matter yield (Wullschleger et al. 2005). Therefore, the plant decreases leaf length against drought stress. Chen et al. (2016) stated that the leaf stalk length and leaf surface decreased in the UV-B radiation application they applied to *M. alba* plant. Exposure to UV-B has been linked to reductions in leaf number, plant height, and dry and fresh biomass (Moradi Rikabad et al. 2019).

Stomata regulate plant water status by adjusting the transpiration rate in the leaf (Sperry et al. 2003). Çobanoğlu (2024) found that the

number of stomata reduced with the effect of severe water deficit in the *Acer negundo* species and increased with both UV-B and severe drought effects. In the *A. pseudoplatanus* species, it was stated that the number of stomata was the least in individuals exposed to both severe drought and UV-B. It was determined that the number of stomata was related to drought and increased when UV-B radiation was the only stress factor. It is claimed that high UV regimes can naturally reduce the effects of increases in exposure to drought (Jansen and Van Den Noort 2000).

Studies show that drought significantly affects stomata number (Candar et al. 2021). Rai and Agrawal (2022) stated that the axial stomatal density in *Wedelia chinensis* (Osbeck) Merr. plant species exposed to UV-B strains increased. Several research have specified that stomatal density increases with the decrease in soil water source (Fraser et al. 2009). In addition, it is known that changes in stomatal number and density develop as a response to water shortage since the larger size of the stomata generates greater water loss from plants (Salsinha et al. 2021). Çobanoğlu (2024) determined that stomatal width enlarged with high dose UV-B in *A. pseudoplatanus* seedlings. Simultaneous exposure to drought stress and UV-B resulted in less detrimental effects on photosynthesis and antioxidant capacity in young *Moringa oleifera* plants compared to exposure to UV-B alone (Araújo et al. 2016).

UV-B radiation is known to have a direct impact on stomata, along with secondary effects resulting from alterations in mesophyll photosynthetic activity. Stomatal closure influences CO₂ assimilation and gas exchange between stomata and the mesophyll, which in turn raises diffusion resistance and promotes metabolic processes that contribute to photodamage (Cornic and Massacci 1996). Findings on this subject are not always consistent, though, according to the literature. For example, scientists have suggested that UV-B exposure can diminish drought stress to a certain degree by altering the structure of the epidermis or promoting the deposition of wax (Gitz et al. 2005). Water

shortage was exhibited to severely diminish leaf area in *Olea europaea* L., *Rosmarinus officinalis* L., and *Lavandula stoechas*, but pre-and co-exposure to elevated UV-B radiation had no noticeable outcomes on growth or photosynthetic performance (Nogués and Baker 2000). Additionally, research has demonstrated that water shortage and UV-B radiation can interact to affect leaf photosynthetic gas exchange (Sullivan and Teramura 1990).

A study of the literature indicates that the effects of UV-B radiation and drought strain on plant stomatal characteristics remain controversial. Şevik et al. (2025) examined the effects of UV-B irradiation at different intensities on the stomatal pore widths in 10 species. They pointed out that although the combined effect was noteworthy in some species, there was no evident linear effect of rising UV-B stress. A detailed investigation is required to determine whether this variation is species-specific or influenced by the nature of the treatment. Because plant phenotypic characters are shaped under the interaction of genetic assembly (Key et al. 2023; Hrivnak et al. 2024) and ecological conditions (Kilicoglu 2024 a,b ; Özdikmenli et al. 2024). For plants to continue their vital activities, their metabolites must function normally. Applying UV-B radiation has been revealed to alter secondary metabolites in plants in a way that promotes structure-specific health benefits without causing damage to the plants (Wiesner-Reinhold et al. 2021).

5. EFFECT OF UV-B RADIATION ON PHOTOSYNTHESIS

Elevated UV-B radiation levels are known to adversely influence plant growth, photosynthetic performance, and overall yield potential (Kataria et al. 2019). In a study conducted on maple species, Çobanoğlu (2024) observed that while increasing drought intensity led to a decline

in net photosynthesis rate, UV-B radiation alone did not significantly alter this parameter. In contrast, Ramamoorthy et al. (2022) exhibited that UV-B exposure caused a direct reduction in net photosynthesis rate. Drought stress is also known to impair chlorophyll biosynthesis and carotenoid production, ultimately reducing photosynthetic efficiency (Hussain et al. 2019).

Declines in photosynthetic rates are largely attributed to stomatal closure, damage to cellular membranes, and decreased enzymatic activity particularly of those enzymes involved in ATP synthesis (Farooq et al. 2009; Farooq et al. 2012). This results in reduced turgor pressure, restricted stomatal aperture, lower CO₂ assimilation, structural impairments in the photosynthetic apparatus (such as PSI and PSII), and increased accumulation of metabolic byproducts (Zargar et al. 2017). As a result, net photosynthesis tends to fluctuate in relation to drought severity. Stress inhibits photosynthesis by simultaneously reducing stomatal conductance and metabolic potential (Lawlor and Tezara 2009).

According to Çobanoğlu and Kulaç (2024), plant transpiration is not significantly affected by UV-B radiation alone; however, a noticeable reduction occurs when drought conditions are also present. Furthermore, drought stress appears to trigger stomatal responses via hormonal regulation, particularly through increased levels of ABA and trans-zeatin-riboside, independent of UV-B intensity (Doupis et al. 2020). This hormonal shift under drought conditions likely induces stomatal closure, reducing water loss as part of the plant's adaptive response. Although this conserves water, it also restricts CO₂ uptake, which may lead to carbon starvation and eventual physiological decline. In woody plants, this is often compounded by impairments in the hydraulic transport system (Rodriguez-Zaccaro and Groover 2019).

UV-B radiation may modulate plant responses to water stress in both beneficial and detrimental ways. Each stressor elicits unique

metabolic adjustments at the cellular level. One common consequence is the accumulation of ROS, which can damage essential macromolecules such as DNA, proteins, lipids, and carbohydrates (Bandurska et al. 2013). Variations in stomatal conductance are closely tied to plant hydraulic regulation, including membrane water transport and associated metabolic pathways (Lawlor and Tezara 2009).

GCC is widely acknowledged to affect all life forms, either directly or indirectly, and is now considered an irreversible process. Within this context, increased drought frequency and rising UV-B radiation are anticipated to impose serious stress on plant life (Ertürk et al. 2024; Isinkaralar et al. 2025). Plant morphology, phenology, and anatomical structure are all subject to modification under these stress conditions (Koç et al. 2022). Water deficit and UV radiation are among the most frequently co-occurring environmental stressors, both of which hinder plant development primarily throughout oxidative destruction (Jan et al. 2022).

It has been documented that while UV-B radiation typically exerts an undesirable influence on stomatal conductance, water stress causes more immediate and pronounced effects (Jansen et al. 2022). Simultaneous exposure to water and UV-B stress significantly suppresses several photosynthetic parameters, including transpiration rate, stomatal conductance, net photosynthesis rate, and intercellular CO₂ concentration. The application of both stressors together worsens the decrease in photosynthesis and transpiration, even though drought alone can significantly lower both parameters. On the other hand, internal water consumption efficiency seems to be essentially unaffected (Zhang et al. 2020; Çobanoğlu 2024). Water shortage and UV-B radiation both reduce chlorophyll content and CO₂ uptake, but their combined effects are frequently less severe than the sum of the impacts of each stressor independently (Jansen et al. 2022). In response to prolonged UV-B exposure, plant species may downregulate pigment production to

diminish excessive energy absorption (Piccini et al. 2020). Similarly, Alemu (2020) revealed that anthocyanin pigments build up inside vacuoles as a defense mechanism due to higher elevations' increased UV-B exposure.

Cantürk (2023) stated that when UV-B radiation and water stress are combined, stomatal conductance reductions. Çobanoğlu (2024) noted that UV-B exposure generally had no substantial effect on stomatal conductance among species, except for *A. negundo*, which had decreased conductance at low UV-B dosages. Alemu (2020) claimed that prolonged exposure to strong UV-B exposure reduced stomatal conductance, particularly through direct effects on guard cells on the adaxial surface. According to these outcomes, UV-B radiation influences stomatal function in two ways: directly by altering guard cell behavior and indirectly by altering mesophyll's photosynthetic activity (Nogués et al. 1999).

6. EFFECT OF UV-B ON WOOD ANATOMICAL CHARACTERS

This section explores how UV-B radiation alters the anatomical features of wood, particularly focusing on changes in libriform fibers, which play a critical role in mechanical support. Research on maple trees revealed that under high UV-B exposure and severe water deficit, fiber length in new shoots decreased drastically compared to unstressed plants (Çobanoğlu 2024). Interestingly, while drought and UV-B stress individually led to wider fibers, their combined effect resulted in narrower fibers with reduced lumen diameter. Additionally, low UV-B exposure caused contrasting responses in two maple species fiber wall thickness decreased in *A. negundo* but increased in *A. pseudoplatanus* (Çobanoğlu and Kulaç 2024). Thicker fiber walls are

known to enhance stem strength and resistance to cavitation (Jacobsen et al. 2005).

Fiber dimensions are crucial for stem stability. In *A. negundo*, neither drought nor UV-B affected lateral branch fiber length, whereas in *A. pseudoplatanus*, low UV-B exposure increased fiber length, but elevated UV-B and drought reduced it (Çobanoğlu 2024). Such species-specific responses may stem from genetic alterations in stress tolerance (Liu et al. 2019). Supporting this, genetic factors were found to influence wood anatomy and growth patterns in oak seedlings more than ecological conditions (Vander Mijnsbrugge et al. 2020).

7. CONCLUSION

Escalating global temperatures and UV-B radiation are intensifying due to climate change (Koç 2021; Çobanoğlu et al. 2023). These shifts, compounded by pollution and urban expansion, are accelerating ecological pressure (Mutlu and Aydın Uncumusaoğlu 2018; Dogan et al. 2023; Aricak et al. 2024; Tokatli et al. 2024; Koç et al. 2025). Without adaptation, these alterations could severely disrupt ecosystems and terrestrial life (Cantürk et al. 2023). Plants, being immobile, face heightened risks as climate change and UV exposure create unprecedented stress combinations (Jansen et al. 2022). Their development is profoundly influenced by genetics, soil quality, and climate, making them particularly vulnerable to prolonged environmental shifts (Sevik et al. 2019; Shults et al. 2020; Kurz et al. 2023).

Mitigating these impacts requires understanding their complexity. While water shortage and elevated UV-B are major concerns, their joined effects on plants remain unclear (Çobanoğlu 2024). Responses vary even among nearby plants due to microclimatic differences (Yiğit et al. 2019). For instance, soil silicon (Si) can mitigate UV-B damage by

enhancing stress resistance (Kaur et al. 2024). Local factors like water access, wind, and species interactions often outweigh broader climatic stresses in shaping plant resilience.

Scientists continue to debate whether elevated UV-B radiation supports or harms plants overall. Çobanoğlu (2024) determined that there was no decrease in root collar diameter in *A. negundo* and *A. pseudoplatanus* seedlings exposed only to UV-B radiation compared to control group. In another study, drought stress or elevated UV-B radiation considerably reduced the growth in stem length and base diameter (Zhang et al. 2020). However, although there are also studies indicating that low-level UV-B increases plant growth, the studies generally focus on the negative effects of high-dose UV-B on plants (Chen et al. 2022; Çobanoğlu 2024; Liaqat et al. 2024). However, since the number of studies conducted in controlled environments is not sufficient, there are many unknown issues regarding UV-B increase and the reactions of plants to the process.

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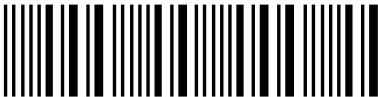
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