

Impact of Climate Change on Crop Physiology and Adaptation Strategies: A Review

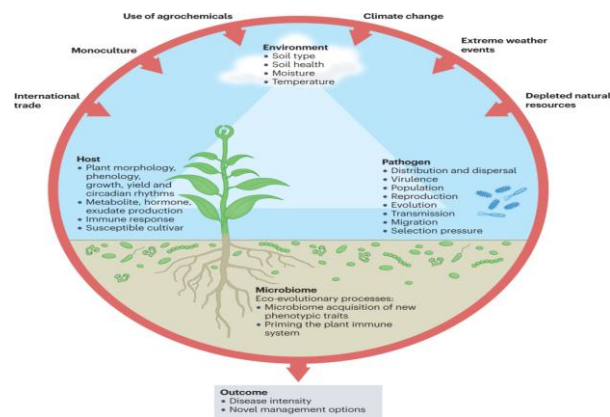
Muhammad Zaib¹, Ali Zeeshan², Humaira Akram², Waheed Amjad², Saira Aslam²,
Samreen Qasim²

¹Department of Soil and Environmental Sciences, College of Agriculture, University of Sargodha,
Punjab, Pakistan

²Department of Biological Sciences University of Veterinary and Animal Sciences Lahore, Punjab,
Pakistan

Corresponding Author:

Muhammad Zaib



Graphical Abstract

Abstract

Climate change poses a significant threat to global agricultural systems, altering environmental conditions and impacting plant physiology. This review explores the intricate relationship between climate change and plant physiology, highlighting the challenges and opportunities for plant adaptation. Through an analysis of current research, this paper examines the effects of changing temperature, CO₂ concentration, water availability, and extreme weather events on plant growth, development, and metabolism. Furthermore, the review delves into various adaptive mechanisms plants employ in response to these changes. The discussion emphasizes the importance of understanding plant responses to climate change to develop effective adaptation strategies for sustaining agricultural productivity. This paper also discusses future prospects, including advancements in genetic modification, breeding techniques, and precision agriculture that can aid plants in coping with the evolving climate.

Key Words: Climate Change, Plant Physiology, Agriculture, Genetic Modification, Ecosystem, CO₂

1. Introduction

The term "climate change" refers to long-term variations in temperature, precipitation, wind, and other atmospheric factors worldwide or in specific regions, mainly resulting from human activities, notably the release of greenhouse gases like carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O) into the atmosphere due to activities such as burning fossil fuels, clearing forests for industrial purposes, and other similar processes. These gases act as a shield for the Earth's atmosphere, gradually warming it up over time, and causing the phenomenon colloquially known as "global warming." Climate change will have extensive and complex impacts on ecosystems, which are groups of living things and their environments that are closely interconnected. Ecosystems help to maintain the planet's overall health and ability to function correctly by performing essential functions such as habitat provision, food production, water purification, and carbon sequestration. Some species may struggle to adapt to changing conditions, and remain viable if temperatures continue to rise. This may result in fluctuations in species distribution and abundance, with some unable to move or adapt quickly enough. Changes in the environment may put many plant and animal species at an increased risk of extinction, according to the Intergovernmental Panel on Climate Change (IPCC). Small changes in temperature and precipitation can cause great instability in numerous ecosystems, leading to habitat loss or degradation. For example, rising temperatures may affect the structure of forests and grasslands, while rising sea levels can reduce the size of coastal ecosystems such as mangroves and salt marshes. As a result of climate change, important biological events such as flowering, hibernation, and migration may have their timing changed. Species reliant on specific signals for these events, such as temperature or the number of daylight hours, may struggle to synchronize their behaviors with changing environmental conditions. This may have a cascading effect on predator-prey relationships and ecosystem function. Warmer temperatures may also expand the geographic range of disease vectors such as mosquitoes and ticks, leading to an increase in diseases such as malaria and Lyme disease. Similarly, pests that were once confined to colder areas may now move to new locations, negatively affecting agriculture and forestry. The oceans are absorbing excessive amounts of carbon dioxide from the atmosphere, leading to increased acidity. This may harm marine ecosystems, particularly coral reefs and shellfish populations, by hindering the ability of creatures to form their shells and skeletons, leading to the destruction of marine life. Carbon sinks, such as forests and peatlands, are ecosystems that remove more carbon dioxide from the atmosphere than they emit. However, these ecosystems may become carbon sources when temperatures rise, due to factors such as increasing wildfires and melting permafrost, releasing stored carbon back into the atmosphere and exacerbating climate change [1]. Plant physiology plays a crucial role in how plants respond to climate change, as it governs their ability to adapt, survive, and contribute to ecosystem stability. Climate change, driven primarily by human activities such as burning fossil fuels and deforestation, leads to elevated temperatures, altered precipitation patterns, and increased atmospheric carbon dioxide (CO₂) concentrations. These changes have profound effects on plant physiology, impacting various physiological processes such as photosynthesis, respiration, water relations, and nutrient uptake. Photosynthesis is a fundamental process

through which plants capture sunlight and convert it into energy, while also absorbing CO₂ from the atmosphere and releasing oxygen. Changes in temperature and CO₂ concentrations significantly influence photosynthesis rates. Rising temperatures can lead to heat stress, affecting enzyme activities and impairing photosynthesis. However, increased CO₂ levels, known as the CO₂ fertilization effect, can stimulate photosynthesis and potentially enhance carbon sequestration. An article by Ainsworth and Long [2] provides insights into the relationship between elevated CO₂ and photosynthesis. Changes in precipitation patterns can affect water availability for plants, which can be worsened by increased evaporation rates due to rising temperatures. The plant's physiology determines how it responds to water stress, affecting its ability to prevent water loss by closing stomata and absorb water by adjusting its osmotic potential. Research by Flexas et al. [3] explores the mechanics of plant water stress responses. Climate change-induced temperature increases impact plant respiration rates. Elevated temperatures can lead to higher respiration rates, potentially offsetting the gains from increased photosynthesis. The balance between photosynthesis and respiration determines whether a plant acts as a carbon sink or source. An investigation by Atkin et al. [4] explores the relationship between temperature and plant respiration. The timing of blooming and leaf emergence in plants is shifting due to climate change, potentially affecting plant-pollinator interactions. Plant physiology governs growth mechanisms that are temperature-dependent. Parmesan and Hanley [5] research illuminates how plants adapt to shifting temperatures.

The article delves into the critical issue of climate change and how it is affecting global agriculture. It emphasizes the urgent need for adaptation strategies to ensure food security and promote sustainable practices.

2. Climate Change Effects on Plant Physiology

Rising temperatures have a significant impact on various physiological and metabolic processes in plants, including photosynthesis and respiration. These effects can vary depending on the plant species, the extent of temperature increase, and other environmental factors. Here, provided an overview of how rising temperatures influence photosynthesis, respiration, and other metabolic processes, along with some references to scientific studies:

2.1. Photosynthesis

Elevated temperatures can influence photosynthesis in both positive and negative ways:

In some cases, moderate temperature increases can lead to improved photosynthetic rates due to increased enzyme activity and improved diffusion of CO₂ through plant tissues. This phenomenon is known as the "temperature response" of photosynthesis. It's often observed in cooler environments, where a slight temperature increase can enhance photosynthetic efficiency. However, as temperatures continue to rise, the positive effects can be offset by the damaging effects of heat stress. High temperatures can lead to the

denaturation of enzymes involved in photosynthesis, impairing their function. Additionally, heat stress can lead to the closure of stomata, limiting CO₂ uptake and inhibiting photosynthesis. This negative impact can outweigh any positive effects of the initial temperature response [6].

2.2. Respiration

Rising temperatures can influence plant respiration rates:

Generally, higher temperatures can lead to increased rates of respiration. This is because temperature affects enzyme activity and reaction rates. As temperatures rise, the metabolic processes of respiration become more rapid, leading to higher energy consumption by the plant. However, if the increase in respiration rates surpasses the increase in photosynthetic rates, it can result in a net loss of energy for the plant. This is particularly problematic in situations where carbon availability is limited due to factors like drought or nutrient deficiencies [7].

2.3. Other Metabolic Processes

Rising temperatures can also impact other metabolic processes in plants:

2.3.1. Protein Denaturation

Proteins and enzymes are vital for cellular processes, but high temperatures can cause denaturation, disrupting their structure and function. Weak interactions, like hydrogen bonds, hold the 3D structure of proteins together. When exposed to high temperatures, these interactions can be disrupted, leading to denaturation. Denatured proteins are biologically inactive and can disrupt cellular processes like signaling pathways, gene expression, and nutrient transport[8].

2.3.2. Oxidative Stress

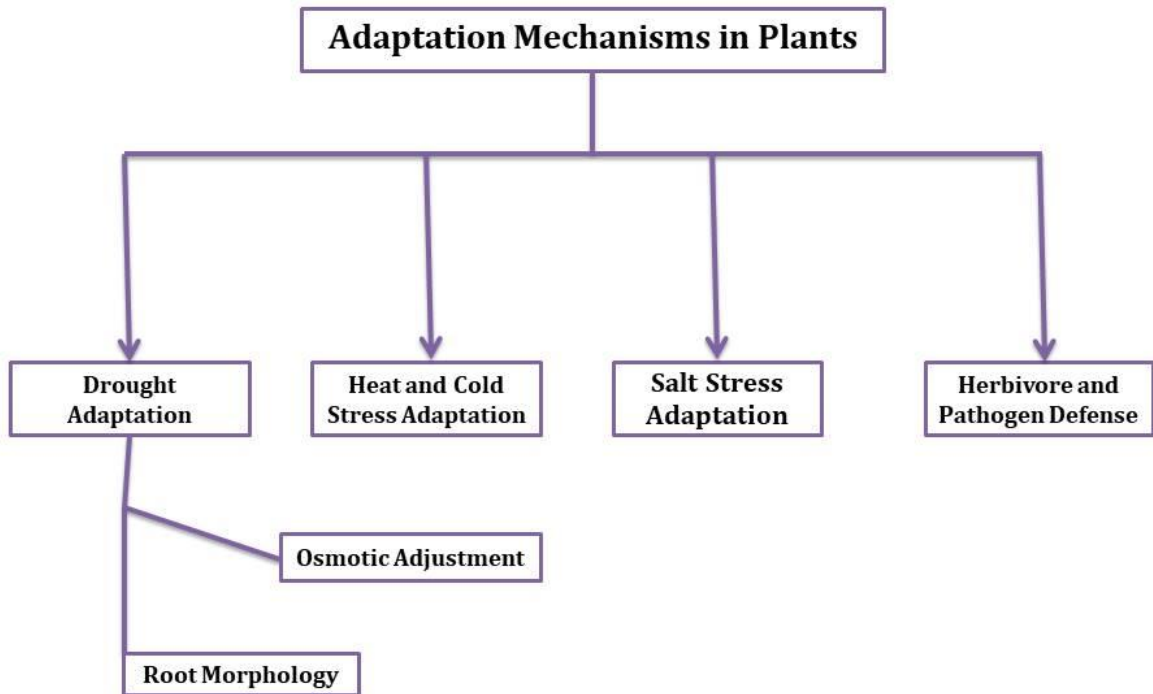
Reactive oxygen species (ROS) are highly reactive molecules containing oxygen that can damage various cellular components. While they occur naturally during cellular processes like energy production in mitochondria, the cell's antioxidant defense mechanisms usually keep them in check. However, external factors like heat stress can disrupt this balance, leading to oxidative stress. This occurs when there's an imbalance between ROS production and the cell's ability to detoxify using antioxidants. Heat stress can cause overproduction of ROS, overwhelming the cell's antioxidant defenses. This excess ROS can attack and destabilize cell membranes, alter protein structure and function, cause damage to DNA, and impair mitochondrial function, leading to various negative outcomes for the cell and organism [8].

Elevated CO₂ concentrations generally enhance photosynthetic rates in C₃ plants (most of the world's crops are C₃ plants). This is because CO₂ is a substrate for photosynthesis, and higher CO₂ levels can lead to increased carbon fixation. This phenomenon is known as the "CO₂ fertilization effect." Increased

photosynthetic rates due to higher CO₂ concentrations can lead to greater plant growth and biomass production, especially under conditions of optimal nutrient availability and water supply. This effect is particularly prominent in fast-growing species. Elevated CO₂ levels can influence nutrient uptake and allocation within plants. Increased carbon fixation may require more nutrients to support growth, affecting nutrient availability in the soil. However, under limited nutrient conditions, the growth response to elevated CO₂ might be limited. Plants grown under elevated CO₂ levels often exhibit improved water use efficiency, as they can maintain higher levels of CO₂ while allowing stomata to partially close, reducing water loss through transpiration. Increased CO₂ levels can affect plant interactions with insects, pathogens, and herbivores. Some studies suggest that elevated CO₂ may alter plant chemistry, making them less nutritious for certain herbivores [9, 10, 11, 12, 13]. Changes in precipitation patterns and drought stress have significant impacts on plant water relations, affecting various physiological systems and overall plant health. These changes can impact water availability, soil moisture, and the plants' ability to manage water stress. Changing precipitation patterns, such as an increase in drought frequency or variations in seasonal rainfall, directly impact soil water availability. Inadequate rainfall or prolonged dry spells can decrease soil moisture levels, making it difficult for plants to obtain water for growth and metabolic functions. Water stress causes plants to adjust the size of their stomatal openings on their leaves, which aids in the regulation of water loss due to transpiration. Under drought stress, plants typically restrict their stomata to conserve water, but this may also limit carbon dioxide uptake, affecting photosynthesis. Drought stress reduces plant cell water potential, creating a gradient that pulls water from the soil into the plant. Consequently, certain plants go through osmotic adjustment, acquiring solutes to reduce their water potential while maintaining turgor pressure. Drought stress can significantly affect plant growth and development. Water scarcity limits cell proliferation, resulting in stunted growth and smaller leaves. It may also interfere with reproductive activities, reducing flower and fruit output. Drought stress can cause an increase in reactive oxygen species (ROS) in plant cells, resulting in oxidative stress. ROS may damage cell membranes, proteins, and DNA, jeopardizing plant life and functioning. Drought acclimation is one of the strategies plants have developed to deal with drought stress, where plants adapt their physiological and biochemical processes to improve water-use efficiency and stress tolerance. If water is provided, plants can recover from drought stress, although the rate and amount of recovery may vary [14, 15, 16, 17, 18].

3. Adaptation Mechanisms in Plants

Plants have developed a range of natural adaptation mechanisms to cope with various stressors in their environments. These mechanisms enable plants to survive and thrive in challenging conditions. Here are some examples of natural adaptation mechanisms that plants employ to cope with stressors, along with relevant references and citations:



Adaptation mechanisms in plants refer to the various strategies and responses that plants have evolved over time to cope with changes in their environment, especially in the face of stressors such as unfavorable climate conditions, nutrient deficiencies, diseases, and herbivore attacks. These mechanisms are vital for the survival, growth, and reproduction of plants, allowing them to thrive in diverse and often challenging habitats. Adaptation mechanisms can be broadly categorized into physiological, molecular, and genetic responses.

3.1. Drought Adaptation

3.1.1. Osmotic Adjustment

Changes in precipitation patterns and drought stress significantly impact plant water relations, affecting various physiological systems and overall plant health. These changes can impact water availability, soil moisture, and the plant's ability to manage water stress. Changing precipitation patterns, such as an increase in drought frequency or variations in seasonal rainfall, directly impact soil water availability. Inadequate rainfall or prolonged dry spells can decrease soil moisture levels, making it difficult for plants to obtain water for growth and metabolic functions. Water stress causes plants to adjust the size of their stomatal openings on their leaves, which aids in regulating water loss due to transpiration. Under drought stress, plants typically restrict their stomata to conserve water, which may also limit carbon dioxide uptake, affecting photosynthesis. Drought stress reduces plant cell water potential, creating a gradient that pulls water from the soil into the plant [19].

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3.1.2. Root Morphology

Plants have evolved various mechanisms to cope with limited water availability in the soil. One of these mechanisms involves modifying their root systems to explore deeper soil layers in search of water. This adaptation is particularly crucial in arid or drought-prone environments where water is scarce. In response to water stress, plants can elongate their existing roots or produce new roots that grow deeper into the soil. Plants can access water resources at greater depths by extending their root length. This allows them to tap into water reserves that might not be accessible by their shallower roots. Plants can also enhance their root systems by increasing branching and density. More branches and finer roots provide a greater surface area for water absorption. This branching network helps capture water from a larger soil volume, increasing the chances of encountering pockets of water even in dry soil. Positive geotropism, or positive gravitropism, is a phenomenon where plant roots grow downward in response to gravity. This natural response can help roots penetrate deeper into the soil. As roots grow downwards, they can explore deeper layers where water might be available. Root plasticity refers to the ability of sources to adjust their growth patterns in response to

environmental cues. When a plant detects water availability in deeper soil layers, it can direct its energy toward producing and extending roots. Conversely, the plant can prioritize root growth deeper into the soil if water is scarce near the surface. Plants gain several advantages by modifying their root systems to explore deeper soil layers. Deeper soil layers often retain water for longer periods, especially in drought-prone regions. Plants that can access this water source have a competitive advantage in surviving extended periods of water scarcity. A well-developed root system that can explore deeper soil layers enhances a plant's resilience to drought. It can sustain the plant's water needs for a longer time, reducing the negative impacts of water stress. Plants with deeper root systems can compete more effectively for water resources with neighboring plants. This can be especially important in ecosystems where water availability is limited [20].

3.2. Heat and Cold Stress Adaptation

Heat Shock Proteins (HSPs), also known as stress proteins, are a group of specialized proteins that play a crucial role in cellular protection and maintenance under stress conditions, particularly heat stress. These proteins are produced in response to various stressors, including high temperatures, and their primary function is to help cells cope with and survive adverse conditions. HSPs are often referred to as "molecular chaperones." Chaperones are proteins that assist in the proper folding of other proteins and help prevent unwanted interactions. When cells are exposed to high temperatures, the increased thermal energy can disrupt the weak interactions that maintain the native 3D structure of proteins. This disruption can lead to protein denaturation, where the protein loses its functional shape and becomes biologically inactive. In response to heat stress, cells upregulate the production of HSPs. These HSPs are critical in stabilizing proteins susceptible to denaturation due to high temperatures. HSPs bind to partially unfolded or denatured proteins, preventing them from aggregating and assisting them in refolding into their functional shapes. By doing so, HSPs help maintain the proper functioning of essential proteins, even under stressful conditions. The prevention of protein denaturation is not the only role of HSPs. They also have a broader protective function. HSPs can stabilize cellular structures, such as membranes and organelles, that might be vulnerable to damage during stress. This helps preserve the integrity of cells and their components. Furthermore, HSPs can help guide misfolded or damaged proteins to degradation pathways, ensuring that potentially harmful or non-functional proteins are efficiently removed from the cell. This is crucial for maintaining cellular health and preventing the accumulation of damaged components. It's worth noting that the production of HSPs is a part of the cell's stress response and serves as a mechanism of adaptation. Different types of HSPs are produced in response to different levels and durations of stress. This allows cells to tailor their response to their specific stressor [21]. Some cold-adapted plants produce antifreeze proteins that prevent ice crystal formation in their cells, protecting them from frost damage [22].

3.3. Salt Stress Adaptation

Plants can selectively transport ions to minimize the uptake of toxic ions (e.g., sodium) from saline soils. This maintains proper ion balance and prevents damage to cells [23]. Similar to drought adaptation, plants accumulate compatible solutes to maintain cellular water potential under salt stress [24].

3.4. Herbivore and Pathogen Defense

Plants can activate their defense responses upon attack by herbivores or pathogens. This involves producing secondary metabolites, such as phytochemicals and toxins, to deter attackers [25]. Some plants release VOCs in response to herbivore attack. These VOCs can attract natural enemies of herbivores, providing indirect defense [26]. Phenotypic plasticity refers to the ability of a single genotype to produce different phenotypes in response to varying environmental conditions. This allows plants to adjust their traits, such as morphology, physiology, and behavior, to optimize their fitness in different environments. For example, plants can alter their root-to-shoot ratio or leaf size in response to nutrient availability or water stress [27]. Plants can adjust their physiological processes, such as photosynthesis and respiration rates, in response to light intensity or temperature changes [28]. Genetic diversity refers to the variety of genetic traits within a population. Higher genetic diversity provides a broader pool of traits that can be selected for under changing conditions, improving the chances of survival and adaptation. Genetic diversity allows populations to respond to new environmental challenges, increasing the likelihood of having individuals with advantageous traits [29]. Genetic diversity can help plants resist pathogens and herbivores by maintaining a range of resistance genes in the population [30]. Epigenetic changes involve modifications to DNA and histones that influence gene expression without altering the DNA sequence. These changes can be reversible and are often responsive to environmental cues. Epigenetic changes, such as DNA methylation, can regulate stress-responsive genes, enabling plants to adapt to changing conditions [31]. Epigenetic changes can be passed on to offspring, allowing plants to "remember" previous stress exposures and potentially providing a head start for the next generation [32].

4. Molecular Responses to Climate Stress

Plants have various receptors on their cell membranes that can detect changes in environmental conditions. These receptors can sense stress factors such as drought, high temperatures, pathogens, and nutrient deficiencies. For instance, receptors like receptor-like kinases (RLKs) or pattern recognition receptors (PRRs) can recognize pathogen-associated molecular patterns (PAMPs) and trigger an immune response [33]. Perception of stress triggers a cascade of events leading to the production of secondary messengers like calcium ions (Ca^{2+}) and reactive oxygen species (ROS). These secondary messengers act as signaling molecules to transmit the stress signal within the cell [34]. Secondary messengers activate various protein kinases, including mitogen-activated protein kinases (MAPKs), calcium-dependent protein kinases (CDPKs), and receptor kinases, initiating signaling pathways. These kinases phosphorylate downstream components, leading to the activation of transcription factors and other regulatory proteins [35]. Signaling pathways activate transcription factors (TFs) that bind to specific DNA sequences in the promoters of stress-responsive

genes. These TFs regulate the expression of genes involved in stress responses, including those coding for enzymes, chaperones, antioxidants, and other protective proteins [36]. Activated transcription factors lead to changes in gene expression, allowing the plant to produce stress-related proteins. These proteins help the plant cope with stress by facilitating osmotic adjustment, heat shock response, ROS detoxification, and other protective mechanisms [37]. Different stress signaling pathways can interact and cross-talk, sharing common components. For example, some components of the abscisic acid (ABA) signaling pathway are also involved in other stress responses, allowing plants to integrate responses to multiple stressors [38].

Stress-responsive genes, transcription factors, and hormones play crucial roles in the plant's ability to sense and respond to environmental stressors. These components form a complex network that coordinates adaptive responses to ensure plant survival and resilience. Stress-responsive genes are those that are activated or upregulated in response to environmental stress. These genes encode proteins that play direct or indirect roles in protecting the plant from stress-related damage. They encompass a wide range of functions, including detoxification, antioxidant defense, osmotic adjustment, protein stabilization, and signaling. Stress-responsive genes code for enzymes that detoxify harmful molecules and scavenge reactive oxygen species (ROS) produced during stress. For example, superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) help counteract oxidative stress. Stress-responsive genes are involved in osmotic adjustment by encoding enzymes that synthesize compatible solutes like proline and sugars. These solutes help maintain cellular water potential and turgor under stress. Genes encoding chaperones and heat shock proteins are activated under temperature stress. These proteins assist in protein folding, prevent denaturation, and protect cellular structures. Transcription factors are regulatory proteins that bind to specific DNA sequences in the promoters of target genes, modulating their transcription rates. TFs play a central role in orchestrating stress responses by activating or repressing stress-responsive genes. Different stressors trigger the activation of specific transcription factors that bind to unique DNA motifs associated with stress-responsive genes. For example, DREBs (dehydration-responsive element-binding proteins) regulate genes involved in drought and cold responses. Some transcription factors participate in cross-talk between different stress pathways, enabling the plant to integrate responses to multiple stressors. This ensures a coordinated and efficient response to various environmental challenges. Plant hormones are signaling molecules that regulate growth, development, and responses to environmental stimuli, including stress. They serve as central mediators in stress signaling pathways, coordinating physiological and biochemical changes in the plant. ABA is a key hormone in stress responses, especially drought and salinity stress. It regulates stomatal closure, reduces water loss, and activates stress-responsive genes. Jasmonic Acid (JA) and Salicylic Acid (SA) hormones are involved in defense responses against pathogens and herbivores. JA regulates wound responses and defense against herbivores, while SA is associated with systemic acquired resistance to pathogens. Ethylene is involved in various stress responses, including responses to flooding, mechanical damage, and pathogen attack. It can regulate programmed cell death and root development under stress. These hormones play roles

in stress responses related to nutrient availability and growth regulation. They can influence root growth and nutrient uptake [39, 40, 41].

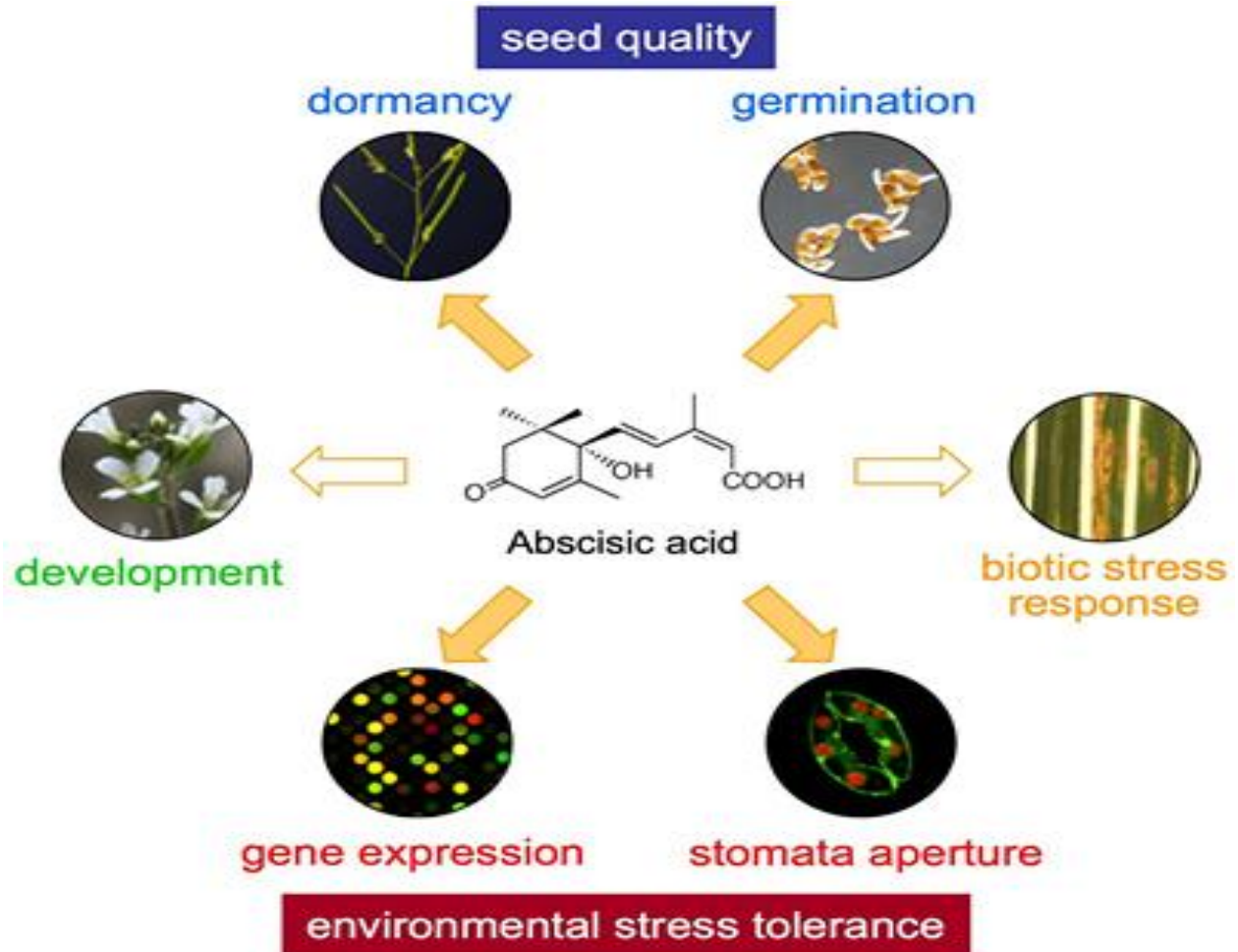
Antioxidants and reactive oxygen species (ROS) are central players in the plant's response to environmental stress. ROS are molecules that include oxygen radicals and other derivatives, such as superoxide (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($OH\cdot$). While ROS are produced as natural byproducts of metabolic processes, their levels increase dramatically under stress conditions. Antioxidants, on the other hand, are molecules that counteract the damaging effects of ROS. The balance between ROS production and antioxidant defense is crucial for stress adaptation. Environmental stresses, such as drought, high light, temperature extremes, and pathogen attack, can trigger the overproduction of ROS within plant cells. This occurs due to disturbances in the balance between ROS production and scavenging mechanisms. Elevated ROS levels can lead to oxidative stress, damaging cellular components like proteins, lipids, and DNA. ROS also function as signaling molecules in stress responses. At moderate levels, ROS can act as secondary messengers, triggering a variety of stress-responsive genes and pathways. ROS play a role in activating stress signaling cascades, such as mitogen-activated protein kinases (MAPKs) and calcium-dependent protein kinases (CDPKs), leading to changes in gene expression. Plants have evolved a complex antioxidant defense system to mitigate the harmful effects of ROS. This system includes both enzymatic and non-enzymatic antioxidants. Enzymes such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX) play critical roles in ROS scavenging. SOD converts superoxide radicals into H_2O_2 , while CAT and POD detoxify H_2O_2 . Non-enzymatic antioxidants include molecules like ascorbic acid (vitamin C), glutathione (GSH), tocopherols (vitamin E), and flavonoids. These antioxidants neutralize ROS directly and help regenerate other antioxidants. Plant hormones, particularly abscisic acid (ABA), salicylic acid (SA), and jasmonic acid (JA), play roles in regulating antioxidant responses to stress. These hormones can induce the expression of genes coding for antioxidant enzymes and molecules, enhancing the plant's ability to scavenge ROS. Elevated ROS levels can lead to programmed cell death (PCD), a controlled process where cells die to protect the plant from spreading damage. PCD helps to contain stress-related injuries and eliminate infected or damaged cells, preventing the spread of pathogens or adverse effects [42, 43].

5. Plant Hormones and Climate Adaptation

Plant hormones play a significant role in climate adaptation by regulating various physiological, developmental, and stress responses that enable plants to survive and thrive in changing environmental conditions. Different hormones are involved in specific aspects of climate adaptation, helping plants adjust their growth, development, and responses to stressors. The interplay between plant hormones and stress responses is a complex and dynamic process that enables plants to adapt and survive in changing environmental conditions. Plant hormones act as signaling molecules, orchestrating various physiological, biochemical, and morphological changes that help plants cope with stressors.

5.1. Abscisic Acid (ABA) and Stress Response

ABA is a central hormone in stress responses, particularly drought and salinity stress. It plays a pivotal role in regulating water relations and stomatal closure. When plants experience water deficiency, ABA levels increase, leading to stomatal closure, reduced transpiration, and water loss. This conserves water and prevents dehydration. ABA also induces the expression of stress-responsive genes involved in osmotic adjustment, antioxidant defense, and stress tolerance [44].



ABA is absolutely essential in preserving seed dormancy, providing protection against untimely germination in unfavorable circumstances. Its crucial functions encompass the regulation of water absorption, inhibition of shoot growth, and initiation of stress-responsive genes [39]. Abscisic Acid (ABA) plays a crucial role in regulating seed dormancy under stressful environmental conditions. This adaptive trait allows seeds to remain dormant during unfavorable periods, such as drought, extreme temperatures, or other stressful circumstances, and then germinate when conditions become more favorable for plant growth. ABA acts as a signal that plants use to perceive environmental stress. When seeds sense stress factors like drought, salinity, or temperature extremes, they respond by producing more ABA. This increased ABA accumulation leads to the suppression of germination-related genes and enhances dormancy. ABA is associated with the development of desiccation tolerance, a crucial trait for seed survival under dry conditions [37]. Abscisic acid (ABA) is a plant hormone that regulates seed development and germination under stress conditions. It promotes desiccation tolerance, induces the synthesis of storage compounds, and enhances the production of antioxidants and enzymes involved in scavenging reactive oxygen species (ROS). ABA also influences nutrient allocation and gene expression, favoring the accumulation of nutrients like nitrogen and phosphorus that are vital for early seedling growth after germination [27]. ABA, or Abscisic acid, is a vital plant hormone that regulates both physiological and molecular responses to environmental stress. Its importance cannot be overstated as it plays a crucial role in drought and salinity responses, inducing gene expression changes, conserving water, and promoting stress adaptation and tolerance [44].

5.2. Auxins and Stress Response

Auxins are involved in various stress responses, including those related to light, gravity, and nutrient availability. They play roles in tropic responses (e.g., phototropism and gravitropism) and root development. In stress conditions, auxins can modulate root growth, enabling plants to explore deeper soil layers for water and nutrients. They also influence lateral root formation, helping plants optimize nutrient uptake [45].

5.3. Cytokinins and Stress Response

Cytokinins regulate cell division, growth, and development. In stress situations, they can modulate stress responses by interacting with other hormones. Cytokinins may counteract the inhibitory effects of ABA on cell division, promoting growth even under stress conditions. They can also influence the allocation of resources between growth and defense responses [46].

5.4. Cross-Talk and Hormonal Balance

The interplay between plant hormones involves cross-talk, where one hormone's action can influence the responses of other hormones. For example, ABA and ethylene often interact to regulate responses to abiotic and biotic stresses. Similarly, auxins and cytokinins can balance growth and stress responses. This cross-talk ensures that plants allocate resources and prioritize responses appropriately in changing environments [47].

6. Genetic and Biotechnological Approaches

Genetic and biotechnological approaches are powerful tools in addressing the challenges posed by climate change on crop production and agriculture. These approaches leverage our understanding of plant genetics, molecular biology, and advanced technologies to develop crops with enhanced resilience, improved yields, and better adaptation to changing environmental conditions. Traditional breeding involves crossing plants with desirable traits to produce offspring with improved characteristics. This approach has been used for centuries to develop crop varieties with better stress tolerance, disease resistance, and yield potential. With the advent of molecular markers and advanced phenotyping techniques, breeders can now select plants with specific genes associated with stress resistance, allowing for more precise and efficient breeding. MAS is a technique that uses molecular markers to identify specific genes or traits of interest in plants. It helps breeders select individuals with desired traits more accurately and rapidly than traditional breeding methods. For climate adaptation, MAS can be used to identify and introduce genes associated with drought resistance, heat tolerance, and other stress-related traits. Genomic selection involves analyzing the entire genome of a plant to predict its potential performance and select individuals with desired traits. This approach takes into account the interactions of multiple genes and provides more accurate predictions of plant performance under varying environmental conditions. Genetic engineering involves directly manipulating an organism's DNA by introducing genes from other species. This approach allows scientists to confer specific traits, such as pest resistance, disease resistance, and stress tolerance, directly into crop plants. For climate adaptation, genetic engineering can produce crops with improved water-use efficiency, enhanced nutrient uptake, and tolerance to extreme temperatures. Genome editing, particularly the CRISPR-Cas9 system, enables precise modifications of specific DNA sequences within a plant's genome. This technology can be used to edit genes responsible for stress responses and improve adaptation to changing climates. CRISPR-Cas9 offers a more targeted and efficient way to develop crops with desired traits compared to traditional genetic engineering. RNA interference is a biotechnological approach that involves silencing specific genes by introducing small RNA molecules. It can be used to downregulate genes responsible for susceptibility to pests, diseases, or abiotic stresses, thereby enhancing resistance and stress tolerance. Synthetic biology involves designing and constructing new biological systems with desired functions. Metabolic engineering, a subset of synthetic biology, focuses on optimizing metabolic pathways within plants to enhance the production of specific compounds, such as antioxidants or osmoprotectants, that improve stress tolerance. Biotechnological tools, including remote sensing, drones, and data analytics, enable precision agriculture. Farmers can monitor crop health, soil conditions, and weather patterns in real-time, allowing for more efficient resource management and targeted interventions to mitigate the impacts of climate change [48].

Advances in genome editing technologies, particularly the CRISPR-Cas9 system, have revolutionized the field of plant biotechnology and hold great potential for climate adaptation in agriculture. CRISPR-Cas9 enables precise and targeted modifications of specific DNA sequences within a plant's genome, allowing researchers

to develop crops with enhanced stress tolerance, improved yields, and better adaptation to changing environmental conditions. CRISPR-Cas9 offers a powerful tool for introducing specific genetic modifications that enhance stress tolerance in crops. By targeting genes involved in stress responses, such as those related to drought resistance, heat tolerance, and disease resistance, researchers can create plants better equipped to withstand adverse environmental conditions caused by climate change. Climate change often results in altered precipitation patterns and increased occurrence of drought. Using CRISPR-Cas9, researchers can modify genes responsible for nutrient uptake and water-use efficiency, allowing plants to thrive in conditions with limited water availability and nutrient resources. CRISPR-Cas9 can be employed to optimize genes related to photosynthesis and carbon fixation. By modifying genes involved in CO₂ fixation, light harvesting, and energy conversion, researchers can improve a plant's ability to capture and utilize sunlight for energy production, potentially leading to higher yields and increased resilience to changing light conditions. CRISPR-Cas9 enables precise control over genes that regulate flowering time and growth patterns. Modifying these genes can help plants adapt to shifting temperature and photoperiod conditions, allowing them to flower at optimal times and maximize reproductive success in changing environments. As climate change alters the distribution and behavior of pests and pathogens, crop plants need enhanced defenses. CRISPR-Cas9 can be used to modify genes involved in plant immune responses, producing crops with improved resistance to various pests and diseases. Traditional breeding methods for climate adaptation can be time-consuming. CRISPR-Cas9 accelerates this process by allowing breeders to directly introduce specific traits into crop plants without the need for lengthy backcrossing and selection cycles. CRISPR-Cas9 can benefit orphan crops—crops not as extensively researched as major staples—by rapidly introducing valuable traits for climate adaptation. This can contribute to food security and livelihoods in regions dependent on these crops. While CRISPR-Cas9 offers immense potential, ethical and regulatory considerations surrounding genetically modified organisms (GMOs) and gene editing must be addressed. Public perception, safety assessments, and regulations vary globally, and responsible use is essential [49].

7. Physiological Strategies for Climate Resilience

Plants have evolved a variety of physiological adaptations to enhance stress tolerance and survive in challenging environmental conditions. Two notable examples are Crassulacean Acid Metabolism (CAM) photosynthesis and the C₄ photosynthetic pathway. These adaptations enable plants to optimize their water and carbon utilization strategies, making them more resilient to factors like drought, high temperatures, and limited resources. CAM photosynthesis is an adaptation mainly found in succulent plants and certain other species. It involves temporal separation of CO₂ uptake and fixation processes to reduce water loss during hot and dry conditions. CAM plants open their stomata at night to take in CO₂. This is when water loss through transpiration is minimized due to cooler temperatures and higher humidity. The absorbed CO₂ is stored as malic acid in vacuoles until daytime. During the day, stomata are closed to conserve water. The stored malic acid is decarboxylated, releasing CO₂ for fixation via the Calvin cycle. By separating CO₂ uptake and fixation, CAM plants reduce water loss and increase water-use efficiency. For examples Pineapple, Agave, Jade

plant. The C_4 pathway is a photosynthetic adaptation that enhances water-use efficiency and CO_2 uptake efficiency, making plants more tolerant to high temperatures, drought, and low CO_2 conditions. C_4 plants spatially separate initial CO_2 fixation (in mesophyll cells) and the Calvin cycle (in bundle sheath cells). CO_2 is initially fixed into a four-carbon compound (oxaloacetate) in mesophyll cells by the enzyme PEP carboxylase. This enzyme has a higher affinity for CO_2 than Rubisco, the enzyme used in the Calvin cycle. The four-carbon compound is then transported to bundle sheath cells, where it releases CO_2 for the Calvin cycle. This spatial separation concentrates CO_2 around Rubisco, reducing oxygen competition and photorespiration, particularly under high temperature and drought conditions. C_4 plants can partially close stomata during hot and dry conditions, reducing water loss, for examples, Maize, sugarcane, sorghum [50].

Root architecture modifications play a critical role in improving water and nutrient uptake in plants, particularly under stress conditions. Plants with well-adapted root systems can explore larger soil volumes, access water and nutrients more efficiently, and enhance their overall resilience. Developing deep and extensive root systems that penetrate deeper soil layers. Deep roots can access water stored at greater depths, even during drought conditions. This enhances the plant's ability to maintain water uptake when surface soils are dry. Promoting the development of root hairs, tiny extensions of root cells that significantly increase the root's surface area. Root hairs are highly efficient in absorbing water and nutrients. They amplify the plant's capacity for nutrient uptake, especially in nutrient-deficient soils. Stimulating the formation of adventitious roots, which develop from non-root tissues such as stems and leaves. Adventitious roots can increase nutrient and water uptake by forming in response to changing environmental conditions, such as flooding or waterlogging. Establishing symbiotic relationships with mycorrhizal fungi, which extend the root's reach and increase nutrient absorption capabilities. Mycorrhizal fungi facilitate the uptake of nutrients, particularly phosphorus, by extending their hyphal networks into the soil and accessing nutrients that might be out of the root's reach. Developing a root system that can adapt its architecture in response to changing conditions. A flexible root architecture allows plants to adjust their root growth in response to fluctuations in water availability and nutrient distribution, optimizing resource uptake. Releasing organic compounds into the rhizosphere (soil surrounding the root) that influence microbial activity and nutrient availability. Root exudates can enhance nutrient availability by promoting beneficial microbial interactions and nutrient mineralization. Utilizing traditional breeding techniques or genetic engineering to develop crops with specific root traits. By breeding for desirable root traits, such as deeper rooting or enhanced nutrient uptake mechanisms, plants can be customized to better match specific environmental conditions and soil types [51].

Metabolic adjustments play a crucial role in enabling plants to thrive in changing environmental conditions. These adjustments involve alterations in biochemical pathways and the production of specific metabolites that help plants adapt to stressors such as drought, high temperatures, and nutrient limitations. Plants regulate their osmotic potential by accumulating compatible solutes, such as proline, sugars, and amino acids. Compatible solutes help maintain cell turgor pressure and water uptake during drought stress, preventing cellular dehydration and damage. Plants increase the production of antioxidants like ascorbate (vitamin C)

and glutathione in response to oxidative stress caused by reactive oxygen species (ROS). Antioxidants scavenge ROS and protect cellular components from oxidative damage, helping maintain cell integrity and function. Elevated temperatures induce the synthesis of heat shock proteins, a class of chaperone proteins that prevent protein denaturation and aggregation. HSPs ensure proper protein folding and stability under heat stress, maintaining cellular function. Plants increase ABA production under drought stress. ABA mediates stomatal closure, reducing water loss through transpiration. It also triggers stress-responsive gene expression and osmotic adjustment. Nitrogen metabolism shifts towards the accumulation of nitrogen-rich compounds, such as amino acids and proteins, under stress conditions. These compounds contribute to osmotic adjustment, ROS scavenging, and protein protection under stress. Plants produce secondary metabolites, such as flavonoids and terpenoids, under stress conditions. Secondary metabolites have roles in defense against herbivores, pathogens, and environmental stresses. Some also have antioxidant properties. Plants accumulate starch during the day and break it down into sugars at night in CAM plants. In C_4 plants, sugars are produced via the C_4 pathway. Starch and sugars serve as energy and carbon storage forms that support growth, maintenance, and stress responses [52].

8. Ecosystem Responses and Feedback Loops

Ecosystems are intricately linked and respond to changes in the environment, including those driven by climate change. These responses can create feedback loops, where changes in one component of an ecosystem lead to further changes in other components. As temperatures rise due to climate change, arctic permafrost begins to thaw, releasing stored carbon dioxide (CO_2) and methane (CH_4) into the atmosphere. The release of CO_2 and CH_4 amplifies the greenhouse effect, further contributing to global warming, which in turn accelerates permafrost thaw [53]. Increased temperatures and drought stress affect forest health and productivity, reducing their ability to sequester carbon. Reduced carbon sequestration decreases the forest's capacity to absorb CO_2 from the atmosphere, contributing to higher atmospheric CO_2 levels and further warming [54].

9. Future Directions in Plant Climate Adaptation

Research on climate change adaptation must include using microbiomes to enhance plant resilience and agricultural sustainability. Understanding how microbial communities interact with plants is crucial to improve stress tolerance, nutrient uptake, and overall fitness. Manipulating these interactions is necessary to enhance stress tolerance, nutrient use efficiency, and productivity. Investigating how microbiomes can enable plants to thrive in marginal and degraded environments is essential to contribute to reclamation efforts. Diverse microbiomes can benefit plants, including enhanced disease resistance and stress tolerance, which must be noticed [55]. Collaboration between plant scientists, ecologists, and climatologists is crucial in understanding the complex relationships between plants, ecosystems, and climate and developing effective adaptation strategies to address climate change. Each discipline provides unique insights and expertise that

complement one another. By combining these perspectives, researchers can better understand how climate change affects plants and ecosystems, leading to the development of holistic and effective solutions [56].

Conclusion

This review presents a comprehensive analysis of the effects of climate change on crop physiology and explores various strategies to enhance crop adaptation. Rising temperatures negatively impact essential metabolic processes, such as photosynthesis and respiration, leading to reduced crop productivity. Climate change disrupts traditional growing seasons, alters precipitation patterns, and intensifies extreme weather events. These changes threaten crop yields, jeopardizing the availability of staple foods and nutrition for billions of people. Agriculture is a critical economic sector worldwide. Crop failures due to inadequate adaptation can lead to income loss for farmers, reduced rural livelihoods, and potential food price hikes affecting global economies. Water scarcity due to climate change puts pressure on agriculture. Understanding plant adaptation is crucial for sustainable water management, resilient crops, and mitigating climate change impacts on ecosystems and human health. Research is essential for effective climate adaptation strategies and interdisciplinary collaboration.

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