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REVIEW

Impact of Soil Microbes and Abiotic Stress on Strawberry Root Physiology and Growth: A Review

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ABSTRACT: Strawberry (*Fragaria ananassa*) is well known among consumers because of its attractive color, delicious taste, and nutritional benefits. It is widely grown worldwide, but its production has become a significant challenge due to changing climatic conditions that lead to abiotic stresses in plants, which results in poor root development, nutrient deficiency, and poor plant health. In this context, the major abiotic stresses are temperature fluctuations, water shortages, and high levels of soil salinity. The accumulation of salts in excessive amounts disrupts the osmotic balance and impairs physiological processes. However, drought reduces fruit size, yield, and quality. Similarly, heat and cold stresses directly affect the rate of photosynthesis. Plants respond to these changes by producing growth-promoting hormones to ensure their survival. In the context of these abiotic stresses, beneficial microbes support plant growth. Among these fungi, the most extensively studied are plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhizal fungi (AMF). When applied as bioinoculants, they are associated with roots and subsequently improve soil health, fruit quality, and overall crop yield. This review highlights the impacts of abiotic stresses on strawberry roots, growth, and hormonal pathways. Moreover, it focuses on the role of beneficial soil microbes in the mitigation of these responses.

KEYWORDS: Abiotic stress factors; crop resilience; hormonal dynamics; microbial interactions; plant-microbe interactions; strawberry

1 Introduction

Strawberry (*Fragaria × ananassa Duch.*), it is a small soft fruit crop that belongs to the Rosacea family and the Fragaria genus. The modern cultivated strawberry is a hybrid of *Fragaria virginia* (meadow strawberry) and *Fragaria chiloensis* (Chilean strawberry) [1]. It is a perennial herbaceous plant with a fibrous root system [2]. It is one of the most widespread fruit crops in the world [3] and is grown commercially throughout temperate and subtropical zones [4], and its global cultivation increased by 9.18 million tons in

2021 [5]. They are well renowned for their antioxidant activities [6] and high mineral contents, including potassium, calcium, and magnesium contents [7]. In addition to nutritional benefits, they offer health benefits such as lowering the risk of cancer, increasing insulin sensitivity, increasing cardiovascular health, and promoting the overall immune system [8]. In addition to being antioxidant and carcinogenic, they are highly anti-hyperglycemic, antidiabetic, and anti-hypersensitive [9]. Additionally, their abundance of bioactive compounds has significantly increased their commercial value [10].

In the past few years, overall global production has reached over 9.1 million tons, with a cost-benefit of approximately 18.41 billion dollars, which has continuously increased since 2010 [11]. They are grown in 73 countries with areas of 390,000 hectares, making them the highest-yielding fruit crop at the global level [12]. China is the largest producer of strawberries, with an annual production of 3.8 million tons, followed by the United States, with an annual production of 1.4 million tons. Similarly, Egypt ranks first in African countries, with a production of 468,000 tons per year [11]. To meet the demands of the growing population, maintaining the quality and production of strawberry plants is necessary. However, its production is limited by poor soil health, nutrient deficiency, and certain abiotic stress factors [13]. In this sense, drought, salinity, and temperature are the main limiting abiotic factors for strawberry production worldwide, as they can influence the anatomical and physiological characteristics of plants by affecting certain molecular pathways and mechanisms [14], which ultimately affects crop production [15], as illustrated in Fig. 1.

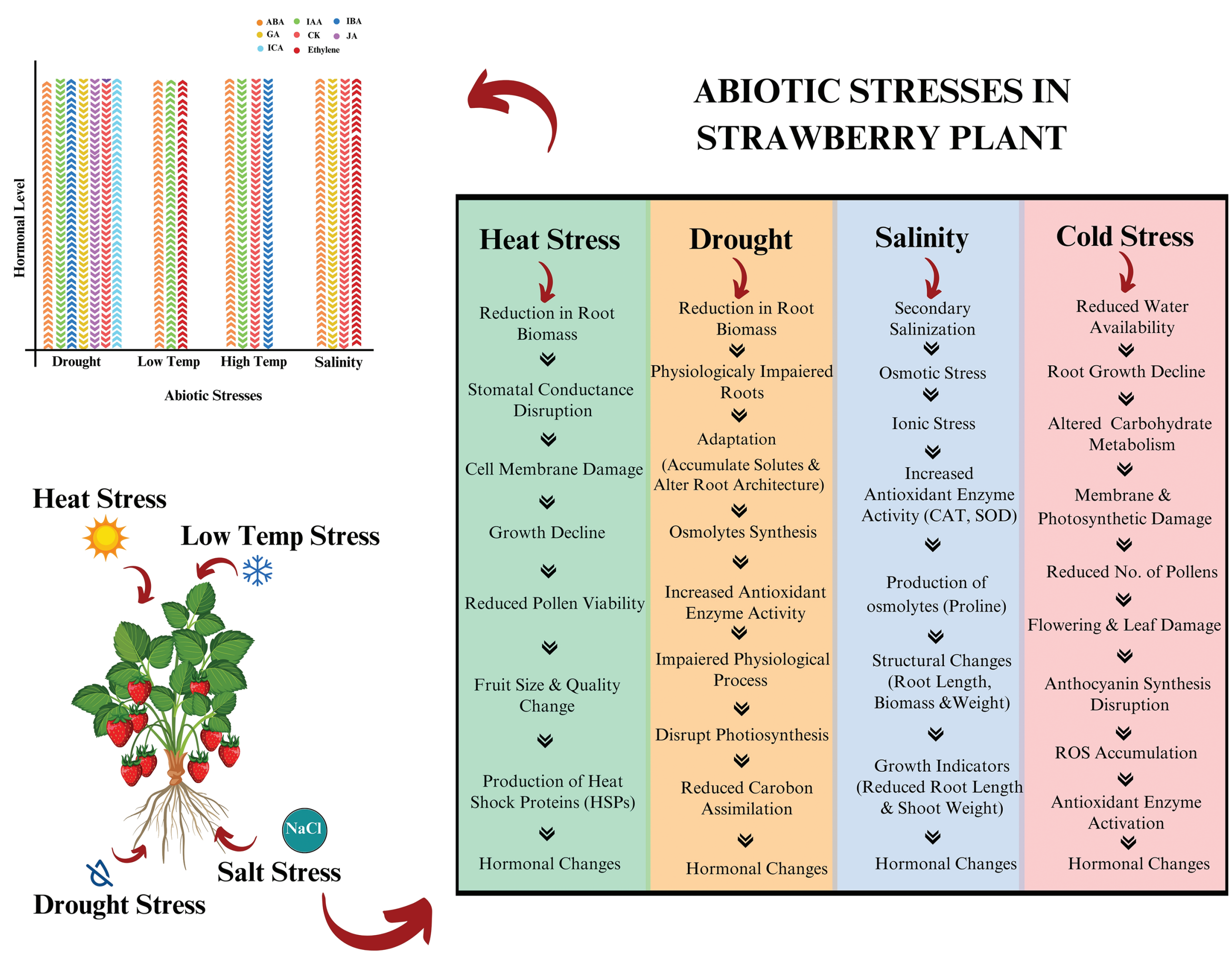

Figure 1: A comprehensive mechanism of abiotic stresses affecting plant roots, growth and hormonal pathways

2 Drought Stress

Drought stress is a serious environmental threat that jeopardizes the yield of crops economically [16]. It is a prevalent environmental stress that limits strawberry productivity and affects strawberry morphology as well as enzymatic and physiological activities [17]. Owing to their shallow root system, large leaf area, and juicy texture, strawberry plants are significantly damaged by water deficiency, thereby reducing their biomass and crop yield [18]. Plants greatly suffer from mineral shortcomings due to the unavailability of enough water in the soil and the lower mobilization of minerals within the plants [19]. This detailed review comprehensively explores the impacts of drought on the growth, physiology, and molecular pathways of strawberry plants, the results of which are summarized in Table 1.

Table 1: Summary of the impacts of drought on the root physiology, crop growth, and hormonal dynamics of strawberry plants

Root physiology	Crop growth	Hormonal dynamics
Loss of root biomass and dry weight.	Reduced turgor pressure and yield.	Accumulation of proline and total sugars to regulate osmotic pressure and to protect macromolecules.
Reduced relative water content and impaired physiological functions.	Stomatal closure, reduced levels of CO_2, and photosynthesis.	Increased activity of antioxidant enzymes (SOD, CAT, POD).
Modified root architecture, solute accumulation, and increased production of ABA.	Increased oxidative stress.	Reduction of GA, IAA, zeatin, and increased production of ABA to promote stomatal closure.
Increased production of proline.	Chlorophyll degradation, lower nitrogen content, and impaired photosynthesis.	Increased production of SA, IBA, and ABA for enhanced stress resistance in moderate drought.
Higher antioxidant enzyme activity (SOD and CAT).	Reduced fruit size, quality, leaf area, plant height, and canopy width.	Reduction of SA, ACC, IAA, and ICA in severe drought.

2.1 Impacts of Drought on Root Physiology

Strawberries are considered the most drought-sensitive crop [18], resulting in substantial losses in root biomass and dry weight. This sensitivity is not constant across all cultivars, with some cultivars appearing to be more resilient than others [17]. In susceptible cultivars, this stress reduces the relative water content of roots, which is required to maintain turgor pressure and overall plant health. A reduced relative water content impairs the physiological functions of plants [20]. Furthermore, plants respond to drought stress via multiple mechanisms, including modifications in root architecture, root structure, increased solute accumulation, osmotic adjustments, and abscisic acid (ABA) production. Moreover, plants minimize the rate of transpiration by closing their stomata and adaptive root structure, which increases water uptake from the soil. The roots of strawberry plants respond to drought stress by synthesizing proline, a type of osmolyte that increases the stability of proteins and cellular structures under dry conditions [17,20]. Additionally, evidence suggests that water shortage results in an increase in the activities of antioxidant enzymes, such as SOD and CAT, in the roots. These enzymes assist in decreasing oxidative stress during water stress [17,21].

2.2 Impacts of Drought on Crop Growth

The susceptibility of plants to water stress depends upon certain factors, including their growth stage, growth pattern, cultivation variety, weather conditions, and duration of stress. However, they are extremely sensitive to water shortages. In the face of water scarcity, strawberry plants frequently lose turgor and actual yield [18]. Additionally, it severely impacts the physiological processes of plants, such as the transpiration rate, photosynthesis, solute transport, and water balance [22]. Stomatal closure in leaves reduces the level of CO_2 under drought stress, which reduces the relative water content and photosynthetic pigments. This results in reduced growth and increased oxidative stress. Water scarcity also causes chlorophyll degradation [23], insufficient nitrogen content [24], and a direct reduction in photosynthesis, severely impacting plant development by hindering cell division, enlargement, and differentiation [23]. Prolonged drought causes a shift in the mechanism of decreased photosynthesis, from stomatal closure to membrane damage in mesophyll cells. This reduces the chlorophyll content and impairs the transport and synthesis of essential compounds [25].

Additionally, reduced leaf gas exchange under drought conditions limits carbon assimilation, ultimately affecting photoassimilation in plants. A decrease in carbon assimilation can inhibit the development of both vegetative and reproductive structures [26,27]. Similarly, reference [28] reported a reduced surface area of leaves, water use efficiency, net assimilation rate, and transpiration due to water shortages. Moreover, the most significant impact of water stress is the reduction in fruit size and yield; however, the extent of this reduction varies among different varieties [18]. Furthermore, inadequate water availability during growth phases lowers fruit quality [12]. Studies have revealed that as the water field capacity decreases from 100% to 25%, parameters such as leaf number, plant height, canopy width, and crown diameter also decline [26].

2.3 Impacts of Drought on Hormonal Dynamics

The increased production of metabolites and various solutes is one of the primary responses of plants to severe drought stress. When plants are under stress, the levels of proline and total sugars begin to increase at relatively high concentrations in certain strawberry species. These solutes perform major functions, including the regulation of osmotic pressure, water retention, and protection of macromolecules from damage [29]. Furthermore, a lack of water increases the levels of anthocyanin and soluble salts, which in turn increase the activity of important enzymes in plants, such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), to neutralize oxidative stress [30]. Drought also led to altered hormonal activities in strawberry plants to mitigate these responses. In this context, the primary hormones are salicylic acid (SA), auxins (IAA, IBA), gibberellins (GA), abscisic acid (ABA), and jasmonic acid (JA). Water shortage typically reduces the production of GA, IAA, and zeatin nucleoside, which results in slower plant growth. When reciprocating, the level of ABA increases. It acts as a signaling molecule that promotes the closure of stomata, reduces the rate of transpiration, and enhances drought resistance. Similarly, under moderate drought conditions, the levels of SA, ABA, and IBA increase, resulting in increased stress resistance. One of the more complex responses to maintain growth is increased levels of GA, JA, and indole-3-carboxylic acid. Moreover, there was an increase in GA, JA, and indole-3-carboxylic acid (ICA) contents, indicating a more complex response to maintain growth. However, severe drought leads to a decline in SA, 1-amminocyclopropane-1-carboxylic acid (ACC), and IAA, suggesting that the plant struggles to maintain normal growth. After rewatering, studies revealed an increase in the levels of ACC, IAA, ICA, and indole-3-propionic acid (IPA) in "Zhangji" strawberry plants, indicating that the recovery phase helps to restore normal growth [31].

3 Heat Stress

In recent years, temperature stress due to global warming has become a significant factor contributing to yield losses and decreased dry matter content, especially in temperate regions [32]. Compared with the period from 1850–1900, global surface temperatures are projected to rise by more than 1.5°C by the end of the 21st century [33]. When strawberries and other plants are exposed to heat stress, several negative effects can occur, including reduced photosynthesis, damage to cell membranes, cell death, and accelerated aging [34]. However, plants can develop a form of heat tolerance, known as thermotolerance, if they are initially exposed to mild, nonlethal heat stress [35]. In light of these challenges, a detailed review of the impacts of heat stress on strawberries is presented below, along with a summary in Table 2.

Table 2: Overview of the effects of heat stress on the root physiology, crop development, and hormonal balance of strawberry plants

Root physiology	Crop growth	Hormonal dynamics
Disruption of enzymatic activities, metabolic pathways, plant structure, growth and yield.	The decline in leaf growth at above 26°C.	Production of heat shock proteins (HSPs).
Reduction in root biomass, water, and nutrient uptake at above 30°C.	Negatively impact reproductive stage, reduced pollen grain adhesion and germination, poor fertilization, and gamete viability.	Disruption in transport and signaling of auxins.
Impaired stomatal conductance and CO_2 absorption lead to a reduction in photosynthesis.	Root zone temperature of 30°C leads to reduced oxygen consumption, fruit size, and wilting of the plant.	Elevated level of ABA, lower transpiration rate, and limited leaf expansion.
Reduction in root and shoot growth.	Reduction in fruit weight and quality.	Impaired root development, growth, and fruit formation.
Damaged cell membranes which results in electrolyte leakage.	Small and irregularly shaped fruits with increased levels of pelargonidin-3-glucoside.	Lower level of CK, cell division, leaf function, and photosynthesis efficiency.

3.1 Impacts of Heat Stress on Root Physiology

Both extreme heat and prolonged exposure to moderately high temperatures negatively impact plants by causing severe damage [36], which leads to changes in plant structure, function, and internal processes due to the disruption of enzymes and metabolic pathways that threaten crop yield and sustainability [37]. High temperatures negatively influence several key aspects of strawberry plants, including vegetative growth, root development, pollen health, fruit size, fruit quality, protein levels in leaves, and fruit production [38]. Research conducted by [39] and [38] revealed that temperatures above 30°C reduce root biomass, which hampers the ability of plants to take up water and nutrients effectively. Additionally, high temperatures significantly decrease photosynthesis by affecting stomatal conductance and CO_2 absorption, with rates decreasing 5 to 9 times lower than those in plants grown at the optimal temperature of 25°C. This decline is crucial for the healthy growth of both roots and shoots. Additionally, Ref. [39] reported that heat stress causes more damage to cell membranes, leading to increased leakage of electrolytes, which indicates cellular stress and damage.

3.2 Impacts of Heat Stress on Crop Growth

Heat stress significantly impacts strawberry plants, leading to various physiological stresses. Research has revealed that leaf growth increases linearly at temperatures below 26°C, whereas growth decreases linearly at temperatures above this threshold. Optimal growth has been reported to occur between 18.3°C and 27.3°C [40]. High temperature particularly affects strawberry plants during their reproductive stages [41]. Furthermore, elevated temperatures have been linked to a reduction in pollen grains, adhesion, and germination. These results in fewer firm stigmas, causing many fertilization attempts to fail due to abnormal pathways taken by pollen tubes. Consequently, there is an increase in immature and unviable female gametes within the pistil, leading to poor pollen performance shortly after pollination [42]. In addition, a high root zone temperature of 30°C led to decreased oxygen consumption and root cell viability, causing most plants to wilt within two months [43] and reducing fruit size [41]. High-temperature stress also negatively affects photosynthesis and overall crop yield [44]. A previous study revealed that the average individual fruit weight and total fruit weight per plant decreased by 70%–80% at 30°C compared with those of plants grown at 25°C. Moreover, the fruits produced under high temperatures were irregularly shaped, small, and had less intense red coloration. However, these fruits presented significantly increased levels of pelargonidin-3-glucoside, which is the primary phenolic compound of strawberry [45].

3.3 Impacts of Heat Stress on Hormonal Dynamics

In strawberry plants, high-temperature stress triggers the production of heat shock proteins (HSPs), which play key roles in protecting plant cells from heat-induced damage. These proteins stabilize other proteins and cellular structures, reducing the impacts of heat stress [46]. These HSPs interact with plant hormones, particularly ABA, and influence their signaling pathways. This influence induces resistance in plants to survive under stress conditions [46]. Additionally, high temperature affects auxin, a hormone essential for cell elongation and division. Disruption of auxin transport and signaling can result in stunted growth and poor root development [47]. Auxins play a key role in fruit and flower development, so their alteration due to heat stress can lead to reduced flowering and fruit set, negatively impacting overall crop yield. Elevated temperatures are known to interfere with auxin-related processes, such as flowering time and fruit formation. Moreover, the level of ABA increases under heat stress. This hormone is crucial for plants to respond to water stress by promoting stomatal closure, thereby reducing water loss during heat stress. Despite its role in mitigating heat stress, higher levels of ABA hinder plant growth by limiting leaf expansion and root development, which can ultimately reduce the overall yield of strawberry plants. Additionally, high temperatures often lead to a decrease in cytokinin (CK) levels, which are important for cell division and delaying leaf aging. Lower CK levels can result in reduced shoot growth and impaired leaf function [48]. This decrease also affects photosynthesis, leading to reduced chlorophyll content and lower photosystem II efficiency under heat stress [49].

4 Low-Temperature Stress

Strawberry seedlings grow best at temperatures between 15°C and 32°C, but temperatures below 10°C can significantly hinder their growth and development. Since strawberries often grow in single-slope greenhouses during the winter and spring, they are frequently exposed to low-temperature and low-light conditions, which negatively affect their growth and fruit quality. Both temperature and light are crucial environmental factors that influence plant growth and development [50], physiological properties, photosynthetic traits [51], and fruit quality [52]. A detailed overview of how low temperature affects the root physiology, crop growth, and hormonal dynamics of strawberry plants is presented in Table 3.

Table 3: A review of the impacts of cold stress on root physiology, crop growth, and hormonal dynamics of strawberries

Root physiology	Crop growth	Hormonal dynamics
Less availability of liquid water, disruption of metabolism, and physiological processes.	Damaged microtubules, microfilaments, and electrolyte leakage impact growth and productivity.	Triggers the production of ROS, damages biomolecules, affects photosynthesis, and plant death if antioxidants are overwhelmed.
Reduction in relative water content, impaired growth, and pressure.	Disrupts photosynthesis (damage thylakoid membrane, electron transport, stomatal conductance, and carbon reduction cycles).	Increases ABA that stabilizes membranes and promotes cold tolerance gene, but excessive production of ethylene causes premature aging.
Altered carbohydrate metabolism.	Impairs fruit color development by hindering anthocyanin accumulation.	Disrupts auxin transport, affecting root and shoot growth.
Damaged cell membranes and reduced membrane fluidity lead to lipid peroxidation.	Low temperature during flowering affects pollen production and germination, reducing fruit set.	Affects IAA levels, influences root growth, and inhibits overall vegetative growth.
Reduction in quantum yield of photosystem II. Impaired root growth and photosynthetic efficiency.	Blossom browning and reduced flowering delay maturation.	Impairs membrane fluidity, hormonal balance, and disruption of cellular functions.

4.1 Impacts of Low-Temperature Stress on Root Physiology

Low-temperature stress affects plants in a way similar to drought, as freezing reduces the availability of liquid water [53], leading to disruptions in physiological processes, metabolism, and plant biology [38]. A study conducted by [54] demonstrated that cold stress reduces the relative water content in strawberry roots. Owing to this reduction, the plant fails to maintain its turgor pressure, cell expansion, and normal growth. This reduction is variable among strawberry cultivars because of genetic differences in terms of cold tolerance. Similarly, there is an alteration in carbohydrate metabolism. Few cultivars respond to cold stress with high levels of soluble carbohydrates. These carbohydrates are used by plants for energy purposes to perform metabolic functions at low temperatures. Similarly, another study conducted by [55] revealed that low temperature affects the structure and function of roots and their ability to take up nutrients, followed by reduced membrane fluidity, lipid peroxidation, and damage to the cell membrane. Additionally, it also results in a reduction in the maximum quantum yield of photosystem II. This reduction reduces photosynthetic efficiency and plant health. Refs. [39] and [38] confirmed that suboptimal temperatures (below 20°C/15°C) restrict root growth, leading to a decline in root biomass and viability.

4.2 Impacts of Low-Temperature Stress on Crop Growth

The exposure of strawberry seedlings to extremely low temperatures leads to significant damage, including depolymerization of microtubules and microfilaments and electrolyte leakage, which can have long-lasting impacts on growth and productivity [55]. It can disrupt photosynthesis by damaging key components, such as the thylakoid membrane, electron transport chain, stomatal conductance, and carbon reduction cycles. For example, stomatal closure after chilling might be a direct response to low temperatures impacting guard cells or an indirect result of increased intercellular CO_2 due to the reduced activity of Rubisco [50]. Cold temperatures also interfere with the accumulation of anthocyanin, which is essential for fruit coloration, by hindering the activation of specific proteins under stress, resulting in poor color development [56]. During flowering, temperatures of approximately 8°C and 10°C can temporarily stop pollen production, as observed in the Chandler cultivar, leading to poor fruit set. Pollen germination rates also decrease at temperatures below 16°C, further affecting fertility [57]. Cold conditions during dormancy reduce the number of blossoms and cause the browning of crown tissues, which is crucial for plant growth. Moreover, exposure to freezing temperatures, such as −6°C, can severely limit flower emergence and leaf size [58]. Similarly, short-term extreme cold conditions delay fruit maturation [59]. Additionally, cold stress triggers the production of reactive oxygen species (ROS), which are harmful to biomolecules such as lipids, proteins, and nucleic acids [60]. To combat ROS, plants activate protective mechanisms via the production of antioxidant enzymes such as CAT, SOD, and POD. These enzymes help to manage ROS levels and prevent severe damage. However, if ROS production overwhelms a plant's defenses, it can lead to irreversible damage, particularly to the photosynthetic machinery and the plant's nuclear gene expression system [61,62].

4.3 Impacts of Low-Temperature Stress on Hormonal Dynamics

Low-temperature stress causes an increase in reactive oxygen species, which activate the plant's antioxidant defense system. However, if cold stress becomes too intense, the defense system cannot effectively eliminate excess ROS, leading to severe damage or even plant death [63]. Moreover, it also results in impaired hormonal dynamics. It disrupts auxin transport and signaling pathways, which impairs root and shoot growth [48]. Additionally, cold stress triggers an increase in ABA, which helps plants tolerate cold conditions by stabilizing their cell membranes and regulating genes that respond to cold stress [64]. The expression of ethylene and the transcription factor ICE1 is also upregulated during cold stress, promoting the expression of cold tolerance-related genes. However, too much ethylene causes premature aging of the plant and deterioration of fruit quality. The hormone IAA is a key auxin for cellular growth that responds variably to low temperatures. In some cases, IAA levels increase, supporting root development, but overall vegetative growth may be inhibited as the plant focuses on stress responses [48]. Cold stress further leads to increased lipid peroxidation and reduced membrane fluidity, which impairs cellular functions. This damage is often intensified by hormonal imbalances, which affect a plant's ability to maintain stability under stress [65].

5 Salinity

Salinity is a major environmental stress that limits plant growth by causing imbalances in ions and water within plants, disrupting their metabolism, stability, and development [66]. According to an estimation, approximately one-third of the world's agricultural land is affected by high salt levels [67]. All plants, particularly strawberry plants, are highly sensitive to salinity [68], with their ideal electrical conductivity ranging between 1 and 1.5 d. Excessive amounts of salts impair the metabolism of strawberry plants [69]. Additionally, when the temperature is high in the absence of rainfall, most of the soil water evaporates and leaves salts behind the soil surface, which leads to their increased concentration, which is referred to as secondary soil salinization. It limits crop growth and reduces yield. All these processes make it important to thoroughly understand the underlying molecular mechanism to makes strawberries resistant to salinity [70], which is summarized in Table 4.

Table 4: Summary of the impacts of salinity on the root physiology, crop growth, and hormonal dynamics of strawberry plants

Root physiology	Crop growth	Hormonal dynamics
Induce osmotic stress that leads to poor hydration, low turgor pressure, and stunted growth.	Induce oxidative stress, leading to ROS production, and damage to cell membranes, proteins, and DNA.	Increases ABA production, reduces transpiration, and limits photosynthesis by closing stomata.
Accumulation of Na^+ and Cl^- ions disrupts nutrient uptake and impairs plant growth.	Leaf necrosis, early aging, reduced photosynthetic area, and lower shoot weight.	Suppress the production of GA.
Increased antioxidant enzyme activity (SOD, CAT), accumulation of proline and carbohydrates to prevent oxidative stress.	Decrease leaf area, shoot (fresh and dry) weight, root biomass, fruit yield, and quality.	Decrease CK levels and reduce leaf size.
Altered root structure (lateral roots, hair development), reduced root length, biomass, and weight that affect water and nutrient uptake, leading to poor root development.	Alters carbohydrates and organic acid levels, affecting the taste and nutritional value of fruits.	Increase ethylene that accelerates early ripening and aging. Lowers the level of auxin that hinders root elongation and cell expansion.

5.1 Impacts of Salinity on Root Physiology

An excessive amount of salt in the root zone leads to osmotic stress in plants. Under these stresses, maintaining plant integrity becomes difficult, resulting in poor hydration, low turgor pressure, stunted growth, and reduced root biomass. In addition, harmful ions such as sodium (Na^+) and chloride (Cl^-) accumulate. This accumulation prevents the plant from maintaining its nutritional balance. As a result, plants fail to take up essential nutrients such as potassium (K), nitrogen (N), and phosphorus (P), which reduces plant growth and development. In response to such types of oxidative stress, there is increased activity of antioxidant enzymes such as SOD and CAT. Their production protects plants from damage caused by oxidative stress [71]. Furthermore, they resist the accumulation of protective substances such as proline and soluble carbohydrates. They help maintain cellular integrity under saline conditions [71,72]. Moreover, certain changes in root structure, including altered lateral root formation and hair development, have been reported. It promotes the uptake of water and nutrients but also leads to deficiencies in the root system [69,71]. Similarly, reduced root length, biomass, and fresh weight hinder the water and nutrient uptake ability of plants [72,73].

5.2 Impacts of Salinity on Crop Growth

Strawberry plants are known to be highly sensitive to salt stress, which negatively impacts their growth and fruit production [73] and affects plants in three ways: osmotic stress, ionic stress, and oxidative stress. Among these, oxidative stress is considered to be the most harmful [74,75]. This leads to the development of harmful reactive oxygen species (ROS) in plant cells, which damage essential components such as membrane lipids, proteins, and DNA [76]. In strawberries, salt stress causes issues such as leaf necrosis, early leaf aging, and a reduction in the photosynthetic area [77]. Additionally, salinity also reduces the number and size of leaves, shoot weight, and number of branch crowns, all of which result in lower fruit yield [78]. Similarly, vegetative growth, leaf water content, chlorophyll levels, and fruit quality are severely affected by salt stress [79]. Important growth indicators, such as the leaf area, fresh and dry weights of plants above ground mass, and root biomass, decrease significantly under high salinity [72,73]. The decrease in water content due to salinity is crucial because of its ability to maintain turgor pressure. In a study conducted by [73], the Rociera cultivar presented a lower water content under high salinity than did Camarosa, which performed better at moderate salinity levels. Moreover, salinity also leads to reduced fruit yield, with reductions in total yield per plant of approximately 21.5% and 29.1% for Camarosa at medium and high salinities, respectively, and of 17.3% and 22.7% for Rociera under the same conditions [73,80]. To withstand salinity, strawberry plants trigger biochemical responses and the production of osmolytes, including proline and soluble carbohydrates. They maintain the cellular structure and integrity under stress conditions [81]. Moreover, there is an alteration in the levels of carbohydrates and organic acids, neglecting their taste and nutritional value [72,81]. In summary, strawberries are highly sensitive to saline soil, followed by wilting; nutritional imbalances; reductions in fruit yield and quality; toxicity from sodium and chlorine; and ultimately death under severe conditions [29].

5.3 Effects of Salinity on Hormonal Dynamics

The hormonal balance of strawberry plants is disrupted by salt stress, especially GA and ABA. A relatively high level of salinity leads to increased production of ABA. It lowers the rate of transpiration through the closure of stomata but also reduces gaseous exchange and photosynthetic activity. On the other hand, the production of GA (required for growth and development) is suppressed, resulting in stunted growth and fruit yield [82]. Additionally, the level of CK (essential for cell division and growth) decreases, which reduces leaf size and disrupts plant health [71,82]. Similarly, an increase in ethylene production causes early fruit ripening and aging, which decreases the texture, flavor, and quality of fruits. A relatively low level of auxins influences root elongation and cell expansion [73], and plants are unable to take up nutrients and water effectively [83].

6 Interplay of Soil Microbes

In the past few years, interest in the use of microorganisms, including PGPR and AMF, as bioinoculants for the mitigation of abiotic stresses in plants has increased [84]. Their activities in soil improve the physical, biological, and chemical properties of the soil, which influences the growth and development of plants. All these factors lead to healthy plants and improved production. Additionally, associations of AMF and PGPR with roots help maintain a balanced ecosystem for plants that improve soil fertility and nutrient availability in the soil through the breakdown of organic compounds, the development of symbiotic relationships, production of iron carriers, and solubilization of minerals [85]. Moreover, they are also used as biofertilizers. They also play a major role in inducing stress tolerance, nutrient cycling, and disease suppression [86,87]. In addition, they provide strength to the defense system of plants during biotic and abiotic stresses, which helps them survive under these changing climatic conditions, highlighting their importance [88].

6.1 Promotion of Rhizobacteria and Abiotic Stress in Plant Growth

PGPR are beneficial microbes that are found in the areas around roots (rhizosphere), where they interact with roots for nutrient exchange [89]. Studies have revealed that several rhizospheric bacterial species have the potential to improve plant growth, fruit quality, and overall yield [90]. The most prominent strains from different genera are Pseudomonas, Azotobacter, Bacillus, Azospirillum, Erwinia, Serratia, Chromobacterium, Caulobacter, Flavobacterium, Agrobacterium, Arthrobacter, Burkholderia and Micrococcus [91]. Bacillus is well known for its ability to survive for longer periods in soil, even under severe environmental conditions [92]. Although the mechanism of plant growth promotion is unknown, these genes are considered to interact with roots directly or indirectly. According to a study by [92], PGPR stimulates growth by increasing systemic resistance to biotic stress through antibiosis (production of antibiotics) and by competing with harmful microbes for nutrients. Similarly, in a study conducted by [93], PGPR was found to mitigate the harmful effects of salinity on strawberry plants, ensuring that their growth and photosynthesis were not compromised by sodium chloride (NaCl) toxicity. Similarly, Ref. [94] found that *Pseudomonas fluorescens* (SBU4) and *Pseudomonas glycinae* (SDK8) are drought tolerant and possess multiple growth-promoting properties, making them suitable as bioinoculants to improve strawberry yield and quality, even during short-term drought stress. In another study, Ref. [95] demonstrated that plant PGPR, especially Pseudomonas and Bacillus, act as early root colonizers, promoting plant growth by increasing seed emergence, increasing plant weight, and improving crop yield. Therefore, we can conclude that although PGPR-based biofertilizers may not completely overcome the negative impacts of abiotic stresses, their influence is still significant, as they have the potential to improve strawberry growth. The detailed mechanism of the interplay of PGPRs in mitigating abiotic stresses is illustrated in Fig. 2.

6.1.1 Cold Stress Suppression

PGPR mitigates cold stress in strawberry plants by increasing the production of beneficial compounds that help stabilize cellular structures under cold stress and promote the synthesis of phytohormones such as IAA. Moreover, PGPR-treated plants present increased production of secondary metabolites, including flavonoids and phenolic compounds, which protect the plants from pathogens during cold stress [96–98]. Additionally, PGPR improves physiological parameters in plants, including chlorophyll content and photosynthesis [97,99,100].

6.1.2 Temperature Stress Suppression

PGPR produces ACC deaminase, an enzyme that breaks down 1-aminocyclopropane-1-carboxylic acid (ACC), which is a precursor to ethylene. Ethylene is directly linked to stress responses in plants, especially under high temperatures. By reducing the level of ethylene, PGPR helps alleviate the negative effects of heat stress, supporting plant growth. Additionally, PGPR improves nutrient uptake under stressful conditions. Some PGPR strains increase root development and water retention, which is important for plants to address drought conditions, particularly during heat waves, when water availability decreases. PGPR also increases the chlorophyll content and improves the nutrient profile of strawberry plants, helping them maintain their photosynthetic efficiency under heat stress [98,101,102].

6.1.3 Salinity Stress Suppression

PGPR plays a key role in increasing the availability and uptake of essential nutrients such as nitrogen, phosphorus, potassium, calcium, and magnesium, even under saline conditions. This nutrient uptake is essential for maintaining plant health when plants are subjected to high salinity [99,103,104]. PGPR treatments reduce electrolyte leakage in plants under saline stress, which indicates better membrane stability and less cellular damage [100,105,106]. A study conducted by [101] revealed that plants treated with PGPR presented lower levels of oxidative stress markers, including malondialdehyde and hydrogen peroxide. Moreover, the growth and yield parameters were greater than those of the untreated plants.

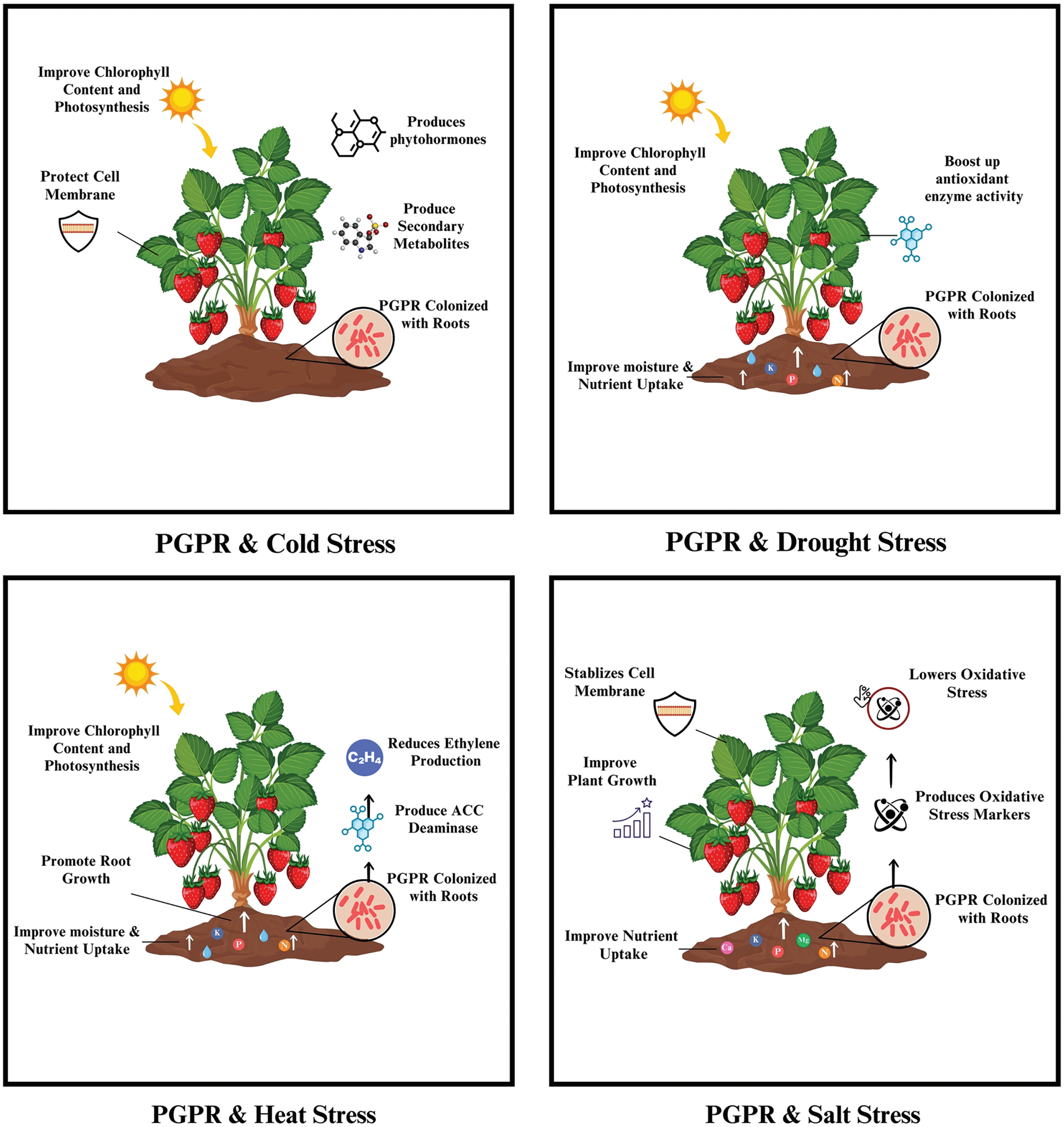

Figure 2: Role of PGPR in the mitigation of abiotic stress

6.1.4 Drought Stress Suppression

The inoculation of plant roots with PGPR increases the chlorophyll content and photosynthetic activity in leaves, root length, root surface area, and water and nutrient uptake during water shortage [97]. PGPR can increase the activity of antioxidant enzymes such as SOD, CAT, and POD [107–109]. These enzymes help mitigate the oxidative damage caused by drought stress, thereby protecting plant cells and enhancing overall plant health [102,110,111]. PGPR inoculation has been shown to maintain better water status in strawberry plants under drought conditions.

6.2 Arbuscular Mycorrhizal Fungi and Abiotic Stress Mitigation

AMF in association with roots plays a primary role in stress mitigation and nutrient and moisture uptake. The role of these genes in maintaining plant health is illustrated in Fig. 3. They capture essential nutrients and water from the soil through their mycelial network and transport them to plants side by side. This interaction of AMF with the host plant is considered a symbiotic relationship [103,112]. In addition, the colonization of plants by AMF alters stomatal behavior by increasing stomatal conductance up to 24% compared with that of non-colonized plants, which exhibit greater production [104,113,114].

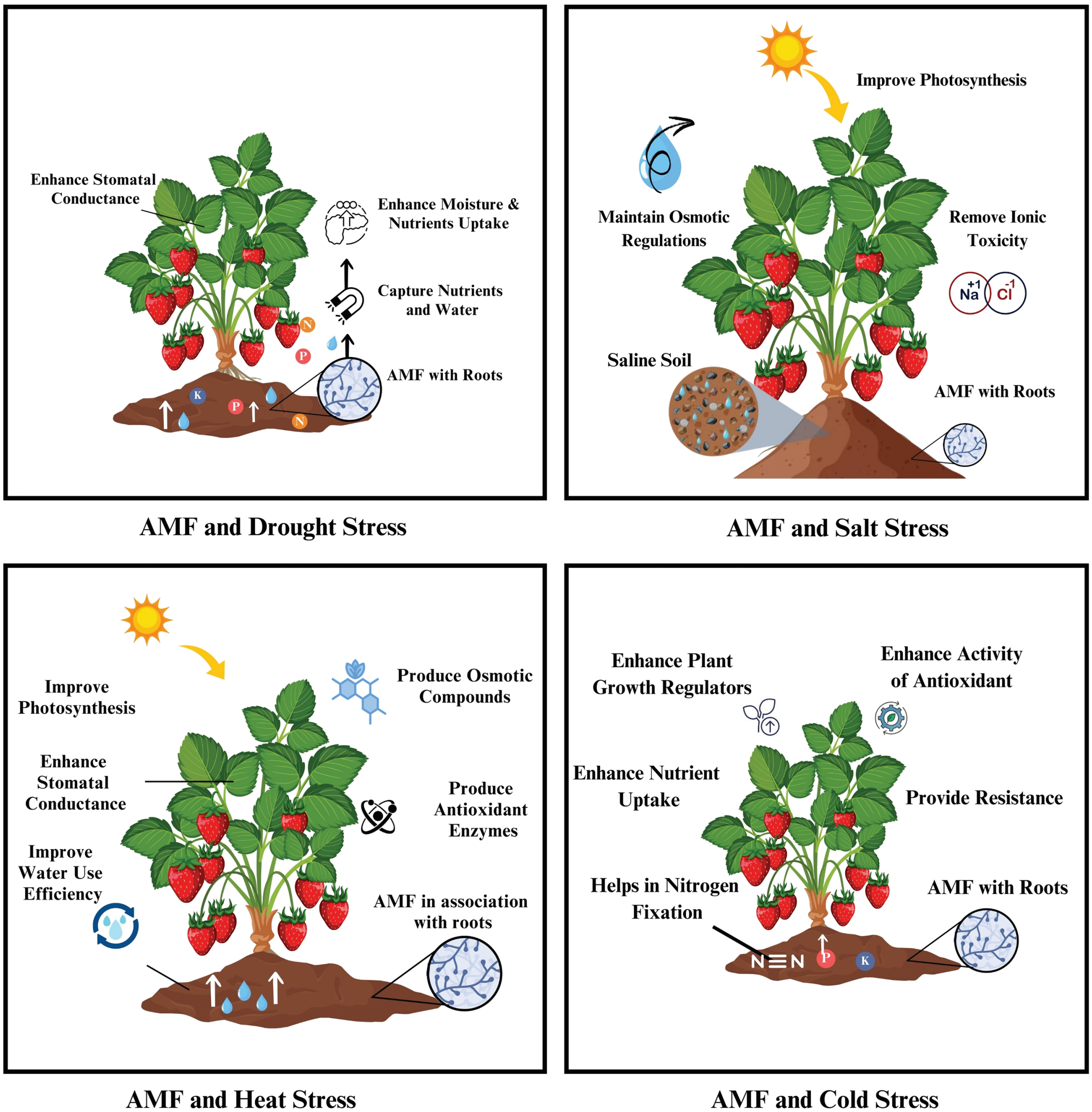

Figure 3: Role of AMF in the mitigation of abiotic stress

AMF, along with other rhizospheric microbes, develop resistance in plants to cold stress through the stimulation of processes such as increased nitrogen fixation, reduced ethylene production, and the production of plant growth regulators, including ABA, auxins, and GA [112–114]. Moreover, they increase the activity of antioxidant enzymes, nutrient uptake, and resistance to low temperatures [105,115–117]. In the face of heat stress, they improve plant biomass, relative water content, and water use efficiency; the production of antioxidant enzymes such as ascorbate POD, CAT, and SOD; and the synthesis of osmotic compounds such as trehalose, glomalin, and proline [118–120]. All these activities increase the rates of photosynthesis, chlorophyll content, stomatal conductance, and carotenoid content. The colonization of these plants improves nutrient assimilation and metabolism and promotes recovery from heat stress [106]. Similarly, AMF also helps mitigate saline stress via osmotic regulation and the maintenance of cellular integrity, turgor pressure, and cellular functions [120–122]. They prevent ionic toxicity by balancing the levels of sodium and potassium ions. All these factors lead to improved photosynthetic activity and water use efficiency and ultimately to healthy plants in saline soil [107].

7 Conclusion

Abiotic stresses significantly influence the root physiology, crop growth, and hormonal dynamics of strawberry plants. In this context, soil microbes act as primary supporters of plant growth, the most prominent of which are PGPR and AMF. They trigger root development, nutrient uptake, stress tolerance, plant growth, and the production of stress-responsive hormones such as ABA and JA. All these activities of beneficial soil microbes help mitigate environmental challenges. It can be concluded that the application of beneficial microbes can increase the production and stress tolerance of plants. Through a thorough understanding of this relationship, it is possible to develop, ecofriendly and innovative approaches for stress mitigation that will be able to minimize food security issues and maximize yield. The study highlights the potential of soil microbes, particularly plant growth-promoting rhizobacteria (PGPR) and mycorrhizal fungi, to mitigate the negative effects of abiotic stress on strawberry growth and root physiology. Their application in strawberry cultivation can enhance nutrient uptake, root architecture, and resilience to stressors like drought and salinity. Farmers are encouraged to adopt microbial inoculants as biofertilizers or biostimulants, which are eco-friendly alternatives to chemical inputs. Additionally, integrating these microbes with practices like organic mulching, optimized irrigation, and stress-tolerant strawberry varieties can further boost productivity under challenging environmental conditions. Field trials are recommended to fine-tune the dosages and combinations of microbial treatments for specific regions and stress scenarios to ensure maximum benefits and economic viability.

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