Chapter 13
Induction of Stress Tolerance in Plants by Metabolic Secretions of Endophytes for Sustainable Development

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Abstract Endophytes are microbes that can survive inside of a plant's stable tissues without wreaking havoc on the host. Endophytes aid plant adaptation by conferring a variety of determining effects that can counteract the harmful impacts of abiotic or biotic stressors. As a result, there is significant potential for long-term agricultural output if endophytic bacteria are used to increase crop performance under stress circumstances including low temperatures, high salt, low humidity, and heavy metal contamination. In order to benefit from symbiotically conferred resistance to abiotic stress, at least two routes must activate host stress response systems soon after stress exposure. That way, plants can prevent or lessen the impact of the stress on their systems. Endophytes increase a plant's resilience to stress through biochemical processes, such as the activation of biomolecules and plant stress genes. Endophytes are essential to sustainable agriculture due to their many beneficial impacts on the host plant. These effects include the regulation of phytohormone signalling, metabolic activity, and plant defence response pathways.

Keywords Endophytes · Metabolites · Abiotic stress · Phytohormones

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13.1 Introduction

De Barry [1] first used the term endophytes, which literally means "in the plant" (edon = within, phyte = plant). This phrase has a wide range of applications, encompassing not only the algae that may live within the algae but also the bacteria, fungus, plants, and insects that may live within them [2]. Consequently, endophytes are symbiotic bacteria that promote plant growth and live within plant tissues. It also plays beneficial roles related with plant responses under conditions of biotic and abiotic stress without being responsible for any disease symptoms on the host plant. There are a variety of methods by which endophytes influence plant growth in response to abiotic stimuli like salt, heat, temperature, heavy metal toxicity, and nutritional stress. These microbial communities generate numerous secondary active chemicals that shield plants from insect and fungal diseases, hence promoting plant growth. In addition, they can produce extracellular enzymes that promote endophyte colonisation of the host plant. Endophytic microbes play a significant role in helping plants adapt to stress and environmental variables that limit growth and output. Symbiotic connections between plants and microbes enable them thrive in harsh environments by facilitating mutually beneficial changes in both partners' rates of evolution and fitness.

It has been shown that endophytic microbes like bacteria, actinomycetes, and fungi create a protective microbial "nest" around their plant hosts, making them more resistant to frost and other environmental stresses [3, 4]. The absence of endophytes in a plant is not a natural condition [5]. Without endophytes, plants can't fight off infections and will easily succumb to environmental stresses [6]. Endophytic microbes, particularly fungi like *Sebacina vermifera* and *Piriformospora indica* and other *Colletotrichum* and *Penicillium* species, differentiate under unfavourable conditions to have more potent effects on plant growth [7, 8].

Generally speaking, the fungus, bacteria, and nematodes that aren't directly hazardous to plants aren't nearly as harmful when they're among plants that have plant growth-promoting microorganisms (PGPM) attached to them. Phytohormones are produced as a result of the primary effects of PGPM. Modifications in chemical or physical plant defence strategies, known as mediated systemic resistance (ISR), may also be affected by PGPM [9]. Under a variety of adverse environmental conditions, PGPM has consistently expanded, proving its usefulness to plant life. Increasing tolerance to environmental stimuli like sun, drought, salinity, cold, and heavy metals has been proved time and time again to be one of the key activities of plant growth-promoting fungus (PGPF) [10–12]. Abscisic acid (ABA)-independent or abscisic acid-dependent pathways convey osmotic stress from salinity and drought [13], and low ABA development levels have been achieved through fungal activity [14, 15]. Treatment with endophytic *Penicillium* spp. brought about water balance in plants, as reported by Miransari [16], so plants didn't have to try very hard to synthesize ABA and shield the progress of stressed cells.

13.2 Role of Endophytes in Abiotic Stress Management

Suboptimal to supra-optimal temperatures, soil pH imbalance (from acidity to salinity), soil moisture deficits and surpluses, heavy metal toxicity, ultraviolet radiation, and many other environmental factors have all been stressors for plants ever since they first appeared [17]. Due to their brief life span, endophytes are able to quickly adapt to their environment and impart a wide variety of stresses on to their host plant [18]. In reaction to abiotic stress, endophytes either (i) activate the host plant's response system or (ii) produce compounds that are toxic to the stress [19]. In the following paragraphs, we will discuss the mechanisms involved in coping with abiotic stresses in greater depth.

Extraction of endophytic fungi from medicinal plants by Chathurdevi and Gowrie [20] revealed that these fungi release extracellular enzymes that aided the plants' growth when subjected to abiotic stress. More than 50 unique endophytic fungal strains rich in enzymes like laccase, amylase, pectinase, cellulase, lipid hydrolase, and proteinase were isolated and identified by Sunitha et al. [21]. Breakdown enzymes for 1-aminocyclopropane-1-carboxylate (ACC) Bacterial endophytes have been studied in relation to the enzymes amylase, deaminase, esterase, pectinase, cellulases, lipids, protease, phytase, asparaginase, and xylanase [22–25]. A group of researchers led by Vijayalakshmi [26] has recently isolated bacterial endophytes from medicinal plants. These endophytes secrete extracellular enzymes such as amylase, protease, and cellulase.

The potential for several different types of endophytic bacteria with molecular weights between 400 and 1500 daltons to create siderophores has been studied [27]. In addition to catecholate and salicylate, bacteria can also produce hydroxamate and carboxylate as siderophores. Streptomyces, Pseudonocardia, Actinopolyspora, Nocardia, Salinispora, Micromonospora, Actinomadura, and Kibdelosporangium are all examples of endophytic actinobacteria that create siderophores [27–29]. To regulate plant growth and confer disease resistance, plants rely on endophytic actinobacteria, which use an exomechanism to produce siderophores [30].

The phytohormone salicylic acid (SA) plays an important role in a wide range of processes, including development of the plant's root system, germination of seeds, induction of flowering, closure of the plant's stomata, and resistance to abiotic and biotic stress. Produced by bacterial endophytes, SA promotes development and protects plants against pathogens such as fungus, making them more resilient to drought [31].

13.3 Endophytes in Biotic Stress Management

Generally speaking, endophytic bacteria are considered to be effective biocontrol agents. Endophytic fungi are extremely important for both grasses and conifers in mitigating the damage caused by insect herbivores. *Bacillus subtilis*, an endophytic bacterium isolated from *Speranskia tuberculata* (Bge.) Baill, has been shown to have antagonistic effect against *Botrytis cinerea*, a fungus responsible for the spoilage of tomato fruits during storage [32]. Poplar canker was the subject of a biocontrol study in which novel endophytes including *Burkholderia pyrrocinia* JK-SH007 and *Bacillus cepacia* were employed [33].

Recombinant endophytic strains, which may be found in many plants, can be used to create a wide variety of anti-pest proteins, which can then be used to combat a wide range of plant pests. Hassan et al. [34] biocontrolled *Culex pipiens* and *Musca domestica* with copper nanoparticles made by the endophyte *Streptomyces capillispiralis* Ca-1. The endophytic actinomycetes *Streptomyces zaomyceticus* Oc-5 and *Streptomyces pseudogriseolus* Acv-11, found in the plant *Oxalis corniculata* L., synthesised copper oxide nanoparticles with antimicrobial activity against four phytopathogenic fungi: *Phoma destructiva*, *Alternaria alternaria*, *Fusarium oxysporum*, and *Curvularia lunata* [35].

In asymptomatic colonisation, the host and the endophyte maintain a dynamic equilibrium in which their antagonistic interactions are roughly balanced. Although only a fraction of endophytes are thought to be dormant pathogens, all endophytes investigated so far have developed the exoenzymes essential to infect and colonise the host [36–39]. Almost all of them can produce compounds that are poisonous to plants (phytotoxins) [2, 40]. Hosts, just like they would in reaction to pathogens, can develop preformed and induced defensive metabolites [2, 41–45]. If the virulence of the fungus and the defence mechanisms of the plant are about equal, there will be no visible signals of danger.

The dynamics of an antagonistic relationship can shift depending on the host and endophyte's tolerance to biotic and abiotic environmental conditions and the state of health of both parties. Many endophytes, for instance, can infect as a pathogen, colonise cryptically, and sporulate as either a pathogen or a saprophyte, making them masters of phenotypic plasticity. Therefore, diversity is required to act as a check on this trend; if this is the case, then endophytic interactions are creative and can drive evolutionary change, with symbioses having the potential to develop into both highly specialised mutualisms and parasitisms or forms of exploitation [46].

13.4 Signalling During Abiotic and Biotic Stresses

Plants have a number of built-in systems that allow them to sense stress signals and continue to grow even in adverse conditions. Information is routinely relayed across pathways and signal molecules/cofactors in the signalling response to any stressor, biotic event abiotic [47]. Reactive oxygen species (ROS) such as NO_2, Ca^{2+}, inositol phosphates, and systemin have a function in signalling as well, complementing the effect of phytohormones. Drought causes osmotic stress, while salt stress causes ionic stress [48]. ROS production has been proposed as a critical mechanism for responding to biotic and abiotic stresses. New research reveals that Ca^{2+} and NO have a large impact on hormone signalling, which is important in stress response pathway crosstalk. Plant defence, ABA-dependent stomata movement, and drought stress responses depend on nitric oxide and Ca^{2+} signalling [49]. MAPK/MPK cascades regulate proliferation, cell differentiation, cell death, development, and stress responses. The mitogen-activated protein kinase (MAPK) cascade drives cellular responses to biotic and abiotic stresses. Cellular responses to biotic and abiotic stressors depend on the MAPK cascade. Plants produce heat shock proteins to avoid protein denaturation and maintain protein homeostasis in severe temperatures [50].

Fungal endophytes have been discovered to contain compounds that counteract the effects of flavonoids, phenols, terpenoids, alkaloids, saponin, nematode polysaccharides, and tannins [51, 52]. Treatment of diseases caused by a wide range of pathogens may be possible in future, with the help of bioactive compounds synthesised by endophytic actinomycetes [53]. In addition to their biocontrol actions, endophytic bacteria also have favourable impacts on abiotic stress.

13.5 Induced Systemic Resistance (ISR)

Plants' natural defences are boosted by endophytic bacteria, making them more resilient to disease. "Induced systematic resistance" (ISR) describes this phenomenon [54]. Endophytic microbes colonise plants by escaping defence responses, as seen in *Bacillus* and *Pseudomonas* [45]. ISR can be activated by several bacterial agents, including salicylic acid, antibiotics, siderophores, N-acyl-homoserine lactones, jasmonic acid, volatiles (such acetoin), and lipopolysaccharides [55]. ISR was associated with the development of defences and immunity against herbivorous insects and diseases. Many types of endophytic bacteria have had their ISR triggered by salicylic acid, but it is also known that the plant hormones ethylene (ET) and jasmonic acid (JA) play crucial regulatory roles in the signalling pathways involved in ISR induction [56]. ISR induction by the endophytic bacterium *Pseudomonas fluorescens* 89B-61 protects cucumbers from the disease anthracnose [45]. Changes in the native endophytic population were associated with improved plant resistance to *Pectobacterium atrosepticum* when the endophytic bacterium *Methylobacterium* sp. IMBG290 was present in potato soil. Correlations between changes in the endophytic community and resistance to disease show the crucial role this population plays in preventing illness [57]. Endophytic fungi have been involved in defence mechanisms via ISR induction to a lesser degree than endophytic bacteria [58]. The ability of endophytic fungi to create metabolites has been linked to both herbivore control and disease prevention. There are numerous different types of metabolites, including alkaloids, steroids, terpenoids, peptides, polyketones, flavonoids, chlorinated compounds, phenols, and quinols [59, 60]. Fungal endophytes cause localised illness in their hosts but have been connected to the discovery of compounds with antibacterial, antiviral, insecticidal, and antifungal activities due to their horizontal spread [61].

13.6 Abiotic Stress Alleviation by Microbial Endophytes

Different extreme situations, such as environmental pressures and strains induced by living communities, limit plant growth and development.

Plants are able to withstand abiotic stress in two ways: (i) by immediately activating response systems after being stressed [62] and (ii) by generating biochemical compounds that act as antistress agents, which are then metabolised by endophytes [40]. Both up- and down regulation of several stress-inducible genes were reduced in pepper plants after inoculation with the endophyte *Arthrobacter* sp. and *Bacillus* sp. Cucumber plants exposed to salt chloride and dehydration stress benefited greatly from inoculation with *Phoma glomerata* and *Penicillium* sp., as measured by increased nutrient absorption (particularly magnesium, potassium, and calcium), increased plant biomass, and enhanced growth metrics, as well as decreased sodium toxicity [63]. Bailey et al. [64] concluded that *Trichoderma* sp. isolated from *Theobroma cacao* improved the cocoa plant's tolerance to abiotic stress, particularly drought, via modifying gene expression.

Plants grown from *Kalmia latifolia* L. tissue cultures were found to be more resilient to drought when inoculated with the endophytic fungus *Streptomyces padanus* AOK-30, according to research by Hasegawa et al. [65]. Under drought stress, sugars and amino acids were shown to be considerably higher in endophyte-colonised plants compared to non-colonised plants [66]. Due to a complex symbiotic interaction, plants with a drought-tolerant phenotype are able to produce more sugar and amino acids, both of which are signs of higher osmolytic activity [67]. Plants that have been colonised by endophytes are more tolerant to environmental challenges such low water availability, high temperatures, and high salt concentrations [7]. A boost in antioxidant activity, as discovered by Chugh et al. [68], was determined to be the cause of accelerated seedling development in response to dryness.

There was also evidence that endophyte colonisation under low-water conditions led to increases in biomass, proline concentrations, and relative water content [69, 70].

13.7 Drought Stress

As an abiotic stressor, drought is particularly detrimental to plant development and output. Due to root water restriction or excessive transpiration, plants experience drought [71]. Most plant species, especially those adapted to temperate climes, experience diurnal water stress during the middle of the day, even when soil moisture levels are within normal range. Growth is stunted due to the temporary drought stress [72]. Drought causes an increase in reactive oxygen species generation, lower germination rates, and membrane disruption [73]. The principal causes of osmotic stress in plants were, in addition, prolonged periods of dryness and high salinity. Cells are affected by osmotic stress, which dryness causes; ionic or ion-toxicity signs appear in high salinity [48]. The effects of drought stress, such as stunted growth and leaf senescence in the shoot system, are counteracted by osmotic stress, induced by salinity [74].

Plants with symbiotic relationships (like rice, tomatoes, dune grass, and panic grass) produce greater biomass with less water.

Endophyte-associated plants may be more resistant to drought because they accumulate more solutes in their tissues than noninfected plants. This could be the result of a slower transpiration rate, a thicker cuticle layer, or reduced leaf conductivity [75]. Changes in a plant's structure, genetic make-up, and metabolic processes may all contribute to its resilience in the face of water stress. Yet, in response to water scarcity, plants primarily increase ABA production and/or decrease ABA breakdown [76]. It is often believed that ABA acts as a signal in drought-stricken plants, primarily regulating transpiration and stomatal closure to decrease water loss [77]. Some evidence also suggests that ABA helps plants develop more extensive root systems, which improves their capacity to take in water [78].

Full scan mass spectrometry was used to isolate ABA from *Azospirillum brasilense* Sp 245 cells that had been grown at a heightened rate due to chemical stimulation. Increased amounts of ABA were seen in *Azospirillum brasilense* Sp 245-infected *Arabidopsis thaliana* seedlings, and the addition of sodium chloride to the growth medium increased the rate of bacterial ABA synthesis [79].

13.8 Salinity Stress

Soil salinisation, caused by the build-up of water-soluble salts, is a problem for farmers all over the world and endangers ecosystem vitality, food supplies, and economic development. Initially, salt has a chilling effect on the distribution and metabolism of soil microorganisms and other creatures that make their home in the soil. It first reduces crop yields and then, in its later phases, completely wipes out the local flora, turning once-productive land into a barren wasteland [80, 81]. Soil is regarded to be saline if its electrical conductivity (EC) in the root zone is greater than 4 dS m^{-1} at 25 ^{0}Celsius and an exchangeable sodium concentration of 15% (almost 40 mMNaCl). Most plant yields are diminished by this degree of salinity. In the world, high salinity affects 20% of all crop land and 33% of irrigated agriculture [82]. By 2050, half of the world's arable land would be affected by salinity, according to a 2017 assessment of the literature by Machado, Rui M.A., and Serralheiro, Ricardo P. They also found that salt accumulation degrade 10 million ha of agriculture land every year. This harm can be hastened by aggressive groundwater use, a rise in the use of low-quality water in agriculture, and climate change.

13.9 Effect of Soil Salinity on Plants

The production of agricultural crops, especially vegetable crops, which have a low tolerance sensitivity to soil saline, is drastically reduced due to soil salinity (Table 13.1). In general, Compared to field crops, vegetable crops offer a better yield per acre under irrigated conditions. Vegetable crops needed higher total water application rates and more frequent irrigation than other agronomic crops. Despite the need for more fertilisers and irrigation, vegetable crop production still takes place in dry and semi-arid regions where rainfall is scarce and temperatures are high. It's common knowledge that vegetables are an excellent source of many different vitamins and minerals, as well as dietary fibre. Salty soil possess a challenges for plants as it hinders their metabolic function, making it difficult for them to thrive. Effects on reproductive development, such as the lengthening of stamen filaments,

Table 13.1 Soil salinity (ECe) tolerance in different crops

Rating group	Crop/Vegetable	Tolerance based on	Soil threshold (dSm^{-1}) ECe	Reference
Tolerant	Barley	Grain Yield	8.0	Maas and Grattan [83]
Tolerant	Canola/Rape seed	Seed yield	9.7	Francois [84, 85]
Tolerant	Cotton	Seed cotton yield	7.7	Maas and Grattan [83]
Tolerant	Rye	Grain yield	11.4	Maas and Grattan [83]
Moderately tolerant	Sorghum	Grain yield	6.8	Maas and Grattan [83]
Moderately tolerant	Wheat	Grain yield	6.0	Maas and Grattan [83]
Moderately tolerant	Sunflower	Seed yield	4.8	Francois [86]
Moderately tolerant	Red beet	Storage root	4.0	Machado and Serralheiro [87]
Moderately sensitive	Onion seed	Seed yield	1.0	Mangal et al. [88]
Moderately sensitive	Eggplant	Fruit yield	1.1	Machado and Serralheiro [87]
Moderately sensitive	Garlic	Bulb yield	3.9	Francois [84, 85]
Moderately sensitive	Potato	Tuber yield	1.7	Machado and Serralheiro [87]
Sensitive	Mung been	Seed yield	1.8	Minhas [89]
Sensitive	Onion bulb	Bulb yield	1.2	Maas and Grattan [83]
Sensitive	Rice	Gran Yield	3.0	Venkateswarlu et al. [90]
Sensitive	Spinach	Top fresh weight	2.0	Machado and Serralheiro [87]

ECe—electrical conductivity (EC) of saturated paste extract of soil the suppression of microsporogenesis, the aborting of ovules, the senescence of fertilised embryos, and the enhancement of cell death in different tissues, can be mediated by high concentrations of K^+, which in turn affect mitosis and meiosis of nucleic acid. When K^+ is replaced by Na^+ in these processes, soil salinity causes ion toxicity. Protein conformational changes are also produced by Cl^- and Na^+. Loss of turgor, cellular dehydration, and cell death can all result from the osmotic stress caused by high soil salt levels. Metabolic imbalance, brought on by osmotic stress and ion toxicity, results in oxidative stress. As salts are also nutrients for plants, too much salt in the soil can disrupt the plant's nutritional balance or prevent it from absorbing key minerals (nitrogen, phosphorus, potassium, iron, and zinc). Salinity decreases photosynthesis by lowering photosystem II capability, chlorophyll content, leaf area, and stomatal conductance in photosynthesis.

Growth is stunted as a result of the high salinity [91]. In addition, cyclin-dependent kinase activity is decreased because of the post translational inhibition that occurs during periods of high salt [92].

13.10 Salinity Stress Alleviation by Microbial Endophytes

Over 20% of farmable soil is at risk from salt right now, and experts predict that by 2050, half of all prime farmland will be under salinity stress. Plant-associated microorganisms use a wide variety of metabolic and genetic methods to better adapt to abiotic and biotic stress. Endophytic bacteria not only react to root-secreted signal molecules but also produce their own signalling molecules, all of which have positive impacts on plant health, such as enhanced root growth, resistance or tolerance to biotic and abiotic challenges, and general plant health [9]. Endophytic fungi *Yarrowia lipolytica* controlled the production of proline in salt stressed maize plant [93]. In another study, Abdelaziz et al. [94] observed that endophytic fungi *Piriformospora indica* caused considerable reduction in shoot proline content in *Solanum lycopersicum* under salinity stress. *Piriformospora indica* also responsible for significant increase in shoot proline in *Trichoderma harzianum* salt stressed plant [95].

13.11 Primary Benefits of Endophytes in Reducing the Negative Effects of Salinity on Plants

13.11.1 Plant Antioxidant Status

Numerous organisms in the microbial world exhibit comparable responses to oxidative stress. That ROS production in plants is mediated by endophytic fungus which was discovered by Hamilton and colleagues in 2012 [96]. Previous research has established a connection between the suppression of antioxidant enzymes and salt tolerance in plants [97]. There are many enzymes in the body that can neutralise reactive oxygen species, including superoxide dismutases (SOD), glutathione reductases (GR), dehydroascorbate reductases (DHAR), catalases (CAT), ascorbate or thiol-dependent peroxidases (APX), and mono-dehydroascorbate reductases (MDHAR) [98]. APX, SOD, and CAT are all direct or indirect participants in the detoxification of reactive oxygen species (ROS). In a 500 mmol NaCl solution, the nonsymbiotic plant *Leymus mollis* (dune grass) shrivels, dries out within in 7 days, and dies after 14 days [99]. After being exposed to 500 mmol NaCl, *Fusarium culmorum*-infected plants became active for 14 days. Barley's salt tolerance is improved by the endophyte *Piriformospora indica ulmus*, which also increases the grain's antioxidant levels [100].

13.11.2 ACC Deaminase

ACC deaminase, produced by endophytic bacteria, is essential to plant growth and stress tolerance but useless to the bacteria [101]. ACC deaminase breaks ACC (1-aminocyclopropane-1-carboxylate) into 2-oxobutanoate and ammonia, lowering ethylene levels and blocking plant ethylene signalling [102]. Ethylene's fundamental involvement in bacterial colonisation of plant tissues affects seed germination and plant responses to various stresses [103].

Over production of ethylene in plants as a response to stress can be harmful to their health and growth [104]. The ACC deaminase enzyme does more than just help plants deal with stress; it also encourages the colonisation of the plant by microorganisms known as endophytes. Silencing the ACC deaminase gene in *Burkholderia phytofirmans* PsJN may prevent a bacterial infection that causes canola seedlings to fail to develop strong roots [105]. Branch invasion by endophytic bacteria has been observed in prior investigations of cut flowers and blocking ACC deaminase helped keep flowers from getting old too quickly [106].

13.11.3 Phytohormone Production

Endophytes produce auxins, most notably indole-3-acetic acid (IAA) that can significantly increase plant growth [107]. Auxins, which counteract the effects of ethylene, are crucial for root growth and development. Endophytic regulation of auxin production in halophytic plants, thus, has the potential to be an important technique for granting salt resistance. There were two groups of bacteria that were found to produce IAA: (i) salinity-tolerant rhizobacteria (*Halomonas* sp., *Arthrobacter* sp., *Pseudomonas mendocina*, *Bacillus pumilus*, and *Nitrinicolalacis aponensis*) and (ii) microorganisms such as *Serratia*, *Bacillus*, *Vibrio*, *Brevundimonas*, and *Oceanobacillus* [108–110]. There were ABA, gibberellins, and IAA generated by the halophytic *Prosopis strombulifera* [111]. Plants produce more of the growth hormone abscisic acid (ABA) when they are under stress.

ABA is primarily responsible for regulating water balance and osmotic stress tolerance in plants [112]. Wheat plants that were grown in salty soil benefited from the presence of IAA-producing rhizobacteria [108]. It is unknown if mycorrhizal or endophytic root fungus get salt tolerance from phytohormones [113].

13.11.4 Nitrogen Fixation

Endophytes help their host plants in many ways, including by preventing disease, creating beneficial hormones, increasing the availability of nutrients, and fixing nitrogen. These mechanisms also contribute to endophytes' buffering effect when the host plant is exposed to unfavourable ecological conditions [113]. Nitrogen could be fixed by a wide range of root endophytes (e.g., *Azoarcus* spp., *Acetobacter diazotrophicus*, and *Herbaspirillum* spp.). Host plant fitness is increased through nitrogen fixation, especially in low-nitrogen conditions. In cases when only a little amount of fixed nitrogen is found in a single species, it is important to determine if this nitrogen is meant to meet the needs of the microbes in the soil or those of the host plants. Poplar trees' endophytic bacteria *Paenibacillus* P22 contributed to the host plant's total nitrogen pool and triggered metabolic shifts [114].

13.11.5 Compatible Solutes

Osmotic pressure results from the accumulation of Na^+ and Cl^- ions in the vacuole of a plant cell. To counteract this force, organelles and the cytoplasm must collect (even at high concentrations) organic solutes that are metabolically compatible. Most commonly found sugars, amino acids, and amino acids are glycine betaine, proline, and proline [115].

Increased salt tolerance in plants colonised by endophytes has been examined, and proline amino acid has been of particular interest because it has been hypothesised that organic solute accumulation is a critical mechanism for halophytic plants to offset osmotic pressure [116]. Proline accumulation appears to be an outcome rather than a cause of salt tolerance, despite contradictory findings about the role of mycorrhizal fungus [117].

Betaines and carbohydrates can also control osmosis. Elevated sugar and betaine levels in mycorrhizal plants have been linked to a potential involvement in salt tolerance [118]. *Pseudomonas pseudoalcaligenes* is an endophyte that increased rice's salt tolerance by encouraging the formation of glycine betaine-like molecules [119].

13.11.6 Temperature Stress

High temperatures have a lethal effect on plants because they cause the proteins inside the cells to get denaturised and agglomerate, ultimately killing the plants. Metabolism slows down as a result of low temperatures because of their effect on enzyme activity, macromolecule interactions, protein structure alterations, and modulation of membrane characteristics [120].

Extreme heat is rarely reported, despite its negative effects, which are frequently linked to a lack of water. The bacterium *Burkholderia phytofirmans* increases cold hardiness in plants [121]. Due to *Curvularia protuberata* and its thermal endurance mycovirus *Curvularia* (CThTV), the grass *Dichanthelium lanuginosum* was able to live in Yellowstone National Park, where soil temperatures ranged from 38 °C to 65 °C [122].

Wheat's endurance to high temperatures has been improved by the presence of fungal endophytes, which has led to higher crop yields and improved germination rates in following generations [123].

Endophyte composition may be affected by a variety of environmental factors, including but not limited to temperature, humidity, and latitude. Lower annual precipitation and higher latitudes favour *Paenibacillus* strains in sweet root (*Osmorhiza depauperata*) endophytes, while greater annual precipitation and lower latitudes favour *Sinorhizobium meliloti* and *Agrobacterium tumefaciens* [124].

Ascorbate and glutathione are oxidised to reduced forms, and lipid peroxidation is reduced in endophyte-colonised plants, which makes them more resistant to temperature and salt stress, as found by Matsouri et al. [125]. By increasing its resistance to cold, endophytes increase a plant's chance of survival. Accumulated phenolic compounds, proline, and starch are downregulated, and cellular damage and photosynthetic activity are elevated in response to cold stress.

Endophytes have a protective effect on wheat development during drought stress due to their positive effect on metabolic balance [70].

13.11.7 Heavy Metal Stress

Heavy metal toxicity is a major abiotic stressor that is responsible for the loss of anywhere from 25% to 80% of many types of farmed crops. Because of toxicity from manganese and aluminium and a lack of potassium, magnesium, phosphorus, and calcium in acidic soils, agricultural output and soil fertility are negatively affected [126]. Exposure to heavy metals significantly slows a plant's root system and is also toxic to plant tissue [126]. Heavy metal toxicity in acidic soils is problematic because it interferes with several vital physiological and biochemical processes, such as nutrition intake, protein and nitrogen metabolism, photosynthesis, and respiration [127].

It is well known that the availability of cations to plants is affected by the immobilisation and mobilisation of metal cations by bacterial endophytes [128]. Higher activity of the antioxidant enzymes was found in Cd-stressed soil when the dark septate endophyte (DSE) *Exophiala pisciphila* was combined with the root of Zea mays [129]. In 2016, Wang et al. DSE-inoculated plants subjected to high amounts of Cd showed upregulation of genes related in Cd detoxification, transport, and absorption, while ZIP was downregulated. Plant ethylene levels are affected by heavy metal tolerance, and *Gigaspora* and *Pseudomonas* can directly affect ethylene levels by varying the amount of 1-aminocyclopropane-1-carboxylate (ACC) [130].

13.11.8 Nutrient Stress

For growth, development, and reproduction, plants need mineral nutrients, light, water, and carbon. Examples of abiotic conditions that can cause damage to plants include hunger and nutrient deficits [131].

Endophytes provide their hosts with both micro and macronutrients.

Amino acids can be synthesised by plants, thanks to nitrogen-fixing bacteria that can metabolise plant root exudates. Growth-promoting gibberellins (GAs), phosphate solubilisation, cytokinins, indole-3-acetic acid (IAA), and siderophore synthesis, as well as important vitamins, are all produced by endophytes and used by the host plant [119]. The solubilisation of phosphate in wheat and rice was found to be enhanced by gibberellic acid generated by *Pseudomonas* sp., according to research by Choi et al. [132]. Zinc uptake in wheat plants can be improved using either *Azotobacter chroococcum* or *Piriformospora indica* [133].

Endophytes have been shown to aid in the biological breakdown of dead host plants. Endophytes colonise plants at first and then they actively work against saprophytic bacteria, speeding up the degradation of plant matter [134–138]). Another study showed that all endophytes can break down lignin, cellulose, and hemicelluloses, which help nutrient cycling [17].

13.12 Role of Microbial Metabolites in Stress Mitigation of Plants

When plants are attacked by the different microbial species belonging to different microbiomes, i.e. rhizosphere microbiome, epiphytic microbiome, endophytic microbiome, seed microbiome, core microbiome, etc., they show differential responses which alter their resistance mechanism against the stresses prevailing. Interaction of microbial metabolites to the plant system leads to the synthesis of different important secondary metabolites, e.g. phenolics, alkaloids, steroids, and flavonoids which are positively correlated with stress resistance in plants [137]. Generally, it is observed that microbe induced production of secondary metabolites that helps in abiotic stress mitigation [138]. Reactive oxygen species level was found to be reduced in crop plants like wheat, soy bean, and peanut due to the activity of metabolites released from different strains of *Pseudomonas* spp. reported by Shaik et al. [139], Kang et al. [140], and Sharma et al. [141]. In another study, by Ghosh and co-workers [142] also observed amelioration of osmotic stresses in *Arabidopsis thaliana* by exopolysaccharides released from *Bacillus* spp., whereas Liu et al. [143], Balsanelli et al. [144], and Mahmood et al. [145] found mitigation of salt stress by IAA, SmR1, and exopolysaccharides released from *Klebsiella oxytoca* Rs-5, *Herbaspirillum seropedicae*, and *Enterobacter cloacae* P6, respectively. Adjustment in production of metabolites for the sake of adaptation to the changing environment is also observed [146], in addition to the enhancement in uptake of plant nutrients, and the formation of soil humus [147]. However, it is also reported by Burkhead et al. [148], Haas and Defago [149], and Sankari et al. [150] that biotic stress can be mitigated by microbial species. The adverse impact of stem rot of chickpea, foot rot of tomato, early blight of tomato, head blight of wheat, and black scurf of potato were observed to be minimised by phenylpropanoid, harzianic acid, siderophores, bacillomycin D, and surfactin by Sathya et al. [151], Manganiello et al. [152], Verma et al. [153], Gu et al. [154], and Kong et al. [155], respectively. Some microbial metabolites which are useful in plant stress mitigation are given in Table 13.2.

Table 13.2 Metabolites from different endophytes

S. No.	Microbe	Metabolite	Stress	Reference
1	*Azospirillum* spp.	IAA/IBA	Inhibition of uptake of nutrients like nitrogen and phosphorus	Malhotra and Srivastava [156]
2	*Pseudomonas putida*	Pyoverdine	Fusarium wilt	Hass and Defago [149]
3	*Pseudomonas fluorescence*	Proline	Salinity stress in *Vicia faba*	Metwali et al. [157]
4	*Bacillus subtilis*	Surfactin	Damping off of cole crops	Kong et al. [155]
5	*Trichoderma koningii*	Koninginin C	Take all disease of wheat	Vinale et al. [158]
6	*Azospirillum brasilense*	Cadaverine	Osmotic stress in rice	Cassan et al. [159]
7	*Pseudomonas aeruginosa*	Glycine betaine	Drought stress in *Vigna radiata*	Sarma et al. [160]
8	*Rhizopus arrhizus*	Raphorin	Fe deficiency in solanaceous crops	Shenker et al. [161]
9	*Streptomyces acidiscabies*	Coelichelin	Nickel stress in *Vigna unguiculata*	Sathya et al. [151]
10	*Azotobacter chroococcum*	Exopolysaccharide	Environmental stress in *Vicia faba*	El-Ghany and Attia [162]
11	*Sphingomonas* sp.	Gibberellic acid	Salinity stress in Tomato	Halo et al. [163]
12	*Streptomyces platensis*	Phenylethyl alcohol	Seedling blight of rice	Wan et al. [164]
13	*Bradyrhizobium* sp.	Nitrogenase	Water stress in Cowpea	Fugyeuredi et al. [165]

13.13 Conclusions

Considering the role of microbes, it can be possible to make a holistic approach which can mitigate the different types of stress in association with other mechanism of mitigation, i.e. avoidance and escape mechanism, genotypic tolerance mechanism, etc. Ultimately, these mechanisms will result in a sustainable and eco-friendly mitigation of the prevailing stress and also make possible the adaptation of crop plants to the changing environment. However, this approach is emerging as a revolution in sustainable development, and it still requires thorough study of mechanism of release and action of the secondary metabolite and the signalling crosstalk in plant-microbiome interactions to make it more effective and reliable. The focus should also be given to understand the genetic controls on plant secondary metabolites and their adjustment according to the changing microbiomes and environmental conditions.

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