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ENDOPHYTE-MEDIATED MODULATION OF CROP RESPONSES TO ABIOTIC STRESS : A REVIEW

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ABSTRACT

Crop productivity is severely constrained by abiotic stress factors such as heat, salinity, drought, flood, and heavy metal toxicity. The increasing frequency and intensity of these stresses with increasing climatic variability further threaten crop performance by disrupting water relations, nutrient acquisition, cellular metabolism, redox balance, and reproductive processes. This necessitates the development of sustainable methods for enhancing crop resilience to abiotic stress. Plant-associated microbial communities influence plant adaptation and resilience by shaping host responses to environmental challenges. Among these, endophytes have attracted attention because of their intimate association with host plants and their multifaceted roles in promoting plant growth and stress tolerance. These include modulation of phytohormone balance, enhancement of antioxidant defense and redox homeostasis, accumulation of osmoprotectants, improved nutrient and water acquisition, and activation of stress-responsive signaling. Endophytic microorganisms can also contribute to induced systemic tolerance, heavy metal detoxification and improved plant health through interactions within the plant–endophyte–pathogen continuum. This review examines the diversity and transmission of endophytes and synthesizes current understanding of their physiological, biochemical, and molecular mechanisms in improving crop tolerance to major abiotic stresses. It further discusses their ecological and functional interactions with host plants and emerging applications as microbial biostimulants and components of sustainable crop production systems. Collectively, these developments position endophytes as promising biological tools for strengthening crop resilience under increasingly variable environmental conditions.

Key words : Plant–microbe interactions, Climate resilience, Antioxidant defense, induced systemic tolerance, Microbial biostimulants.

Introduction

Abiotic stresses such as drought, salinity, extreme temperatures, flooding, and soil contamination constitute major constraints to global crop productivity and agricultural sustainability. These stressors disrupt plant physiological and metabolic processes, resulting in substantial yield losses in major food crops, particularly under rain-fed and coastal agroecosystems (Kopecká *et al.*, 2023). Ongoing climate change has intensified both the frequency and severity of abiotic stresses, further threatening food security and farmer livelihoods, especially in climate-vulnerable regions of the tropics and subtropics (Zhang *et al.*, 2021).

Plants possess inherent adaptive mechanisms to cope with environmental stress, including stomatal regulation, osmotic adjustment, antioxidant defense, and stress-responsive gene expression. However, these intrinsic responses are often insufficient under prolonged or combined stress conditions, leading to impaired growth, reproductive failure, and yield instability (Munns and Tester, 2008; Zhang *et al.*, 2023). Conventional approaches such as breeding stress-tolerant cultivars and improving agronomic practices have provided partial solutions but are frequently time-consuming, resource-intensive, and stress-specific, limiting their effectiveness

under rapidly changing climatic scenarios (Zhang *et al.*, 2021).

In recent years, plant-associated beneficial microorganisms, especially bacterial and fungal endophytes that colonize internal plant tissues without causing disease symptoms have gained increasing attention as next-generation plant bio-stimulants. Endophytes contribute to plant stress tolerance by modulating phytohormone levels, enhancing antioxidant capacity, improving nutrient and water uptake, and regulating stress-induced ethylene accumulation (Bhupenchandra *et al.*, 2025; Ameen *et al.*, 2024). Unlike conventional inputs, endophytes often confer multi-stress tolerance and function synergistically with host metabolic and signaling pathways, making them particularly attractive for sustainable agriculture.

Several studies demonstrate that endophytic microorganisms such as *Bacillus*, *Pseudomonas*, *Trichoderma*, and *Serendipita*(*Piriformospora*) *indica* can significantly improve plant performance under drought, salinity, heat, and flooding stress in diverse crop species (Kamran *et al.*, 2022). Advances in molecular biology and omics technologies have further revealed that endophytes influence host gene expression, redox signaling, and stress memory, emphasizing their role in priming plants for enhanced tolerance to recurring environmental stresses (Pandey *et al.*, 2023).

Despite these advances, the translation of endophyte-based solutions into field-level applications remains limited. Variability in host endophyte compatibility, inconsistent performance under complex field conditions, and challenges related to formulation, delivery, and regulatory approval constrain large-scale adoption (Busby *et al.*, 2017; Sena *et al.*, 2024). Moreover, most of existing studies focus on single-stress conditions, leaving significant gaps in understanding how endophytes function under combined and fluctuating stresses typical of real agricultural systems. This review synthesizes current knowledge on endophyte-mediated abiotic stress tolerance in crops, with emphasis on physiological, biochemical, and molecular mechanisms of action. It further examines recent advances in endophyte application technologies, including bio-stimulant formulations and nano technological approaches, and highlights critical research gaps and future directions for developing endophyte-based strategies in climate-resilient agriculture.

Abiotic stresses limiting crop productivity

Abiotic stresses which arise from non-living factors often occur unpredictably, persist for extended periods,

and act in combination, thereby intensifying their negative effects on plant growth and yield stability. The major abiotic stresses affecting crops include drought, salinity, temperature extremes, flooding or waterlogging, heavy metal toxicity, and excess light (He *et al.*, 2018).

Drought is the most pervasive abiotic stress and primarily results from inadequate soil moisture availability. It disrupts plant-water relations by reducing cellular turgor, inducing stomatal closure, and limiting carbon assimilation, ultimately impairing biomass accumulation and reproductive development (Farooq *et al.*, 2009). Prolonged drought stress leads to reduced leaf area, restricted root growth, premature senescence, and substantial yield losses, particularly in rain-fed cropping systems (Kopecká *et al.*, 2023).

Salinity stress predominantly affects irrigated and coastal agricultural lands, where excessive accumulation of soluble salts imposes both osmotic stress and ion toxicity. Elevated concentrations of sodium (Na⁺) and chloride (Cl⁻) ions disrupt nutrient homeostasis, impair photosynthetic processes, and induce oxidative stress, resulting in suppressed growth and reduced productivity (Munns and Tester, 2008). Unsustainable irrigation practices and climate-driven seawater intrusion intensify this problem.

Temperature extremes, including both heat and cold stress, significantly alter plant metabolic processes. Heat stress destabilizes cellular membranes, denatures proteins, and enhances the generation of reactive oxygen species, thereby impairing photosynthesis and reproductive success, especially during flowering and grain filling (Bita and Gerats, 2013; Mahajan *et al.*, 2025). In contrast, cold stress impairs enzyme activity, alters membrane fluidity, and induces cellular dehydration, thus arresting growth and development in temperature-sensitive crops (Theocharis *et al.*, 2012).

Flooding and waterlogging result from excessive rainfall or inadequate drainage and create hypoxic or anoxic conditions in the root zone. Oxygen deficiency restricts root respiration and nutrient uptake, causing chlorosis, leaf epinasty, and root necrosis, which collectively reduce plant growth and yield (Aldana *et al.*, 2014). Such stresses are increasingly prevalent in low-lying and deltaic regions due to changing precipitation patterns.

Heavy metal toxicity arises from the accumulation of elements such as cadmium, lead, arsenic, and mercury in agricultural soils, often due to industrial activities and intensive agrochemical use. These metals interfere with enzymatic functions, disrupt nutrient uptake, and trigger

oxidative damage, ultimately constraining crop growth and productivity (Sharma *et al.*, 2012). Excess light, particularly under high irradiance conditions, induces photo-oxidative stress when absorbed energy exceeds photosynthetic capacity, leading to chloroplast damage and reduced photosynthetic efficiency, especially when combined with drought or heat stress (Foyer and Noctor, 2005).

Agronomic and economic impacts of abiotic stress

Abiotic stresses exert profound agronomic and economic consequences by reducing crop yield, compromising produce quality, and destabilizing farming livelihoods and food systems. It is estimated that abiotic stresses collectively account for more than 50% of potential yield losses in major food crops worldwide, with drought exerting the greatest impact, followed by salinity and temperature extremes (Kopecká *et al.*, 2023).

Yield losses due to drought generally range from 30–70%, depending on crop species, developmental stage, and stress duration, particularly in rain-fed systems (Farooq *et al.*, 2009; Kopecká *et al.*, 2023). Salinity stress typically reduces yields by 20–30% through osmotic constraints and ionic toxicity, while heat stress can cause 15–40% yield penalties when high temperatures coincide with flowering or grain filling (Munns and Tester, 2008; Bitá and Gerats, 2013). Flooding and waterlogging can result in complete crop failure under prolonged submergence, especially in poorly drained soils (Aldana *et al.*, 2014).

Beyond quantitative losses, abiotic stresses substantially deteriorate crop quality. Heat and drought stress during reproductive stages reduce grain filling, starch accumulation, and protein composition in cereals, leading to lower grain density, increased chalkiness, and reduced milling quality (Zhang *et al.*, 2021). Salinity and heavy metal stress alter nutrient composition and can increase the accumulation of toxic elements in edible plant parts, compromising food safety and market value (Sharma *et al.*, 2012).

The cumulative impact of yield and quality losses directly affects farmer livelihoods and food security, particularly for smallholder farmers who lack access to irrigation, insurance, or adaptive technologies. Reduced and unstable production increases income volatility, heightens vulnerability to poverty, and contributes to price fluctuations in regional and global markets (Kopecká *et al.*, 2023). In developing economies, repeated abiotic stress events exacerbate rural distress and undermine long-term agricultural sustainability, reinforcing the

urgency for resilient and low-input stress mitigation strategies.

Plant responses to abiotic stress: physiological, biochemical and molecular basis

Plants are continuously exposed to fluctuating environmental conditions and have evolved complex adaptive mechanisms to perceive and respond to abiotic stresses. These responses operate at multiple levels—physiological, biochemical, and molecular—to maintain cellular homeostasis and ensure survival under adverse conditions (Figure 1). However, prolonged or severe stress often overwhelms these protective systems, leading to metabolic disruption, growth inhibition and yield loss.

Physiological responses

Abiotic stresses primarily disrupt core physiological processes that govern plant growth and productivity. Photosynthesis is one of the earliest and most sensitive targets. Drought, salinity, heat, and excess light impair photosystem stability, reduce chlorophyll content, and inhibit the activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), thereby limiting carbon assimilation and biomass accumulation (Muhammad *et al.*, 2021; Li *et al.*, 2024).

Stomatal conductance is tightly regulated under stress to minimize water loss. Drought and salinity induce stomatal closure, largely mediated by abscisic acid (ABA), which restricts CO₂ uptake and further suppresses photosynthesis (Farooq *et al.*, 2009). Under flooding conditions, impaired root function similarly triggers stomatal closure, resulting in physiological drought despite abundant soil moisture content (Aldana *et al.*, 2014).

Altered water relations are central to stress-induced growth inhibition. Reduced soil water potential or impaired root uptake decreases relative water content, leading to cellular dehydration, loss of turgor, and restricted cell expansion (Kopecká *et al.*, 2023). Nutrient uptake is also disrupted as drought limits mass flow and diffusion, salinity interferes with ion homeostasis, and waterlogging restricts root respiration and nutrient transport. These nutrient imbalances further weaken plant metabolic capacity and productivity (Munns and Tester, 2008).

Biochemical responses

Abiotic stress conditions provoke pronounced biochemical adjustments, many of which are linked to oxidative stress. Disruption of cellular metabolism under drought, salinity, temperature extremes, or heavy metal exposure leads to excessive production of reactive oxygen species (ROS) such as superoxide radicals, hydrogen peroxide, and hydroxyl radicals (Sharma *et al.*, 2012).

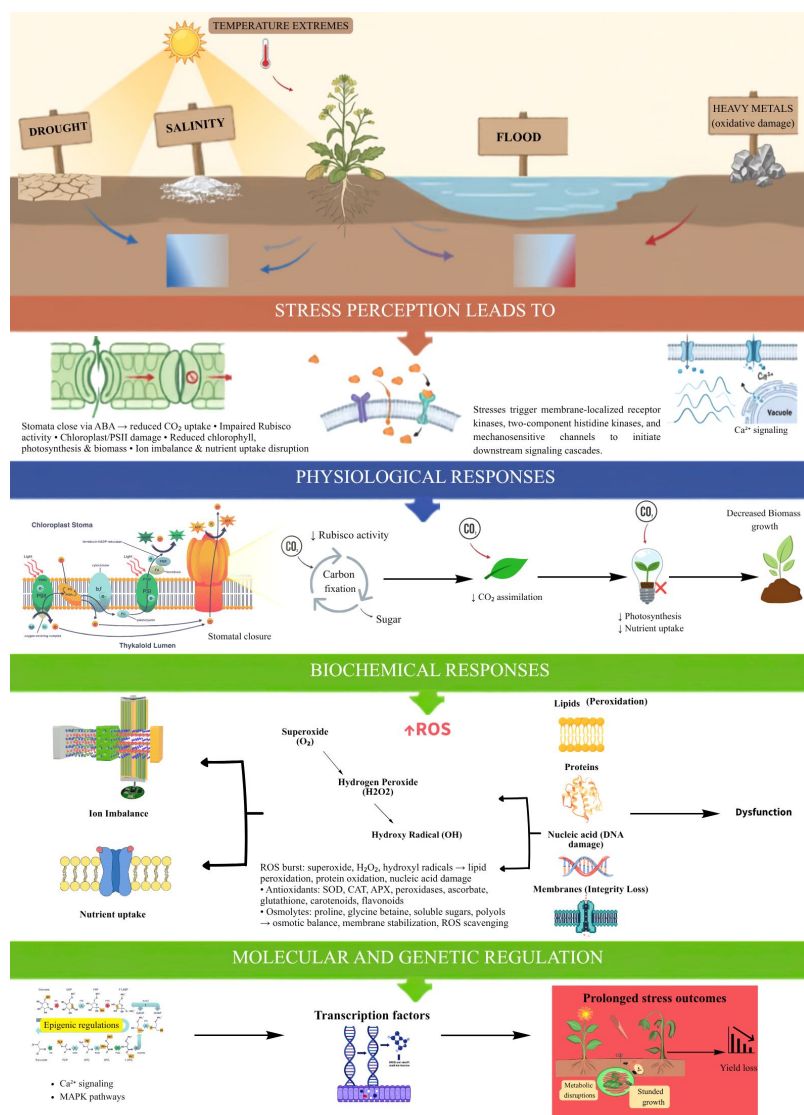


Fig. 1 : A comprehensive overview of plant responses to the fluctuating environmental conditions.

While ROS function as signaling molecules at low concentrations, their overaccumulation damages lipids, proteins, nucleic acids, and cellular membranes.

To counteract oxidative damage, plants activate antioxidant defense systems comprising enzymatic and non-enzymatic components. Major antioxidant enzymes are superoxide dismutase, catalase, ascorbate peroxidase, and peroxidases while non-enzymatic antioxidants include ascorbate, glutathione, carotenoids, and flavonoids (Foyer and Noctor, 2005). Stress-tolerant genotypes typically exhibit more effective antioxidant responses, reinforcing the importance of redox homeostasis in stress adaptation.

Another key biochemical response to stress is the accumulation of osmolytes, including proline, glycine betaine, soluble sugars, and polyols. These compatible solutes stabilize proteins and membranes, maintain cellular

osmotic balance, and scavenge ROS under stress conditions (Zhang *et al.*, 2021). Osmolyte accumulation is strongly correlated with improved drought and salinity tolerance, particularly during prolonged stress exposure.

Molecular and genetic regulation

At the molecular level, abiotic stress perception initiates complex signaling cascades that reprogram gene expression and metabolic pathways. Stress signals activate stress-responsive genes encoding transcription factors, molecular chaperones, osmoprotectant biosynthesis enzymes, and antioxidant proteins, enabling plants to adapt to hostile environments (Zhang, 2023).

Key signaling pathways include mitogen-activated protein kinase (MAPK) cascades, which transmit extracellular stress signals to the nucleus, and transcriptional regulators such as DREB/CBF (dehydration-responsive element-binding/C-repeat binding factors) that control the expression of drought-, salinity-, and cold-responsive genes (Zhu, 2016; Zhang *et al.*, 2021). ABA signaling plays a central role in coordinating stomatal regulation, stress gene expression, and metabolic adjustment, often integrating with MAPK and calcium signaling networks.

Recent evidence also highlights the role of epigenetic regulation and stress priming in plant adaptation. DNA methylation, histone modifications, and chromatin remodeling influence the expression of stress-responsive genes and can confer a form of stress memory, enabling faster and stronger responses upon subsequent stress exposure (Pandey *et al.*, 2023). These mechanisms are particularly relevant under recurring or combined abiotic stresses common in agricultural environments.

Endophytic microorganisms: diversity, ecology and plant colonization

Endophytes are defined as microorganisms, primarily bacteria and fungi, that colonize internal plant tissues for at least part of their life cycle without causing visible disease symptoms (Petrini, 1991; Hardoim *et al.*, 2015). Early studies initially viewed internal plant colonization as indicative of latent pathogenicity; however, advances in microscopy, culturing, and molecular techniques have demonstrated that many endophytes confer neutral or beneficial effects on host fitness. The modern concept of endophytes emphasizes their ecological roles in nutrient

acquisition, stress tolerance, and modulation of host physiological and molecular processes rather than mere asymptomatic colonization (Hardoim *et al.*, 2015; Bhupenchandra *et al.*, 2025). Their ecological significance lies in their ability to persist within internal plant tissues while establishing functionally beneficial, non-pathogenic associations with their hosts. Understanding the diversity, colonization strategies, and host specificity of endophytes is essential for harnessing their potential as bio-stimulants in agriculture.

Diversity of endophytic microorganisms

Endophytic communities are taxonomically diverse and encompass a broad range of microorganisms adapted to distinct plant niches and environmental conditions.

Bacterial endophytes are the most extensively studied group and are dominated by genera such as *Bacillus*, *Pseudomonas*, *Enterobacter*, *Azospirillum*, and *Burkholderia*. These bacteria frequently exhibit traits associated with plant growth promotion, including phytohormone production, nutrient solubilization, and stress ethylene regulation, enabling them to function as key mediators of abiotic stress tolerance (Kandel *et al.*, 2017; Compant *et al.*, 2019).

Fungal endophytes include both root- and shoot-associated taxa, with notable genera such as *Serendipita* (*Piriformospora*), *Trichoderma*, *Fusarium*, *Chaetomium*, and *Cladosporium*. Many fungal endophytes establish long-term associations with host plants and influence root development, nutrient uptake, and systemic stress responses (Ajit *et al.*, 1999; Lata *et al.*, 2018).

Actinomycetes, particularly members of the genus *Streptomyces*, constitute a distinct group of filamentous bacterial endophytes with high metabolic versatility. These organisms produce a wide array of secondary metabolites, including antibiotics and antioxidants, and contribute to plant stress tolerance and pathogen suppression. Although less studied than bacterial and fungal endophytes, actinomycetes are increasingly recognized for their ecological and biotechnological significance (Golinska *et al.*, 2015).

Colonization routes and host specificity

Endophytic colonization is a dynamic, multistep process governed by microbial traits, host physiology, and environmental factors. Entry mechanisms include penetration through root hairs, lateral root emergence zones, stomata, hydathodes, and wounds, with roots serving as the primary gateway for most endophytic microorganisms (Hardoim *et al.*, 2015). Successful colonization often requires microbial motility, biofilm

formation, secretion of cell wall modifying enzymes, and evasion or modulation of host immune responses (Kandel *et al.*, 2017).

Endophytic fungi are transmitted through both vertical and horizontal routes. Vertical transmission, primarily via seeds, can facilitate persistence across plant generations. In wheat, Salamon *et al.* (2025) identified 27 fungal OTUs shared between parental and progeny plants under controlled sterile conditions, suggesting potential intergenerational transmission. Horizontal transmission involves recruitment from external sources such as soil, air, rain, and insects, followed by colonization through wounds, natural openings, or direct penetration. Experimental inoculation of axenic wheat seedlings demonstrated cultivar-dependent recolonization by selected *Fusarium*, *Penicillium*, and *Trichoderma* taxa, highlighting the importance of host fungus compatibility in endophytic establishment.

Once inside the plant, endophytes display marked tissue specificity, colonizing roots, stems, leaves, seeds, or vascular tissues depending on microbial identity and host compatibility. Root tissues generally harbor the highest diversity and density of endophytes due to continuous interaction with the soil microbiome, whereas aerial tissues often support more specialized communities (Compant *et al.*, 2019).

Endophyte-host compatibility is a critical determinant of functional outcomes. Colonization success and persistence depend on genetic compatibility, host developmental stage, and environmental context. Compatible endophytes integrate into host signaling networks without triggering strong defense responses, enabling stable mutualistic interactions. Conversely, incompatible associations may result in transient colonization or activation of plant immune pathways that restrict microbial establishment (Hardoim *et al.*, 2015; Bhupenchandra *et al.*, 2025). This specificity underscores the importance of host adapted strain selection for effective endophyte-based applications in agriculture.

Mechanisms of endophyte-mediated abiotic stress tolerance

Endophytes enhance plant tolerance to abiotic stress through a coordinated set of physiological, biochemical, and molecular mechanisms that modulate host metabolism and signaling pathways (Table 1). Rather than acting through a single trait, endophytes function as integrated bio-stimulants, enabling plants to maintain growth and homeostasis under adverse environmental conditions.

Phytohormone modulation

One of the most extensively documented mechanisms

of endophyte-mediated stress tolerance is the modulation of plant phytohormone balance. Many bacterial and fungal endophytes synthesize or regulate indole-3-acetic acid (IAA), which promotes root elongation, lateral root formation, and root hair development, thereby enhancing water and nutrient acquisition under drought and salinity stress (Spaepen *et al.*, 2007; Ameen *et al.*, 2024).

Endophytes also influence abscisic acid (ABA) signaling, a central regulator of abiotic stress responses. Certain endophytes modulate ABA accumulation or sensitivity, contributing to optimized stomatal regulation and improved water-use efficiency during drought stress without excessive growth inhibition (Tsai *et al.*, 2020). In addition, endophyte-derived cytokinins delay stress-induced senescence and maintain photosynthetic capacity, while gibberellins support cell elongation and recovery growth following stress exposure (Kandel *et al.*, 2017). Through this hormonal fine-tuning, endophytes balance stress defence with sustained growth.

Abiotic stress often induces excessive ethylene production, which inhibits root elongation and accelerates senescence. Many endophytic bacteria produce 1-aminocyclopropane-1-carboxylate (ACC) deaminase, an enzyme that degrades ACC, the immediate precursor of ethylene (Glick, 2014). By lowering stress-induced ethylene levels, ACC deaminase-producing endophytes alleviate growth inhibition and maintain root development under drought, salinity, and flooding stress. This mechanism is particularly important during early growth stages, where ethylene sensitivity strongly influences plant establishment and survival (Naing *et al.*, 2021).

Regulation of oxidative stress

Abiotic stresses commonly induce overproduction of reactive oxygen species (ROS), leading to oxidative damage of membranes, proteins, and nucleic acids. Endophytes play a critical role in maintaining ROS homeostasis by enhancing host antioxidant capacity. Numerous studies report increased activities of superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and peroxidases in endophyte-colonized plants under drought, salinity, and temperature stress (Kamran *et al.*, 2022).

In addition to enzymatic antioxidants, endophytes stimulate the accumulation of non-enzymatic antioxidants such as ascorbate, glutathione, phenolics, and flavonoids, further buffering oxidative stress (Jasim *et al.*, 2016). This enhanced antioxidant network limits lipid peroxidation and preserves cellular integrity, enabling plants to tolerate prolonged stress conditions more effectively.

Osmolyte accumulation and cellular homeostasis

Osmotic stress induced by drought and salinity disrupts cellular water balance and turgor maintenance. Endophyte association promotes the accumulation of compatible solutes, including proline, glycine betaine, soluble sugars, and polyols, which stabilize proteins and membranes and protect cellular structures (Rani *et al.*, 2022).

Root endophytes such as *S. indica* have been shown to significantly enhance proline and sugar accumulation in host plants, improving osmotic adjustment and stress resilience under water-limited conditions (Baltruschat *et al.*, 2008; Mani *et al.*, 2023). These metabolites also function as ROS scavengers and signaling molecules, linking osmoprotection with redox regulation.

Improved nutrient and water acquisition

Endophytes improve plant performance under stress by enhancing nutrient availability and water uptake. Several bacterial endophytes possess nitrogen-fixing capabilities, supplying bioavailable nitrogen to plants under nutrient-limited or stress-affected soils (Doty *et al.*, 2016).

Endophytes also influence root system architecture and regulate the expression of aquaporin genes, thereby increasing root hydraulic conductivity and water-use efficiency. For example, *S. indica* colonization has been associated with upregulation of aquaporins, resulting in improved water transport and drought tolerance (Jogawat *et al.*, 2013). Collectively, these effects enable plants to sustain nutrient and water uptake under suboptimal conditions.

Endophyte-induced systemic tolerance

Beyond immediate physiological effects, endophytes induce systemic tolerance and stress priming, enabling plants to respond more rapidly and robustly to subsequent stress events. Primed plants exhibit enhanced baseline expression of stress-responsive genes, elevated antioxidant capacity, and improved metabolic readiness even before stress onset (Pandey *et al.*, 2023).

This priming effect often confers cross-tolerance to multiple abiotic stresses, reflecting the integration of hormonal, redox, and transcriptional regulation. Endophyte-mediated priming is increasingly recognized as a key mechanism underpinning durable stress resilience in fluctuating field environments.

Endophyte–host–stress interaction networks

Plant responses to abiotic stress are governed by

Table 1 : Major mechanisms of endophyte-mediated abiotic stress tolerance in plants.

Mechanism	Functional outcome	References
Phytohormone modulation	Root growth, stomatal regulation, delayed senescence	Spaepen <i>et al.</i> (2007), Tsai <i>et al.</i> (2020)
Antioxidant activation	ROS detoxification, membrane protection	Kamran <i>et al.</i> (2022)
Osmolyte accumulation	Osmotic balance, protein stabilization	Baltruschat <i>et al.</i> (2008), Rani <i>et al.</i> (2022)
Nutrient & water uptake	Improved N and P availability, hydraulic conductivity	Doty <i>et al.</i> (2016), Jogawat <i>et al.</i> (2013)
ACC deaminase activity	Reduced stress ethylene, sustained root growth	Glick (2014), Naing <i>et al.</i> (2021)
Systemic priming	Faster and stronger stress responses	Pandey <i>et al.</i> (2023)

interconnected physiological and molecular pathways rather than isolated mechanisms. Endophytes operate within this networked system by simultaneously influencing multiple stress-response processes, thereby improving the plant's ability to cope with adverse environmental conditions.

An important feature of endophyte-mediated stress tolerance is the crosstalk between major stress signaling pathways. Abiotic stress responses share common regulatory components, including reactive oxygen species (ROS), calcium signaling, mitogen-activated protein kinase (MAPK) cascades, and phytohormones such as abscisic acid (ABA) and ethylene. Endophytes modulate these shared signaling nodes by regulating ROS levels, adjusting hormone balance, and influencing stress-responsive gene expression, which helps maintain cellular homeostasis without excessive growth inhibition (Pandey *et al.*, 2023).

This coordinated regulation enables multi-stress tolerance, an important advantage of endophyte-assisted plants. In field conditions, crops are often exposed to overlapping stresses such as drought combined with heat or salinity. Endophyte-colonized plants frequently show improved performance under such combined stresses through common protective mechanisms, including strengthened antioxidant systems, better osmotic regulation, and stabilized photosynthesis (Zandalinas *et al.*, 2018). These overlapping responses allow plants to respond efficiently to multiple stresses using shared defence pathways.

From a systems-level perspective, endophytes act as modulators of plant stress readiness rather than direct stress protectants. Endophyte association can subtly enhance baseline defence capacity and metabolic flexibility, enabling faster and more effective responses when stress occurs. This phenomenon underlies stress priming and contributes to cross-tolerance across different abiotic stresses (Busby *et al.*, 2017). The outcome of

these interactions depends on host genotype, microbial strain, and environmental context, emphasizing the importance of compatible endophyte–host combinations.

Emerging applications of endophytes

The multifunctional traits of endophytes have positioned them as promising tools across agriculture, environmental management, and biotechnology. Advances in formulation technologies, microbial ecology, and systems biology have accelerated the transition of endophytes from experimental systems toward practical applications.

Endophytes as biostimulants in sustainable agriculture

Endophytes are increasingly explored as biological stimulants to enhance crop growth, nutrient efficiency, and stress resilience while reducing reliance on synthetic agrochemicals. Unlike conventional fertilizers or pesticides, endophytes function by improving intrinsic plant physiological capacity through hormonal regulation, improved root architecture, antioxidant enhancement, and stress priming (Bhupenchandra *et al.*, 2025).

Several commercial and pre-commercial microbial products already incorporate endophytic bacteria and fungi such as *Bacillus*, *Pseudomonas*, *Trichoderma*, and *Serendipita indica*. These biostimulants have demonstrated benefits under drought, salinity, and nutrient-limited conditions, particularly in cereals, legumes, and horticultural crops (Kamran *et al.*, 2022). Importantly, endophyte-based biostimulants often provide multi-stress benefits, making them well suited for climate-resilient and low-input farming systems.

However, field-level consistency remains a challenge due to host specificity, environmental variability, and formulation stability. Current research therefore emphasizes strain selection, host compatibility testing, and improved delivery methods such as seed coating and root

inoculation to enhance agronomic reliability (Busby *et al.*, 2017).

Endophyte-mediated nanotechnology in crop stress management

A recent and rapidly expanding application area is the use of endophytes in green synthesis of nanoparticles. Endophytic microorganisms can reduce metal ions to form nanoparticles using their enzymes and secondary metabolites, offering an eco-friendly alternative to chemical synthesis routes (Choudhary *et al.*, 2023).

Endophyte-derived nanoparticles such as silver, zinc oxide, and iron oxide have shown potential to enhance nutrient delivery, improve stress tolerance, and suppress plant pathogens at low concentrations. When combined with endophyte inoculation, these nano-formulations can synergistically enhance antioxidant activity, nutrient uptake, and stress resilience in crops under drought and salinity conditions (Farooq *et al.*, 2009).

Despite promising experimental results, endophyte-mediated nanotechnology is still in an early developmental stage. Key challenges include dosage optimization, long-term environmental safety, and regulatory acceptance. As such, its application should be viewed as a complementary strategy rather than a standalone solution in sustainable agriculture.

Industrial, environmental and biomedical applications

Beyond agriculture, endophytes possess considerable industrial and environmental relevance due to their metabolic diversity. Many endophytic microorganisms produce enzymes, antibiotics, and secondary metabolites with applications in bioremediation, pharmaceuticals, and biotechnology (Kusari *et al.*, 2012).

Endophytes have demonstrated the ability to degrade environmental pollutants, immobilize heavy metals, and assist phytoremediation processes in contaminated soils. Their capacity to survive within plant tissues allows them to function effectively under harsh environmental conditions where free-living microbes often fail (Shahzad *et al.*, 2017).

In the biomedical domain, endophytes are recognized as reservoirs of bioactive compounds like alkaloids, terpenes, and steroids with antimicrobial, antioxidant, anti-inflammatory, and anticancer properties. Several endophyte-derived metabolites structurally resemble known therapeutic compounds, highlighting their potential for drug discovery (Strobel and Daisy, 2003). While large-scale commercialization remains limited, ongoing advances in microbial fermentation and metabolomics are

accelerating translational research in this area.

Challenges and limitations in the adoption of endophyte-based technologies

Despite the growing evidence supporting the role of endophytes in enhancing abiotic stress tolerance, several challenges limit their large-scale adoption and consistent performance in agricultural systems. Addressing these constraints is essential for translating experimental success into reliable field-level applications.

One of the primary limitations is field inconsistency. While many endophytes demonstrate strong stress-mitigating effects under controlled or greenhouse conditions, their performance often declines or becomes variable under open-field environments. Factors such as soil physicochemical properties, native microbial communities, climatic variability, and agricultural practices strongly influence endophyte survival, colonization efficiency, and functional expression (Busby *et al.*, 2017; Compant *et al.*, 2019). This context dependency remains a major barrier to predictable agronomic outcomes.

Host specificity further constrains endophyte deployment. Many endophytes exhibit host or genotype-specific interactions, where strains effective in one crop or cultivar may fail to colonize or confer benefits in another. This specificity is governed by plant immune responses, root exudate composition, and developmental stage, making universal or “one-size-fits-all” inoculants unrealistic (Hardoim *et al.*, 2015). Consequently, successful application often requires careful matching of endophyte strains to target crops and environments. Even in a suitable host, changes in environmental conditions and nutrient status can tilt the beneficial association towards pathogenicity. For example, light conditions and nitrogen content have been reported to change the colonization strategies and host responses of fungal endophytes (Kumar and Nautiyal, 2026).

Another significant challenge lies in formulation, delivery, and shelf life. Endophytes must remain viable, stable, and effective during storage, transport, and application. Many microbial inoculants suffer from reduced viability over time, sensitivity to temperature and moisture, and inconsistent colonization following application. Developing robust carrier materials, protective formulations, and efficient delivery methods such as seed coating or encapsulation remains an active area of research (Bashan *et al.*, 2014). Without reliable formulation strategies, commercialization and farmer adoption remain limited.

Finally, biosafety and regulatory concerns present

important hurdles. Although endophytes are generally regarded as safe due to their natural association with plants, the introduction of non-native or genetically modified strains raises concerns regarding ecological balance, horizontal gene transfer, and unintended effects on native microbiota. Regulatory frameworks for microbial bio-stimulants vary widely across countries and are often less developed than those for chemical inputs, creating uncertainty for product approval and commercialization (Compant *et al.*, 2019). Rigorous risk assessment, transparent regulatory guidelines, and long-term environmental monitoring are therefore essential.

Collectively, these challenges highlight that while endophyte-based technologies hold strong promise, their successful integration into sustainable agriculture will depend on improved strain selection, formulation technologies, multi-location field validation, and supportive regulatory frameworks.

Future perspectives and research directions

The successful integration of endophytes into sustainable agriculture will depend on advancing beyond single-strain inoculation approaches toward system-oriented, technology-enabled solutions. Future research must prioritize scalability, predictability, and alignment with climate-resilient agricultural policies.

Microbiome engineering and synthetic consortia

Natural plant microbiomes function as complex communities rather than isolated microorganisms. Accordingly, future endophyte-based strategies are shifting toward synthetic microbial consortia that combine complementary functional traits such as hormone modulation, nutrient mobilization, antioxidant enhancement, and stress priming. Rationally designed consortia offer greater functional stability and resilience across variable field conditions compared to single-strain inoculants (Busby *et al.*, 2017).

Advances in microbiome ecology and community assembly theory are enabling targeted selection of compatible endophytes with reduced functional redundancy and improved persistence within host plants. However, understanding inter-microbial interactions and host-mediated selection remains essential to ensure consistent performance under multi-stress environments.

Smart delivery systems and nano-formulations

Effective field application of endophytic microorganisms depends on reliable delivery systems that maintain microbial viability, facilitate their establishment

in the plant environment, and ensure consistent expression of beneficial functions under field conditions. Conventional inoculant formulations include liquid, granular, powder and carrier-based systems, while more advanced approaches involve seed coating and encapsulation technologies designed to improve microbial survival, application uniformity and persistence after inoculation (Bashan *et al.*, 2014).

Seed coating represents a promising strategy for the precise delivery of beneficial microorganisms to the seed and emerging root environment. Appropriate coating materials can improve microbial adherence to seeds and protect inoculants from environmental stresses during storage and establishment. Recent research has demonstrated the potential of microbial seed coating for improving plant growth and tolerance to both biotic and abiotic stresses (Paravar *et al.*, 2023).

Encapsulation provides another promising approach in which microbial cells are incorporated within protective matrices such as alginate, chitosan and other biopolymers. Such systems can help protect microorganisms from adverse environmental conditions and facilitate their gradual or controlled release following application. The integration of nano polymers with microbial formulations has further expanded the potential for nano-biofertilizer and nano-enabled inoculant development, although their performance depends on microbial compatibility, release characteristics, environmental safety, scalability and regulatory considerations (Thirumurugan *et al.*, 2024).

Nano-enabled delivery systems may additionally improve the stability and functionality of microbial inoculants and may facilitate the co-delivery of nutrients or other biologically active components. However, the application of nanomaterials in plant–microbe systems remain an emerging area, and potential effects on microbial communities, plants and the surrounding environment require careful evaluation. Therefore, integrating advanced delivery technologies with microbial ecology, plant–microbe interactions and field environmental conditions will be essential for developing reliable and reproducible endophyte-based formulations for agricultural applications.

Climate-smart agriculture and policy integration

Endophyte-based technologies align strongly with the principles of climate-smart agriculture, offering low-input solutions that enhance productivity, resilience, and resource-use efficiency. However, their broader adoption will depend on supportive policy frameworks, harmonized regulatory guidelines, and farmer-oriented extension

services.

Future efforts must emphasize multi-location field validation, cost-benefit analysis, and clear communication of application protocols to stakeholders. Collaboration among scientists, policymakers, industry, and farmers will be essential to translate endophyte research into scalable, climate-resilient agricultural practices.

Conclusion

Abiotic stresses remain a major constraint to global crop productivity and are intensifying under climate change, underscoring the urgent need for sustainable and resilient agricultural solutions. Endophytes have emerged as powerful biological allies capable of enhancing plant tolerance to environmental stress through coordinated modulation of physiological, biochemical and molecular processes. By influencing hormone balance, redox homeostasis, nutrient and water acquisition and stress priming, endophytes enable plants to maintain growth and productivity under adverse conditions.

Advances in microbiome science, omics technologies, and formulation strategies have significantly expanded the translational potential of endophyte-based bio-stimulants. However, realizing this potential will require addressing challenges related to host specificity, field consistency, formulation stability and regulatory frameworks. Future progress will depend on rational strain selection, synthetic microbial consortia, robust multi-location field validation and integration with climate-smart agricultural practices.

Overall, endophyte-mediated approaches represent a promising, low-input pathway for enhancing crop resilience and sustainability. Strategic integration of endophytes into modern agricultural systems has the potential to contribute meaningfully to food security, environmental protection, and climate-resilient crop production.

References

- Aldana, F., García P.N. and Fischer G. (2014). Effect of waterlogging stress on the growth, development and symptomatology of cape gooseberry (*Physalis peruviana* L.) plants. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, **38(149)**, pp.393-400. <https://doi.org/10.18257/raccefyn.114>
- Ameen, M., Mahmood A., Sahkoo A., Zia M.A. and Ullah M.S. (2024). The role of endophytes to combat abiotic stress in plants. *Plant Stress*, **12**, 100435. <https://doi.org/10.1016/j.stress.2024.100435>
- Baltruschat, H., Fodor J., Harrach B.D., Niemczyk E., Barna B., Gullner G., Janeczko A., Kogel K.H., Schäfer P., Schwarczinger I. and Zuccaro A. (2008). Salt tolerance of barley induced by the root endophyte *Piriformospora indica* is associated with a strong increase in antioxidants. *New Phytologist*, **180(2)**, 501-510. <https://doi.org/10.1111/j.1469-8137.2008.02583.x>
- Bashan, Y., de-Bashan L.E., Prabhu S.R. and Hernandez J.P. (2014). Advances in plant growth-promoting bacterial inoculant technology: formulations and practical perspectives (1998–2013). *Plant and Soil*, **378(1)**, 1-33. <https://doi.org/10.1007/s11104-013-1956-x>
- Bhupenanchandra, I., Chongtham S.K., Devi A.G., Dutta P., Sahoo M.R., Mohanty S., Kumar S., Choudhary A.K., Devi E.L., Sinyorita S. and Devi S.H. (2025). Unlocking the potential of arbuscular mycorrhizal fungi: exploring role in plant growth promotion, nutrient uptake mechanisms, biotic stress alleviation and sustaining agricultural production systems. *J. Plant Growth Regul.*, **44(12)**, 6802-6840. <https://doi.org/10.1007/s00344-024-11467-9>
- Bitá, C.E. and Gerats T. (2013). Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. *Front. Plant Sci.*, **4**, 273. <https://doi.org/10.3389/fpls.2013.00273>
- Busby, P.E., Soman C., Wagner M.R., Friesen M.L., Kremer J., Bennett A., Morsy M., Eisen J.A., Leach J.E. and Dangel J.L. (2017). Research priorities for harnessing plant microbiomes in sustainable agriculture. *PLoS Biol.*, **15(3)**, e2001793. <https://doi.org/10.1371/journal.pbio.2001793>
- Choudhary, N., Dhingra N., Gacem A., Yadav V.K., Verma R.K., Choudhary M., Bhardwaj U., Chundawat R.S., Alqahtani M.S., Gaur R.K. and Eltayeb L.B. (2023). Towards further understanding the applications of endophytes: enriched source of bioactive compounds and bio factories for nanoparticles. *Front. Plant Sci.*, **14**, 1193573. <https://doi.org/10.3389/fpls.2023.1193573>
- Compant, S., Samad A., Faist H. and Sessitsch A. (2019). A review on the plant microbiome: ecology, functions and emerging trends in microbial application. *J. Adv. Res.*, **19**, 29-37. <https://doi.org/10.1016/j.jare.2019.03.004>
- Doty, S.L., Sher A.W., Fleck N.D., Khorasani M., Bumgarner R.E., Khan Z., Ko A.W., Kim S.H. and DeLuca T.H. (2016). Variable nitrogen fixation in wild *Populus*. *PLoS One*, **11(5)**, e0155979. <https://doi.org/10.1371/journal.pone.0155979>
- Farooq, M., Wahid A., Kobayashi N.S.M.A., Fujita D.B.S.M.A. and Basra S.M. (2009). Plant drought stress: effects, mechanisms and management. *Agron. Sust. Develop.*, **29(1)**, 185-212. <https://doi.org/10.1051/agro:2008021>
- Foyer, C.H. and Noctor G. (2005). Oxidant and antioxidant signalling in plants: a re evaluation of the concept of oxidative stress in a physiological context. *Plant, Cell Environ.*, **28(8)**, 1056-1071. <https://doi.org/10.1111/j.1365-3040.2005.01327.x>
- Glick, B.R. (2014). Bacteria with ACC deaminase can promote plant growth and help to feed the world. *Microbiological Research*, **169(1)**, 30-39. <https://doi.org/10.1016/>

[j.micres.2013.09.009](https://doi.org/10.1186/1745-0718-10-009)

- Golinska, P., Wypij M., Agarkar G., Rathod D., Dahm H. and Rai M. (2015). Endophytic actinobacteria of medicinal plants: Diversity and bioactivity. *Antonie Van Leeuwenhoek*, **108**(2), 267-289. <https://doi.org/10.1007/s10482-015-0502-7>
- Hardoim, P.R., Van Overbeek L.S., Berg G., Pirttilä A.M., Compant S., Campisano A., Döring M. and Sessitsch A. (2015). The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. *Microbiol. Mole. Biol. Rev.*, **79**(3), 293-320. <https://doi.org/10.1128/MMBR.00050-14>
- He, M., He C.Q. and Ding N.Z. (2018). Abiotic stresses: general defenses of land plants and chances for engineering multistress tolerance. *Front. Plant Sci.*, **9**, 1771. <https://doi.org/10.3389/fpls.2018.01771>
- Jasim, B., Mathew J. and Radhakrishnan E.K. (2016). Identification of a novel endophytic *Bacillus* sp. from *Capsicum annuum* with highly efficient and broadspectrum plant probiotic effect. *J. Appl. Microbiol.*, **121**(4), 1079-1094. <https://doi.org/10.1111/jam.13214>
- Jogawat, A., Saha S., Bakshi M., Dayaman V., Kumar M., Dua M., Varma A., Oelmüller R., Tuteja N. and Johri A.K. (2013). *Piriformospora indica* rescues growth diminution of rice seedlings during high salt stress. *Plant Signaling & Behavior*, **8**(10), e26891. <https://doi.org/10.4161/psb.26891>
- Kamran, M., Imran Q.M., Ahmed M.B., Falak N., Khatoon A. and Yun B.W. (2022). Endophyte-mediated stress tolerance in plants: a sustainable strategy to enhance resilience and assist crop improvement. *Cells*, **11**(20), 3292. <https://doi.org/10.3390/cells11203292>
- Kandel, S.L., Joubert P.M. and Doty S.L. (2017). Bacterial endophyte colonization and distribution within plants. *Microorganisms*, **5**(4), 77. <https://doi.org/10.3390/microorganisms5040077>
- Kopecká, R., Kameniarová M., Ěerný M., Brzobohatý B. and Novák J. (2023). Abiotic stress in crop production. *Int. J. Mole. Sci.*, **24**(7), 6603. <https://doi.org/10.3390/ijms24076603>
- Kumar, V. and Nautiyal C.S. (2026). From hidden allies to precision symbionts: unleashing endophytes for sustainable agroecosystems. *World J. Microbiol. Biotechnol.*, **42**(4), 172. <https://doi.org/10.1007/s11274-026-04896-z>
- Kusari, S., Hertweck C. and Spiteller M. (2012). Chemical ecology of endophytic fungi: origins of secondary metabolites. *Chemistry & Biology*, **19**(7), 792-798. <https://doi.org/10.1016/j.chembiol.2012.06.004>
- Lata, R., Chowdhury S., Gond S.K. and White Jr J.F. (2018). Induction of abiotic stress tolerance in plants by endophytic microbes. *Lett. Appl. Microbiol.*, **66**(4), 268-276. <https://doi.org/10.1111/lam.12855>
- Li, X., Zhang W., Niu D. and Liu X. (2024). Effects of abiotic stress on chlorophyll metabolism. *Plant Science*, **342**, 112030. <https://doi.org/10.1016/j.plantsci.2024.112030>
- Mahajan, S., Thakur P., Das S., Sharma R.P., Manuja S., Jha P.K., Saini A., Sahoo C. and Fayeizadeh M.R. (2025). Impression of contemporary heat stress complexities in agricultural crops: a review. *Plant Growth Regulation*, **105**(6), 1805-1823. <https://doi.org/10.1007/s10725-025-01382-8>
- Mani, K.M., Ameena M., Johnson J.M., Pillai S., John J. and Beena R. (2023). Root endophyte *Piriformospora indica* significantly affects mechanisms involved in mitigating drought stress in rice (*Oryza sativa*). *Indian J. Agron.*, **68**(3), 324-327. <https://doi.org/10.59797/ija.v68i3.2815>
- Muhammad, I., Shalmani A., Ali M., Yang Q.H., Ahmad H. and Li F.B. (2021). Mechanisms regulating the dynamics of photosynthesis under abiotic stresses. *Front. Plant Sci.*, **11**, 615942. <https://doi.org/10.3389/fpls.2020.615942>
- Munns, R. and Tester M. (2008). Mechanisms of salinity tolerance. *Annu. Rev. Plant Biol.*, **59**, 651-681. <https://doi.org/10.1146/annurev.arplant.59.032607.092911>
- Naing, A.H., Maung T.T. and Kim C.K. (2021). The ACC deaminase producing plant growth promoting bacteria: influences of bacterial strains and ACC deaminase activities in plant tolerance to abiotic stress. *Physiologia Plantarum*, **173**(4), 1992-2012. <https://doi.org/10.1111/1751-7915.13963>
- Pandey, P., Tripathi A., Dwivedi S., Lal K. and Jhang T. (2023). Deciphering the mechanisms, hormonal signaling and potential applications of endophytic microbes to mediate stress tolerance in medicinal plants. *Front. Plant Sci.*, **14**, 1250020. <https://doi.org/10.3389/fpls.2023.1250020>
- Paravar, A., Piri R., Balouchi H. and Ma Y. (2023). Microbial seed coating: An attractive tool for sustainable agriculture. *Biotechnol. Rep.*, **37**, e00781. <https://doi.org/10.1016/j.btre.2023.e00781>
- Petrini, O. (1991). Fungal endophytes of tree leaves. In: *Microbial ecology of leaves* (pp. 179-197). New York, NY: Springer New York. https://doi.org/10.1007/978-1-4612-3168-4_9
- Rani, S., Kumar P., Dahiya P., Maheshwari R., Dang A.S. and Suneja P. (2022). Endophytism: a multidimensional approach to plant-prokaryotic microbe interaction. *Front. Microbiol.*, **13**, 861235. <https://doi.org/10.3389/fmicb.2022.861235>
- Salamon, S., Mikołajczak K., Basińska-Barczak A., Banachewicz P. and Błaszczuk L. (2025). Intergenerational and horizontal transmission of wheat endophytic fungi. *Scientific Reports*, **15**(1), 42275. <https://doi.org/10.1038/s41598-025-26280-x>
- Sena, L., Mica E., Valè G., Vaccino P. and Pecchioni N. (2024). Exploring the potential of endophyte-plant interactions for improving crop sustainable yields in a changing climate. *Front. Plant Sci.*, **15**, 1349401. <https://doi.org/10.3389/fpls.2024.1349401>
- Shahzad, R., Khan A.L., Bilal S., Waqas M., Kang S.M. and Lee I.J. (2017). Inoculation of abscisic acid-producing endophytic bacteria enhances salinity stress tolerance in *Oryza sativa*. *Environ. Exp. Bot.*, **136**, 68-77. <https://doi.org/10.1016/j.envexpbot.2017.05.011>

doi.org/10.1016/j.envexpbot.2017.01.010

- Sharma, P., Jha A.B., Dubey R.S. and Pessarakli M. (2012). Reactive oxygen species, oxidative damage and antioxidative defense mechanism in plants under stressful conditions. *J. Bot.*, **2012**(1), 217037. <https://doi.org/10.1155/2012/217037>
- Spaepen, S., Vanderleyden J. and Remans R. (2007). Indole-3-acetic acid in microbial and microorganism-plant signaling. *FEMS Microbiol. Rev.*, **31**(4), 425-448. <https://doi.org/10.1111/j.1574-6976.2007.00072.x>
- Strobel, G. and Daisy B. (2003). Bioprospecting for microbial endophytes and their natural products. *Microbiol. Mole. Biol. Rev.*, **67**(4), 491-502. <https://doi.org/10.1128/MMBR.67.4.491-502.2003>
- Theocharis, A., Clément C. and Barka E.A. (2012). Physiological and molecular changes in plants grown at low temperatures. *Planta*, **235**(6), 1091-1105. <https://doi.org/10.1007/s00425-012-1641-y>
- Thirumurugan, N.K., Velu G., Murugaiyan S., Maduraimuthu D., Ponnuraj S., DJ S. and Subramanian K.S. (2025). Nanobiofertilizers: utilizing nanopolymers as coating matrix—a comprehensive review. *Biofabrication*, **17**(1), 012007. <https://doi.org/10.1088/1758-5090/ad94a8>
- Tsai, H.J., Shao K.H., Chan M.T., Cheng C.P., Yeh K.W., Oelmueller R. and Wang S.J. (2020). *Piriformospora indica* symbiosis improves water stress tolerance of rice through regulating stomata behavior and ROS scavenging systems. *Plant Signaling & Behavior*, **15**(2), 1722447. <https://doi.org/10.1080/15592324.2020.1722447>
- Varma, A., Verma S., Sudha N., Sahay N., Butehorn B. and Franken P. (1999). *Piriformospora indica*, a cultivable plant-growth-promoting root endophyte. *Appl. Environ. Microbiol.*, **65**(6), 2741-2744. <https://doi.org/10.1128/AEM.65.6.2741-2744.1999>
- Zandalinas, S.I., Mittler R., Balfagón D., Arbona V. and Gómez Cadenas A. (2018). Plant adaptations to the combination of drought and high temperatures. *Physiologia Plantarum*, **162**(1), 2-12. <https://doi.org/10.1111/ppl.12540>
- Zhang, X., Wang Z., Jiang C. and Xu J.R. (2021). Regulation of biotic interactions and responses to abiotic stresses by MAP kinase pathways in plant pathogenic fungi. *Stress Biology*, **1**(1), 5. <https://doi.org/10.1007/s44154-021-00004-3>
- Zhang, Y., Xu J., Li R., Ge Y., Li Y. and Li R. (2023). Plants' response to abiotic stress: Mechanisms and strategies. *Int. J. Mole. Sci.*, **24**(13), 10915. <https://doi.org/10.3390/ijms241310915>
- Zhu, J.K. (2016). Abiotic stress signaling and responses in plants. *Cell*, **167**(2), 313-324. <https://doi.org/10.1016/j.cell.2016.08.029>