



Leveraging microorganisms and biostimulants: mitigating salinity stress in crops with agricultural biologicals

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Received: 3 March 2025 / Accepted: 18 May 2025
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Abstract

Background and Aims Soil salinity is an increasing threat to crop production and, as a consequence, improving the level of salinity tolerance has become a priority in plant research. Biologicals, including microorganisms and biostimulants, can play a significant role in enhancing plant tolerance to salinity stress, which is further fueled by soil degradation and climate change.

Methods This review explores the mechanisms by which these agents contribute to salinity tolerance.

Results Microorganisms such as plant growth-promoting rhizobacteria, mycorrhizal or endophytic fungi improve plant resilience by facilitating nutrient uptake, producing phytohormones, and enhancing antioxidant activities. They alter root architecture and exude signals that improve water use efficiency, allowing plants to better manage osmotic stress. Biostimulants, comprising amino acids, humic substances, plant and seaweed extracts, further bolster

Responsible Editor: Christopher Ngosong.

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plant tolerance by regulating ion balance and stimulating metabolic pathways associated with the stress response. Some of these substances enhance photosynthetic efficiency, thus maintaining plant growth and productivity under saline conditions. Collectively, the synergistic interaction of microorganisms and biostimulants cultivates a robust soil-plant interface, providing a sustainable strategy to mitigate the impacts of salinity.

Conclusion Continued research is needed to optimize their application methods and to understand the complex interactions within specific crop and soil systems, enabling agricultural systems to adapt to increasing soil salinity levels.

Keywords Salinity tolerance · Microorganisms · Biostimulants · Plant resilience · Saline agriculture

Introduction

The impact of global warming has intensified environmental stresses, including heat, salinity, and drought (Chele et al. 2021). Soil salinity poses a severe challenge to agriculture because it reduces crop productivity and soil health, particularly in arid and semi-arid regions. The global scope of this problem is highlighted by recent estimates that over 1,125 million hectares of land in more than 100 nations are impacted by salinity (Mannan et al. 2024). Projections suggest that nearly 10% more land undergoes salinization annually, with around 50% of arable land expected to be salt affected by 2050 (Kumar and Sharma 2020).

Traditional methods for managing soil salinity, such as leaching and chemical amendments, are often costly and unsustainable in the long term (Wang et al. 2023). As an alternative, the use of microorganisms and biostimulants offers a promising solution

to mitigate the adverse effects of salinity on plant growth. This approach not only improves yields but also contributes to the sustainability of agricultural practices by reducing reliance on synthetic chemicals and fertilizers (Kumar et al. 2019). Microorganisms, such as plant growth-promoting rhizobacteria (PGPR) and mycorrhizal or endophytic fungi, establish symbiotic relationships with plant roots, enhance nutrient uptake and promote plant health (Brokate et al. 2024). These microorganisms can induce systemic tolerance to saline stress by producing phytohormones, solubilizing essential nutrients, and enhancing the plant's antioxidant defense systems (Brokate et al. 2024). Biostimulants include a diverse range of natural substances such as amino acids, humic acids, and plant and seaweed extracts that can promote plant growth and development (Bhat et al. 2020). The strategic use of microorganisms and biostimulants can enhance plant resilience and productivity on salt-affected fields without requiring significant adjustments to farm management practices for specific crop species.

In this review, we aim to delve into the practical application of these biological solutions, assessing their effectiveness and scalability in various agroecosystems. We will discuss recent advances in research that elucidate the mechanisms of action in the application of microorganisms and biostimulants, providing insights into how these biologicals can be integrated into current farming practices.

The challenge of salinization

One of the biggest current challenges in global agriculture is the salinization of arable land as well as coastal regions worldwide, that are increasingly threatened by rising soil and water salinity (Hossain and Li 2024). The effects of salinization in organisms are characterized by osmotic stress and ion toxicity (Acosta-Motos et al. 2017; Munns and Tester 2008). These arise from soluble salts moving to the soil surface during evaporation, leading to salt accumulation at the surface and in the root zone (Epstein et al. 1980). Salinity can result from natural processes or anthropogenic activities, such as poor irrigation practices, excessive fertilizer use, and insufficient drainage systems. In arid regions, the lack of adequate rainfall for leaching exacerbates salt accumulation from irrigation water (Munns 2002). A saline soil is

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typically defined as one where the electrical conductivity (EC) of the saturation extract in the root zone exceeds 4 dS m^{-1} (approximately 40 mM NaCl) at 25°C , with an exchangeable sodium (Na^+) ion percentage of 15% (Acosta-Motos et al. 2017; Shrivastava and Kumar 2015). Most current crops are glycophytes, which exhibit low salt tolerance, with severe growth inhibition occurring at NaCl concentrations of $100\text{--}200 \text{ mM L}^{-1}$.

The temporal and spatial variations in soil salinity can be influenced by several environmental factors, leading to non-uniform salinity patterns in the soil (Xiong et al. 2024). Considerable research has been conducted on the physiological and molecular responses of plants to heterogeneous salinity (Valenzuela et al. 2022), although the interactions between salinity and biotic factors, such as symbiotic relationships and pathogens, remain underexplored. It was reported that organic matter applied to saline soils is beneficial for the diversity of soil microorganisms (Çiçek and Yücedağ 2023). Split-root system seems to be a promising approach for testing and solving the questions of plant response to different abiotic stresses, including non-uniform salinity conditions, and application of a broad range of beneficial biologicals (Kafle et al. 2022; Xiong et al. 2024). As reported by Xiong et al. (2024), the Na^+ content was significantly reduced in *Medicago sativa* under conditions of non-uniform salinity, while the net photosynthetic rate, stomatal conductance and transpiration rate were increased in uniform salinity conditions. Moreover, the shoot dry weight and plant growth rate were higher under non-uniform conditions and both the uniform and non-uniform salinity treatments significantly increased the contents of stress indicators such as hydrogen peroxide (H_2O_2) and malondialdehyde (MDA) in leaves.

At the shoot level, salt stress severely disrupts photosynthesis and water balance. Plants often respond by closing their stomata to reduce water loss, which inadvertently also limits CO_2 uptake, reducing photosynthesis and stunting growth (Ait-El-Mokhtar et al. 2020). Accumulation of high Na^+ and chloride (Cl^-) ions within leaves hinders chlorophyll synthesis, resulting in chlorosis and necrosis. Photosynthetic impairment has also been observed, with degradation of carotenoid and chlorophyll pigments (Hniličková et al. 2017) and reduced photosynthetic pigment biosynthesis leading to impaired photosynthesis and

lower biomass accumulation (Chaves et al. 2009; Ounoki et al. 2021, 2023; Parida and Das 2005; Soti et al. 2023). Furthermore, hormonal dysregulation occurs, as elevated salinity triggers changes in phytohormone levels, such as an increase in abscisic acid (ABA) to regulate stomatal closure (Peleg and Blumwald 2011; Zhang et al. 2016). Metabolic disruptions, including effects on nitrogen (N) assimilation, carbohydrate metabolism, and protein synthesis, have also been documented (Ashraf and Harris 2004; Bose et al. 2014). At the root level, elevated salinity restricts water uptake, causing wilting and loss of turgor pressure in leaves. Excessive Na^+ and Cl^- ions compete with essential nutrients, such as potassium (K^+), calcium (Ca^{2+}), and magnesium (Mg^{2+}) ions, limiting their absorption and disrupting critical metabolic processes (Ben-Laouane et al. 2021). Additionally, alkaline conditions prevalent in saline soil reduce the bioavailability of micronutrients like iron (Fe^{3+}), zinc (Zn^{2+}), copper (Cu^{2+}), and manganese (Mn^{2+}) ions, which can exacerbate developmental disorders in plants.

Limitations of conventional methods to deal with salinity

Conventional breeding has long been employed to enhance crop tolerance to several kinds of stresses, including salinity. However, limited genetic variation, complexity of stress tolerance mechanisms, environmental variability and lack of precision in genetic background have limited the development of more tolerant cultivars (Mastrangelo et al. 2012). Genetic variety is crucial for successful breeding programs, especially for developing salt-tolerant cultivars. Morphological, physiological and biochemical markers have critical roles to evaluate variability under salinity stress (Awaad 2023).

Complex physiological and biochemical processes regulated by numerous genes govern stress tolerance, making it difficult for traditional breeding to successfully select for such polygenic traits. The process is further complicated by the multilevel interactions between different genes and environmental conditions, which frequently lead to only a slight increase in salinity tolerance (Mastrangelo et al. 2012). Additionally, the performance of traits selected through traditional breeding can vary significantly across

different environments. Due to variations in environmental conditions, a cultivar that exhibits stress tolerance in one area may not perform exactly the same in another area, resulting in inconsistent performance under a variety of stress settings (Mastrangelo et al. 2012). Creating new cultivars through traditional breeding is a time-consuming procedure that most of the time takes years or even decades. This prolonged time frame is particularly problematic when addressing urgent agricultural challenges, such as the rapid escalation of soil salinity and climate change impacts. Traditional breeding is progressing slowly, delaying the release of new cultivars and limiting farmers' prompt answers to pressing problems (Mastrangelo et al. 2012). The limitations of conventional methods in creating salt-tolerant cultivars are further highlighted by the time-consuming and occasionally unsatisfactory results of these drawn-out breeding procedures (Pandita 2023).

Biotechnological interventions, such as the development of salt-tolerant crop cultivars through genetic engineering and marker-assisted breeding, have shown promise in enhancing crop productivity in saline soils (Munns et al. 2020; Zhu 2016). For example, Zhang et al. (2022) reported that overexpression of *GhABF3* enhanced drought and salt tolerance in *Arabidopsis thaliana* and cotton by promoting root elongation, reducing leaf wilting and water loss, increasing antioxidant capacity, and upregulating ABA-inducible genes, whereas its silencing increased sensitivity to these stress factors.

Key drivers for soil salinization include improper irrigation, inadequate drainage, over-fertilization and deforestation. To address these challenges, mitigation strategies such as mulching, improved drainage, and crop rotation, along with adaptation measures like cultivating salt-tolerant plants and using bioremediation are advised. The application of organic and inorganic soil amendments can effectively reduce root-zone salinity by binding Na^+ ions. Organic amendments reduce oxidative damage and improve plant growth and yield in saline environments by modifying ionic homeostasis, enhancing photosynthetic efficiency, and bolstering antioxidant defenses (Hoque et al. 2022). Sensitive fruit species, such as apples and cherries, are already affected by low salt concentrations (Maas and Hoffman 1977). However, traditional soil reclamation methods are costly and time intensive.

Emerging strategies, such as the utilization of nanotechnology, have further enhanced the efficiency of soil amendments and nutrient delivery under saline conditions (Kah et al. 2018). Monitoring soil salinity at both local and regional scales is essential for implementing appropriate management strategies. Advancements in remote sensing technologies and geographic information systems (GIS) have facilitated the development of accurate salinity maps, enabling site-specific interventions and real time monitoring (Allbed et al. 2014).

Microorganisms as allies in mitigating salt stress

Recent advances have highlighted the potential of beneficial soil microorganisms, such as plant growth-promoting bacteria (PGPB), including PGPR and endophytic bacteria, in addition to various mycorrhizal fungi, including ectomycorrhizal fungi and arbuscular mycorrhizal fungi (AMF), as well as endophytic fungi, which have emerged as crucial players in enhancing plant resilience to salinity (Acosta-Motos et al. 2020; Etesami and Beattie 2018a). These microorganisms contribute to plant tolerance via multiple mechanisms, including ion homeostasis, osmotic adjustment, hormonal regulation, and antioxidant defense activation (Chaffai et al. 2024; Sagar et al. 2021). Their ability to interact with host plants under saline conditions represents an environmentally sustainable alternative to traditional soil amendments and genetic modifications. Integrating beneficial soil microorganisms, including mycorrhizal fungi, can further enhance nutrient uptake and salt tolerance, providing a comprehensive strategy to improve plant growth and productivity in saline environments (Korkmaz and Çiçek 2024).

The role of plant growth-promoting rhizobacteria (PGPR) in alleviating salt stress

Beneficial microorganisms have been proven as a promising and sustainable approach to alleviate salinity stress (Hafez et al. 2021; Karlidag et al. 2010). Native beneficial microorganisms are crucial for plant nutrient uptake, soil nutrient cycling, and the production of bioactive compounds that stimulate plant growth (Van der Heijden et al. 2008). However, their populations can be depleted in degraded soils or

disrupted by agricultural practices such as intensive tillage (Alfonzetti et al. 2023; Lienhard et al. 2014). Despite these challenges, PGPR have been recognized as a key component of sustainable agriculture, reducing reliance on synthetic fertilizers and pesticides while promoting plant growth and soil health. PGPR include diverse genera such as *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Klebsiella*, *Pseudomonas*, *Serratia*, and *Variovorax*, all of which contribute to plant growth under both normal and stressful conditions (Goswami and Suresh 2020). In particular, halo-tolerant PGPR can survive in saline soils and enhance plant adaptation to high salinity by activating multiple stress-mitigation pathways (Ilyas et al. 2020; Khoshru et al. 2020). Similar to halophytic plants, these bacteria have evolved diverse adaptations to thrive in highly saline environments, with one key strategy being the accumulation of compatible osmolytes to maintain intracellular osmotic balance (Etesami and Beattie 2018b; Sharma et al. 2016). Notably, halo-tolerant bacteria can adapt to a broad range of salinity levels, from 1 to 33% NaCl, and are also capable of growing in NaCl-free environments (Etesami and Beattie 2018a; Larsen 1986). Flemer et al. (2022) demonstrated that the microbiota endosphere of tomato adapted to drought or salinity stress conditions and that, in turn, root microbes isolated from salt-stressed plants had an increased halo-tolerance and were able to promote plant growth under salinity.

PGPR increase plant resilience to salinity stress through several mechanisms. PGPR solubilize essential elements such as N, P, K^+ and Fe^{2+} ions, thereby supporting plant growth under saline conditions (Billah et al. 2019; Kumar et al. 2020). For example, Kural et al. (2024) reported that P-solubilizing rhizobacteria reduced the need for chemical inorganic P in apple (*Malus domestica*) nursery production by 50% under conditions where this element is present in the soil but largely unavailable to plants.

Salinity stress disrupts ion homeostasis in plants by promoting the excessive accumulation of Na^+ and Cl^- ions in plant tissues (Bose et al. 2017), while simultaneously inhibiting the uptake of essential nutrients such as K^+ ions (Mohapatra et al. 2021) and Ca^{2+} ions (Cabanero et al. 2004). These imbalances result in reduced K^+/Na^+ and Ca^{2+}/Na^+ ratios, which adversely affect metabolic functions, impair photosynthesis, and ultimately reduce yield (Ibrahimova et al. 2021;

Paul et al. 2024; Zhang et al. 2024a). PGPR play a critical role in restoring ion balance through several complementary mechanisms. Under salt stress, PGPR inoculation reduces Na^+ and Cl^- accumulation in root tissues, thereby alleviating ion toxicity and preserving cellular integrity (Carreiras et al. 2022; Etesami and Maheshwari 2018; Nadeem et al. 2013). Concurrently, PGPR enhance the uptake and accumulation of K^+ and Ca^{2+} in the leaves, reflecting improved selective ion transport and nutrient delivery to metabolically active tissues (Gao et al. 2022; Pan et al. 2019; Zhang et al. 2024a). These improvements are strongly associated with increased K^+/Na^+ and Ca^{2+}/Na^+ ratios in both roots and shoots, better nutrient status, and enhanced photosynthetic performance, ultimately contributing to improved plant growth and salinity tolerance (Etesami and Maheshwari 2018; Kumar et al. 2020; Pan et al. 2019; Zhang et al. 2024a). PGPR have also been shown to influence the expression of high-affinity K^+ transporters, such as members of the HKT1 family, thereby promoting selective K^+ uptake under saline conditions (Rojas-Tapias et al. 2012). PGPR are associated with improved K^+/Na^+ homeostasis in salt-stressed plants through enhanced ion selectivity (Etesami and Maheshwari 2018; Pan et al. 2019; Paul and Lade 2014). Additionally, PGPR support ion balance indirectly by boosting nutrient acquisition and mitigating oxidative stress effects that can be further strengthened when used in combination with AMF (Zhang et al. 2024a).

Many PGPR facilitate osmotic adaptation by producing osmoprotectants and extracellular polymeric substances (EPS). These compounds, including sucrose, proline and sugar alcohols, stabilize cell membranes, regulate stomatal function and increase water retention (AbuQamar et al. 2024; Kumar et al. 2020; Naseri et al. 2022). In addition, EPS-producing PGPR bind cations such as Na^+ , improve water-holding capacity and promote biofilm formation, which helps plants withstand saline environments (Kumar et al. 2020; Riseh et al. 2021).

PGPR also modulate phytohormone levels by balancing growth-promoting hormones such as indole-3-acetic acid (IAA), gibberellic acid (GA), and cytokinin (CK), while reducing stress-related ABA, thereby optimizing root system development and stress adaptation (Barnawal et al. 2017; Etesami and Maheshwari 2018). Under stress conditions, rhizobacteria adhere to plant surfaces and secrete IAA,

which plays a key role in cell division, elongation, differentiation and phototropic responses (Sivasankari et al. 2011; Zukauskaitė et al. 2023). PGPR that produce 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase degrade ACC, the ethylene precursor, effectively reducing ethylene levels, alleviating stress and promoting root and shoot development (Errickson and Huang 2023; He et al. 2024). This regulation increases root biomass, chlorophyll content, total sugar production and antioxidant enzyme activity, all of which contribute to salinity tolerance (Gupta et al. 2022).

PGPR also play a crucial role in enhancing antioxidant defenses by increasing enzymatic (e.g. catalase [CAT], superoxide dismutase [SOD], peroxidase [POD]) antioxidant activity and non-enzymatic antioxidants (e.g. carotenoids, tocopherols, flavonoids), reducing reactive oxygen species (ROS) accumulation and preventing lipid peroxidation in plants (Kumar et al. 2020; Singh et al. 2022). PGPR significantly increased antioxidant enzymes activities in salt-stressed plants, thereby enhancing oxidative stress defense mechanisms (Slimani et al. 2023; Xie et al. 2024).

Mycorrhizal and endophytic fungi in alleviating salt stress

Arbuscular mycorrhizal fungi (AMF)

The partnership between AMF and the root system of plants has numerous benefits for plant growth and performance (Boorboori and Lackóová 2025; Evelin et al. 2019; Pooja et al. 2024). The symbiosis between naturally occurring and/or artificially inoculated AMF and host plants can facilitate the adaptation of plants to various biotic and abiotic stress conditions, including salinity stress (Baron and Rigobelo 2022; Boorboori and Lackóová 2025; Dastogeer et al. 2020; Evelin et al. 2019; Navarro-Torre et al. 2023; Tang et al. 2024). Under saline conditions, when water sources are often scarce and limited, inoculation of plants with AMF stimulates better uptake of water and nutrients from the soil, especially P, N, Ca^{2+} , and K^{+} ions, both through root modification and the spread of hyphal networks (Delaeter et al. 2024; Evelin et al. 2019; Pan et al. 2020; Porras-Soriano et al. 2009). Meanwhile, the absorption and transport of Na^{+} is greatly reduced, and as a consequence, the ratios of

$\text{K}^{+}/\text{Na}^{+}$ and $\text{Ca}^{2+}/\text{Na}^{+}$ are enhanced to ensure osmotic balance without the accumulation of toxic levels of Na^{+} in host plants (Ait-El-Mokhtar et al. 2019, 2020). Plant-AMF symbiosis induces upregulation of genes involved in both intracellular and transmembrane water transport, including aquaporins, in several host plants (Ouziad et al. 2006; Puccio et al. 2023). Liu et al. (2023) showed that inoculation of tomato (*Solanum lycopersicum*) with *Paraglomus occultum* under 150 mM NaCl stress impacted the expression of several host stress-responsive genes, potentially related to the exchange of $\text{Na}^{+}/\text{H}^{+}$.

Compared to non-mycorrhizal plants under salt stress, photosynthetic activity in AMF-inoculated plants is made more efficient by improving leaf water status, stomatal conductance, gas exchange, as well as increasing chlorophyll and carotenoid content (Boorboori and Lackóová 2025; Hamzehzadeh et al. 2025; Liang et al. 2021). Several authors have reported that components of primary and secondary mechanisms responsible for the defense processes triggered under salt stress are more active in AMF-inoculated plants compared to those activated in plants without symbiotic association (Borde et al. 2017; Li et al. 2024a). Mitigation action of AMF in co-symbiosis with plants in saline conditions has promoted plant growth parameters in several plant species, including plant height, plant biomass, and leaf area, for example, in *Zea mays* inoculated with *Rhizophagus irregularis* (Abbaspour et al. 2021), *M. sativa* inoculated with *Rhizophagus intraradices* (Achiary et al. 2024), and peanut (*Arachis hypogaea*) inoculated with *R. irregularis* and *Funneliformis mosseae* (Qin et al. 2021).

Salinity heterogeneity is the natural state of soil in rain-fed and irrigated systems, and this includes heterogeneous root-zone salinity levels. This leads to the observation that controlled experiments using stable salinity levels usually overestimate crop response and underestimate the effect of beneficial microbes. A recent study by Xiong et al. (2024) investigated how soil salinity heterogeneity influenced the mitigating effect of AMF application. Authors investigated the association of *M. sativa* and *R. irregularis* under uniform (200/200 mM NaCl) and non-uniform (0/200 mM NaCl) saline conditions using a split-root system. Their findings indicate that mycorrhizal inoculation improved growth parameters and locally alleviated several parameters under heterogeneous salinity conditions, including the levels of H_2O_2 and MDA,

which are indicators of oxidative stress in cells and peroxidation of membrane lipids, respectively. In addition, the mycorrhizal plants promoted the activities of antioxidant enzymes (mainly CAT, SOD, and POD), photosynthetic rate, and nutrient homeostasis under both non-uniform and uniform salt treatment compared to non-inoculated plants.

Existing findings underscore the potential of interactions between different soil microorganisms, including AMF, and host plants to mitigate the detrimental effects of salt stress on the quality and productivity of crops (Delaeter et al. 2024; Emmanuel and Babalola 2020). Boorboori and Lackóová (2025) discuss the pros and cons of AMF adaptation to saline environments. Although it is undeniable that AMF-plant symbiosis makes these fungi valuable biostimulants for the maintenance of plants under these conditions, the mechanisms by which these benefits arise are still unclear (Puccio et al. 2023). Identifying missing gaps, especially in understanding the intricacies of complex networks involved in gene expression under saline stress, need to be further elucidated (Puccio et al. 2023; Tang et al. 2024). Moreover, it is necessary to include careful selection and cultivation of salt-resistant plants and microbial species in the management of soil salinization (Baron and Rigobelo 2022; Costa et al. 2018; Saubenova et al. 2023).

Ericoid and orchid endomycorrhiza

When compared to data available on the effect of AMF or ectomycorrhiza on salt tolerance of plants, there is only limited literature available on ericoid endomycorrhiza (e.g. *Oidiodendron maius* and *Meliniomyces variabilis* inoculation of *Vaccinium myrtilloides*, *Vaccinium vitis-idaea* and *Rhododendron groenlandicum*), but they show similar positive effects of infection on seedlings to the other mycorrhizal symbioses (Fadaei et al. 2020). It is assumed that orchid mycorrhizal symbiosis also positively affects salt stress tolerance, however, data about its role in salt tolerance are missing.

Ectomycorrhizal (ECM) fungi

The ECM symbiosis represents mutualistic associations between certain soil fungi and the roots of plants, especially trees. Evidently, fungi exhibit different levels of salt tolerance with Basidiomycota

generally being less salt tolerant than Ascomycota. Studies on ECM fungal communities reveal lower species diversity in saline environments, suggesting that only a few specialized fungal species and strains are well adapted to these environments (Guerrero-Galán et al. 2019; Sa et al. 2019). Such studies are especially important as ECM colonization is reduced in soils having increased NaCl concentrations (Bandou et al. 2006; Dixon et al. 1993). Thus, identification of salt-tolerant fungal species and strains may be especially promising for saline agriculture. However, further research is necessary to improve our understanding of the mechanisms underlying the salt tolerance of such strains (Li et al. 2022).

At the same time, literature data have clearly shown that ECM symbiosis can effectively alleviate the negative physiological effects of salinity primarily through the improved osmoregulation, nutrient (including Ca^{2+} , K^+ , N, P) and water status (Guerrero-Galán et al. 2019). Although the underlying mechanisms still need to be elucidated, they appear to prevent Na^+ entry into the root cortex, to inhibit its transport towards photosynthetic organs, while they enhance K^+ uptake, resulting in a better K^+/Na^+ ratio in the root cells (Luo et al. 2011; Wen et al. 2022; Zwiazek et al. 2019).

Increased antioxidant enzyme activity and osmotic adjustment substance levels was observed in salt-stressed *Quercus mongolica* seedlings in the presence of the ECM fungi *Gomphidius viscidus* or *Suillus luteus*, which also increased plant growth and photosynthetic activity (Bai et al. 2021). Similarly, the presence of *Paxillus involutus* ECM fungus resulted in alleviation of poplar (*Populus x canescens*) leaf chlorosis, improved water status, higher photosynthetic activity and K^+/Na^+ ratio, lower accumulation of major amino compounds and lower unsaturated-to-saturated fatty acid ratio than those of non-mycorrhizal plants (Luo et al. 2011). A study analyzing two different *P. involutus* strains on the same poplar species has clearly shown that the ECM-stimulated plasmalemma proton ATPases were responsible for the well retained nitrate (NO_3^-) uptake of plants under salt stress (Sa et al. 2019). It should be noted, however, that although *Scleroderma* ECM fungi alleviated salt stress in *Populus nigra*, this was not accompanied by improved N status in this case (Otgonsuren et al. 2016).

Higher growth rates and reduced shoot Na^+ accumulation have been reported in *Pinus contorta* seedlings inoculated with soil from urban saline areas containing *Tuber*, *Suillus*, and *Wilcoxina* ECMs (Zwiazek et al. 2019). Inoculation with *Laccaria amethystina*, *Pisolithus tinctorius* and *Cenococcum geophilum* improved leaf chlorophyll content and seedling survival of *Pinus thunbergii* in saline soils (Wen et al. 2022). Similar positive effects of *Sclerotinia bermudense* ECM fungus was reported on the salt tolerance of seagrape (*Coccoloba uvifer*) (Bandou et al. 2006; Bullaín Galardis et al. 2022). Improved N (Sa et al. 2019), K^+ (Bullaín Galardis et al. 2022) and P (Bandou et al. 2006) status of ECM colonized and salt-stressed plants was also reported.

Data related to the beneficial effects of ECMs in saline agriculture could be used in forestry, ecological reforestation and urban restoration (e.g. of trees located close to roads exposed to ice-melting salting during winter) (Wen et al. 2022; Zwiazek et al. 2019). However, it has to be emphasized that most of the research was performed on seedlings or young trees, mostly under controlled environments, and that long-term observations on adult trees and under natural conditions are lacking. Similarly, further research is needed to elucidate the role of ECM in plant defense mechanisms, antioxidant systems, and hormonal signaling under salt stress (Guerrero-Galán et al. 2019). Combined treatments may also open up new research directions. The beneficial effect of the combined application of ECM (*Schizophyllum commune*) and PGPR (*Bacillus paramycoides* JYZ-SD5) in *Metasequoia glyptostroboides* has been efficient to alleviate salt stress (Kong et al. 2023).

Endophytic fungi

In addition to AMF, endophytic fungi that inhabit the inner plant tissues have also been identified in recent years as promising microbials that could protect plants against various environmental stresses, including salinity, without obviously harming the host plants (Baron and Rigobelo 2022; Margarita et al. 2023; Saubenova et al. 2023; Zhang et al. 2024c).

Among them, *Trichoderma* species are well known and widely used fungi to support sustainable agricultural production (Ahmad et al. 2015; Khalmuratova et al. 2020; Margarita et al. 2023; Saubenova et al. 2023). Saha et al. (2025) reported that

inoculation of *Brassica juncea* with the endophytic fungus *T. harzianum* mitigates the impact of salt stress by increasing chlorophyll and proline content, activating several antioxidant enzymes (SOD, CAT, ascorbate peroxidase [APX], and POD) and reducing the synthesis of H_2O_2 and MDA, leading to increased nutrient uptake and overall higher growth and yield. Similarly, Seshagiri et al. (2025) demonstrated that inoculation of *Piriformospora indica* had a positive effect on ameliorating 200 mM NaCl stress in *Solanum melongena*. The inoculated plants were able to improve growth attributes, showed lower oxidative damage, higher chlorophyll content and increased POD activity compared to non-inoculated plants under saline conditions. *Piriformospora indica* inoculation resulted in improved salt tolerance and higher grain yield in barley, which was attributed to a systematically improved “defense readiness” of the inoculated plants due to the activation of the glutathione-ascorbate cycle (Waller et al. 2005). In tomato, it improved water status, foliar K^+/Na^+ ratio, N, P and Ca^{2+} accumulation likely affecting signal transduction processes (Ghorbani et al. 2019). Analyses on the influence of salt stress and the colonization of the root by the endophyte on the plant proteome revealed proteins involved in photosynthesis, cell antioxidant defense, protein translation and degradation, energy production, and cell wall arrangement (Alikhani et al. 2013). In addition to AMF and ECM fungi, several endophytes have also been shown to alleviate salt stress in young *P. nigra* by improving the resilience of plants to abiotic stress (Kulczyk-Skrzeszewska and Kieliszewska-Rokicka 2022).

Melanin-producing and thus dark-colored so-called dark septate endophytes (DSE), which belong to *Ascomycota*, have been isolated from the roots of more than 600 plant species (Gaber et al. 2023). Some DSE (*Periconia macrospinoso*, *Cadophora* sp., *Leptodontidium* sp.) have been shown to alleviate salt stress in tomato without affecting the K^+/Na^+ ratio, but by improving P and N uptake, leading to a higher biomass at stable nutrient contents (Gaber et al. 2023). Similarly, the DSE inoculation (*Sordariomyces* sp. and *Melanconiella elegans*) improved N and P nutrition of cowpea (*Vigna unguiculata*), resulting in better growth and photosynthesis under salt stress without affecting ion contents (Farias et al. 2020).

Similarly, the DSE *Penicillium* sp. improved tomato biomass under salt stress (Morsy et al. 2020).

Future research directions should aim at better understanding the osmo-adaptive strategies of various endophytes (e.g. *Aspergillus montevidensis*) that enable them to thrive in hypersaline habitats (Liu et al. 2017).

Existing findings highlight the potential of interactions between different soil microorganisms (including AMF, ECM fungi and endophytes) and host plants to mitigate the detrimental effects of salt stress on the quality and productivity of favored crops (Delaeter et al. 2024; Emmanuel and Babalola 2020). Although it is undeniable that the AMF-plant symbiosis makes these fungi valuable potential biologicals for the maintenance of plants under saline conditions, the mechanisms by which these benefits arise are still underexplored. The rapid development of molecular and genomic approaches offers the opportunity to recognize and identify missing gaps, particularly, the intricacies of the complex networks involved in gene expression under saline stress and the specific plant-fungal symbiosis (Puccio et al. 2023; Tang et al. 2024). In addition, it is necessary to conduct field trials in the near future and to include careful selection and cultivation of salt-resistant plants and specific microbes in the management of soils vulnerable to salinity (Baron and Rigobelo 2022; Costa et al. 2018; Kakabouki et al. 2023; Margarita et al. 2023). These microbial biostimulants need to find strategies to adapt and thrive in environments with high salinity, as their activities and generally also their abilities to colonize plant roots are reduced by NaCl stress (Baron and Rigobelo 2022; Boorboori and Lackóová 2025; Kakabouki et al. 2023; Klinsukon et al. 2021). Other emerging issues that should be considered is potential co-existence of both synergistic and competitive relationships of these beneficial microbes with other naturally occurring microflora in a soil, as well as the recovery of biodiversity in the soil microbiome (Wang et al. 2025; Yarzabal Rodríguez et al. 2024; Zhang et al. 2024b) and the above-mentioned problem of spatio-temporal salinization. This could be of great importance for the long-term sustainability of salt-affected soils and enhanced agricultural efficiency.

Effects of yeast-based products

Yeast-based products, including *Saccharomyces cerevisiae* (baker's or brewer's yeast), are increasingly studied in agriculture due to their multifunctional role in promoting plant growth and enhancing stress tolerance (Emam 2013). As a taxonomically diverse group of unicellular fungi, yeasts contribute to plant performance through various biochemical pathways, despite an estimated 99% of yeast species still remaining undescribed (Li et al. 2020). The composition of soil yeast communities is influenced by environmental factors such as pH, similar to bacterial communities (Masinova et al. 2017).

Functionally, yeasts improve plant resilience under abiotic stress conditions by producing phytohormones (e.g. auxins, CKs), facilitating nutrient solubilization (e.g. P), and enhancing overall soil health (Alzandi et al. 2022; Devi et al. 2025). Additionally, yeasts are rich in essential amino acids, vitamins (e.g. B1, B2, B3, B5, B6, B7, B9, and biotin), and trace elements such as chromium and zinc, all of which support key physiological processes including cell division, chlorophyll biosynthesis, and root development (Abdel Latef et al. 2019; Emam 2013; Taha et al. 2021).

Under saline conditions, amino acids such as proline function as osmoprotectants by regulating ion homeostasis, stomatal conductance, detoxification of heavy metals, redox balance, and stress-responsive gene expression (Abdelkader et al. 2023). Cheng et al. (2016) demonstrated that exogenous application of amino acids like glycine, cysteine, serine, and methionine alleviated salt-induced inhibition of seed germination, potentially through elevated cytosolic Ca^{2+} levels via activation of Ca^{2+} -permeable channels.

However, high salinity can also impair amino acid uptake in yeast, leading to intracellular amino acid starvation (Li et al. 2003). In a study on flax, Emam (2013) reported that yeast application to salinized seeds enhanced the accumulation of total free amino acids, particularly proline, while significantly reducing peroxidase (POX) and polyphenol oxidase (PPO) activities, which subsequently stimulated the accumulation of phenolic compounds. These findings suggest a key physiological mechanism through which yeast mitigates salt-induced oxidative stress and contributes to improved plant tolerance.

Knowledge gaps and future directions related to microorganism-based salt stress alleviation

Research to date has predominantly centered on the performance of microbial inoculants, such as PGPR and AMF, under static or uniformly saline conditions (Xiong et al. 2024). However, these controlled experiments fail to capture the complexity of fluctuating salinity conditions commonly observed in agricultural soils, where salinity levels can vary both temporally and spatially due to factors like irrigation practices, rainfall, and evapotranspiration (Li et al. 2025; Ren et al. 2019; Sui et al. 2025). The dynamic nature of these environments poses unique challenges to microbial communities, influencing not only their survival and functionality, but also their ability to establish and maintain beneficial interactions with host plants (Nizamani et al. 2024). Current knowledge gaps include understanding how microbial inoculants respond to rapid shifts in salinity at both physiological and molecular levels (Anas et al. 2025; Díaz-Rodríguez et al. 2025; Palanisamy et al. 2025). It remains unclear how these fluctuations affect microbial community stability, diversity, and the resilience of symbiotic relationships (Li et al. 2024b; Qin et al. 2021).

Furthermore, the plasticity of microbial genomes in response to environmental stressors is an emerging area of interest. Adaptive mechanisms such as horizontal gene transfer, regulation of stress-responsive pathways, and epigenetic modifications could play significant roles in enhancing microbial tolerance to salinity fluctuation (Acharya et al. 2024; Roy et al. 2021). Despite these potential mechanisms, comprehensive studies integrating omics approaches are limited. Such approaches could provide deeper insights into the regulatory networks governing microbial adaptation and the downstream effects on plant physiology (Patel et al. 2024; Srikanth et al. 2024).

Another critical aspect that remains underexplored is the impact of fluctuating salinity on the metabolic interactions between plants and their microbial partners (Balestrini et al. 2024; Tang et al. 2024). Changes in root exudation patterns under stress can alter the composition of the rhizosphere microbiome and potentially influence the efficacy of microbial inoculants. Additionally, while some research has highlighted the capacity of certain PGPR and AMF strains to maintain their functional roles under moderate salinity shifts, the consistency of these effects

under field conditions with unpredictable salinity dynamics is poorly documented.

Future research should aim to fill these gaps through long-term field trials that simulate natural salinity fluctuations, coupled with advanced analytical techniques to monitor microbial activity and plant health in real time. Investigating the synergistic effects of microbial consortia rather than single-strain inoculants could also offer new perspectives on enhancing resilience to salinity stress. Ultimately, a better understanding of how microbial inoculants adapt to and influence plant responses under fluctuating salinity conditions will be pivotal for developing sustainable agricultural practices in salt-affected regions. Microbes inhabiting the roots and leaves of halophytes may contribute significantly to their salinity tolerance and have been identified as promising sources for microbial isolates (Ruppel et al. 2013). The ongoing identification of halophyte-associated bacteria and fungi, the analysis of their interaction with the host and how this interaction contributes to the survival of both partners will provide essential novel routes to identify strains conferring salt stress tolerance to glycophytes.

Microbial communities are not static entities; but exhibit dynamic changes in their composition, structure, and functionality in response to environmental stressors, including salinity fluctuations. This dynamic nature is particularly evident in saline-affected soils, where changes in salt concentrations can rapidly alter microbial diversity and ecosystem functioning. Salinity acts as a selective pressure, favoring halotolerant and halophilic species while suppressing the growth of salt-sensitive microorganisms. As a result, the microbial community undergoes reorganization, with shifts in the abundance of key taxa and changes in microbial interactions (Sviatoslav et al. 2023). Current research has shown that increasing salinity levels generally lead to a reduction in microbial diversity, with bacterial communities being more sensitive to salt stress than fungal communities. Halophilic bacteria, such as the genera *Halomonas* and *Marinobacter*, often become dominant under moderate-salinity conditions, while *Actinobacteria* and certain *Proteobacteria* show resilience to low salinity and salinity fluctuations (Mani et al. 2020). Fungal communities, particularly AMF, exhibit varying degrees of tolerance, with some species adapting

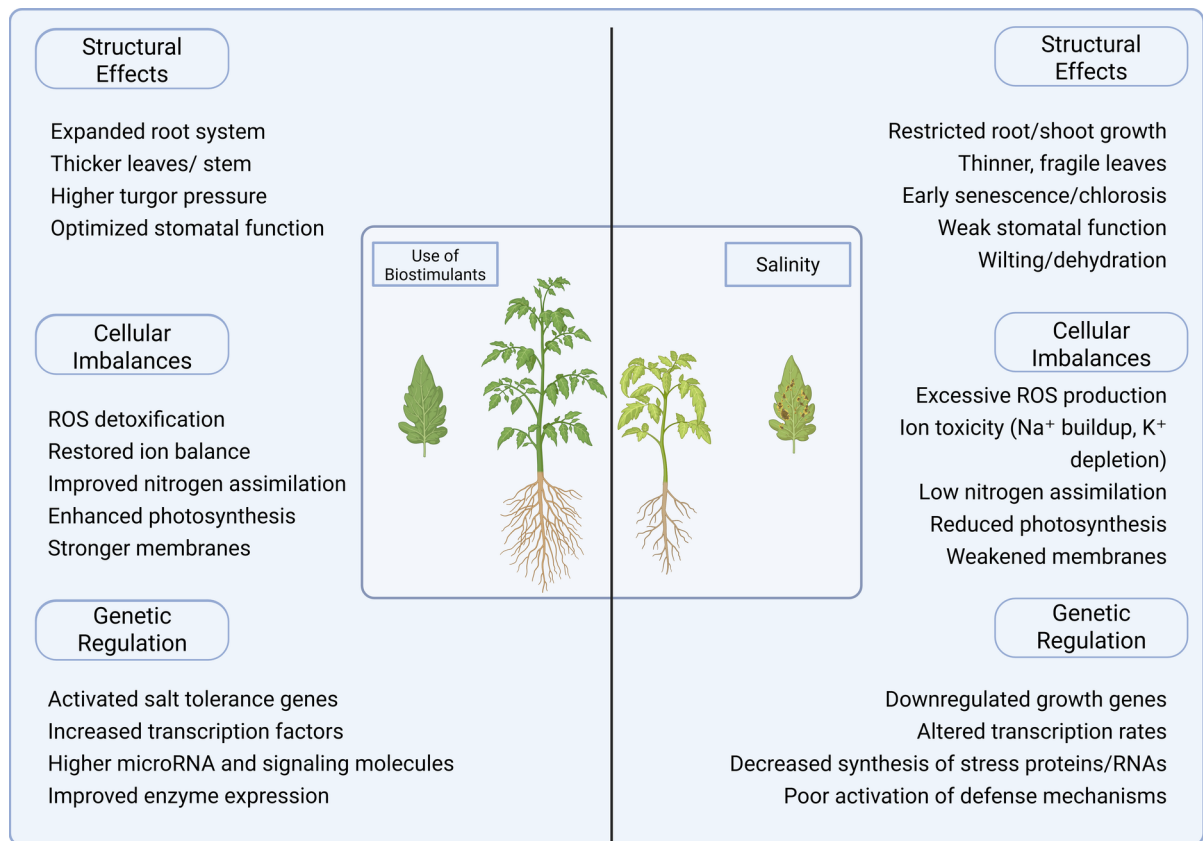


Fig. 1 Impact of salinity on plant structure, cellular reaction and gene expression and the mitigating effects by the application of biostimulants

through modifications in spore morphology and hyphal structures (Qin et al. 2021). Longitudinal studies that track changes in microbial communities over time are needed to capture the transient and adaptive responses to salinity fluctuations. Such studies should incorporate high-throughput sequencing technologies, metagenomics, and metabolomics to unravel the complex interactions within microbial networks.

Additionally, the functional implications of these community shifts are not yet fully understood. Changes in microbial composition can influence nutrient cycling, soil structure, and plant health, potentially affecting agricultural productivity (Morsy et al. 2020). For example, the loss of key functional groups involved in N fixation or P solubilization could compromise soil fertility. Conversely, the proliferation of stress-adapted microbes might enhance plant resilience through the production of stress-alleviating compounds (Yarzabal Rodríguez et al. 2024).

Role of biostimulants

Biostimulants are a relatively new approach to mitigate abiotic stress caused by salinity, with varying degrees of success (Fig. 1). Biostimulants are natural plant or algal extracts and derivatives which typically contain a wide range of active compounds, most of these compounds are still unknown (Calvo et al. 2014). However, there are promising studies that have shown that biostimulants can improve the salt resistance of glycophytes. In the study by Ikuyinminu et al. (2022), protein hydrolysates and *Ascophyllum nodosum*-derived biostimulants were tested as treatments for improving salinity resistance in glycophytes, such as tomatoes. These biostimulants effectively mitigated salinity-induced yield losses and improved fruit quality. According to the findings, tolerance was enhanced by promoting osmotic adjustment, ion

homeostasis, and physiological resilience, including a boost in photosynthetic pigments.

Finding a suitable extract to alleviate salinity stress is important, but it is also essential to understand which specific symptoms of salt stress the extract alleviates. If the mechanisms of action of these extracts were to be determined, future research could optimize their efficacy, either by improving the extraction method (e.g. aqueous extraction, ethanol-based methods) or by identifying better isolation sources, such as halophytes. This could involve genetic selection or the development of plants with higher concentrations of the active substances that alleviate salt stress symptoms (e.g. through genetic engineering).

To follow this direction a more detailed understanding of the induced biochemical pathways needs to be provided. For example, salicylic acid (SA), a plant hormone with natural protective properties rather than a biostimulant, might be used as a tool to explore the underlying mechanisms associated with salinity tolerance. Salicylic acid is a signaling molecule that can help identifying pathways involved in the plant's stress response (Ben Youssef et al. 2025; Karimi et al. 2025). It has shown potential in mitigating the adverse effects of salt stress through multiple regulatory mechanisms when applied to soil (Gunes et al. 2005). Activating effects of SA on the antioxidant defense system in plants plays an important role in reducing oxidative stress by modulating ROS, thereby preserving cell membranes and organelles from damage caused by salt-induced stress. Additionally, SA enhances water retention under osmotic stress by regulating stomatal opening and closing, maintaining cellular hydration and reducing water loss. This osmotic regulation is complemented by the role of SA in ion homeostasis. In particular, by balancing Na^+ and K^+ levels, SA limits Na^+ related ion toxicity and improves the plant's cellular function. Research demonstrates that SA application not only preserves chlorophyll content and enhances photosynthetic capacity in plants under salt stress but also regulates the levels of stress-regulating molecules such as proline and enzymes that mitigate oxidative damage, such as those involved in lipid peroxidation and hydrogen peroxide detoxification. These physiological adjustments collectively contribute to enhanced growth rates, improved morphological features (e.g. leaf structure and root development), and greater overall resilience of plants in saline environments (Gunes et al. 2005;

Kereçin and Öztürk 2024). Consequently, SA application partially alleviates the detrimental impacts of salt stress, supporting plants in maintaining morphological integrity, crop quality and sustaining productivity under salt affected soil conditions. In this context, the morphological and physiological characteristics of cucumber (Toksoy and Doğru 2021) and maize (Kereçin and Öztürk 2024) have been shown to benefit from the application of SA under salt stress. Under this condition, SA increases the plant's tolerance and enhances the microorganisms in the rhizosphere when applied to saline soils with the appropriate dose and method (Aydın et al. 2022; Gül et al. 2008). Future implications of this approach include leveraging SA treatment to elucidate key pathways and mechanisms. This significantly contributes to understanding salinity tolerance at a molecular level, rather than attributing biostimulant properties to SA. The inclusion, therefore, might be evaluated as a means to deepen mechanistic insights.

In addition to SA, another promising element in combating salt stress is silicon (Si), an element known to be involved in mitigating various abiotic stresses in plants. Silicon improves the physical, chemical, and biological conditions in saline soils, and enhances the tolerance of plants and microorganisms to salt stress. In particular, Si application reduces oxidative stress by activating antioxidant enzymes (SOD, CAT, APX) (Kireççi and Yürekli 2019). Furthermore, Si is a crucial element that regulates ion balance in plant cells and fortifies the cell wall. In particular, it increases resilience to environmental stressors such as drought, salt, and heavy metals. Silicon also has various effects on increasing the diversity and quantity of microorganisms in saline soils and is known to help create a more balanced environment for them (Ahmad et al. 2024).

Numerous studies have already highlighted the use of biostimulants, such as seaweed extracts, to combat salt stress (Ikuyinminu et al. 2022). According to this study, seaweed extract enhances plant resistance to salt stress by activating antioxidant enzymes, balancing stress hormones, increasing membrane stability, and boosting plant resistance through various plant regulators (auxins and gibberellins), vitamins, and plant nutrients it contains (Kara et al. 2019; Korkmaz and Çiçek 2024). Seaweed extracts improve the likelihood of plants thriving in saline soils due to their chemical composition, organic carbon, and nutrients.

The morphological and physiological characteristics of *Lavandula officinalis* cultivated in saline environment were enhanced by the application of seaweed extract at varying concentrations (Korkmaz and Çiçek 2024). Moreover, in this study, seaweed extract was found to increase chlorophyll levels and regulate proline content. It is also expected that the application of seaweed extract has a positive effect on soil enzymes and encourages the growth of beneficial bacteria and fungi in the root zone. On the other hand, seaweed extract is thought to enhance the resistance of weakened microorganisms to salt stress by providing them with a rich organic carbon source in saline soils.

Waste sheep wool, a byproduct of the wool industry, has also been explored as a sustainable solution for improving plant resilience under salt stress. Due to the complex structure of keratin, sheep wool waste is highly resistant to decomposition (Petek and Logar 2021). This waste is a natural raw material that is biodegradable in the soil without harming the environment and does not contain any chemicals (Adi and Pacurar 2015). The application of wool waste significantly improves soil fertility, with notable increases in organic carbon and N. Additionally, this waste leads to an increase in soil enzyme activities (Lal et al. 2020). Sheep wool improves water use efficiency in plants with short cultivation periods, acts as a water conservation substrate (Kadam et al. 2013; Zoccola et al. 2015), and has positive effects on soil salinity when used as a soil conditioner and fertilizer in agricultural applications (Gorecki and Gorecki 2010). According to a study by Öztürk et al. (2025), sheep wool enhanced the morphological and physiological characteristics of *L. officinalis* cultivated in soils with varying degrees of salt stress and increased the plant's resistance to salt. Sheep wool is also an excellent product for soil conditioning. It is known to promote beneficial microorganisms due to its high levels of carbon, N, and creatine.

There are already numerous studies cited on the use of biostimulants against salt stress, such as seaweed extracts as already mentioned (Deolu-Ajayi et al. 2022; Ikuyinminu et al. 2022). However, there is little to no research on the use of halophyte extracts. Halophytes possess numerous mechanisms that enable them to adapt to salt stress. Some of these, such as the storage of salt in vacuoles through specialized ion transporters (Munns and Tester 2008; Zhu 2001), are not transferable when used in plant extracts. However,

others, such as the production of proline and glycine betaine for osmotic adjustment (Flowers and Colmer 2008), antioxidant enzyme activity to mitigate oxidative stress (Mittler 2002), and the biosynthesis of protective proteins (Hasegawa et al. 2000), could, in theory, be transferable. These transferable traits, combined with their ability to thrive in saline environments, make halophytes prime candidates for developing extracts to combat salinity stress in crops. Since some of these plant species store salt in their vacuoles, the extract made from these plants could contain some salt, particularly if it is an obligate halophyte and not a facultative one. However, small amounts of salt have been proven to be beneficial as a foliar spray (Vucko et al. 2021). For this reason, both types of halophytes are possible candidates for plant extracts. These extracts could contain proline and glycine betaine for osmotic adjustment (Flowers and Colmer 2008) and antioxidant enzymes to mitigate oxidative stress (Mittler 2002).

Other natural compounds, such as humic substances, formed by chemical and biological transformations of plant and animal matter and by microbial metabolism, have been applied as biostimulants for a long time (Canellas et al. 2015). The application of humic and fulvic acids, has been shown to increase nutrient uptake, plant growth and crop yield by biostimulating of plants as well as by improving soil structure (Guo et al. 2019). The application of humic substances to alleviate salt stress-related growth restraints highlights the great potential of this class of compounds, as the use of natural organic matter, especially in field production systems, will increase soil productivity and soil health in the long term.

Treatment application windows

In agricultural techniques that promote crop production, the timing and method of treatment application, such as seed priming (Ma et al. 2024; Marthandan et al. 2020), seedling treatments (Campobenedetto et al. 2020), dose dependency (Canellas et al. 2015) and interventions throughout vegetative growth (Peláez-Vico et al. 2024) are crucial. Each stage-specific strategy provides unique advantages tailored to the conditions and period of plant development.

A pre-sowing procedure known as "seed priming" is designed to enhance the vigor and germination rates

of seedlings. Typically employed techniques include osmopriming, hydropriming, and biopriming (Amir et al. 2024). These methods increase metabolic readiness for growth, promote uniform seedling emergence, and enhance stress tolerance. Osmopriming, which involves soaking seeds in osmotic solutions such as polyethylene glycol, promotes enhanced germination under stress by preserving a controlled water uptake. According to Marthandan et al. (2020), this method has been effective in enhancing salinity tolerance by modulating osmotic balance and reducing ion toxicity. Amir et al. (2024) examined the principles underlying priming techniques and highlighted the ways that they can be applied to mitigate abiotic stresses including salinity and drought.

Biopriming has been demonstrated to enhance plant development and stress tolerance by combining beneficial bacteria with seed hydration. Noble et al. (2023) found that biopriming can enhance tolerance to abiotic stresses and generate systemic resistance against pathogens by activating defense-related genes. A straightforward and affordable technique that improves germination by shortening the imbibition period and triggering vital metabolic processes is hydropriming, which involves soaking seeds in water. According to Marthandan et al. (2020), hydropriming may improve drought tolerance by promoting faster seedling establishment and enhancing the activity of enzymes that are antioxidants. In order to improve crop resilience over the long term, Louis et al. (2023) discovered that primed seeds can preserve stress tolerance features that are transferred to succeeding generations through epigenetic alterations. By targeting early plant development, treatments administered to seedlings protect plants against biotic and abiotic stressors. Applying growth regulators, nutrients, or microbial inoculants during the first establishment period is crucial, as seedlings are most vulnerable during this period. According to Campobenedetto et al. (2020), applying biostimulants to cucumber seeds to increase seed germination tolerance to different abiotic stress greatly improved their resistance to heat stress, which in turn led to higher output and growth. This stage-specific approach enables the rapid establishment of robust seedlings that can withstand challenging circumstances.

Opportunities for interventions that directly affect biomass accumulation, photosynthesis, and nutrient uptake occur during the vegetative growth phase.

During this phase, foliar spraying, fertigation, and soil amendments are frequently utilized to provide vital nutrients and biostimulants. Peláez-Vico et al. (2024) highlight that multifactorial stress combinations significantly impair reproductive tissues and grain yield in crop plants by reducing pollen viability, seed set, and grain filling, emphasizing the need for integrated stress-mitigation strategies. Depending on the crop and environment, each stage of treatment has distinct advantages. Although seed priming is cost-effective and prepares seeds for rapid germination, its benefits could only be felt in the early stages of growth. Although they offer targeted resilience, seedling treatments need to be handled and managed carefully. Crop productivity is immediately impacted by applications made during vegetative growth, but long-term effects may require repeated treatments. As evidenced by integrated nutrition and biostimulant management approaches, combining these tactics can have synergistic benefits (Amir et al. 2024).

Despite our improved understanding of the treatment phases, there are still research gaps. The optimization of priming, seedling treatments, and vegetative applications in relation to particular crop species and stress conditions should be the primary goal of future studies. The efficiency and long-term viability of these interventions could be improved by incorporating emerging technologies, such as precision agriculture tools and nanotechnology.

A path forward and conclusion

Recent scientific research in the field of sustainable saline agriculture has focused on the development of adaptable, cost-effective and environmentally friendly technologies that would increase agricultural efficiency and reduce the negative impact of changing environmental conditions on crop yields. As indicated by numerous studies (e.g. Boorboori and Lackóová 2025), one promising strategy is the application of beneficial soil microbes, including AMF, in order to increase crop salt tolerance. Given the difficulties in plant breeding for many crops and the limitations of genetic engineering, the development of natural alternatives holds great promise for achieving more sustainable agriculture (Baron and Rigobelo 2022). The present review demonstrates the current benefits in mitigating crop salt stress through the application

of several well-described agricultural biologicals, which represent a promising new bio-strategy for basic research and targeted agricultural sustainability. However, plants are continuously stressed under field conditions and often a simultaneous exposure to salinity, drought and other constraints occurs. Until now, research on the effect of biologicals to mitigate multiple stresses is scarce since the vast amount of data has resulted from field, greenhouse or growth chamber experiments using single stressor treatments. Providing data on the efficiency of agricultural biologicals under multistress natural growth conditions will bridge the gap between controlled experiment and crop performance in the field.

Biostimulants offer economical solutions that include many positive features as well as being environmentally friendly. In arid and semi-arid areas and other salt-affected areas, it is foreseen that they will offer important solutions to both improve crop quality and regulate the soil to some extent. The lack of information provided to farmers and crop producers about beneficial microbes and biologicals is one of the biggest bottlenecks in the translation of research results into practical application. The farmers who produce crops under saline conditions should be made aware of the importance of biostimulants, which not only serve as fertilizers but also regulate the physical, chemical and biological structure of the soil.

Acknowledgements Katalin Solymosi is grateful for the support of the Bolyai Janos Research Scholarship of the Hungarian Academy of Sciences.

Authors' contribution All authors whose names appear on the submission.

1) made substantial contributions to the conception or design of the work; or the acquisition, analysis, or interpretation of data; or the creation of new software used in the work;

2) drafted the work or revised it critically for important intellectual content;

3) approved the version to be published; and.

4) agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

Funding Open Access funding enabled and organized by Projekt DEAL. This publication is based upon work from COST Action SUSTAIN (CA22144) supported by COST (European Cooperation in Science and Technology).

Declarations

Competing interests The authors have no conflict of interests related to this publication.

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