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Alleviation of salinity stress in plants by endophytic plant-fungal symbiosis: Current knowledge, perspectives and future directions

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Abstract Salinization of soil with sodium chloride ions inhibits plant functions, causing reduction of yield of crops. Salt tolerant microorganisms have been studied to enhance crop growth under salinity. This review describes the performance of endophytic fungi applied to crops as a supplement to plant genetics or soil management to alleviate salt stress in crops. This is achieved via inducing systemic resistance, increasing the levels of beneficial metabolites, activating antioxidant systems to scavenge ROS, and modulating plant growth phytohormones. Colonization by endophytic fungi improves nutrient uptake and maintains ionic homeostasis by modulating ion accumulation, thereby restricting the transport of Na^+ to leaves and ensuring a low cytosolic Na^+:K^+ ratio in plants. Participating endophytic fungi enhance transcripts of genes encoding the high Affinity Potassium Transporter 1 (HKT1) and the inward-rectifying K^+ channels KAT1 and KAT2, which play key roles in regulating Na^+ and K^+ homeostasis. Endophytic-induced interplay of strigolactones play regulatory roles in salt tolerance by interacting with phytohormones. Future research requires further attention on the biochemical, molecular and genetic mechanisms crucial for salt stress resistance requires further attention for future research. Furthermore, to design strategies for sustained plant health with endophytic fungi, a new wave of exploration of plant-endophyte responses to combinations of stresses is mandatory.

Keywords Endophytic fungi · Biochemical changes · Ionic homeostasis · Osmoregulation · Hormones · Salinity · Roots · Soil · Inoculants · Microorganisms

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Soil salinity affects agriculture globally

The beginning of the 21st century has been marked by global scarcity of water resources, increased environmental pollution and salinization of soil and fresh water. Two major threats for agricultural sustainability are increased human population and reduction in arable land available for crop cultivation (Shahbaz and Ashraf 2013). Several environmental stresses such as high winds, extreme temperatures, drought, salinity and flood have impacted on the production and cultivation of agricultural crops. Among these, soil salinity is one of the most significant environmental stresses resulting in major reductions in cultivatable land area, and decreased crop productivity and quality. It is estimated that 50% of all arable land will be impacted by salinity by 2050 (Shrivastava and Kumar 2015) and that globally, soil salinity results in more than US$12 billion in annual losses due to reduced crop productivity (Jägermeyr and

Frieler 2018). Salinity is recognized as the main threat to environmental resources in several countries, affecting almost 1 billion ha worldwide, which represents about 7% of the earth's continental area (Shrivastava and Kumar 2015). Consequently, it is important to understand the crop responses to this major soil and plant stress to minimize economic loss and improve food security.

Soil is defined as being saline when the electrical conductivity (EC) of the saturation extract (ECe) in the root zone exceeds 4 dSm^{-1} at 25^oC and has an exchangeable sodium of 15% (w/v). Salinization also includes excessive accumulation of ions such as calcium (Ca^{2+}), magnesium (Mg^{2+}), sodium (Na^+), sulphates (SO_4^{2-}), and chlorides (Cl^-) in the soil, inhibiting plant growth and cellular functions. The most abundant ion in most salt-affected soils is Na^+ and hence the exchange phase is dominated by Na^+. A secondary process often associated with saline soils is alkalinisation, creating a condition known as sodicity. This results in the degradation of soil physical properties and porosity, leading to reduced water and air flow and increased soil hardness and crusting.

Apart from affecting soil physical properties, high soil salinity directly and adversely affects plants- both native vegetation and introduced crops, severely affecting seed germination, root growth, and the physiological functions of crops (Oster and Jayawardane 1998). It has been estimated that worldwide 20% of total cultivated and 33% of irrigated agricultural land is affected by high salinity. This is mainly due to the toxicity of the salt ions directly on the plant cells but also through general osmotic effects of the soil around the roots of the plant. High osmotic potentials at the soil-root interface reduce the ability of the plant to absorb water from the soil (Machado and Serralheiro 2017).

Native plants have evolved mechanisms to tolerate low rainfall and high salinity over hundreds of thousands of years (Steffen et al. 2009). However, in the past 200 years, human activities have intensely disrupted the natural hydrological balance in many regions of the globe. This has resulted in significant consequences for the distribution of salt in all landscapes leading to severe degradation of both natural and agricultural environments. It is predicted that the total area of land affected by salinity will increase drastically over the next few decades if effective solutions are not implemented. These solutions would involve significant changes to our present systems of management

including research and development of strategies to improve salt tolerance in crops and improve mechanisms to mitigate its consequences (Rengasamy 2002, 2006).

Effects of salt stress on above-ground and below-ground organs of plants

Plants have two major systems, the above-ground organs (shoots) and below-ground organs (roots). Each system has morphological, physiological and anatomical differences that affect plant performance differently (Gregory 2007). However, while these two systems grow and function as a separate site for the uptake of nutrients and other resources, they are coupled, and their functions need to form an integrated system. The above-ground system is highly dependent on the development of below-ground organs and without a sufficiently developed root system, the above-ground system cannot fully mature (de Willigen and van Noordwijk 1987).

Salinity limits vegetative and reproductive development by inducing physiological dysfunctions, and this has profound implications on different harvested organs such as leaf, stem, root, shoot, fruit or grain. The complex phenomenon of tolerance and response to salt stress involves dynamic changes in growth, physiology, metabolic pathways and gene expressions (Atkinson and Urwin 2012; Munns and Tester 2008). Strategies used to mitigate against salt stress include proline accumulation within cells (Matysik et al. 2002), modulation of hormones and accumulation of glycine betaine and polyols (Gupta and Huang 2014). They also involve generation of nitric oxide (NO) and compounds to combat formation of reactive oxygen species (ROS). NO directly or indirectly triggers expression of several redox-regulated genes. NO also reacts with lipid radicals thus preventing lipid oxidation, exerting a protective effect by scavenging superoxide radicals and formation of peroxynitrite that can be neutralised by other cellular processes. NO also helps in the activation of many antioxidant enzymes including catalase (CAT), ascorbate or thiol-dependent peroxidases (APX), glutathione reductases (GR) and superoxide dismutase (SOD).

The effect of salinity on leaf growth, biomass production and grain yield on several crops are well documented (Hasanuzzaman et al. 2013; Munns et al. 2011; Munns and Tester 2008; Sun et al. 2014). The extent to which plants are damaged by salinity depends on several

factors including species, genotype, plant growth phase, ionic strength, duration of salinity exposure, composition of salinizing solution and, most importantly, which plant organ is exposed (Robin et al. 2016).

Munns (2005) hypothesized that salinity damage in plants occurs in two temporal phases. The first phase of growth reduction occurs rapidly after exposure and is due to an osmotic effect, while the second phase, which is a slower process, is due to the accumulation of salt ions, mainly in older leaves. Early symptoms of the second phase of growth reduction include damage to old leaves and a reduced photosynthetic capacity (Munns et al. 2006). At the plant organ level, shoots have been demonstrated to be more sensitive to salinity than roots (Munns and Tester 2008). However, roots are exposed to salinity stress before leaves and can respond rapidly through changes in elongation (Rahnama et al. 2011) and function (Shelden et al. 2016). The roots are crucial for a myriad of physiological processes including water and nutrient uptake, preventing toxic substances from reaching photosynthetic tissue, signal exchange with shoots, anchoring of plants, and providing mechanical support to the above-ground organs.

The root-soil interface/ The rhizosphere

Roots and their growing substrate are intrinsically connected, and they mutually influence each other at all stages of plant life (Gregory 2006). The interface between roots and the soil is a complex and often ill-defined zone. Compounds are released from roots into the surrounding soil matrix resulting in changes to its chemical and physical properties. The narrow zone of soil that surrounds and is influenced by plant roots is known as the rhizosphere. The term rhizosphere was first defined over a century ago by Hiltner (1904) and recently, redefined by Pinton et al. (2007) as the most dynamic interface on earth that includes soil influenced by the root, along with the root tissues. The rhizosphere is home to a vast number of microorganisms (Morgan et al. 2005; Pinton et al. 2007), and consists of three distinct zones: (a) the endorhizosphere, which includes part of the cortex and endodermis in which microbes occupy the apoplastic space; (b) the rhizoplane, which is the medial zone immediately next to the root consisting of the root surface and mucilages; and (c) the ectorhizosphere, which extends from the rhizoplane out into the bulk soil (Lynch 1990).

The root system architecture is greatly influenced by soil conditions (Rich and Watt 2013), including nutrient gradients and concentrations of nitrate and phosphorus (Ho et al. 2005; Paterson et al. 2006). Roots also affect the surrounding nutrient composition by the release of organic compounds that play a vital role in mineralizing nutrients. The compounds released from the roots into the surrounding soil are generally part of rhizodeposits (Jones et al. 2009), which include a range of substances from sloughed-off root cells and tissues, mucilages, volatiles, and soluble lysates and exudates from damaged and intact cells (Curl and Truelove 1986; Dakora and Phillips 2002; Watt 2009). Abiotic factors influence the root system (Bekkara et al. 1998; Brimecombe et al. 2000; Groleau-Renaud et al. 1998; Watt and Evans 1999) with roots responding by secreting a different combination of compounds to protect against negative effects and encourage positive microbial interactions (Badri and Vivanco 2009). These secreted compounds usually induce an interactive metabolic cross-talk involving diverse biosynthetic networks and pathways.

Root exudates include both secretions (including mucilage) that are actively released from the root and diffusates which are passively released because of osmotic differences between soil solution and the root cells (McNear 2013). Inorganic root exudates include ions, water, ubiquitous H^+ and electrons. Although the concentration of inorganic compounds make up far less of the root exudate composition compared to organic compounds but their role is still significant (Khorassani 2008; Uren 2000). Organic compounds can be classified into high molecular weight compounds, such as complex molecules including polysaccharides secreted by root cap cells and epidermal cells at the apical zone, and low molecular weight compounds that include arabinose, fructose, glucose, amino acids, organic acids, plant hormones and phenolic compounds (Bertin et al. 2003). Due to the richness of inorganic and organic compounds in rhizodeposits, the rhizosphere is home to specialised microbes that are able to utilise these compounds as an energy source.

Several recent and comprehensive reviews have been written covering the diversity and activity of microorganisms at within roots and in the rhizosphere, as well as the functions and effects of microorganisms in nutrient turnover and supply to the plant (Garcia et al. 2016; Jacoby et al. 2017; Smith and Smith 2011; Udvardi and Poole 2013). In the following section, the use of microorganisms as one of the key approaches used to alleviate

abiotic stresses, with the focus on using fungi as a major beneficial microbe will be discussed.

Alleviating salt stress by association with endophytic fungi

Diverse metabolic and genetic strategies used by plant-associated microbes can reduce the impact of salt stress and other abiotic stresses arising from extreme environmental conditions (Gopalakrishnan et al. 2015; Singh 2014). Induced Systemic Tolerance (IST) is the term used to describe microbe-mediated induction of abiotic stress responses (Meena et al. 2017). In these beneficial situations, rhizosphere microorganisms not only perceive and respond to signal molecules secreted by plant roots, they also release diverse signalling molecules that influence plants, resulting in increased biotic and abiotic stress resistance or tolerance, as well as root development and plant growth (Zhang et al. 2017a). Microbial interactions with plants induce several local and systemic responses that improve the metabolic capacity of plants to respond to salt stress (Nguyen et al. 2016). This microorganisms-based plant biotechnology has proven to be more efficient in many cases than plant breeding and genetic modification approaches (Smith 2014).

Beneficial effects due to plant root interactions with endophytic fungi

In recent years the ability of mycorrhizal fungi to induce tolerance against salt stress in crops has been documented (Gangwar and Singh 2018) (Fig. 1). In a mycorrhizal association, the fungus colonizes the host plant's root tissues, either intracellularly as in arbuscular mycorrhizal fungi (AMF), or forms extracellular exchange mechanisms outside of the root cells, as in ectomycorrhizal fungi. Thus, mycorrhiza fungi can be categorised as endo- inside plant tissue, or ecto- associated with the external rhizosphere or not penetrating root cells. For the purpose of clarity, this review will only focus on endomycorrhizal (termed as endophytic for this review) fungi.

Penetration and colonisation of plant roots appears to be essential for some endophytic fungal strains that are reported to promote plant growth and provide protection against pathogens. For example, some species belonging to the genus *Trichoderma* can colonize local sites (Metcalf and Wilson 2001) on roots, mediated by

hydrophobins- (Viterbo et al. 2004) and expansin-like proteins (Brotman et al. 2008) present in the outermost cell wall layer that coats the fungal cell surface. Other rhizosphere-competent Trichoderma spp. colonize entire root surfaces for long periods of time (Harman 2000; Thrane et al. 1997) or penetrate the epidermis and the cortex (Yedidia et al. 1999). Once hyphae penetrate roots, a series of fungal bioactive compounds can be produced inducing plant biochemical mechanisms (Harman 2006). The callose-enriched wall appositions in the root cell limit the growth of the Trichoderma spp. to a small area (epidermis and cortex), preventing the entry of Trichoderma spp. into the vascular stele (Hermosa et al. 2012; Yedidia et al. 1999). Arbuscular mycorrhiza fungi (AMF) are another group of endophytic fungi. Their hyphae penetrate plant cells, producing structures that are either balloon-like (vesicles) or dichotomously branching invaginations (arbuscules) as a means of nutrient exchange. The fungal hyphae do not in fact penetrate the protoplast (i.e. the interior of the cell), but invaginate the cell membrane. Dark septate endophytic (DSE) fungi are also root endophytes, characterized by intense dark pigmentation and the formation of septate and melanized hyphae and occasionally microsclerotia (Knapp et al. 2015; Yuan et al. 2016). They can be found in plant cortical cells inter- and intracellularly and are present in several environments (Li et al. 2019; Santos et al. 2017). In contrast to the vast information on AMF, information on the role of DSE fungi in the ecosystem is limited.

Colonization of several crops with endophytic fungi has been reported to induce systemic resistance to pathogens, mitigate stress by increasing the levels of protective metabolites and osmoprotectants, activate antioxidant systems to prevent damage caused by ROS, decreasing salt induced root respiration and modulate the phytohormone profile to minimize salt effects on growth of plants (Ghaffari et al. 2016; Jogawat et al. 2013; Li et al. 2017; Nia et al. 2012; Rewald et al. 2015; Zhang et al. 2019a). These effects are in coordinated to improve plant growth and resilience to salinity stress. These ameliorative effects can be evaluated in terms of improved plant growth exhibited by endophyte colonized (ENC) plants in comparison to non-endophytic (NENC) colonized plants.

Salinity triggers a decrease in stomatal conductance, thus decreasing the $CO_2:O_2$ ratio and increasing photorespiration (Kangasjärvi et al. 2012). This causes an increase in stomatal resistance to transpiration and an
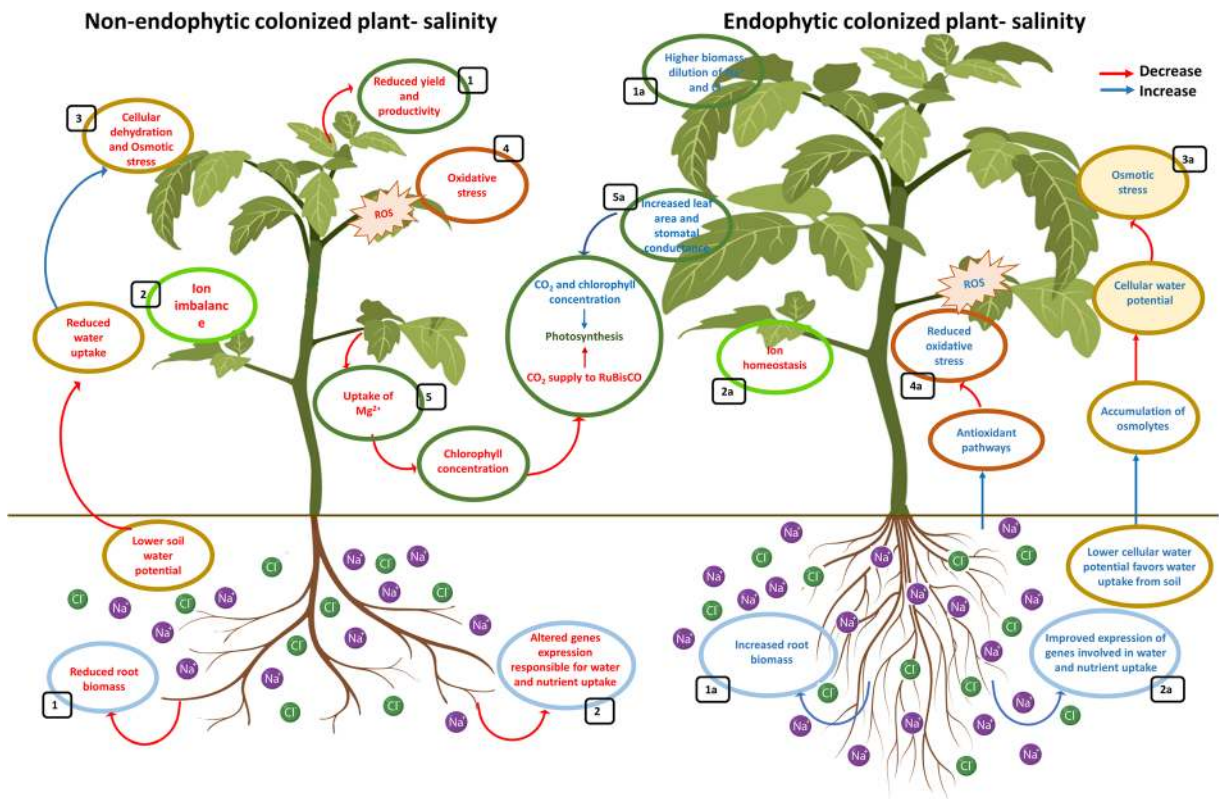
Fig. 1 Potential beneficial effects of root colonisation of plants by endophytic, symbiotic fungi in saline soil conditions, summarised from the literature. Salinity results in reduced root biomass due to salt-induced inhibition of cell division and affect the total biomass yield (1) (left). Plant colonized with endophytic fungi improves biomass accumulation by modifying root architecture and increased nutrient absorption (1a) (right). Salt accumulation creates competition for nutrient uptake and transport. This results in imbalance of the ionic composition of plant, affecting plant's physiological traits (2) (left). Endophytic fungi improve expression of genes and upregulate several cation transporters, resulting in improved nutrient uptake and maintenance of ionic homeostasis (2a) (right). Increase of salt in soil lowers soil water potential resulting in cellular dehydration (3) (left). Endophytic fungi negate this effect by mediating accumulation of osmolytes consequently improving plant's water status (3a) (right). Increasing salinity causes oxidative stress due to imbalance in reactive oxygen species generation and quenching activities of antioxidants (4) (left). Endophytic fungi improve the antioxidant systems of plants reducing oxidative stress under salt stress (4a) (right). Salt stress hinders photosynthesis by reducing uptake of magnesium and decreasing chlorophyll concentration which eventually reduces carbon dioxide supply to RuBisCo (5) (left). Endophytes have a positive effect on photosynthesis under salt stress (5a) (right). See text for relevant references and further details

increase in the rate of tissue respiration. Under these conditions, photosynthetic capacity is limited, and the plant uses its own photo-assimilates, resulting in decreased growth. Rewald et al. (2015) showed that in NENC *Ulmus glabra* seedlings there was a significant increase in fine root respiration under salt stress as compared to their ENC counterparts. This suggested that colonization by endophytic fungi can prevent a major increase of root respiration under moderate NaCl stress, enabling trees to deploy more assimilated C for growth and, theoretically, improve defence mechanisms against other stress factors occurring in urban environments.

Endophytic fungi are effective against several root diseases (Azcón-Aguilar and Barea 1997; Borowicz 2001) and impart stress tolerance to plants (Duc et al. 2018; Evelin et al. 2019; Yasmeen et al. 2019),but can also enhance susceptibility to biotrophic leaf pathogens (Gernns et al. 2001; Waller et al. 2005). These endophytes have been frequently reported to not only protect against plant pathogens and pests but also impart strong tolerance against several abiotic stresses in crops (Gangwar and Singh 2018).

In the past decade, significant progress has been made to understand several mechanisms of salt tolerance imparted by endophytic fungi. In the following sections,

current understanding of biochemical and physiological changes that occur in salt stressed plants inoculated with endophytic fungi will be covered. This will include advances made recently toward better understanding of the mechanisms that contribute to salt stress alleviation in ENC plants. Finally, gaps in our understanding of the mechanisms will be identified and research challenges to be met in future studies will be discussed.

Mechanisms of salt tolerance in ENC plants

Increase in total biomass

Total biomass is usually evaluated as an indicator of the plant's ability to tolerate salinity. Several studies have highlighted that endophytic fungi impart salinity tolerance in host plants by virtue of higher biomass as compared to NENC plants. Endophytic fungus colonization has been demonstrated to increase biomass in *Zea mays* L. (Rho et al. 2018), soybean (Hamayun et al. 2017), *Vochysia divergens* Pohl (Farias et al. 2019), *Solanum lycopersicum* (Azad and Kaminskyj 2016), *Brassica juncea* (Ahmad et al. 2015), *Oryza sativa* L. (Saddique et al. 2018) and, *Triticum aestivum* L. (Zhang et al. 2019b).

The total biomass can also be assessed by measuring plant relative growth rate (plant weight increment per plant weight unit). This includes measurement of the net assimilation rate (NAR) (the increase in plant weight per leaf area unit), the leaf area ratio (LAR) and root relative growth rate (RGR$_{plant}$). Balliu et al. (2015) investigated the effects of commercially available AMF inoculant (*Glomus* sp. mixture) on growth and nutrient acquisition in tomato (*Solanum lycopersicum* L.) plants grown in media with different levels of salinity. Salinity stress immediately and significantly reduced the LAR, NAR and RGR$_{plant}$ in NENC as compared to ENC plants. Similarly, Sallaku et al. (2019) showed that AMF alleviates the salinity stress in cucumber plants by extending their root length and root surface area and even more through enhancing their photosynthetic rate (NAR) as compared to NENC plants.

Alteration of root architecture

Root branching and root system architecture play a significant role in determining the composition of exudates (Badri and Vivanco 2009). Changes in the root system architecture for regulating salt acquisition and translocation are crucial for enhancing plant resistance to salt stress (Jung and McCouch 2013). Barley plants experienced a decline in primary root growth under saline conditions due to salt-induced inhibition of cell division and elongation of root epidermal cells, while simultaneously stimulating lateral root development (Rahnama et al. 2011). Endophytic fungi can modulate the plant's ability to modify root architecture (Salope-Sondi et al. 2015; Vahabi et al. 2016). Yun et al. (2018) observed that the length and volume of roots were greater in ENC than in NENC maize plants under saline conditions and similar observations have been reported in *Hordeum vulgare* (Waller et al. 2005) and *Oryza sativa* L. (Kord et al. 2019). Improved root systems enable the plant to utilize water and minerals from non-saline areas until exploitation of areas affected by salt cannot be avoided (Jogawat et al. 2013). Though few studies have shown the ability of endophytic fungi to alter root architecture under saline conditions for beneficial purposes, much remains to be investigated on endophytic fungi influenced root architecture for better water and nutrient uptake in saline conditions.

Osmoregulation

Upon exposure to saline environments, plants undergo a reduction in water absorbing capacity from the soil, disrupting cell water relations and inhibiting cell expansion. In order to negate these effects, plants employ osmoregulation as a mechanism to tolerate salt stress (Munns and Tester 2008). This is achieved by accumulation of osmolytes in the form of proline, glycine betaine, sugars, organic acids, polyamines and amino acids contributing to osmotic adjustment (Hasegawa et al. 2000). These osmolytes, often termed as compatible solutes, are organic compounds of low molecular weight that are water soluble and non-toxic at high concentrations (Chen and Murata 2011).

Under salt stress, ENC plants have been shown to possess higher osmotic potential than NENC plants (Contreras-Cornejo et al. 2014) due to accumulation of osmolytes (Ahmad et al. 2015; Song et al. 2015) (Fig. 2). Osmolytes are also involved in quenching reactive oxygen species (ROS), maintaining membrane integrity, and stabilizing enzymes. Osmolytes are also described as osmoprotectants (Azad and Kaminskyj 2016; Li et al. 2017). Endophytic symbiosis can influence the concentration and profile of polyamines and organic acids in plants (Chen et al. 2019; Zhao et al.
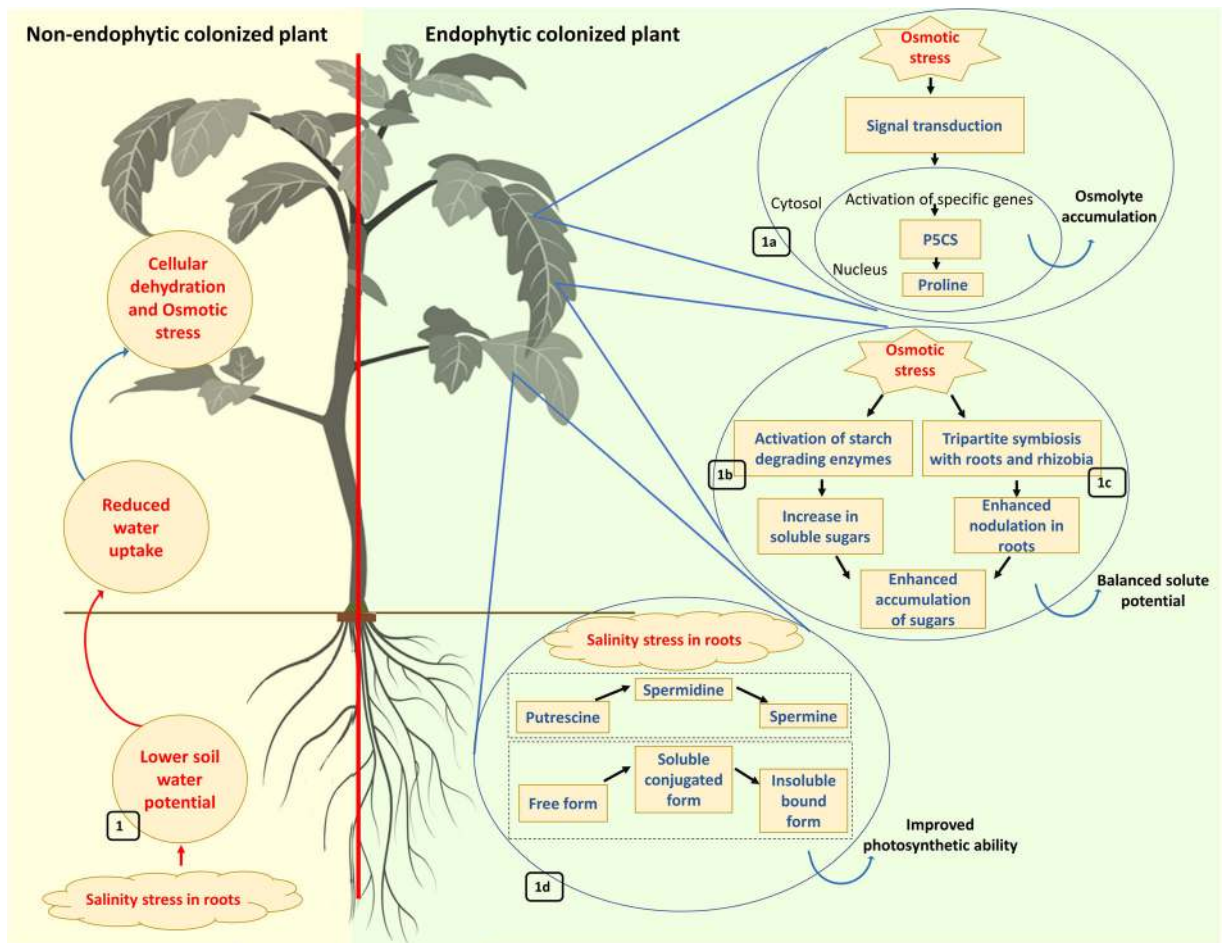
Fig. 2 Salinity stress induced osmotic stress tolerance mechanisms in plants. Increase in salt in soil lowers the soil water potential of plant cells. This reduces water uptake by plants and consequently causes cellular dehydration (1) (left). To combat this issue, plants accumulate osmolytes, such as proline, sugars and polyamines in higher concentration. Osmolyte accumulation results in lowering of cellular water potential and maintains a favourable gradient for water uptake from soil to roots. Endophytic fungi alleviate osmotic stress by influencing the expression of specific genes, P5CS, pyroline-5-carboxylate synthase (1a) (right), involved in the biosynthesis of the osmolyte proline, activation of starch degrading enzyme, glucan-water dikinase (1b) (right) and forming tripartite symbiosis with roots and rhizobia (1c) (right) to elevate the accumulation of sugars and by increasing the biosynthesis of polyamines such as spermidine and spermine (1D) (right). See text for relevant references and further details

2014). Polyamines help retain ion homeostasis in plant cells by enhancing the uptake of nutrients and water (Pang et al. 2007). Organic acids may increase the availability of nitrogen, phosphorus and potassium (N, P and K) in soil (Samolski et al. 2012). The role of specific osmolytes in improving salt tolerance is ENC plants are discussed below.

Proline

Proline is one of the most common osmoprotectants that accumulates in plants during salt stress, thereby ameliorating the negative effects of salinity. Proline has been observed to protect cell walls under osmotic stress, protect protein integrity and to increase enzymatic activity by acting as a molecular chaperone. Proline also has a role in scavenging ROS and shows singlet oxygen quenching ability (Kaur and Asthir 2015). Despite these benefits, there are conflicting reports on the role of endophytic fungi in proline accumulation in salt stressed plants. Several studies reported increases in proline contents in ENC plants compared to NENC plants, while others have reported lower proline contents in ENC plants (Table 1). Higher proline content in ENC

Table 1 Examples of studies on effects of salt stress and endophytic fungi on osmotic regulation in plants

S. No.	Salt level (mM NaCl)	Plant	Fungus	Parameters assessed	Effects of		References
					Salinity	Endophytic fungi on salt stressed plants	
1	0, 100	Zea mays	Yarrowia lipolytica	Shoot proline content, total flavonoid, total phenolics, phytohormone analysis	Increased	Controlled the production of proline	Jan et al. (2019)
2	0, 100, 200, 300	Hordeum vulgare	Epichloë bromicola	Free, soluble conjugated and insoluble bound forms of polyamine (proline), putrescine, spermidine and spermine content	Increased proline	Proline, Spermidine, total spermine- increased under higher stress conditions, Putrescine, free form of spermine- significantly decreased at higher salt treatments	Chen et al. (2019)
3	0, 50	Solanum lycopersicum	Piriformospora indica	Shoot proline content	Highly increased	Significantly reduced	Abdelaziz et al. (2019)
4	40, 100, 175, 250	Medicago truncatula	Piriformospora indica	Shoot proline content	Continually enhanced in line with the increased salt concentration	Significantly increased than un-colonized plants	Li et al. (2017)
5	0, 100, 200	Brassica juncea	Trichoderma harzianum	Oil and proline content, pigments, enzymatic assay	Increased with maximum accumulation of 59.12% at 200 mM NaCl	Further increase to 70.37%	(Ahmad et al. 2015)
6	0, 150	Triticum aestivum	Trichoderma longibrachiatum	Water content in leaves and roots, chlorophyll content, shoot proline content	Increased	Highest increase win plants pretreated with fungus under 150 mM NaCl stress	Zhang et al. (2016)
7	0, 70, 150, 240	Oryza sativa	Five isolates of Trichoderma sp.	Leaf water content, chlorophyll content, proline content, membrane stability, lipid peroxidation and expression of stress related genes	Increased	Further increased	Rawat et al. (2016)
8	0, 100, 200, 300, 400, 500	Triticum aestivum	Piriformospora indica	Total biomass, photosynthetic pigments, compatible solutes	Increased	Further increased	Zarea et al. (2012)

plants has been attributed to – (i) favouring a decline in ionic influx inside cellular masses thus helping plants to maintain their osmotic balance; (ii) increasing the expression of the gene encoding Pyrroline-5-carboxylate synthase (P5CS) enzyme which is involved in proline biosynthesis; and (iii) increasing activity of the P5CS enzyme (Rawat et al. 2016). Besides its role as an osmolyte proline can act as a stress marker. In ENC tomato plants, proline accumulation was reduced when the toxic effects of salinity were reduced following colonization of an endophytic fungus, *Piriformospora indica* (Abdelaziz et al. 2019).

Sugars

In salt stressed plants, the accumulation of total soluble sugars, such as glucose, sucrose, dextrins and maltose, serves as an osmoprotection as they can stabilize the cell membrane and protoplast. These sugars also protect water soluble enzymes from high intracellular concentrations of inorganic ions (Liang et al. 2018). The synthesis of soluble sugars from starch and sucrose in plants is upregulated by the activities of sucrose anabolizing enzymes such as α- and β-amylase, which convert starch into dextrins and maltose, respectively (Preiss 2018). Sucrose phosphate synthase and sucrose synthase catalyse the synthesis of sucrose, while β-fructofuranosidase catalyses the breakdown of sucrose to glucose and fructose (Peng et al. 2016). In plants grown under saline conditions, sucrose undergoes decomposition in order to meet the requirements for glucose (Munns and Tester 2008).

There have been reports that show the role of endophytic fungi in enhancing accumulation of soluble sugars in salt stressed plants (Qi and Zhao 2013; Uma Shaanker 2014; Zhang et al. 2019b). These sugars act as chemoattractant signals to soil rhizobia (el Zahar Haichar et al. 2014). These chemoattractants can direct movement to microorganisms in response to chemical gradients- a behaviour known as chemotaxis. This chemotactic response of microorganisms to root exudates play key role in initiating communication between plant roots and microbes. Yang et al. (2015) reported that the colonization by *Phomopsis liquidambari* could stimulate sugar secretion from the rhizodeposition of sloughed off cells and root debris of rice, thereby providing carbon to the endophytic fungi. Another study of *P. liquidambari* on peanut showed increased soluble sugar contents in leaves. This was due to the ability of

the fungus to form tripartite symbiotic associations with peanut roots and rhizobia. This tripartite association significantly enhanced peanut nodulation (Zhang et al. 2017b). Here, sucrose derived from photosynthesis was transported to bacterial inoculated root nodules and was hydrolysed by sucrose synthase into UDP-glucose and fructose. This was due to the allocation of more carbon by the endophyte toward peanut and rhizobia symbionts by increased soluble sugar content, leading to more active nodule carbon metabolism in ENC plants.

Furthermore, Sherameti et al. (2005) also suggested that one of the major starch-degrading enzymes, glucan-water dikinase, activated by the fungus in colonized roots, is responsible for the increase in soluble sugars in ENC plants. Similar results were obtained by Ghabooli (2014) with *Piriformospora indica* increasing the level of soluble sugars, including glucose, fructose, and sucrose, in inoculated plants under salt stress conditions. Recently, Zhang et al. (2019a) demonstrated that *T. harzianum* improved salt tolerance of cucumber seedlings by enhancing accumulation of sugars. This results in adjustment of the osmotic potential for cellular water retention and turgor maintenance, thereby minimizing the adverse effects of salt stress by balancing the solute potential (Bai et al. 2019).

Organic acids

Other important osmolytes in plants are organic acids such as citric acid and malic acid. They are found in plant vacuoles and the regulation of their metabolism plays a crucial role in providing tolerance to salt stress (Guo et al. 2010). Fungal endophytes have been reported to induce the release of organic compounds by the roots (Yang et al. 2015; Zhang et al. 2014), thus influencing the concentrations and profile of organic acids in plants. One of the major plant nutritional disorders associated with increased salinity in soil is iron (Fe) deficiency. Endophytes can enhance Fe acquisition by their host through their ability to secrete organic acids which chelate and solubilise iron in the soil (Chen et al. 1998; Khan et al. 2006). A study by Zhao et al. (2014) demonstrated that the release of organic acids from endophytes, resulted in ferric solubilization to form organic ferric salts that can be assimilated directly by plants under saline conditions. It has also been shown that ENC plants have better nutrient uptake capacity and distribution within plant tissues due to modulation of the root architecture and nutrient availability in the soil.

These benefits are imparted by increases in organic acids produced by ENC plants (Samolski et al. 2012; Zhao et al. 2014). Limited research has been done on understanding the mechanisms underlying the changes in organic acids in ENC plants, thus this topic calls for further investigation.

Polyamines

Polyamines (PA) are low molecular weight nitrogenous aliphatic molecules that participate in physiological processes such as activation of antioxidant systems, cell growth and development, and in cellular osmoregulation in plants under salt stress (Singh et al. 2018). PA also regulate ion channels, either by direct binding or via PA-induced signalling molecules (ROS and NO). PAs also regulate the activity of ion channels indirectly by membrane depolarization. The hyperpolarization-activated Ca^{2+} influx and the NO-induced release of intracellular Ca^{2+} result in a higher cytoplasmic Ca^{2+} concentration, which is a major component in general stress responses such as stomatal movements (Wani 2018; Williams 1997). They are either present in free, soluble conjugated (covalently conjugated with small molecules such as phenolic acids) or insoluble (bound with macromolecules such as proteins, DNA and RNA) forms. These compatible solutes accumulate under salt stress and include putrescine (Put, diamine), spermidine (Spd, triamine) and spermine (Spm, tetramine) (Minocha et al. 2014; Todorova et al. 2013).

Differences in PA (Put, Spd, Spm) responses under salt-stress have been reported in several species (Singh et al. 2018) and it remains unclear which polyamine plays the major role in imparting salt tolerance. Chen et al. (2019) demonstrated that the putrescine content was significantly reduced in ENC plants compared to NENC plants in high stress conditions whereas spermidine and spermine content showed the opposite pattern. It was suggested that salinity stress tolerance induced by endophytic fungus *Epichloë bromicola* correlated with enhanced conversion of putrescine to spermidine and spermine. The fungus also converted the free forms and soluble conjugated forms of polyamines to insoluble bound forms of polyamines.

Modulation of the polyamine pool to help tolerate salt stress by arbuscular mycorrhizal fungi (AMF) is well explored (Evelin et al. 2009). However, research on polyamine metabolism during the interactions between endophytic fungi and plants under salt stress is underrepresented and many questions remain unanswered. For example, most plant polyamine research relates to changes in free polyamines, and where polyamine conjugates have been measured, substantial changes have been detected. The precise role of polyamines, free or conjugated, in ENC plants remains unclear. Further investigations, focusing on understanding endophyte-facilitated modulation of polyamines, including the intracellular localization of free polyamines and conjugates associated with salt tolerance in plants, is needed. Already some of the key genes involved in the biosynthetic pathways have been cloned making it possible to manipulate polyamine metabolism using molecular genetic approaches (Malmberg et al. 1998). Hence, genetic manipulation of polyamine levels in ENC plants may allow valuable insights into the role of these compounds especially in studies of plant tolerance to salt stress.

Nutrient acquisition and ionic homeostasis

High salt (Na^+ and Cl^-) in the soil disturbs nutrient availability by imposing competition during uptake, translocation or distribution within the plant. This may suppress nutrient associated activities resulting in undesired ratios of $Na^+:K^+$, $Na^+:Ca^{2+}$, and $Ca^{2+}:Mg^{2+}$ (Munns et al. 2011). This in turn results in imbalance among ionic composition of the plant subsequently affecting plants physiological traits (Hasegawa et al. 2000; Munns et al. 2006). However, endophytic symbiosis has been shown to improve assimilation of nutrients and assist in maintenance of ionic homeostasis in host plants grown in saline conditions (Table 2).

Although the effects of AM fungi on plant nutrient acquisition are commonly discussed based on the differences of nutrient concentration in plant tissues, the relative uptake rate of nutrient elements (RUR) has recently been suggested as a better tool to distinguish the differences among treatments over a short period, as the nutrient concentration could be largely influenced by the dilution effect of fast growth in young plants. Balliu et al. (2015) found that RUR values of ENC tomato plants grown in both non-saline and moderate saline conditions were higher than in non-inoculated seedlings. Similarly, another study showed the enhancement effect of AMF inoculation on the nutrient uptake capacity of cucumber seedlings after salt stress (Sallaku et al. 2019).

Table 2 Examples of studies on the effects of salinity and endophytic fungi on nutrient concentration and ionic ratios in plants

S. No.	Salt level (mM NaCl)	Plant	Fungus	Parameters assessed	Effects of		References
					Salinity	Endophytic fungi on salt stressed plants	
1	0, 140	Cucumis sativus	Phoma glomerata LWL2 and Penicillium sp. LWL3	Na^+, K^+, Ca^{2+}, Mg content	Significant increases in Na^+ and decreases in K^+, Mg^{2+} and Ca^{2+} levels	Significantly higher levels of K^+, $Mg2^+$ and $Ca2^+$ ions, particularly in case of Penicillium sp. and P. glomerata and inhibit the uptake of Na^+	Waqas et al. (2012)
2	0, 100, 200	Zea mays	Piriformospora indica	Na^+, K^+ content	Increased Na^+ in roots and shoots, K^+ in shoots and decreased K^+ in roots	Significant decreased levels of Na^+ and K^+ in roots and increase in shoots	Yun et al. (2018)
3	0, 75, 100	Arabidopsis thaliana	Piriformospora indica	Transcript levels of several genes known to encode proteins involved in Na^+ and K^+ homeostasis and the abiotic stress marker gene relative to Desiccation A (RD29a)	Increased- expression of the stress marker gene, RD29a, expression level of AtHKT1, K^+ content in roots and shoots, Decreased Na^+ content in roots and shoots	Decreased- expression of the stress marker gene, RD29a, further decrease in Na^+ content, Further increased expression level of AtHKT1, and K^+ content	Abdelaziz et al. (2017)
4	0, 100	Arabidopsis thaliana	Trichoderma virens and Trichoderma atroviride	Na^+ content	Decreased Na^+ content in roots	Further decreased NA^+ content in roots	Contreras-Cornejo et al. (2014)
5	0, 150, 300, 450, 600	Hordeum vulgare	Epichloe	Na^+, C, P, N, K^+ content, C:N, C:P, Na^+:K^+, N:P ratios	Increased Na^+, N, P and K^+ contents, ionic ratios, no significant effect on C content	Further increased N, P and K^+ contents, N:P ratios; Decreased C:N, C:P, Na^+:K^+ ratios	Song et al. (2015)
6	0, 100, 300	Hordeum vulgare	Piriformospora indica	Na^+, K^+, Ca^{2+}, ionic ratios	Increased Na^+, Ca^{2+}, Decreased K^+:Na^+, Ca^{2+}:Na^+ ratios	Increased K^+, K^+:Na^+, Ca^{2+}:Na^+, Decreased Na^+ content	Ghabooli (2014)
7	0, 50, 100, 150	Lolium arundinaceum	Neotyphodium coenophialum	Na^+, K^+, Ca^{2+}, and Mg^{2+} content in leaves, roots and sheath	At lower salt concentration- in leaves, decreased K^+, similar Na^+, Ca^{2+}unaffected; in sheath, decreased K^+, similar $Na^+$and Ca^{2+} At higher salt concentration- in leaves, decreased Na^+, similar K^+, Mg^{2+}unaffected	At lower salt concentration- in leaves, increased K^+, similar Na^+, Ca^{2+}unaffected; in sheath, increased K^+, similar $Na^+$and Ca^{2+} At higher salt concentration- in leaves, increased Na^+, similar K^+, Mg^{2+}increased at all concentrations	Yin et al. (2014)

Phosphorus

Phosphorus (P) and nitrogen (N) are two of the most important and essential elements for plant growth with crucial roles in cell function and metabolism (Uchida 2000). Increased salt in soil occludes P to plants due to its precipitation with other cations (de Aguilar et al. 1979), thereby creating soil-induced P deficiency in plants. This affects the normal growth of the plant and causes older leaves to die prematurely (Niu et al. 2012). Increased P acquisition in ENC plants under saline conditions is attributed to (i) increased availability of phosphates in soil due to the conversion of insoluble phosphates into soluble forms through the process of acidification, chelation and exchange reactions; (ii) ability of endophytic fungi to absorb P at lower thresholds owing to the expression of a high affinity Pi transporter, PiPT, and (iii) ability of endophytic fungi to interact with diverse rhizobacteria which have inorganic phosphate-solubilizing capabilities by virtue of production of a variety of organic acids and acid phosphatases (Johri et al. 2015; Meena et al. 2010; Ngwene et al. 2016; Singh et al. 2009; Srividya et al. 2009; Swetha and Padmavathi 2016). This effective P uptake in ENC plants aids in transporting absorbed phosphorus to leaves, prompting plant growth; increasing absorption of nutrients and biomass accumulation (Wu et al. 2019), consequently alleviating the adverse effects of salinity.

Nitrogen

Nitrogen plays a crucial role in cell function and metabolism (Chokshi et al. 2017). Plants absorb N as nitrate (NO_3^-), ammonium (NH_4^+) ions, and also as organic compounds such as amino acids and peptides (Rentsch et al. 2007; Tegeder and Rentsch 2010) but absorption is compromised by salinity due to N immobilisation. Nitrate reductase (NR, E.C.1.6.6.1) catalyses reduction of NO_3^- to NO_2^- and its activity is nitrate-inducible. The NR activity is the limiting step in the conversion of NO_3^- to amino acids (Campbell 1999). Nitrate reductase activity in leaves is largely dependent on nitrate flux from roots (Ferrario-Méry et al. 1998) and is severely affected by osmotic stress induced by NaCl (Baki et al. 2000). A number of reports have shown that endophytic fungal colonization assists in N uptake under stress conditions (Khan et al. 2011a; Sherameti et al. 2005; Song et al. 2015). Recruitment of N in endophytic interactions differs from mycorrhizal interactions in

which the fungus preferentially recruits ammonium rather than nitrate from the soil (Boukcim and Plassard 2003; Gage 2004). Song et al. (2015) showed that in ENC plants, N content increased in both the shoots and roots with increasing salt concentrations. The fungus was suggested to be involved in the cell's antioxidant and ROS-scavenging enzymes where N is an essential component (Cabot et al. 2014; Khan et al. 2014). Another study by Sherameti et al. (2005) showed a significant increase in growth of ENC plants that was proposed to be associated with a stimulation of the NADH-dependent NR, the key enzyme of nitrate assimilation in plants.

Na^+:K^+ ratio

Increased levels of Na^+ in cells impairs important biochemical mechanisms required for plant growth and survival. Sodium accumulation alters cellular Na^+:K^+ ratios thereby reducing the availability of K^+ that is required for activity of various enzymes and for the regulation of osmotic pressure and stomatal closure. Increased Na^+ also competes with K^+, disrupting cellular metabolism in roots and leaf tissues (Abdelaziz et al. 2017). This eventually increases the Na^+:K^+ ratios in the cytosol, and subsequently disrupts enzyme activity, protein synthesis, turgor maintenance, photosynthesis and stomatal movement (Evelin et al. 2019).

High Na^+:K^+ ratios in plants indicate higher levels of stress. Hence, plants must maintain low levels of Na^+ to be able to resist the deleterious effects of salinity. ENC plants consistently have lower Na^+:K^+ ratios than NENC plants under saline conditions. Reza Sabzalian and Mirlohi (2010) demonstrated that the toxic effect of Na^+ was mitigated in grasses inoculated with endophytic fungi by increasing K^+ concentration and thus maintaining the Na^+:K^+ ratio in plants. Similar results were found by Song et al. (2015) and Alikhani et al. (2013) where endophytic fungi modulated ion accumulation in colonized barley plants by decreasing the foliar Na^+:K^+ ratio. Restricting the transport of Na^+ to leaves and ensuring a low cytosolic Na^+:K^+ ratio are important ways plants can increase their tolerance to high salt levels (Berthomieu et al. 2003; Cuin et al. 2003). Increase of K^+ concentration is also related to mechanisms that control turgor pressure (Beckett and Hoddinott 1997). Song et al. (2015) also showed that the lower Na^+:K^+ ratios observed in ENC plants decreased the level of toxic ions and osmotic influence on plants under

salt stress. Another study on barley plants inoculated with endophytic fungi showed a decreased Na$^+$:K$^+$ ratio compared to uninoculated plants, indicating that this ratio is a reliable indicator of the severity of salt stress, or for screening plant genotypes for high Na$^+$ tolerance (Ghabooli 2014) (Table 2).

Plants control Na$^+$ homeostasis through a variety of membrane proteins, antiporters, nonspecific cation channels, Na$^+$ and K$^+$ transporters, vacuolar ATPases and aquaporins, and the plasma membrane (PM) (Grabov 2007). Recently, Abdelaziz et al. (2017) postulated a molecular basis of establishing a balanced ion homeostasis of Na$^+$:K$^+$ ratio in ENC plants. Inoculated Arabidopsis plants had enhanced transcript levels of the genes encoding the high Affinity Potassium Transporter 1 (HKT1) and the inward-rectifying K$^+$ channels KAT1 and KAT2, which play key roles in regulating Na$^+$ and K$^+$ homeostasis. Subsequently, lower Na$^+$:K$^+$ ratios were confirmed in the Arabidopsis line gl1-HKT:AtHKT1;1 that expresses an additional AtHKT1;1 copy driven by the native promoter. This study demonstrated that endophytic colonization promotes plant growth under saline conditions by modulating the expression level of the major Na$^+$ and K$^+$ ion channels, which helps in the establishment of a balanced ion homeostasis of Na$^+$ and K$^+$ under salt stress conditions (Abdelaziz et al. 2017).
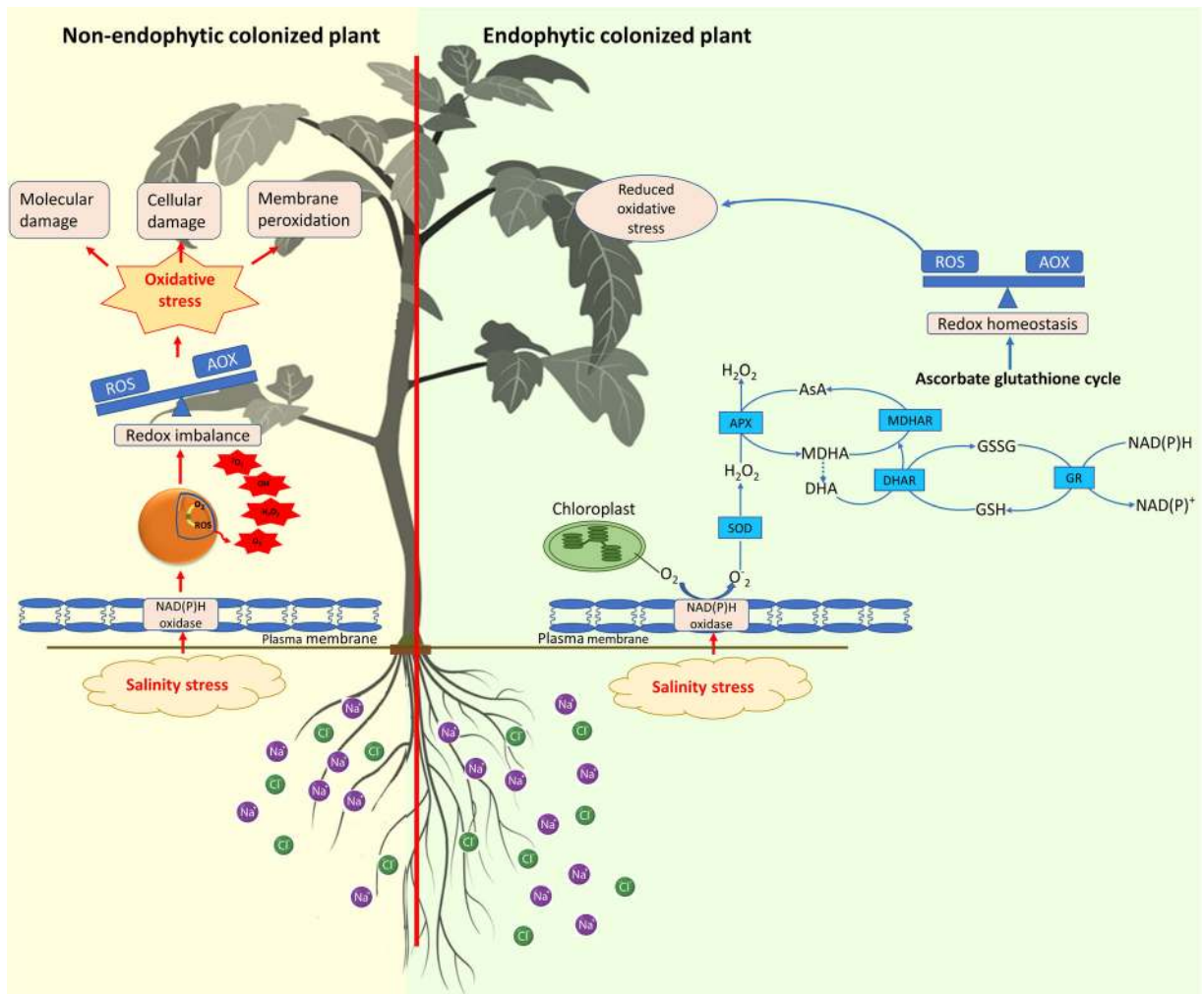
Oxidative stress

Salt stress (osmotic and ionic stress) also interferes with proper cellular functions of plants due to enhanced production of ROS, which can lead to oxidative damage in several cellular components such as lipids, proteins and DNA (Gupta and Huang 2014). ROS consist of a group of chemically reactive oxygen molecules such as hydroxyl radical (OH-), H_2O_2, O_2^- and O^{2-} and are produced as a result of interrupted pathways in plant metabolism that cause transfer of high energy electrons to molecular oxygen (Gill and Tuteja 2010). Broad host range endophytic fungi can confer effective tolerance to ROS under abiotic stress conditions such as salinity (Mastouri et al. 2010; Rodriguez et al. 2008). (Redman et al. 2011); Singh et al. (2011) reported that exposure to high salt conditions caused ROS accumulation in tomato, rice, panic grass, and dunegrass without endophytic associations, whereas the ENC plants had decreased ROS accumulation through various pathways (Fig. 3).

Plants have two ways to counteract the adverse consequences of ROS, mainly enzymatic and non-enzymatic antioxidative systems. The enzymatic system includes catalase (CAT), ascorbate peroxidase (APX), superoxide dismutase (SOD), glutathione reductase (GR), dehydroascorbate reductases (DHAR) and monodehydroascorbate reductases (MDHAR). The non-enzymatic antioxidant system consists of ascorbic acid (AsA), glutathione (GSH), carotenoids and osmoprotectants that play roles in quenching toxic by-products of ROS.

Baltruschat et al. (2008) reported increased activity of CAT, APX, GR and DHAR in the root tissues of barley under saline conditions. Increased activity of DHAR was seen in *P. indica* colonized barley leading to detoxification of ROS and an enhanced ratio of ascorbic acid to neutralize oxygen free radicals (Foryer and Noctor 2000). Azad and Kaminskyj (2016) used H_2O_2 localization as a proxy to assess accumulation of ROS and showed that ENC plants had lower H_2O_2 levels in their leaves following NaCl-stress, confirming the role of endophytes to reduce stress-induced ROS generation.

Also, Zhang et al. (2016) reported that ENC plants had higher SOD, peroxidase (POD) and CAT activity suggesting that the coordination of POD and CAT activity along with SOD activity played a central protective role in the O_2^- and H_2O_2 scavenging process in ENC plants (Ahmad et al. 2015). Increased activity was a result of increased expression of the genes encoding the enzymes (Zhang et al. 2016). Under saline conditions, endophytic colonization also increases the concentrations of non-enzymatic antioxidant molecules such as AsA, GSH and carotenoids in plants as shown by several studies (Jan et al. 2019; Jogawat et al. 2013; Prasad et al. 2013; Waller et al. 2005).

Salinity increases the level of lipid peroxidation (Hernández 2019; Yu et al. 2020) which results in higher membrane permeability and loss of ions from the cells (Gupta and Huang 2014). NaCl treatment of ENC plants resulted in higher rates of lipid peroxidation in salt-sensitive plants than in salt-tolerant plants suggesting that the rate of lipid peroxidation can be used as an indicator to measure how effectively ENC plants cope with salt stress (Baltruschat et al. 2008). Another study showed that ENC plants contained higher ascorbate concentrations in roots compared with NENC plants, while the ratio of ascorbate to dehydroascorbate was not significantly altered and CAT, APX, GR,

Fig. 3 Oxidative stress tolerance mechanisms in salt stressed plants. Increase in salinity causes oxidative stress in plants due to redox imbalance between ROS (reactive oxygen species) and antioxidants. This results in molecular and cellular damage and membrane peroxidation eventually disturbing the normal functioning of the cell. Several antioxidant enzymes are induced to combat salt stress including catalyse (CAT), ascorbate peroxidase (APX), superoxide dismutase (SOD), peroxidase (POX), glutathione reductase (GR), dehydroascorbate reductase (DHAR) and monodehydroascorbate reductase (MDHAR). Ascorbate (AsA), glutathione (GSH) and carotenoids are non-enzymatic antioxidants that are produced to counteract the adverse consequences of salt stress. In endophyte colonized (ENC) plants, the tolerance mechanism in reinforced by activating an efficient antioxidant system that abates the oxidative damage caused due to salt stress

DHAR and MDHAR activities were increased. These changes were consistent with the decrease of leaf lipid peroxidation observed in these experiments (Waller et al. 2005). Similar results were shown by Mastouri et al. (2010) and Zhang et al. (2001) where ENC plants had significantly reduced accumulation of lipid peroxides than control plants under salt stress. Malondialdehyde (MDA), a product of lipid peroxidation, is generally regarded as an indicator of free radical damage to cell membranes caused by oxidative stress.

Zhang et al. (2016) reported that salt stressed ENC plants had a 15% reduction in MDA compared to salt stressed NENC plants. Table 3 lists some of the studies reporting changes in lipid compositions due to endophytic symbiosis in salt stressed plants.

Photosynthesis

Salt stress hinders photosynthesis resulting in an enormous loss in crop productivity (Sudhir and Murthy

Table 3 Examples of studies on the effects of salinity and endophytic fungi on lipid peroxidation in plants

S. No.	Salt level (mM NaCl)	Plant (Family)	Fungus	Parameters assessed	Effects of Salinity	Endophytic fungi on salt stressed plants	References
1	0, 100, 200, 300	*Oryza sativa*	*Piriformospora indica*	Total soluble proteins, lipid peroxidation (measured thiobarbituric acid reactive substances in shoots and roots), free proline content, and enzyme antioxidants(catalase(CAT: EC1.11.1.6), glutathione reductase(GR: EC1.6.4.2), superoxide dismutase(SOD: EC 1.15.1.1), ascorbate peroxidase(APX: EC 1.11.1.11)) activity	Increased lipid peroxidation, SOD, APX, CAT, GR; Decreased total soluble proteins, free proline content	Increased total soluble proteins, proline, further increase in SOD, APX, CAT, GR; Decrease in lipid peroxidation	Bagheri et al. (2013)
2	0, 100	*Glycine max*	*Fusarium verticillioides*	Lipid peroxidation, antioxidant enzyme analysis, gibberellins, ABA, salicylic acid	Increased ABA, SA, lipid peroxidation; Decreased CAT, SOD, POD, SA, ABA	Increased CAT, SOD, POD; Decreased lipid peroxidation, ABA, SA significantly	Radhakrishnan et al. (2013)
3	0, 100	*Glycine max*	*Fusarium verticillioides and Humicola sp*	Protein content, catalase activity, ABA content, SA content, lipid peroxidation (measured in terms of malondialdehyde-MDA content)	Increased ABA, SA, lipid peroxidation; Decreased CAT, SOD, POD, SA, ABA, lipid peroxidation	Significant three-fold reduction in MDA level, ABA, SA; Increased CAT, SOD, POD	Radhakrishnan et al. (2015)
4	0, 100, 175, 250	*Medicago truncatula*	*Piriformospora indica*	Proline, MDA, Sodium ion, antioxidant enzymes	Increased MDA, NA+ in shoots, slight increase in proline content; Decreased POD, SOD, CAT	Highest increased in proline content with increase in POD, SOD, CAT; decreased MDA, NA+ in shoots	Li et al. (2017)
5	0, 200	*Cucumis sativus*	*Trichoderma harzianum*	Antioxidant enzymes, K+ content, K+/Na+ ratio, Na+ content, ethylene levels, MDA levels as a measure of lipid peroxidation	Increased MDA levels, Na+ content, ethylene levels; Decreased antioxidant enzymes, K+ content, K+/Na+ ratio	Improved activities of antioxidant enzymes, increased K+ content, K+/Na+ ratio; decreased Na+ content, ethylene levels, MDA levels	Zhang et al. (2019a)

2004). Salt stress has been shown to degrade D1 and D2 proteins of the photosystem II reaction centre. These proteins play crucial roles in protein phosphorylation coupled with the flow of electrons (Jansen et al. 1996). Salt stress also results in decreased photosynthetic pigments by reducing the activity of enzymes that synthesize them. Osmotic shock resulting from salt stress leads to reduced leaf area and decrease in stomatal and mesophyll conductance (Chaves et al. 2009). This limits CO_2 availability and assimilation which consequently affects RuBisCO (Seemann and Critchley 1985). Decreasing CO_2 assimilation also increases the risk of the accumulation of electrons in thylakoid membranes and predisposes the photosynthetic apparatus to increased energy dissipation. Thus, to dissipate this energy, photosystem II loses excess electrons causing injury to photosynthetic tissues and affecting the net photosynthetic rate (Redondo-Gómez et al. 2010).

Plants can protect the photosystems from light induced inhibition and damage in several ways such as minimizing harvesting of light and dispersion of excess energy by non-photochemical quenching (NPQ) (Lima Neto et al. 2015). An increase in NPQ can limit quantum yield (Baker 2008) but ENC plants are reported to have lower NPQ, therefore symbiosis enhances photosynthetic efficiency by proficient conversion of harvested light into chemical energy and minimizing NPQ (Pehlivan et al. 2017). Endophytic fungi are also known to reinforce these mechanisms and reduce the negative effects of salinity on plant photosynthetic capacity (Jogawat et al. 2013; Molina-Montenegro et al. 2018). Table 4 lists some of the studies in the last decade on effect of salinity and endophytes on photosynthesis in plants. Endophytic symbiosis combats the negative effects of salt stress on photosynthesis in several ways. ENC plants have shown improved water status resulting in larger leaf area and higher stomatal conductance and eventually better assimilation of carbon dioxide (Zarea et al. 2012).

Magnesium (Mg) is one of the essential macronutrients for plant growth and is involved in numerous physiological and biochemical processes such as photosynthesis, enzyme activation and synthesis of nucleic acids ad proteins (Chen et al. 2018). It is the central atom of the tetrapyrrole ring of chlorophyll *a* and *b* molecules, which are the major pigments for photosynthetic light absorption (Wilkinson et al. 1990). Salt reduces uptake of Mg^{2+} thus also reducing the concentration of chlorophyll in leaves (Sudhir and Murthy 2004). ENC plants

maintain higher chlorophyll concentration by improving the uptake of Mg^{2+} (Jogawat et al. 2013; Yin et al. 2014) and this leads to maintenance of plastid integrity and enhanced photosynthetic efficiency (Johnson et al. 2014).

Another way in which endophytes induce defence systems in plants under saline conditions is by upregulating the ascorbate-glutathione (ASH-GSH) cycle; for example Kumar et al. (2012) described that during salt stress, the endophytic fungus *P. indica* maintains a high antioxidative environment by defence system priming, especially the ascorbate–glutathione (ASH–GSH) cycle leading to maintenance of plastid integrity and therefore enhanced photosynthetic efficiency in colonised plants during abiotic stress (Johnson et al. 2014). ENC plants also confer the benefit of maintaining the integrity of photosystem II by repairing salt-induced degradation of D1/D2/Cytb 559 complex by the accumulation of glycine betaine in ENC plants (Rivero et al. 2014). Glycine betaine is also known to stabilise PSII pigment-protein complexes and protect the activities of RuBisCO and rubisco activase enzymes responsible for fixing CO_2 in AM fungi (Talaat and Shawky 2014).

Hormonal regulation

Induction of phytohormones is also one of the strategies plants use to mitigate abiotic stresses that ultimately enhance plant growth and productivity in stressful environments (Ryu and Cho 2015). Phytohormones, often regarded as plant growth regulators, are compounds that are derived from plant biosynthetic pathways acting either locally or via transport to other sites within the plant to mediate growth, development and nutrient allocation (Peleg and Blumwald 2011). These include abscisic acid (ABA), gibberellins (GA), ethylene (ETHY), cytokinins (CKs), brassinosteroids (BRs) and auxins, particularly indole acetic acid (IAA). To initiate suitable plant responses to environmental stimuli, there is interplay between these hormones to modulate biochemical and physiological processes (Saeed et al. 2017).

It is known that some strains of endophytic fungi can produce plant hormones, especially gibberellins (GAs), to help the plant to tolerate or avoid abiotic stress (Contreras-Cornejo et al. 2009; Khan et al. 2011b; Waller et al. 2005). Hamayun et al. (2010) reported that inoculation with the endophytic fungi *Phoma herbarum* showed increased plant biomass and elevated

Table 4 Examples of studies on the effects of salinity and endophytic fungi on photosynthesis in plants

S. No.	Salt level (mM NaCl)	Plant	Fungus	Parameters assessed	Effects of		References
					Salinity	Endophytic fungi on salt stressed plants	
1	0, 200, 300	Oryza sativa	Piriformospora indica	Photosynthetic pigment content [chlorophyll (Chl) a, Chl b]	Decreased	Increased	Jogawat et al. (2013)
2	0, 50, 150	Lactuca sativa (lettuce var. Romaine) and Solanum lycopersicum (tomato var. Moneymaker)	Colobanthus quitensis (AFE001) and Deschampsia antarctica (AFE002)	The net photosynthesis rate (A), and transpiration rate (EC), water use efficiency (WUE) for photosynthesis as the ratio between photosynthetic rate and transpiration (A/EC)	Decreased Amax, WUE	Significantly increased Amax, WUE	Molina-Montenegro et al. (2018)
3	0, 100, 200, 300, 400, 500	Triticum aestivum	Piriformospora indica and Azospirillum spp.	Photosynthetic pigments (Chl a, b, ab)	Decreased	Significantly increased with inoculation of both organisms	Zarea et al. (2012)
4	0, 300, 500	Solanum lycopersicum	Fusarium culmorum	Photosystem II (PsII) efficiency	Decreased	Increased	Azad and Kaminskyj (2016)

production of active GAs including GA_1, GA_3, GA_4, and GA_7 in salt-stressed soybean. Similar results were shown by Waqas et al. (2012), where salt-stressed cucumber plants inoculated with *Penicillium* sp. had larger shoot growth and plant biomass that was attributed to the secretion of bioactive GAs. A study on salt-stressed cucumber plants inoculated with *Trichoderma asperellum* Q1 alleviated the suppression effects of salt stress by altering the phytohormone levels (IAA, GA and ABA) and the phosphate solubilization ability (Lei and Zhang 2015). Three bioactive GAs, i.e. GA_4, GA_9 and GA_{12} were more abundant in ENC plants grown under salt stress compared to NENC plants (Khan et al. 2011c), and this mitigated the adverse effects of salinity and improved growth.

Endophytic symbiosis under saline conditions has a positive influence on the endogenous concentration of auxins (Contreras-Cornejo et al. 2009). Contreras-Cornejo et al. (2014) evaluated the expression of the auxin-responsive marker gene *DR5:uidA* which was upregulated in ENC plants compared to their counterparts under saline conditions speculating that, by providing auxins, *Trichoderma* spp. could restore auxin homeostasis and, consequently growth and development could be normalized when grown under salt stress.

Perspectives and future directions

Evolution has led to complex interactions between a wide diversity of microorganisms and plants; many of them resulting in the establishment of a symbiotic relationship between them (Hassani et al. 2018). These interactions beneficially impact plant survival, biodiversity, fitness and ecosystem function (Bai et al. 2018; Rosier et al. 2016; Sasse et al. 2018). Growing evidence indicates that endophytic associations can also be important for plant fitness, development of the immune system, tolerance to abiotic stresses, nutrient acquisition and disease suppression (Hiruma et al. 2016; Khan et al. 2015; Khare et al. 2018; Soliman et al. 2015; Terhonen et al. 2016; Zuccaro et al. 2014). This review highlights some of the numerous mechanisms by which endophytic symbiosis promotes salt tolerance in plants. However, there are several challenges and issues that future research should address for comprehensive understanding of these mechanisms. It is well established how osmotic adjustment in plants under salt stress via enhanced accumulation of osmolytes is achieved using endophytic symbiosis. However, the biochemical, molecular and genetic mechanisms are largely unexplored. Therefore, there is a need to understand these phenomena by investigating genes encoding enzymes used for the synthesis of molecules that are crucial for salt stress resistance. Therefore, dedicated research into unravelling the molecular basis of osmolyte accumulation in ENC plants will broaden our understanding of the mechanisms involved.

In recent years, new compounds, such as polyamines, and strigolactones have been implicated in improving plant tolerance to salt stress (Fahad et al. 2015). Strigolactones (SL) play regulatory roles to combat abiotic stress, including salinity, and in order to be fully effective, they need to modulate and interact with other phytohormones, especially auxin and ABA. SLs are also involved in several aspects of plant development; suppression of secondary branches in shoots, regulation of leaf senescence, stimulation of internode length and induction of endophytic symbiosis (de Saint Germain et al. 2013; Lopez-Raez et al. 2017; Yamada et al. 2014). This group of sesquiterpene lactones is responsible for hyphal branching and successful colonisation within roots by producing 5-deoxy-strigol, followed by the formation of a pre-penetration apparatus (Genre et al. 2005). Recently, SL secreted by roots of *Arabidopsis thaliana* was found to act as a signal molecule for colonization of endophytic *Mucor* sp. (Rozpądek et al. 2018). Studies on auxin and ABA involvement with endophytes under salt stress has been explored, but further research is required to investigate the role of strigolactones secreted by ENC plants in ameliorating salt stress.

The root is the primary location in plants that senses salt stress. The PM constitutes the interface between a cell and its surroundings and plays an important role in cell wall biosynthesis, ion transport, endocytosis, sensing of environmental stimuli, and cellular signal transduction (Mansour et al. 2015). PM lipids and proteins in salt tolerant plants are protected from oxidative attack through enhanced antioxidant systems, a mechanism that minimizes lipid and protein oxidation while retaining PM integrity (Mansour 2013). Though lipid peroxidation has been elucidated in ENC plants under salt stress, lipid metabolism in the PM in root tissues is yet to be investigated. Hence future research that evaluates how endophytic symbiosis influences these changes under saline conditions is warranted.

Limited studies are available to understand the role of endophytic fungi in modifying the photosynthetic

capacity of plants to alleviate the negative effects of salinity as described in previous sections. Salt stress has been shown to degrade proteins of the PSII reaction centre. These proteins play fundamental roles in phosphorylation of proteins (Jansen et al. 1996). Studies in the past have focused on understanding how AMF symbiosis acts to maintain the integrity of PSII showing the upregulation of the genes encoding these proteins under salt stress (Chen et al. 2017). However, research on maintenance of these proteins by endophytic fungi under salt stress is a field to explore.

Metabolomics is increasingly being utilized for generating deep insights into abiotic stress responses. Several studies have focused on exploring and discovering compounds that stimulate ENC plant growth by alleviating stress using various technologies (Chetia et al. 2019; Kusari and Spiteller 2012; Mazlan et al. 2019; Tawfike et al. 2018). However, molecular signalling mechanisms employed by endophytic fungi under saline conditions are yet to be explored. The high-throughput mass spectrometric profiling of cellular metabolites of plant-associated endophytes under the influence of salt stress could help to reveal the level of interference by the stressor in overall cellular homeostasis. Thus, future 'omics-based research is required to generate comprehensive information on specific plant-endophytic fungi-salt stress systems to resolve facts behind precise mechanisms of stress tolerance in crop plants.

Although this review covers mechanisms and strategies employed by plants under salt stress, in nature plants often face multiple biotic and abiotic stresses instead of a single stress. These combinations of stresses exert more complex effects on plant fitness which eventually results in potential differences from the responses elicited under single stresses. (Bai et al. 2018) demonstrated that tomato developed integrated responses via genetic components and cross-talk of signalling pathways under combined salinity and pathogen stresses. This shows that plants must have evolved to mitigate a combination of stresses. Addressing specific questions related to multiple stresses such as how beneficial microorganisms and pathogens or combined abiotic stresses interact would facilitate the design of strategies for sustained plant health under diverse environmental stresses.

In conclusion, directing future research on endophytic symbiosis under salinity in order to understand the above-mentioned challenges will help improve our knowledge and understanding of the mechanisms of endophyte facilitated salinity tolerance in host plants.

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