

# Fungal biopriming increases the resistance of wheat to abiotic stress

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**Abstract** Increasing soil salinity is one of the global challenges that the agriculture sector in Egypt has been facing; 33% of the cultivated land in Egypt, which includes merely 3% of the entire land area, is already salinized. The present review sheds light on the role of fungal biopriming, a technique in which hydrated seeds are inoculated with beneficial fungal flora, in mitigating the deleterious influence of NaCl tension. Endophytic fungi were recognized to be able to interact with several plant species, markedly contributing to the mitigation of NaCl stress in these plants, such that some plants get impoverished to their absent associated microbes under stressful conditions.

**Keywords** Fungal biopriming, Abiotic stress, Wheat salt stress

## Introduction

Seed priming approaches were initially nominating for alleviating the plant environmental stresses. Several approaches of priming were reported such as hydropriming, osmopriming, hormopriming, thermopriming, nutripriming, chemical priming and biopriming (Heydecker et al. 1973; Lutts et al. 2016). Compiling the process of seeds hydration and microbial inoculation using beneficial microbes has been nominated as biological priming “biopriming”. It plays vital roles in increasing seed viability, germination

so, enhancing the growth of plant and also, decrease other stresses on the plant (Afzal et al. 2016; Lutts et al. 2016). The fungal endophytes are able to interplay with plants and significantly participate in their tolerance to different forms of both stresses (biotic and abiotic) such as salinity, heat, drought, plant pathogens, herbivores, shortage of elements of nutrition to great limit that some plants get impoverished to their absent associated microbes under stressful conditions (de Zelicourt et al. 2013; El-Sayed et al. 2019). Stress control by phytosymbiotic are mainly occurred by stimulation of systems responsible for stress in the host cell, and anti-stress compounds produced by endophytes. These phytohormones could promotes the root hairs growth by increasing the total area of root, ease the nutrients uptake, inducing the activity of 1-aminocyclopropane-1-carboxylate deaminasee (Lata et al. 2018; Milošević et al. 2012; Prasad et al. 2016; Singh et al. 2011; Vardharajula et al. 2017).

## Salt Stress

Agriculture is the prime activity for the Egyptian population, however, degradation of soils through salinity was the major agricultural problem. Soils in the Nile Delta are affected by different types of salts comes from three distinct sources named logging, water irrigation, and the interruption of saline water. Salinity can affect the uptake of nutrients and water absorption as well as the permeability of cell membranes, and this appears clearly by the balance water and nutrients, and mutually effect the metabolic process in the plant, hormones production, exchange of gases, and the accumulation of reactive oxygen species (ROS) (Gheyi et al. 2016). Visual signs of salt harm in plant growth seem progressive: wilting, leaves yellowing and abnormal growth, followed by losing of green colour and appearance pf chlorotic lesion on the green parts, burning of the upper parts of leaves, and necrotic lesions on the leaves, then finally, the oldest leaves takes the scorched appearance

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(Machado and Serralheiro 2017). Salinity decreases the plant growth because owing to salinity the plant may face four types of stresses firstly, water stress induced by osmosis. Secondly, the ion toxicity stress because of the high ions concentrations as sodium and chloride. Thirdly, the imbalance ions nutrients, because higher levels of sodium and chloride can decrease the uptake of other ions as  $K^+$ ,  $NO_3^-$ ,  $PO_4^{3-}$ . Fourthly, the stress caused by high production of ROS which causes macromolecules damage.

Soil salinity diminishes the net photosynthetic process by decreasing the stomatal conductance,  $CO_2$  pressure in leaves, and cell content of chlorophyll, altering the structure of chloroplasts, decreasing the photo dependent chemical reactions, and increasing the tissues content of soluble sugars (Iqbal et al. 2014). Osmoregulators (proline, protein, mannitol, sorbitol, glycine and betaine) build up in salt stressed plants to reduce the osmotic potential, thereby maintaining cell turgidity that provides in turn the driving gradients for uptake of water (Rasool et al. 2013). The main cations associated with salinity are usually sodium, calcium and magnesium, while the main anions associated with salinity were  $Cl^-$ ,  $SO_4^{2-}$  and  $HCO_3^-$  (Yadav et al. 2011). Plants are either glycophytes or halophytes depending on their potency for growing on different concentrations of salt. Halophytes are completely grows on steep dose of salt, *Atriplex nummularia* (a saltbush). A lot of the terrestrial plants are classified as glycophytic with low tolerance to salt high concentrations (Rasool et al. 2013). Plants with salt sensitivity and tolerance are differs in the speed of progression of salt toxicity, may be days or weeks or months, relying on the species of plant and salinity degree, is the timescale (Carillo et al. 2011). To study the effects of osmotic and ionic salt stress, (Munns et al. 1995) proposed a model of two-phase in which the first, osmotic phase, which commence instantly (within minutes) after the accumulation of salt near the roots increases to a threshold level which is nearly 40 mM of sodium chloride for most plants, or less in plants sensitive for salt such as *Arabidopsis* and rice, leading to a significant reduction in shoot growth because the root system hardly gets the needed water and also, due to a loss of cell wall extensibility (Läuchli and Grattan 2007; Le Gall et al. 2015; Munns and Tester 2008; Tilbrook and Roy 2013).

Ion-specific, the second phase, is the stage at which plants respond to salinity (in days, weeks or months): salt accumulation in old leaves reaches to its toxic concentrations (which in turn stop their growth and prevent the dilution of salt arrives to them as occur in younger leaves)

leading to their death, the inescapable destiny. If the death rate exceeds the production rate of new leaves, the photosynthesis process of the plant will not be able to cover carbohydrate demand of the newly growing leaves, which subsequently decreases the rate of their growth (Läuchli and Grattan 2007; Munns and Tester 2008).

#### Pre-Sowing Seed Treatment

Different methods were used from past to present trying to adapt to different stresses, including traditional methods of breeding “hybridization and selection” and modern technologies as “mutation, polyploidy breeding and genome editing” (Jisha et al. 2013). Genetic engineering possesses in a reasonable manner being the affordable method due to the incorporation of targets, and heterologous traits to the elite crop lines. However, these methods are expensive, cumbersome requiring biosafety regulations that hinders the implementation of transgenic plants to the field (Jisha et al. 2013). The alternative solution would be more affordable, cost effective and can be adopted without complications (Jisha et al. 2013). Different research has been done to decrease the time between planting to development as this plays a fundamental role in the production of different crops. Seed priming technique is one of the results these researches. This technique was proposed for the first time by (Heydecker et al. 1973). Priming technique is an effective method for enhancing the quality of seed, increasing the rates for germination resulting in high resistance levels of stress and high yields production, improving the product competitiveness, correlating to seed vigour, that limited by various genetic and environmental traits (Paparella et al. 2015).

Priming of seeds is a pre-sowing of seeds by exposing to particular solutions for a specific time that enables partial entrance of water before emerging of radicle. When a dry non-dormant seeds were kept in water, imbibition, lag phase, and appearance of the radicle by the testa follows one another during the process of germination (Dalil 2014; Lutts et al. 2016; Singh et al. 2015). During priming the water supply to the seed is a limiting step, because it makes the level of seed moisture below its required level for exact germination. At this level the physiological processes controlling the pre-germination metabolism can be started but the transition of seed towards its full germination is prevented. This precludes seeds from going through the third phase of hydration (growth) by stretching and detaining seeds within the lag phase (activation) (Ibrahim 2016; Singh et al. 2015). Being desiccation-tolerant, seeds have to be re-dried again to its initial

content of moisture before radicle emergence to preserve the benefits of the priming method (Ibrahim 2016; Mondal and Bose 2014). The seed should be dried at imbibition phase (I) or activation (II), but growth phase III is an advanced phase allowing re-drying keeping the seed quality. Post-radicle emergence seed dehydration leads to seed vigour damage and losing seed viability. Life expectancy of primed seeds is usually long on condition of a successful drying-back and storage (Ibrahim 2016; Paparella et al. 2015).

Numerous factors affect priming efficiency and extremely relies on types of plant species and priming technique, namely osmotic, water potential, priming agent, duration, light, aeration, and seed type. All of these factors plays an important role in priming success and germination requirements (Lutts et al. 2016). The common priming techniques include hydropriming, osmopriming, hormoprimer, thermoprimer, chemoprimer, and bioprimer. Using osmotic solution with low water potential to soak the seeds in is known as osmopriming. The low potential of water used in the osmotic solutions, enables water to enter into seed slowly allowing the gradual activation of germination phases without occurrence of radicle emergence (Jisha et al. 2013; Lutts et al. 2016; Paparella et al. 2015).

In priming by solid matrix (matricconditioning), solid or semi-solid matrix has been used replacing the liquid one (Jisha et al. 2013). Solid priming has been emerged as an alternative approach of osmopriming because of the high price and technical problems of osmopriming. In contrast to osmopriming in which liquid solutions (liquid priming) are used, in solid priming, a solid matrix is to coat the seeds, due its ability to adjust the moisture content and controlling water uptake (Fig. 1). This solid matrix allows slowly hydration of seeds (Jisha et al. 2013; Lutts et al. 2016; Paparella et al. 2015). We can improve the seed germination of different crops by adding hormones and PGPR during priming process (Jisha et al. 2013). For example in hormoprimer different regulators are used as ABA, auxins, GAs, polyamines, and SA (Lutts et al. 2016). Pre-sowing seeds at different temperatures is referred to as thermoprimer, generally, the best results can be achieved at low temperatures. Although in some species priming with higher temperatures is preferable and gives a good germination results mainly for crops growing in warm climates (Paparella et al. 2015).

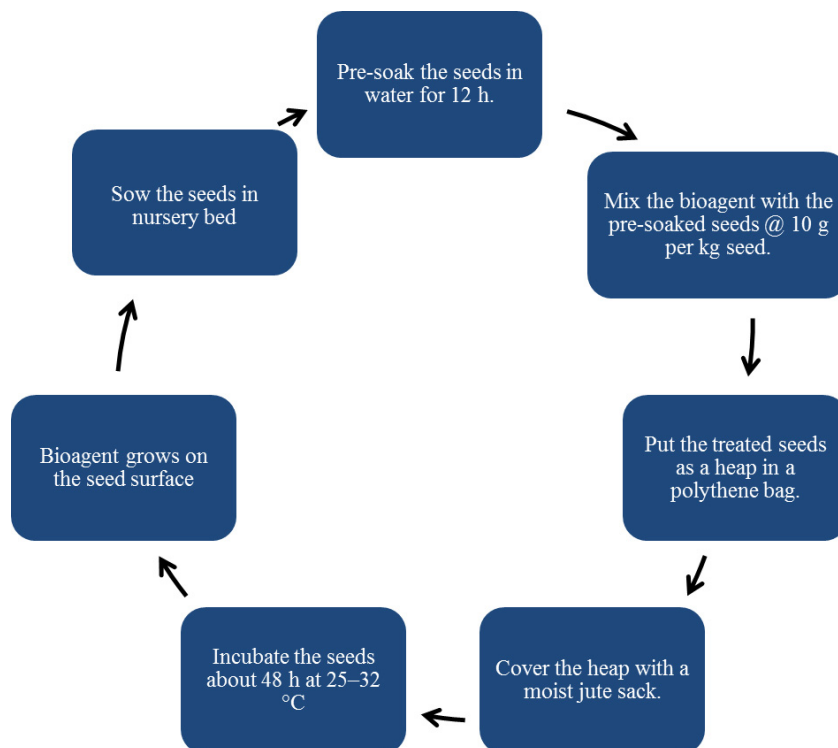
Chemoprimer is the process in which seeds are treated with various chemicals before its germination. The priming process in this case can use different compounds (natural or synthetic) some of these compounds are ascorbic acid, urea, chitosan, sodium nitroprusside, and so on (Jisha et

al. 2013; Lutts et al. 2016). In nutripriming, seeds were soaked in water containing different limiting nutrients instead of water alone. This method prove the important role of mineral nutrition in increasing the plant resistance to different types of stress (Jisha et al. 2013; Lutts et al. 2016).

In hydropriming, soaking the seeds in water (distilled and sterilized) at room temperature (in a range from 5 to 20°C) till hydration level in seeds equal to 10-20% of full absorption. As mentioned, it is important to dry the seeds soaked to their initial weights with air (Jisha et al. 2013; Paparella et al. 2015). Bioprimer is the process in which seed hydration by soaking in water containing beneficial microbes, thus improving the viability of seed, germination rate, plant growth, protecting the plants from the diseases (microbial or physiological). Immersion of the seeds for 12 h in water, is the recommended method of bioprimer. The formulated of the microorganisms were added to the seeds (pre-immersed) at the level of 10 g/kg of the crop seeds and mixed with each other. The seeds were collected in polythene bags, and to maintain high level of humidity, the bags were covered with moist jute sack for two days at 30°C, allowing to the adherence biological agent to the seeds surface making a protective layer surrounding the seed coat (Afzal et al. 2016; Lutts et al. 2016; Prasad et al. 2016).

### Role of Bioprimer in Salt Stress Resilience

Several reports document that plants can better withstand salt stress by seed bioprimer approach. Bioprimer of durum wheat grains with *Bacillus pumilus*, *Virgibacillus* sp., *B. pumilus*, and *B. tequilensis* gave the highest protection against *Fusarium* disease, promote the plant growth, and salinity adaptation (Feto et al. 2019). Seed bioprimer of rice (*Oryza sativa*) with five salinity adaptive isolates of *Trichoderma harzianum* gave a significant increase in length of shoot and root, leaves number, leaf area, rate of photosynthesis process, leaf content of chlorophyll and plant fresh weight comparing to salt stressed control plant (Rawat et al. 2012). Effect of *Trichoderma lixii* on *Zea mays* as a seed fungal bioprimer agent was studied under sodium chloride stress. Authors observed a decrease amount of both hydrogen peroxide and MDA along with an increase in the content of soluble protein and proline (Pehlivan et al. 2017). Bioprimer of Seeds using *Pseudomonas geniculata* (salt tolerant endophyte) caused a growth promotion and mitigated the salt stress in *Zea mays*. Application of *P. geniculata* reduced the sodium uptake and increased the uptake of potassium and calcium



**Fig. 1** The common recommended method for seed bio-priming

in the roots of maize showing its role in controlling the ionic balance/homeostasis in the roots of maize under high salt stresses (Singh et al. 2020). Several studies studied the ability of five salinity tolerant isolates of *T. harzianum* applied via seed biopriming by attenuating the severity of salinity on wheat (*Triticum aestivum* L.). Fungal biopriming resulted in improved germination percentage, lengths of shoot and root systems, leaves content of chlorophyll and membrane stability index than control at all salt stress levels (Rawat et al. 2011). Biopriming of *Brassica napus* (canola) seeds using *B. subtilis* and *Macrophomina phaseolina* could enhance the germination index and alleviates the effects of salinity (Mousavi and Omidi 2019). Researchers should thereby study more to show the impact of seed biopriming with microbial inoculants on the removal of environmental stresses.

#### Stress Tolerance in Plants via Fungal Neighbours

Plants lives in close association with the microorganisms either as neighbours in the soil, or especially those microorganisms lives internally in plants as endophytes (El-Baz et al. 2011a; El-Baz et al. 2017, 2018; Hardoim et al. 2015). endophytic fungi can interact with many species and hence cause a significant contribution in the plant adaptation to different environmental stresses such as

drought, heat, pathogens infect, insects infection, or nutrients limitation to the level at which some plants cannot preserve stress conditions in the absence of their endophytic microbes (Alsaggaf et al. 2020; de Zelicourt et al. 2013; El-Mekay et al. 2013, El-Baz et al. 2011b; El-Sayed et al. 2010, 2012). A growing interest in symptomless parasitic fungi ‘endophytes’ since the discovery of paclitaxel (Taxol, anticancer drug), from *Pestalotiopsis microspora*, a endophytic fungus that lives internally in the Himalayan yew tree *Taxus wallichiana*, without causing injury to its host plant (Maheshwari 2006). As well as, several fungal endophytes namely *A. flavipes*, *A. terreus* inhabiting *Podocarpus gracilior* were reported as potent Taxol producers, without any effect diseases symptoms on the plant (El-Sayed et al. 2015e, 2019a, 2019b, 2020, 2021). Also, *Penicillium polonicum* as endophyte of *Ginkgo piloba* were reported as potent Taxol producers without any apparent effect on the plant health (Abdel-Fatah et al. 2021). The endophytic fungus *Aspergillus fumigatus* of *Vinca* was reported for first time as Epothilones producer without any undesirable effect on the plant health (El-Sayed et al. 2021; El-Sayed et al. 2015a, 2015b, 2015c, 2015d, 2015e, 2016, 2019a). The potency of endophytic fungi for inhabiting various medicinal plant for production of diverse bioactive compounds were extensively studied (El-Sayed et al. 2020a, 2020b, 2021). They lives entirely in the plant

**Table 1** Common priming techniques and the agents utilized in each case

Priming Concept	Priming technique
Osmopriming/osmotic priming halopriming	Immersion of the seeds in an osmotic solution of water with a low potential, rather than pure water. <b>Priming agents:</b> Polyethylene glycol (PEG), mannitol, sorbitol, glycerol, and inorganic salts, such as sodium chloride (NaCl), potassium chloride (KCl), potassium nitrate (KNO <sub>3</sub> ), potassium phosphate (K <sub>3</sub> PO <sub>4</sub> ), and calcium chloride (CaCl <sub>2</sub> ).
Solid matrix priming (SMP)/ solid priming	The seeds are mixed with a solid matrix (organic or inorganic) capable of adjusting the moisture content and controlling the uptake of water. <b>Priming agents:</b> Vermiculite, peat moss, charcoal, sand, clay
Hormopriming	The seeds are soaked in water with plant growth regulators and hormones, leading to an enhancement of seed germination. <b>Priming agents:</b> Abscisic acid (ABA), auxins (AU), gibberellins (GAs), kinetin, ethylene, polyamines, and salicylic acid (SA).
Thermopriming	Pre-sowing seeds at different temperatures is referred to as thermopriming. <b>Priming agent:</b> Low temperatures or high temperatures.
Chemopriming	The seeds are soaked in different chemical solutions. <b>Priming agents:</b> Ascorbic acid, glutathione, tocopherol, melatonin, and proline, H <sub>2</sub> O <sub>2</sub> , sodium nitroprusside, urea, thiourea, mannose, chitosan, fungicides, etc.
Hydropriming/ On-farm priming	The seeds are soaked in sterilized distilled water and then re-dried using air to their original case. <b>Priming agent:</b> Sterilized distilled water
Biopriming/ biological seed treatment	A combination of seed hydration by soaking; then, the seeds can be inoculated with beneficial microbes. <b>Priming agents:</b> Beneficial microbes

tissues for whole or small part of their life cycle and cause no apparent infections and may grow inside the roots, stems and/or leaves, tending to forms spores with aging of their host-tissue (El-Sayed, 2009; Hallmann and Sikora 2011; Maheshwari 2006; Mishra et al. 2014).

Fungal endophytes can affect both of plant growth and its responses to different factors as pathogenic organisms, grazing animals and environmental stresses through their ability to produce beneficial metabolites (Abdella et al. 2018a, 2018b; Abdel-Monem et al. 2012; Porrás-Alfaro and Bayman 2011). Endophytic fungi can be classified into two groups depending on their food uptake strategies: (1) facultative endophytes (obtaining their food from living and non-living dead organic matter), and (2) obligate endophytes (obtaining their food from living plant cells only) (Hallmann and Sikora 2011). Recently, by molecular analysis it was suggested that endophytic fungi can colonize the green plants by before plants colonized the land, by establishing a close contact (intercellularly and intracellularly) with the plant cells (Maheshwari 2006). Endophytes can suppress the defence mechanism of plants to prevent the pathogen attack to the plant depending on the way used by plants to detect the pathogens and endophytes as the plant uses the same set of genes (Maheshwari 2006).

Successful endophytic colonization undergoes numerous significant steps: finding the host plant, surface colonization of the plant and invasion of the internal tissue in plant. Some factors ease the entrance process of endophytic microbes to the plant tissues includes natural factors such as hydathodes, stomata and lenticels, and artificial factors as wounds caused by physical factors. Penetration of microbes to the cuticle surface and cell walls requires secretion of cell wall-degrading enzymes like cutinase, pectinase, cellulase, hemicellulase, protease and lignin-peroxidases. Plant endophytes can easily transmitted from one generation to another through plant seeds (Lata et al. 2018). To show whether *Piriformospora indica* infested plants would be more resistant to biotic stress or not, the barley was grown in soil infected with macroconidia of *Fusarium culmorum* a necrotrophic fungal pathogen (Waller et al. 2005). They found that fresh weight of shoot and root was decreased by two folds in plants infested with *P. indica* comparing to 12-fold reduction in controls with *F. culmorum* alone. Kannadan and Rudgers (2008). found that fungal endophyte *Neotyphodium* sp symbiosis positively affects the survival and growth of grove bluegrass '*Poa alsodes*' under altered water availability. It was reported that under water-limitation stress for grove bluegrass, two treatments were used the first disinfected plants and the second endophyte-harboring

plants and the result showed that disinfected plants had bigger leaf aging than endophyte-harboring plants, showing the positive role of endophytes symbiosis in amelioration the negative drought stress effects (Kannadan and Rudgers 2008). In another work, Song et al. (2015) demonstrated that *Epichlë* sp. endophyte infected wild barley plants producing significantly higher content of chlorophyll in leaves, high lengths of roots and shoots and higher plant biomass comparing to plants free of endophytes under waterlogging stress. They also had more proline production, low content of malondialdehyde and low leakage of electrolyte, meaning that the endophytic microbe alleviated the damage in waterlogged barley host plants.

In terms of investigating the role of fungal endophytes in ameliorating the heavy metal stressor, Yamaji et al. (2016) found that in absence *Clethra barbinervis* (root endophytic fungus), could hardly grow under the high levels of heavy-metal, showing chlorosis. Waqas et al. (2015) reported that endophytic association of *Paecilomyces formosus* without any stress and increase heat stress conditions significantly, enhanced the growth of japonica and resulted in an increase in height, fresh and dry weight, and plant content of chlorophyll. *P. formosus* also increased the total protein content and lowered endogenous level of stress-signalling compounds such as jasmonic and abscisic acid and finally protected the rice plants from heat stress comparing to the controls. Redman et al. (2011) assessed the ability of *Curvularia protuberata* to confer cold tolerance to rice plants (below 20°C). Results showed that symbiotic seedlings had development (appearance of roots and shoot) frequencies of greater than 90% at all of the temperatures tested. In agreement with the studies above, some other works showed the positive impact of fungal endophytes on salt-stressed plants as well. For instance, Ahmad et al. (2015) showed that adding of *Trichoderma harzianum* to NaCl treated mustard "*Brassica juncea*" seedlings showed enhancement in lengths of root and shoot, plant dry weight, pigment and proline contents, SOD, POD, APX, GR, GST, GPX, GSH, and GSSG comparing to plants treated with sodium chloride (200 mM) alone. Also, a decrease in the accumulation of both hydrogen peroxide and MDA was reported by adding of *T. harzianum* to NaCl fed mustard seedlings. The effect of moderate (100 mM NaCl) salt stress was abolished completely by *Piriformospora indica*, as reported the infested plants produced large biomass than produced by control (non-stressed) plants under the same condition conditions (Waller et al. 2005). Similarly, while working with barely, it has been reported recently that the endophytic fungus *Epichloë*

*bromicola* might help the *Hordeum brevisubulatum* plants to stand salt stress by stimulating the conversion of putrescine to spermine and spermidine, as well as shifting the ability of polyamines free and soluble conjugated forms to its bound insoluble forms (Chen et al. 2019).

#### Phytohormones: Alleviation Mechanism adopted by Endophytic Fungi

Plants adaptation to stress follow two mechanisms: (1) activation of stress response systems in the host quickly after exposure to stress, and (2) secondary metabolites biosynthesis (anti-stress compound) by endophytic microbes (Lata et al. 2018; Singh et al. 2011). Plant hormones works as central connector that link and reprogram the complex development and stress adaptation signalling cascades (Golldack et al. 2014). In this section we will consider how phytohormones come into play to avoid salt injury. In a study, on two rice varieties differ in their sensitivity to salt, growth reprogramming and building up of an adaptation program leading to specific responses (morphological and physiological) and growth yield under salt stress was backed to the speed of hormonal metabolism regulation in the tolerant variety (Formentin et al. 2018; Patel et al. 2016). The plant growth and development are mainly regulated by auxins. different studies showed the role of auxin in plants response to salinity stress, but unfortunately, there is no enough available information about auxin mechanisms in salt stress regulation (Fahad et al. 2015; Ryu and Cho 2015). It has been reported that auxin-induced mitigation of the salinity effects of on maize plants was linked with the increment in the concentration of photosynthetic pigments and leaf sodium/potassium ratio and the reduction in membrane permeability (Kaya et al. 2013). Overexpression of TaSAUR75, small auxin upregulated RNAs (SAURs), was regulated by auxin and different environmental factors, intensified drought and salt adaptation in *Arabidopsis*. Genetically modified plant lines displayed higher length of root and survival rate and the expression of some stress-response genes was high than that of control plants (Guo et al. 2018).

Gibberellins are important for plants during their life cycle for growth-stimulation purpose (Wani et al. 2016). During plants exposure to salinity stress a rapid accumulation of gibberellic acid (GA) will occur (Kaya et al. 2009). In a study conducted by (Iqbal and Ashraf 2013), induced increase in grain yield was linked to the gibberellins-priming stimulated modulation of ions uptake under salinity stress. Similarly, while working with *Olea europaea*, researchers

found that using gibberellin via reducing the concentrations of sodium and chloride in olive plants, but increasing the amount of potassium chlorophyll and proline (Shekafandeh et al. 2017).

Cytokinins (CKs) achieve abiotic stress adaptation in higher plants, may be through modulating various components of the photosynthetic machinery under abiotic stress conditions (Fahad et al. 2015; Gururani et al. 2015). A transcriptomic analysis showed that under salt stress, CK triggered transcriptional reprogramming in *Arabidopsis* leaves that resulted in decreasing stress-dependent inhibition of vegetative growth and reduce premature plant aging (Golan, et al. 2017). Ma et al. (2016) showed that using of 6-benzylaminopurine alleviated the bad effects caused by salt stress in Perennial ryegrass by increasing the ability of enzymes associated with reactive oxygen species scavenging and suppression of sodium ion accumulation to keep a higher potassium/sodium ratio attributed to the increased high-affinity K<sup>+</sup> transporter expression.

Accumulation of abscisic acid can alleviate the bad effect of salt stress on growth, photosynthesis, and translocation. High levels of abscisic acid hormone aids plants to grow under low water content by closing stomatal openings and accumulates virous proteins and osmoprotective agents for osmotic control (Gupta and Huang 2014; Ryu and Cho 2015). The *Arabidopsis* abscisic acid -deficient mutants, *aba1-3*, died after exposure to higher salt concentration, implying that ABA provides a protective role in higher salt concentration (Cramer 2002). In a study, on rice, researchers reported the implication of ABA in the control of salt-induced cellular mechanisms resulting in sodium ion defatation from the cytoplasm (Pons et al. 2013).

Foliar spray of salt stressed-soybean with salicylic acid (SA) led to significant increase in chlorophyll, sugar, starch and proline contents, indicating that application of SA can overcome salinity (Jaiswal et al. 2014). Treatment of salicylic acid to saline soils enhanced also the salt tolerance in rice plants via less accumulation of sodium and chlorine ions, an increased concentration of endogenous SA level and augmented antioxidant enzymes such as superoxide dismutase, catalase and peroxidase (Jini and Joseph 2017; Khan et al. 2017). The cyclopentanone is a phytohormones produced from the metabolism of membrane fatty acids as jasmonates (methyl jasmonate (MeJA) and jasmonic acid) can activate the defence mechanisms of plant in response to wounding caused by insect, pathogenic organisms, and environmental stresses, such as drought, low or high temperature, and salts (Mann et al. 2015; Wani et al. 2016). OsJAZ9 is a member of the JAZ

subfamily that belonging to the TIFY gene family in rice "*Oryza sativa*", suppression of this gene resulted in reduction of salt tolerance. The altered salt adaptation was mainly due to changes in homeostasis of ion (especially K<sup>+</sup>), which was proved by the different expression levels of several ion transporters (Wu et al. 2015). Zhao et al. (2014), reported that salinity-response gene in bread wheat (TaAOC1 gene), encoding allene oxide cyclase involved in the metabolic pathway of  $\alpha$ -linolenic acid, was highly expressed in both *Arabidopsis* and bread wheat. In both species, genetically modified lines showed an enhanced level of adaptation to salt (Zhao et al. 2014).

Different groups of organisms, such as fungi, bacteria, and plants are harbouring soils. Plant roots are the richest place colonized by microorganisms (compared to soil and other habitats) because of root exudates which are rich with nutrients. The rhizosphere area attracts different microbes that utilize the different nutrients released in the root exudates. Hence, these microbes plays an effective role in nutrition uptake and development and growth by producing biologically active secondary metabolites, as phytohormones (auxins, cytokinins, gibberellins and abscisic acid), and antimicrobial compounds. Also, they can increase plant resistance to different factors of biotic and abiotic stress, enhancing nutrient uptake and protect plants from different pathogenic soil-borne microbes (Egamberdieva et al. 2017). Microbes adopt their ability for synthesizing phytohormone in the rhizosphere for improving both plant growth and stress resistance. In plant tissue, microbial phytohormones affect the metabolic pathway of endogenous growth regulators and it are a limiting factor in changing root morphology upon exposure to different stresses as drought, salt, low and high temperature and toxicity of heavy metal (Chakraborty et al. 2015; Egamberdieva et al. 2017). For example, Bastías et al. (2018) indicated the important role of salicylic acid a in regulating the acquired resistance by endophyte against herbivores. In addition, the culture application and endophytic-association of *Phoma glomerata* and *Penicillium* sp. significantly reprogrammed the growth of host cucumber plants during salt and drought stress conditions by means of secreting gibberellins and indole acetic acid (Waqas et al. 2012). Kang et al. (2014) found that the endogenous SA and GA4 contents were significantly higher in *B. cepacia*, *A. calcoaceticus* and *Promicromonospora* sp inoculated plants than non-inoculated cucumbers under both salinity and drought stresses.

Iqbal et al. (2016) showed that inoculation of maize with auxin producing rhizobacterial stains enhanced grain yield, fresh biomass and grains contents of phosphorous

under saline field conditions. Results of Khan et al. (2012) revealed that upon salinity stress *Paecilomyces formosus*, a GAs and indole acetic acid secreting fungal strain, inoculation higher endogenous gibberellins (GA<sub>3</sub>, GA<sub>4</sub>, GA<sub>12</sub> and GA<sub>20</sub>) contents in the tissue of cucumber plants which resulted in salinity stress modulation. *Penicillium janthinellum* association helped Sitiens plants, tomato abscisic acid (ABA)-deficient mutants, that had reduced the growth under normal and salt stress to synthesis significantly higher abscisic acid to modulate stress responses (Khan et al. 2013; Selvakumar et al. 2014).

A study by Sajjad Asaf and colleagues reported that the combined treatment of soybean plants with *Sphingomonas* sp. along with trehalose improved endogenous jasmonic (JA) and abscisic (ABA) acid contents and alleviated the negative effects of osmotic stress induced by drought (Asaf et al. 2017; Maamoun et al. 2021). It has also been reported that most of the alfalfa plants inoculated with engineered *Sinorhizobium* strains which overproducing zeatins survived under severe drought stress and the no apparent change for nitrogenase activity in their root nodules was reported (Rodriguez et al. 2009; Xu et al. 2012).

In conclusion, preceding data presented in this review underpin the view that seed biopriming approach is a promising pre-sowing treatment conferring better tolerance to plants against diverse abiotic stressors. Steering research on fungal biopriming under salt stresses will help to enhance our knowledge and understanding of the action mechanisms adopted by fungal endophytes to reach to salinity tolerance in host plants.

## References

- Abdel-Fatah SS, El-Batal AI, El-Sherbiny GM, Khalaf MA, El-Sayed AS (2021) Production, bioprocess optimization and  $\gamma$ -irradiation of *Penicillium polonicum*, as a new Taxol producing endophyte from Ginko biloba Biotechnology Reports, 30, art. no. e00623
- Abdella A, El-Baz AF, Ibrahim IA, Mahrous EE, Yang S-T (2018a) Biotransformation of soy flour isoflavones by *Aspergillus niger* NRRL 3122  $\beta$ -glucosidase enzyme. Natural Product Research 32:2382-2391
- Abdella A, El-Baz AF, Mahrous EE, El Maksoud AAA, Ibrahim IA, Abdel-Monem AR, Yang S-T (2018b) Response surface methodology for optimization of genistein content in soy flour and its effect on the antioxidant activity. Iranian Journal of Pharmaceutical Research 17:1026-1035
- Abdel-Monem OA, El-Baz AF, Shetaia YM, El-Sabbagh SM (2012) Production and application of thermostable cellulase-free xylanase by *Aspergillus fumigatus* from agricultural wastes. Industrial Biotechnology 8:152-161
- Alsaggaf MS, El-Baz AF, Badawy SE, Moussa SH (2020) Anticancer and antibacterial activity of cadmium sulfide nanoparticles by *Aspergillus niger*. Advances in Polymer Technology 4909054:1-13
- Afzal I, Rehman HU, Naveed M, Basra SMA (2016) Recent advances in seed enhancements, New Challenges in Seed Biology-Basic and Translational Research Driving Seed Technology. InTech
- Ahmad P, Hashem A, Abd-Allah EF, Alqarawi A, John R, Egamberdieva D, Gucel S (2015) Role of Trichoderma harzianum in mitigating NaCl stress in Indian mustard (Brassica juncea L) through antioxidative defense system. Frontiers in plant science 6
- Asaf S, Khan AL, Khan MA, Imran QM, Yun BW, Lee I-J (2017) Osmoprotective functions conferred to soybean plants via inoculation with *Sphingomonas* sp. LK11 and exogenous trehalose. Microbiological research 205:135-145
- Bastías DA, Alejandra Martínez-Ghersa M, Newman JA, Card SD, Mace WJ, Gundel PE (2018) The plant hormone salicylic acid interacts with the mechanism of antiherbivory conferred by fungal endophytes in grasses. Plant, cell & environment 41:395-405
- Carillo P, Annunziata MG, Pontecorvo G, Fuggi A, Woodrow P (2011) Salinity stress and salt tolerance, Abiotic Stress in Plants-Mechanisms and Adaptations. InTech
- Chakraborty U, Chakraborty B, Dey P, Chakraborty AP (2015) Role of microorganisms in alleviation of abiotic stresses for sustainable agriculture. Abiotic stresses in crop plants 232-253
- Chen T, Li C, White JF, Nan Z (2019) Effect of the fungal endophyte Epichloë bromicola on polyamines in wild barley (Hordeum brevisubulatum) under salt stress. Plant and soil 436:29-48
- Cramer GR (2002) Response of abscisic acid mutants of Arabidopsis to salinity. Functional plant biology 29:561-567
- Dalil B (2014) Response of medicinal plants to seed priming: a review. International Journal of Plant, Animal and Environmental Sciences 4:741-745
- de Zelicourt A, Al-Yousif M, Hirt H (2013) Rhizosphere microbes as essential partners for plant stress tolerance. Molecular Plant 6:242-245
- Egamberdieva D, Wirth SJ, Alqarawi AA, Abd\_Allah EF, Hashem A (2017) Phytohormones and beneficial microbes: essential components for plants to balance stress and fitness. Frontiers in microbiology 8:2104
- El-Mekay A, Hegab HM, El-Baz A, Hudson SM (2013) Kinetic properties and role of bacterial chitin deacetylase in the bioconversion of chitin to chitosan. Recent Patents on Biotechnology 7:234-241
- El-Baz AF, Shetaia MY, Elkhoul RR (2011a) Xylitol production by candida tropicalis under different statistically optimized growth conditions. African Journal of Biotechnology 10: 15353-15363
- El-Baz AF, Shetaia YM, Elkhoul RR (2011b) Kinetic behavior of



- Candida tropicalis* during xylitol production using semi-synthetic and hydrolysate based media. African Journal of Biotechnology 10:16617-16625
- El-Baz AF, El-Enshasy HA, Shetaia YM, Mahrous H, Othman NZ, Yousef AE (2018) Semi-industrial Scale Production of a New Yeast with Probiotic Traits, *Cryptococcus* sp. YMHS, Isolated from the Red Sea. Probiotics and Antimicrobial Proteins 10:77-88
- El-Baz FN, Gamal RF, El-Baz AF, Ibrahim NE, ElMekawy A (2017) Biochemical and biotechnological studies on a novel purified bacillus cholesterol oxidase tolerant to solvent and thermal stress. Biocatalysis and Biotransformation 35(3): 205-214
- El-Sayed ASA (2009) L-Methioninase production by *Aspergillus flavipes* under solid-state fermentation. Journal of Basic Microbiology 49(4):331-341
- El-Sayed ASA, Abdel-Azeim S, Ibrahim HM, Yassin MA, Abdel-Ghany SE, Esener S, Ali GS (2015a) Biochemical stability and molecular dynamic characterization of *Aspergillus fumigatus* cystathionine  $\gamma$ -lyase in response to various reaction effectors. Enzyme and Microbial Technology 81: 31-46
- El-Sayed AS, Shindia AA, Zaher Y (2012) L-Amino acid oxidase from filamentous fungi: Screening and optimization Annals of Microbiology 62(2):773-784
- El-Sayed ASA, Shindia AA, Zeid AAA, Yassin AM, Sitohy MZ, Sitohy B (2019a) *Aspergillus nidulans* thermostable arginine deiminase-Dextran conjugates with enhanced molecular stability, proteolytic resistance, pharmacokinetic properties and anticancer activity. Enzyme and Microbial Technology 131:109432
- El-Sayed ASA, George NM, Yassin MA, Alaidaroos BA, Bolbol AA, Mohamed MS, Rady AM, Aziz SW, Zayed, RA, Sitohy MZ (2019b) Purification and Characterization of Ornithine Decarboxylase from *Aspergillus terreus*; Kinetics of Inhibition by Various Inhibitors. Molecules (Basel, Switzerland), 24(15)
- El-Sayed ASA, Hassan AEA, Shindia AA, Mohamed SG, Sitohy MZ (2016) *Aspergillus flavipes* methionine  $\gamma$ -lyase-dextran conjugates with enhanced structural, proteolytic stability and anticancer efficiency. Journal of Molecular Catalysis B: Enzymatic 133:S15-S24
- El-Sayed AS, Khalaf SA, Abdel-Hamid G, El-Batrik MI (2015b) Screening, morphological and molecular characterization of fungi producing cystathionine  $\gamma$ -lyase. Acta Biologica Hungarica 66:119-132
- El-Sayed MT, El-Sayed ASA (2020a) Biocidal activity of metal nanoparticles synthesized by *Fusarium solani* against multidrug-resistant bacteria and mycotoxigenic fungi. Journal of Microbiology and Biotechnology 30:226-236
- El-Sayed MT, El-Sayed ASA (2020b) Tolerance and mycoremediation of silver ions by *Fusarium solani*. Heliyon 6:e03866
- El-Sayed AS, Khalaf SA, Abdel-Hamid G, El-Batrik MI (2015c) Screening, morphological and molecular characterization of fungi producing cystathionine  $\gamma$ -lyase. Acta Biologica Hungarica 66:119-132
- El-Sayed ASA, Shindia AA, Ali GS, Yassin MA, Hussein H, Awad SA, Ammar HA (2021) Production and bioprocess optimization of antitumor Epothilone B analogue from *Aspergillus fumigatus*, endophyte of *Catharanthus roseus*, with response surface methodology. Enzyme and Microbial Technology 143:109718
- El-Sayed ASA, Yassin MA, Ibrahim H (2015d) Coimmobilization of L-methioninase and glutamate dehydrogenase: Novel approach for L-homoalanine synthesis Biotechnology and Applied Biochemistry 62:514-522
- El-Sayed ASA, Yassin, MA, Ali GS (2015e) Transcriptional and proteomic profiling of *Aspergillus flavipes* in response to sulfur starvation PLoS ONE, 10 (12), art. no. e0144304
- El-Sayed ASA, Fathalla M, Yassin MA, Zein N, Morsy S, Sitohy M, Sitohy B (2020) Conjugation of *Aspergillus flavipes* taxol with porphyrin increases the anticancer activity of taxol and ameliorates its cytotoxic effects. Molecules 25(2):263
- El-Sayed ASA, Fujimoto S, Yamada C, Suzuki H (2010) Enzymatic synthesis of  $\gamma$ -glutamylglutamine, a stable glutamine analogue, by  $\gamma$ -glutamyltranspeptidase from *Escherichia coli* K-12. Biotechnology Letters 32:121877-1881
- Fahad S, Hussain S, Matloob A, Khan FA, Khaliq A, Saud S, Hassan S, Shan D, Khan F, Ullah N (2015) Phytohormones and plant responses to salinity stress: a review. Plant growth regulation 75:391-404
- Feto N, Brahim A, Jlidi M, Daoud L, Ben-Ali M, Akreimi A, Hmani H (2019) Seed-Biopriming of Durum Wheat with Diazotrophic Plant Growth Promoting Bacteria (PGPB) Enhanced Tolerance to Fusarium Head Blight (FHB) and Salinity Stress
- Formentin E, Barizza E, Stevanato P, Falda M, Massa F, Tarkowskà D, Novák O, Lo Schiavo F (2018) Fast regulation of hormone metabolism contributes to salt tolerance in rice (*Oryza sativa* spp. Japonica, L.) by inducing specific morpho-physiological responses. Plants 7:75
- Gheyi H, Dias NdS, Lacerda Cd, Gomes Filho E (2016) Physiology and biochemistry of plants growing under salt stress
- Golan Y, Shirron N, Avni A, Shmoish M, Gepstein S (2017) Cytokinins Induce Transcriptional Reprogramming and Improve Arabidopsis Plant Performance under Drought and Salt Stress Conditions. Front. Abiotic Stresses in Agroecology: A Challenge for Whole Plant Physiology 4:125
- Golldack D, Li C, Mohan H, Probst N (2014) Tolerance to drought and salt stress in plants: unraveling the signaling networks. Frontiers in plant science 5:151
- Guo Y, Jiang Q, Hu Z, Sun X, Fan S, Zhang H (2018) Function of the auxin-responsive gene TaSAUR75 under salt and drought stress. The Crop Journal 6:181-190
- Gupta B, Huang B (2014) Mechanism of salinity tolerance in plants: physiological, biochemical, and molecular characterization. International journal of genomics 2014
- Gururani MA, Mohanta TK, Bae H (2015) Current understanding of the interplay between phytohormones and photosynthesis under environmental stress. International journal of molecular sciences 16:19055-19085
- Hallmann J, Sikora RA (2011) Endophytic Fungi, p. 227-258. In K. Davies and Y. Spiegel (ed.), Biological Control of Plant-

- Parasitic Nematodes: Building Coherence between Microbial Ecology and Molecular Mechanisms. Springer Netherlands, Dordrecht
- Hardoim PR, Van Overbeek LS, Berg G, Pirttilä AM, Compant S, Campisano A, Döring M, Sessitsch A (2015) The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. *Microbiology and Molecular Biology Reviews* 79:293-320
- Heydecker W, Higgins J, Gulliver R (1973) Accelerated germination by osmotic seed treatment. *Nature* 246:42
- Ibrahim EA (2016) Seed priming to alleviate salinity stress in germinating seeds. *Journal of plant physiology* 192:38-46
- Iqbal M, Ashraf M (2013) Gibberellic acid mediated induction of salt tolerance in wheat plants: Growth, ionic partitioning, photosynthesis, yield and hormonal homeostasis. *Environmental and Experimental Botany* 86:76-85
- Iqbal MA, Khalid M, Zahir ZA, Ahmad R (2016) Auxin Producing Plant Growth Promoting Rhizobacteria Improve Growth, Physiology and Yield of Maize under Saline Field Conditions. *International Journal of Agriculture & Biology* 18
- Iqbal N, Khan NA, Umar S (2014) PHOTOSYNTHETIC INHIBITION UNDER SALINITY CHALLENGED ENVIRONMENT: AN INSIGHT INTO REGULATION OF RUBISCO. FUNCTIONAL GENOMICS, PHYSIOLOGICAL PROCESSES AND ENVIRONMENTAL ISSUES:167
- Jaiswal A, Pandurangam V, Sharma S (2014) Effect of salicylic acid in soybean (*Glycine Max L. Meril*) under salinity stress. *The Bioscan* 9:671-676
- Jini D, Joseph B (2017) Physiological mechanism of salicylic acid for alleviation of salt stress in rice. *Rice Science* 24:97-108
- Jisha K, Vijayakumari K, Puthur JT (2013) Seed priming for abiotic stress tolerance: an overview. *Acta Physiologiae Plantarum* 35:1381-1396
- Kang S-M, Khan AL, Waqas M, You Y-H, Kim J-H, Kim J-G, Hamayun M, Lee I-J (2014) Plant growth-promoting rhizobacteria reduce adverse effects of salinity and osmotic stress by regulating phytohormones and antioxidants in *Cucumis sativus*. *Journal of Plant Interactions* 9:673-682
- Kannadan S, Rudgers J (2008) Endophyte symbiosis benefits a rare grass under low water availability. *Functional Ecology* 22:706-713
- Kaya C, Ashraf M, Dikilitas M, Tuna AL (2013) Alleviation of salt stress-induced adverse effects on maize plants by exogenous application of indoleacetic acid (IAA) and inorganic nutrients-A field trial. *Australian Journal of Crop Science* 7:249
- Kaya C, Tuna A, Yokaş I (2009) The role of plant hormones in plants under salinity stress, p 45-50, *Salinity and Water Stress*. Springer
- Khan AL, Hamayun M, Kang S-M, Kim Y-H, Jung H-Y, Lee J-H, Lee I-J (2012) Endophytic fungal association via gibberellins and indole acetic acid can improve plant growth under abiotic stress: an example of *Paecilomyces formosus* LHL10. *BMC microbiology* 12:3
- Khan AA, El-Sayed A, Akbar A, Mangravita-Novo A, Bibi S, Afzal Z, Norman DJ, Ali GS (2017) A highly efficient ligation-independent cloning system for CRISPR/Cas9 based genome editing in plants. *Plant Methods* 13:86
- Khan AL, Waqas M, Khan AR, Hussain J, Kang S-M, Gilani SA, Hamayun M, Shin J-H, Kamran M, Al-Harrasi A (2013) Fungal endophyte *Penicillium janthinellum* LK5 improves growth of ABA-deficient tomato under salinity. *World Journal of Microbiology and Biotechnology* 29:2133-2144
- Lata R, Chowdhury S, Gond SK, White Jr JF (2018) Induction of abiotic stress tolerance in plants by endophytic microbes. *Letters in applied microbiology* 66:268-276
- Läuchli A, Grattan S (2007) Plant growth and development under salinity stress, p 1-32, *Advances in molecular breeding toward drought and salt tolerant crops*. Springer
- Le Gall H, Philippe F, Domon J-M, Gillet F, Pelloux J, Rayon C (2015) Cell wall metabolism in response to abiotic stress. *Plants* 4:112-166
- Lutts S, Benincasa P, Wojtyła L, Kubala S, Pace R, Lechowska K, Quinet M, Garnczarska M (2016) Seed priming: New comprehensive approaches for an old empirical technique, New Challenges in Seed Biology-Basic and Translational Research Driving Seed Technology. InTech
- Ma X, Zhang J, Huang B (2016) Cytokinin-mitigation of salt-induced leaf senescence in perennial ryegrass involving the activation of antioxidant systems and ionic balance. *Environmental and Experimental Botany* 125:1-11
- Maamoun HS, Rabie GH, Shaker I, Alaidaroos BA, El-Sayed ASA (2021) Biochemical properties of tyrosinase from *Aspergillus terreus* and *Penicillium copticola*; undecanoic acid from *aspergillus flavus*, an endophyte of *Moringa oleifera*, is a novel potent tyrosinase inhibitor. *Molecules* 26(5):1309
- Machado R, Serralheiro R (2017) Soil salinity: effect on vegetable crop growth. Management practices to prevent and mitigate soil salinization. *Horticulturae* 3:30
- Maheshwari R (2006) What is an endophytic fungus. *Curr Sci* 90:1309
- Mann A, Bishi S, Mahatma M, Kumar A (2015) Metabolomics and Salt Stress Tolerance in Plants, p. 251-266, *Managing Salt Tolerance in Plants*. CRC Press
- Milošević NA, Marinković JB, Tintor BB (2012) Mitigating abiotic stress in crop plants by microorganisms. *Zbornik Matice srpske za prirodne nauke* 2012:17-26
- Mishra Y, Singh A, Batra A, Sharma M (2014) Understanding the biodiversity and biological applications of endophytic fungi: a review. *J Microb Biochem Technol* 8:2
- Mondal S, Bose B (2014) An impact of seed priming on disease resistance: a review, p 193-203, *Microbial Diversity and Biotechnology in Food Security*. Springer
- Mousavi M, Omidi H (2019) Seed priming with bio-priming improves stand establishment, seed germination and salinity tolerance in canola cultivar (Hayola 401). *Plant Physiology* 9:2807-2817
- Munns R, Schachtman D, Condon A (1995) The significance of a two-phase growth response to salinity in wheat and barley. *Functional Plant Biology* 22:561-569

- Munns R, Tester M (2008) Mechanisms of salinity tolerance. *Annu Rev Plant Biol* 59:651-681
- Patel JS, Vitoreli A, Palmateer AJ, El-Sayed A, Norman DJ, Goss EM, Brennan MS, Ali GS (2016) Characterization of *Phytophthora* spp. Isolated from ornamental plants in Florida. *Plant Disease* 100:500-509
- Paparella S, Araújo S, Rossi G, Wijayasinghe M, Carbonera D, Balestrazzi A (2015) Seed priming: state of the art and new perspectives. *Plant cell reports* 34:1281-1293
- Pehlivan N, Yesilyurt AM, Durmus N, Karaoglu SA (2017) *Trichoderma lixii* ID11D seed biopriming mitigates dose dependent salt toxicity in maize. *Acta Physiologiae Plantarum* 39:79
- Pons R, Cornejo MJ, Sanz A (2013) Is ABA involved in tolerance responses to salinity by affecting cytoplasm ion homeostasis in rice cell lines? *Plant physiology and biochemistry* 62:88-94
- Porrás-Alfaro A, Bayman P (2011) Hidden fungi, emergent properties: endophytes and microbiomes. *Annual review of phytopathology* 49
- Prasad SR, Kamble UR, Sripathy K, Bhaskar KU, Singh D (2016) Seed bio-priming for biotic and abiotic stress management, p 211-228, *Microbial inoculants in sustainable agricultural productivity*. Springer
- Rasool S, Hameed A, Azooz M, Siddiqi T, Ahmad P (2013) Salt stress: causes, types and responses of plants, p 1-24, *Eco-physiology and responses of plants under salt stress*. Springer
- Rawat L, Singh Y, Shukla N, Kumar J (2011) Alleviation of the adverse effects of salinity stress in wheat (*Triticum aestivum* L.) by seed biopriming with salinity tolerant isolates of *Trichoderma harzianum*. *Plant and soil* 347:387
- Rawat L, Singh Y, Shukla N, Kumar J (2012) Seed biopriming with salinity tolerant isolates of *Trichoderma harzianum* alleviates salt stress in rice: growth, physiological and biochemical characteristics. *Journal of Plant pathology* 94:353-365
- Redman RS, Kim YO, Woodward CJ, Greer C, Espino L, Doty SL, Rodriguez RJ (2011) Increased fitness of rice plants to abiotic stress via habitat adapted symbiosis: a strategy for mitigating impacts of climate change. *PLOS one* 6:e14823
- Rodriguez R, White Jr J, Arnold A, Redman R (2009) Fungal endophytes: diversity and functional roles. *New phytologist* 182:314-330
- Ryu H, Cho Y-G (2015) Plant hormones in salt stress tolerance. *Journal of Plant Biology* 58:147-155
- Selvakumar G, Kim K, Hu S, Sa T (2014) Effect of salinity on plants and the role of arbuscular mycorrhizal fungi and plant growth-promoting rhizobacteria in alleviation of salt stress, p. 115-144, *Physiological mechanisms and adaptation strategies in plants under changing environment*. Springer
- Shekafandeh A, Sirooenejad S, Alsmoushtaghi E (2017) Influence of gibberellin on increasing of sodium chloride tolerance via some morpho-physiological changes in two olive cultivars. *Agriculturae Conspectus Scientificus* 82:367-373
- Singh H, Jassal RK, Kang J, Sandhu S, Kang H, Grewal K (2015) Seed priming techniques in field crops-A review. *Agricultural Reviews* 36:251-264
- Singh LP, Gill SS, Tuteja N (2011) Unraveling the role of fungal symbionts in plant abiotic stress tolerance. *Plant signaling & behavior* 6:175-191
- Singh S, Singh UB, Trivedi M, Sahu PK, Paul S, Paul D, Saxena AK (2020) Seed biopriming with salt-tolerant endophytic *Pseudomonas geniculata*-modulated biochemical responses provide ecological fitness in maize (*Zea mays* L.) grown in saline sodic soil. *International Journal of Environmental Research and Public Health* 17:253
- Song M, Li X, Saikkonen K, Li C, Nan Z (2015) An asexual *Epichloë* endophyte enhances waterlogging tolerance of *Hordeum brevisubulatum*. *Fungal Ecology* 13:44-52
- Tilbrook J, Roy S (2013) Salinity tolerance, p 133-178, *Plant Abiotic Stress*. John Wiley & Sons, Inc
- Vardharajula S, SkZ A, Shiva Krishna Prasad Vurukonda S, Shrivastava M (2017) Plant growth promoting endophytes and their interaction with plants to alleviate abiotic stress. *Current Biotechnology* 6:252-263
- Waller F, Achatz B, Baltruschat H, Fodor J, Becker K, Fischer M, Heier T, Hückelhoven R, Neumann C, von Wettstein D (2005) The endophytic fungus *Piriformospora indica* reprograms barley to salt-stress tolerance, disease resistance, and higher yield. *Proceedings of the National Academy of Sciences of the United States of America* 102:13386-13391
- Wani SH, Kumar V, Shriram V, Sah SK (2016) Phytohormones and their metabolic engineering for abiotic stress tolerance in crop plants. *The Crop Journal* 4:162-176
- Waqas M, Khan AL, Kamran M, Hamayun M, Kang S-M, Kim Y-H, Lee I-J (2012) Endophytic fungi produce gibberellins and indoleacetic acid and promotes host-plant growth during stress. *Molecules* 17:10754-10773
- Waqas M, Khan AL, Shahzad R, Ullah I, Khan AR, Lee I-J (2015) Mutualistic fungal endophytes produce phytohormones and organic acids that promote japonica rice plant growth under prolonged heat stress. *Journal of Zhejiang University SCIENCE B* 16:1011-1018
- Wu H, Ye H, Yao R, Zhang T, Xiong L (2015) OsJAZ9 acts as a transcriptional regulator in jasmonate signaling and modulates salt stress tolerance in rice. *Plant Science* 232:1-12
- Xu J, Li X-L, Luo L (2012) Effects of engineered *Sinorhizobium meliloti* on cytokinin synthesis and tolerance of alfalfa to extreme drought stress. *Appl. Environ. Microbiol.* 78:8056-8061
- Yadav S, Irfan M, Ahmad A, Hayat S (2011) Causes of salinity and plant manifestations to salt stress: a review. *Journal of Environmental Biology* 32:667
- Yamaji K, Watanabe Y, Masuya H, Shigetou A, Yui H, Haruma T (2016) Root Fungal Endophytes Enhance Heavy-Metal Stress Tolerance of *Clethra barbinervis* Growing Naturally at Mining Sites via Growth Enhancement, Promotion of Nutrient Uptake and Decrease of Heavy-Metal Concentration. *PLoS one* 11:e0169089
- Zhao Y, Dong W, Zhang N, Ai X, Wang M, Huang Z, Xiao L, Xia G (2014) A wheat allene oxide cyclase gene enhances salinity tolerance via jasmonate signaling. *Plant physiology* 164:1068-1076