

REVIEW

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REVIEW

Alleviation of abiotic and biotic stresses in crops through beneficial rhizospheric bacteria

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Plants do not live in isolation but constantly interact with an array of microorganisms in the soil and in the atmosphere. This interaction is again affected by various environmental factors, and when the environmental conditions become unfavourable they impose different stresses on the plant. With increasing urbanization and population leading to adverse conditions such as extremes of temperatures, water deficit, salinity, increase of heavy metal pollutants in the soil ways and means are now being sought to make plants more resilient. Use of beneficial microorganisms with multiple traits not only for plant growth promotion and disease reduction, but also for alleviation of abiotic stresses is now being considered. Plant growth promoting rhizobacteria (PGPR), endophytic bacteria and other beneficial bacteria including those responsible for biocontrol are being evaluated for such multiple uses in sustainable agriculture. Such bacteria mainly act by mechanisms which reduce the effects such as oxidative stress or cellular metabolic disruptions brought about by different stresses. The various beneficial plant microbial interactions which lead to amelioration of abiotic stresses as well as promotion of growth in plants have been discussed here and along with the various mechanisms involved in the observed beneficial effect.

Key words: Abiotic Stress; biotic Stress; rhizosphere bacteria; defense enzymes; oxidative burst

INTRODUCTION

It is now confirmed scientifically that the earth's climate is rapidly changing and due to rising concentrations of CO₂ and other atmospheric trace gases, global temperatures have increased by about 1°C over the course of the last century, and will likely rise even more rapidly in coming decades. Increased drought and salinization of arable land are expected to have devastating global effects. Abiotic stress is already the primary reason of crop loss worldwide, reducing average yields for most major crop plants by more than 50%. It will soon become even more severe as desertification will further increase and the current amount of annual loss of arable area may double by the end of the century because of global warming. Simultaneously, rapid population growth increasingly

generates pressure on existing cultivated land and other resources. Population migration to those arid and semiarid areas increases the problems of water shortage and worsens the situation of land degradation in the destination, and in turn causes severe problems of poverty, social instability, and population health threats. Water scarcity and desertification could critically undermine efforts for sustainable development, introducing new threats to human health, ecosystems, and national economies of various countries.

Agriculture is one of the most vulnerable sectors to changing environmental conditions such as salinity, drought and flooding, high and low temperatures, change in pH, strong light, UV as well as incidences of diseases caused by pests and pathogens. It is quite obvious that adverse environmental conditions will have a negative impact on crop production, which has the potential to become major problems for food security, particularly in tropical regions.

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Besides natural changes in environmental conditions, the most compounding factors are the population explosion and human activities, which in turn aggravate the adverse effects. Abiotic stress management is one of the greatest challenges of agricultural scientists and needs careful consideration. Various strategies to cope with abiotic stresses, include development of heat and drought tolerant varieties, shifting the crop calendars, resource management practices etc (Venkateswarlu and Shanker 2009). Development of stress tolerant plants (STPs) is another option being considered and this includes manipulation of stress associated genes and proteins for over-expression of metabolites, production of transgenics or conventional plant breeding combined with the use of molecular markers and QTLs.

However, though some of these technologies have shown promise, they are cost-intensive and laboratory oriented. Hence these technologies may not be the solution for the common farmer. In this scenario, recent studies indicate that there is another strategy which has high potential to alleviate stresses in plants, is highly eco-friendly and cost effective. It involves the utilization of multifaceted traits of several beneficial microorganisms which have been known earlier for their role in plant growth promotion, nutrient management and disease control. Several reports on the use of microorganisms, specially plant growth promoting rhizobacteria (PGPR) for induction of tolerance against abiotic stresses have been forthcoming in the last 2-3 decades. Interestingly, researches in several laboratories have now confirmed that several of these PGPR can also help the plant in withstanding against abiotic stresses (Bashan and Bashan 2010). Reports are now accumulating on application of PGPB (plant growth promoting bacteria) as elicitors for tolerance to abiotic stresses, such as drought, salt and nutrient deficiency in plants and raising possibility for incorporation of microbial genes into plant and diverse microbial species (Chakraborty *et al.* 2015). The beneficial plant microbial interactions are very frequent in nature, where PGPB help the plants to overcome various stresses. Besides bacteria, beneficial fungi such as endophytes or mycorrhizal fungi also confer tolerance to plants against different abiotic stresses. Microbial communities offer a potentially powerful

opportunity for understanding these beneficial interactions (Khanna *et al.* 2019). Consequently, changes in the structure or function of microbial communities may have a major impact on ecosystem activities (Khan *et al.* 2011). Yang *et al.* (2009) proposed the term 'induced systemic tolerance' (IST) for PGPR-induced physical and chemical changes in plants that result in enhanced tolerance to abiotic stress, as against the well known ISR or 'induced systemic resistance' by PGPR (plant growth promoting rhizobacteria) against plant pathogens. Besides bacteria, plants live in close symbiotic association with a group of fungi, known as arbuscular mycorrhizal fungi (AMF) which confer on the plants an improved ability for nutrient uptake as well as increased tolerance to abiotic and biotic stresses while the fungi themselves acquire protected ecological niche and plant photosynthates (Ruiz-Lozano 2003). This interaction of plant-AMF can be successfully exploited for development of abiotic stress management strategies. Reports are also available currently on the role of established biocontrol agents such as *Trichoderma* in alleviation of abiotic stresses and plant growth promotion. The present review is confined to a discussion of the alleviation of abiotic and biotic stresses by beneficial rhizospheric bacteria and the biochemical changes involved therein.

ALLEVIATION OF ABIOTIC STRESSES

Temperature stress alleviation

The effects of temperature varies depending on type of plant and its optimal requirements. Plants growing in colder climates, when exposed to higher temperatures will suffer from elevated temperature stress whereas the same temperature would be optimal for those growing in warmer climates. Similar is the case with tropical plants which when exposed to colder temperatures suffer from cold stress or in colder conditions, to freezing. With global warming and other related phenomena, earth is now witnessing several extreme temperature conditions varying from very high to very low and is now a major concern in agriculture. Water scarcity also leads to temperature increase. Microorganisms also have optimal temperature conditions for growth and hence, the ability of rhizospheric bacteria to alleviate temperature stress will also vary.

It is clear that temperature and soil type may affect the performance of plant-beneficial bacteria interaction (Egamberdiyeva and Hoflich 2003). Those bacteria which can themselves grow better at higher / lower temperatures could be of use for application in agriculture under elevated/ low temperature conditions. In addition, bacteria colonizing distinct sites may react differently to different environmental conditions. In studies using several rhizospheric bacteria, it was observed that many bacteria such as *Mycobacterium* sp. 44, a *Pseudomonas fluorescens* and a *Pantoea agglomerans* strain isolated from a semi-continental climate were found to significantly increase the root and shoot growth of winter wheat at 16°C compared with that at 26°C in loamy sand (Compant *et al.* 2010). On the other hand, bacteria isolated from semi arid climate such as *Mycobacterium phlei* strain MbP18 as well as *Mycoplanabullata* MpB46 were not affected by temperature change, indicating genotype-specific preferences for certain environmental conditions. A study with the endophyte *Burkholderia phytofirmans* strain PsJN demonstrated that a temperature increase from 10 to 30°C reduced the colonization of this strain in the tomato rhizosphere, whereas endophytic abundance was not affected. After successful colonization, rhizosphere as well as endophytic bacteria may alleviate temperature by inducing a systemic response (Yang *et al.* 2009).

Srivastava *et al.* (2008) also isolated a thermotolerant *P. putida* strain NBR10987 from drought stressed rhizosphere of chickpea. The thermotolerance of the strain was attributed to the over expression of stress sigma factor and enhanced biofilm formation at high temperatures. The ability of a thermo-tolerant strain of *Pseudomonas* AKM-P6 was used to alleviate the heat stress in sorghum seedlings (Ali *et al.* 2009). They reported that inoculation induced the biosynthesis of high molecular weight proteins in leaves under elevated temperature, reduced membrane injury, and improved the level of cellular metabolites like proline, chlorophyll, sugars, amino acids, and proteins. Analysis of proteins from inoculated and uninoculated sorghum seedlings exposed to ambient and elevated temperature revealed the presence of three additional polypeptides in the seedlings exposed to elevated temperature, indicating a possible role of inducible proteins in microbial mediated heat tolerance mechanism.

Ashraf and Foolad (2007) reported that *Pseudomonas putida* strain AKMP7 increases the thermotolerance of wheat plants by stimulating accumulation of proline, which binds to cell membrane, maintain membrane permeability and direct osmotic balance within tissue. Certain oligosaccharides belonging to raffinose oligosaccharide family, galactinol and stachyose as well as sugars, such as trehalose, glucose and sucrose, are known to be associated with responses to environmental stress. The over expression of galactinol synthase gene (GolS), a heat shock factor in *Arabidopsis* under abiotic stress and steady state expression of trehalose phosphate synthase 5 (TPS5) gene in wheat plants (cv. Olivin) after *Bacillus amyloliquefaciens* 5113 treatment clearly indicating their probable contribution to overall fitness of plant against abiotic stress. Likewise, *P. putida* strain AKMP7 neutralizes negative impact of heat stress on wheat and increase yield, spike length and count, grain size and quality. In another study, wheat seedlings (cv. Olivin and Sids1) treated with two PGPR strains *Bacillus amyloliquefaciens* 5113 and *Azospirillum brasilense* NO40, transcript expression level of several heat response transcription regulator homologs (HsfB1, HsfA3, MBF1c), HSP17.8, which maintain protein conformation under stressed condition, MSFB1 remained unaffected unlike untreated heat stressed seedlings (Islam *et al.* 2014). RT PCR expression analysis of heat stressed bacteria untreated and treated wheat plants using APX1 (forward, 52 - GGAGGCTTCCTGATGCTG-32 reverse, 52 -CGGCGTAGTCCTTGAAGAAT-32 ; AF387739.1) and TmSAMS1 (forward, 52 - GACCCAGGTGACTGTGGAGT-32 reverse, 52 - AGGCACGCCAATAGCATAAG-32 ; EU399630.1) gene specific primer showed reduced expression of these two genes in bacterial primed plants. In addition, higher basal levels of other enzymes of ascorbate-glutathione pathway DHAR, MDHAR and GR were observed in bacteria primed plants. Similarly, *P. putida* strain AKMP7 inoculated wheat plants had reduced ROS production pointing towards preventive measure against ROS production and avoiding expensive adaptations tied to ROS detoxification mechanism (Ali *et al.* 2011).

It is thus obvious that such beneficial bacterial strains have the potential to be used in agriculture under temperature stressed conditions in the era of global warming and changing environmental scenario.

Several plants including maize, soybean, cotton, banana are sensitive to temperatures below 10–15 °C and exhibit signs of injury. Frost injury is common in many plants and they exhibit different phenotypic symptoms in response to chilling stress which include reduced leaf expansion, wilting, chlorosis and may lead to necrosis and also reproductive development (Mahajan and Tuteja 2005). Several workers have also reported the ability of cold-tolerant bacteria to induce cold tolerance in plants (Chang *et al.* 2007; Mishra *et al.* 2009). The potential of novel cold tolerant plant growth promoting bacterial species viz., *Pantoea dispersa*, *Serratia marcescense*, *Pseudomonas fragi*, *Exiguobacterium acetylicum* and *Pseudomonas lurida* in promoting plant growth at cold temperatures was demonstrated by Selvakumar *et al.* (2008a,b). They attributed the observed effects mainly due to auxin production and phosphate solubilization by bacterial species. Under low temperature, such bacteria can sustain their metabolic processes and aid in plant growth promotion. Since ice nucleation has been recognized as a cause of frost damage of plants, recent development in the use of microbial technology is the identification of naturally occurring phyllospheric bacteria with low ice nucleating activity, so that they can be sprayed on leaves to overcome frost damage (Selvakumar *et al.* 2012).

In order to determine the effect of a PGPR on growth and physiological activity of grapevines at low temperature, *in vitro* inoculation of *Vitis vinifera* cv. Chardonnay explants with *Burkholderia phytofirmans* strain PsJN, was carried out. Bacterization enhanced both growth and physiological activity of grapevine at low temperature. A relationship between endophytic bacterial colonization of the grapevine plantlets and their growth at both ambient (26°C) and low (4°C) temperatures and their sensitivities to chilling was evident. The major benefits of bacterization were observed on root growth and plantlet biomass. The inoculation with PsJN also significantly improved plantlet cold tolerance compared with that of the non-bacterized control. Moreover, relative to the non-inoculated controls, bacterized plantlets had significantly increased levels of starch, proline, and phenolics. These increases correlated with the enhancement of cold tolerance of the grapevine plantlets (Barka *et al.* 2006). In another study, Mishra *et al.* (2009)

examined the effect of seed inoculation with 12 cold tolerant plant growth promoting *Pseudomonas* strains on wheat growth and physiological changes under green house conditions at 10°C. They reported that bacterization with pseudomonads significantly improved root length, shoot length, dry root biomass, dry shoot biomass compared with non-bacterized control. Further, bacterized wheat plants showed enhanced levels of total chlorophyll, anthocyanin, free proline, total phenolics, and starch contents, while a decrease was observed in the ratio and electrolyte leakage values which indicate enhanced tolerance to cold stress conditions. Inoculation of wheat seeds with *Serratia marcescens*, strain SRM, and *Pantoea dispersa*, strain 1A increases the seedlings biomass and nutrients uptake at low temperatures (Milosevic *et al.* 2012). Sarkar *et al.* (2018) reported the alleviation of high temperature stress in wheat by the use of multi faceted bacteria such as *Bacillus safensis* and *Ochrobactrum pseudogrignonense*. Thus, use of plant growth promoting bacteria, which are themselves cold tolerant is now being considered very useful because such bacteria, besides promoting growth of plants also provide them the ability to survive under freezing conditions (Chakraborty *et al.* 2019 a)

WATER AND SALINITY STRESS ALLEVIATION

Drought, flooding and salinity lead to osmotic stress and water deficit like conditions due to limitations in available water supply. This condition affects the water relations of a plant at both cellular and whole plant level decreasing productivity. Since this has a serious implication in agriculture and food production, attempts are continuously being made for development of strategies so that plants can overcome osmotic stresses. Among the several options, one of the most promising ones in terms of ease of use, cost-benefit and eco-friendliness is the use of those microbes which themselves can grow in such stressed environments and also confer on plants the ability to tolerate such stresses to a great extent. It has been reported by several authors that beneficial microorganisms such as plant growth promoting microorganisms (PGPM)-bacteria or fungi, promote plant growth and increases tolerance to stresses such as drought, flooding or salinity (Marulanda *et al.* 2008; Grover *et al.* 2011; Timmusk *et al.* 2014). It has been suggested that use of these microorganisms per se can alleviate stresses in agriculture thus

opening a new and emerging application of microorganisms. Microbial elicited stress tolerance in plants may be due to a variety of mechanisms proposed from time to time based on studies done (Shrivastava and Kumar 2015).

It has now been proved beyond doubt that inoculation of plants by certain rhizospheric bacteria leads to enhanced tolerance to abiotic stresses, especially to drought and salinity. In the last decade or so, bacteria belonging to different genera including *Pseudomonas*, *Bacillus*, *Paenibacillus*, *Pantoea*, *Burkholderia*, *Azospirillum*, *Achromobacter*, *Microbacterium*, *Methylobacterium*, *Enterobacter* etc. have been reported to provide tolerance to host plants under different abiotic stress environments (Grover *et al.* 2011). Inoculation of *Azospirillum brasilense* Sp245 in wheat (*Triticum aestivum*) under drought stress resulted in a better water status and an additional 'elastic adjustment' leading to better grain yield and mineral quality (Mg, K, and Ca) (Creus *et al.* 2004). Chakraborty *et al.* (2013) showed that two rhizospheric bacteria with plant growth promoting ability could also induce tolerance in wheat against drought. These were *Bacillus safensis* and *Ochrobactrum pseudogrignonense*. Timmusk *et al.* (2014) also reported that two bacteria- *Bacillus thuringiensis* and *Paenibacillus polymyxa*, originally isolated from stressed environments could induce tolerance in wheat against drought. There are also several reports that halotolerant plant growth promoting rhizobacteria alleviate salt stress and help plants to maintain better growth. In a study by Shukla *et al.* (2012), six PGPR strains were analyzed for their involvement in salt-stress tolerance in *Arachis hypogaea*. Of the six, three – *Brachybacterium saurashtrense*, *Brevibacterium casei*, and *Hatererohalobacter* showed the best growth of *A. hypogaea* seedlings under both stressed and salt stressed conditions. Plant length, shoot length, root length, shoot dry weight, root dry weight, and total biomass were significantly higher in inoculated plants compared to uninoculated plants. Similar results were reported for salt tolerance in various plants induced by PGPR (Mayak *et al.* 2004; Saravankumar and Samiyappan 2007; Zahir *et al.* 2009).

While the exact mechanisms of plant drought and salinity stress tolerance enhancement by rhizosphere bacteria still remain largely speculative, possible explanations include: (i)

production of hormones like abscisic acid, gibberellic acid, cytokinins, and auxin; (ii) production ACC deaminase leading to reduced level of ethylene in the root of developing plants; (iii) induced systemic tolerance by the bacteria and (iv) formation of bacterial biofilm i.e. extracellular matrix (Yang *et al.* 2009; Timmusk *et al.* 2011; 2014; Kim and Timmusk 2013). Extracellular matrix formed by bacterial biofilm can provide almost infinite range of macromolecules such as sugars and oligo- and polysaccharides beneficial for plant development and growth. The water retention capacity of some polysaccharides can exceed several-fold their mass (Timmusk *et al.* 2011). In fact, it has been demonstrated that even a small polysaccharide alginate content in the biofilm facilitates maintenance of hydrated microenvironment (Chang *et al.* 2007). The EPS producing *Pseudomonas putida* strain GAP-P45 forms biofilm on the root surface of sunflower seedlings and impart tolerance to plants against drought stress. The inoculated seedlings showed improved soil aggregation and root-adhering soil and higher relative water content (RWC) in the leaves (Sandhya *et al.* 2009; 2011).

Involvement of auxins in stress responses have been indicated in several studies. There are earlier reports that water and salt stresses affect auxin transport by altering the expression of PIN genes and/or by inhibition of polar auxin transport (Potters *et al.* 2009). Interestingly, over-expression of an auxin-amidohydrolase in *Arabidopsis* is associated with a reduced inhibition of root elongation and increased resistance to salt stress which may probably due to the increase in the content of free auxin sufficiently to provide protection against salt stress (Junghans *et al.* 2006). Changes in plant root morphology have been observed repeatedly upon *Azospirillum* inoculation and have been attributed to the production of plant-growth promoting substances-auxins, cytokinins and gibberellins, with auxin production being quantitatively the most important (Spaepen *et al.* 2008). Ansary *et al.* (2012), from their studies on maize concluded that, inoculation with *Pseudomonas fluorescens* led to improved tolerance to water deficit and a concomitant increase in secretion of phytohormones such as auxin, cytokinins and gibberellins.

Besides the direct involvement of IAA on root growth and stress responses, it has also been

postulated that the observed positive effects of IAA on root growth may be an indirect effect due to reduction in ethylene levels since a close relationship exists between IAA and ethylene precursor ACC (Dimkpa *et al.* 2009; Lugtenberg and Kamilova 2009). In plants, production of ethylene occurs at two different phases in response to stress. In the first phase, relatively small amount of ethylene is produced which promotes the activity of stress-related genes, while the larger amount of ethylene produced in the second phase (1–3 days after) leads to inhibition of growth and harmful effects on plants including senescence, chlorosis, and abscission (Glick *et al.* 2007).

The ability of several PGPR to produce ACC deaminase which degrades ACC (1-aminocyclopropane-1 carboxylate), the immediate precursor of ethylene leads to reduction in ethylene biosynthesis in plants treated with these PGPR. The ACC-deaminase function seems to be mutually beneficial between plants and PGPR, because ethylene in plants can be reduced by continuous ACC secretion and degradation by bacteria, and bacteria can use metabolized ACC. This characteristic of several PGPR have made them useful in protecting different plant species against growth inhibition caused by various environmental stresses. In a study by Mayak *et al.* (2004) they reported that *Achromobacter piechaudii* having ACC deaminase activity significantly increased the fresh and dry weights of tomato seedlings grown in the presence of NaCl salt (up to 172 mM). Similarly, inoculation of maize plants with *Pseudomonas fluorescens* which could produce ACC deaminase enhanced root elongation and fresh weight significantly under saline conditions (Kausar and Shahzad 2006). Siddiqui *et al.* (2010) have also confirmed that inoculation with 14 halotolerant bacterial strains ameliorate salt stress in canola plants through the reduction of ethylene production via ACC deaminase activity.

Accumulation of certain specific metabolites such as amino acids, amides, imino acids, proteins, glycine betaines and polyamines have been correlated with drought and salt tolerance in plants by several authors (Parida and Das, 2005; Shukla *et al.*, 2012). It is well known that when plants face drought or salt stress, proline accumulates in the cytosol and helps substantially in cytoplasmic

osmotic adjustment. Very high accumulation of cellular proline (up to 80% of the amino acids pool under stress and 5% under normal conditions) due to increased synthesis and decreased degradation under a variety of stress conditions such as salt and drought has been documented in many plant species (Szabados and Savaure 2009). While it is clear that proline accumulates during stress conditions, it is not clear whether proline has a role in tolerance. While several authors (Shukla *et al.* 2012; Tiwari *et al.* 2016) have shown that alleviation of stress by PGPR correlates with decreased accumulation of proline, others have reported increased accumulation of proline during stress alleviation (Jha *et al.* 2010; Vardharajula *et al.* 2011). Chen *et al.* (2007) also correlated proline accumulation with drought and salt tolerance in plants. Introduction of proBA genes derived from *Bacillus subtilis* into *A. thaliana* resulted in production of higher levels of free proline resulting in increased tolerance to osmotic stress in the transgenic plants. Increased production of proline along with decreased electrolyte leakage, maintenance of relative water content of leaves and selective uptake of K⁺ ions resulted in salt tolerance in *Zea mays* coinoculated with *Rhizobium* and *Pseudomonas* (Bano and Fatima, 2009). However, in studies using *Pseudomonas putida* in chickpea, Tiwari *et al.* (2016) showed that proline and total soluble sugar increased significantly with progression of drought stress; however while inoculation with *P. putida* increased drought tolerance several fold, it also led to significant decline in proline and TSS content at all stress durations. Authors suggested that this may be due to bacteria-induced IST response of chickpea plants since its inoculation may have stimulated root exudation, biofilm formation and conservation of soil moisture which may have resulted in enhanced root growth and nutrient uptake thereby improving plant health under stress condition. Further degradation of ethylene precursor ACC by bacterial deaminase may also be one of the reasons for relieving plant stress and rescuing normal plant growth under drought stress as reported earlier by Yang *et al.* (2009).

It is well known that abiotic stresses cause oxidative stress injuries in cells but in many cases plants are able to overcome the oxidative stress by their in-built antioxidant mechanisms. In several cases it has been reported that enhancement of antioxidant machinery is one of the mechanisms

by which microbes alleviate abiotic stresses. The antioxidant machinery is known to involve a battery of enzymes such as peroxidase (POX), ascorbate peroxidase (APOX), catalase (CAT), superoxide dismutase (SOD) and glutathione reductases (GR) as well as small antioxidants such as carotenoids, glutathione, ascorbate etc. (Chakraborty and Pradhan 2012; Roy and Chakraborty 2018). Chakraborty *et al.* (2013), from their studies on wheat, showed that in susceptible cultivars GY and MW, both superoxide dismutase (SOD) and catalase (CAT) declined from the onset of drought; application of either *Bacillus safensis* or *Ochrobactrum pseudogregnonense* helped to maintain higher levels of the two enzymes and thus helped alleviate drought. One of the mechanisms of alleviation of water stress seems to be the ability to tilt the balance from oxidatively stressed condition to a more antioxidative state, thereby resisting the effects of stress. However, there are also reports that inoculation of plants with PGPR which also provide protection against drought or salt stress, lead to reduced antioxidative enzyme activities. In a study by Sandhya *et al.* (2010), it was shown that alleviation of drought in maize plants inoculated with species of different species of *Pseudomonas*- *P. entomophila*, *P. stutzeri*, *P. putida*, *P. syringae*, and *P. montelli*, led to lower activity of antioxidant enzymes as compared to uninoculated plants. According to Tiwari *et al.* (2016), comparatively less activity of SOD and CAT in PGPR inoculated chickpea plants than the uninoculated ones at all stress durations suggests that low level of oxidative stress is perceived by the plants inoculated with the bacterium. Significantly lower level of expression of genes encoding antioxidant enzymes namely CAT, APX, and GST in PGPR-inoculated chickpea plants of both varieties exposed to drought stress indicates that this bacterium is capable of relieving stress and restoring normal growth conditions for inoculated plants as compared to the uninoculated ones. These results, which apparently seem to be in contradiction with the more common observation that stress resistance in plants is related to more effective antioxidant systems may be an indication that inoculated plants felt less stress as compared to uninoculated plants.

Disruption in the requisite Na⁺-K⁺ ratio is one of the common effects of osmotic disbalance caused by stresses such as salinity. Under saline conditions, plants are forced to uptake more Na⁺

ions leading to lesser uptake of K⁺ ion which is more essential for plants. Potassium plays a key role in plant metabolism such as activation of a number of enzymes, and also plays an important role in stomatal movements and protein synthesis. Since these functions cannot be replaced by Na⁺ ions a higher Na⁺:K⁺ ratio generated due to salinity disrupts the ionic balance in the cytoplasm, consequently disrupting various metabolic pathways. In this context, experiments have shown that PGPR can modulate the Na⁺/K⁺ ratio under salinity stress by restricting Na⁺ uptake and enhancing K⁺ uptake. In a study conducted by Shukla *et al.* (2012), authors obtained a low Na⁺ content and a higher K⁺ content in the presence of PGPR under salinity leading to a higher K⁺ / Na⁺ ratio in plants under salt stress. Similarly, several earlier workers have also reported that PGPR reduce the salt toxicity in plants by lowering the Na⁺ concentration and increasing the K⁺ concentration (Nadeem *et al.* 2006; Yildirim *et al.* 2006; Bano and Fatima 2009). Repression of expression of some of the salt induced genes such as NHX1, SOS1 maybe one of the mechanisms by which PGPR restrict entry of Na⁺. The SAPK4 gene acts as regulatory factor in salt stress acclimatization, ion homeostasis, growth and development, therefore its 1.3-fold upregulation in SN13 alone implies SN13 mediated low Na⁺ & Cl⁻ intake under hydroponic system (Diedhiou *et al.* 2008).

Bacillus subtilis GB03, a species which was earlier used as a commercial biocontrol agent was reported to induce systemic tolerance in *Arabidopsis* to salt stress (Zhang *et al.* 2008). Interestingly, some of the volatile organic compounds (VOCs) that are emitted from *B. subtilis* GB03 and which had earlier been considered to be involved in the biocontrol activity (Ryu *et al.* 2004) of the bacterium have subsequently been shown to be also the bacterial determinants involved in IST. In *Arabidopsis*, transcriptional expression of HIGH-AFFINITY K⁺ TRANSPORTER 1 (HKT1), which controls Na⁺ import in roots, was decreased. HKT1 has been shown to adjust Na⁺ and K⁺ levels differentially being tissue specific. Exposure of an *athkt1* mutant to bacterial VOCs not only resulted in typical salt-stress phenotypes, such as stunting, but also led to the inhibition of seedling growth. Transcriptional validation revealed that bacterial VOCs down-regulated HKT1 expression in roots, but

upregulated it in shoot tissues, thereby orchestrating lower Na⁺ levels in the whole plant. Furthermore, no difference was observed in IST to salt stress in the Na⁺-export mutant salt overly sensitive3 (*sos3*), suggesting that HKT1 functions in shoots to retrieve Na⁺ from the xylem, thereby facilitating shoot-to-root Na⁺ recirculation. Overall, plant perception of bacterial VOC causes a tissue-specific regulation of HKT1 that controls Na⁺ homeostasis under salt stress.

Salinity stress alleviation in wheat using *Bacillus safensis* and *Ochrobactrum pseudogrignonense*, two salt tolerant PGPR, have been reported by Chakraborty *et al.* (2018,2019). Microarray analysis revealed that 282 genes were down-regulated and 6022 up-regulated after application of *O. pseudogrignonense* under salt stress induction by 200 mM sodium chloride. Among the up-regulated genes were those of peroxidase, phenylalanine ammonia-lyase, chitinase, glucanase, as well as germin-like proteins, histone H2B, and sulfur-rich thionin-like proteins. Genes for ascorbate peroxidase, lipid transfer proteins, and salt stress responsiveness were among the down-regulated ones.

ALLEVIATION OF BIOTIC STRESSES

Exploitation of symbiotic association of microbes with plants has currently become an important tool to protect the plant health in eco friendly manner (Gaiero *et al.* 2013; Gupta *et al.* 2015). Significant attempts have been made to replace fertilizers and pesticides with various biocontrol agents (Chakraborty and Chakraborty 2017), such as plant growth promoting rhizobacteria (Bent 2006; Chakraborty *et al.* 2014) and plant growth promoting fungi (Hossain *et al.* 2017). PGPR improve plant health and growth promotion by array of mechanisms that include formation of soil structure, disintegration of organic matter, reprocessing of essential elements, mineral nutrients solubilisation and producing copious amount of plant growth regulators which act as stimuli of root growth. These increase soil fertility also protect plants from broad spectrum of soil and seed borne pathogens by induced systemic resistance (Sivasakthi *et al.* 2014). Jasmonate and ethylene signalling along with a range of defense enzymes and phenolic compounds induce systemic resistance within the plant and incite the host plant's defense reactions against a range of

plant pathogens (Glick 2012). The beneficial microbes may also inhibit the pathogen growth directly by secreting antimicrobial compounds into the soil, thereby restricting growth and entry of the pathogen into the host.

Deepthi *et al.* (2016) reported the antifungal activity of *Lactobacillus plantarum* MYS6 against *Fusarium proliferatum* MYS9. They have reported 10-Octadecenoic acid, methyl ester as one of the major antifungal compounds produced by the isolate by its volatile substances. Chemoprofiling of this volatile substance secreted from root endophyte *Pseudomonas putida* BP25 identified Pyrrolo [1,2-a] pyrazine-1,4-dione, an antifungal compound inhibited broad range of pathogens such as *Gibberella moniliformis*, *Phytophthora capsici*, *Pythium myriotylum*, *Rhizoctonia solani*, *Colletotrichum gloeosporioides*, *Athelia rolfsii*, and plant parasitic nematode, *Radopholus similis* (Sheorn *et al.* 2016). Antagonistic activity of different species of *Bacillus* (*B. amyloliquefaciens*, *B. pumilus*, *B. subtilis*) against *B. sorokiniana* were reported by Kilic-Ekici and Yuen (2004). Different species of *Ochrobactrum*, such as *Ochrobactrum lupini* KUDC1013 induced systemic resistance (ISR) in tobacco against soft rot disease caused by *Pectobacterium carotovorum* subsp. *carotovorum* (Sumayo *et al.* 2013) and *Ochrobactrum anthropi* BMO-111 against blister blight disease of tea (Sowndhararajan *et al.* 2012).

Plant phenolics and proteins are directly or indirectly involved in various metabolic pathways and play vital role in disease resistance. Fungal infection accelerates phenolic metabolism and lignin synthesis. Phenolic compounds, including phenolic acids and cell wall bound ferulic acid, can give mechanical strength to the cell wall to guard against infection, ferulic acid crosslinking of phenylpropanoid esters directs to the formation of lignin-like polymers, such hydroxycinnamic acids and their derivatives (Maurya *et al.* 2007).

Increased protein expression perhaps involved in modulation of enzyme expression, signal transduction, degradation of plant metabolism, transport, biocontrol (Yaoyao *et al.* 2017). Chloroplastic Hsp70 induced JA-dependent signal transduction pathway which plays a key role in induction of defense responses in stripe rust infected wheat plants (Duan *et al.* 2011; Yu *et al.*

2015). Kumar *et al.* (2009) reported that HsfB1 and HsfB2b family interacted with class A-Hsfs and upregulated many heat shock proteins including Hsp17.6, Hsp70, Hsp83.1, and Hsp101 and induced resistance against many pathogens (*P. syringae*, *P. infestans*, *B. cinerea*, *A. brassicicola*). To impede pathogen attack PGPR modulate expression of an array of defense enzymes which are already present in plants as intrinsic defense against any pathogen attack. Among the defense enzymes POX is one of the key enzymes countering pathogen attack and provide defense against plant pathogens (Anand *et al.* 2007). Different isoforms of POX provide resistance against plant pathogens by lignin and suberin deposition, polymerization of hydroxyl proline rich glycoprotein on cell walls guarding cells against fungal hyphae invasion and also reduce oxidative damage by H₂O₂ scavenging (Maksimov *et al.* 2014). Other than POX, application of two PGPR significantly increase expression of PR proteins, such as β -1,3 glucanase (PR 2) and chitinase (PR 3) in infected plants at the same time reduce disease incidence. Chitinase and β 1,3 glucanase accumulate around necrotic region. These two enzymes destroy fungal hyphae and restrict hyphae penetration within cells (Armijo *et al.* 2016).

Another vital enzyme and part of phenyl propanoid pathway PAL activity also increases significantly after PGPR application. PAL is the principal enzyme in the phenylpropanoid metabolism and has important function in the production of several defense-related secondary compounds such as lignin and phenols (Tahsiliet *al.* 2014). Boominathan *et al.* (2013) reported *B. megaterium* (AUM72) mediate induction of defense related enzymes against rhizome rot causing fungus *Pythium aphanidermatum*. Plant growth promotion in wheat by rhizosphere bacteria with multi-functional traits was reported by Chakraborty *et al.* (2013). Chakraborty *et al.* (2016) also reported the role of PGPR as plant growth promoter in tea and biocontrol agent against root rot pathogens. Elevated expression defense-related genes, namely puoindoline protein, β -1,3-glucanase and chitinases in wheat during *Tilletia indica* infection was reported by Tripathi *et al.* (2013). Overexpression of pathogenesis related (PR) proteins like peroxidase, β -1,3-glucanase and chitinase, polyphenol oxidase (PPO), phenylalanine ammonia lyase -an integral part of phenyl propanoid pathway, phenols and also chlorophyll

contents induced systemic resistance (ISR) in infected plants (Sundaramoorthy *et al.* 2014). β -1,3-glucanase and chitinase can break down the cell wall components of pathogens, PAL and peroxidase was found to induce defense responses in many crops under fungal attack. Coordinated accumulation of these enzymes systemically and locally are linked to the development of systemic acquired response (SAR) (Ferreira *et al.* 2007). Investigation expression patterns of involved genes in production of these metabolites e.g. PAL and CHS, for a better understanding of defence mechanisms towards various stresses appears significantly useful. According to Compant *et al.* (2010) application of PGPR increased accumulation of phenylalanine ammonia lyase, peroxidase, phytoalexins, polyphenol oxidase, and/or chalcone synthase. Induction of these plant defense compounds (e.g., chalcone synthase) perhaps triggered by the chemical PGPR use for intraspecific signaling.

Plants enduring hypersensitive response due to pathogen attack accumulate proline to protect the plants from oxidative injury and cell death. Increased level of proline in plants tissues during hypersensitive response was most likely due to upregulation of the key enzyme in proline biosynthesis, P5CS, at and around the sites of HR (Deuschle *et al.* 2004). Biosynthesis of the polyamines putrescine, spermidine, and spermine is induced in response to pathogen infection of plants (Lou *et al.* 2016). This is consistent with ODC and ADC2 induction being part of the coordinated defense response to *Fusarium* head blight. (Gardiner *et al.* 2010). Egg plants expressing the oat ADC gene exhibited tolerance to the wilt-causing fungus *Fusarium oxysporum* (Prabhavathi and Rajam 2007). These results were similar to others found in barley, where the levels of free PUT and SPN and conjugated forms of PUT, SPD and SPN were increased following inoculation with the powdery mildew. *Ustilago maydis* induced accumulation of putrescine in maize leaves (Rodríguez-Kessler and Jiménez-Bremont, 2009).

Plants are unceasingly exposed to enormous number of latent pathogens and to protect themselves plants have developed complex defense machinery (Abdullah *et al.* 2017). With onset of disease and pathogen recognition an oxidative burst of reactive oxygen species (ROS)

Table 1: Microorganisms used in alleviation of different stresses in plants

Microorganisms	Stress	Crop	References
<i>Aeromonas hydrophila</i> , <i>Bacillus</i> sp., <i>B. insolitus</i>	Temperature	Wheat	Ashraf (2004)
<i>Azospirillum</i> sp.	Drought	Wheat	Creus <i>et al.</i> (2004)
<i>Pseudomonas mendocina</i>	Salinity	Lettuce	Kohler <i>et al.</i> (2006)
<i>Burkholderia phytofirmans</i>	Temperature	Grape vine	Barka <i>et al.</i> (2006)
<i>Bacillus megaterium</i> , <i>Ochrobactrum anthropi</i>	Root rot disease	Tea	Chakraborty <i>et al.</i> (2006, 2009)
<i>Pseudomonas putida</i>	Temperature	Rapeseed	Chang <i>et al.</i> (2007)
<i>Pseudomonas syringae</i> , <i>Pseudomonas fluorescens</i> , <i>Enterobacter aerogenes</i>	Salinity	Maize	Nadeem <i>et al.</i> (2007)
<i>Bacillus</i> sp.	Drought	Lettuce	Arkhipova <i>et al.</i> (2007)
<i>Bacillus megaterium</i>	Drought	Clover	Marulanda <i>et al.</i> (2007)
<i>Paenibacillus polymyxa</i> , <i>Rhizobium tropici</i>	Drought	Mung bean	Figueiredo <i>et al.</i> (2008)
<i>Pseudomonas</i> sp.	Drought	Pea	Arshad <i>et al.</i> (2008)
<i>Pseudomonas mendocina</i>	Drought	Lettuce	Kohler <i>et al.</i> (2008)
<i>Pseudomonas putida</i> strain NBR10987,	Temperature	Chickpea	Srivastava <i>et al.</i> (2008)
<i>Pseudomonas</i> sp. AMK-P6	Temperature	Sorghum	Ali <i>et al.</i> (2009)
<i>Pseudomonas syringae</i> , <i>Rhizobium phaseoli</i>	Salinity	Mung bean	Ahmad <i>et al.</i> (2011)
<i>Pseudomonas putida</i> GR12-2	Temperature	Canola	Glick (2012)
<i>Brachy bacterium saurashtrense</i> , <i>Brevibacterium casei</i>	Salinity	Groundnut	Shukla <i>et al.</i> (2012)
<i>Ochrobactrum anthropi</i>	Blister blight	Tea	Sowndhararajan <i>et al.</i> (2012)
<i>Pseudomonas putida</i>	Salinity	Wheat	Nadeem <i>et al.</i> (2013)
<i>Pseudomonas fluorescens</i>			
<i>Ochrobactrum lupini</i>	Soft rot disease	Tobacco	Sumayo <i>et al.</i> (2013)
<i>Bacillus safensis</i> , <i>Ochrobactrum pseudogrignonense</i>	Drought	Wheat	Chakraborty <i>et al.</i> (2013, 2018, 2019)
	Salinity		
<i>Pseudomonas pseudoalcaligenes</i> , <i>Bacillus pumilus</i>	Salinity	Rice	Jha and Subramanian (2014)
<i>Bacillus amyloliquefaciens</i> 5113	Temperature	Wheat	Islam <i>et al.</i> (2014)
<i>Acinetobacter</i> spp., <i>Pseudomonas</i> sp.	Salinity	Barley and oats	Chang <i>et al.</i> (2014)
<i>Bacillus altitudinus</i>	Soft rot disease	Mung bean	Sunar <i>et al.</i> (2015)
<i>Pseudomonas putida</i>	Drought	Chickpea	Tiwari <i>et al.</i> (2016)
<i>Bacillus safensis</i>	Temperature	Wheat	Sarkar <i>et al.</i> (2018, 2018a)
<i>Ochrobactrum pseudogrignonense</i>	Spot Blotch disease		

like hydrogen peroxide, superoxide occurs which on one side are important signals interceding defense gene activation and act as activator of induced systemic response (ISR) while excess amount of ROS is toxic for cell and causes lipid peroxidation and membrane damage (Montillet *et al.* 2005).

Sarkar *et al.* (2018 a) carried out experiments to appraise various biochemical and metabolic changes during spot blotch disease development caused by *Bipolaris sorokiniana* and efficiency of two plant growth promoting rhizobacterial (PGPR) strains *Bacillus safensis* and *Ochrobactrum pseudogrignonense* in promoting resistance against *Bipolaris sorokiniana*. *In vitro* studies had revealed the ability of both of these bacteria to inhibit the growth of *B. sorokiniana* (Fig.1).



Fig. 1 : *In vitro* antagonism of selected bacteria to *B. sorokiniana*. Control (L), *B. safensis* + *B. sorokiniana* (M) and *O. pseudogrignonense* + *B. sorokiniana* (R)

In PGPR primed plants which were challenge inoculated with *B. sorokiniana*, disease index reduced markedly. Application of PGPR decreased stress indicators like hydrogen peroxide and malonaldehyde accumulated in infected plant tissue as a response to oxidative damage promoted by lipid peroxidation under elevated free radical formation. Increased activity of defense enzymes such as, chitinase, β -1,3 glucanase, phenyl alanine ammonia lyase and peroxidase were observed in plants following application with PGPR and challenge inoculated with *B. sorokiniana* in comparison with untreated healthy control plants. Besides, accumulation of proline and biochemical components such as total soluble protein and total phenol in higher concentration in PGPR treated and pathogen inoculated plants was evident. Analysis of phenols by high performance liquid chromatography revealed higher accumulation of phenols such as ferulic acid, salicylic acid and caffeic acid.

CONCLUSION

It is thus clear that in the current scenario plants are subjected to extreme environmental conditions

causing high degrees of stresses. Agricultural productivity is affected; and on the other hand, population is on the rise, specially in India. Thus, ways and means to help plants overcome the stresses is a very important aspect of present day agriculture. While techniques such as genetic engineering, breeding etc. are lengthy and out of reach of most agriculturists, the best solution

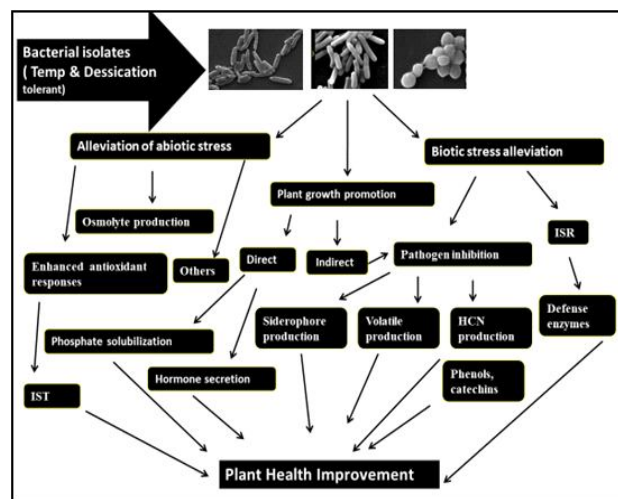


Fig. 2 : Schematic representation of mechanisms of abiotic and biotic stress alleviation in plants by bacteria

seems to be the use of microorganisms which are themselves tolerant to different stresses. Research in this area has thrown up a number of extremely beneficial microorganisms which not only promote growth, but also alleviate both abiotic and biotic stresses (Table 1). It is now time to commercialize such microorganisms and provide to the farmers for sustainable agriculture. Overall mechanisms by which the bacteria alleviate abiotic and biotic stress have been schematically presented in Fig 2.

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