Microbes for Plant Stress Management

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Foreword

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As the world marches towards the year 2050 with the predicted population of 9.7 billion, the daunting task faced by the agricultural scientists is to find out methods to feed the growing population with shrinking natural resources. It is also predicted that the demand for food has to be raised by about 60% compared to the current food production. This challenge gets more complicated with the current threat of global climate change resulting in increased temperature, drought, salinity, etc. These abiotic stresses will vigorously affect the agricultural productivity. It has already been observed that yield of crops is reduced due to various stresses. Abiotic stresses predominantly affect the genetic potential of food crops to the tune of nearly 69%. Drought is the most serious environmental factor limiting the production of agricultural crops with serious economical and social impacts. Salinity is another severe environmental stress decreasing crop productivity, mainly in irrigated land, worldwide. Hence there is an urgent need to address the abiotic stresses in order to achieve the goal of increased food production. Certain agronomic and breeding strategies are recommended for mitigating abiotic stresses. Microorganisms could play an important role in adaptation strategies and increase tolerance to abiotic stresses in agricultural crops. The mechanisms adopted by microorganisms to mitigate abiotic stresses in crop plants are many. The information available on the utilization of microbes for plant stress management is limited.

Viewing from the above stated perspective, the book on "Microbes for Plant Stress Management" by Dr. D.J. Bagyaraj and Dr. Jamaluddin is very timely. The book will be a valuable companion to students, teachers, researchers, administrators and policy makers who foresee the need for managing stresses affecting crop productivity using microbes for feeding mankind in the years to come.

S. Ayyappan

Preface

The world population is predicted to reach about 9.7 billion by the end of the year 2050 and to feed this population the current food production levels have to be raised by nearly 60% with limited land resource. This challenge gets compounded by the threat of global climate change leading to erratic rainfall, drought, salinity, increased temperature, etc. These abiotic stress consequences will seriously threaten the sustainable agricultural production. Hence there is a need to address this issue by all available means in order to achieve the goal of enhanced food production. Certain agronomic strategies like change in sowing dates, alley cropping, zero tillage, etc. have been proposed to mitigate stress. Breeding strategies recommend mitigating abiotic stresses by choice of resistant cultivars, use of hyper-accumulator plants, etc. A lesser explored potential option for abiotic stress alleviation is in the utilization of stress tolerant microbial resources, which have the ability to promote and sustain crop growth during adverse environmental conditions. This approach has gained popularity in the recent years and seems to be a potential option for the future. Thus the present book brings out the role of different groups of microorganisms like plant growth promoting rhizomicroorganisms (PGPR), arbuscular mycorrhizal fungi (AMF), endophytes, etc. in alleviating abiotic stress in crop plants.

The book contains 14 chapters written by distinguished scientists of the country having expertise in dealing with microorganisms and exploiting them for the benefits of mankind. Chapters 1 and 2 deal with exploring microbes from extreme environments and rhizomicrobiome respectively, for use in sustainable agriculture. Chapter 3 describes the recent developments in utilizing microorganisms for abiotic stress management in crop plants. Chapter 4 helps to understand the innate stress management mechanisms in plants. Chapter 5 deals with nanoparticles synthesized by microorganisms for use in agricultural ecosystem. Chapter 6 covers the role of plant growth promoting rhizomicroorganisms in supporting the growth of plants under stressed environment. Chapters 7 and 8 discuss the role of endophytic microorganisms in alleviation of abiotic stress in crop plants. Chapters 9 to 12 cover the role of arbuscular mycorrhizal fungi in alleviating drought and salt tolerance in different crops important in agriculture and horticulture. Chapter 13 is devoted to bioconversion of municipal solid wastes and its use in soil fertility. Chapter 14 provides an overview of microbial inoculants for quality seedling production in forestry. Thus the book is a comprehensive and detailed analysis of the subject.

We profusely thank all the authors for their keen interest, kind efforts and rich contributions in making this book highly informative and productive. Special thanks are due to Mr. R. Ashwin for his help in bringing out this book. We are also thankful to New India Publishing Agency, New Delhi for taking keen interest in bringing out this book in time.

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Application of Endophytic Microorganisms for Alleviation of Abiotic Stresses in Crop Plants

Kamal K. Pal and Rinku Dey

Abstract

A majority of the plants studied in natural ecosystems are symbiotic with microorganisms that either reside entirely (endophytes) or partially within plants. These microorganisms express different associations ranging from mutualism to parasitism. These symbiotic relationships appear to impart tolerance to various types of abiotic stresses such as heat, drought, salinity, heavy metals, etc. and sometimes may be responsible for the survival of both plant hosts and microbial symbionts in high stress habitats. The amelioration of the abiotic stresses by the endophytes assumes increasing significance in the light of rapidly changing global climate, which is likely to face frequent incidences of extreme weather conditions like high temperature, droughts, etc. To compensate the loss in crop productivity due to vagaries of nature and depleting areas of cultivable land, the application of endophytic microorganisms in agriculture is seen as a potential and ecologically sound means of maintaining profitability and sustainability in crop production. Apart from providing tolerance to abiotic stresses, majority of the endophytes are also known to confer tolerance to biotic stresses such as diseases, pests, etc. The endophytic microorganisms have also found application in remediation of heavy metal contaminated sites or polluted soils through phytoremediation. Here, we describe the role of endophytic microorganisms in alleviation of abiotic stresses in plants and the different ways by which this symbiosis can potentially mitigate the impacts of climate change and anthropogenic activities on crop plants.

Keywords: Abiotic stress, Endophyte, Phytoremediation, Stress tolerance, Symbiosis

1. Introduction

Throughout evolutionary time plants have been confronted with changing environmental conditions, forcing them to adapt or succumb to selective pressures such as extreme temperatures, insufficient water and toxic chemicals (Rodriguez *et al*. 2004). During recent years, the pace of climate change has accelerated resulting in elevated levels of CO_2, temperature, ultraviolet radiations, etc. The incidences of extreme drought may increase in the future due to global warming (IPCC 2014), and predicted increases in drought- and temperature- related stresses are expected to reduce crop productivity (Ciais *et al*. 2005, Larson 2013). These changes adversely affect the rainfall pattern and distribution, photosynthetic activities of plants, utilization of water, etc. Added to this is the rapid expansion of human population, causing changes in the natural and agricultural ecosystems. The agricultural ecosystems are facing limitations of decreasing area and availability of water. The rapid changes at the global level are causing abiotic and biotic stresses to crop plants. In future, local climate changes may require crops to have a greater tolerance of stresses such as drought, salinity, high temperature, etc. in order to produce an economic crop. While plant-breeding programmes and genetic modification can produce crop cultivars with much improved drought tolerance (Cattivelli *et al*. 2008), supplementary techniques and practices using micro-organisms may help to alleviate the worst effects of drought (Reynolds and Tuberosa 2008; Coleman-Derr and Tringe 2014). The same is true for other stresses like salinity, high temperature, water-logging, etc. Providing food security to an ever-growing population is a major challenge which will require cultivation of additional farmland along with improvements in crop yield. This will increase the burden of farming on arid and semi-arid lands resulting in heat- and drought-related stresses on crops.

Plants show, to a certain extent, some degree of adaptation to the different stresses. Due to lack of locomotion plants have to depend on complex physiology in order to escape the different types of stresses or to mitigate their effects to certain extent. There may be several reasons for the tolerance shown by the plants to different stresses. One of these reasons could be the symbiotic associations of plants with microorganisms – bacteria, fungi, etc. Endophytes are microorganisms (bacteria, fungi and unicellular eukaryotes) which can live at least part of their life cycle inter- or intracellularly inside of plants usually without inducing pathogenic symptoms. This can include competent, facultative, obligate, opportunistic and passenger endophytes. Endophytes can have several functions and/or may change function during their life cycle (Murphy *et al.* 2014a, b). Under stress conditions, endophytic plants exhibit different types of stress responses including the production of osmolytes, altering water movement, scavenging reactive oxygen species, etc.

The endophytic microorganisms are ubiquitous in the plants (Table 1). It has been reported that all plant life on Earth is symbiotic with fungi (Rodriguez *et al*. 2004), which contribute to and may be responsible for the adaptation of plants to environmental stresses (Clay and Holah 1999; Morton 2000; Redman *et al*. 2002a). The fungal symbiosis with plants is of two categories – 1) Fungal endophytes reside inside the plant tissues of roots, stems, leaves, etc, and 2) Mycorrhizal fungi residing only in the plant roots, but may extend into the rhizosphere. In natural ecosystems, symbiosis plays an important role in plant adaptation and survival. Endophytic fungi may help plants to adapt to high stress environments and mitigate the effects of such stresses. Fungal endophytes confer tolerance to drought, heavy metals, high temperature, besides promoting growth and nutrient acquisition sometimes. Recent developments in this field are the aspects of symbiotic lifestyle switching (Redman *et al*. 2001) and the phenomenon of habitat-adapted symbiosis (Rodriguez *et al*. 2008), which allows the plants to establish in high stress habitats. Similar is the case with bacterial endophytes, which are also widely present in the plant kingdom. The bacterial endophytes may also confer tolerance to a wide range of biotic and abiotic stresses in plants.

Another type of stress faced by plants growing in metal polluted sites or mines is the heavy metal stress. Man-made activities such as industrial productions, mining activities, agrochemicals usage, biosolids waste disposals, etc. are primary sources of heavy metal contaminations. Phytoremediation is suggested to be an environment-friendly approach for the clean- up of metal contaminated sites. Endophytes can also play an important role in accelerating phytoremediation (Table 2). The plant-endophyte partnership can accelerate the phytoremediation process; improve the plant growth by sequestration of heavy metals.

Table 1: Non-exhaustive list of endophytic bacteria associated with crop plants

Endophyte	Plant species	Endophyte	Plant species
Azorhizobium caulinodans	Rice	*Pantoea* sp.	Rice, soybean
Azospirillum brasilense	Banana	*Pantoea agglomerans*	Citrus plants, sweet potato
Azospirillum amazonense	Banana, pineapple	*Pseudomonas chlororaphis*	Marigold (*Tagetes* spp.), carrot
Bradyrhizobium japonicum	Rice	*Pseudomonas fluorescens*	Carrot
Methylobacterium extorquens	Scots pine, citrus plants	*Pseudomonas citronellolis*	Soybean
Rhizobium leguminosarum	Rice	*Pseudomonas synxantha*	Scots pine
Rhizobium (Agrobacterium) radiobacter	Carrot, rice	*Serratia* sp.	Rice
Gluconacetobacter diazotrophicus	Sugarcane	*Bacillus* spp.	Citrus
Sinorhizobium meliloti	Sweet potato	*Bacillus megaterium*	Maize, carrot, citrus plants
Azoarcus sp.	Callar grass	*Clostridium*	Grass *Miscanthus sinensis*
Burkholderia sp.	Banana, pineapple, rice	*Paenibacillus odorifer*	Sweet potato
Herbaspirillum seropedicae	Sugarcane, rice, maize, sorghum, banana	*Staphylococcus saprophyticus*	Carrot
Herbaspirillum rubrisulbalbicans	Sugarcane	*Kocuria varians*	Marigold
Citrobacter sp.	Banana	*Streptomyces* spp.	Wheat
Enterobacter spp.	Maize, citrus	*Pseudomonas fluorescens*	Carrot
Enterobacter cloacae	Citrus	*Burkholderia cepacia*	Lupine, citrus
Enterobacter agglomerans	Soybean	*Arthrobacter globiformis*	Maize
Enterobacter asburiae	Sweet potato	*Curtobacterium flaccumfaciens*	Citrus plants
Klebsiella sp.	Wheat, sweet potato, rice	*Microbacterium esteraromaticum*	Marigold
Klebsiella pneumoniae	Soybean	*Microbacterium testaceum*	Maize
Klebsiella terrigena	Carrot	*Nocardia* sp.	Citrus plants
Klebsiella oxytoca	Soybean	*Streptomyces*	Wheat
Serratia sp.	Rice	*Stenotrophomonas*	Dune grasses

Source: Rosenblueth and Martínez-Romero, 2006

Table 2: Application of endophytes in phytoremediation

Compound	Plant association	Organism
Mono- and dichlorinated benzoic acids	Wild rye (*Elymus dauricus*)	*Pseudomonas aeruginosa* strain R75 and *Pseudomonas savastanoi* strain CB35
2,4-D	Poplar and willow	*P. putida* VM1450
Methane	Poplar	*Methylobacterium populi* BJ001
TNT, RDX, HMX	Poplar	*Methylobacterium populi* BJ001
MTBE, BTEX, TCE	Poplar	*Pseudomonas* sp
Toluene	Poplar	*B. cepacia* Bu61
TCP and PCB	Wheat	*Herbaspirillum* sp. K1
Volatile organic Compounds and toluene	Lupine	*Burkholderia cepacia* G4

Source: Newman & Reynolds 2005

2. Fungal endophytes and stress tolerance

The fungal endophytes reside entirely within the host tissues and comprise a phylogenetically different group that are members of the dikarya (Girlanda *et al.* 2006; Arnold and Lutzoni 2007). Though most of the fungal endophytes belong to the Ascomycota clade, some belong to the Basidiomycota. Fungal endophytes are widespread in occurrence and reportedly found in major taxonomic groups of plants thriving under various environments. The endophytic fungi express a range of symbiotic lifestyles spanning from mutualism to parasitism and this is known as symbiotic continuum (Schardl and Leuchtmann, 2005).

Endophytic fungi provide tolerance to plants to many types of abiotic stresses such as drought, high temperature, heavy metals, etc. Mutualistic fungi may confer several benefits to plants such as tolerance to drought. The stress tolerance provided to the plants due to the symbiotic association with endophytic fungi may involve two mechanisms: 1) rapid activation of host stress response systems upon exposure to stress (Redman *et al.* 1999), or 2) synthesis of anti-stress biochemicals by the fungus (Bacon and Hill 1996). The mechanisms by which endophytes activate host stress response systems are not known.

2.1 High temperature stress

In response to high temperature stress, plants are known to initiate complex biosynthetic responses involving heat shock proteins, antioxidant systems, and adjustments in osmotic potential, and membrane lipids (Iba 2002). The stress tolerance conferred by some endophytes involves habitat-specific fungal adaptations. Some plants have been reported to thrive in geothermal soils tolerating high temperature and drought stress, due to the symbiotic association with endophytic fungi. Studies conducted by Rodriguez *et al*. (2004) indicated that the endophytic fungus *Curvularia protuberata* conferred thermotolerance to *Dichanthelium lanuginosum* and this symbiosis was responsible for the survival of both the species in geothermal soils of Yellowstone National Park. It was also observed that the individual partners could not tolerate the stress, when exposed to heat stress >38^{o}C, but the symbiotic association provided the tolerance to the habitat-specific stress. The ability of the endophyte to confer heat tolerance was due to the presence of a fungal RNA virus, which provides biochemical functionality to the fungus for conferring heat tolerance (Ma´rquez *et al*. 2007).

2.2 Moisture-deficit stress

To address the issues of providing food security to an ever growing human population, efforts are needed for enhancement in crop yield and bringing additional farmland under cultivation. For this, we may need to bring marginal, arid and semi-arid lands under cultivation, resulting in the crops facing more stresses like heat and drought related stresses. These stresses will reduce the crop productivity, with strong adverse effects on regional, national, and household livelihood and food security (IPCC 2014). Plants need to show adaptation to drought stress in order to survive (Seki *et al*. 2007).

Plants respond to moisture-deficit stress conditions by several mechanisms including osmotic adjustments, production of antioxidants, altered transcriptional and translational regulation, and altered stomatal activity (Griffiths and Parry 2002). The physiological and biochemical responses to drought stress include stomatal closure (Roelfsema and Hedrich 2005), reduction of growth and photosynthesis (Flexas *et al*. 2004), and activation of respiration (Rennenberg *et al*. 2006).

Very few plant species show drought-tolerance, though all the plants respond to moisture-deficit stress to certain extent. Some fungal and bacterial functional groups have been reported to enhance drought tolerance in a variety of crop hosts (Table 3), including mycorrhizal (Boyer *et al*. 2014) and endophytic fungi (Oberhofer *et al*. 2014). There are reports suggesting fungal symbionts conferring drought-tolerance to some plants (Clay and Schardl 2002), the mechanisms of which may involve osmotic adjustments and/or altered stomatal activity. The mutualistic *Colletotrichum magna* mutants have been reported to provide drought tolerance to watermelon plants. Interestingly, both the non-pathogenic mutants as well as the wild type *C. magna* asymptomatically colonize non-cucurbit hosts including tomato and pepper (Redman *et al*. 2001), which allows these plants to survive desiccation for longer duration as compared to the non-symbiotic plants. The host genotype plays a very important role in

Table 3: Non-exhaustive list of beneficial endophytes capable of alleviating abiotic stress and plant growth promotion

Endophyte	Crop/plant	Function(s)	Reference
Pseudomonas pseudoalcaligenes	Rice	Salinity tolerance	Jha *et al*. 2010
Penicillium minioluteum LHL09	Soybean	Salinity	Khan *et al*. 2011
Pseudomonas aeruginosa PW9	Cucumber	Abiotic stress tolerance	Pandey *et al*. 2012
Clavibacter sp.	*Chorispora bungeana*	Chilling stress tolerance	Ding *et al*. 2011
Piriformospora indica	*Prosopis juliflora*, *Z. nummularia*, Wheat, mustard, tomato, cabbage	Salinity, moisture & biotic stress tolerance and plant growth, nutrient uptake, etc.	Walker *et al*. 2005

determining the expression and magnitude of benefits of endophytic fungi. It is now thought that the host range of these fungi may be wider and provide benefits to unrelated plant species also (Rodriguez *et al*. 2004).

Fungal root endophytes isolated from a wild barley species (*Hordeum murinum* subsp. *murinum*) induced significant improvements in agronomic traits for a severely drought-stressed barley cultivar grown in a controlled environment, including number of tillers, grain yield, and shoot biomass (Murphy *et al*. 2015). This group studied the inoculation effects of five endophytes, and the trait that showed maximum significant difference was the number of tillers per plant that was more in all the inoculated treatments.

An endophytic fungus *Piriformospora indica* has been widely studied and used worldwide for alleviation of abiotic stresses. This fungus belongs to the Sebacinaceae family, which colonizes the roots of many plant species, and has been reported to impart benefits to plants under drought-stress conditions (Sahay and Varma 1999; Shahollari *et al*. 2005, 2007). Besides, the fungus has also been reported to promote nutrient uptake; helps the plants to circumvent moisture, temperature and salt stress, confers resistance to toxins, heavy metals, pathogens; and also promote plant growth and seed production (Verma *et al*. 1998; Waller *et al*. 2005, 2008; Oelmüller *et al*. 2009). *P. indica* was isolated from the roots of *Prosopis juliflora* and *Zizyphus nummularia* plants grown in the Thar desert of India (Verma *et al*. 1998), and root colonization and association of fungal hyphae with roots have been found to result in promotion of plant growth and higher seed yield under drought-stress conditions. This fungus colonises the roots by growing inter- and intracellularly and forms pear shaped spores within the cortex, but does not invade the aerial parts of the plants. The fungus does not show host specificity. It has a wide host range including bryophytes (*Aneura pinguis*), pteridophytes (*Pteris ensiormis*), gymnosperms (*Pinus halepensis*), and a large number of angiosperms (Varma *et al*. 2001; Shahollari *et al*. 2005; Waller *et al*. 2005; Serfling *et al*. 2007). This includes the cereal crops like rice, wheat, barley, etc. Some drought-inducible genes have been identified (Seki *et al*. 2002), which are mainly classified into two major groups: proteins that function directly in abiotic stress tolerance and regulatory proteins, which are involved in signal transduction or expression of stress-responsive genes (Shinozaki *et al*. 2003). Under drought-stress conditions, many genes for signaling components themselves are upregulated. Using *Arabidopsis* as a model system, Sherameti *et al*. (2008) demonstrated that *P. indica* conferred drought tolerance by priming the aerial parts of the plants for the expression of a set of quite diverse (drought) stress-related genes. *P. indica* also promotes the expression of the two genes *MDAR2* (At3g09940) and *DHAR5* (At1g19570) in the aerial parts of drought-stressed seedlings. These two genes are crucial for the beneficial interaction between *P. indica* and *Arabidopsis*, because reduced ascorbate maintains a constant redox balance in the cytoplasm (Vadassery *et al*. 2009b). The mutualistic interactions between microorganisms and plants have been utilized for enhancing growth, biomass and seed production, often in poor soils, with little extraneous application of chemical fertilizers and pesticides. *P. indica* has the advantage of rapid and large scale propagation for field level applications.

Arbuscular-mycorrhizal (AM) fungi are important group of endophytic microorganisms playing significant role in sustainable agriculture. They provide multiple benefits to their plant hosts by increasing drought resistance (Allen and Allen 1986; Nelsen 1987), mineral uptake and providing resistance to diseases. The symbiotic relationship between AM fungi and their host plants is generally nonspecific in nature. There are considerable differences at the species level and within the geographic isolates, and thus great biodiversity exists for the AM endophytes (Bethlenfalvay *et al*. 1989). Suitable endophytes need to be selected for a particular environmental condition based on the specific plant host and compatibility with the environmental conditions. AM endophytes may alleviate the effects of reduced photosynthesis due to reduction in leaf water status and stomatal closure by altering the physiological parameters of the plants so that the plant can adapt to low soil moisture content (Ruiz-Lozano *et al*. 1995). AM fungi mediated improved host nutrition, particularly phosphorus nutrition has also been reported to improve the water balance of plants (Giovannetti and Mosse 1980; Graham and Syvertson 1984). The several mechanisms by which AM fungi improve drought-tolerance in their host plants, are increased CO_2 assimilation, changes in stomatal conductance (Auge´and Duan 1991) and transpiration. Potassium nutrition plays a significant role in stomatal movement with any changes in leaf water status. Accumulation of proline in the leaves has been reported to enhance osmotic adjustments. Ruiz-Lozano *et al* (1995) reported higher proline content in drought-stressed plants as compared to well-watered plants and a lower proline content was stated to be an indication of better tolerance to drought. AM fungal isolates need to be carefully selected based on the situation or the problems for which they are intended. Suitable AM fungal isolates have great potential for restoring drought-prone degraded lands.

2.3 Salinity stress

The problem of high soil salinity, particularly in arid and semi-arid regions, is a limiting factor for agricultural productivity in such areas (Flowers *et al*. 1977). Accumulation of salts in the rhizosphere zone reduces the water potential and its availability to the plants (Heyster and Nabors, 1982). Salinity stress affects the metabolic processes of plants. But, the plants growing in saline environments have developed mechanisms to circumvent the detrimental effects of high salt concentrations that include compartmentalization or translocation of salt, exclusion, cellular osmotic adjustments, and/or antioxidant systems (Gilbert *et al*. 2002, Yoshida *et al*. 2003). They may produce amino acids such as proline and accumulate inside the cells to maintain osmotic balance. Most of the crops of arid and semi-arid regions are mycorrhizal. Some mycorrhizal fungi have been reported to confer salt tolerance through symbiosis (Yano-Melo *et al*. 2003). The fungus-plant symbiotic association confers salinity tolerance in some plant species including banana, tomato and lettuce. In plants such as tomato (Al-Karaki 2006) and soybean (Sharifi *et al*. 2007) increased growth under saline conditions was observed when their roots were colonized by AM fungi.

Salinity stress affects the growth parameters of plants, irrespective of their being mycorrhizal or non-mycorrhizal. However, the reduction in biomass production is observed to be more in non-mycorrhizal plants. The improvement in growth of salinity stressed plants inoculated with AM fungi was reported by Tain *et al*. (2004). According to Zandavalli *et al*. (2004), better nutritional status of plants may be the reason for enhancement in growth and salt tolerance of mycorrhizal peanuts. It is a well known fact that beneficial effects of AM fungi on plant growth is to a large extent due to higher uptake of P. Rabie and Almadini (2005) reported enhancement in contents of N and K as a result of AM association. Investigations conducted by Al-Khaliel (2010) revealed that *Glomus mosseae* could improve growth of peanuts under salinity stress through enhanced nutrient absorption and photosynthesis. This association helped in the establishment of peanuts under salinity and phosphorus deficiency conditions.

There are reports of alleviation of moderate salt stress by *P. indica* (Waller *et al*. 2005). Barley plants exposed to moderate (100 mM NaCl) salt concentrations in hydroponic culture showed leaf chlorosis and reduced growth. The harmful effects of moderate salt stress were completely alleviated by *P. indica*, as shown by the higher biomass than non-stressed control plants.

Antioxidants are molecules that function to reduce oxidative stress by scavenging or quenching ROS and these molecules are crucial for beneficial plant/microbe interactions (Alguacil *et al*. 2003). Generally, ROS and H_2O_2 are produced as a result of abiotic and biotic stresses. The fungus *P. indica* has been found to enhance the antioxidative capacity of plants. Baltruschat *et al*. (2008) studied the *P. indica* - mediated salt tolerance in barley. It was reported that the fatty acid composition, lipid peroxidation, ascorbate concentration and activities of catalase, ascorbate peroxidase, dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR) and glutathione reductase enzymes were strongly influenced by the fungus under salt-stress condition.

Also, the endophytic fungus significantly elevated the amount of ascorbic acid and increased the activities of antioxidant enzymes in barley roots under salt stress conditions. Fungal endophyte induced increase in antioxidants was reported in barley grown under salt and pathogen stress (Harrach *et al*. 2013).

There are instances of cross-species alleviation of abiotic stresses in literature. Recently, Khan *et al*. (2011) demonstrated that the endophytic fungus *Exophiala* sp. LHL08 isolated from cucumber roots could confer salinity and drought stress tolerance in rice seedlings by modulating stress responses.

2.4 Habitat-adapted symbiosis

A new term was coined by Rodriguez *et al*. (2008) which defines habitat-specific, symbiotically-conferred stress tolerance as habitat-adapted symbiosis. This was hypothesized to be responsible for the establishment of plants under high-stress habitats. It was observed that grass endophytes from coastal areas conferred salt tolerance, geothermal endophytes conferred heat tolerance and endophytes from agricultural crops conferred disease tolerance, respectively, to plants under the respective habitats. But, the same fungal species isolated from plants in habitats devoid of salt or heat stress did not confer these stress tolerances. Further studies also showed that the agricultural, coastal and geothermal plant endophytes also colonized tomato (a model eudicot) and conferred disease, salt and heat tolerance, respectively. Strengthening the idea of habitat-adapted symbiosis was the observation that the coastal plant endophyte colonized rice (a model monocot) and conferred salt tolerance. These endophytes showed a broad host range covering both monocots and eudicots.

2.5 Heavy metal stress

Fast paced industrialization has resulted in widespread environmental pollution. The use of chemicals such as pesticides, agrochemicals, industrial solvents, etc., have gone into the environment polluting soil, air and water. Among the pollutants, heavy metals are of particular concern for human health because of their cytotoxicity and carcinogenicity. The use of plants for remediation of polluted soils (phytoremediation) is an eco-friendly and cost-effective option. Many plants are known to be capable of hyperaccumulating heavy metals in their tissues. The association of metal tolerant endophytes with hyperaccumulating plants results in enhanced uptake of heavy metals by plants and increase in biomass of the plants.

Fungal endophytes also show instances of imparting tolerance to their host plants against heavy metals or trace metals. The AM fungus *Glomus intraradices* was shown to enhance growth of *Helianthus annuus* in Ni contaminated soil (Ker and Charest, 2010) along with significantly increased activity of glutamine synthetase, indicating an enhanced Ni tolerance. AM fungal symbiosis may enhance plant growth and tolerance to trace elements like Ni, As, etc. in hyperaccumulating plants growing in metal contaminated sites.

3. Bacterial endophytes and stress tolerance

Like their fungal counterparts, endophytic bacteria are also widely present in the plant kingdom colonizing internal tissues of their host plants and forming relationships like symbiotic, mutualistic, commensalistic and trophobiotic (Ryan *et al*. 2008). Endophytic bacteria may benefit their plant hosts by improving growth and development. This may involve the facilitating of primary and secondary nutrient uptake by processes such as atmospheric nitrogen fixation, siderophore production, and solubilization of minerals such as phosphate (PO_4^{3-}), potassium (K^+) and zinc (Zn^{2+}). Endophytic bacteria may also supply plant roots with phytohormones like auxin, cytokinin and gibberellins (Table 4). Some endophytic bacteria provide tolerance to stresses such as pathogen infections, drought, soil salinity, etc. by inhibiting the production of the plant hormone ethylene (Siddikee *et al*. 2010).

Table 4: Production of phytohormones by beneficial bacterial endophytes

Endophyte	Plant origin	Beneficial action
Azospirillum sp. BS10	Rice	ACC deaminase, BNF, IAA, Siderophore
Burkholderia phytofirmans	Onion	ACC deaminase, IAA, Siderophore
Enterobacter sp. 638	Poplar	IAA, Siderophore, Volatiles
Gluconacetobacter diazotrophicus Pal5	Sugarcane	Gibberellins, IAA and Volatiles
Herbaspirillum seropedicae SmR1	Sorghum	ACC deaminase, IAA
Pseudomonas putida W619	Poplar	IAA
Bacillus sp.*, Micrococcus* sp., *Pseudomonas* sp.*, Serratia* sp.	Legume	IAA, Gibberellins, Cytokinins

Source: Sturz *et al*. 2000.

3.1 Moisture-deficit stress

In the interaction of plants with bacterial endophytes, production and modulation of hormones such as auxins and ethylene play an important role in plant development and stress (e.g. drought) tolerance. Stress tolerance in such interactions is reportedly influenced by endophyte-derived hormones. The hormones abscisic acid and gibberellins produced by the endophyte *Azospirillum lipoferum* was found to alleviate drought stress symptoms in maize (Cohen *et al*. 2009).

3.2 Salinity stress

Salinization of agricultural soils is a serious threat to crop production. It is estimated that by the year 2050 approximately 50% of the arable land will be affected by salinity (Munns and Tester, 2008). Not only climatic conditions but also human activities are responsible for soil salinization. Such conditions limit the growth of vegetation and the number of plant species growing in these situations. However, in saline conditions also certain plant populations are successfully adapted and exhibit strategies of salt tolerance. One of the mechanisms of coping with salt stress or other abiotic stresses is the association of plants growing under such conditions with the endophytic microorganisms. These microorganisms along with rhizospheric microorganisms may be involved in the biogeochemical cycling of nutrients under saline conditions. Cassán *et al.* (2009) coined the term plant stress homeoregulating bacteria (PSHB), that can either directly or indirectly facilitate the plant growth in optimal, biotic, or abiotic stress conditions. The PSHB may benefit plants by providing stress-related phytohormones, like abscisic acid (Cohen *et al*. 2008); plant growth regulators like cadaverine (Cassán *et al*. 2009); and catabolism of ACC deaminase. Many plant species have been reported to thrive under saline environments by developing effective associations with endophytic bacteria. A halophyte *Prosopis strombulifera* is reported to be naturally associated with different endophytes having plant growth-promoting physiological and biochemical capabilities (Sgroy *et al*. 2009). These workers mentioned the production of phytohormones by many isolates and also production of ABA and ACC deaminase activity as homeostasis regulation mechanisms by some isolates. Some endophytic bacteria can produce the enzyme 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase that breaks down ACC, the direct precursor of ethylene, into ammonia and á-ketobutyrate. ACC is used by bacteria as a source of nitrogen and carbon and thereby the deleterious effect of ethylene on plant tissues is reduced (Glick *et al*. 2007). Under environmental stress conditions, the availability of auxin, ACC deaminase and the nutrients produced by endophytic bacteria is important to minimize the deleterious effects of physiological stress and to support the level of growth and development required to complete the lifecycle of the plants (Timmusk *et al*. 2011).

Yaish *et al*. (2015) isolated and characterized endophytic bacteria from date palm (*Phoenix dactylifera* L.) seedling roots, and tested for their ability to help plants grow under saline conditions. Molecular characterization showed that the majority of these strains belonged to the genera *Bacillus* and *Enterobacter* . These endophytic bacteria had a likely role to play in salinity tolerance due to their ability to produce the growth regulator IAA and reduce the production of stress hormone ethylene through the production of ACC deaminase, besides providing essential nutrients such as ammonia, K^+, Fe^{3+}, PO_4^{3-}, and Zn^{2+}.

Certain endophtyic bacteria can also bring about cross-species alleviation of abiotic stresses. A salt-tolerant endophytic bacteria *Pseudomonas aeruginosa* PW09 isolated from wheat stem could alleviate salinity stress in cucumber (Pandey *et al*. 2012). There was enhanced biomass accumulation under salinity stress along with higher antioxidant activities and proline accumulation in cucumber plants inoculated with *P. aeruginosa* PW09. This endophyte could also reduce plant mortality in cucumber due to *Sclerotium rolfsii* infection.

3.3 Heavy metal stress

Contamination of soil with heavy metals has become a serious environmental problem and threat to the delicate ecological balance. Phytoremediation is the use of plants to extract pollutants from soil in an eco-friendly way. However, many metal accumulating plants exhibit slow growth and often are inhibited by high concentrations of heavy metals. Studies involving plant-associated microorganisms have shown that such microorganisms can enhance seedling emergence and growth of plants under metal polluted conditions (Chen *et al*. 2010). Recent studies have demonstrated that endophytic bacteria improve the tolerance of plants to heavy metals and increase heavy metal translocation factors, biomass, and trace element concentrations of hyperaccumulators (He *et al*. 2009). Endophytic bacteria are influenced by the physicochemical properties of the soil and have evolved with the progress of heavy metal contamination (Chen *et al*. 2012). It is important to study the abundance and composition of bacterial endophytes in the metal contaminated sites for understanding their interactions with the environment, and also for exploring the possible uses of these bacterial species for the bioremediation of heavy metals.

Phytolacca americana is reported to be a Mn-hyperaccumulating plant that has great potential for remediation of Mn-contaminated soils. Wei *et al*. (2014) investigated the diversity of the endophytic bacterial populations in the tissues of *P. americana* growing in Mn mine by PCR-DGGE. Phylogenetic analyses of the recovered DNA sequences classified the bacteria into 10 different divisions, indicating a high level of diversity amongst the endophytic bacterial species of *P. americana*. From the sequencing results it was observed that Proteobacteria, specifically the γ, δ and α subclasses, may be the dominant endophytic bacterial genera of *P. americana*. These endophytic bacteria may have an important role in assisting *P. americana* in phytoremediation.

Endophytic bacteria can improve trace element uptake by plants and the efficiency and rate of phytoextraction. Zinc-resistant endophytes were isolated from Zn-accumulating willows (*Salix caprea*), comprised mostly *Sphingomonas* spp., *Methylobacterium* spp. and various actinobacteria (Kuffner *et al*. 2010). Endophytic bacteria isolated from both the root and shoot tissues of the Cd/Zn-hyperaccumulator *Sedum alfredii* were closely related to *Pseudomonas*, *Bacillus*, *Stenotrophomonas* and *Acinetobacter* (Long *et al*. 2011). Inoculation with these endophytes resulted in increase in plant growth and biomass, along with increase in concentration of metals. Inoculation of *Nicotiana tabacum* with Cd-resistant seed endophyte *Sanguibacter* sp. S_d2 increased shoot Cd concentrations compared to non-inoculated plants (Mastretta *et al*. 2009). Pea plants inoculated with an endophyte *Pseudomonas* sp., capable of degrading the organochlorine herbicide, 2,4-dichlorophenoxyacetic acid (2,4-D), showed no accumulation of the herbicide in the tissues and no signs of phytotoxicity when exposed to 2,4-D (Germaine *et al*. 2006). Thus, endophytes can alleviate the toxic effects of agrochemicals and reduce the impact of hazardous chemicals.

Certain endophytic bacteria are capable of metal biosorption and result in phytostabilization. These endophytes show increased biosorption and bioaccumulation of the metals. Inoculation with endophytic bacteria, *Magnaporthe oryzae* and *Burkholderia* sp. increased plant growth but reduced the Ni and Cd accumulation in roots and shoots of tomato and also their availability in soil (Madhaiyan *et al*. 2007). Certain endophytes produce metabolites such as siderophores, biosurfactants and organic acids and alter the availability/toxicity of the heavy metals to the plant (Sheng *et al*. 2008). A plant growth promoting endophyte (PGPE) *Pseudomonas* sp. A3R3 effectively promoted the phytoremediation of both host (*Alyssum serpyllifolium*) and non-host (*Brassica juncea*) plants by improving either the Ni accumulation or biomass production (Ma *et al*. 2011). Metal tolerant endophytic bacteria have great potential for reclamation of heavy metal and chemically polluted sites.

Conclusion

Many beneficial endophytic fungi and bacteria have been identified in the past and the basis for their molecular interaction with plants has been studied. The primary interest of these endophytic microorganisms is to gain access to photoassimilates by the plants. The endophytic microorganisms often take shelter inside the plant tissues to escape the harsh environment outside and also to get access to carbon compounds. However, the mutualistic association involves many recognition and signaling processes between the endophytes and the host plants.

Though not much is known about the biochemical basis of stress tolerance in plants mediated by endophytes, in near future it may be possible to develop effective symbiosis between specific fungi and plants to achieve stress tolerance for a particular geographic region. Such symbiosis may be effective and environment friendly strategy for mitigating the adverse effects of stresses on plant communities. Though much has been studied on the symbiotic association between endophytes and their plant hosts but some questions still need answers as to why only few plant species are adapted to severe stress conditions and whether plants can adapt to such habitats without the endophytic association. The effectiveness and performance of each endophyte may differ from each other, depending on environmental factors. Endophytes need to be selected for a particular crop growing conditions. Endophytes mediated drought-tolerance will have far-reaching consequences in light of current and future climate change brought by global warming. This will help the marginal farmers to raise crops in vast areas of arid land and help the crop to adapt to drier areas. It is known that majority of plants have endophytes residing in them, but their diversity in the different plant species is yet to be discovered. Thus, scope exists for finding many potentially beneficial endophytes from the different plant species thriving in different ecosystems. Sustainable agricultural practices must exploit the potential of endophytes for mitigating the impacts of abiotic stresses on crop plants. The endophytes can also have biotechnological potential in large-scale remediation of polluted sites and sustainable production of bioenergy and biofuel crops.

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