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Unraveling the role of fungal symbionts in plant abiotic stress tolerance

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Fungal symbionts have been found to be associated with every plant studied in the natural ecosystem, where they colonize and reside entirely or partially in the internal tissues of their host plant. Fungal endophytes can express/form a range of different lifestyle/relationships with different host including symbiotic, mutualistic, commensalistic and parasitic in response to host genotype and environmental factors. In mutualistic association fungal endophyte can enhance growth, increase reproductive success and confer biotic and abiotic stress tolerance to its host plant. Since abiotic stress such as, drought, high soil salinity, heat, cold, oxidative stress and heavy metal toxicity is the common adverse environmental conditions that affect and limit crop productivity worldwide. It may be a promising alternative strategy to exploit fungal endophytes to overcome the limitations to crop production brought by abiotic stress. There is an increasing interest in developing the potential biotechnological applications of fungal endophytes for improving plant stress tolerance and sustainable production of food crops. Here we have described the fungal symbioses, fungal symbionts and their role in abiotic stress tolerance. A putative mechanism of stress tolerance by symbionts has also been covered.

Introduction

Generally, vascular plants have been considered as autonomous organisms especially when their performance has been interpreted at the genomic and cellular level. But in reality, vascular plants provide a unique ecological niche for diverse communities of cryptic symbiotic microbes which often contribute multiple benefits, such as enhanced photosynthetic efficiency, nutrient and water use and tolerance to abiotic and biotic stress.[1] Fossil records indicate that fungi have been associated with plants since at least 400 million years ago[2,3] and fungal symbiosis is thought to be responsible for the movement of plants onto land.[4] Now, it is a well recognized fact that symbiosis is a common and fundamental condition of plants in nature.[5] Modern research suggests that all plants in native ecosystems are symbiotic with fungi and other microbes (bacteria, yeast) on their leaf and root surfaces, rhizosphere and internal tissues that influence their performance.[6,7] It was suggested in the late 1800's and now confirmed by DNA based detection technology that plastids and mitochondria of the eukaryotic cell were derived from a consortium of primitive microbes.[5,8,9] The continuity of microbial associations with plants from their origin suggests that plants have not functioned as autonomous individuals, but their internal tissues provide a unique ecological environment for diverse communities of symbiotic microbes, which have had a major influence on plant adaptation and evolution.[5,10,11]

Recent studies indicate that fitness benefits conferred by mutualistic fungi contribute to or are responsible for plant adaptation to stress.[12,13] Collectively, mutualistic fungi may confer tolerance to drought, metals, disease, heat and herbivory, and/or promote growth and nutrient acquisition. It has become apparent that at least some plants are unable to tolerate habitat-imposed abiotic and biotic stresses in the absence of fungal endophytes.[14] Abiotic stresses, such as drought, salinity, extreme temperatures (heat and cold), heavy metal toxicity and oxidative stress are serious threats to agriculture and result in the deterioration of the environment.[15] Abiotic stress is the primary cause of crop loss worldwide, reducing average yields for most major crop plants by more than 50%.[16,17] Abiotic stress leads to a series of morphological, physiological, biochemical and molecular changes that adversely affect plant growth and productivity.[18] Drought, salinity, extreme temperatures and oxidative stress are often interconnected, and may induce similar cellular damage.[15] For example, drought and/or salinization are manifested primarily as osmotic stress, resulting in the disruption of homeostasis and ion distribution in the cell.[19,20] High temperature stress causes extensive denaturation and aggregation of cellular proteins, which, if unchecked, lead to cell death. Heat response is characterized by inhibition of normal transcription and translation, higher expression of heat shock proteins (hsps) and induction of thermotolerance.[21] Low temperature stress causes impairment of metabolic processes, by alterations in membrane properties, changes in structure of proteins and interactions between macromolecules as well as inhibition of enzymatic reactions.[22] Heavy metal like Cu is taken up by plant cell by specific transport systems. Inside the cell, chaperones serve intracellular Cu transport to vesicular storage sites and to target enzymes such as Cu/Zn-SOD, ethylene receptors, etc. "Free" Cu is extremely dangerous because it will reduce molecular oxygen leading to increased formation

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Table 1. Some examples of class I fungal endophytes that conferred abiotic stress tolerance

Fungal endophyte/species/strain	Abiotic stress	Host plant/cultivar	Reference
Neotyphodium sp.	Drought	*Festuca pratensis*	Malinowski, et al. 1997[105]
		Perennial Ryegrass	Barker, et al. 1997[250]
		F. arizonica	Morse, et al. 2002[237]
N. lolii	Drought	Perennial Ryegrass	Latch, et al. 1985[99] and Ravel, et al. 1997[94]
N. coenophialum	Drought/Water Stress	Tall fescue	Belesky, et al. 1989[96] and de Battista, et al. 1990[97]
N. uncinatum	Water Stress	Meadow fescue	Malinowski, 1995[241]
Acremonium sp.	Drought	Tall fescue	White, et al. 1992[240]
Phialophora sp.	Drought	*F. pratensis*	Malinowski, et al. 1997[105]
Curvularia protuberate	Heat	*Dichanthelium lanuginosum*	Redman, et al. 2002a[14]
C. protuberate (Cp4666D)	Drought	*D. lanuginosum*	Rodriguez, et al. 2008[36]
		Leymus mollis	
		Oryza sativa	
		Lycopersicon esculentum	
C. protuberata	Heat	*L. esculentum*	Rodriguez, et al. 2008[36]
C. protuberata (CpMH206)	Drought	*D. lanuginosum*	Rodriguez, et al. 2008[36]
		L. esculentum	
C. protuberate (Cp4666D)	Drought	*Triticum aestivum*	Rodriguez, et al. 2008[36]
		Watermelon	
Curvularia sp.	Heat/Drought	*L. esculentum*	Rodriguez and Redman, 2008[29]

of superoxide, hydrogen peroxide and hydroxyl radicals switching normal metabolism to programmed cell death.[23] Oxidative stress, which frequently accompanies high temperature, salinity or drought stress, may cause denaturation of functional and structural proteins.[24]

Plant responses to abiotic stresses are complex, involving signal reception and transduction followed by genetic and physiological responses. It is perceive that all plants are capable of perceiving and responding to stress.[25] Some biochemical processes which are common to all plant stress responses are—the production of osmolytes, altering water movement and scavenging reactive oxygen species (ROS).[26-28] Even though there has been extensive research in plant stress responses, we still could not make out why so few species are able to colonize high stress habitats. On the other hand, plant stress research rarely takes into consideration a ubiquitous aspect of plant biology—fungal symbiosis.[29]

Fungal Symbioses

Symbiosis, defined as "the permanent association between two or more specifically distinct organisms, at least during a part of the life cycle",[30] is known to be an ubiquitous and important aspect of life on Earth. Most animals and plants live in close associations with a series of microorganisms. Evolutionarily, plants require some specialized microbial partners in order to adapt to certain ecological niches and maintain their normal growth and development.[31] Rhizobium, actinorhizal and mycorrhizal symbionts have long been investigated and considered as the primary mutualistic microbial symbionts associated with plant roots.[32,33] In addition, aboveground plant-fungal mutualistic interactions also exist in some temperate and tropical grasses and it is well known that endophytic systemic clavicipitaceous fungi colonize inner grass leaf tissue and exert beneficial effects on hosts through increased resistance to herbivores, pathogens and drought stresses.[34]

There are several outcomes of symbiotic interactions defined by the fitness benefits realized by each partner.[35] In plant-fungal symbiosis the benefits to fungal symbionts can be positive (mutualism, commensalism and parasitism), neutral (amensalism and neutralism) or negative (competition). Benefits to host plants can also be positive (mutualism), neutral (commensalism and neutralism) or negative (parasitism, competition and amensalism).[36] Successful plant-fungal symbioses involve at least three events: penetration by the fungus into plant tissues; colonization of plant tissues by the invading fungus; expression of a fungal symbiotic lifestyle. However, symbionts as well as pathogens must be able to overcome or manipulate hosts surveillance system to establish a compatible interaction.[37,38] It is assume that some form of biochemical and/or genetic communication occurs between the symbionts and hosts that allow mutualists to confer physiological benefits to hosts. Yet, what type of communication occurs between the partners that result in the expression of different symbiotic lifestyles, or if symbionts are recognized by hosts before lifestyle expression is still not clear.[39] However, in different cases, different strategies have been used, like disturbing plants' defense signaling networks or even reprogramming host metabolism such as modifications on hormonal homoeostasis and antioxidant contents.[38,40] In general, plant hormones can quickly and potentially affect plant physiology.[41]

Table 2. Some examples of class II fungal endophytes that conferred abiotic stress tolerance

Fungal endophyte/species/strain	Abiotic stress	Host plant/cultivar	Reference
Colletotrichum magna (path-1)	Drought	*L. esculentum* *Capsicum annuum*	Redman, et al. 2001[39]
C. magna (L2.5)	Drought	*L. esculentum* *C. annuum*	Redman, et al. 2001[39]
C. musae (927)	Drought	*L. esculentum* *C. annuum*	Redman, et al. 2001[39]
C. orbiculare (683)	Drought	*L. esculentum*	Redman, et al. 2001[39]
C. gloeosporioides	Drought	*C. annuum*	Redman, et al. 2001[39]
C. gloeosporioides (95-41A)	Drought	*L. esculentum*	Redman, et al. 2001[39]
Fusarium culmorum (Fc18)	Drought	*Leymus mollis* *Oryza sativa* *L. esculentum*	Rodriguez, et al. 2008[36]
F. culmorum (FcRed1)	Salinity	*L. mollis* *O. sativa* *L. esculentum* *D. lanuginosum*	Rodriguez, et al. 2008[36]
F. culmorum (FcRed1)	Drought	*L. mollis* *O. sativa* *L. esculentum* *D. lanuginosum*	Rodriguez, et al. 2008[36]
Colletotrichum sp.	Drought	*L. esculentum*	Rodriguez, et al. 2004[13]
Fusarium sp.	Heat/Drought	*L. esculentum*	Rodriguez and Redman, 2008[29]
Alternaria sp.			
C. orbiculare	Drought	*L. esculentum* cv. Big Beef	Rodriguez and Redman, 2008[29]
C. magna	Drought	*Triticum aestivum* *L. esculentum* cv. Big Beef and Seattle's Best *C. annuum* cv. Calif. Wonder Watermelon	Rodriguez and Redman, 2008[29]
C. gloeosporioides	Drought	*L. esculentum* cv. Big Beef *C. annuum* cv. Calif. Wonder	Rodriguez and Redman, 2008[29]
C. musae	Drought	*C. annuum* cv. Calif. Wonder	Rodriguez and Redman, 2008[29]
Piriformospora indica	Salinity	*Hordeum vulgare*	Waller, et al. 2005[86]
P. indica	Salinity	*Hordeum vulgare* cv. Ingrid	Baltruschat, et al. 2008[71]
P. indica	Drought	Arabidopsis sp.	Sherameti, et al. 2008a[125]
P. indica	Drought	*Brassica campestris* ssp. Chinensis	Sun, et al. 2010[122]
Trichoderma hamatum (DIS 219b)	Drought	*Theobroma cacao*	Bae, et al. 2009[176]

Earlier, fungal symbionts were thought to be restricted to specific symbiotic lifestyles (e.g., mutualism, commensalism or parasitism).[35] However, current studies suggest that fungi may express different symbiotic lifestyles in response to host genotypes or environmental factors. For example, depending on the physiological status of plants, some mycorrhizal fungi may be mutualistic or parasitic.[42-44] Furthermore, more often than not, both pathogenic and nonpathogenic fungi are isolated from asymptomatic plant tissues, implying that both mutualists and pathogens infect plants and remain dormant until plant senescence.[45] One of the most interesting aspects of lifestyle expression is that the initial phases of infection and colonization by pathogens, mutualists and commensals are identical for many fungi.[13] Thus, the mode of recognition and early signaling processes are crucial in understanding how a plant can differentiate between a beneficial and a detrimental microbe[46] and express a lifestyle accordingly. A very early event in the interaction of pathogenic, mycorrhizal or endophytic microbes with a plant cell is an increase in the intracellular calcium (Ca^{2+}) levels within seconds or minutes after the recognition of the two partners. How this information is decoded into the appropriate responses in the plant cell it is not clear yet. Ca^{2+} ion is a second messenger in numerous plants signaling pathways, coupling extracellular stimuli to intracellular and whole-plant responses. The cellular Ca^{2+} level is tightly regulated and even a small change in its concentration provides information for protein activation and signaling.[46]

Evaluation on host genotype versus symbiotic lifestyle expression revealed that individual isolates of some fungal species could extent the symbiotic continuum by expressing either mutualistic or pathogenic lifestyles in different host plants.[39] For example, Colletotrichum spp. are classified as virulent pathogens, yet several species can express mutualistic lifestyles in non-disease hosts. Mutualistic benefits conferred by Colletotrichum spp. include disease resistance, growth enhancement and/or drought tolerance.[39] Although the genetic basis of symbiotic communication is not yet known, subtle differences in host genomes have profound effects on the outcome of symbiotic interactions.[29] For example, commercially grown tomato (*Solanum lycopersicum*) is known to possess relatively few genetic differences between varieties yet, it is able to express high levels of phenotypic plasticity.[47-49] When *C. magna* is introduced into different tomato cultivars, the fungus may express either mutualistic, commensal or parasitic lifestyles. Whereas parasitic and mutualistic lifestyles are easily observed, commensal lifestyles are often designated when no host fitness benefit is observed. However, depending on the traits being assessed, the commensal designation may be misleading.[29] For example, *C. gloeosporioides* was designated a pathogen of strawberry and a commensal of tomato because it conferred no disease protection.[39] Nevertheless, *C. gloeosporioides* increased plant biomass and conferred drought tolerance to tomato plants and was therefore designated a mutualist.[29] Endophytic fungi inside plant roots and rhizosphere fungi near plant roots can benefit plants in various ways, including through an improved nutrient supply, protection against pathogens or high temperature and production of phytohormones that may benefit the plant.[50]

Habitat-adapted symbiosis. The ability of endophytes originally isolated from grasses to confer the same functional stress tolerance to genetically distant plants such as tomato is intriguing as the evolutionary divergence of these plants occurred approximately 140–235 million years ago.[51-53] The concept that fungal endophytes adapt to stress in a habitat-specific manner has been confirmed with different fungal and plant species, and different environmental stresses.[36] While performing laboratory and field studies of Class II endophytes from plants from geothermal soils, coastal beaches and agricultural fields, Rodriguez and co-researchers observed a new ecological phenomenon and defined as habitat-adapted symbiosis. They have determined that endophytes from these habitats confer habitat-specific stress tolerance to plants. This habitat-specific phenomenon provides an intergenomic epigenetic mechanism for plant adaptation and survival in high-stress habitats.[14,36]

It is interesting that the stress tolerance conferred by some endophytes involves habitat-specific fungal adaptations. For example, within the geothermal soils of Yellowstone National Park, WY, a plant species (*Dichanthelium lanuginosum*) has been studied and found to be colonized by one dominant endophyte (*Curvularia protuberata*). *C. protuberate* confers heat tolerance to the host plant, and neither the fungus nor the plant can survive separate from one another when exposed to heat stress >38°C.[14] A comparative study of *C. protuberata* isolates from geothermal and nongeothermal plants revealed that the ability to confer heat tolerance was specific to isolates from geothermal plants hence; the ability to confer heat tolerance is a habitat-adapted phenomenon.[36] Another example of habitat-specific fungal adaptation involves a native dunegrass (*Leymus mollis*) on coastal beaches of Puget Sound, WA. *L. mollis* which is colonized by one dominant fungal endophyte (*Fusarium culmorum*). *F. culmorum* confers salt tolerance to the host plant which cannot survive in coastal habitats without the habitat-adapted endophyte. A comparative evaluation of *F. culmorum* isolates from *L. mollis* and a non-coastal plant revealed that the ability to confer salt tolerance was specific to isolates from the coastal plants, indicating that the ability to confer salt tolerance is a habitat-adapted phenomenon.[36] Evaluation of *C. protuberata, F. culmorum* and *C. magna* isolates further supports habitat-specific adaptation of endophytes: *C. protuberata* confers heat but not disease or salt tolerance; *F. culmorum* confers salt but not heat or disease tolerance; and *C. magna* confers disease but not heat or salt tolerance.[36] These symbiotically conferred stress tolerances conform to the evolutionary dynamics that must play out in the different habitats, with fungi adapting to habitat-specific stresses and conferring stress tolerance to host plants. This habitat-specific adaptation is defined as HA-symbiosis, and it is hypothesized that this allows plants to establish and survive in high stress habitats.[29]

Tripartite symbiosis. As plants represent communities of fungi, bacteria, viruses and/or algae, all of these micro-organisms contribute to the outcome of symbiosis and hence increase the complexity of studying plant biology. Furthermore, fungal symbionts may also harbor bacteria and viruses that can have dramatic effects on symbiotic communication.[29] Fungal viruses or mycoviruses can modulate plant-fungal symbioses. The best known example of this is the hypovirus that attenuates the virulence (hypovirulence) of the chestnut blight fungus, *Cryphonectria parasitica*.[54] Virus regulation of hypovirulence has been demonstrated experimentally in several other pathogenic fungi.[55,56] However, the effect of mycoviruses on mutualistic fungal endophytes is unknown. Fungal virus genomes are commonly composed of double-stranded RNA (dsRNA).[57] Large molecules of dsRNA do not normally occur in fungal cells and, therefore, their presence is a sign of a viral infection.[58] A mutualistic association between a Class II endophyte fungal endophyte [*C. protuberate* isolate (Cp4666D)], originally isolated from a tropical panic grass (*D. lanuginosum*) growing in geothermal soils allows both the organisms to grow at high soil temperatures where a double-stranded RNA (dsRNA) virus from this fungus is involved in the mutualistic interaction. In the absence of the virus, Cp4666D asymptomatically colonizes plants but could not confer heat tolerance. However, when the virus is reintroduced the heat tolerance is restored.[59] Thus, a three-way symbiosis (a virus in a fungus in a plant) is required for thermal tolerance.[29] The ability of the endophyte to confer heat tolerance requires the presence of a fungal RNA virus.[59] The virus-infected fungus confers heat tolerance not only to its native monocot host (*D. lanuginosum*) but also to a eudicot host (*Solanum lycopersicon*), which suggests that the underlying mechanism involves pathways conserved between these two groups of plants.[59]

Xu et al.[60] illustrates an unexpected but a very intrigue beneficial aspect of plant-pathogen interactions. Ten monocot and dicot plant species (*Beta vulgaris*, *Capsicum annuum*, *Cucumis lanatus*, *Cucumis sativus*, *Solanum lycopersicum*, *Oryza sativa*, *Cucurbita pepo*, *Chenopodium amaranthicolor*, *Nicotiana benthamiana* and *Nicotiana tabacum*) inoculated with the specific RNA viruses CMV (Cucumber mosaic virus), BMV (Brome mosaic virus), TMV (Tobacco mosaic virus) and TRV (Tobacco rattle virus) exhibited better tolerance and survival in response to drought and/or cold stress, implying that the viral infection induced a reaction that may be part of an elaborate mechanism used by plants to survive under various environmental challenges. It is likely that the presence of the viruses upregulated a specific set of stress-related genes which allows the infected plant to survive for a longer period when subjected to additional abiotic stresses,[61] which are also known to generate the production and accumulation of ROS.[62] The contact with the virus or pathogen induced molecular changes in the plant hosts which made them more tolerant to other stresses. Following these experiments, one wonders whether pathogens can also provide useful metabolites or enzymes that could be of benefit to their hosts. These studies demonstrate that the molecular limits between pathogenic and mutualistic associations are sometimes very narrow.[61]

Tripartite interactions among *Paenibacillus lentimorbus* NRRL B-30488, *Piriformospora indica* DSM 11827 and *Cicer arietinum* L. (Chick pea), enhance root nodulations and plant growth, which is evident by N, P and K uptake by plants. Principal component analysis (PCA) of carbon source (trehalose, proline, pectin, lysine, lignin, glycolic acid, glutamine, glutamic acid, chitin, cellulose and betaine) utilization pattern did not show any clustering. Proline, lysine, glutamine and glutamic acid were maximally utilized. While reverse was applicable for lignin, chitin, cellulose and betaine, trehalose and glycolic acid had no correlation.[63] In general, proline, lysine, glutamine and glutamic acid are associated with imparting abiotic stress tolerance,[64,65] while lignin, chitin and cellulose are associated with providing defense against pathogenic fungi.[66,67] Higher activity of lignin, chitin and cellulose utilizing microbial communities in the rhizosphere being stimulated by root exudates and, in turn, that should have encourage beneficial symbiotic or mutualistic microorganisms that can act as plant growth promoting and biocontrol agents. However, betaine an important metabolite involved in imparting abiotic tolerance was not grouped with proline, lysine, glutamine and glutamic acid but with lignin, chitin and cellulose, instead. Therefore, these results comparing the discriminant ability of carbon sources shows variable results.[63] The reasons why certain carbon sources increase the discrimination of this technique may be as discriminatory power of multivariate techniques lies not in the use of many different carbon sources, but in the use of combinations of carbon sources.[68,69] Plant root exudates, as such are a complex mixture of chemicals and organic compounds secreted into the soil by the roots that drive underground interactions and the exact composition of the exudates is determined by many factors, including species and nutritional status of the plant, soil structure and micronutrient status,[70] which makes it further more difficult to opt for carbon sources which might, therefore, be expected to differentiate to a greater extent between microbial populations.[63]

While the genetic/biochemical role of the virus in symbiotically conferred heat tolerance is not known, it is assumed that the virus provides biochemical functionality to the fungus and it is not the virus that directly confers heat tolerance. This astonishing result reflects our limited understanding of symbiotic systems and how they function. It also indicates the need to study plants from a symbiotic systems perspective to elucidate the contributions of all symbionts.[29] By and large, these studies indicate that the increased plant tolerance to abiotic stresses (whether drought, salt or cold/thermal stress) recorded when plants are in contact with a microbe, either a pathogen or a mutualist, is in part correlated with an increase in antioxidant or osmolyte concentrations and/or in the activities of antioxidant enzymes,[61] with ascorbate apparently playing a major role in the plant cells.[71] These observations may somehow be related to the systemic acquired resistance observed in some pathogenic interactions where healthy parts of the host plant become more resistant to a subsequent infection by either the same microbe or another one. Seemingly, there is no molecular evidence for the involvement of the above-mentioned antioxidants in this process.[61] Of course, in addition to ascorbate, several other compounds are also crucial and it is well known that glutathione and several hormones [abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA) and ethylene] are important players both in the abiotic stress response of plants and in plant-microbe interactions.[72-74] However, the status of the beneficial effect of viral infection as an alternative measure for abiotic stress tolerance in terms of improving agricultural yields is still not more than a last option. Indeed, whilst the beneficial effect of viral infection can temporarily delay the negative effects of a given abiotic stress, it cannot protect indefinitely against them.[61]

Fungal Symbionts

There are two major classes of fungal symbionts associated with plants: (1) Endophytic fungi, which reside entirely within plant tissues and may be associated with roots, stems and/or leaves; and (2) Mycorrhizal fungi, that reside only in roots but extend out into the rhizosphere. Fungal symbionts express a variety of symbiotic lifestyles including mutualism, commensalism and parasitism.[35] Mutualistic symbioses confer host fitness benefits that can result in drought and metal tolerance,[75] disease resistance, thermotolerance, growth enhancement,[14,76,77] herbivore resistance,[78] and enhanced nutrient acquisition.[75] Commensal symbioses have no beneficial or detrimental effects on hosts whereas, parasitic symbioses negatively affect host fitness by decreasing growth rates and/or fecundity, or inducing disease symptoms that may result in lethality.[39] Mutualistic benefits for endophytes may involve acquiring nutrients from hosts, abiotic and biotic stress avoidance and dissemination by seed transmission.[79,80]

Fungal endophytes. Endophytic fungi are those fungi that live entirely within plant tissues and may grow within roots, stems and/or leaves, emerging to sporulate at plant or host-tissue senescence.[81-83] Thus, endophytes encompass a wide range of fungi, including latent pathogens and dormant saprophytes. However, recent phylogenetic data demonstrate that some endophytes are genetically distinct from known parasites in the same host despite their morphological identity.[6,82] Carroll[82] defined two different types of endophytic fungi: constitutive mutualists (Class I endophyte) and inducible mutualists (Class II endophyte). It is usually proposed that most Class I clavicipitaceous endophytes (*Epichloë/neotyphodium*) are systemic and vertically transmitted through seeds and exclusively infect grass. Whereas, nonsystemic Class II endophytes are taxonomically diverse, horizontally transmitted from plants to plants and colonize almost all plants in ecosystems.[36] Currently, endophytes can be subdivided into four classes based on host range, colonization pattern, transmission and ecological function (For a review in ref. 84).

Stress tolerance confer by fungal endophytes. Numerous studies have shown that fungal endophytes confer stress tolerance to host species and play a significant role in the survival of at least some plants in high-stress environments.[13] For example, Class II endophytes confer heat tolerance to plants growing in geothermal soils,[14] the extent of tree leaf colonization by endophytes correlates with the ability to resist pathogens[85] and endophytes confer drought tolerance to multiple host species.[86]

Clavicipitaceous or class I endophytes. Class I endophytes represent a small number of phylogenetically related clavicipitaceous species that are fastidious in culture and limited to some cool- and warm-season grasses.[87] Distinctively these endophytes live their entire life cycle within the aerial portion of the host grass, forming nonpathogenic, systemic and usually intercellular associations.[88] Class I endophytes frequently increase plant biomass, confer drought tolerance (Table 1)and produce chemicals that are toxic to animals and decrease herbivory.[89] However, the benefits conferred by these fungi appear to depend on the host species, host genotype and environmental conditions.[90-92]

The frequency of endophyte infection often increases in grass populations over time, which suggests that endophytes confer an adaptive advantage on their hosts, even though they grow at the expense of host metabolism. Endophyte infection increases growth rate of perennial ryegrass and tall fescue.[89] Neotyphodium endophytes also increase drought tolerance in grasses, by means of osmoregulation and stomatal regulation[93] and also entail plant protection against nitrogen starvation or water stress.[94] These mechanisms have allowed perennial ryegrass to colonize large areas of the south-eastern US that would otherwise be too hot and dry. Production of plant hormones may be part of the mechanism of action.[95] Several studies conducted in controlled environments on single cultivars and natural ecotypes of tall fescue, meadow fescue (*Lolium pratense = Festuca pratensis*) and perennial ryegrass, suggest that their epichloe endophytes (*Neotyphodium coenophialum*, *N. uncinatum* and *N. lolii*, respectively) have positive effects on plant growth. Enhanced biomass production, tiller numbers, seed production and root growth have been reported in reference 96–99. Endophytes can induce in tall fescue and meadow fescue increased root growth and longer root hairs and decreased root diameter.[100,101]

Endophyte-infected grasses express a range of adaptations to biotic[78] and abiotic stresses, including drought,[102,103] mineral imbalance,[101,104,105] and soil acidity.[106,107] As a result, endophyte-infected grasses are more competitive and thrive better than noninfected grasses with limited resources.[93,108,109] Recent approaches to endophyte-grass interactions focus on isolated endophyte strains that, in association with grasses, show minimal or no production of alkaloids toxic to livestock yet retain the pest- and drought-resistance benefits of symbiotic plants.[110-112] These associations are crucial for improved livestock performance on fescue and ryegrass. Once alkaloid production has been altered, it is essential to understand mechanisms involved in abiotic stress tolerance of endophyte-infected grasses for their continued improvement and persistence for a range of applications.[100] While systemic endophytes in agronomic grasses have been well-studied, the interactions between host plants and endophytes in natural populations and communities are poorly understood.[113]

Nonclavicipitaceous or class II endophytes. Nonclavicipitaceous or Class II endophytes colonize roots, stems and leaves; are capable of forming extensive infections within plants; are transmitted via seed coats and/or rhizomes; have low abundance in the rhizosphere; confer habitat-adapted fitness benefits in addition to nonhabitat-adapted benefits; and typically have high infection frequencies (90–100%) in plants growing in high-stress habitats.[84] Currently, nonsystemic (Class II) endophytic fungi isolated and identified in a very wide range of host plant species have met with increasing attention due to their striking species diversity and multiple functions.[36] It is considered to be the largest group of fungal symbionts, are readily culturable on artificial media and are thought to colonize almost all plants in natural ecosystems.[114] Unlike other plant-microbe symbiotic relationships, plant-fungal endophyte associations generally occur in both aboveground and belowground plant tissues.[113] Strongly supported evidence has revealed that Class II endophytes represent more or less phylogenetic diversity when compared to Class I endophytes and mycorrhizal symbionts.[113,115,116] It has been assume that the endophyte and its host has a balanced antagonism or conditional mutualism,[117,118] which depends on the status of two partners. The plant's physiology and genotype, the genotype and virulence of the fungi, together with the environmental context ultimately determine the outcome of plant-endophyte interactions.[39,118,119] It appears that variability is the nature of the endophyte-plant interaction.[31]

Nevertheless, fungal endophytes have been known to confer fitness benefits to host plants including tolerance to herbivory, heat, salt, disease and drought (Table 2) and increased below- and above-ground biomass.[29,36,39,59,71,85,86,93,120-122] For instance, *C. protuberata* colonizes all nonembryonic tissues of the geothermal plant *D. lanuginosum*.[14,59] When grown nonsymbiotically, neither the plant nor the fungus can tolerate temperatures above 40°C. However, the symbiosis allows both partners to tolerate temperatures up to 65°C. Similarly trend was observed with *F. culmorum* which colonizes all nonembryonic tissues of coastal dunegrass (*L. mollis*): when grown nonsymbiotically, the host plant does not survive and the endophyte's growth is retarded when exposed to levels of salinity experienced in their native habitat.[36] However, both partners tolerate sea water levels of salinity (300–500 mM NaCl) when grown symbiotically. Evidently, *C. protuberata* and *F. culmorum are* able to avoid the detrimental effects of temperature and salt stress by residing in plant tissues. Based on these observations described above, it has been concluded that at least some Class II endophytes are mutualistic, conferring positive fitness benefits to hosts while also obtaining nutrition for growth and reproduction from host tissues and avoiding abiotic stress via symbiosis.[84]

A very unique and fascinating trait of Class II endophytes is the ability of individual isolates to asymptomatically colonize and confer habitat-adapted fitness benefits on genetically distant host species representing monocots and eudicots.[36] This phenomenon was discovered by comparing fitness benefits conferred by Class II endophytes in plants growing in geothermal soils (*C. protuberata*), coastal beaches (*F. culmorum*) and agricultural fields (Colletotrichum spp.). A series of laboratory studies indicated that *C. protuberata* conferred heat but not salt or disease tolerance, *F. culmorum* conferred salt but not heat or disease tolerance and Colletotrichum spp. conferred disease resistance but not heat or salt tolerance.[14,36,39] Field studies in geothermal soils and coastal beaches confirmed laboratory results indicating that nonsymbiotic plants could not survive stresses imposed in their natural habitats without colonization by these habitat specific endophytes. Further investigations revealed that the ability of endophytes to confer habitat-specific stress tolerance is an adaptive process defined at the subspecies level.[36] For example, isolates of *C. protuberata* (CpMH206) and *F. culmorum* (Fc18) from habitats devoid of heat or salt stress asymptomatically colonize plants to the same extent as isolates from habitats imposing heat and salt stress, but CpMH206 and Fc18 do not confer either heat or salt tolerance. Though all of these fungi establish nonpathogenic symbioses, the fitness benefits conferred on hosts were dependent on the habitat-specific stresses. Furthermore, investigation on the symbiotic lifestyle expressed by nonstress-adapted endophytes (CpMH206 and Fc18), their abilities to confer drought tolerance and growth enhancement revealed that all of the fungi conferred drought tolerance and growth enhancement on various host species,[36] suggesting that they were expressing mutualistic lifestyles. Hence, the ability of endophytes to confer habitat-adapted fitness benefits as habitat-adapted symbiosis and this allows plants to establish and survive in high-stress habitats.[84] While it is fairly uncomplicated to determine the impact of symbiosis on host fitness, it is more challenging to determine the benefits for fungal endophytes.[36]

The fact that individual Class II fungal isolates can asymptomatically colonize and confer specific stress tolerances on both monocot and eudicot hosts implies that the symbiotic communication required for stress tolerance predates the divergence of these plant lineages between 140 and 235 million year ago.[51-53] It is no wonder, as plant endophyte associations are represented in the fossil record at least 400 Million years ago,[3] placing endophyte symbioses in the same geological time frame as mycorrhizal symbioses.[2] The ability of many symbiotic fungi to confer drought tolerance is generally go well together with the suggestion that symbiotic fungi were involved in the movement of plants onto land.[4] Although fungal endophytes likely arose throughout evolutionary time and differed in host range and temporal distribution, their persistence throughout geologic time and their ubiquitous distribution are a testament to their significance in plant ecology and evolution.[84]

Piriformospora indica. Piriformospora indica, a new root colonizing endophytic fungus was discovered by Verma et al.[123] *P. indica* colonizes a wide range of monocot and dicot plants. *P. indica* can also convey several benefits to host plants like, better tolerance to various biotic and abiotic stresses, as well as improved plant fitness by increasing growth performance under normal and stress conditions.[86,124] The contribution of *P. indica* symbiosis to improve plant drought and salinity tolerance might point towards the natural habitat of its desert origin.[71,86,125] *P. indica* is analogous to AM fungi with regard to plant growth promotional effects. However, conversely to AM fungi, *P. indica* has the potential to grow axenically without the requirement of a living hosts[123] and can colonize members of the Brassicaceae (e.g., *A. thaliana*) and Chenopodiaceae, known to be non-host plants of mycorrhiza.[126,127] The ability of *P. indica* to improve growth rate of various host plants is well documented.[77,86,126] It also has a stimulatory effects on adventitious root formation in ornamental stem cuttings. However, the exact nature of plant growth promotional effects is still unclear.[128,129] *P. indica* was reported to activate nitrate reductase that plays a major role in nitrate acquisition and also a starch-degrading enzyme, glucan-water dikinase, involved in early events of starch degradation in the plants such as tobacco and Arabidopsis.[130] In addition, improvement of plants tolerance to biotic and abiotic stresses following colonisation by *P. indica* have also been widely documented and considered as a promising means to achieve sustainable agricultural production.

Drought. Drought resistance mechanisms have been divided into several types. At the first level the phenomenon may be distinguished into desiccation postponement (ability to maintain tissue hydration), desiccation tolerance (ability to function when dehydrated) which are sometimes referred to as drought tolerance at high and low water potentials respectively and drought escape which comprises plants that complete their lifecycles during the wet season, before the onset of drought. These are the only true drought avoiders. Among the desiccation postponers are water savers and water spenders. The water savers use water conservatively saving some in the soil for later use in the life cycle, whereas the water spenders aggressively absorb water, often using prodigious quantities.[131,132]

Drought stress induces a range of physiological and biochemical responses in plants such as stomatal closure,[133,134] repression of growth and photosynthesis,[135] and activation of respiration.[136] Many drought-inducible genes have been identified,[137] which can be 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.[138] Many genes for drought stress signaling components themselves are upregulated under drought stress. ABA-dependent and -independent signaling pathways have been shown to convert stress signal information into the alteration of the expression of responding genes. Since *P. indica* was isolated from a desert, it is likely that the fungus may confer drought tolerance to plants. When Arabidopsis is exposed to mild drought stress, seedlings co-cultivated with the fungus continue to grow, while the uncolonized controls do not and show symptoms of withering. When seedlings are first exposed to drought stress and then transferred to soil, many colonized seedlings reach the flowering stage and produce seeds, while the percentage for uncolonized seedlings is much lower. After exposure to drought stress, the message levels for many proteins involved in drought tolerance are faster upregulated in the leaves of *P. indica*-colonized seedlings when compared to the uncolonized controls.[125] An Arabidopsis EMS mutant is less resistant to drought stress and the stress-related genes are not upregulated in the presence of *P. indica*. Thus, *P. indica* confers drought stress tolerance to Arabidopsis and this is associated with the priming of the expression of a quite diverse set of stress-related genes in the leaves.[139]

P. indica colonize the roots of Chinese cabbage and promotes root and shoot growth and lateral root formation. When colonized plants were exposed to polyethylene glycol to mimic drought stress, the activities of peroxidases (POX), catalases (CAT) and superoxide dismutases (SOD) in the leaves were upregulated within 24 h. The fungus retarded the drought-induced decline in the photosynthetic efficiency and the degradation of chlorophylls and thylakoid proteins. The expression levels of the drought-related genes DREB2A, CBL1, ANAC072 and RD29A were upregulated in the drought-stressed leaves of colonized plants. Furthermore, the CAS mRNA level for the thylakoid membrane associated Ca^{2+}-sensing regulator and the amount of the CAS protein increased. Antioxidant enzyme activities, drought-related genes and CAS are three crucial targets of *P. indica* in Chinese cabbage leaves during the establishment of drought tolerance. *P. indica*-colonized Chinese cabbage provides a good model system to study root-to-shoot communication.[122]

Salinity. Soil salinization is an extensive and ever-present threat to crop productivity. Approximately, 7% of the global land surface is covered with saline soils.[140] Out of 1.5 billion ha cultivated land, about 77 million ha (5%) are affected by excess salt content mainly induced by irrigation with ground water of high salt content.[141] It is well known that crop production is low in saline soil, mainly due to salt toxicity to plants leading to a decrease in plant water holding capacity, the imbalance of nutrient uptake and toxicity of ions towards plant photosynthesis.[142,143] The responses to salt stress comprise an array of changes at the molecular, biochemical and physiological levels.[144]

Barley plants exposed to moderate (100 mM NaCl) salt concentration in hydroponic culture showed leaf chlorosis and reduced growth. Though, the detrimental effects of moderate salt stress is completely eliminated by *P. indica* colonization, as shown by the fact that colonized plants produce higher biomass than do nonstressed control plants under these conditions. A possible mechanism that confers drought tolerance in barley might be the establishment of a cellular environment with elevated antioxidative capacities.[86] *P. indica* protects barley even from high salt stress (300 mm NaCl). However, the mechanism of *P. indica*-induced salt tolerance has not yet been investigated. Previous studies suggested that salt-induced increase in lipid peroxidation[145,146] and reduction in metabolic heat production[147] in salt-sensitive plants, while unchanged in salt-tolerant cultivars. Salt induced responses indicated by heat emission and ethane production in the *P. indica*-infected salt-sensitive barley cv. Ingrid resemble those found in salinity-tolerant plants. Calorimetric studies indicated that the rate of metabolic activity increased in leaves of *P. indica*-infected plants after salt treatment. Hence, the endophyte seemed to overcompensate the salt-induced inhibition of leaf metabolic activity.[71] Prior studies have shown that the extent of natural herbicide resistance of wild oat biotypes is tightly correlated with the rate of heat production upon herbicide exposure, owing to the activation of metabolic pathways required for defence responses.[148] This suggests that enhanced tolerance to salt stress can be associated with higher metabolic activity in *P. indica*-colonized barley.[71] Exogenously applied unsaturated fatty acids can protect barley during NaCl-induced stress.[149] Lipid desaturation could be an important component of plant tolerance in response to salt stress.[71] Salt stress reduced the proportion of oleic acid in barley roots.[150,151] Similarly, *P. indica* colonization leads to a significant reduction in the proportion of oleic acid in barley leaves. *P. indica* also induces changes in fatty acid composition similar to those induced by salinity.[71] Such effects on the fatty acid composition of host plants may display a symbiotic adaptive strategy mediated by the endophyte to cope with salt stress in hostile environments.[36] *P. indica* might induce similar effects on fatty acid composition of the host plants in its original habitat, the arid Thar desert.[71]

Earlier studies have suggested that tolerance of plants to salt stress is associated with the induction of antioxidant enzymes.[152-154] Salt stress increases the activities of CAT, APX, DHAR, MDHAR and GR in roots of barley. Although enzyme activities decreased after an initial induction in both salt-sensitive and salt-tolerant cultivars, their decline was delayed and less pronounced in *P. indica*-colonized salt-sensitive cultivar than in the salt-tolerant cultivar. These results emphasize the importance of these enzymes in tolerance of barley to salinity.[71] Overexpression of CAT, APX or DHAR in transgenic plants enhanced tolerance to salt stress.[155,156] Surprisingly, Arabidopsis double mutant plants deficient in cytosolic and thylakoid APX also show enhanced tolerance to salinity, suggesting that ROS such as H_2O_2 could be responsible for activation of an abiotic stress signal that leads to enhanced stress tolerance.[157]

P. indica colonization enhances the ratio of reduced to oxidized ascorbate and induces DHAR activity in colonized barley.[86] Ascorbic acid acts as a primary substrate in the ascorbate-glutathione cycle for detoxification of hydrogen peroxide. Moreover, it acts directly to neutralize oxygen free radicals.[158] Ratio of ascorbate to DHA decreased in the salt-sensitive *L. esculentum* under salt stress and increased in the salt-tolerant *L. pennellii*.[159] Similarly, ascorbate content and the ratio of reduced to oxidized ascorbate dramatically decreased in roots of salt-treated barley plants soon after one week of salt exposure.[71] Earlier, investigation have shown that ascorbate content decreased in salt-sensitive and salt-tolerant pea cultivars as well, but the decline was greater in the NaCl-sensitive plants.[152] The importance of ascorbate in cellular protection under salt stress has also been demonstrated on an ascorbate deficient Arabidopsis mutant. Impaired in the ascorbate-glutathione-cycle, this mutant accumulated high amounts of ROS and showed increased sensitivity to salt stress.[160]

Consistently, exogenously applied ascorbate increased the resistance to salt stress and attenuated the salt-induced oxidative burst.[161] Alternatively, ascorbate can improve the tolerance of barley to high salinity via processes related to root growth. Ascorbic acid and high ratio of reduced to oxidized ascorbate accelerate root elongation and increase root biomass.[162]

The exact mechanism responsible for *P. indica*-mediated upregulation of the plant antioxidant system is not yet recognized. It has been shown recently *P. indica* is able to produce auxin when associated with plant roots.[163] Exogenous auxin has been found to transiently increase the concentration of ROS and then prevent H_2O_2 release in response to oxidative stress (caused by paraquat) and enhance APX activity, while decreasing CAT activity.[164,165] On the other hand, *P. indica* increased the amount of methionine synthase, which plays a crucial role in the biosynthesis of polyamines and ethylene.[127] Transgenic tobacco plants overproducing polyamines also have enhanced tolerance toward salt stress and salt treatment induces antioxidant enzymes such as APX, superoxide dismutase and glutathione S-transferase more significantly in these transgenic plants than in wild-type controls.[166] *Sebacina vermifera*, an endophyte closely related to *P. indica*, downregulates ethylene production in *Nicotiana attenuata*.[167] It has been suggested that *P. indica* induces ethylene biosynthesis in barley roots. Ethylene signaling may be required for plant salt tolerance,[168] and ethylene may induce some antioxidant enzymes when plants are exposed to heat stress.[169] However, further experiments are necessary to clarify the function of phytohormones in *P. indica*-induced salt tolerance in barley.[71]

It has been demonstrated that a high-saline environment is well tolerated by salt-sensitive barley when previously inoculated with the mutualistic *P. indica*, at least partly, through the upregulation of ascorbate and antioxidant enzymes. However, several possible symbiotic mechanisms could account for salt tolerance.[71] For example, root endophytes may act as a biological mediator allowing symbiotic plants to activate stress response systems more rapidly and strongly than nonsymbiotic plants.[13] Since *P. indica* has a broad host range and can easily be propagated in axenic culture on a large scale, it has been emphasize the high potential of the endophyte in protecting crops against salt stress in arid and semiarid agricultural regions.[71]

Trichoderma spp. Numerous organisms colonize plant roots, including fungi in the genus Trichoderma. Trichoderma spp. has been known for decades as biocontrol fungi; however, some strains are endophytic plant symbionts. They invade and colonize roots, thereby inducing plant resistance, which results in localization of the fungi. Some strains can invade and colonize twigs and stems too. As a root symbiont, they establish chemical communication with plant which results in reprogramming of plant gene expression and changes plant physiology. Earlier, it was considered that antibiosis and mycoparasitism were the primary mechanisms of biocontrol, but now a phenomenon/mechanism known as induced systemic resistance (ISR) has been discovered and considered to be more important. Though, biocontrol is only a subset of the advantages that effective endophytic Trichoderma strains can confer. They can also promote growth and induce resistance to a variety of abiotic stresses, including water deficit, temperature, salt and osmotic stress. In addition, improved photosynthetic and respiratory rates and nitrogen used efficiency (NUE) is also takes place. It is anticipated that we can reduce nitrogen use for selected crops by 30% without reducing yields. These applications have major implications for plant agriculture. For instance, NUE can reduce air and water pollution from agriculture and can improve food security for small holders who cannot afford sufficient nitrogen fertilizer to obtain maximum yields of plants.[170,171] However, specific knowledge of mechanisms, abilities to control multiple plant stress factors, is still lacking.[172]

Recent research has identified isolates of many Trichoderma spp. that are endophytic on *Theobroma cacao* including aboveground tissues.[173,174] Trichoderma spp. are primarily being studied for their ability to control disease in cacao.[174] Characterization of *Trichoderma/cacao* revealed changes in gene expression patterns which imply the possibility that Trichoderma spp. could induce tolerance to abiotic stresses, possibly including drought, in cacao.[175] Colonization of cacao seedlings by endophytic Trichoderma resulted in a delay in many aspects of the drought response. Thus, it is proposed that this effect is mediated through enhanced root growth, resulting in an improved water status allowing cacao seedlings to tolerate drought stress.[176] Colonization of cacao seedlings by *T. hamatum* isolate DIS 219b enhanced seedling growth, altered gene expression and delayed the onset of the cacao drought response in leaves at the molecular, physiological and phenotypic levels, a response that could prove valuable in the production of this important tropical crop.[176] Seed treatment with *T. harzianum* strain T22 increases seedling vigor and ameliorates stress by inducing physiological protection in plants against oxidative damage. Under multiple abiotic stress (osmotic, salt or suboptimal temperatures), biotic stress (seed and seedling disease caused by *Pythium ultimum*) and physiological stress (poor seed quality induced by seed aging), *T. harzianum* strain T22 treated seed germinated consistently faster and more uniformly than untreated seeds. The consistent response to varying stresses suggests a common mechanism through which the plant-fungus association enhances tolerance to a wide range of abiotic stresses as well as biotic stress. A common factor that negatively affects plants under these stress conditions is accumulation of toxic reactive oxygen species (ROS). However, T22 reduced damages resulting from accumulation of ROS in stressed plants. Seeds treatment reduced accumulation of lipid peroxides in seedlings under osmotic stress or in aged seeds. The effect of exogenous application of an antioxidant, glutathione, or application of T22, resulted in a similar positive effect on seed germination under osmotic stress or in aged seed as well.[172]

The ability of some Trichoderma spp. to overcome extreme environments facilitates their presence in very diverse geographical locations.[177] Owing to their ubiquity and rapid substrate colonization, it is no wonder that they have been commonly used as biocontrol organisms in agriculture under different environmental conditions.[178] Subsequently, isolation of genes from this biocontrol agent and their further transfer to a plant genome may result in a significant improvement in plant tolerance to biotic or abiotic stresses,[179] and such genes represent an important resource in the development of agricultural biotechnology and the exploitation of soil resources.[178] However, for successful use of Trichoderma spp. against biotic and abiotic stresses call for discovery or production of highly efficient strains.[171]

Mycorrhizal Fungi

Arbuscular mycorrhizal fungi (AMF), which are microscopic filamentous fungi, colonize the roots and their rhizosphere simultaneously and spread out over several centimeters in the form of ramified filaments.[180] AM fungi is the most extensively studied fungal symbionts which are associated with approximately 90% of all land plants and contribute multiple benefits to their host plants.[1] This filamentous network dispersed inside as well as outside the roots allows the plant to have access to a greater quantity of water and soil minerals required for its nutrition. In return, the plant provides the fungus with sugars, amino acids and vitamins essential to its growth.[181] Numerous studies support the fact that plant colonized by mycorrhizal fungi is better nourished and better adapted to its environment. It gains increased protection against environmental stresses,[182] such as drought,[183] cold,[184] salinity and heavy metal toxicity,[185] micronutrient imbalances, industrial effluents,[186] biocide treatment,[187] slurry application,[188] sulfur dioxide fumigation,[189] wild fire recovery[190] and pathogens.[191,192] On the whole, the growth and health of colonized plants is improved and at the same time, obtain increased protection against biotic and abiotic stresses detrimental to their survival.[180] However, attempts to incorporate these valuable symbionts into mainstream agricultural production practices have not yet been successful.[193]

Drought. Some AM fungi are adapted to adverse conditions therefore; they can benefit plants under a variety of environmental stresses.[194] Mycorrhizal plants may avoid drought to some extent through enhanced water uptake at low soil moisture levels. In onion, the effects seem to be conferred through improved phosphorus nutrition,[195] while in Bromus and rose, some other mechanism prevails.[196] An influence on host osmotic potential has been observed in wheat.[197] Extensive amount of research literature indicates that mycorrhizae often have a substantive impact on water movement into, through and out of host plants, with consequent effects on plant tissue hydration and leaf physiology.[180] They usually increase host growth rates during drought, by affecting nutrient acquisition and possibly hydration and typically water use efficiency, which are influenced by the kind of fungi involved.[198]

AM fungal hyphae contributed extensively in terms of improving soil structure and its water holding capacity.[199] Not only can mycorrhizal fungi influence overall plant growth (and hence soil water regimes), mycorrhizal plants can also exhibit different water relations from their non-mycorrhizal counterparts.[198,200] AM symbiosis has been reported to result in altered rates of water movement into, through and out of host plant, with consequent effects of tissue hydration and leaf physiology.[180] For example, higher stomatal conductance and transpiration can occur in the mycorrhizal states.[201] More efficient exploration of water by mycorrhizal fungi may lead to more extreme wet/dry cycles, which could have very strong consequences for soil aggregation.[202] Furthermore, the symbiosis can allow leaves to fix more carbon during water stress,[203] carbon inputs into the soil would be expected to be increased, which might be especially important in more arid environment. Hyphae and roots can be viewed as a "sticky string bag" from a mechanistic point of view because mainly the hyphae of AM fungi contribute to the entanglement and enmeshment of soil particles to form aggregates, the basic building blocks of soil structure. Moreover, the glycoprotein, glomalin, deposited on the cell wall of the AM fungus is rather stable hydrophobic glue that might enable the fungus to cope with gas-water interfaces during aerial growth. The hydrophobicity of the deposited glomalin may reduce macro-aggregate disruption during wetting and drying events as well.[199]

Salinity. Mycorrhizal symbiosis is a key component in helping plants survive under adverse environmental conditions.[204] Arbuscular mycorrhizal fungi widely occur in salt stressed environment.[205] Recent literatures suggest that AM fungi play a vital role in alleviating the effects of salinity[206] and enhance the ability of the plants to cope with salt stress[207] by compensating nutritional imbalances imposed by salinization through improved nutrient acquisition,[182] improving plant nutrient uptake,[208] and ion balance,[209] protecting enzyme activity[210] and facilitating water uptake.[211] It has been suggested that salt stress could decrease photosynthetic ability and induce physiological drought in plants which leads to a decrease in crop production.[212] There are also few reports which indicate that AM colonization could enhance relative water content in Zuchhini leaves,[213] water potential of maize plants[214,215] and chlorophyll concentration in the leaves of several plant species like *Sesbania aegyptica*, *S. grandiflora* and *Lotus glaber*.[213,216,217] Mycorrhizal maize plants had greater biomass than non-mycorrhizal plants under salt stress, thus implying that mycorrhizal plants grow better than non-mycorrhizal plants under saline conditions.[218] Similar trend were also reported in various crops other e.g., tomato,[219] cotton,[220] barley.[221]

Increased antioxidative enzyme activities could be involved in the beneficial effects of mycorrhizal colonization on the performance of plants grown under semiarid conditions. Many of the physiological and biochemical processes of *Cajanus cajan* (pigeon pea) were affected by salt stress as a result of triggering premature nodule senescence along with a reduction in N-fixing ability of the nodules.[222] AM significantly improved nodulation, leghemoglobin content and nitrogenase activity under salt stress. Activities enzymes involved in detoxification of O_2^- radicals and H_2O_2 namely, superoxide dismutase, catalase and peroxidase and enzymes that are important components of the ascorbate glutathione pathway responsible for the removal of H_2O_2, namely, glutathione reductase and ascorbate peroxidase increased markedly in mycorrhizal-stressed plants.[144] Similar trend were also noticed in soybean under drought stress.[223,224]

AM symbiosis has also been reported to increase resilience of host plants against salinity stress, perhaps with greater consistency than to drought stress.[225] Salt resistance was improved by AM colonization in maize,[226] mung bean[227] and clover,[228] with the AM effect correlated with improved osmoregulation or proline accumulation. AM colonization also improved NaCl resistance in tomato, with extent of improvement related to salt sensitivity of the cultivar.[206] AM improvement of salt resistance has usually been associated with AM-induced increase in P acquisition and plant growth, although two of three AM fungi tested were able to protect cucumber plants from NaCl stress compared to similarly sized non-AM plants.[229] Alfalfa was also more effectively protected against salinity stress by AM symbiosis than by P-supplementation,[230] and the improvement of NaCl resistance in lettuce induced by several AM fungi was not attributed to nutrition.[140]

Since solutes can concentrate in the soil solution just outside roots as soil dries,[231] and AM symbiosis often increases plant resistance to salinity stress, one can contemplate that the amount of salts in drying soil may be one factor that can elucidate why AM fungi increased drought resistance in some studies but not in others i.e., perhaps AM effects on drought resistance are linked to AM effects on salt resistance; in those reports where AM symbiosis did improve drought resistance, AM fungi may have helped to overcome plant susceptibility to an osmotic or NaCl stress that developed as soil dried. Salinity stress tended to nullify an AM-induced change in drought response in *Sorghum bicolor* plants.[225] In case of squash leaves, across all AM and NaCl treatments, the leaf hydraulic conductance change in synchrony with stomatal conductance corroborating leaf tendency towards hydraulic homeostasis under varying rates of transpirational water loss.[183] AM also plays positive role in protecting plants from pH extremes.[182]

Stress Tolerance Mechanism(s)

Symbiotically conferred stress tolerance involves at least two mechanisms: (1) activation of host stress response systems soon after exposure to stress, allowing the plants to avoid or mitigate the impacts of the stress;[45,232] and (2) biosynthesis of antistress biochemicals by endophytes.[233,234] Besides biosynthesis of antistress chemicals, plant-fungal mutualisms have been maintained over evolutionary time because endophytes control the activation of host stress response systems by acting as biological triggers.[13] Some of the mechanisms used by the cool season grass endophytes to alter the drought response include drought avoidance through morphological adaptations, drought tolerance through physiological and biochemical adaptations and enhanced drought recovery.[100]

Osmotic adjustment. Drought, heat and salt stress affect plant-water relations triggering complex plant responses, which include increased production of osmolytes.[15,235] Osmotic potential is determined primarily by two components: solute potential and matrix potential, and it is likely that symbiotic fungi contribute to the matrix potential, which is particularly important in helping plants retain water and thereby enhance plant drought tolerance. Upon exposure to heat stress, nonsymbiotic panic grass and tomato plants significantly increased osmolyte concentrations as predicted. Increased osmolyte concentrations correlated with the development of subsequent wilting and desiccation symptoms prior to plant death.[36] In contrast, symbiotic plants either maintained the same (panic grass and Rutgers tomato),[59] or lower (Tiger-Like tomato),[36] osmolyte concentrations when compared to non-stressed controls. The differences in osmolyte patterns in tomato may be reflective of differences in the varieties (Rutgers versus Tiger-Like). Most investigations of epichloë effects on stress tolerance focus on osmotic adjustment, water relations and drought recovery,[236,237] accumulation of drought-protective osmolytes in the grass tissues,[238] and photosynthetic rates under water or heat stress.[239] Under water stress, the tall fescue endophyte is also associated with a significant increase in cell wall elasticity as measured by bulk modulus tissue elasticity, and by turgid weight to dry weight ratio (TW/DW).[240] Likewise, *N. uncinatum* increases TW/DW in water-stressed meadow fescue.[241] Whatever the case may be, the overall pattern of osmotic concentrations in plants that succumb to heat stress (nonsymbiotic) differs from plants that are heatstress tolerant, suggesting that symbiotic plants use approaches other than increasing osmolyte concentrations to mitigate the impacts of heat stress.[36]

Osmotic protection. Osmotic protection is more likely than stomatal conductance to be involved in drought protection in tall fescue,[242] but reduced stomatal conductance might be important to conserving water in *Festuca arizonica-Neotyphodium* sp. interactions.[237] Some speculation regarding osmoprotectants centers around the fungal loline alkaloids, which are abundant in those symbiota for which the endophyte has a documented and consistent positive effect on drought tolerance.[100] Lolines fit several prerequisite criteria, being nontoxic to plant cells, highly water soluble, and generally increasing in response to heat or drought. However, it is unclear if lolines reach sufficient levels to significantly affect osmotic balance. If these alkaloids are involved, they might protect macromolecules from denaturation and/or scavenge reactive oxygen species associated with drought stress, possibilities not yet tested.[79] Other potential osmoregulators and protectants are soluble sugars and sugar alcohols, produced by the endophyte, plant or both.[238]

Water-use efficiency. Symbiotic plants consumed significantly less water than nonsymbiotic plants regardless of the colonizing endophyte. Panic grass, rice, tomato and dunegrass plants all used significantly less fluid than nonsymbiotic plants. Since these symbiotic plants achieve increased biomass levels, decreased water consumption suggests more efficient water usage. Decreased water consumption and increased water-use efficiency may provide a unique mechanism for symbiotically conferred drought tolerance.[36] Substantial (>50%) stand losses in tall fescue were reported after removing the endophyte from this grass.[243] These losses are typically associated with drought periods, and endophyte-infected tall fescue exhibits improved recovery after drought compared to endophyte-free tall fescue.[244] It was suggested that grass endophytes, particularly *N. coenophialum* in tall fescue, affect plant water relations, nutrient acquisition, as well as allocation and photosynthetic assimilation.[102] Overall, there appears to be a trend toward improved physiological responses of endophyte-infected grasses to adverse environmental conditions.[79] However, studies with several grass species confirm complex interactions between endophyte status, plant genotype, water and nutrient availability and spatial competition.[91,236]

Reactive oxygen species (ROS). A plant biochemical process common to all abiotic and biotic stresses is the accumulation of ROS. ROS are extremely toxic to biological cells causing oxidative damage to DNA, lipids and proteins. On the other hand, ROS can act as signaling molecules for stress responses and generation of ROS is an early event in plant response to stress.[62,245] In their natural environment, plants establish relationships with many microorganisms like fungi, bacteria and viruses which can either be pathogens or symbionts. In the case of pathogenesis, one possibility for the plant to prevent or minimize microbe infection is to generate an oxidative burst, the purpose of which is to kill bacteria and plant cells surrounding the infection site.[61] However, recent data shows that reactive oxygen species (ROS) and reactive nitrogen species (RNS) are produced by both partners in many symbiotic and pathogenic systems.[246,247] Therefore, in a pathogenic or symbiotic association, both the plant and the microbe must be able to deal with a complex mixture of ROS coming from both sides. ROS are not necessarily harmful for the partners and, depending on the model considered, they can also help to signal and limit/control the interaction.[61] For example, the development of a mutualistic association between *Epichloë festucae*, a fungal endophyte, and the grass *Lolium perenne* requires the production of superoxide or hydrogen peroxide by a fungal NADPH oxidase, whilst inactivation of this gene changes the interaction from mutualistic to antagonistic.[246] Whatever the case may be, both partners (the plant and the microbe) have developed an impressive array of nonenzymatic and enzymatic antioxidant systems, whose function is to maintain adequate concentrations of ROS in their own cells. Certainly, low ROS concentrations are known to be required for signalling, growth and development, while high concentrations are detrimental to the cell and can damage various macromolecules. It is of primary importance for the development of plant-microbe interactions that ROS produced at the interface between the partners, that is, in the extracellular matrices, cell walls and more generally the apoplast compartment. NADPH oxidases, plasma membrane-situated proteins, are key players in this subcellular compartment for the generation of ROS species including superoxide ions and hydrogen peroxide.[61]

Symbiotic and nonsymbiotic plants when exposed to ±stress (panic grass and tomato to heat stress and dunegrass and tomato to salt stress) revealed that in the absence of stress, both nonsymbiotic and symbiotic plant leaf tissues for all plants (panic grass, tomato, dunegrass) remained green indicating the absence of ROS generation and hence lack of stress response. In contrast, when exposed to stress, nonsymbiotic tissues bleached white indicating the generation of ROS while symbiotic tissues remained green. This suggests that endophytes either scavenge ROS or induces plants to more efficiently scavenge ROS, or prevents ROS production when exposed to abiotic stress. It has been presumed that the role of ROS in plant symbioses with Class I and Class II endophytes may differ.[36] The Class I endophyte *Epichloe festucae* appears to generate ROS to limit host colonization and maintain mutualisms,[246] while the Class II endophytes Cp4666D and FcRed1 reduce ROS production to possibly mitigate the impact of abiotic stress. Further studies may clarify if these are general differences between Class I and Class II endophytes or a reflection of individual isolates.[36]

Antioxidant enzymes. It is a common belief that antioxidant enzymes plays an important role in fungal symbiosis conferring abiotic stress tolerance.[61] The antioxidants include the low molecular-weight compounds glutathione, ascorbate and tocopherol and the enzymes superoxide dismutases, catalases, ascorbate- or thiol-dependent peroxidases, glutathione reductases, dehydroascorbate reductases and monodehydroascorbate reductases.[248] These enzymes are involved in the removal of ROS either directly (superoxide dismutases, catalases and ascorbate- or thioldependent peroxidases) or indirectly through the regeneration of the two major redox molecules in the cell, ascorbate and glutathione (glutathione reductases, dehydroascorbate reductases and monodehydroascorbate reductases).[61] An interesting feature of the interplay between oxidants and antioxidants is that it occurs in all subcellular compartments including plastids and mitochondria, two sites of extensive ROS production.[249]

Under salt stress conditions *P. indica* increases the tolerance of a salt-sensitive barley (*Hordeum vulgare*) cultivar to severe salt stress. *P. indica*-colonized plants contained higher ascorbate concentrations in roots compared with noncolonized plants, while the ratio of ascorbate vs. dehydroascorbate was not significantly altered and catalase, ascorbate peroxidase, glutathione reductase, dehydroascorbate reductase and monodehydroascorbate reductase activities were increased. These modifications are consistent with the decrease of leaf lipid peroxidation observed in these experiments.[71,86]

Conclusion

As plants in nature do not function as autonomous individuals, but accommodate diverse communities of symbiotic microbes, the role of these microbes in plant development and protection can no longer be ignored. These symbiotic microbial interactions are significant for the survival of both the host and microbe in stressed environments.[1] Numerous studies suggest that fungal endophytes confer stress tolerance to host species and play a significant role in the survival in high-stress environmental conditions such as drought, salinity, extreme temperature (cold/heat), heavy metal pollution, etc., and increase growth. It is our common belief that all the indigenous/native plants thrive and flourish in various abiotically stressed ecosystems because of endosymbiotic organisms that have co-evolved and were essential for their adaptation to stressed environments.[1] Some of these microbial components are non-cultivable and vertically transmitted from generation to generation. They represent a vast reservoir of heritable DNA that can enhance plant performance in changing environments and add genetic flexibility to adaptation of long-lived plants.[13,82] Unculturable endosymbiotic microbes may be vertically transferred in succeeding generations. If such endophytes can be identified that not only persist in progeny of novel hosts, but can confer benefits in mechanized, agricultural systems, they would be increasingly important in agricultural production and lead to a rapid and economical method of providing novel germplasms of native and crop plants.[1] Furthermore, studies indicate that fungal endophytes generally have wide host range (e.g., Colletotrichum spp.). Fungal endophytes that express non-mutualistic lifestyles in specific hosts may establish mutualistic symbioses with genetically unrelated plant species and confer stress (disease and/or drought) tolerance. If this is common to all the fungal endophytes, it may be possible to use endophytes from the hosts thriving in high stress environments to confer desirable traits such as drought, temperature, disease and salt tolerance to genetically unrelated stress-sensitive plant species. This would allow native plants and agricultural crops to be generated with new capabilities for tolerating specific environmental stresses brought by global change.[36]

In order to achieve these objectives, we need to discover or develop efficient fungal endophytes for abiotic stress tolerance through assessing the endophyte species found in the nature (different stressed habitats), because it has been assume that many endophytes have not yet been discovered and the ecological roles of these fungi are not fully understood. Most researches on endophytes are still at greenhouse experimental phase, field experiments and trials must be promoted to evaluate their efficiency under natural conditions because ultimately, both the host and fungal endophyte have to deal with the natural environment and survive. Since, plant growth and development cannot be adequately described without acknowledging microbial interactions thus; we need to study plants from a symbiotic systems perspective to understand the functions and contributions of all symbionts for better plant health and protection.

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