Rhizosphere Microbes as Essential Partners for Plant Stress Tolerance

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Ever since plants colonized land, they evolved mechanisms to respond to changing environmental conditions and settle in extreme habitats. Recent studies show that several plant species require microbial associations for stress tolerance and survival. Although many plants lack the adaptive capability to adapt to stress conditions, the ability of a variety of plants to adapt to stress conditions often appears to depend on their association with certain microbes, raising a number of questions: What distinguishes the microbes and plants that can adapt to extreme environmental conditions? Can all plants improve stress tolerance when associated with appropriate microbial partners? Answers to these questions should modify our concepts of plant physiology and could lead to new ways towards a sustainable agriculture.

THE ROLE OF RHIZOSPHERE MICROBES IN PLANT STRESS TOLERANCE

Due to their sessile nature, plants have always been confronted with various abiotic and biotic stresses in their immediate environment. As a consequence, the survival of plants depends on their ability to rapidly adjust their physiology, development, and growth to escape or mitigate the impacts of stress. All plants are known to perceive and respond to stress signals such as drought, heat, salinity, herbivory, and pathogens (Hirt, 2009). Some responses are common to various stresses, including the production of certain proteins and the adjustment of the primary metabolism.

Due to photosynthesis, plants can produce carbohydrates, of which a considerable fraction passes to root-associated microorganisms, commonly denoted as the rhizosphere. Plant growth also requires significant quantities of nitrate, phosphate, and other minerals which are often not available in free form or in limited quantities in the soil. This is where root-associated beneficial microbes are important partners. The best-known beneficial microbes are mycorrhizal fungi and rhizobia. Approximately 80% of all terrestrial plant species interact with mycorrhiza which make phosphate and nitrate available to plants. Free-living or endophytic rhizobia can fix atmospheric nitrogen, but only the family of leguminosae profits from such an interaction through their ability to house rhizobia in root nodules. The interaction of plants with mycorrhizal fungi and rhizobial bacteria is well documented (Corradi and Bonfante, 2012; Geurts et al., 2012). Non-symbiotic rhizosphere microbes have received much less attention and are therefore treated in this review.

Soil-grown plants are immersed in a sea of microbes and diverse beneficial microorganisms such as plant-growth-promoting bacteria (PGPB) as well as plant-growth-promoting fungi (PGPF) can stimulate plant growth and/or confer enhanced resistance to biotic and abiotic stresses (Lugtenberg and Kamilova, 2009). The establishment of beneficial plant-microbial interactions requires the mutual recognition and a considerable orchestration of the responses at both the plant and the microbial side. Rhizobial and mycorrhizal symbioses share a common plant-signaling pathway that is activated by rhizobial and mycorrhizal factors (Corradi and Bonfante, 2012) and this signaling pathway also seems to be activated by certain beneficial bacteria, suggesting that different beneficial and pathogenic microbes initiate common plant-signaling pathways. Recent evidence indicates that beneficial and pathogenic microbes also suppress the host defense system by various strategies, including the production of effectors, exopolysaccharides, or phytohormones (Zamioudis and Pieterse, 2012).

THE ROLE OF PLANT GROWTH-PROMOTING BACTERIA

PGPBs belong to a number of different bacterial families, including \textit{Rhizobium}, \textit{Bacillus}, \textit{Pseudomonas}, \textit{Burkholderia}, etc. PGPBs can improve the growth of vegetables and crops under abiotic stress conditions (Egamberdieva and Kucharova, 2009) and might therefore open new applications for a

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sustainable agriculture. Enhanced salt tolerance of Zea mays upon co-inoculation with Rhizobium and Pseudomonas is correlated with decreased electrolyte leakage and maintenance of leaf water contents (Bano and Fatima, 2009). Some microorganisms produce plant hormones, such as indole acetic acid and gibberellic acid, which induce increased root growth and thereby lead to enhanced uptake of nutrients (Egamberdieva and Kucharova, 2009).

Plants have the ability to acquire a state of induced systemic resistance (ISR) to pathogens after inoculation with PGPBs. In association with plant roots, PGPBs can prime the plant innate immune system and confer resistance to a broad spectrum of pathogens with a minimal impact on yield and growth (Van Hulten et al., 2006). Several PGPBs, including Pseudomonas fluorescens, Pseudomonas putida, Bacillus pumilus, Serratia marcescens, Paenibacillus alvei, Acinetobacter Iwoffii, Chryseobacterium balustinum, and Azospirillum brasilense colonize roots and protect on a large variety of plant species, including vegetables, crops, and even trees, against foliar diseases in greenhouse and field trials (Van Loon, 2007).

**PLANT-ASSOCIATED FUNGI CONFER STRESS TOLERANCE TO PLANTS**

Mycorrhizal and/or endophytic fungi can interact with many plant species and thereby significantly contribute to the adaptation of these plants to a number of environmental stresses (Rodriguez et al., 2008). These conditions include drought, heat, pathogens, herbivores, or limiting nutrients. Moreover, some plants are unable to withstand stress conditions in the absence of their associated microbes (Redman et al., 2002). It appears that stress tolerance of the host plant can be a habitat-specific feature of the interaction. For example, Curvularia protuberata confers heat tolerance to its geothermal host plant Dichanthelium lanuginosum. However, neither the fungus nor the plant can survive alone at temperatures above 38°C (Redman et al., 2002). Moreover, only C. protuberata isolates from geothermal plants can confer heat tolerance (Rodriguez et al., 2008).

A comparison of different fungal endophytes unravels a further layer of specificity: C. protuberata confers heat but neither disease nor salt tolerance. In contrast, Fusarium culmorum only confers salt tolerance and Curvularia magna only disease tolerance (Rodriguez et al., 2008). It appears that these specific features contribute to the ability of some plants to establish and survive in extreme habitats.

Symbiotically conferred disease tolerance appears to involve different mechanisms depending on the endophyte. For example, a non-pathogenic Colletotrichum strain that confers disease resistance does not activate host defense in the absence of pathogen challenge (Redman et al., 1999). Moreover, disease resistance is localized to tissues that the fungus has colonized, but is not systemic.

In contrast, Piriformospora indica confers disease resistance systemically. *P. indica* colonizes the roots of many plant species and stimulates growth, biomass, and seed production of the hosts (Fig. 1). *P. indica* promotes nitrate and phosphate uptake and confers resistance against abiotic (Waller et al., 2005) and biotic stress (Stein et al., 2008). Colonization by the fungus stimulates the host to synthesize phosphatidic acid,


