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Microbially Mediated Plant Salt Tolerance and Microbiome-based Solutions for Saline Agriculture

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ABSTRACT

Soil salinization adversely affects plant growth and has become one of the major limiting factors for crop productivity worldwide. The conventional approach, breeding salt-tolerant plant cultivars, has often failed to efficiently alleviate the situation. In contrast, the use of a diverse array of microorganisms harbored by plants has attracted increasing attention because of the remarkable beneficial effects of microorganisms on plants. Multiple advanced ‘-omics’ technologies have enabled us to gain insights into the structure and function of plant-associated microbes. In this review, we first focus on microbe-mediated plant salt tolerance, in particular on the physiological and molecular mechanisms underlying root–microbe symbiosis. Unfortunately, when introducing such microbes as single strains to soils, they are often ineffective in improving plant growth and stress tolerance, largely due to competition with native soil microbial communities and limited colonization efficiency. Rapid progress in rhizosphere microbiome research has revived the belief that plants may benefit more from association with interacting, diverse microbial communities (microbiome) than from individual members in a community. Understanding how a microbiome assembles in the continuous compartments (endosphere, rhizoplane, and rhizosphere) will assist in predicting a subset of core or minimal microbiome and thus facilitate synthetic re-construction of microbial communities and their functional complementarity and synergistic effects. These developments will open a new avenue for capitalizing on the cultivable microbiome to strengthen plant salt tolerance and thus to refine agricultural practices and production under saline conditions.

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Contents

1. Introduction	0
2. Roots, microorganisms and soil: belowground interaction networks	0
3. How do microbes help plants tolerate salt stress?	0
3.1. Rhizospheric and endophytic bacteria as helpers for alleviating plant salt stress	0
3.2. Fungal symbionts of roots: underestimated roles in improving plant salt adaptation	0
4. Broad horizons: understanding rhizosphere microbiome assembly and functioning at a community level	0
4.1. How is the rhizosphere microbiome assembled and what factors shape its structure?	0
4.2. Tools used to study the functional traits of microbial communities	0
4.3. Experimental framework for characterizing microbiome-mediated plant phenotypic traits at a community level	0
5. Practical applications of the concept of a core (minimal) microbiome and principles for reconstructing synthetic microbial communities	0
5.1. Core (minimal) microbiome.	0
5.2. Synthetic microbial communities: bridging the gap between basic research and agricultural practice	0
6. Concluding remarks.	0
Acknowledgments	0
References	0

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1. Introduction

Climate change-induced soil salinization is a constant threat to agriculture and ecology worldwide. Approximately 15–50 % of the irrigated lands have been severely damaged by salinity (Pitman and Läuchli, 2002). In China, 7 million hectares (ha) of land area are affected by salinity (Brandon and Ramankutty, 1993). To feed the ever-growing population, a boost in crop productivity is required. It is therefore worthwhile to explore the question of how to mitigate the adverse effects of salt stress, enhance plant salt tolerance and eventually increase crop yields in high-salinity soils.

The physiological and molecular mechanisms of salinity tolerance in plants have been thoroughly reviewed (Deinlein et al., 2014; Hasegawa et al., 2000; Kawasaki et al., 2001; Mickelbart et al., 2015; Munns and Tester, 2008; Rus et al., 2005). It is acknowledged that plants have readily evolved an array of genetic and epigenetic regulatory systems to respond to abiotic stresses such as salinity and drought (Liu et al., 2015; Vannier et al., 2015). This valuable information is useful for developing practical strategies for alleviating crop salinity stress. For example, the integration of conventional plant breeding and molecular techniques has been widely deployed to increase crop abiotic tolerance (Bresghele and Coelho, 2013; Ishitani et al., 2004). Transgenic plants overexpressing a wide range of genes adapt well to high salt environments under laboratory and greenhouse conditions (Roy et al., 2014). In general, however, such approaches have not been very successful at increasing salinity tolerance or yield, although they are still being actively pursued. There are several reasons for this failure. First, these approaches are both time-consuming and labor-intensive (Coleman-Derr and Tringe, 2014) and frequently result in unstable mutants due to the simultaneous manipulation of numerous genes involved in abiotic stress responses (Jewell et al., 2010). Second, it is still uncertain whether transgenic crops will become generally publicly acceptable (Fedoroff et al., 2010). Third, molecular techniques are not widely applicable to important *Brassica* and *Triticum* species that are tetraploid or hexaploid (Birch, 1997; Kumar et al., 2015). Fourth, saline and alkaline stresses are frequently linked in nature (Bui et al., 2014). The tolerance of transgenic salt-tolerant plants to high soil alkalinity (pH) and/or salt-alkaline mixed conditions in fields has yet to be fully evaluated (Yamaguchi and Blumwald, 2005). Finally, transgenic salt-tolerant crops, especially those whose transcription factors have been genetically modified, sometimes suffer yield penalties (Roy et al., 2014). Thus, care should be taken to maintain yield stability in transgenic crops. To bypass these limitations, it is necessary to investigate additional alternative strategies. In past decades, efforts were made to understand plant abiotic tolerance from an ecological perspective. There is now increasing recognition that plant fitness and adaptation is not only related to the genome of a plant but might also be intricately linked to multiple biotic factors of the environment (Munns and Gilliam, 2015; Vannier et al., 2015).

2. Roots, microorganisms and soil: belowground interaction networks

Root-associated microbial communities (primarily bacteria and fungi) are active partners interacting with host plants (Lebeis, 2014; Tikhonovich and Provorov, 2011). Surprisingly, plant roots growing in soil are in contact with highly diverse microbes (Vandenkoornhuysen et al., 2002, 2007), and numerous groups of mutualistic microbes are uncultivable and/or taxonomically novel. These microbes have coevolved with their hosts and have tailored their community structure to specific environmental pressures (Lau and Lennon, 2012). It is therefore assumed that the belowground ecological interaction network between the root, soil and microorganisms plays a crucial role in supporting normal growth and defending against unsuitable conditions for both the host and its associated organisms. The major exception to this rule, however, may be the agricultural soils used for

crop production that have been microbially impoverished by tilling, chemical fertilizers, pesticide input, and monoculture (Altieri, 1999).

It is thus reasonable to focus our attentions on identifying how much of the plant phenotypic traits (growth and stress tolerance) are related to specialized belowground microbial communities. Although a small proportion of plant parasites and pathogens are commonly recorded in soils, which is typically the result of intensive farming, at least some important mutualistic microorganisms can reduce the incidence of plant diseases (Spence et al., 2014), promote nutrient utilization, and enhance a plant's ability to resist abiotic stress (Friesen et al., 2011; Lugtenberg and Kamilova, 2009; Yang et al., 2009; Zelicourt et al., 2013). This microbe-based plant biotechnology has proven to be more efficient than plant breeding and genetic modification approaches (Smith, 2014). In return, the plants sustain and protect these microorganisms through rhizodeposition (Jones and Nguyen, 2009), provide carbon sources for growth and influence the activities and composition of the microbial communities (Bais et al., 2006; Mendes et al., 2013). While many excellent reviews have discussed a wide range of plant beneficial traits provided by diverse microbial groups (Bulgarelli, 2013; Friesen et al., 2011; Hardoim et al., 2008; Harman et al., 2004; Lugtenberg and Kamilova, 2009; Rodriguez et al., 2009; Rosenblueth and Martínez-Romero, 2006; Singh et al., 2011), the present review first seeks to give a holistic overview of current knowledge of microbe-mediated plant salt tolerance. We then shift the focus from plant-microbe to plant-microbiome interactions, which is becoming a popular research topic. We hope that this information gives tremendous impetus to further attempts in the direction of microbiome-based solutions for saline agriculture.

3. How do microbes help plants tolerate salt stress?

There is clear evidence that a diverse group of root-associated microbes is essential for promoting plant adaptation to salinity (Munns and Gilliam, 2015; Tkacz and Poole, 2015; Turner et al., 2013; Zelicourt et al., 2013). To describe how microbes help plants tolerate salt stress, in this section, we aim to summarize current knowledge regarding the mechanisms of action of beneficial microbes accompanied by the plant physiological and molecular response to salinity stress. Indeed, most studies have focused on elucidating microbial modes of action in simplified systems (using single isolates as inoculants). Both direct and indirect mechanisms underlying the well-studied bacteria and fungi that confer plant salt tolerance will be discussed in detail (Fig. 1).

3.1. Rhizospheric and endophytic bacteria as helpers for alleviating plant salt stress

Any community of root-associated microorganisms is dominated by plant-growth-promoting rhizobacteria (PGPR) and endophytic bacteria. Notably, PGPR have been used worldwide for many years as biofertilizers owing to their remarkable positive effects on crop yield and a range of biotic and abiotic stress tolerance (Lugtenberg and Kamilova, 2009; Mayak et al., 2004; Upadhyay et al., 2012). Whole genome sequences of a handful of bacteria provide sufficient information for determining the benefits of interest in PGPR (Gupta et al., 2014). In this section, we focus on the role of PGPR in eliciting tolerance to a variety of abiotic stresses in plants, a process referred to as induced systemic tolerance (IST) (Yang et al., 2009). It seems plausible that multiple bacterial determinants are involved in IST, including phosphate solubilization, 1-aminocyclopropane-1-carboxylic acid (ACC)-deaminase activity, and the production of volatiles, siderophores, indole-3-acetic acid (IAA), and exopolysaccharides (Farag et al., 2013; Kumari et al., 2015; Nadeem et al., 2016).

Plants when subjected to salinity, drought, and pathogen stresses are known to produce excessive ethylene, which severely retard root development (Mahajan and Tuteja, 2005). One of the most striking

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