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Review

Bacterial-mediated drought tolerance: Current and future prospects

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ABSTRACT

With ongoing climate change, the severity, frequency and duration of drought in cotton (*Gossypium hirsutum* L.), soybean (*Glycine max* L.), and corn (*Zea mays* L.) producing areas around the world are predicted to increase. Plants' tolerance to drought stress needs to be improved in order to allow growth of crops that satisfy food demands under limited water resource availability. Plant-associated microbial communities, such as mycorrhizal fungi, nitrogen-fixing bacteria, and plant growth-promoting rhizobacteria (PGPR), enhance crop productivity and provide stress resistance. PGPR represent a wide range of root-colonizing bacteria with excellent root colonizing ability and capacity to produce a wide range of enzymes and metabolites that help plants tolerate both biotic and abiotic stresses. Their roles in the management of abiotic stresses such as drought are only beginning to gain attention. In this review, we synthesize research concerning bacterial-mediated drought tolerance in agricultural crop plants. We summarize in a table and provide details of most relevant and recent studies about the crop system studied, experimental system, means of applying drought stress, and physiological traits measured (such as relative water content, photosynthesis). Furthermore, we highlight the research needed to understand mechanisms behind observed bacterial-mediated drought tolerance and the need to homogenize and develop screening protocols.

Contents

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1. Introduction

1.1. Definitions and concepts of drought

One of the key obstacles to increasing crop growth and productivity in many parts of the world is drought (Vinocur and Altman, 2005; Naveed et al., 2014). Due to differences in hydrometeorological variables, socioeconomic factors, and the stochastic nature of water demands in different regions of the world, many definitions of drought have been proposed (Yevjevich, 1967; Dracup et al., 1980; Wilhite and Glantz, 1985; American Meteorological Society, 2004). Depending on the variable used to describe drought, drought definitions are classified into four different categories (Wilhite and Glantz, 1985; American Meteorological Society, 2004): (1) meteorological drought, defined as a lack of precipitation for a period of time; (2) hydrological drought, defined as a lack of adequate surface and subsurface water resources for established water uses of a given water resources management system; (3) socio-economic drought, defined as the failure of water resources systems to meet water demands; and (4) agricultural drought, defined as a period with declining soil moisture resulting in crop failure. In this review, we focus on agricultural drought.

Drought is one of the major limitations to food production worldwide and is estimated to have reduced national cereal production by 9–10% (Lesk et al., 2016). Drought is expected to cause serious plant growth problems for crops on more than 50% of the earth's arable lands by 2050 (Vinocur and Altman, 2005). With ongoing global climate change, the severity, frequency and duration of drought in cotton (*Gossypium hirsutum* L.), soybean (*Glycine max* L.), and corn (*Zea mays* L.) in many crop-producing areas around the world are predicted to continue to increase (IPCC, 2007; EEA, 2011). In addition, the world population is expected to reach 9 billion by 2050, necessitating continued increases in crop production to assure food security (Gatehouse et al., 2011; Foley et al., 2011). Therefore, there is a renewed interest in finding solutions to water-related problems such as drought and its impacts on food security (Alexanratos and Bruinsma, 2012). In particular, there is a need to find solutions that increase plants' tolerance to drought stress and allow growth of crops that satisfy food demands under limited water resource availability (Editorial, 2010; Mancosu et al., 2015).

1.2. Concepts of drought adaptations

The ability of plants to sustain growth and survive during periods of drought stress has been termed drought resistance (Levitt, 1980; Chaves et al., 2003). Plants have developed several mechanisms allowing them to cope with drought stress including morphological adaptations, osmotic adjustment, optimization of water resources, antioxidant systems that diminish the harmful effects of reactive oxygen species (ROS) linked to drought, and induction of a variety of stress-responsive genes and proteins (Farooq et al., 2009). These and other adaptations have been detailed in multiple research articles and reviews (e.g. Chaves et al., 2003; Boomsma and Vyn, 2008; Farooq et al., 2009; Lopes et al., 2011; Huang et al., 2014) and are not be included in this review. These adaptations of plants to drought broadly fit into three categories. First is drought escape, in which the plant completes its life cycle before the onset of drought and undergoes dormancy before the onset of the dry season (Levitt, 1980; Turner et al., 2001; Farooq et al., 2009). Second is drought avoidance and phenotypic flexibility, which is the ability of a plant to sustain its normal water status under drought conditions (Blum, 2005). This can be achieved when the plant obtains more water from the soil or minimizes water loss through transpiration. Third is drought tolerance, which occurs when normal plant growth and metabolic activities are maintained even under water stress. These activities include strategies such as osmotic adjustment, maintenance of root viability and membrane stability under dehydration as well as accumulation of proteins and other metabolites that work directly or indirectly in structural stabilization (Nilsen and Orcutt, 1996; Huang et al., 2014).

1.3. How bacteria in soil experience water stress

Soil microorganisms including beneficial soil bacteria experience drought (Schimel et al., 2007; Barnard et al., 2013). Drought stress affects soil bacteria through osmotic stress and resource competition (Schimel et al., 2007; Chodak et al., 2015) and can result in nucleic acids damages (Dose et al., 1991) that may occur via chemical modifications (alkylation or oxidation), cross-linking, or base removal (Potts, 1999). Drought stress results in an accumulation of free radicals due to conformational protein changes, restricted enzyme efficiency, and changes in electron transport chains (Vriezen et al., 2007; Bérard et al., 2015). Accumulation of free radicals induces protein denaturation and lipid peroxidation that ultimately leads to cell lysis (Potts, 1999). Moreover, drought stress can induce protein conformational changes and affect the membrane characteristics of microbes through phospholipid fatty acid composition changes (Russell et al., 1995; Bérard et al., 2015).

Soil microbes are small, in intimate contact with soil water, and have semipermeable membranes (Schimel et al., 2007). As water potentials decline and soils dry due to drought, cells have to accumulate solutes to decrease their internal water potential to avoid dehydration and death (Schimel et al., 2007). To survive drought and protect cell structures and organelles, soil bacteria employ a variety of physiological mechanisms including accumulation of compatible solutes, exopolysaccharide production, and the production of spores (Conlin and Nelson, 2007; Schimel et al., 2007; Allison and Martiny, 2008; Bérard et al., 2015). Accumulation of compatible solutes such as proline, glycine betaine and trehalose increases thermotolerance of enzymes, inhibits proteins thermal denaturation, and helps maintain membrane integrity (Welsh, 2000; Conlin and Nelson, 2007; Schimel et al., 2007; Bérard et al., 2015). Bacteria also synthesize heat shock proteins (HSPs) that recognize and bind to other proteins if they are in non-native conformations (Hecker et al., 1996; Feder and Hofmann, 1999). Alternatively, some bacteria store high quantities of ribosomes, which allow them to respond with rapid protein synthesis when the stress is released (Placella et al., 2012). Other mechanisms that help bacteria to cope up with water stress include increased efficiency of resource use and re-allocation within microbial cells (Tiemann and Billings, 2011) and the production of extracellular polymeric substances (EPS). EPS serve to protect the cell as well as the local environment in which the cell is embedded (Rossi et al., 2012).

The strategies used by soil bacteria to withstand drought stress have also been reported as some of the key adaptation strategies that are employed by plants to survive drought. For example, many of the compatible solutes (proline and glycine betaine) that help bacteria to cope with drought stress also help plants to tolerate drought stress.

1.4. Bacterial-mediated drought tolerance

To date, creation of drought-tolerant cultivars has been the approach used to mitigate the negative effects of drought stress on crops and crop yields (Barrow et al., 2008; Eisenstein, 2013). Conventional plant breeding techniques have allowed the development of high-yielding, drought- tolerant crop varieties. The