

Review Article

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Review on Drought Tolerance in Plants Induced by Plant Growth Promoting Rhizobacteria

Zaffar Mahdi Dar^{1*}, Amjad Masood², Arshad Hussain Mughal¹,
Malik Asif¹ and Mushtaq Ahamd Malik¹

¹Division of Basic Sciences, ²Division of Agronomy, Faculty of Agriculture,
SKUAST- K Kashmir J&K, India

*Corresponding author

ABSTRACT

Abiotic stresses are major constraints which adversely affect the plant growth and productivity. Among all abiotic stresses, drought is considered as one of the major constraints on agricultural productivity worldwide and is likely to further increase. Hence the need of the hour is to formulate the strategies that can minimize the loss in crop production under drought conditions. One of them being the exploitation of soil microbes which have the capacity to overcome the adverse effects of drought stress. In the current scenario, microbial role in plant adaptation towards drought stress is gaining more attention. In this regard plant growth promoting rhizobacteria (PGPR) can be employed to mitigate the drought adversities in the plants. This review deals with the mechanisms through which the PGPR minimize the harmful effects of drought stress in plants. In several studies it has been reported that these beneficial microorganisms colonize the plant rhizosphere and impart drought tolerance by altering the level of plant hormones like IAA (indole acetic acid) and ABA (abscisic acid), enzymes like ACC (1-amino, cyclo propane 1-carboxylic acid) deaminase, promoting root growth and nutrient uptake, inducing accumulation of osmolytes and antioxidants.

Keywords

Abiotic, Plant growth promoting rhizobacteria, Drought, Tolerance, Hormones

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Introduction

Crop growth and development are constantly influenced by environmental stresses which are the most important yield reducing factors in the world (Dennis, 2000). Drought stress is considered as the most destructive abiotic stresses that increased in intensity over the past decades affecting world's food security. It may range from moderate and short to extremely severe and prolonged duration, restricting the crop yields (Bottner *et al.*,

1995). Drought affects cell water potential and turgor pressure, enough to interfere with normal functions, physiological and morphological traits in plants (Rahdari and Hoseini, 2012). Drought stress decreases nutrient diffusion and mass flow of water soluble nutrients (Selvakumar *et al.*, 2012). Drought also induces the formation of free radicals such as superoxide radicals, hydrogen peroxide and hydroxyl radicals resulting in oxidative damage to cell through lipid peroxidation and membrane deterioration

(Nair *et al.*, 2008). Besides, the stomatal closure during drought conditions reduces the CO₂ uptake by the plants, hence reducing the photosynthetic rate and plant yield.

Keeping in view the dangers posed by the drought stress and the increasing demand for food, a wide variety of efforts focusing on agro ecosystem and soil biological system as a whole is required to understand the stability of process. One of them being the exploitation of soil microbes which have the capacity to overcome the adverse affects of drought stress (Navnita *et al.*, 2015). In the current scenario, microbial role in plant adaptation towards drought stress is gaining more attention. This strategy is not only easier but also cost effective. Millions of microbes inhabit plant root system forming a complex ecological community that influences plant growth and productivity through its metabolic activities and plant interactions (Schmidt *et al.*, 2014).

The term PGPR was proposed by Kloepper *et al.*, (1980) who defined it as a group of bacteria capable to actively colonize the plant root system and improve their growth and yield (Wu *et al.*, 2005). A wide range of species belonging to the genus *Pseudomonas*, *Azospirillum*, *Azotobacter*, *Klebsiella*, *Enterobacter*, *Alcaligenes*, *Arthrobacter*, *Burkholderia*, *Bacillus* and *Serratia* were reported to have PGPR properties (Saharan and Nehra, 2011). PGPR represent about 2 to 5% of total rhizospheric bacteria (Antoun and Kloepper, 2001). They colonize all ecological niches of root to all stages of plant development, even in the presence of a competing microflora. The effects of PGPR depend on ecological and soil factors, plant species, plant age, development phase and soil type (Werner, 2001). For example, a bacterium which promotes plant growth through nitrogen fixation or phosphorus solubilization, certainly not produce beneficial effects to the plant when the soil

receives chemical fertilizers. It has been reported in several studies that PGPR improves plant growth even under drought conditions through one or more mechanisms. Hence in the following sections, efforts have been made to appraise the role and underlying major mechanisms of PGPR in inducing tolerance to drought stress.

Mechanism of PGPR mediated drought tolerance

There are various strategies and mechanisms studied for enhancement of plant drought tolerance mediated by rhizobacteria but, the exact mechanism is still speculative. However, the literature suggests the involvement of the following possible mechanisms in promoting the drought tolerance by PGPR.

Effect of PGPR on phytohormonal level

Phytohormones such as indole acetic acid, gibberellins, ethylene, abscisic acid and cytokinins are produced by plants, which are important for their growth and development (Egamberdieva, 2013). Indole-3-acetic acid (IAA) is the best-characterized auxin produced by many plant associated bacteria, including PGPR (Spaepen *et al.*, 2007a). PGPRs stimulate plant cell growth and division to become tolerant against environmental stresses mediated through biosynthesis of phytohormones (Glick and Pasternak, 2003). Various plant species inoculated with IAA producing bacteria increased root growth and/or enhanced formation of lateral roots and roots hairs (Dimkpa *et al.*, 2009) thus increasing water and nutrient uptake (Mantelin and Touraine, 2004), helping plants to cope with water deficit (Egamberdieva and Kucharova, 2009). Bacterial treatment in wheat (Arzanesh *et al.*, 2011) induced decrease in leaf water potential and increase in leaf water content, which was

attributed to the production of plant hormones such as IAA by the bacteria that enhanced root growth and formation of lateral roots their by increasing uptake of water and nutrients under drought stress resulting in better grain yield and higher mineral quality as compared to untreated plants. Similarly, inoculation with *A. brasilense* Cd and *B. thuringiensis* in common bean (German *et al.*, 2000) and *Lavandula dentate* plants (Armada *et al.*, 2014) respectively increased root projection area, specific root length and specific root area, nutritional physiology and metabolic activities of plant. *A. brasilense* produces nitric oxide, a small diffusible gas which acts as a signaling molecule in IAA inducing pathway and helps in adventitious root development in tomato plants (Molina Favero *et al.*, 2008).

Cellular dehydration induced biosynthesis of ABA, a stress hormone during water deficit condition (Kaushal and Wani, 2015). In addition to IAA, production of ABA by *Azospirillum lipoferum* alleviated drought stress in maize plants (Cohen *et al.*, 2009). ABA is involved in water loss regulation by controlling stomatal closure and stress signal transduction pathways (Yamaguchi-Shinozaki and Shinozaki, 1994). Arabidopsis plants inoculated with *A. brasilense* had elevated levels of ABA compared to non-inoculated plants. PGPR *Phyllobacterium brassicacearum* isolated from the rhizosphere of *Brassica napus* enhanced osmotic stress tolerance in inoculated Arabidopsis plants by elevating ABA content, leading to decreased leaf transpiration conferring drought stress resistance (Bresson *et al.*, 2013).

Effect of PGPR on plant root system

Many PGPR are able to produce phytohormones among which IAA is the best-characterized auxin produced by many plant associated bacteria, including PGPR (Spaepen

et al., 2007a). Exogenous IAA controls a wide variety of processes in plant development and plant growth: low concentrations of IAA can stimulate primary root elongation, whereas high IAA levels stimulate the formation of lateral roots, decrease primary root length and increase root hair formation (Remans *et al.*, 2008). IAA is usually synthesized by rhizobacteria from tryptophan, which is found at different concentrations in root exudates according to plant genotype (Kamilova *et al.*, 2006). In PGPR strains, several IAA biosynthetic pathways have been described depending on the metabolic intermediates (Spaepen *et al.*, 2007a).

It has also been reported that certain PGPR produce some secondary metabolites such as 2,4-diacetylphloroglucinol (DAPG), and nitric oxide (NO). Several PGPR strains like *Azospirillum brasilense* have nitrite reductase activity and consequently are able to produce NO during root colonization (Pothier *et al.*, 2007). NO is involved in the auxin signaling pathway controlling lateral root formation (Molina-Favero *et al.*, 2008). DAPG is a well-known antimicrobial compound produced by pseudomonads (Couillerot *et al.*, 2009). At lower concentrations, DAPG can also be a signal molecule for plants, inducing systemic resistance (Bakker *et al.*, 2007), stimulating root exudation (Phillips *et al.*, 2004), and enhancing root branching (Walker *et al.*, 2011). DAPG can interfere with an auxin dependent signaling pathway (Brazelton *et al.*, 2008). Indeed, applications of exogenous DAPG, at a concentration around 10 μ M, inhibited primary root growth and stimulated lateral root production in tomato seedlings.

PGPR has been found to modify the chemical composition of root cell walls that directly promote plant growth. El Zembrany *et al.*, (2007) concluded that roots inoculated with *Azospirillum lipoferum* had lower lignin

content than uninoculated ones facilitating cell elongation by rapid water uptake, and therefore overall root elongation. Similarly, *Azospirillum irakense* produces pectate lyases that are capable of degrading the pectate content of root cell wall and might allow its progression between root cortex cells and its functioning as an endophyte (Bekri *et al.*, 1999).

Modifications of root cell wall ultrastructure are thought to result mainly from PGPR triggered changes in plant gene expression. Indeed, *Bacillus subtilis* GB03 promotes *Arabidopsis* growth by producing volatile organic compounds that were shown to modulate the expression of 38 genes with known functions associated with cell wall structure (Zhang *et al.*, 2007). Among them, 30 were implicated in cell wall expansion or loosening. The endophytic PGPR *Azospirillum irakense* was also shown to stimulate the expression of polygalacturonase genes in inoculated rice roots (Sekar *et al.*, 2000).

Effect of PGPR on ACC deaminase activity

Under biotic and abiotic stresses plant drought tolerance is regulated by ethylene level (Hardoim *et al.*, 2008). In the biosynthetic pathway of ethylene, S-adenosylmethionine (S-AdoMet) is converted by 1-aminocyclopropane-1-carboxylate synthase (ACS) to 1-aminocyclopropane-1-carboxylate (ACC), the immediate precursor of ethylene. Under stress conditions, the plant hormone ethylene endogenously regulates plant homeostasis resulting in reduced root and shoot growth. It has been reported that ACC deaminase producing PGPR *Achromobacter piechaudii* ARV8 significantly increased the fresh and dry weights of both tomato and pepper seedlings and reduced the ethylene production under drought stress (Mayak, 2004). ACC deaminase producing bacteria *Pseudomonas*

fluorescens biotype G (ACC-5) eliminated the effects of drought stress on growth, yield, and ripening of pea in both pot and field trials (Arshad *et al.*, 2008). In addition to it the bacteria induced longer roots, which led to an increased uptake of water from soil under drought stress (Zahir *et al.*, 2008) which resulted in more seed yield, seed number and seed nitrogen accumulation and restoring nodulation which was depressed in drought stress conditions (Dodd *et al.*, 2005). Rhizobacteria populating the sites where water is limited with repeated dry periods are likely to be more stress adapting and promote plant growth than those bacteria isolated from the sites where water sources are abundant (Mayak, 2004).

Actually, PGPR are more widely able to lower plant ethylene levels through deamination of 1-aminocyclopropane-1-carboxylic acid (ACC). Many genomes of PGPR do contain a gene (*acdS*) coding for an ACC deaminase, which degrades ACC into ammonium and α -ketobutyrate (Prigent Combaret *et al.*, 2008). By lowering the abundance of the ethylene precursor ACC, the PGPR *AcdS* activity is thought to decrease root ethylene production, which can in turn alleviate the repressing effect of ethylene on root growth (Glick, 2005). Plant ACC is sequestered and degraded by ACC deaminase producing bacteria to supply nitrogen and energy.

Impact of PGPR on plant nutrition

Plant growth-promoting rhizobacteria can directly increase nutrient supply in the rhizosphere and stimulate ion transport systems in root. With regards to increased nutrient supply, two main types of bacterial activities can be considered. Firstly, phosphate solubilization is one key effect of PGPR on plant nutrition. Soils generally contain a large amount of phosphorus, which accumulates in the wake of regular fertilizer

applications, but only a small proportion of the latter is available for plants. Plants are able to absorb on their own the mono and dibasic phosphate; however, organic or insoluble forms of phosphate need to be mineralized or solubilized by microorganisms (Ramaekers *et al.*, 2010). Many PGPR such as *Pseudomonas*, *Bacillus*, *Rhizobium* are able to dissolve insoluble forms of phosphate (Richardson *et al.*, 2009) through two of the main processes: acidification of the external medium through the release of low molecular weight organic acids such as gluconic acid that chelates the cations bound to phosphate (Miller *et al.*, 2009), and production of phosphatases/phytases that hydrolyse organic forms of phosphate compounds. Capsicum plants inoculated with PGPR had a P and K uptake 40% higher than that on uninoculated. In addition to N and P PGPR application in tomato has been found to improve iron and zinc uptake. Secondly, many associated bacteria can fix N₂ so that they could provide nitrogen to the plant. Evidence in favor of the participation of PGPR to the plant N budget has been reported for several plants, especially sugarcane (Boddey *et al.*, 2003).

It is commonly hypothesized that nutrient uptake is increased as a consequence of increased root surface area triggered by PGPR. However, root ion transporters are under the control of regulatory processes that adjust their activity to the plant nutritional demand (Nazoa *et al.*, 2003), so that regulations of root development and ion transporter activities are antagonistically coordinated to maintain steady nutrient acquisition rate (Touraine, 2004).

Impact of PGPR on osmoregulation

Plant adaptation to drought stress is associated with metabolic adjustments that lead to the accumulation of several compatible solute like proline, sugars, polyamines, betaines, quaternary ammonium

compounds, polyhydric alcohols and other amino acids and water stress proteins like dehydrins (Close, 1996). These small, uncharged, soluble molecules, which include proline, glycine betaine, polyamines, and melatonin, do not affect cellular function directly. These solutes decrease the hydric potential of cells by trapping water molecules or by retaining the water molecules they are already associated with which is termed as osmoregulation and the accumulated solutes are called as compatible solutes because their accumulation in the plant cell does not have any harmful effect on the cell physiology. Compatible solutes can increase the stability and integrity of membranes and proteins, preventing or lessening cellular damage. It has been reported in several studies that PGPR secrete osmolytes in response to drought stress, which act synergistically with plant produced osmolytes and stimulate plant growth (Paul *et al.*, 2008). PGPR *Pseudomonas putida* GAP-P45 inoculation improved plant biomass, relative water content and leaf water potential by accumulation of proline in maize plants exposed to drought stress (Sandhya *et al.*, 2010) hence adding to its existing concentrations (Ansary *et al.*, 2012).

Drought tolerance of *L. dentate* showed that PGPR *B. thuringiensis* (Bt) inoculation enhanced shoot proline accumulation under drought stress (Armada *et al.*, 2014). Similarly, tomato treated with phosphate solubilizing bacteria (PSB) (*Bacillus polymyxa*) secreted excess proline to cope up with the drought condition (Shintu and Jayaram, 2015). PGPR consortia containing *Pseudomonas jessenii* R62, *Pseudomonas synxantha* R81 and *Arthrobacter nitroguajacolicus* strain YB3, strain YB5 enhanced plant growth in both drought tolerant and drought sensitive cultivars of rice. PGPR inoculation increases proline content in plants due to up regulation of its biosynthesis pathway hence maintaining cell

water status and protects the cell membranes and proteins from the injury caused by drought stress (Sandhya *et al.*, 2010).

Impact of PGPR on plant antioxidative system

Studies have shown that water deficit is a major environmental factor limiting the productivity of plants and may cause damage to plant tissues, especially roots, through the formation of reactive oxygen species (ROS) such as H₂O₂, O₂⁻ and OH⁻, due to high susceptibility of root meristem activity to ROS. ROS are toxic molecules capable of causing oxidative damage to the lipids, DNA and proteins (Miller *et al.*, 2010). If these molecules are not managed properly, they cause significant damage to the membranes and cause catastrophic effects on cell metabolism. Therefore, efficient quenching of ROS is very crucial for survival and cell metabolism under stress conditions. Oxidative stress occurs when the antioxidant defence system is overloaded and is unable to maintain an adequate cellular redox balance. The antioxidant system includes both enzymatic (e.g., superoxide dismutases, ascorbate peroxidases, and catalases) and non-enzymatic molecules (e.g., glutathione, flavonoids, carotenoids, and tocopherols) (Mittler, 2002).

In order to decrease the deleterious effects of ROS, antioxidant promoting systems are required, such as PGPR application. Basil plants (*Ocimum basilicum* L.) treated with *Pseudomonas* sp. under drought stress significantly increased the catalase enzyme activity, similarly when treated with microbial consortia containing *Pseudomonas* sp., *Bacillus lentus* and *A. brasilense* highest activity of glutathione peroxidase and ascorbate peroxidase was observed (Heidari and Golpayegani, 2011). PGPRs, *P. jessenii* R62, *P. synxantha* R81 and *A.*

nitroguajacolicus strain YB3 and strain YB5 used as consortia's enhanced plant growth and induction of stress related enzymes superoxide dismutase, catalase (CAT), peroxidase (PX), ascorbate peroxidase (APX) and lower level of H₂O₂, malondialdehyde (MDA) in Sahbhagi (drought tolerance) and IR-64 (drought sensitive) cultivars of rice under drought stress compared to control (Gusain *et al.*, 2015). Maize plants inoculated with five drought tolerant plant growth promoting *Pseudomonas* spp. strains namely *P. entomophila*, *P. stutzeri*, *P. putida*, *P. syringae*, and *P. montelli* subjected to drought stress showed significantly lower activity of antioxidant enzymes as compared to uninoculated plants (Sandhya *et al.*, 2010). In another experiment on maize plants it was found that plants inoculated with *Bacillus* species developed protection against drought stress by reducing activity of the antioxidant enzymes APX and Glutathione peroxidase (GPX) (Vardharajula *et al.*, 2011). Effectiveness of autochthonous PGPR *B. thuringiensis* (Bt) in *Lavandula dentata* and *Salvia officinalis* under drought conditions promoted growth and drought avoidance by decrease of glutathione reductase (GR) and ascorbate peroxidase (APX) activity (Armada *et al.*, 2014). The reduction in the antioxidant activity by inoculation with PGPR is related to less generation of free radicals hence reducing the antioxidant activity. These studies provide evidence for beneficial effect of PGPRs application in enhancing drought tolerance of plants by altering the antioxidants activity and reduction in active oxygen species under water deficit conditions (Gusain *et al.*, 2015).

It is quite clear from the above discussion that PGPR mediates plant drought tolerance by overcoming the deleterious effects posed by drought stress through changes in hormonal level like IAA and ethylene which in turn promote root elongation as well as its

architecture favorable for the increased water uptake which is additionally being favored by enhancement in the accumulation of solutes in the plant cell that prevents the loss of water from the cell. The danger posed by the free radical to the plant through different means is prevented by PGPR through enhancement in the level of different antioxidants followed by the reduction in the ROS hence preventing the cell death.

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