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Minireview

MINIREVIEW

Seed biopriming with plant growth promoting rhizobacteria: a review

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One sentence summary: The article reviews the potential of seed priming with plant growth promoting bacteria over conventional methods of bacterial application to the soil in improving plant productivity.

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ABSTRACT

Beneficial microbes are applied to the soil and plant tissues directly or through seed inoculation, whereas soil application is preferred when there is risk of inhibitors or antagonistic microbes on the plant tissues. Insufficient survival of the microorganisms, hindrance in application of fungicides to the seeds and exposure to heat and sunlight in subsequent seed storage in conventional inoculation methods force to explore appropriate and efficient bacterial application method. Seed priming, where seeds are hydrated to activate metabolism without actual germination followed by drying, increases the germination, stand establishment and stress tolerance in different crops. Seed priming with living bacterial inoculum is termed as biopriming that involves the application of plant growth promoting rhizobacteria. It increases speed and uniformity of germination; also ensures rapid, uniform and high establishment of crops; and hence improves harvest quality and yield. Seed biopriming allows the bacteria to enter/adhere the seeds and also acclimatization of bacteria in the prevalent conditions. This review focuses on methods used for biopriming, and also the role in improving crop productivity and stress tolerance along with prospects of this technology. The comparison of methods being followed is also reviewed proposing biopriming as a promising technique for application of beneficial microbes to the seeds.

Keywords: biopriming; plant growth promoting rhizobacteria; inoculation

INTRODUCTION

Soil microbes since their discovery in late 18th century have been used extensively in crop production. Advent of technology allowed the researchers to study more about the microbial populations, and Kloepper and Schroth (1978) first time used the term plant growth promoting rhizobacteria (PGPR) explaining them as bacteria which are closely related to rhizosphere. Kloepper, Lifshitz and Zablotowicz (1989) also used the term rhizobacteria. Functions and mechanisms of growth promotion by these microbes have been discussed, and microorganisms have been categorized in different classes (Hayat *et al.* 2010). Microbes actively involved in crop production are generally termed as

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plant growth promoting bacteria (PGPB), whereas the bacteria isolated from the root zone are termed as plant growth promoting rhizobacteria (Kloepper and Schroth 1978). Major functions of these beneficial microbes are supply of nutrients to crops, stimulation of plant growth namely producing phytohormones, biocontrol of phytopathogens, improving soil structure, bioaccumulation of inorganic compounds and bioremediation of metal contaminated soils (Brierley 1985; Davison 1988; Ehrilch 1990; Middeldorp, Briglia and Salkinoja-Salonen 1990; Wilson and Lindow 1993; Burd, Dixon and Glick 2000; Zaidi *et al*. 2006).

Interaction between beneficial soil microbes and plants determines the plant health and soil fertility (Jeffries *et al*. 2003). The concept of sustainable agriculture has given much importance to the use of rhizospheric bacteria to help plants easy nutrient uptake and solubilization of fixed nutrients such as phosphorus (Hayat *et al*. 2010). It is the need of the time to reduce the agricultural inputs through combining beneficial microorganisms for better and sustainable agriculture. Several symbiotic such as *Rhizobium* spp. and *Frankia* spp. and asymbiotic bacteria such as *Azotobacter*, *Azospirillum*, *Bacillus* and *Klebsiella* spp. are used throughout the world to increase the crop growth and yield (Staley and Drahos 1994). Bacteria inhabiting plant rhizosphere are called PGPR which can promote the growth and productivity of plants through various mechanisms (Kloepper, Lifshitz and Zablotowicz 1989; Cleyet-Marcel *et al*. 2001). These rhizosphere inhabiting bacteria have also been categorized as nodule promoting rhizobacteria which is an important interaction of microbes with plants and plant health promoting rhizobacteria (Burr and Caesar 1984). PGPRs can also be categorized based on their relationships i.e. symbiotic and free-living soil inhabiting bacteria (Khan 2005). Gray and Smith (2005) also classified intercellular PGPR (iPGPR) called symbiotic bacteria and extracellular PGPR which are free-living bacteria. Rhizobia are famous iPGPR as they produce nodules in leguminous plants (Sriprang *et al*. 2003).

Podile and Kishore (2006) conclude several plant growth promoting (PGP) mechanisms of PGPR such as modification and increased branches in root hair, improvement in germination of seeds, enhanced and faster nodule performance, increase in leaf area per plant, release of certain phytohormones, augmented nutrients and water uptake by plants, increased biomass of the plants with more vigor growth and better carbohydrate accumulation which increases the growth of plant species. On the other hand, Glick (2003) categorizes the bacterial assisted plant growth in three different ways, including plant hormone production (Dobbelaere, Vanderleyden and Okon 2003), bacterial assisted better nutrient uptake by plants (Çakmakçi *et al*. 2006) and avoiding the diseases in plants through biological control (Saravanakumar *et al*. 2008). Dey *et al*. (2004) suggest the need of exploring other mechanisms of plant growth promotion by PGPR apart from the list already studied. Listing all the explored and investigated mechanisms of PGPR, following can be included: (a) solubilization and mineralization of nutrients notably phosphorus (Richardson 2001; Banerjee and Yesmin 2002); (b) nitrogen fixation through symbiosis and asymbiosis (Kennedy, Choudhury and Kecskés 2004); (c) release of certain plant hormones such as gibberellic acid and cytokinins (Dey *et al*. 2004), indole acetic acid (Patten and Glick 2002) and abscisic acid (Dobbelaere, Vanderleyden and Okon 2003); (d) production of 1-aminocyclopropane-1-carboxylate (ACC)-deaminase helping to lower ethylene level in roots this increasing length and vigor of roots (Li *et al*. 2000; Penrose and Glick 2001); (e) antagonism toward plant pathogens by producing substances such as cyanides and antibiotics (Glick and Pasternak 2003); (f) increasing the availability of nutrients specifically of iron through chelating by producing siderophores (Glick and Pasternak 2003); (g) tolerance against deveral abiotic stresses such as oxidative (Stajner *et al*. 1995, 1997) and drought stress (Alvarez, Sueldo and Barassi 1996); (h) water soluble vitamin production including biotin, niacin, thiamine and riboflavin (Revillas *et al*. 2000); (i) detoxification of heavy metals (Ma *et al*. 2011); (j) tolerance of salinity (Tank and Saraf 2010); and (k) biological control of pests and insects (Russo *et al*. 2008).

Several studies have documented beneficial effects of certain rhizobial strains in improving growth of legumes as well as non-legumes. Second, inoculation of rhizobium in consortium with free-living rhizospheric bacteria has also given excellent results in improving crop growth and productivity (Kishore, Pande and Podile 2005; Tilak, Ranganayaki and Manoharachari 2006; Wani, Khan and Zaidi 2007). These PGPRs can be used effectively to meet the nutrient-deficient conditions and their use can be favorable to reduce the uses of chemical fertilizers and support of environment friendly crop productivity (Herrera, Salamanka and Barea 1993; Requena *et al*. 1997). The beneficial and plant growth enhancing effects of PGPR are well reported and explained. PGPR inoculation has increased different crop yields in normal and stress conditions. From the recent literature, PGPR inoculation increased the stress resistance and production of the crops, including tomato (Almaghrabi, Massoud and Abdelmoneim 2013), lettuce (Kohler *et al*. 2009), wheat (Jaderlund *et al*. 2008; Chakraborty *et al*. 2013; Nadeem *et al*. 2013; Islam *et al*. 2014; Kumar, Maurya and Raghuwanshi 2014), rice (Bal *et al*. 2013; Jha, Saxena and Sharma 2013; Lavakush *et al*. 2014), soybean (Masciarelli, Llanes and Luna 2014), groundnut (Paulucci *et al*. 2015), broad bean (Younesi and Moradi 2014), maize (Rojas-Tapias *et al*. 2012) and chickpea (Patel *et al*. 2012). The increase in yields and other yield parameters can be different in different crops and environments and normally range from 25% to 65%. Local reviews also indicate the growth promotion of crops by application of PGPR including wheat and barley (Ozturk, Caglar and Sahin 2003; Salantur *et al*. 2005; Turan, Çakmak and Şahin 2013), sugar beet (Sahin, Çakmakçi and Kantar 2004), strawberry (Esitken *et al*. 2010), apple (Aslantas, Cakmakci and Sahin 2007), grapes (Köse, Güleryüz and Demirtaş 2005) and raspberry (Orhan *et al*. 2006).

Bacterial inoculation to enhance the productivity of different crops is being practiced since the discovery of beneficial effects of these bacteria. The methods used for augmentation of the beneficial bacteria include seed coating, pelleting, foliar application and direct soil application where most commonly used is inoculation. Every method has been used with modifications according to the requirements. However, inoculation is most commonly used because it is easy to use and is practiced since the advent of this technique. Availability of sticking agent although is a limitation in this method but is still the most trusted method throughout the world. PGPR application through seed priming, soaking the seeds for premeasured time in liquid bacterial suspension, starts the physiological processes inside the seed while radicle and plumule emergence is prevented (Anitha *et al*. 2013) until the seed is sown. The start of physiological process inside the seed enhances the abundance of PGPR in the spermosphere (Taylor and Harman 1990). This proliferation of antagonist PGPR inside the seeds is 10-fold than attacking pathogens which enables the plant to survive those pathogens (Callan, Mathre and Miller 1990) increasing the use of biopriming for biocontrol too.

Method of application contributes mainly to the survival efficiency of the bacteria in the soil and on the seeds. Most common methods developed and explored include seed treatment, soil amendment and roots dipping in the bacterial suspensions

before transplanting particularly in rice. Other uncommon methods include foliar spray or application of bacteria through drip irrigation (Podile and Kishore 2006). PGPR are applied to the soil or seeds and/or to the plant parts when there is risk of inhibitors or antagonistic microbes on the plant tissues (Gindrat 1979). Diverse carrier materials have been tried and are being used depending on their quality to keep the bacteria viable for longer times as well as to reduce the desiccation chances along with the adhesive ability to the plant parts (Chao and Alexander 1984; Elegba and Rennie 1984). Proper inoculation procedures are followed as survival of bacterial cells depends mainly on the environmental conditions. Several carriers such as broth cultures, agar cultures and powder carriers have been used (Strijdom and Deschodt 1976; Thompson 1980), yet peat-based inoculants have shown good results and have been used widely but there are issues with peat-based inoculants such as exposure of peat based inoculants to high temperatures or water scarcity, presence of antagonist microorganisms and quality of peat strictly affects the bacterial viability (Chao and Alexander 1984). Exposure of the inoculated seed to sun causes the death of the bacterial cells as well as its exposure to environment can lead to contamination. Therefore, peat-involving inoculants are not yet considered as the best option as there can be pathogenic microbes causing plant diseases.

Use of proper carrier strongly influences the survival and colonization ability of the bacteria in the soil as well as in the roots. Peat soil is most preferred carrier material being used for inoculation of bacteria but its availability is a major limitation (Boonkerd and Singleton 2002). Similarly, rice husk is also being used in Asian countries. Trevors *et al.* (1992) found that mixing of bentonite clay in the carrier increased the survival of bacteria in fine textured soils. A similar study also suggested that mixing of 1% bentonite clay in fresh grown or freeze-dried *Rhizobium leguminosarum* suspension enhanced the bacterial survival markedly when compared to no amendment (Heijnen, Hok-A-Hin and Van Veen 1992). Heijnen, Hok-A-Hin and Van Elsas (1993) also reported that fresh cells showed less survival ability and colonization as compared to starved bacterial cells. Different soil amendments and chemical polymers have also been tried to entrap the bacteria in the carrier material, but a more promising report is use of barley straw which increased the survival of bacteria and also improved the root colonizing ability of the strains (Stephens 1994). Inoculation techniques are yet to be explored as there is scarce information available regarding the delivery and application of bacteria to the soil or the seeds. However, it is quite clear that population of the bacteria in soil is mainly dependent on initial stack of inoculums on the seed (Milus and Rothrock 1993). Hebbar *et al.* (1992) stated that application of more inoculums per seed can increase the efficiency but results are not always steady. Bacteria need to compete with other microbes to colonize so it can be concluded that introduced bacteria should be competitive enough to efficiently compete and colonize the roots.

Variety of methods have been used and studied by researchers for producing better inoculums which can survive better in the soil. The simplest strategy as explained by Paau (1989), local strains should be selected which are competent, adapted and dominant in a particular geographical area, and then mutant from the parent strain having more nitrogen fixing and competitive ability should be used in that particular area. This method or strategy is also used in preparation of microbial pesticides (Watrud *et al.* 1985) where mutation has been used. Effectiveness of the inoculum in the soil depends on the conditions after the release in the soil and if the conditions are optimum, inoculum will survive better. Several laboratory microcosm and field studies have been conducted on bacterial survival potential in soil (van Elsas and Heijnen 1990). Presence of microniches in the soil enables the bacteria to survive after their application to soil otherwise reduction in bacterial number has been observed (van Elsas *et al.* 1986; Heijnen *et al.* 1988; Postma, Scheffers and van Dijken 1988; van Elsas and Heijnen 1990). Other factors affecting the bacterial survival in the soil include certain abiotic factors including soil temperature and moisture, nutrient presence and pH of the soil (García *et al.* 2010). Several studies have documented the effects of biotic and abiotic factors on survival of bacteria in soil (Bashan *et al.* 1995; Bashan and Vazquez 2000; Oliveira *et al.* 2004). Environmental factors affect the survival of bacteria in the soil, as an example fluorescent pseudomonad strain survived 10-fold better in sandy loam soil as compared to clay loam (Bahme and Schroth 1987; Pathma, Kennedy and Sakthivel 2011). Amending the soil with bentonite mineral increased the bacterial survival in loamy sand soil (Heijnen *et al.* 1988) through protection against protozoa (van Elsas and Heijnen 1990). It can be concluded that both biotic and abiotic factors affect bacterial survival and root colonization by bacteria in the soil (Campbell and Ephgrave 1983; Postma, Hok-A-Hin and Van Veen 1990). Most of studies indicate bottlenecks in various techniques of bacterial application either to the soil or to the plant tissues. Among different methods being used for introducing beneficial bacteria include seed coating and covering, root dipping, foliar application, direct soil application and seed Inoculation which have various merits and demerits reviewed in Table 1.

Seed coating and covering is a general term where liquids or suspending solids are applied to the seed coat, prospectively to cover it homogenously. This method requires use of adhesives to ensure proper coating of the seed which hinder the further application of pesticides to the seeds (Bardin and Huang 2003). Bacterial survival and nitrogen fixation was reduced when pelleting of the molybdenum was carried out along with bacterial inoculation and 99% bacteria were dead after 4 days (Burton and Curley 1966). Campo, Araujo and Hungria (2009) has also reported the drawback of applying micronutrient to seeds and inoculants together. Seed coating also hinders the gaseous exchange to the leguminous seeds which causes reduction in nitrogen fixation (Duarte *et al.* 2004), along with problems such as reducing the number of bacteria on the seeds due to desiccation. This technique is usually used for application of biocontrol agents (Paulitz, Zhou and Rankin 1992).

Dipping the roots in bacterial suspension has been used for biocontrol, and very few evidences can be found. Srinivasan *et al.* (2009) applied this technique and found that it is possible option in controlling *Fusarium wilt* of tomato. Munif, Hallmann and Sikora (2013) studied the effect of endophytic bacteria against *Meloidogyne incognita* using root dipping technique and found less number of galls on treated plants. Another report is from Esitken *et al.* (2010), who used root dipping along with foliar application and have reported significant increases in yield parameters of strawberry. Root dipping however needs prepared plant nursery which is not very economical in most of the crops.

Foliar application is not widely practice by the researchers or the farmers for the augmentation of these significant bacteria to the plants. However, in some cases such as biocontrol of fungus, this application has been used (Obradovic *et al.* 2004). Another research group has applied the PGPR through both root dipping and foliar application and have concluded that it increased the yield and yield parameters of fruits such as strawberry (Esitken *et al.* 2010), apricot (Esitken *et al.* 2002), sweet cherry (Esitken *et al.*

Table 1. Advantages and disadvantages of different application methods.

Method	Advantages	Disadvantages	Reference
Career-based inoculation	Easy availability Easy to prepare Lower cost	Contamination of the inoculants by unwanted microbes from career such as peat No uniformity on the career Short-term storage ability	Brockwell (1977); Brockwell, Gault and Chase (1977); Bezdicek *et al.* (1978); Gault, Chase and Brockwell (1982); Bashan, Levanony and Ziv-Vecht (1987); Brockwell, Holliday and Pilka (1988); Rice and Olsen (1988); Kosanke *et al.* (1992); Smith (1992); Bashan (1998)
Seed coating and covering	Easier to apply No specific machinery needed Practiced by farmers in case of pesticide application to seeds	Application of pesticides to the seeds Sticking agents harmful to bacteria Flexibility in seeding is less	Brockwell (1977); Brockwell, Holliday and Pilka (1988); Bashan and Levanony (1990); Bashan and Carrillo (1996); Bashan and Holguin (1997); Bashan (1998)
Pelleting	Easy to apply Favored by farmers Flexibility in seeding and application Lime pellets can be used for acid soils	Survival of bacteria is hindered due to lower moisture levels Special machinery needed to prepare thus increases cost	Brockwell (1977); Bezdicek *et al.* (1978); Bordeleau and Prevost (1981); Bashan and Levanony (1990); Bashan (1998)
Direct soil application	Injection in the root zone is possible Easy and simple	Exposure to the sun Desiccation problems Needs more volume	Brockwell (1977); Bordeleau and Prevost (1981); Bashan and Levanony (1990); Bashan (1998)
Root dipping	Nursery required Simple and easy	Large amount of liquid media and bacterial cells needed Contamination from environment quite normal	Brockwell (1977); Bordeleau and Prevost (1981); Bashan and Levanony (1990); Bashan (1998)

2006) and apple (Pirlak *et al.* 2007). Sudhakar *et al.* (2000) also investigated the effect of foliar application of *Azotobacter*, *Azospirillum* and *Beijerinckia* on mulberry and have reported positive effects.

Application of the inoculum directly to the soil is favored when there is threat of presence of antagonistic microbes or pesticides on the plant tissues (Gindrat 1979). Presence of inhibitory compounds on the plant tissues also inhibits plant part inoculation. Soil application needs large amount of inoculants which contradicts with the economics of the farming. Solid inoculants are easy but if there are liquid inoculants, it needs special care from the transportation and after the application to the field.

Application of beneficial bacteria to the seeds is generally called as inoculation. It is the most common method been used since the beneficial bacteria have been studied and discovered. Seed inoculation involves use of carrier material for better transportation and application, use of adhesives to ensure the sticking of bacteria to the seeds and sometimes other materials avoiding desiccation of the inoculum (Elegba and Rennie 1984). Peat-based inoculants are most common and extensively used since the discovery of rhizobium for leguminous crops. Peat being easily available and a cheap source is sterilized and milled so used as carrier for most of the inoculation material (Walker, Rossall and Asher 2004). Most favored and commonly used method of inoculation includes application of adhesive agents on the seeds followed by inoculum spreading under shade (Vincent, Thompson and Donovan 1962). Among the adhesive agents, most commonly used are Arabic gum, sugar solution, methylcellulose, polyvinylpyrollidone, caseinate salts and polyvinylacetate (Deaker, Roughly and Kennedy 2004). Inoculation usually produces favorable results with rhizobia; however, their development limit has been reached (Burton 1976; Thompson 1980). As discussed above, extreme environmental factors such as high temperatures decrease the viable cell count in the inoculum (Chao and Alexander 1984). Apart from this, it has several drawbacks depending on the nature and type of peat and issues of peat availability in different countries (Bashan *et al.* 2002). Polymer-based inoculants can be used over peat-based inoculants but they are expensive and need more biotechnical handling (Fages 1992). As far as polymer-based inoculants are concerned, they are also being opposed as they are hazardous to environment (Cassidy, Lee and Trevors 1996). Merits and demerits of different application methods are described in Table 1.

MECHANISMS INVOLVED IN SEED COLONIZATION

Efficient colonization supports better functioning of plant beneficial bacteria (Compant, Clément and Sessitsch 2010). Diverse endophytic bacteria which spend part of their life inside the plant tissue without causing any disease (Döbereiner 1992); colonize different parts of plants without causing any damage (Bacon and Hinton 2006; Ali *et al.* 2014) and similar to phytopathogens, they enter the plants through various mechanisms. Entry through wounded plant parts (Agarwhal and Shende 1987), stomatal openings (Roos and Hattingh 1983), lenticels (Scot *et al.* 1996), germinating radicles (Gagné *et al.* 1987) and root cracks (Sørensen and Sessitsch 2006) includes different colonization processes where root cracks entry helps root inoculation by bacteria (Ali *et al.* 2014).

Bacteria after soil application tend to colonize rhizosphere (Gamalero *et al.* 2003) followed by adherence to root surfaces and finally to the rhizodermis making a string of bacteria (Hansen

et al. 1997). Bacteria form biofilms or microcolonies on the rhizodermal cells where the colonization occurs (Benizri, Baudoin and Guckert 2001). Rhizosphere colonization is linked to photosynthates translocation to roots and exudation (Lugtenberg and Dekkers 1999; Bais *et al.* 2006) along with root mucilage (Knee *et al.* 2001). These exudates include diverse kind of organic acids, amino acids and carbohydrates which serve as food for most of bacteria inhabiting rhizosphere (Walker *et al.* 2003). This chemotaxis helps bacteria in multiplication along with colonization (Lugtenberg and Kamilova 2009) but when limited results in reduced root colonization (de Weert *et al.* 2002). Concentration and composition of root exudates also influences colonization where colonization occurs on different levels proportional to concentration of exudates (Gamalero *et al.* 2004). Soil characteristics and nutrient availability have also been reported as factors influencing colonization (Kraffczyk, Trolldenier and Beringer 1984; Paterson and Sim 2000). Plant pathogenic infection also affects the root colonization processes, e.g. plant released malic acid to attract bacteria against the infection of pathogen where the bacteria protected the roots of the plants by creating biofilm (Rudrappa *et al.* 2008).

Plant beneficial bacteria also have to compete with the local bacteria and other soil organisms in the root zone for colonization (Walker *et al.* 2003) and under severe competitive conditions, PGPB also secrete siderophores and lytic enzymes to limit growth of plant pathogens (Compant, Clément and Sessitsch 2010), metabolites (Haas and Défago 2005), and they also release certain antibiotic compounds for better colonization (van Loon and Bakker 2005). Production of several other compounds such as amino acids, vitamins, enzymes and polysaccharides has also been reported enhancing root colonization (Vesper 1987; de Weger *et al.* 1989; Simons *et al.* 1997; Dekkers *et al.* 1998; Camacho *et al.* 2002). Physically, flagella of the bacteria help them making contact with exudates (Turnbull *et al.* 2001) but are not always important for root colonization (Scher *et al.* 1988). Quorum sensing based on cell density is also involved in colonization of rhizosphere and rhizoplane (Soto, Sanjuán and Olivares 2006), which might be linked to enhancing competitive ability of PGPB (Compant, Clément and Sessitsch 2010).

Legumes show symbiosis with members of Rhizobiaceae family and this symbiosis needs exchange of resources (Giordano and Hirsch 2004; Ahemad and Kibret 2014). Endophytic colonization needs penetration of bacteria inside the plant tissues which then show the PGP traits (Hallmann and Berg 2006). Nodulating bacteria have evolved certain processes of entry like introduction through cortex and lateral root fissures and intercellular cracks forming specialized organs called nodules by penetrating in the roots through utilizing flavonoids and nod genes from such microbes (Garg and Geetanjali 2007; Compant, Clément and Sessitsch 2010). This type of colonization involves physical (Böhm, Hurek and Reinhold-Hurek 2007) and further chemical mechanisms including cell-wall-degrading enzyme production (Lodewyckx *et al.* 2002). Most of the *Rhizobium* species have been found to produce indole acetic acid (Ahemad and Khan 2012), which is essential for process of nodule formation through cell division and differentiation along with vascular tissue formation (Ahemad and Kibret 2014). Thus, higher auxin levels in legume plants are responsible for nodule formation (Spaepen, Vanderleyden and Remans 2007; Glick 2012) and symbiotic relationships. The PGPR showing non-symbiotic interaction with plants often contribute very small amount of nitrogen (Glick 2012). Diazotrophs being free-living nitrogen-fixing soil bacteria show non-obligate relationship with the non-legumionous plants (Glick *et al.* 1999).

HOST SPECIFICITY IN PGPR APPLICATIONS

Host specificity depends on particular bacterial strains to non-specific traits of host plant or non-specific bacterial strains to particular traits of the host plants, but evolution has played its role in preferential interaction between host and bacterial strains (Drogue *et al.* 2013). Bacterial association with particular hosts involves interaction and recognition process (Benizri, Baudoin and Guckert 2001). The recognition process involves root exudates concentration and composition where composition of root exudates depends on the cultivars, stress condition and plant growth stage (Haichar *et al.* 2008). In other studies, claiming no particular host specificity found in *Azospirillum* indicated that chemotaxis was however strain specific, and the bacteria showed preference toward exudates of their isolated host (Bacilio-Jimenéz *et al.* 2003; Pedraza *et al.* 2010). Chemical signals from the plants as root exudates serve as attractants to microbes (Doty 2011). Host specificity can be influenced by chemotaxis and metabolic activities can be its determinant and provision of nutrients by the host plant also plays important role in specifying bacteria to the plants (Reinhold, Hurek and Fendrik 1985; Buyer, Roberts and Russek-Cohen 2002; Reis, dos Santos Teixeira and Pedraza 2011). Plant genetic makeup is important in determining microbiome associations with roots and rhizosphere (Bulgarelli *et al.* 2015). In detailed study regarding genome wide study in *Arabidopsis-Pseudomonas*, it was observed and concluded that plants genetics is the core element of benefiting from PGPR and identification of genes responsible for host specificity is needed (Wintermans, Bakker and Pieterse 2016). Several genes responsible for chemotaxis, flagella formation, transportation and metabolic pathways are involved in root colonization which complete recognition and chemotaxis (Compant, Clément and Sessitsch 2010). Studies regarding host specificity and microbial presence in the plant roots have been made easy through use of next-generation sequencing techniques in recent years (Bai *et al.* 2015), but yet extensive research in this area is lacking. Nitrogen-fixing bacteria can be applied to unrelated plants (Doty 2011), and application of such bacteria in non-leguminous plants enhanced growth and productivity (Bhattacharjee, Singh and Mukhopadhyay 2008). Different PGPR can promote the growth and productivity of diverse crops depending on genetics of the host and exudates released, and also ability of beneficial bacteria to compete and colonize rhizosphere and roots (Vessey 2003).

Keeping in mind the prospects of biopriming, this review focuses on (i) the comparison of past bacterial application methods with their drawbacks, (ii) suggesting the technique biopriming as a promising method for bacterial application in increasing stress resistance and crop productivity.

BIOPRIMING

Since the advent of seed priming, a lot of work has been done on this aspect of seed treatment and is now common in most of the areas for delayed sowing and to obtain vigorous plant growth. As defined by McDonald (1999), seed priming is soaking the seeds in any solution containing our required priming agent followed by redrying the seeds which result into start of germination process except the radicle emergence. Among different priming techniques, hydration using any biological compound is termed as biopriming (Ashraf and Foolad 2005). Seed priming creates ideal conditions for the bacterial inoculation and colonization in the seed (McQuilken, Rhodes and Halmer 1998). Soaking the seeds in the bacterial suspension for precalculated period of time to

Table 2. Role of biopriming in different PGP activities.

Strains under study	Crop	PGP activities	Reference
Azotobacter chroococcum, A. lipoferum	Barley	Increase in 1000-grain weight, dry matter accumulation, grain yield, biological yield and harvest index	Mirshekari *et al.* (2012)
Pseudomonas spp.	Safflower	Increased number of branches, heads per plant, diameter of head, grain number per head, grains per plant, 1000 grain weight, oil content and grain yield	Sharifi (2012)
Azotobacter chroococcum Azospirillum lipoferum, A. chroococcum A. lipoferum	Maize	Grain yield, crop growth rate and dry matter accumulation	Sharifi (2011)
Azotobacter and *Azospirillum* spp.	Maize	Increase in grain yield, plant height, number of kernels per ear and number of grains per ear row	Sharifi and Khavazi (2011)
Pseudomonas fluorescens	Sunflower	Shoot height, root length and seedling weight	Moeinzadeh *et al.* (2010)
Clonostachys rosea, P. chlororaphis, *P. fluorescens*, *T. harzianum, T. viride*	Carrot and onion	Increase in emergence and yield	Bennett, Mead and Whipps (2009)

allow the bacterial imbibition into the seed is known as biopriming (Abuamsha, Salman and Ehlers 2011). Reddy (2013) explained biopriming more in biocontrol aspect as application of beneficial bacterial inoculum to the seeds and their hydration to protect seeds against disease control. This soaking of seeds in bacterial suspension initiates the physiological processes in the seed where plumule and radicle emergence is prevented (Anitha *et al.* 2013), until the seeds have temperature and oxygen after being sown. PGPR keep on multiplying in the seed and proliferate in the spermosphere (Taylor and Harman 1990) even before sowing. Seed biopriming is being focused as it ensures the entrance of endophytic bacteria into the sides along with avoiding the effect of high temperature. Biopriming treatment is potentially able to promote quick and even germination as well as better plant growth (Moeinzadeh *et al.* 2010). Biopriming with rhizospheric bacteria has been reported in crops such as carrot (Jensen *et al.* 2002), sweet corn (Callan, Mathre and Miller 1990, 1991) and tomato (Harman and Taylor 1988; Legro and Satter 1995; Warren and Bennett 1999). In case of efficacy and survival of biological agents, priming has been reported beneficial and been reported to enhance the plant growth and yield (Harman, Taylor and Stasz 1989; Callan, Mathre and Miller 1990, 1991; Warren and Bennett 1999). Germination and enhanced seedling establishment is obtained through seed priming with PGPR (Anitha *et al.* 2013). Bio-osmopriming can significantly enhance the uniformity of the germination and plant growth traits when associated with bacterial coating (Bennett 1998). Uniformity in germination and better stand establishment options when considered, biopriming is favored method. Biopriming has been practiced and explained by different researchers (Callan, Mathre and Miller 1991; Bennett, Mead and Whipps 2009; Moeinzadeh *et al.* 2010; Chakraborty *et al.* 2011; Sharifi 2011, 2012; Sharifi and Khavazi 2011; Gururani *et al.* 2012; Mirshekari *et al.* 2012) in several ways, but still is an ambiguous approach which needs to be explored and discussed.

There are different methods used explaining biopriming varying in the temperature and time duration of soaking the seeds (Miché and Balandreau 2001; Gholami, Shahsavani and Nezarat 2009; Abuamsha, Salman and Ehlers 2011; Sharifi and Khavazi 2011; Sharifi, Khavazi and Gholipouri 2011; Carrozzi *et al.* 2012; Firuzsalari, Mirshekari and Khochebagh 2012; Saber *et al.* 2012; Kasim *et al.* 2013; Reddy 2013). Some of the researchers have also surface disinfected the seeds before soaking into the bacterial suspension (Sharifi, Khavazi and Gholipouri 2011; Firuzsalari, Mirshekari and Khochebagh 2012; Saber *et al.* 2012; Reddy 2013).

BIOPRIMING AND CROP PRODUCTIVITY

Biopriming contributes to various PGP activities which has been studied by researchers as reviewed in Table 2. Saber *et al.* (2012) used the technique biopriming with a commercial biofertilizer having different bacterial species including *Bacillus lentus, B. subtilis, Pseudomonas fluorescens, P. putida* and *Azospirillum* spp. They observed increase in several agromorphological traits of wheat plants. In addition, they also postulate that requirement of nitrogen and phosphorus was decreased in bioprimed plants as compared to control plants. Stem and total seedling fresh weight was increased with the priming of PGPR in maize seedlings in a laboratory experiment (Gholami, Shahsavani and Nezarat 2009). Barley seed priming with a consortium of *Azotobacter chroococcum* and *Azospirillum lipoferum* in combination with 80 kg ha^{-1} urea and 60 kg ha^{-1} P_2O_5 significantly increased the yield attributes such as thousand grain weight, dry matter accumulation, biological yield, grain yield and harvest index (Mirshekari *et al.* 2012). In maize, different *Azotobacter* and *Azospirillum* strains were used for biopriming of the seeds, and the results showed that biopriming significantly increased the crop growth rate, dry matter accumulation and grain yield (Sharifi 2011). Different bacterial strains were also investigated for biopriming in safflower, and it was observed that seed priming with *Pseudomonas* strain 186 with coapplication of 180 kg ha^{-1} increased the number of branches, heads per plant, diameter of head, grain number per head, grains per plant, 1000 grain weight and grain yield of the plants (Sharifi 2012).

ROLE OF BIOPRIMING IN RESISTANCE AGAINST ABIOTIC STRESSES

Kasim *et al.* (2013) used the technique biopriming to document its effects against drought stress. They used two strains including *A. brasilense* and *B. amyloliquefaciens* and observed that

Table 3. Role of biopriming in abiotic stress tolerance.

Strains under study	Mechanism of action	Crop	Role in stress tolerance	PGP activities	Reference
Bacillus pumilus, B. furmus	ACC-deaminase activity, IAA production, phosphate solubilization, phytate mineralization, siderophore production	Potato	Salinity, drought, heavy metal stress tolerance	Increase in plant height, No. of leaves plant^{-1}, No. of tubers plant^{-1}, tuber yield plant^{-1}	Gururani *et al.* (2012)
Bacillus cereus	Phosphate solubilization, IAA, catalase, protease, chitinase and siderophore production, nitrate reduction, starch hydrolysis	Rice, mungbean, chickpea	Salinity tolerance	Increase in seedling height, number and length of leaves, root and shoot biomass	Chakraborty *et al.* (2011)
Agrobacterium rubi, Burkholderia gladii, P. putida, B. subtilis, B. megaterium	–	Radish	Improved seed germination under saline conditions	Increase in seed germination	Kaymak *et al.* (2009)

Table 4. Role of biopriming in biotic stress tolerance.

Strains under study	Crop	Role in stress tolerance	Reference
Trichoderma harzianum	Maize	*Fusarium verticillioides* and fumonisins tolerance	Nayaka *et al.* (2010)
Pseudomonas fluorescens	Sunflower	*Alternaria blight* tolerance	Rao *et al.* (2009)
Clonostachys rosea	Carrot	*Alternaria dauci* and *Al. radicina* tolerance	Jensen *et al.* (2004)
Pseudomonas fluorescens	Pearl millet	Downy mildew tolerance	Raj, Shetty and Shetty (2004)
Pseudomonas aureofaciens	Sweet corn	*Pythium ultimum* tolerance	
Pseudomonas fluorescens	Sweet corn	Damping-off tolerance	Callan, Mathre and Miller (1991)

biopriming with these strains increased drought tolerance in wheat plants through upregulation of genes related to stress. Role of biopriming has been studied in various crops using different PGPR as compiled in Table 3. Role of biopriming in salinity stress tolerance is widely studied and promising results have been recorded. Most notable genus used in abiotic stress tolerance is *Bacillus* which is used in potato (Gururani *et al.* 2012), radish (Kaymak *et al.* 2009) rice, mungbean and chickpea (Chakraborty *et al.* 2011).

ROLE OF BIOPRIMING IN RESISTANCE AGAINST BIOTIC STRESSES

Biopriming has been applied in various crops for the biocontrol of several diseases (Table 4). Abuamsha, Salman and Ehlers (2011) applied *Serratia plymuthica* and *P. chlororaphis* to the different oilseed rape cultivars for the control of a pathogen *Leptosphaeria maculans* causing blackleg disease, and it was observed that disease extent was reduced up to 71.6% by *S. plymuthica* and 54% by *P. chlororaphis*. Seed biopriming gave the highest control over *Verticillium longisporum* as compared to coating the bacteria on the seeds (Müller and Berg 2008). Biopriming has been reported to control damping-off disease in various crops such as cucumber (Pill *et al.* 2009), maize (Callan, Mathre and Miller 1990), pea (Taylor, Harman and Nielsen 1994) and soybeans. Rao *et al.* (2009) applied a biocontrol agent *P. fluorescens* through seed biopriming and observed that incidence of *Alternaria blight* was reduced and biopriming helped the plants to tolerate the disease incidence efficiently. In maize, biocontrol agent *Trichoderma harzianum* was applied which resulted in better control of *F. verticillioides* and *fumonisins* (Nayaka *et al.* 2010). Similarly, different biocontrol agents were applied to the seeds through biopriming, and better biocontrol was observed in radish (Kaymak *et al.* 2009), carrot (Jensen *et al.* 2004), sweet corn (Bennett 1997) and pearl millet (Niranjan, Shetty and Shetty 2004).

Microbes capable of colonizing the rhizosphere and plant roots can protect the plants to pathogens through antagonistic interaction (Buchenauer 1998, Berg *et al.* 2001, Whipps 2001). They can also induce systemic resistance to the plants which can reduce the fungal infection (Compant *et al.* 2005). During the seed germination, successful antagonizing microbe colonization helps in reducing the pathogenic attack on the plant (Weller 1983). They can also induce systemic resistance to the plants which can reduce the fungal infection (Compant *et al.* 2005). Jensen *et al.* (2004) reported that death of carrot plants due to seedborne pathogens such as *Al. radicina* and *Al. dauci* was significantly reduced with biopriming of the seeds with *Clonostachys rosea* and was as effective as use of fungicide iprodione. Root rot caused by different pathogens such as *Macrophomina phaseolina*, *F. solani* and *Rhizoctonia solani* was reduced in cowpea through biopriming of the seeds with *T. harzianum* by 56.3%–64% at the pre-emergence and 57.1%–64% at the post-emergence stage (El-Mohamedy, Abd-Alla and Badiaa 2006). In faba bean, biopriming with different bacterial strains was tested to reduce the incidence of root rot, and it was observed that use of the biopriming technique can be used as economical, safe and easy to apply biocontrol method (El-Mougy and Abdel-Kader 2008). *Trichoderma harzianum* is the main focus of the researchers in terms of biopriming and has been used widely in different crops. Another evidence of *T. harzianum* with coapplication of *P. fluorescens and B. subtilis* as biopriming significantly reduced the incidence of root rot pathogenic disease caused by *F. solani* and *R. solani* in pea under greenhouse and field conditions (El-Mohamedy and Abd-El-Baky 2008).

ECONOMICS OF BIOPRIMING

Several workers have encouraged this technique being a cost-effective approach for the biocontrol of different pathogenic microbes (Rao *et al.* 2009) and application of beneficial bacteria to the soil. Along with the crop productivity, biopriming can also be favored as the potential technique for biocontrol of several plant pathogens. Control of these plant pathogens is usually carried out by using costly pesticides where we can promote this technique as dual purpose technology enhancing the plant productivity and stress resistance side by side.

CONCLUSION AND FUTURE PROSPECTS

Regarding the application of the bacteria, it has been explained by the scientists that biopriming can be used effectively in application of the bacteria as it gives enough number of bacteria in the seeds. Competition of the our desired inoculants with local bacteria is also a problem which can be addressed by biopriming as our desired bacteria will already be inside the seeds reducing the chance of desiccation as well as harmful effects of any pesticides applied to the field. On the other basis, it can also be an alternative approach for the application of bacteria to small seeded crops which can imbibe the bacterial suspension resulting in entrance of bacteria inside the seed. Biopriming gives equal or better control against several root rot diseases so can be used commercially as an alternative to fungicides successfully. In the application, there is need to search for the more better media for application due to cost hurdles which can definitely be reduced by further research. Second, this method can be implied to other crops yet not experimented which will give better picture of potential of this technology.

Conflict of interest. None declared.

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