



Review

Plant growth-promoting rhizobacteria act as biostimulants in horticulture



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ABSTRACT

To overcome the challenge of increasing food production with a significant reduction of agrochemical use and environmental pollution, and an increase of natural resource productivity, the use of soil microorganisms in horticulture is essential. One group of microorganisms consists of plant growth-promoting rhizobacteria (PGPR), which have been studied from the beginning of the twentieth century and their mode of action at the physiological level is currently well understood. PGPR mechanisms include hormone release or hormonal changes within plants, the production of volatile organic compounds, the improvement in the availability of nutrients and the enhancement of tolerance to abiotic stresses. All these mechanisms are described in the present review. However, to maximize the effects of these mechanisms, the proper PGPR strain needs to be selected in each soil–plant–PGPR system and the mode of inoculation must be optimized in both greenhouse and open-field experiments. This review summarizes recent progress in our understanding of the PGPR–plant interaction and highlights future lines of research that should increase our knowledge on plant–bacterial communication and that can help to improve the effective use of PGPR in horticulture.

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1. Introduction

In recent decades, the importance of reducing chemical inputs into horticultural systems has been growing, and governments and growers are aiming to decrease them. The chemical contamination of underground water and rivers and the salinisation of soils caused by horticultural practices have risen in recent years (Phogat

et al., 2014). Therefore, solutions are required to maintain crop productivity and to simultaneously reduce chemical inputs in terms of chemical fertilizers and pesticides. Another resource that limits plant productivity is water. According to global-change predictions, several areas of the globe could become arid or semi-arid regions due to a reduction in precipitation (Sivakumar, 2011). Therefore, any strategy that reduces the amount of water added to crops without a loss in yield, is desirable.

To fulfill the above desired practices, one possibility is the use of soil microorganisms that increase the nutrient- and water-use efficiency and uptake capacity (Armada et al., 2014). Among

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these potential soil microorganisms, plant growth-promoting rhizobacteria (PGPR) are the most promising. The first report of the use of soil bacteria to promote plant growth apart from in a *Rhizobium*–legume symbiosis came from Bottomley (1909). This study showed that a consortium of *Pseudomonas radicola* and *Azotobacter* sp. increased the growth of oat (*Avena sativa*), the yield of barley (*Hordeum vulgare* L.), and the bulb weight of summer hyacinth [*Galtonia candicans* (Baker) Decne], effects that were ascribed to an increase in nitrogen (N) availability. However, the term PGPR was not adopted until almost 70 years later than this initial study, at the Annual Meeting of the American Phytopathological Society (Kloepper and Schroth, 1979), where the mechanism of PGPR function was suggested to be via modification of the soil microflora. One year later, Kloepper et al., proposed that PGPRs produced siderophores, which remove iron from the soil and reduce the growth of deleterious soil microorganisms (Kloepper et al., 1980). Nevertheless, from the end of the 1990s, the term plant growth-promoting bacteria was also used (Glick and Bashan, 1997), although plant growth-promoting bacteria also include non-soil microorganisms that inhabit the aerial parts of the plant (Martínez-Rodríguez et al., 2014). This review focuses only on rhizobacteria,

The term PGPR includes three types of soil bacteria, depending on their lifestyle: free-living bacteria inhabiting the zone around the root (rhizosphere), those that colonize the root surface (rhizoplane), and endophytic bacteria that live within roots. However, this division is not exclusive, since any individual bacterial strain might adopt all three lifestyles, depending on the soil environment conditions and the host-root partner involved (Alavi et al., 2013; Mitter et al., 2013).

The group of PGPR therefore includes all bacteria inhabiting the rhizosphere and the rhizoplane that promote plant growth. Clearly, this promotion capacity can be more easily determined under controlled conditions using sterile substrates, but under uncontrolled conditions, the inoculated PGPR will compete with the soil microflora, and sometimes the positive effects are lost (Sturz and Christie, 1995). Despite this, several examples exist, where inoculation by PGPR induced plant growth, including that of vegetables (Table 1), fruit crops (Table 2), and flower and ornamental plants (Table 3).

Rhizobacteria with PGP-activity occur in a number of bacterial phyla (Actinobacteria, Proteobacteria and Firmicutes), including strains belonging to genera *Bacillus*, *Pseudomonas*, *Azospirillum*, *Azotobacter*, *Alcaligenes*, *Arthobacter*, *Agrobacterium*, *Burkholderia*, *Comamonas*, *Pantoea*, *Rhizobium*, *Serratia*, and *Variovorax* (Tables 1–3; Kloepper et al., 1989).

The modes of action of PGPR are clearly diverse and not all bacteria possess the same mechanisms (Dey et al., 2004). These mechanisms vary from changes in hormonal content, the production of volatile compounds, increasing nutrient availability or enhancing abiotic stress tolerance (Choudhary et al., 2011). Since the term biostimulants refers to any substance or microorganisms used to enhance plant growth, but that does not act against pathogens (Calvo et al., 2014), the use of PGPR to control plant diseases will not be covered in this review. The review will firstly outline the different modes of action of PGPR, and then describe the difficulties in isolating PGPR from the soil and finally, will describe the use of PGPR in horticultural crops.

2. Mode of action

2.1. Plant hormonal changes

It is well known that plant growth is regulated in part, by hormonal changes, therefore, one of the possible mechanisms used by PGPR to promote plant growth might be changes in

the hormonal content of the host plant. In 1994, Glick et al., found that a *Pseudomonas putida* mutant strain lacking the enzyme 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase was unable to promote the root growth of canola seedlings (Glick et al., 1994). This provided the first evidence for a role of a reduction in ethylene content by PGPR in increasing plant growth. ACC is the immediate precursor of ethylene, therefore, decreasing the levels of ACC will decrease the levels of ethylene and inhibit the growth reduction effect of this plant hormone (Van de Poel and Van der Straeten, 2014). Some PGPR hydrolyse ACC to ammonia and α -ketobutyrate by the enzyme ACC deaminase, and use the latter as a carbon source (Van de Poel and Van der Straeten, 2014). In fact, several PGPR can lower ethylene levels in the plant host and thereby enhance plant growth (Bal et al., 2013; Chen et al., 2013). Additionally, soil bacteria that can synthesise ethylene have a negative effect on plant growth (Shaharoon et al., 2007). However, Chen et al. (2013) also found that the complete ethylene signal transduction pathway was necessary to enhance *Arabidopsis thaliana* growth by the PGPR *Variovorax paradoxus* strain 5C-2. Therefore, although several PGPRs might enhance plant growth by reducing the ethylene content, the ethylene signaling pathway is also crucial for the action of these other PGPRs (Chen et al., 2013).

Other plant hormones implicated in growth promotion by PGPR are auxins; a positive correlation was found between the in vitro production of auxins by several PGPR strains and their growth-promotion effects (Asghar et al., 2002; Khalid et al., 2004). Auxins are well-characterised plant hormones that promote plant growth, their effects being known since 1939 (Thimann and Schneider, 1939; for review see Enders and Strader, 2015). Therefore, the release of auxins by bacteria can induce plant growth. In fact, auxin efflux carrier genes have been used to detect the activity of some PGPR in the soil (Lim et al., 2011). It has also been shown that several PGPR induce the expression of auxin-responsive genes in host-plant roots (O'Callagan et al., 2001; Lakshmanan et al., 2013). Contesto et al. (2010) showed that the PGPR *Phyllobacterium brassicacearum* caused increased levels of auxins in the host plant, although it was unable to produce auxins, and that the action of this particular PGPR was mediated by the auxin signaling pathway. Therefore, to induce an auxin response in the plant, auxin synthesis by the PGPR is not necessary.

Other plant hormones are also involved in the effects of PGPR in plants, but are less-well studied, including abscisic acid (ABA), cytokinins (CKs) and gibberellins (GAs). The beneficial effects of increasing CK levels in the host plant to the PGPR appears to be via an increase in the excretion rate of root exudates, which contain among other substances, amino acids (Kudoyarova et al., 2014). Abscisic acid is known to reduce plant growth, although a certain amount of ABA is required for normal growth, since it regulates stomatal aperture and therefore water loss and CO₂ uptake (Pospisilova, 2003). Some PGPR can reduce the levels of ABA in the host plant and then indirectly increase plant growth (Belimov et al., 2014). Moreover, a reduction in growth was observed when tomato plants deficient in ABA were inoculated with a *Bacillus megaterium* strain, mainly due to an overproduction of ethylene (Porcel et al., 2014). Thus, the positive effects of PGPR depend on the endogenous levels of ABA of the host plant. Under water-stress conditions, some PGPR can increase the ABA content of host plants and thereby reduce water loss (Salomon et al., 2014). Most recently, Fan et al. (2015) found that *Burkholderia* sp. LD-11 can increase the sensitivity of maize (*Zea mays* L.) plants to ABA. The role of ABA in PGPR action is still not well understood and more researches are required.

Plant hormones cannot be studied in isolation, since they functionally interact with each other in plants and result in a specific response. For example, Liu et al. (2013a) found that a cytokinin-producing *Bacillus subtilis* strain decreased the ABA content of the host plant under optimal watering conditions, to increase stoma-

Table 1
Effects of plant growth-promoting rhizobacteria (PGPR) application on vegetable crops.

Crop	PGPR (species/strain)	Application mode	Experimental conditions	Effects	References
Broccoli	<i>Brevibacillus reuszeri</i> ^a <i>Rhizobium rubi</i> ^b	Root-dipping of seedlings for 60 min (10 ⁸ CFU mL ⁻¹)	Field	Increased yield, plant weight, head diameter, chlorophyll content, macronutrient and micronutrient uptake	Yildirim et al. (2011)
	<i>Pseudomonas fluorescens</i> strain MTCC103 ^d	Root-dipping of seedlings for 5 min	Pots, greenhouse conditions	Enhanced plant growth, nutrient uptake and broccoli's yield when combined with the recommended dose of superphosphate fertilizer	Tanwar et al. (2014)
Cabbage	<i>Pantoea agglomerans</i> strain RK-92 ^d	Seed-dipping (10 ⁸ CFU mL ⁻¹) before planting	Pots, greenhouse conditions	Enhancement of growth, nutrient, and hormone content	Turan et al. (2014)
Carrot	<i>Rhizobium leguminosarum</i> strain PEPV16 ^b	Seed-dipping (1.5 10 ⁹ CFU per seed) before planting	Pots, greenhouse conditions	Increased dry matter of shoots and roots, increased root length and root hair number	Flores-Félix et al. (2013)
Cucumber	<i>P. agglomerans</i> strain FF ^d	Foliar spray (10 ⁸ CFU mL ⁻¹), at ten days interval, for three times during seedling development	Greenhouse conditions (unheated)	Increased plant length, dry matter and mineral content of fruits, as well as number, weight and width of fruits	Dursun et al. (2010)
	<i>Serratia plymuthica</i> strain RR-2-5-10 ^d , <i>Stenotrophomonas rhizophila</i> strain e-p10 ^d , <i>Pseudomonas extremorientalis</i> strain TSAU20 ^d , <i>P. fluorescens</i> strain PCL1751 ^d and SPB2145 ^d	Seed-dipping for 15 min (10 ⁸ CFU mL ⁻¹)	Pots, greenhouse under semi-controlled environmental conditions	Increased plant height (up to 15%), dry weight (up to 62%) and fruit yield (up to 32%) in a soil amended with 3% NaCl.	Egamberdieva et al. (2011)
	Microbial consortium (<i>Bacillus cereus</i> strain AR156 ^a , <i>Bacillus subtilis</i> strain SM21 ^a , and <i>Serratia</i> sp. strain XY21 ^d)	Soil drench (10 ¹¹ CFU per plant)	Pots, greenhouse conditions	Induced systemic tolerance to drought stress, by maintaining photosynthetic efficiency and root vigor and increasing some of anti-oxidase activities (<i>i.e.</i> superoxide dismutase activity)	Wang et al. (2012)
	<i>Azospirillum brasilense</i> strain Sp7 ^b and Sp245 ^b , <i>Herbaspirillum seropedicae</i> ^c	Seed-dipping for 60 min (10 ¹¹ CFU per seed)	Petri dishes, temperature-controlled growing cabinet	Increased germination, increased length and weight of roots, improved vigor index of germinating seeds	Mangmang et al. (2015a)
Lettuce	<i>Rhizobium leguminosarum</i> biovar phaseoli strain P31 ^b	Seed-dipping for 60 min	Field	Beneficial effect on growth in a soil with low fertility	Chabot et al. (1996)
	<i>Rhizobium leguminosarum</i> strain VF39SM ^b	Seed-dipping for 60 min	Petri dishes, controlled growth chamber	Beneficial effect on early seedling growth and increase in root length	Noel et al. (1996)
	<i>Agrobacterium</i> sp. ^b , <i>Alcaligenes piechaudii</i> ^c , <i>Comamonas acidovorans</i> strain 26 ^c	Direct inoculation of axenic seedlings	Petri dishes, controlled growth chamber	Root promotion or inhibition is correlated to indole-3-acetic acid levels produced by rhizobacteria (indole-3-acetic acid overproduction is deleterious to plants)	Barazani and Friedman (1999, 2000)
	<i>Serratia proteamaculans</i> strain ATCC35475 ^d , <i>Rhizobium leguminosarum</i> bv <i>viciae</i> strain 128C56G ^b	Root inoculation	Greenhouse conditions	Alleviated the negative effects of salinity on the plant, increased photosynthesis and total chlorophyll content, stomatal conductance, fresh weight, leaf area, N, P, and K uptake, and activity of some antioxidant enzymes	Han and Lee (2004)
	<i>A. brasilense</i> strain Sp245 ^b	Seed-dipping for 180 min (10 ⁷ CFU per seed)	Pots, controlled growth chamber	Better germination and increase in the vegetative growth after exposure to NaCl	Barassi et al. (2006)
	<i>Pseudomonas mendocina</i> Palleroni strain ^d	Soil drench (10 ¹⁰ CFU per plant; two treatments)	Pots, greenhouse conditions	Increase in the plant biomass under moderately and severely saline conditions and increase in the antioxidant enzyme activities in response to severe salinity	Kohler et al. (2009)
	<i>A. brasilense</i> strain Sp245 ^b	Seed-dipping for 90 min (10 ⁹ CFU per seed)	Pots, greenhouse conditions (under natural light)	Promoted early germination, seedling settlement of seeds and increased leaf dry weight, leaf area and chlorophyll content when plants were grown at 40 mmol ⁻³ NaCl	Fasciglione et al. (2012)
	<i>A. brasilense</i> strain Sp7-S ^b	Seed-dipping for 60 min and re-inoculation by drenching 7 days later	Petri dishes, temperature-controlled growing cabinet	Increased in the number of leaves, seedling height, and root length	Mangmang et al. (2015b,c)
Pepper	<i>Bacillus</i> strains ^b	Seed-dipping	Field	Increased fresh root and shoot weights, stem diameter, dry root, and dry shoot weights	Kokalis-Burelle et al. (2002)
	<i>P. fluorescens</i> strain IISR-6 ^d , IISR-11 ^d and IISR-51 ^d	Seed-dipping for 30 min (10 ⁸ CFU mL ⁻¹)	Pots, greenhouse conditions	Increased root length, total root area, and number of root tips	Paul and Sarma (2006)
	<i>Bacillus licheniformis</i> strain K11 ^a	Soil drench (7 10 ⁸ CFU mL ⁻¹ per plant; one treatment)	Pots, greenhouse conditions	Increased in the root and shoot length, and dry weight under drought stress	Lim and Kim (2013)

^a Bacilli.

^b Alphaproteobacteria.

^c Betaproteobacteria.

^d Gammaproteobacteria.

^e Actinobacteria.

Table 2
Effects of plant growth-promoting rhizobacteria (PGPR) application on fruit crops.

Crop	PGPR (species/strain)	Application mode	Experimental conditions	Effects	References
Apple	<i>Bacillus</i> sp. strain M3 ^a and OSU-142 ^a , <i>Microbacterium</i> sp. strain FS01 ^e , <i>Pseudomonas</i> sp. strain BA-8 ^d (alone or in combinations)	Root-dipping (10 ⁹ CFU mL ⁻¹)	Field	Increased cumulative yield, fruit weight, shoot length, and shoot diameter in apple cv. Granny Smith and Stark Spur Golden	Karlidag et al. (2007); Aslantas et al. (2007)
	<i>Bacillus</i> sp. ^a	Foliar application of spores (10 ⁷ spores g ⁻¹)	Field	Enhanced growth of apple leaves and improved fruit quality parameters (sweetness and moisture content)	Ryu et al. (2011)
Apricot	<i>Bacillus</i> sp. strain OSU-142 ^a	Foliar application (10 ⁹ CFU mL ⁻¹)	Field	Increased yield, shoot development and reduced shot-hole disease severity and incidence	Esitken et al. (2002, 2003)
Banana	<i>Pseudomonas fluorescens</i> strain CHAO ^d	Soil application of cells (2.5–3 × 10 ¹⁰ CFU) with or without chitin (treatment repeated three times)	Field	Increased growth, leaf nutrient contents and yield of banana plants under perennial cropping systems	Kavino et al. (2010)
Cherry	<i>Pseudomonas</i> sp. strain BA-8 ^d and <i>Bacillus</i> sp. strain OSU-142 ^a (alone or combinations)	Foliar application (spray; 10 ⁹ CFU mL ⁻¹)	Field	Stimulated plant growth, increased yield per trunk, fruit weight and shoot length and resulted in significant yield increase	Esitken et al. (2006)
Grape	<i>Pseudomonas putida</i> strain BA-8 ^d and <i>Bacillus simplex</i> strain T7 ^a (alone or combinations)	Grafted plant-dipping (10 ⁹ CFU mL ⁻¹) for 60 min	Experimental glasshouse	Increased graft callusing, scion shoot growth, cane hardening, and nursery survival rate, as well as fruitfulness of the grapes in following year	Sabir (2013)
Hazelnut	N ₂ -fixing and P-solubilizing bacteria	Seed-dipping (10 ⁹ CFU mL ⁻¹), on one-year old seedlings	Pots, greenhouse conditions	Increased seedling and total branch length, branch number, trunk diameter, and nutrient uptake	Erturk et al. (2011)
Kiwifruit	<i>Bacillus</i> sp. ^a , <i>Paenibacillus polymyxa</i> ^a and <i>Comamonas acidovorans</i> ^c	Seed-dipping (10 ⁹ CFU mL ⁻¹) for 30 min	Greenhouse conditions	Stimulation of rooting and root growth	Erturk et al. (2010)
Strawberry	<i>Bacillus subtilis</i> strain GBO3 ^a and <i>Bacillus amyloliquefaciens</i> strain IN937a ^a	Seed-dipping with a formulation that contains both strains in a 2.5% chitin carrier	Field	Addition of PGPR to plug transplants resulted in healthier roots, earlier and higher total yields	Kokalis-Burelle (2003)
	<i>Bacillus</i> sp. FS-3 ^a	Root drench (3.5 × 10 ⁷ cell g ⁻¹), repeated five times within 7-D intervals	Pots, greenhouse conditions	Increased fruit and leaf nutrient concentrations (N, P, K, Ca, and Fe)	Güneş et al. (2009)
	<i>Azospirillum brasilense</i> strain REC3 ^b , RLC1 ^b , PEC5 ^b	Root-dipping (10 ⁶ CFU mL ⁻¹) for 30 min	Pots, greenhouse conditions	Increased root length, root area, and dry weight of root and shoot	Pedraza et al. (2010)
	<i>Pseudomonas</i> sp. strain BA-8 ^d and <i>Bacillus</i> sp. strain OSU-142 ^a and M3 ^a (alone or combinations)	Root-dipping (10 ⁹ CFU mL ⁻¹) for 30 min or foliar application	Field	Increased fruit yield, plant growth, phosphorus and zinc content of leaves	Esitken et al. (2010)
	<i>Bacillus sphaericus</i> GC subgroup B strain EY30 ^a , <i>Staphylococcus kloosii</i> strain EY37 ^a and <i>Kocuria erythromyxa</i> strain EY43 ^e	Root-dipping (10 ⁸ CFU mL ⁻¹) for 30 min	Pots, greenhouse conditions	Increased plant growth, fruit yield, chlorophyll content, relative water content of leaves, mineral uptake (N content of leaves and P content of roots), and reduced membrane injury under saline conditions (35 mM NaCl)	Karlidag et al. (2010)
	<i>P. fluorescens</i> strain Pf4 ^d , <i>Pseudomonas</i> sp. strain 5Vm1K ^d	Root drench with the two PRGB (5 × 10 ⁹ CFU) and/or with arbuscular mycorrhizal fungi	Pots, greenhouse conditions	Increased anthocyanin concentration in fruits of plants grown under conditions of reduced fertilization	Lingua et al. (2013)
	<i>Alcaligenes</i> sp. strain 637Ca ^c	Root-dipping (10 ⁸ CFU mL ⁻¹) for 30 min	Pots, greenhouse conditions	Increased fruit yield, number and weight under high calcareous soil conditions	Ipek et al. (2014)
Walnut	<i>Pseudomonas chlororaphis</i> ^d and <i>Arthrobacter pascens</i> ⁵	Seed-dipping (10 ⁹ CFU mL ⁻¹), on one-year old seedlings	Greenhouse conditions	Increased plant height, shoot and root dry weight, phosphorus and nitrogen uptake	Yu et al. (2012)

tal aperture and photosynthesis rate. However, under water-stress conditions, the levels of ABA increased and the stomatal conductance was lower than that of non-inoculated plants, preventing water loss. Furthermore, some GA-producing rhizobacteria also cause a decrease in the ABA content under optimal growth conditions, but an increase under cold conditions, to improve cold tolerance in pepper plants (Kang et al., 2015). Therefore, to study how specific PGPR alters the concentration of one plant hormone, it is important also to analyse how other plant hormones respond to any particular PGPR.

2.2. Volatile organic compounds

Several PGPR emit volatile organic compounds (VOCs), which promote plant growth (Table 4; Bailly and Weisskopf, 2012). These VOCs have been largely studied in relation to their function as inducers of resistance against plant pathogens (Frag et al., 2013). However, they also promote plant growth in the absence of pathogens, and can confer tolerance against abiotic stresses (Bhattacharyya et al., 2015). The VOCs for which a plant growth promotion effect has been confirmed by using bacterial mutants

Table 3
Effects of plant growth-promoting rhizobacteria (PGPR) application on flower and ornamental plants.

Crop	PGPR (species/strain)	Application mode	Experimental conditions	Effects	References
Broom	<i>Variovorax paradoxus</i> strain 5C-2 ^c	Root drench (3.5 × 10 ⁷ cell g ⁻¹ dry weight of soil)	Pots, temperature controlled glasshouse and regulated deficit irrigation conditions	Reduced level of ethylene production, leaf necrosis and abscission under drought stress	Sharp et al. (2011)
Chrysanthemum	<i>Pseudomonas fluorescens</i> strain 51 ^d	Soil drench (10 ¹¹ CFU per plant)	Pots, greenhouse conditions	Increased plant height, leaf surface area and number of flowers per plant	Göre and Altin (2006)
Dahlia	<i>P. fluorescens</i> strain 51 ^d	Soil drench (10 ¹¹ CFU per plant)	Pots, greenhouse conditions	Increased root length and number of flowers per plant. Enhancement in fresh and dry weight	Göre and Altin (2006)
Gladiolus	<i>Bacillus</i> group ^a	Foliar spray	Field, sodic soil conditions	Induced salt tolerance and improvement of growth characters (plant height, spike length, number of floret, corm weight and diameter)	Damodaran et al. (2014)
	<i>Azospirillum</i> sp. ^b	Corm dip for 30 min in the bacterial suspension followed by shade drying before planting	Field	Increased plant height, length of spike, dry and fresh weight of leaves, number of florets, as well as total chlorophyll content, protein content, total soluble sugars, and accumulation of nutrients (N, P and K)	Qasim et al. (2014)
Jasmine	<i>Azospirillum</i> sp. ^b , <i>Pseudomonas striata</i> ^d , <i>P. fluorescens</i> ^d	Lignite based cultures used at 8 kg ha ⁻¹ each	Field	In combination with <i>Trichoderma viridae</i> , improved flower yield, flower quality characteristics, chlorophyll content, and total microbial population in the rhizosphere	Jayamma et al. (2014)
Pelargonium	<i>P. fluorescens</i> strain 51 ^d	Soil drench (10 ¹¹ CFU per plant)	Pots, greenhouse conditions	Increased plant height, leaf surface area and number of flowers per plant	Göre and Altin (2006)
Peppermint	<i>P. fluorescens</i> strain WCS417 ^r ^d	Plant exposed to bacterial volatile organic compounds without physical contact	Petri dishes, growth chamber with controlled conditions of light, temperature and relative humidity	2-fold increase in essential oil production [(+) pulegone and (-) menthone]	Santoro et al. (2011)
Petunia	<i>Azospirillum lipoferum</i> ^b and <i>Bacillus polymxa</i> ^a	Foliar spray	Pots, greenhouse conditions	Increased plant height, leaf area, shoot and root dry weight, flowering date, number of flower/branch, and flowering period	El-Mokadem and Mona (2014)
Photinia	<i>Azospirillum brasilense</i> strain Cd ^b and Sp7 ^b combined with auxin inductive pulses	Direct inoculation of shoots (10 ⁷ CFU per shoot)	Pots, growth chambers	Earlier rooting of photinia shoots; increased root fresh and dry weight, root surface area and shoot fresh and dry weight	Larraburu et al. (2007)
Zinnia	<i>P. fluorescens</i> strain E6 ^d	Root-dipping of seedlings (10 ⁸ CFU ml ⁻¹)	Pots, greenhouse conditions	Effect on root microflora that determined an enhancement of plant growth	Yuen and Schroth (1986)

Table 4
Volatile-mediated effects of plant growth-promoting rhizobacteria (PGPR) on plants.

VOC	PGPR (species/strain)	Plant	Effect	Reference
2,3-butanediol and 3-hydroxy-2-butanone (acetoin)	<i>Bacillus subtilis</i> strain GB03, <i>Bacillus amyloliquefaciens</i> strain IN937a	<i>Arabidopsis thaliana</i>	Increased leaf surface area and induced systemic resistance (ISR)	Ryu et al. (2003)
Indole	<i>Escherichia coli</i>	<i>A. thaliana</i>	Increased biomass and lateral root number	Bailly et al. (2014)
Mixture of volatile compounds including β-Caryophyllene	<i>Fusarium oxysporum</i> and a bacterial consortium consisting of <i>Gammaproteobacteria</i> (96%), <i>Alfaproteobacteria</i> (2%), <i>Betaproteobacteria</i> (1%) and <i>Firmicutes</i> (1%)	Lettuce	Induced shoot length, root length, and fresh weight of lettuce seedlings	Minerdi et al. (2011)
Mixture of volatile compounds	<i>Pseudomonas palleroniana</i> strain R43631, <i>Bacillus</i> sp. strain R47065, R47131, <i>Paenibacillus</i> sp. strain B3aR49541, <i>Bacillus simplex</i> strain M3-4 R49538	Potato	Increased potato yield in field conditions (more evident at the lower fertilizer level)	Velivelli et al. (2014)

unable to synthesize these particular VOCs or by application of the pure compounds (Ryu et al., 2003).

Apart from the VOCs shown in Table 4, other VOCs have been identified as the putative causal agents of the growth promotion by PGPR (Kanchiswamy et al., 2015). Among these VOCs, 2-pentylfuran was shown to increase *A. thaliana* fresh weight, with an optimum dose of 10 µg (Zou et al., 2010). Almost all the studies performed to date concerning the effects of VOCs on plant growth have been carried out using *A. thaliana* as a target for bacterial volatiles (Bailly and Weisskopf, 2012). This is because to ascribe a

PGPR effect to VOCs, no contact between the bacteria and the roots can occur, therefore, this type of experiment has been performed in vitro using a divided petri dish setup, where the bacteria or plant are present on two different compartments and are not in direct contact. Kai and Piechulla (2009) proposed that the VOC effects of PGPR might be caused by CO₂ released by the bacteria. Therefore, although the composition of VOCs has been determined in several experiments, and some compounds have been proven to promote growth, it is not possible to conclude that PGPR activity is due to a specific VOC, apart from the use of bacterial mutants lacking the

synthesis of a specific VOC. Moreover, it should be considered that many VOCs exert inhibitory effects on plant growth at high concentration and some of them are toxic (Bailly and Weiskopf, 2012). Thus, for a proper field application of VOCs, either by exposing crops to volatiles or inoculating plants with volatile-producing bacteria, it is essential to elucidate the signaling cascades and the subsequent metabolic changes that are triggered in the plant by VOCs.

Another important point to mention is that recent studies performed in the open field indicated that the effect of volatile compounds varies from laboratory to field conditions. For instance, drench treatment of cucumber with 2,3-butanediol (2,3-BD)-related compounds, 3-pentanol and 2-butanone, was effective in eliciting induced resistance against aphids and bacterial pathogens at field conditions, but had no effect on plant growth, other than an unexpected increase in fruit yields (Song and Ryu, 2013). 2,3-BD and its precursor acetoin are the two most abundant compounds released from *B. subtilis* GBO3 and *B. amyloliquefaciens* IN937a, two PGPR strains present in a commercially available formulation (BioYield®) that consistently increase the growth and yield of cucumbers, peppers, and tomatoes (Kloeppe et al., 2004). Thus, it is necessary to test VOCs on different crop species both at laboratory and field conditions to evaluate their ability to modulate growth and defense of crop plants and to assess their resulting outcomes on plant growth and productivity. In addition to studies in *A. thaliana*, Santoro et al. (2011) found that VOCs from several PGPR could increase the production of essential oils in peppermint (*Mentha piperita* Huds) plants. Thus, VOCs-producing PGPR can be used in horticultural crops, even though the specific compound or the mixture of compounds that causes the growth promotion are unknown. For example, Velivelli et al. (2014) identified VOCs from Andean rhizobacteria with *in vitro* antagonistic activity against the potato pathogen *Rhizoctonia solani* and positive effects of selected rhizobacterial inoculants on potato tuber growth under field conditions, but were unable to elucidate possible synergistic or antagonistic effects of the different compounds of the mixture. Nevertheless, results from their trials in Bolivia, Ecuador and Peru clearly demonstrated that it is possible to evaluate the relevance of rhizobacterial volatiles in agronomical contexts performing open field experiments in different geographical locations and under different climatic conditions and seasons. A general conclusion that can be drawn from this example is that the formulation of an inoculant that is compatible with routine field practices, which gives reproducible results under different field conditions and types of soil and on different crops, and is safe for humans, non-targeted plants, animals, and the environment, requires both greenhouse and open field experiments.

2.3. Nutrient availability and uptake by plants

It has been known for a long time that inoculation with PGPR can increase the nutrient concentration in the host plant (Canbolat et al., 2006; Wani et al., 2007; Lai et al., 2008); however, the mechanisms that underlie this effect are far from elucidated. Moreover, each nutrient element responds differentially. To favour nitrogen (N) uptake by plants, free-living bacteria able to grow in media without the addition of N were selected (Canbolat et al., 2006), and these bacteria subsequently increased N uptake by the plant and the tissue N concentration, mainly because more nitrogen was available in the soil (Canbolat et al., 2006). In contrast, other free-living bacteria that were able to fix atmospheric nitrogen (N₂), did not subsequently increase the N concentration in the host plant (Lai et al., 2008), because not all bacterial traits selected *in vitro* are also expressed *in vivo*. This will be discussed in the following section. The facilitation of N uptake and assimilation by PGPR are not only due to their nitrogen-fixing ability; Parra-Cota et al. (2014) found that in addition to fixing N₂, the PGPR *Burkholderia ambifaria*

increased the expression of the nitrate transporter *NRT1* in amaranth (*Amaranthus hypochondriacus* L.) plants. Mantelin et al. (2006) had previously shown that the PGPR *Phyllobacterium* sp. decreased the expression of several nitrate transporters, but increased the expression of others, depending on the external nitrate concentration. Therefore, some PGPR cause plants to respond differently to the external N concentration, to potentially maximize N availability (Mantelin et al., 2006). Growth promotion by PGPRs is actually enhanced under non-fertilized conditions (Mantelin et al., 2006; Parra-Cota et al., 2014). It has also been shown that exudates from nutrient-deficient plants (especially N- and P-deficient plants) modify the transcriptome of the PGPR *B. amyloliquefaciens* (Carvalhais et al., 2013).

Similar to N, several PGPR can solubilise phosphates (Canbolat et al., 2006; Lai et al., 2008), resulting in an increased availability of phosphate (P) in the soil that can be taken up by the plant. Recently, Talboys et al. (2009) found that a strain of *B. amyloliquefaciens* increased root growth of wheat (*Triticum aestivum* L.) plants but also decreased the uptake rate of inorganic phosphate (Pi) under P-deficiency conditions, most probably as a compensatory mechanism. This decrease in Pi uptake was correlated with a down-regulation of Pi transporter genes, and an up-regulation of Pi remobilizing genes, which were all controlled by auxin release by the bacteria. Some PGPR can facilitate the uptake of potassium (K) by the plant host (Bertrand et al., 2000; Singh et al., 2010), due to the ability of some PGPR to release K from its immobile forms in the soil (Liu et al., 2013b) and thus, to increase the availability of K in the soil (Sheng, 2005). This better acquisition of K also is involved with the higher salt-stress tolerance of plants inoculated with some PGPR, which limit the deleterious effects of sodium ions (Abd El-Azeem et al., 2012; Nadeem et al., 2013). The effects of PGPR on the assimilation of other nutrients and deeper explanations about nutrient assimilation and PGPR are discussed Pii et al. (2015).

2.4. Abiotic stress tolerance in plants

Timmusk and Wagner (1999) described how the PGPR *Paenibacillus polymyxa* enhanced drought tolerance in *A. thaliana* plants. However, these experiments were performed *in vitro*, and the drought treatment consisted of leaving the petri-dish open for three days. Subsequently, Pishchik et al. (2002) reported that three different PGPR could attenuate the toxic effect of cadmium pollution on the barley yield, mostly because these bacteria could remove cadmium ions from the soil by binding mechanisms, thereby decreasing cadmium availability in the soil.

The mechanisms behind the higher tolerance of plants to several abiotic stresses following inoculation by some PGPR are extremely broad. This section will focus on effects on the antioxidant system and the alleviation of stress caused by leaf dehydration. Other mechanisms have been described in previous sections, such as the regulation of hormonal changes or improvements in nutrient acquisition. It should be borne in mind that all the mechanisms are interconnected, and all favour to some extent the promotion of growth and tolerance to abiotic stress conferred by PGPR (Zhu and Gong, 2014).

Almost all stresses cause an increase in the production of reactive oxygen species (ROS) and subsequent oxidative damage (Gill and Tuteja, 2010). Oxidative damage can be alleviated by limiting the production of ROS, or by improving the ability to remove them (Gill and Tuteja, 2010; Pinto-Marijuan and Munne-Bosch, 2014). The best-known mechanism to reduce the production of ROS is the dissipation of excess of energy in the chloroplasts via carotenoids, especially via the xanthophyll cycle (Bassi and Caffarri, 2000). No information is available concerning the effect of PGPR on the xanthophyll cycle; however, several studies observed an increase in the carotenoid content of plants inoculated with PGPR (Tiwari et al.,

2011; Chakraborty et al., 2013). Nevertheless, there is no evidence for the role of carotenoids in the enhancement of abiotic stress tolerance in plants by PGPR, which will necessitate reverse genetic studies.

Cakmakci et al. (2007) found that the PGPR strains that increased glutathione reductase activity in wheat plants to the greatest extent, also promoted higher growth. However, this relationship was not confirmed in spinach plants using the same PGPR strain. Glutathione reductase is an enzyme that reduces oxidized glutathione to be reused as an antioxidant compound (Gill and Tuteja, 2010). Therefore, the mechanism of action of different PGPR varies, depending on the host plant. Nautiyal et al. (2008) found that the PGPR *Bacillus lentimorbus* increased the antioxidant capacity of the edible parts of lettuce, spinach and carrot plants, as well as caused an increase in growth. These results are important, to improve the nutrient content of these horticultural crops.

Although an enhancement of the antioxidant capacity of plants inoculated with some PGPR has been observed at the biochemical level, molecular studies remain scarce. Recently, Sarma and Saikia (2014) demonstrated that a strain of *Pseudomonas aeruginosa* improved the growth of *Vigna radiata* plants under drought conditions and also increased the activity of several antioxidant enzymes: an increase in the activity of catalase (an enzyme that removes hydrogen peroxide) was correlated with the up-regulated expression of the *calatase1* gene. The involvement of the antioxidant system in the induction of abiotic stress resistance by PGPR needs to be investigated using reverse genetic analyses, via plants that lack single or multiple components of this system.

Another important effect of PGPR inoculation on plants under abiotic stress conditions is the improvement of leaf water status, especially under drought and salt stress (Ahmad et al., 2013; Naveed et al., 2014). To maintain a constant water status under stress conditions, plants need to balance water-loss by the leaves (which is mostly regulated by the stomatal aperture) and water taken up by the roots. In the two studies cited above, stomatal conductance was higher in inoculated plants than in non-inoculated ones under stress conditions. In other studies, the leaf transpiration rate hardly changed following inoculation with PGPR, but growth was increased (Stefan et al., 2013). Therefore, PGPR-inoculated plants tend to have higher values of water-use efficiency (the ratio between the gain in dry weight and water consumed; Stefan et al., 2013; Naveed et al., 2014). This interesting trait could be exploited to save water in environmentally friendly horticulture.

Another factor that regulates plant water status is the ability to absorb water by roots. Marulanda et al. (2010) demonstrated that inoculation with a *B. megaterium* strain increased the ability of maize roots to absorb water under salt stress conditions. This increased ability was associated with a higher gene expression and protein abundance of some plasma-membrane aquaporins (membrane proteins implicated in the transport of water across cell membranes, see Li et al. 2014). More recently, Gond et al. (2015) also observed an increase in the expression of aquaporin genes in the roots of maize plants inoculated with *Pantoea agglomerans* under salt conditions. Thus, some aquaporin genes might be involved in the enhancement of stress tolerance by some PGPR, but this hypothesis needs to be validated using aquaporin mutants.

Multiple effectors govern the response of plants to PGPR inoculation, which are interconnected. One of the next steps in the study of PGPR is to understand which plant genes are involved in the response of plants to PGPR, considering that each plant–PGPR combination might behave differently, increasing the difficulty of such studies. In the following sections, criteria for the selection of PGPR strains and their validity are described and discussed, together with examples of the effects of PGPR on horticultural crops, including ornamental plants and application methods.

3. Selection of PGPR

Based on the mode of action described above for PGPR, several bacterial traits can be used to select a candidate PGPR strain isolated from the rhizosphere of several plant species. The bacteria pre-selected might thus originate from the rhizosphere soil, from the rhizoplane or from within the root, and all might demonstrate PGPR activity, independent of the lifestyle (da Costa et al., 2014). The most common bacterial traits that have been screened are auxin production, ACC deaminase activity, P solubilisation, the ability to fix N₂, and siderophore production. Several examples of the use of these different traits are shown in Table 5. The percentage of isolated bacteria that demonstrate PGP-activity varies from very few (about 5%) to 100% (Table 5).

However, cases where 100% PGPR activity was observed might be because only active bacteria were shown in the publication and the number of isolates in fact was low (four to six isolates; Aslantas et al., 2007; Ipek et al., 2014). In the study of Ipek et al. (2014), in addition to the common bacterial traits shown in Table 5, five out of six isolates also showed the ability to solubilise calcium carbonate. Ipek et al. (2014) grew strawberry plants in a calcareous soil, thus, this ability was potentially crucial. Bacteria without the ability to solubilise calcium carbonate also increased the yield of strawberry plants, although the quality of the berries was lower than that of plants inoculated with other bacteria.

The exact mechanism by which PGPR promote plant growth in different crops and under different environmental conditions is not fully understood, though it is becoming clear that some or all the plant growth promoting traits do not work independently of each other but additively (Ahemad and Kibret, 2014). The most general conclusion that can be drawn from the above example is that to isolate effective PGPR is better to analyze the soil characteristics where the plants will be grown and the specific requirements of the particular crop, and then to identify bacterial traits that might be beneficial to these particular conditions (Ipek et al., 2014).

4. Effects of PGPR on horticultural crops

Tables 1–3 show examples where PGPR application increased the yield of horticultural crops in laboratory, greenhouse or field conditions. For vegetable crops, most experiments were carried out in greenhouse and only in few cases, with lettuce, pepper, potato and tomato, similar experiments were also performed in open field conditions (Table 1). Interestingly, in the latter cases inoculation with PGPR always determined an increase in plant root length and plant productivity, which is a good evidence of the efficacy of candidate PGPR strains that were tested. In contrast, several experiments with fruit crops, as expected, were carried out in open field conditions and PGPR formulations, in these cases, were applied as a foliar spray (Table 2). Bacterial strains used as PGPR with fruit crops mainly belong to the genus *Pseudomonas* and *Bacillus* and some of these strains (i.e. *Bacillus* sp. OSU-142) determined beneficial effects (increased yield, weight and quality parameter of fruits) on several crops (apple, apricot, cherry and strawberry) in field conditions (Table 2).

As mentioned in the Section 1, one of the problems in the use of PGPR in horticultural production is the persistence of the PGPR in the soil following application, and the survival of the bacteria in the inoculation formulation during storage. For instance, Aslantas et al. (2007) found up to a 2.4-fold higher yield in an apple-tree orchard two years after *Pseudomonas* spp. application, demonstrating that the effect of PGPR application was persistent over time. The method of inoculation used by Aslantas et al. (2007) was to inoculate the plants by dipping the roots into the bacterial suspension for 60 min before transplanting the young trees. Stefan et al. (2013) found up

Table 5
Traits used to select bacteria with potential plant growth-promoting activity.

Reference	Auxin production	ACC deaminase	P solubilization	N ₂ fixation	Siderophores production	Positives (%) ^a	PGPR (%) ^b
Stefan et al. 2013	+ ^c	n.d.	+	n.d.	+	88	8
Aslantas et al. 2007	+	n.d.	+	n.d.	n.d.	100	100
Cakmakci et al. 2007	+	n.d.	+	+	n.d.	100	89
Rodrigues et al. 2008	+	n.d.	n.d.	+	n.d.	84	16
Bal et al. 2013	n.d.	+	n.d.	n.d.	n.d.	100	53
Ipek et al. 2014	+	+	+	+	n.d.	50	100

^a Percentage of isolates that at least had one of the characteristics.

^b Percentage of isolates that had PGP-activity.

^c + means that the trait was checked. n.d. non determined.

to a 1.3-fold higher yield of bean following the simultaneous inoculation with two PGPR strains. In this case, the inoculation method consisted of soaking the seeds in the bacterial culture medium prior to sowing. In each of the above cases, the persistence of the introduced bacteria in the soil or in the roots was monitored. Very few studies have analysed the persistence of bacteria introduced at harvest time, partly due to the difficulty in recovering the specific strain inoculated (Von Felten et al., 2010).

The inoculation methods described above are not practical from a commercial point of view, since they involve fresh bacterial medium. Therefore, techniques that facilitate the use of dry inocula are crucial to extend the use of PGPR in horticulture. One of these techniques is the encapsulation procedure, which consists of immobilizing bacterial cells within a polymer matrix. The most common polymer matrix used is calcium alginate, which in some cases also contains other substances, such as humic acids, skimmed milk, starch or bentonite (Young et al., 2006; Minaxi, 2011; Wu et al., 2012). A further common method of inoculation is to inoculate seeds with alginate beads (Grandlic et al., 2009). The most important advantage of using encapsulated PGPR is not the improvement in the inoculation efficiency (Young et al., 2006; Minaxi, 2011), but the ability to store them for several months, during which time, cell release is maintained and the bacteria are protected from predation and other environmental constraints. A comprehensive review on this topic (Bashan et al., 2014) sets the scene to apply knowledge about inoculation methods in the field.

This review has cited several examples concerning the effect of PGPR on vegetables or fruit plants. However, another relevant horticultural aspect is the propagation of flower and ornamental plants, including representative members of *Asteraceae* (*Chrysanthemum*, *Dahlia*, *Zinnia*), *Geraniaceae* (*Pelargonium*), *Iridaceae* (*Gladiolus*), *Oleaceae* (*Jasmine*) and *Solanaceae* (*Petunia*). As shown in Table 3, PGPR strains used with these plants mainly belong to *Pseudomonas* and *Azospirillum* genus and, in most cases, a relevant effect of the inoculation with PGPR is an increase in the number of flowers per plant. *Azospirillum brasilense* strains were also used, in combination with indole-3-butyric acid, to induce the early rooting of *Photinia* shoots (Larraburu et al., 2007). Interestingly, inoculation with *A. brasilense* strains also increased the shoot and root fresh weight of the propagated plants (Table 3). Similar results with the same *A. brasilense* strains were observed in the propagation of *Handroanthus impetiginosus* (Larraburu and Llorente, 2015).

Moreover, PGPR have been used after the transplantation of ornamental plants and Sharp et al. (2011) found that inoculated plants of *Cytisus* × *praecox* and *Aquilegia* × *hybrida* were more tolerant to drought stress than non-inoculated plants and showed less necrosis, less leaf abscission and fewer flowers.

5. Conclusions and perspectives

It is clear that the use of PGPR as biostimulants in horticulture is a reality. Although several physiological studies have been

performed and much knowledge has been generated, the molecular mechanisms that underlie this growth promotion effect are far from understood. This lack of knowledge applies to both bacteria and plant partners. Although some progress has been made on the bacterial side, including VOC experiments (Table 4) or the involvement of the ACC deaminase enzyme (Ali et al., 2014), the study of other bacterial traits is required. On the plant side, several transcriptomic and proteomic studies have been performed, but these have not been conclusive. More recently, the use of knock-out mutants of *A. thaliana* that lack gene functions implicated in the ethylene response have shown the importance of this pathway in PGP-activity (Chen et al., 2013). In the future, these studies need to be applied to horticultural crop species.

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