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REVIEW

Proven and potential involvement of vitamins in interactions of plants with plant growth-promoting bacteria—an overview

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Abstract Plant growth-promoting bacteria (PGPB) can improve plant performance in many different ways, operating via a multitude of physiological, molecular, and biochemical pathways. One of the lesser known involvements in these interactions is the role of vitamins. Vitamins can be produced by plants and bacteria and also by PGPB. The main function of vitamins is to (1) act as a cofactor in diverse metabolic pathways, (2) facilitate production of essential compounds for plants and bacteria, (3) induce resistance against pathogens, (4) directly promote plant growth, and (5) participate in energy conversion in the plant from stored compounds. Most of the roles of specific vitamins in PGPB–plant interactions are still little known or completely unknown. This overview presents what is known about vitamins detected in potential PGPB, presents proposals for the potential role of vitamins in PGPB–plant interactions based on the known function of these vitamins in plants and bacteria, and proposes research avenues in this topic that are worth exploring.

Keywords Plant growth-promoting bacteria · PGPB · PGPR · Vitamins

Dedication This review is dedicated to the memory of the Israeli soil microbiologist Prof. Yigal Henis (1926–2010) of the Faculty of Agriculture, The Hebrew University of Jerusalem in Rehovot, Israel, one of the pioneers of phytobacteriological studies in Israel

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Abbreviations

PGPB	Plant growth-promoting bacteria
PGPR	Plant growth-promoting rhizobacteria
CoA	Coenzyme A
PQQ	Pyrroloquinoline quinone

Introduction

Plant growth-promoting bacteria (PGPB; Bashan and Holguin 1998), also commonly known as plant growth-promoting rhizobacteria (PGPR) for rhizosphere interactions (Kloepper and Schroth 1978) are bacteria that, via numerous independent or linked mechanisms, are capable of positively affecting plant growth for sustainable agriculture (Bashan and de-Bashan 2005; Compant et al. 2010; Hayat et al. 2010; Lugtenberg and Kamilova 2009; Reddy et al. 2010), counteract many stress effects in plants (Compant et al. 2005; Kang et al. 2010; Kim et al. 2012; Yang et al. 2009), and assist in the recovery of damaged or degraded environments (de-Bashan et al. 2012).

Many types of molecules facilitate interactions of PGPB with plants. These include all known plant hormones (Babalola 2010; Bashan and de-Bashan 2010; Spaepen et al. 2007), hydrolytic enzymes (Hallmann et al. 1999), antibiotics (Haas and Keel 2003; Raaijmakers et al. 2002), flavonoids (Cesco et al. 2012), other signal molecules (Bashan et al. 1992; Faure et al. 2009; Gantner et al. 2006; Juhas et al. 2005), toxic molecules (Schippers et al. 1990; Voisard et al. 1989), siderophores (Kloepper et al. 1980a, b; Kurek and Jaroszuk-Scisel 2003), exopolysaccharide (Kyungseok et al. 2008), volatiles (Cohen et al. 2010; Ping and Boland 2004; Ryu et al. 2003), polyamines (Cassan et al. 2009), lectins (Alen'kina et al. 2006; Castellanos et al. 1998), elevated

concentration of CO_2 in the atmosphere (Drigo et al. 2008), and vitamins (Dahm et al. 1993).

Given the significant importance of vitamins for human and animal health and diet, numerous reviews over the last decade summarized in great detail many of their features, biosynthetic and degradation metabolic pathways, and molecular mechanisms that are involved (Asensi-Fabado and Munné-Bosch 2010; Begley et al. 1999; Burgess et al. 2009; Conklin and Barth 2004; Jurgenson et al. 2009; Lim et al. 2001; Martens et al. 2002; Mooney et al. 2009; Moore and Warren 2012; Mukherjee et al. 2011; Raschle et al. 2005; Roje 2007; Smirnoff and Wheeler 2000; Streit and Entcheva 2003; Survase et al. 2006). This specific overview concentrates solely on 11 vitamins produced by potential PGPB, specifically regarding their proven or potential roles in maintaining interactions of these bacteria with plants. Synthesis, genetics, biochemistry, and functions of these vitamins in other organisms are only briefly mentioned and are accompanied by the related references. This specific review is intended to highlight points that need to be addressed by future research in this lesser studied field of science.

Vitamins are essential micronutrients synthesized by numerous photosynthetic plants and bacteria, but not by animals (Survase et al. 2006). Because vitamins are necessary cofactors in diverse metabolic pathways and serve as antioxidants (Asensi-Fabado and Munné-Bosch 2010; Smith et al. 2007), they need to be provided to an organism that cannot produce them. Specifically, during plant–microbe interactions, vitamins can influence the proliferation of PGPB in and around the root system. Vitamins are from root exudates or are produced by the rhizosphere bacteria and fungi. Some vitamins exuded by plant roots are not entirely plant-synthesized, but are microbial-produced vitamins taken up and later exuded by the plant roots. Because of the common occurrence of microbial vitamin production in the rhizosphere and assimilation of microbially synthesized vitamins by plants, it appears that vitamins have a role in plant development and rhizosphere interactions (Baya et al. 1981). Some plant species that cannot produce some vitamins but are essential in their metabolism are alfalfa, soybean, pea, bean, red clover, and *Pleurochrysis carterae* (Shaukat-Ahmed 1961; Marek-Kozaczuk and Skorupska 2001; Miyamoto et al. 2002; Campbell et al. 2006). Therefore, a theoretical solution for these plants to obtain these vitamins is to maintain interactions with PGPB in a rhizosphere environment that can make these vitamins available. From the perspective of bacteria, production of vitamins, including biotin, niacin, pyrroloquinoline quinone, pantothenic acid, and thiamine, by plants can facilitate bacterial growth and synthesis of diverse compounds, thus, establishing mutual interaction.

The hypothesis leading all studies on involvement of vitamins in plant–PGPB interaction is based on the assumption that such complicated and sometimes difficult-to-produce vitamins would have not been synthesized unless they participate in important cellular mechanisms, either in each of the partners (plant or PGPB) or during their interaction. Far more is known about other cellular and molecular mechanisms involved in plant–bacteria interactions than involvement of vitamins in these interactions. At least 11 vitamins are known to be produced by PGPB in relation to interactions with plants, where the B group vitamins are the most studied (Burgess et al. 2009). The suggested possible roles of vitamins in mutualistic interaction between plant and PGPB are summarized in Table 1.

General considerations of vitamin production by PGPB

Culture medium

Rarely has production of vitamins by PGPB been demonstrated in situ. Production of vitamins was mainly demonstrated in vitro, where growth parameters of the culture media play the major role in which vitamin is produced and in what quantity. The nature of the compound used as the sole carbon source strongly influences the pattern of vitamin release by a bacterial strain (Sierra et al. 1999). For example, in *Rhizobium* sp. strain GR4B, the greatest quantity of vitamins exuded into the medium occurred in the presence of sodium succinate, where glucose reduced production of vitamins, especially thiamine and riboflavin (Sierra et al. 1999). Other preferences occurred in *Rhizobium* sp. strain GRH28, where the highest

Table 1 Suggested possible roles of vitamins in mutualistic interaction between plants and PGPB

Vitamin	Function
Thiamin	Cofactor of cell metabolism Synthesis of plant hormones Plant defense reaction. Antioxidant Plant growth promotion
Riboflavin	Cofactor of cell metabolism Plant defense reaction. Antioxidant Plant growth promotion Quorum sensing. Signal molecule Mitigation of salt stress
Pyridoxine	Cofactor of cell metabolism Plant defense reaction. Antioxidant
Cobalamin	Cofactor of cell metabolism Plant growth promotion
Biotin	Cofactor of cell metabolism Quorum sensing. Signal molecule
Pantothenic acid	Cofactor of cell metabolism
Niacin	Plant defense reaction. Antioxidant Mitigation of salt stress
Ascorbic acid	Plant defense reaction. Antioxidant
Pyrroloquinoline quinone	Cofactor of cell metabolism Plant growth promotion

quantity of vitamins occurred with succinate as a carbon source for production of niacin, yielding more thiamine, riboflavin, pantothenic acid, and biotin in the culture medium when mannitol or glucose was added as the sole carbon sources (Sierra et al. 1999). Another example is *Pseudomonas fluorescens* strain 267 that produced thiamine, niacin, biotin, pantothenic acid, pyridoxine, and cobalamin, yielding amounts of each vitamin that were strongly dependent on the amount and nature of the carbon source. In this case, citrate provided the best support for production of biotin and thiamine, glucose for pyridoxine, and glycerol for cobalamin. Another factor affecting vitamin production in this strain was the pH of the medium. Production of pyridoxine and cobalamin increased sevenfold in an acid medium (pH 5.5), and production of thiamine, niacin, and pantothenic acid increased at pH 7.5 (Marek-Kozaczuk and Skorupska 2001). Similar preferences were also found in *Azospirillum* spp. and *Azotobacter* spp. *Azospirillum brasilense* produced thiamine from malate and fructose, but not from gluconate (Rodelas et al. 1993). Niacin was produced in malate, gluconate, and glucose medium. Small quantities of riboflavin were produced in a medium containing malate and fructose, but not in a medium containing gluconate. Apart from the carbon source, production of vitamins is highly influenced by the duration of incubation (Rodelas et al. 1993), temperature (Dahm et al. 1993), and source of nitrogen (Gonzalez-Lopez et al. 1983; Revillas et al. 2000). Other species of *Azospirillum*, isolated from ectomycrorrhizae, showed different patterns of vitamin production. Riboflavin was synthesized in large quantities at neutral pH, but contrary to the above, thiamine was detected in these strains at pH 5.5. These strains produced pantothenic acid with an increase in temperature and pH (Dahm et al. 1993). *Azotobacter vinelandii* produced biotin, pantothenic acid, riboflavin, niacin, cobalamin, and thiamine, depending mainly on the combination of carbon sources in the culture media (Gonzalez-Lopez et al. 1983), whereas *Azotobacter chroococcum* strain H23 and *A. vinelandii* ATCC 12837 preferred soil phenolic compounds for production of biotin, niacin, thiamine, pantothenic acid, and riboflavin, which was similar to other species of *Azotobacter*. Quantities of all vitamins were affected by the use of different C and N substrates (Revillas et al. 2000). Adding glucose and NH_4NO_3 to a N-free medium was very important for production of vitamins by *A. vinelandii* ATCC 12837 (Gonzalez-Lopez et al. 1983). In another strain of *A. vinelandii*, pantothenic acid and thiamine were produced in large amounts in a culture medium containing glucose and NH_4Cl. Liberation of these vitamins increased under nondiazotrophic conditions and an excess of a carbon source (Martinez-Toledo et al. 1996). Taken together, the evidence of the two latter studies suggests a competing mechanism between nitrogen fixation and vitamin production.

Microelements were also required for production of vitamins. A strain of *Azotobacter chroococcum* produced a considerable amount of cyanocobalamin, especially when cultivated in a medium enriched with NH_4Cl (El-Essawy et al. 1984). Yet, molybdenum, Fe^{2+}, cobalt, and ascorbic acid were required for optimal production.

In summary, during in vitro cultivation, medium composition (N, P, and microelements), combined with environmental parameters (pH, temperature), dictates which vitamins were produced and at what quantities.

Varying production of vitamins among strains

Not all PGPB strains, even those belonging to the same species, show similar features in regard to vitamin production. Assays of the synthesis and extracellular release of riboflavin into the culture filtrate from root nodules of 30 strains of bacteria from tumbleweed (of the legume genus *Psoraleae*) and standard laboratory strains of the genera *Rhizobium*, *Bradyrhizobium*, *Mesorhizobium*, and *Sinorhizobium* revealed significant differences. Production did not only vary among rhizobial isolates, but also sometimes between paired bacterial isolates from root nodules of the same *Psoralea* species (Kanu et al. 2007). Another bacterial species that has shown varying production is *A. brasilense*; some strains produce biotin (Dahm et al. 1993) and others do not (Rodelas et al. 1993).

Potential interactions of vitamins with PGPB and plants

Nearly every photosynthetic organism produces its own vitamins, yet many species have strategies that allow them to survive without synthesizing vitamins (Croft et al. 2005, 2006). Because vitamins play an important role in the physiology of photosynthetic plants and algae and the biosynthesis of some vitamins is very complex, it is advantageous for plants to associate with microorganisms that can produce vitamins for them. For example, culturing of as many as 306 species of algae was possible only when the media were supplemented with vitamins. Thiamin, cobalamin, and biotin are most commonly required by auxotroph freshwater algae (Croft et al. 2006). Phytohormone effects, combined with vitamins, are linked to the beneficial influence of PGPB on the function of rhizobia–legumes and PGPB–plants. The information is mostly circumstantial or logically deduced, but direct experimental data is mostly lacking. For example, Revillas et al. (2000) proposed that, because exogenous applications of B vitamins affect plant cellular functions, the production of these vitamins by PGPB, such as *Azotobacter* spp., is a mechanism that explained positive effects of these bacteria on plants and their interactions with other microorganisms in the rhizosphere; for example, fluorescent *Pseudomonas* sp. strain 267 promoted growth of nodulated clover under gnotobiotic conditions. Plant growth promotion was attributed to secretion of B vitamins by *P. fluorescens*.

Adding vitamins to the plant medium increased symbiotic nitrogen fixation by clover (Deryło and Skorupska 1993).

One of the better known examples over the past half century involves cobalamin, rhizobia, and growth of legumes. When small quantities of cobalt were added to soybean (*Glycine max*), nitrogen, chlorophyll, and cobalamin in nodules dramatically increased, compared to growth conditions without cobalt (Shaukat-Ahmed 1961). Similarly, when cobalt was added to alfalfa (*Medicago sativa*) grown with *Sinorhizobium meliloti*, dry weight of alfalfa more than doubled. Nitrogen content was approximately nine times greater than alfalfa grown without cobalt; roots and nodules in the presence of added cobalt possess a greater capacity for nitrogen fixation than those grown without added cobalt. This pattern also occurs in subterranean clover *Trifolium subterranean* (Hallsworth et al. 1960) and in leguminous and nonleguminous plant nodules, including *Pisum sativum*, *Trifolium pretense*, *Phaseolus vulgaris*, *Alnus oregona*, and *Ceanothus velutinus* (Kliewer and Evans 1963b).

Pesticides used in agriculture affect the production of vitamins by PGPB. For example, the effect of diazinon on cells of *Azospirillum brasilense* grown in a chemically defined medium had no negative impact on *A. brasilense*, but profenofos significantly reduced nitrogen fixation, intracellular levels of ATP, production of pantothenic acid, thiamine, niacin, and growth of cells (Gómez et al. 1999). Adding the herbicide simazine to culture media negatively affected the amount of thiamin, niacin, pantothenic acid, cyanocobalamin, and biotin produced by *Azotobacter vinelandii* strain ATCC 12837 and *A. chroococcum* strain H23 (Murcia et al. 1997). An earlier study demonstrated the existence of a possible relationship between vitamin release and the ability to dissolve dicalcium phosphate by PGPB. Among rhizosphere and rhizoplane isolates producing one or more of cobalamin, riboflavin, and niacin, the isolates solubilized phosphate; production of these vitamins by rhizosphere isolates was correlated with their ability to solubilize phosphate (Baya et al. 1981).

The following sections will describe and evaluate vitamins that are known to be produced by PGPB, potential PGPB, or are known to be involved in the interaction of PGPB with plants (Table 2).

B-group vitamins

Of the large number of vitamins in this group, only seven vitamins are produced in significant quantities by PGPB.

Thiamine (vitamin B_1)

Thiamine pyrophosphate is the active form of the vitamin and functions as a cofactor with a number of important enzymes in carbohydrate and amino acid metabolism (Schyns et al. 2005).

Table 2 Direct evidence for function of vitamins produced by PGPB in plants during their interaction

Vitamin	PGPB	Potential function in plant		Plant or microalgae	Reference
		Direct	Indirect		
Thiamin	*Pseudomonas* sp.		Stimulates shoot and nodule weight by *Rhizobium leguminosarum*	Red clover (*Trifolium pratense*)	Deryło and Skorupska (1993))
Riboflavin and lumichrome	*Sinorhizobium meliloti*	Enhance root respiration		Alfalfa (*Medicago sativa* L.)	Phillips et al. (1999)
Cobalamin	*Sinorhizobium meliloti*	Cofactor in enzymes related to invasion of root plant		Alfalfa	Campbell et al. (2006)
Biotin	*Sinorhizobium meliloti*	Promotes root colonization, root nodule formation, and N_2 fixation		Alfalfa	Streit et al. (1996) Hofmann et al. (2000)
Niacin	*Pseudomonas fluorescens*		Promoter of root colonization and nodulation by *Rhizobium leguminosarum* bv. *trifolii*	Red clover	Marek-Kozaczuk and Skorupska (2001))
Ascorbic acid	*Rhizobium* sp.	Plant cell division, growth, development (theory not checked in the plant)		Legume pulse (*Phaseolus mungo*)	Ghosh et al. (2008)
Pyrroloquinoline quinine (PQQ, methoxantin)	*Pseudomonas fluorescens*	Promotes plant growth Antioxidant		Tomato (*Solanum lycopersicum*) Cucumber (*Cucumis sativus*)	Choi et al. (2008)

Two of the major metabolic pathways in which the vitamin acts as a cofactor are the enzyme complexes of pyruvate dehydrogenase and α-ketoglutarate dehydrogenase of the citric acid cycle and transketolase in the pentose phosphate pathway (Belanger et al. 1995).

Biosynthesis of thiamine involves the separate formation of pyrimidine and thiazole. These are coupled to form thiamine phosphate. Twelve genes involved in thiamin biosynthesis have been identified in bacteria. Of these, six genes are required for biosynthesis of thiazole (*thiFSGH*, *thiI*, and *dxs*), one is involved in biosynthesis of pyrimidine (*thiC*), and one is required for linking thiazole and pyrimidine (*thiE*). All are involved in the de novo synthesis of thiamine, and four (*thiD*, *thiM*, *thiL*, and *pdxK*) are kinase genes (Begley et al. 1999).

There are some differences in the genes involved in thiamine synthesis in rhizobia. *Sinorhizobium meliloti*, *Mesorhizobium loti*, and *Rhizobium etli* use the *thiCOGE genes* for novo thiamine synthesis; the genome of *R. leguminosarum* lacks *thiCOGE*, but has the salvage *thiMED* pathway. *thiMED* operates when thiamine is in short supply, thereby aiding their survival (Karunakaran et al. 2006). Some rhizobia exclusively use the de novo *thiCOGE* pathway; others use only the *thiMED* salvage pathway (thiamine kinase and thiamine phosphate kinase that permit bacteria to obtain thiamine diphosphate from dephosphorylated thiamine from culturing media). *Rhizobium etli* strain CFN42 uses both. An additional pathway in the salvage of base-degraded forms of thiamine is widely distributed among bacteria, archaea, and eukaryotes. In this pathway, thiamine can be formed by thiaminase II, a thiamin-degrading enzyme, which is involved in regeneration of the thiamin pyrimidine. Rather than thiamin degradation, it allows bacteria to reuse compounds from degradation of thiamine to produce de novo thiamine (Jenkins et al. 2007).

Production of thiamine has been reported in different potential PGPB, including *Azotobacter vinelandii*, *Azospirillum brasilense*, *Azospirillum* spp., *Pseudomonas fluorescens*, *Rhizobium leguminosarum*, *Rhizobium etli*, *Sinorhizobium meliloti*, *Mesorhizobium loti*, and *Bacillus subtilis* (Dahm et al. 1993; Karunakaran et al. 2006; Marek-Kozaczuk and Skorupska 2001; Martinez-Toledo et al. 1996; Rodelas et al. 1993; Sierra et al. 1999; Zhang et al. 1997).

Several documented properties of thiamine make it valuable for maintaining mutualism with plants as one of the mechanisms that assists plant growth. The direct evidence for this is emerging (Fig. 1).

1. The main role of thiamine is to act as a cofactor for several enzymes. As described above, it acts as a cofactor for transketolase, pyruvate dehydrogenase, and α-ketoglutarate in the following metabolic pathways: glycolysis, pentose phosphate, tricarboxylic acid cycle, synthesis of amino acids, and synthesis of nucleic acids (Bunik and Fernie 2009; Depeint et al. 2006; Goyer 2010; Krampitz 1969; Leclere et al. 2004; Schenk et al. 1998). Thiamine also acts as a cofactor of the principal enzyme (indolepyruvate decarboxylase) in synthesizing indole-3-acetic acid (IAA) in PGPB. IAA plays a major role in many PGPB interactions with plants (see "Introduction"). This involves participation of the inactive monomer of indolepyruvate decarboxylase (Koga et al. 1992).
2. Several biocontrol PGPB (Bashan and Holguin 1998) induce systemic resistance in plants against pathogens (Zhang et al. 2004; Paré et al. 2005; Kloepper and Ryu 2006; Ryu et al. 2007; Park et al. 2008). Thiamine and riboflavin (described below) showed comparable tendencies. Thiamine was involved in activating a plant's defense reactions. Thiamine-treated rice, arabidopsis (*Arabidopsis thaliana*), tobacco, and cucumber showed resistance to fungal, bacterial, and viral infections. Treatment with thiamine induced a transient expression of several pathogenesis-related genes. The effects of thiamine on disease resistance and expression of defense-related genes were mobilized systemically throughout the plant and last for more than 15 days after treatment. Induction of acquired systemic resistance happened through two different signaling pathways: salicylic acid and cytoplasmic-free Ca^{2+} (Ahn et al. 2005). To put this effect in a broader perspective, salicylic acid is well

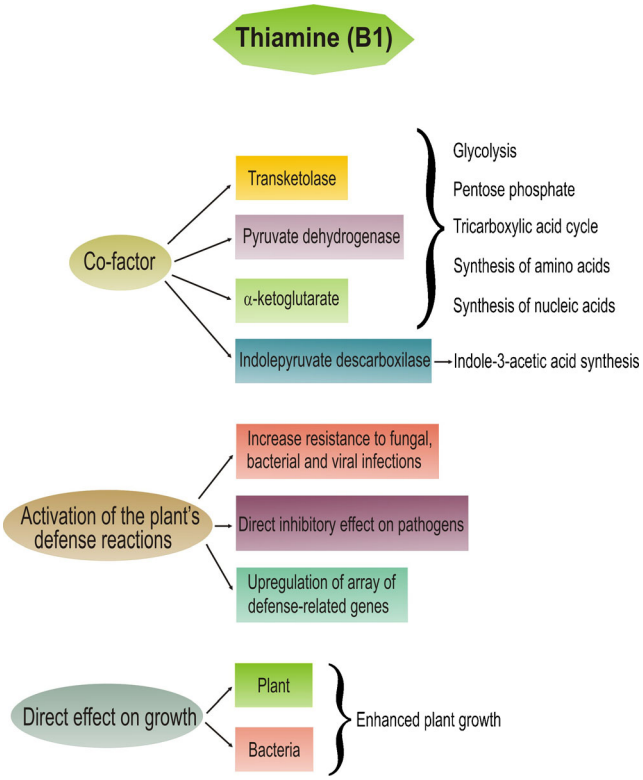

Fig. 1 Properties of thiamine that assist PGPB to maintain mutualism with plants to promote plant growth

known as a signal molecule in the pathway leading to local and systemic disease resistance (Klessig et al. 2000), and cytoplasmic-free Ca^{2+} serves as a messenger in plant processes as diverse as root nodule formation, phytochrome phototransduction, stomatal closure, geotropism, circadian rhythm, growth of pollen tubes, and adaptation to stress (Rudd and Franklin-Tong 1999). In parsley (*Petroselinum crispum*), transient influx of Ca^{2+} constitutes an early element of signaling cascades that trigger pathogen defense responses in the cells. Sustained concentrations of cytoplasmic-free Ca^{2+} are required for activation of defense-associated responses (Blume et al. 2000). Recently, thiamine was shown to be an efficient factor in significantly reducing the effect of downy mildew in grapevine caused by *Plasmopara viticola*. Thiamine-induced resistance in grapevines by a dual mode of action involves direct antifungal activity and elicitation of host-defense responses. These effects involve production of hydrogen peroxide, upregulation of an array of defense-related genes, and induction of additional defense responses, including callose deposition in stomata cells, accumulation of phenolic compounds, and a hypersensitive response leading to cell death (Boubakri et al. 2012).

3. Thiamine produced by fluorescent *Pseudomonas* sp. stimulated shoot growth and nodule weight by *Rhizobium leguminosarum* bv. *trifolii*, growth of the bacteria, and enhanced nitrogen fixation in clover under gnotobiotic conditions when using bacterial mutants that could not produce vitamin B (Deryło and Skorupska 1993).

Riboflavin (vitamin B_2)

Riboflavin is a water-soluble vitamin required for the production of the flavin cofactors, flavin mononucleotide (FMN), and flavin adenine dinucleotide (FAD) (Reihl and Stolz 2005); both are essential cofactors for electron transport functions of proteins involved in basic energy metabolism of the cell (Bereswill et al. 1999). Riboflavin can be produced by plants and many species of bacteria and yeast, using a similar metabolic pathway that starts with guanosine triphosphate (GTP) and ribulose-5-phosphate. This involves seven enzymatic activities: GTP cyclohydrolase II; 2,5-diamino-6-ribosylamino-4 (3H)-pyrimidinone 5′-phosphate deaminase; 5-amino-6-ribosylamino-2,4 (1H, 3H)-pyrimidinedione 5′-phosphate reductase; phosphatase; lumazine synthase; dihydroxybutanone phosphate synthase, and riboflavin synthase (Hümbelin et al. 1999; Stahmann et al. 2000). The best studied riboflavin biosynthesis pathway in bacteria is the *rib* operon in *Bacillus subtilis* that encodes a pyrimidine deaminase/reductase (*ribG*), α-subunit of riboflavin synthase (*ribB*), β-subunit of riboflavin synthase (*ribH*), and GTP cyclohydrolase/dihydroxybutanone phosphate synthase (*ribA*) (Hümbelin et al. 1999; Mack et al. 1998; Vitreschak et al. 2002). The riboflavin operon has also been studied in *Bacillus amyloliquefaciens*, *Actinobacillus pleuropneumoniae*, and *Bartonella* spp. (Bereswill et al. 1999; Vitreschak et al. 2002). In *Photobacterium phosphoreum* and *Photobacterium leiognathi*, the riboflavin genes are localized within the *lux* operon (Lee et al. 1994; Vitreschak et al. 2002). In contrast, the riboflavin synthesis genes in *Escherichia coli* are not clustered in an operon, but are scattered on the chromosome (Lee et al. 1994; Vitreschak et al. 2002).

Among the potential PGPB that produce riboflavin are *Azotobacter vinelandii*, *Azotobacter chroococcum*, *Azospirillum brasilense*, *Azospirillum* spp., *Micrococcus luteus*, *Pseudomonas fluorescens*, *Sinorhizobium meliloti*, *Rhizobium* spp., and *Bacillus subtilis* (Dahm et al. 1993; Hümbelin et al. 1999; Pridham 1952; Revillas et al. 2000; Rodelas et al. 1993; Sierra et al. 1999; Sims and O'Loughlin 1992; Stahmann et al. 2000).

Possible roles of riboflavin in plant–PGPB interactions

Riboflavin functions as a coenzyme in many physiological processes in animals, plants, and microbes. Riboflavin has at least four demonstrated functions in plants; its degradation products also have physiological functions in plants (Fig. 2). Thus:

1. Riboflavin is involved as a cofactor in antioxidation and peroxidation; both processes affect the production of reactive oxygen intermediates (H_2O_2, O_2^-, OH, ROIs) that participate in oxidative bursts. The latter is an immediate response to inoculation with virulent pathogens or treatment with resistance elicitors. The result of oxidative bursts is a consequent hypersensitive response, programmed cell death associated with disease resistance in plants. Oxidative bursts involve complex redox processes that require participation of specific signal molecules, such as H_2O_2, nitric oxide, and antioxidants, such as tocopherols and riboflavin. Foliar application of riboflavin effectively controls several diseases in tobacco (Dong et al. 1995), and it reduces powdery mildew of strawberry plants when combined with methionine, metal ions, and surfactants (Wang and Tzeng 1998). Based on these studies, riboflavin may function as a resistance elicitor or a mediator of resistance signal transduction. Furthermore, riboflavin induced a different type of systematic resistance. Normally, systemic-acquired resistance in many plants refers to a distinct signal transduction pathway that is mediated exclusively by salicylic acid and activates defense genes, such as pathogenesis-related genes. For example, application of riboflavin to *Arabidopsis* developed systemic resistance to the phytopathogens *Peronospora*

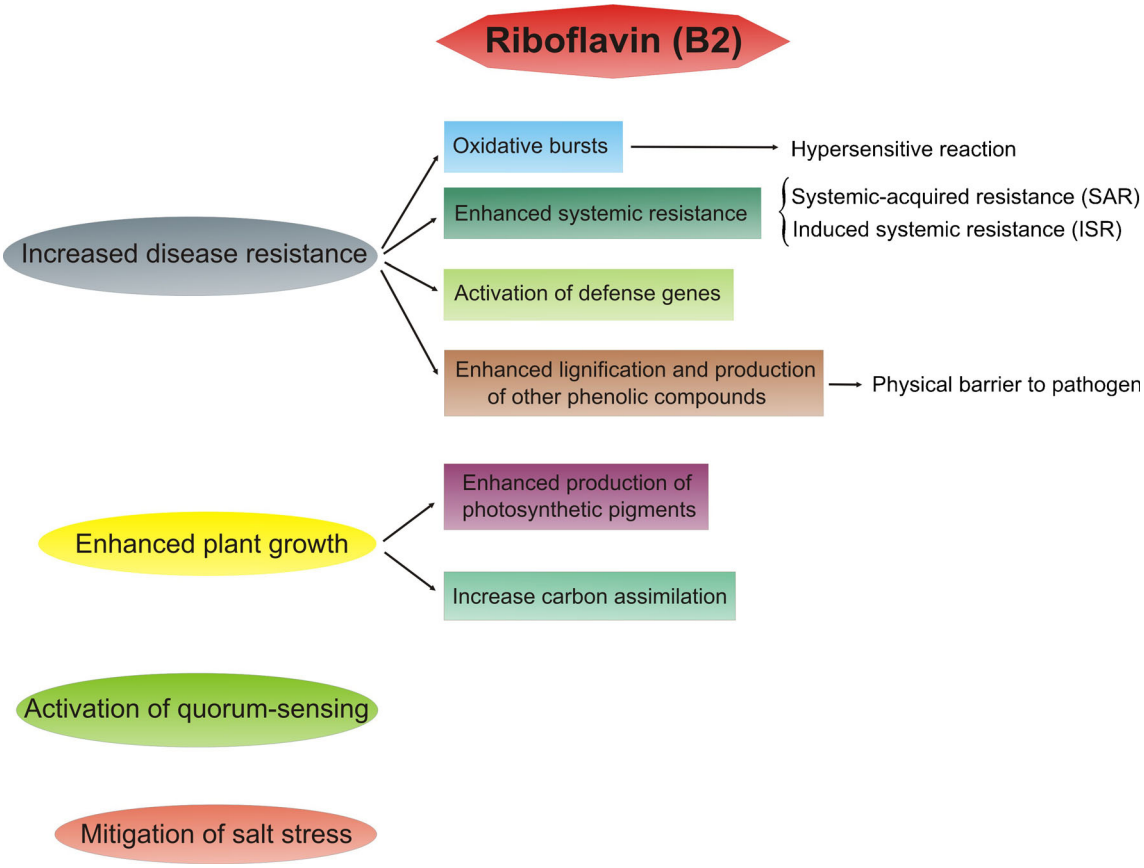

Fig. 2 Properties of riboflavin that assist PGPB to maintain mutualism with plants to promote plant growth

parasitica and *Pseudomonas syringae* pv. *tomato*. Tobacco developed systemic resistance to tobacco mosaic virus and to *Alternaria alternata*. In these plants, riboflavin induced expression of pathogenesis-related genes, suggesting its ability to trigger a signal transduction pathway that leads to systemic resistance. But, in contrast to common systemic-acquired resistance, riboflavin induced resistance and pathogenesis-related gene expression without accumulating salicylic acid (Dong and Beer 2000; Zhang et al. 2009). Riboflavin also acts as a defense activator in rice against sheath blight disease caused by *Rhizoctonia solani*, which, through octadecanoid-mediated priming of the phenylpropanoid pathway, leads to lignification. Riboflavin induced expression of lipoxygenase, a key enzyme in the octadecanoid pathway, and enhanced lignification as a structural barrier. This occurs via generation of H_2O_2. Lignin is extremely resistant to microbial degradation, reinforces the cell wall, and functions as a physical barrier against pathogens. This phenomenon is similar to exogenous application of jasmonic acid, which is known to induce resistance against *R. solani* and other necrotrophic phytopathogens. These results indicate that riboflavin-induced resistance is not based on direct triggering of defense mechanisms but rather on inducing plant tissues to express basal defense responses stronger and/or faster upon subsequent pathogen infection (Taheri and Tarighi 2010). In rice blast disease caused by *Pyricularia oryzae*, riboflavin and its dimethylated amino-derivative roseo-flavin were effective in inducing systemic resistance (Aver'yanov et al. 2000). Riboflavin elicited the defense responses and secondary metabolism in tobacco *Nicotiana tabacum* cell suspensions and protected tobacco seedlings against two phytopathogens, *Phytophthora parasitica* var. *nicotianae* (black shank disease) and *Ralstonia solanacearum* (bacterial wilt). The series of defense responses and secondary metabolism elicited by riboflavin in tobacco cells were an oxidative burst, production of $H_2O_2^-$, alkalinization of the extracellular medium, expression of four defense-related genes with different kinetics and intensities, and accumulation of two phenolic compounds (scopoletin and lignin), yielding together a protection of ~50 % against both diseases (Liu et al. 2010; Zhao et al. 2005).

2. Although riboflavin is susceptible to light and to the enzyme riboflavin hydrolase, one compound, lumichrome, a common breakdown product of riboflavin, can stimulate plant growth in the presence of light. Several PGPB enhance net photosynthesis and production of photosynthetic pigments in various plant species (Bashan et al. 2006). Lumichrome may be one of the factors responsible for that

effect. Lumichrome enhances root respiration in alfalfa (*Medicago sativa*) and also triggers a compensatory increase in whole-plant net carbon assimilation (Phillips et al. 1999). Inoculation with *Sinorhizobium meliloti* increases CO_2 availability by enhancing alfalfa root respiration with production and excretion of this compound (Volpin and Phillips 1998). Lumichrome at nanomolar concentrations, following irrigation of seedlings, promoted growth of monocots and dicots (cereals and legumes). This was manifested as accelerated initiation of trifoliate leaf development, enhanced leaf expansion, and increased stem elongation in soybean and cowpea, yielding increased shoot and plant total biomass. Increased biomass was also observed in leaf area and shoot and total biomass in corn and sorghum (Matiru and Dakora 2005). Lumichrome increased photosynthesis rates in corn and soybean and showed significant effects on the growth of soybean by increasing leaf area and shoot and total dry mass (Khan et al. 2008). How lumichrome acts as an inducer of respiration is unclear. Concentration of CO_2 in the plant increased and stomatal conductance decreased, the latter reducing water loss. Coupled to these functions, this substance affects photosynthesis by unknown mechanisms (Khan et al. 2008; Matiru and Dakora 2005; Phillips et al. 1999).

3. Activation of quorum-sensing receptors of *Pseudomonas aeruginosa* is a function of lumichrome found in the microalgae *Chlamydomonas*. It mimics quorum-sensing signals that allow the host to manipulate quorum-sensing that regulates gene expression in bacteria (Rajamani et al. 2008). Many bacteria, including several PGPB, use quorum sensing as an intercellular signaling mechanism to regulate gene expression in local populations. Quorum-sensing facilitates establishment of diverse mutualistic interactions between plants and bacteria (Cha et al. 1998). The mechanisms by which lumichrome activates quorum sensing is unclear. One of the principal difficulties is the specificity of the acyl-homoserine lactone, the common signal molecules of quorum sensing, to the receptors because lumichrome does not have a molecular structure similar to acyl-homoserine lactone (Rajamani et al. 2008).
4. Mitigation of salt effects in microalgae. Metabolic interactions between single cell microalgae and PGPB are very similar and sometimes identical to interactions of PGPB with higher plants (de-Bashan and Bashan 2008). Application of riboflavin led to a significant increase in growth and biosynthesis of pigments in salt-treated microalgae *Chlorella vulgaris* and *Chlorococcum humicola*. Salinity decreased the contents of carbohydrates and proteins, while riboflavin treatments increased their contents in these microalgae (Abdel-Rahman et al. 2005). PGPB, such as *A. brasilense*, affects many biochemical and physiological growth parameters of *Chlorella vulgaris* (de-Bashan and Bashan 2008); *Azospirillum* spp. are known to produce riboflavin.

Pyridoxine (vitamin B_6)

The term vitamin B_6 encompasses six biologically interconvertible forms of pyridoxine that include pyridoxine and its vitamers (isomers of the vitamin pyridoxine) pyridoxal and pyridoxamine, and their phosphorylated derivatives, such as pyridoxal 5′-phosphate. All living organisms require vitamin B_6. Pyridoxal 5′-phosphate is the most active form and is used as a cofactor for 140 enzymatic reactions in all organisms, primarily involved in amino acid metabolism, but in fatty acid and carbohydrate metabolism and biosynthesis of chlorophyll and ethylene. Vitamin B_6 can be produced by fungi, plants, archaea, and most bacteria and is an essential nutrient in human diets (Mittenhuber 2001; Mooney et al. 2009; Roje 2007). Also, B_6 is a potent antioxidant that effectively quenches reactive oxygen species and is essential for cellular well-being (Bilski et al. 2000).

Pyridoxine is synthesized from 1-deoxy-D-xylulose 5-phosphate and 4-hydroxy-L-threonine (Tazoe et al. 2000). Six genes that are specifically involved in synthesizing pyridoxine include *pdxA*, *pdxB*, *pdxJ*, *pdxF* (*serC*), *dxs*, and *pdxH*. 4-Hydroxy-L-threonine is synthesized from D-erythrose 4-phosphate in a reaction catalyzed by PdxB and PdxF (SerC) proteins. 1-Deoxy-D-xylulose 5-phosphate is formed from pyruvate and D-glyceraldehyde 3-phosphate by 1-deoxy-D-xylulose 5′-phosphate synthase. The two intermediaries are combined by PdxA and PdxJ proteins to generate pyridoxine 5′-phosphate (PNP), which is finally oxidized to the active form PLP by PNP/PMP (pyridoxamine 5′-phosphate) oxidase (PdxH) (Osmani et al. 1999; Tazoe et al. 2005).

The bacteria that have been reported as producing pyridoxine and are also PGPB are *Bacillus subtilis*, *Pseudomonas fluorescens*, *Mesorhizobium loti*, and *Sinorhizobium meliloti* (Marek-Kozaczuk and Skorupska 2001; Sierra et al. 1999; Tazoe et al. 1999).

Possible roles of pyridoxine in plant–PGPB interaction

Pyridoxine produced by PGPB may have several effects on plants, but so far lack experimental evidence regarding PGPB–plant interaction.

1. Pyridoxine is a principal cofactor of amino acid, fatty acid, and carbohydrate metabolism, and its function is reported in different groups of enzymes, such as aminotransferases, aminomutases, lyases, synthases, deaminases, and phosphorylases (Mooney et al. 2009). Nitrogen, lipid, and carbohydrate metabolism, as well as

effects of chlorophyll and ethylene biosynthesis, are well known to be altered by many species of PGPB (Bashan and de-Bashan 2005, 2010; Lugtenberg and Kamilova 2009). It is possible that some of the derivatives of vitamin B_6 have a role that is yet to be discovered.

2. A secondary function of pyridoxine is generating protection against oxidative stress as a strong quencher of O_2 by interacting with singlet oxygen. The $^1O_2$ is a nonradical, a strong oxidizer, and a potent initiator of radical oxidation in biological systems during photo-oxidative stress. In that process, pyridoxine is degraded. So far, this has been demonstrated in the fungal plant pathogen *Cercospora nicotianae*. It provides protection for the pathogen against its own toxin, cercosporin, which generates the toxic $^1O_2$. While it is difficult to separate potential antioxidant properties of B_6 vitamers from their enzymatic role (listed above), pyridoxine appears to contribute strongly to the resilience of *Cercospora* fungi to photo-oxidative stress (Bilski et al. 2000). In *Arabidopsis*, supplementing the growth media with pyridoxine alleviates osmotic and oxidative stress (Chen and Xiong 2005; Havaux et al. 2009).
3. Another demonstrated potential function of pyridoxal-5-phosphate is to regulate Na^+ and K^+ homeostasis by modulating the activities of ion transporters in the plant cell, thus conferring tolerance of plants to saline stress (Shi et al. 2002).

Cobalamin (vitamin B_{12})

Vitamin B_{12} is a family of related vitamins containing cobalt. Its production is restricted to certain members of the prokaryotic world, but it is an essential nutrient for animals and protists. Although plants do not contain cobalamin because they have no cobalamin-dependent enzymes, many algae are rich in vitamin B_{12}, suggesting that the acquisition of this vitamin is through a symbiotic interaction between algae and bacteria (Croft et al. 2005) In humans, trace amounts of cobalamin are used primarily to assist two enzymes, (R)-methylmalonyl-CoA mutase, which is involved in the metabolism of propionyl, and CoA assimilation and methionine synthase, which methylates homocysteine to form methionine (Martens et al. 2002).

Its complex chemical nature requires more than 30 enzymatic steps for the entire de novo biosynthesis of cobalamin (Moore and Warren 2012). There are two distinct biosynthetic routes in bacteria. One is the well-studied aerobic pathway, which is present in *Pseudomonas denitrificans* and *Sinorhizobium meliloti*, where genes (*cobA-V*) were isolated by complementation of mutants and could be functionally assigned (Campbell et al. 2006; Rodionov et al. 2003; Roessner et al. 2002). The anaerobic alternative pathway has been partly studied in *Salmonella typhimurium* and *Bacillus megaterium* (Raux et al. 2003) and *Propionibacterium shermanii* (Wang et al. 1996). In the anaerobic pathway, the genes are *cysG*, *cbiA-Q*, and *cobSTU*. However, there is no convention followed when naming the genes for the two pathways. Therefore, many of the genes encoding the same enzyme have different names, whereas some of the genes with the same name encode different enzymes (Roessner et al. 2002). Both pathways share the *hemB-D* genes.

The potential PGPB that produce cobalamin are *Azotobacter vinelandii*, *Azotobacter chroococcum*, *Pseudomonas fluorescens*, *Bacillus megaterium*, *Bacillus firmus*, and *Sinorhizobium meliloti* (El-Essawy et al. 1984; Gonzalez-Lopez et al. 1983; Kliewer and Evans 1963b; Marek-Kozaczuk and Skorupska 2001; Moore and Warren 2012; Sierra et al. 1999).

Possible roles of cobalamin in plant–PGPB interactions

Plants usually do not directly need cobalamin for their metabolism, yet it appears in several species. One case is the presence of a coenzyme cobalamin-dependent enzyme, leucine-2,3-aminomutase in *Phaseolus vulgaris*, *Solanum tuberosum*, and *Candida utilis* (Poston 1978; Poston and Hemmings 1979). Several functions were indirectly demonstrated, while others only show a potential.

1. Several rhizobacteria produce cobalamin, yet it is unknown whether the bacteria are the sole users or perhaps have some effects on plants or the plant–bacteria interaction process is the beneficiary, so that the plant is indirectly influenced by cobalamin. It has been known for a very long time that several *Rhizobium* species (Lowe et al. 1960; Lowe and Evans 1962) and legumes (Delwiche et al. 1961; Shaukat-Ahmed 1961) grown without a fixed source of nitrogen require cobalt for normal growth. *Sinorhizobium meliloti* and nodules of seven legumes and alder contain a cobamide coenzyme (Kliewer and Evans 1963a) that serves as a cofactor for enzymatic conversion of glutamate to β-methyl aspartate during the synthesis of amino acids. Thus, cobalamin in plant nodules suggests that cobalamin is important during the nitrogen-fixation process (Kliewer and Evans 1963b). A *Sinorhizobium meliloti bluB* mutant, defective in the *bluB* gene, suggests that this gene is involved in the synthesis of cobalamin because, when the mutant fails to establish a symbiosis with alfalfa, the defect can be reversed by adding vitamin B_{12} or the lower ligand of cobalamin, 5,6-dimethylbenzimidazole. Consequently, presence of cobalamin-dependent enzymes is essential for invading alfalfa plant cells by *Sinorhizobium meliloti* (Campbell et al. 2006).

2. Cobalamin functions as an essential cofactor in chloroplasts, mitochondria, microsomes, and cytosol of the photosynthetic protozoan *Euglena gracilis* and the periwinkle *Catharanthus roseus*. Cobalamin also functions as a cofactor in methionine synthetase, which catalyzes formation of methionine and various methylation reactions (Eichel et al. 1995; Isegawa et al. 1984).
3. Adding vitamin B_{12} to a culture of the marine single-cell microalga *Pleurochrysis carterae* led to conversion of most of the B_{12} to the coenzyme forms of B_{12}, including methylmalonyl-CoA mutase, which acts in fatty acid metabolism (Miyamoto et al. 2002).
4. Finally, cobalamin produced by three *Rhizobium* spp. isolated from a forest soil was found to enhance methane oxidation by the aerobic methanotroph *Methylovulum miyakonense* (Iguchi et al. 2011). Methanotrophs play a key role in the global carbon cycle, in which they affect methane emissions and help to sustain diverse microbial communities by converting methane to organic compounds. Aerobic methanotrophs are the major microorganisms responsible for the methane sink and are widespread in many ecosystems. Thus, microbial interactions, through cobalamin, play a role in methane oxidation in at least some ecosystems.

Biotin (vitamin B_7)

The principal function of this vitamin is as a cofactor for three classes of carboxylases that bind CO_2 as a bicarbonate. It is produced by microorganisms and plants, but not by animals; it regulates its own synthesis at very low concentrations of itself (Knowles 1989).

In microorganisms, D-biotin is synthesized from L-alanine and pimelic acid through pathway intermediates pimeloyl-CoA, 7-keto-8-aminopelargonic acid, 7,8-diaminopelargonic acid, and D-dethiobiotin (Roje 2007; Sakurai et al. 1993). The genes involved in biotin synthesis are generally located in the *bio* operon (Guillén-Navarro et al. 2005; Sullivan et al. 2001), which is subjected to strict feedback repression by biotin (Sakurai et al. 1993). The orthodox pathway, common to many microorganisms, including rhizobia, *Mesorhizobium loti*, and *Bradyrhizobium japonicum*, involves four enzymes. These are the products of *bioF* (BioF; 8-amino-7-oxononanoate synthase), *bioA* (BioA; 7,8-diaminopelargonic acid synthase), *bioD* (BioD; dethiobiotin synthase), and *bioB* (BioB; biotin synthase) (Guillén-Navarro et al. 2005). Biotin synthesis in *Sinorhizobium meliloti* is limited by poor functioning or complete absence of the key genes *bioA*, *bioC*, *bioD*, or *bioZ*, while *bioB* and *bioF* genes are not localized in a biotin-synthesis operon. However, Entcheva et al. (2002) suggested that *S. meliloti* can grow in exogenous biotin because genes *bioM* and *bioN* are present; they play an important role in biotin transport. In *E. coli* and many enteric bacteria, the *bio* operon is bidirectional. The rightward transcription unit includes the genes *bioB*, *bioF*, *bioC*, and *bioD* and the leftward transcription unit includes the *bioA* gene and an additional open reading frame, *orfX*, whose function is not clear. A sixth gene (*bioH*) is located in a different part of the genome (Streit and Entcheva 2003).

Biotin production has been reported in PGPB, including *Pseudomonas fluorescens*, *Sinorhizobium meliloti*, *Mesorhizobium loti*, *Mesorhizobium* sp., *Bradyrhizobium japonicum*, *Bacillus subtilis*, *Achromobacter* sp., *Azotobacter vinelandii*, *Azotobacter chroococcum*, and *Azospirillum* spp. (Dahm et al. 1993; Entcheva et al. 2002; Frappier and Marquet 1981; Gonzalez-Lopez et al. 1983; Guillén-Navarro et al. 2005; Heinz et al. 1999; Marek-Kozaczuk and Skorupska 2001; Revillas et al. 2000; Sakurai et al. 1993; Streit and Entcheva 2003; Sullivan et al. 2001).

Possible role of biotin in plant–PGPB interaction

Despite its basic role as a cofactor for carboxylases, its role in the PGPB–plant interaction is yet to be found. During an interaction between plant and PGPB in the rhizosphere, the sole function reported for this vitamin is a signal molecule for rhizobia. For *Sinorhizobium meliloti*, biotin is not essential but promotes growth in culture medium and soil. When the population of these species in soil is low, plant-derived biotin in alfalfa is an important factor that stimulates growth of *S. meliloti* in the rhizosphere and promotes root colonization (Streit et al. 1996). The biotin produced by plants acts as a signal molecule and induces the expression of the *bioS* gene, a biotin-inducible gene that affects competitive growth and biotin uptake and accumulation. The latter happens at the stationary phase of growth of this bacterium, where it is expressed most strongly (Heinz et al. 1999; Streit and Phillips 1997). The BioS protein is probably involved in sensing plant-exuded biotin. This further indicates a possible role of biotin in the signaling process between plant and bacterium and possible involvement in the nodulation process (Heinz et al. 1999). In the presence of biotin, the BioS protein can be detected in the cell. Yet, under biotin-limiting conditions, BioS protein is almost undetectable. Under biotin-limiting conditions, rhizobial cells are filled with polyhydroxybutyrate (PHB) granules, the typical carbon storage compound of free-living *S. meliloti*, other species of rhizobia (Encarnación et al. 1995), and numerous other PGPB (Tal and Okon 1985; Castro-Sowinski et al. 2010). When biotin exudes from plants, its availability to the bacteria induces the use of the internal PHB in *S. meliloti*. This provides more energy for the bacterium to compete in the rhizosphere. This induction happens by expression of 3-hydroxybutyrate dehydrogenase, which is central to PHB degradation in *S. meliloti*. This enzyme is regulated by the

availability of biotin. As a result of this process, a rapid catabolism of stored PHB, in response to plant-exuded biotin, allows the bacterium to rapidly colonize the plant rhizosphere and contribute immediately to root nodule formation and N_2 fixation (Hofmann et al. 2000).

Pantothenic acid (vitamin B_5)

Pantothenic acid is a metabolic precursor to coenzyme A (CoA) and acyl carrier protein, which are cofactors required by a large number of metabolic enzymes (White et al. 2001). Biosynthesis of pantothenic acid occurs in microbes and plants only, whereas animals obtain it in their diet.

In bacteria, pantothenic acid is synthesized by the condensation of pantoic acid, derived from α-ketoisovalerate, an intermediate in valine biosynthesis, and β-alanine, produced by the decarboxylation of L-aspartate (Primerano and Burns 1983; White et al. 2001). The *panB-E* genes encode the four enzymes required for pantothenic acid biosynthesis, and were first described in *Salmonella typhimurium* and *E. coli* (Cronan et al. 1982).

Among the PGPB that produce pantothenic acid are *Pseudomonas fluorescens*, *Azotobacter vinelandii*, *Azotobacter chroococcum*, *Sinorhizobium meliloti*, *Rhizobium* spp., *Azospirillum brasilense*, and *Azospirillum* spp. (Dahm et al. 1993; Marek-Kozaczuk and Skorupska 2001; Martinez-Toledo et al. 1996; Revillas et al. 2000; Rodelas et al. 1993; Sierra et al. 1999).

Possible role of pantothenic acid in plant–PGPB interaction

Little is known about this interaction. Over seven decades ago, *S. meliloti* was reported to produce and provide pantothenic acid that may have a significant effect on carbohydrate anabolism, but without experimental evidence of the latter (McBurney et al. 1935). No further study has been done since then.

Niacin (vitamin B_3)

The term "niacin" is accepted as a broad descriptor of vitamers that have the biological activity associated with nicotinamide, which includes nicotinic acid and a variety of pyridine nucleotide structures (Kirkland 2007). The biologically active forms of niacin compounds are the nicotine adenine dinucleotide (NAD) and nicotine adenine dinucleotide phosphate (NADP) coenzymes, which intervene virtually on every metabolic pathway in the cell (Noctor et al. 2006).

Most microorganisms can synthesize the pyridine ring of NAD de novo from aspartic acid and dihydroxyacetone phosphate. *Pseudomonas fluorescens*, *Azospirillum brasilense*, *Azotobacter vinelandii*, *A. chroococcum*, *Sinorhizobium meliloti*, and *Rhizobium* spp. are some of the bacteria known as potential PGPB that produce niacin (Marek-Kozaczuk and Skorupska 2001; Revillas et al. 2000; Rodelas et al. 1993; Sierra et al. 1999).

Possible roles of niacin in plant–PGPB interaction

The most important function of niacin is production of cofactors that participate in diverse cellular oxidation–reduction reactions (Kirkland 2007) and have potential importance under stress conditions (Noctor et al. 2006), where PGPB are known to mitigate stress in many plant species, including microalgae (Bashan and de-Bashan 2005; de-Bashan and Bashan 2008; de-Bashan et al. 2005; Lucy et al. 2004). Another function of niacin is to act as a promoter of root colonization and nodulation of red clover by *Rhizobium leguminosarum* bv. *trifolii* (Marek-Kozaczuk and Skorupska 2001).

Other vitamins

Ascorbic acid (vitamin C)

Ascorbic acid acts as an antioxidant by directly scavenging reactive oxygen species, which are formed from photosynthetic and respiratory processes and by regenerating α-tocopherol in plant cells (Ghosh et al. 2008; Rao and Sureshkumar 2000). In plants, it participates in a variety of processes, including photosynthesis, photoprotection, cell wall growth and cell expansion, resistance to environmental stresses, and synthesis of ethylene, gibberellins, anthocyanins, and hydroxyproline (Smirnoff and Wheeler 2000).

Although the direct biosynthesis of ascorbic acid from a carbohydrate source by yeast, plant, and animal cells is well documented, it has not been widely found in bacteria (Rao and Sureshkumar 2000; Smirnoff and Wheeler 2000). Rao and Sureshkumar (2000) report a direct biosynthesis of ascorbic acid from glucose by *Xanthomonas campestris* as an adaptive response to induced free radicals. Some bacteria that may be PGPB, such as *Gluconobacter*, *Acetobacter*, *Pseudomonas*, and *Bacillus megaterium*, are able to transform D-glucose, D-sorbitol, or L-sorbose to 2-keto-L-gulonic acid (2-KLGA) in a very efficient way, a key intermediate that can be converted to L-ascorbic acid by esterification (Bremus et al. 2006; Lee and Pan 1999). Ghosh et al. (2008) propose that *Rhizobium* spp. could also produce ascorbic acid from glucose in nodules.

Possible roles of ascorbic acid in plant–PGPB interaction

Because many potential PGPB can synthesize intermediates of ascorbic acid, it is possible that these bacteria may facilitate production of this vitamin by plants. Two potential roles of this vitamin, which is most abundant in green leaves, are listed here.

1. Antioxidant during photosynthesis. Initially, Mapson (1962) proposed that ascorbic acid and its oxidized forms function as electron carriers in plant respiration and as an electron transferring system during photosynthesis. Later, the specific role of ascorbate was described as antioxidant in photosystems I and II. The mechanism by which this vitamin acts is that the H_2O_2 that is produced is reduced to water by ascorbate catalyzed with ascorbate-specific peroxidase (Asada 1999). In alfalfa, pea, common bean, and lotus, ascorbate in the infected zone of the nodule is primarily involved in the protection of host cells against peroxide damage. Likewise, the high ascorbate and levels of the enzyme L-galactono-1,4-lactone dehydrogenase that catalyze the last step of ascorbate biosynthesis in plants is found in the apex of indeterminate nodules, which suggests participation of ascorbate in additional functions during symbiosis, possibly related to cell growth and division (Matamoros et al. 2006). Similarly, the root nodules of black gram *Phaseolus mungo*, an herbaceous leguminous pulse, contain high amounts of ascorbic acid, where the respective *Rhizobium* sp. could produce ascorbic acid in vitro at high quantities. Part of the nodular ascorbic acid may have been contributed by the host. Yet, the host plant may further induce the symbiont to produce excess ascorbic acid when necessary for its own benefit (Ghosh et al. 2008). Ascorbic acid also has a role as a protectant against ozone by reducing cellular damage. Sensitivity to ozone is correlated with total ascorbic acid levels, and a first line of defense against reactive oxygen species generated in the apoplastic space in leaves by ozone is ascorbic acid. For activity in situ, ascorbic acid must be in a highly reduced state (Conklin and Barth 2004).
2. Modulator of plant defenses. In *Arabidopsis* plants deficient in ascorbic acid, many defense genes are activated, specifically those that encode pathogenesis-related proteins and those related to synthesis of salicylic acid, which elicits systemic acquired resistance to the pathogen. By modifying gene expression, vitamin C not only acts to regulate defense, but also acts via phytohormones to modulate plant growth under optimal conditions (Barth et al. 2004; Pastori et al. 2003). Higher levels of glutathione and ascorbic acid in salicylic acid-deficient *Arabidopsis* plants may contribute to alleviate symptoms against RNA virus infections (Wang et al. 2011).

Pyrroloquinoline quinone (methoxatin)

Pyrroloquinoline quinone is an aromatic, tricyclic orthoquinone that serves as the redox cofactor for several bacterial dehydrogenases (Puehringer et al. 2008). Kasahara and Kato (2003) identified a PQQ-dependent dehydrogenase enzyme crucial for the degradation of the amino acid lysine in mice. Consequently, they suggested PQQ should be placed in the B group of vitamins; however, its role as a vitamin has been challenged (Rucker et al. 2005, 2009). Tyrosine and glutamic acid may be the precursors of bacterial PQQ; however, the biosynthetic pathway of PQQ has not yet been fully solved (Goosen et al. 1989; Meulenberg et al. 1992; Velterop et al. 1995). Although a number of *pqq* genes (*pqqABCDEF*) involved in PQQ biosynthesis have been isolated from several bacteria, the biological function of the encoded proteins is largely unknown (Choi et al. 2008; Meulenberg et al. 1992; Velterop et al. 1995). The amount and type of genes that are involved, as well as their regulation at transcriptional level, depends on microbial species (Biville et al. 1989; Gliese et al. 2010; Goosen et al. 1989; Meulenberg et al. 1992; Ramamoorthi and Lidstrom 1995;). The potential PGPB that have to be studied for PQQ synthesis are *Acinetobacter calcoaceticus*, *Acinetobacter iwoffi*, *Azotobacter vinelandii*, *Rhizobium* spp., *Pseudomonas fluorescens*, and *Pseudomonas* spp. (Choi et al. 2008; Goosen et al. 1989; Van Schie et al. 1987; Schnider et al. 1995).

Possible roles of PQQ in plant–PGPB interaction

The main function of this compound is as a cofactor in several bacterial dehydrogenases (Smidt et al. 1991). PQQ can act indirectly to promote growth of plants by enzyme PQQ synthase. The metabolic function of the PQQ synthase is the biosynthesis of the cofactor PQQ, which is necessary for the assembly of glucose dehydrogenase (GDH), which acts in the oxidation of glucose to gluconic acid (Rodríguez et al. 2000). The latter is the major organic acid involved in phosphate solubilization (Bashan et al. 2013). However, this venue has to be shown in plants.

There have been few studies of the functional roles of PQQ in plants, which can act directly as a plant growth-promoting factor. Wild-type *Pseudomonas fluorescens*, isolated from the roots of graminaceous plants, produces PQQ, whereas mutants defective in plant growth promotion do not. Inoculation of wild-type *P. fluorescens* on tomato (*Solanum lycopersicum*) plants cultivated in a hydroponic system significantly increased several plant growth parameters, whereas none of the strains that did not produce PQQ promoted growth of tomato. Synthetic PQQ conferred a significant increase in the fresh weight of cucumber (*Cucumis sativus*) seedlings. Treatment of cucumber leaf disks with PQQ and wild-type *P. fluorescens* resulted in scavenging of reactive oxygen species and hydrogen peroxide, suggesting that PQQ acts as an antioxidant in plants (Choi et al. 2008). A mutant strain of an undefined bacterium from Pakistan, defective in the *pqq* gene, could not stimulate growth of the mung bean *Vigna radiata*, compared to the wild-type strain with this gene, which stimulated 25 % improvement in growth the of mung bean (Ahmed and Shahab 2010).

Conclusions and future research avenues

In contrast to the vast knowledge on the role of vitamins in human and animal nutrition, less is known of their role in bacteria, and very little is known about their potential roles in the interactions of PGPB and plants. Less than a dozen vitamins have been detected in PGPB or potential PGPB, and several of these only have a potential role in these interactions. The hypothesis of all the studies listed in this review is based on the assumption that an organism will not synthesize any compound unless it is essential for its metabolism, function, or interaction with its environment. The roles of these vitamins, some produced in large quantities in in vitro culturing, have yet to be discovered.

There are many reasons for PGPB to synthesize vitamins. Apart from self-consumption for its metabolism, several vitamins facilitate interaction with plants, essential parameters for living and survival of these bacteria. A healthier plant provides more exudates, which supports a larger bacterial community (including the PGPB), thus reducing predation and increasing survival.

Because vitamins are needed in minute quantities and some plants are self-sufficient in most, presumably the role of the PGPB is to provide the vitamins for specific functions within plant–PGPB interactions. Consequently, highly valuable research themes might be the following:

- Define which vitamin is produced in situ in the presence or absence of the plant. Production of most vitamins was demonstrated only in culture media with mostly an unlimited supply of carbon sources.
- Determine at what concentration these vitamins are involved in PGPB–plant interaction.
- Less than a dozen vitamins are produced by PGPB in vitro. Because there are many more vitamins, perhaps some of them are produced only in situ and are not produced in vitro; thus, they escape detection by current methods.
- Develop techniques to detect these vitamins in situ in inoculated plants. Most studies of vitamins involve animals or bacteria in culture media, using techniques specific for these fields. Furthermore, because molecular structures of the same vitamins produced by the plant or a PGPB are similar, but not always identical, there is a need to develop techniques sensitive enough to distinguish between vitamins that are exclusively synthesized by prokaryotes and those which can be produced by plants and PGPB.
- Some derivatives or degradation products of vitamins also affect plant metabolism. A search for them in other vitamins will open the field for other options.
- In many cases, it is not realistic to trace vitamins or their degradation products in plants. Consequently, genetic studies using mutants and also cloning biosynthetic operons in strains that are deficient in the respective vitamin biosynthesis pathway are needed.
- Sometimes, it is unclear why a PGPB is producing a vitamin where the plant is capable of producing this vitamin. What is the benefit of each partner from this capacity?
- Knowledge of the role of vitamins is common in human/animal sciences because of their importance. Less is known about their role in plants and substantially less in PGPB–plant interactions. Some of the established roles of vitamins as cofactors of universal enzymes and antioxidants processes in plants and animals should be tested for their interactions.
- As genome information of various PGPB becomes increasingly available, it would be worthwhile to screen whole genome data of sequenced PGPB for the presence of involved genes.
- Use of vitamins produced by plants for the benefit of their associated PGPB is unknown and should be explored.
- In the rhizosphere, plants sustain a careful balance with their adjacent environment and react to chemical signals emitted by the soil microbiome, including PGPB. These signals are received and recognized, and then the plant responds via the release of root exudates of many kinds (Brimecombe et al. 2007; Chaparro et al. 2012). In this dynamic process, vitamins naturally released by both plants and PGPB are hypothetically part of the "dialogue" and yet to be explored.

The importance of vitamins in PGPB/rhizobia–plant interactions is at an emerging stage, even if they were sporadically studied over many decades. The amount of knowledge we have does not permit a critical analysis about their importance in these interactions before more data is collected. Consequently, this field is at the exploratory stage.

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