

Ureide metabolism in plant-associated bacteria: purine plant-bacteria interactive scenarios under nitrogen deficiency

María Luisa Izaguirre-Mayoral · George Lazarovits ·
Bikash Baral

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Abstract

Background The erratic alterations in climate being experienced in agriculture, such as extended periods of drought or heavy rainfalls, are bringing increasing concerns about nitrogen (N) management. Even in high-input farming systems, unpredictable weather patterns can cause N deficiencies and result in nutrient losses that contribute to major pollution issues in groundwater, lakes, and even the oceans. Our present understanding of the beneficial interactions between N-deficient-challenged plants and plant-associated bacteria (PAB), mainly of the phyla Actinobacteria, Bacteroidetes, Firmicutes, and Proteobacteria, is largely based on

studies performed at the level of whole-plant fitness and impacts of crop yields via the abilities of bacteria to synthesize indole acetic acid and/or produce the enzyme 1-aminocyclopropane-1-carboxylate deaminase which reduces endogenous ethylene levels. Much less is known about the complex interaction that occur from the PAB's abilities to produce N ureide (allantoin and allantoate) and how these purine intermediaries function as an N source and prime stress signals for the growth of both partners.

Methods This review examines the noteworthy progress made on understanding the bacterial ureide pathway with the aim to elaborate possible scenarios to unravel the complex nature of PAB-plant interactions at the purine level. Tables with updated information on PAB growth-promoting activities, N metabolism, and abilities to hydrolyze purine intermediates as well as allantoin for colony growth are included.

Results As in plants, the metabolism of ureides in PAB covers the pathways from the deamination of the nucleobase guanine up to its conversion into glyoxylate, NH_4^+ , and/or NH_3 to recycle C and N. More important, in PAB, the full set of riboswitch-modulated genes encoding the enzymes involved in the synthesis and catabolism of ureides, as well as purine transporters, is expressed primarily under stressful conditions leading to N deficiency. Thus, PAB might act as a stress-induced source of purines for the plant N metabolism, or could become scavengers of the plant-synthesized purines for colony replication. Consumption of purine intermediaries or ureides by PAB may hinder the symbiotic

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M. L. Izaguirre-Mayoral
Academia de Ciencias de America Latina, Palacio de las
Academias, Distrito Federal, Apartado Postal 1121-A, Caracas,
Venezuela

G. Lazarovits
A&L Biologicals, Agroecological Research Services Centre,
London, ON N5V 3P51, Canada

B. Baral (✉)
Department of Biochemistry, University of Turku, 20500 Turku,
Finland
e-mail: bikash.baral@utu.fi

efficiency of rhizobia-nodulated N₂-fixing legumes. The impact of soil xanthine, hypoxanthine, and allantoin pools on the plants or PAB ureide synthesis is also discussed.

Conclusions Given widespread concerns for crop losses due to the drastically changing climate and prevailing agricultural practices, the understanding of the interactive signaling for the purine metabolisms between PAB and plants takes on a major importance, as it may support management decisions necessary to maintain PAB biodiversity and the agricultural services provided by PAB to crops.

Keywords ACC deaminase · Allantoin · Growth-promoting bacteria · Indole acetic acid · N₂-fixers · Xanthine · Hypoxanthine

Introduction

Nitrogen (N) is a crucial factor limiting crop productivity in many terrestrial ecosystems and its availability in soils largely depends on the rates of the microorganisms driven mineralization of organically bound N into plant-available inorganic forms of ammonium (NH₄⁺) and nitrate (NO₃⁻) (Cronan 2018). However, there is an increasing concern about the more frequent occurrence of N deficiency in agricultural soils, even in farming systems with large inputs of N fertilizer, as a result of more frequent and severe drought spells brought about by climate change (Wang et al. 2018) that negatively impacts soil microbial biomass (Nguyen et al. 2018). Even transitory reductions in the amount of rainfall decrease the size of soil microbial populations as well as the plant microbiome recruitment traits (Naylor and Coleman-Derr 2018; Ren et al. 2018). Evidences to support the negative impact of drought on the size of soil microbial populations involved in N cycling are (i) the reduced activity of microbial urease enzyme involved in the hydrolysis of urea to CO₂ and NH₃ in dry soils (Xue et al. 2017) and (ii) the negative correlation between aridity and the gross soil N mineralization ($p < 0.01$) or NH₄⁺ immobilization ($p < 0.05$) (Kou et al. 2018). This situation is also complicated by the accumulation of high salt concentrations in drying soils that negatively impact soil microbial activity limiting soil N mineralization (Numan et al. 2018). Seasonal drought and salinity are known to be accompanied by soil N deficiency and this also negatively impacts plant

growth, physiology, and N-ureide metabolism (Baral and Izaguirre-Mayoral 2017). Moreover, carbon (C) starvation of belowground organs and soil microorganisms (brought about by the reductions in photosynthesis created under drought and salinity) enhances competition for the limited soil N between soil microbiome and active roots (Simon et al. 2017).

To survive under stressful conditions, plants and plant-associated bacteria (PAB) developed adaptative-strategic associations via inter- and intraspecies signaling as well as the modulation of plant immunity process to allow PAB to colonize the surface of roots (rhizospheric) and leaves (phyllospheric) and/or different plant tissues (endophytic) (Chagas et al. 2018; Fitzpatrick et al. 2018). In general, soils are largely the main source of bacterial diversity, with the greatest plethora of potentially effective PAB being concentrated in the bulk soil (Castellano-Hinojosa et al. 2016; Rauwane et al. 2017). The largest, but less diverse microbial populations occur in the rhizosphere. Selection here is linked to utilization of plant nutrient sources, but such organisms are also under the influence of faster dehydration associated to salinity brought about by the increased plant transpiration rates required to sustain low stomatal resistance during drought spells (Ibekwe et al. 2017). This can result in the survival of only abiotic stress-tolerant bacteria, as constrained also by the selection of plant genetic traits (Wu et al. 2018). However, to maintain metabolic functionality under these stressful N-deficient conditions, the stress-tolerant bacteria should enhance their rates of soil N uptake to mineralize C causing a severe N mining of the plant-available soil N (Meyer et al. 2017; Simon et al. 2017). Overall, interactions between prevailing environmental conditions and various operons within the bacterial N-regulation system (*ntr*), responsible for the degradation and/or uptake of diverse N sources, seem to be the key factors to modulate N utilization and production of N scavenging enzymes in bacteria (Ghosh et al. 2017). The expression of at least nine genes associated to the N metabolism allows *Brucellas abortus* to survive under culture conditions of nutrient starvation (Zai et al. 2017).

PAB species belonging to the phyla Actinobacteria (Supplemental Table S1), Bacteroidetes (Supplementary Table S2), and Firmicutes (Supplementary Table S3), as well as subphyla α , β , and γ -Proteobacteria (Supplementary Tables S4, S5, S6) are commonly found in all agricultural soils (de Matos et al. 2017). The

phylum Actinobacteria plays an important role as soil organic matter decomposers; whereas, the phyla Firmicutes and Proteobacteria, generally categorized as copiotrophs—fast growing organisms—prefer soil C-rich environments as energy source to sustain high growth rates (Rebollar et al. 2017). Plants also host a consortium of a taxonomically diverse group of PAB, all positively strengthening the performance of abiotically challenged plants (Numan et al. 2018; Shameer and Prasad 2018), mostly of the genera *Acinetobacter*, *Alcaligenes*, *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Beijerinckia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, and *Serratia*. Members of the *Curtobacterium* genus were described mainly in the phyllosphere and seldom are associated with roots or as endophytic symbionts (Chase et al. 2016). A typical example of PAB was reported for plants of the *Poaceae* family (maize, wheat, pearl millet, sorghum, and rice) of Gujarat region in India revealing the average presence of 37% Actinobacteria (*Aeromicrobium* sp., *Arthrobacter* sp., *Microbacterium* sp., *Staphylococcus* sp.), 23% β -Proteobacteria (*Achromobacter* sp. and *Ralstonia* sp.), 20% α -Proteobacteria (*Rhizobium* sp., *Brevundimonas* sp., and *Methylobacterium* sp.), 10% γ -Proteobacteria (*Acinetobacter* sp., *Pseudomonas* sp., and *Pantoea* sp.), and 10% Firmicutes (*Streptomyces* sp. and *Bacillus* sp.) (Patel and Archana 2017). For agricultural purposes, the positive synergism shown by PAB consortia on stress-challenged plants, when compared with single bacteria inoculations, may be most promising for increasing crop fitness (Chinnaswamy et al. 2018; Hajnal-Jafari et al. 2018). Moreover, the consortia of bacterial endophytes in seeds are of particular importance because they facilitate seed germination in stress-constrained soils and are the source of inoculum to successive plant generations via vertical transmission (see *Plant and Soil* special issues 1–2 Volume 422, January 2018). Noteworthy is the influence of belowground PAB on floral traits that mediate interactions between plants and pollinators (Rolli et al. 2015), and the impact of the size of soil particles on the bacterial diversity found in soils (Hemkemeyer et al. 2018). The mechanisms for the entry of PAB to plant cells and their translocation to different plant organs were recently discussed by Chagas et al. (2018) and Rodríguez et al. (2018).

The magnitude of the positive effects exerted by PAB on drought- and salinity-challenged plants seems to be enhanced by the bacterial ability to cleave plant-synthesized 1-aminocyclopropane-1-carboxylate

(ACC), the immediate biosynthetic precursor of ethylene, into NH_3 and α -ketobutyrate via the enzyme ACC deaminase (ACCD), as a way to use this additional N source (Nascimento et al. 2018). Bacterial ACCD is a sulfhydryl multimeric enzyme with a monomeric subunit molecular mass between 35 and 42 kDa and pyridoxal 5-phosphate as co-factor encoded by *acdS* genes (Soni et al. 2018). In *Sinorhizobium meliloti*, *acdS* has a polyphyletic origin obtained through horizontal gene transfer, its expression is induced by root exudates of legumes and non-leguminous plants, and it is negatively regulated by a putative leucine-responsive regulator (LrpL) located upstream to *acdS* sequence (*acdR*) (Checcucci et al. 2017). High rates of ACCD production under drought and salinity conditions were reported in *Bacillus simplex* (Soleimani et al. 2017), and ACCD activity linked to plant growth-promoting traits was described for the first time in the genus *Citrobacter* and *Empedobacter* isolated from wheat rhizosphere (Gontia-Mishra et al. 2017). In the case of drought-challenged rhizobia-nodulated legumes, the presence of PAB expressing ACCD activity counteracts the negative effects of high ethylene levels on root nodulation (Nascimento et al. 2018). On the other hand, synthesis of indole acetic acid (IAA) in PAB is enhanced under conditions of limited N (Otanga et al. 2018) and plays a pivotal role on PAB promoting plant growth. The negative effects of drought and salinity seem to be further counteracted in plants co-inoculated by PAB expressing ACCD activity and IAA production, in spite of the IAA stimulating the activity of ACC synthase in plants (Vargas et al. 2017). Bacteria expressing ACCD activity and/or producing IAA are listed in Supplementary Tables S1 to S6.

In parallel, N-deficient crops may also benefit from the N_2 -fixing abilities in a large number of PAB belonging to the agriculturally important α -Proteobacteria (order Rhizobiales) in symbiosis mainly with legumes and β -Proteobacteria (order Burkholderiales) as well as in the phylum Firmicutes (Order Bacillales) (Supplementary Tables S1–S6). In nodulated N_2 -fixing legumes, the effectiveness of the symbiosis with rhizobia, nutrient uptake, and seed yield are enhanced by the plant co-inoculation with non- N_2 -fixing PAB such as *Streptomyces griseoflavus* (Htwe et al. 2018). The use of the *nifH* gene encoding the nitrogenase reductase subunit, the most widely established molecular marker for the study of N_2 -fixing prokaryotes, as indicator of the N_2 -fixing properties of PAB was recently questioned

(Emmyrafedziawati and Stella 2018). In the case of nodulated N_2 -fixing legumes, the abundance of C and N in the root exudates triggers the profusion of rhizospheric PAB (Gao et al. 2017). Moreover, the N_2 -fixing nodules in legumes are C, N, and phosphorus (P) enriched and thus are readily colonized by diverse groups of PAB in intimate co-existence with the nodulating rhizobia (Table 1). As indicated by Xiao et al. (2017), the taxonomic composition of nodule endophytes is primarily determined by plant species. Although, new evidences suggest the predominant influence of the soil type as major driver for the composition of the microbiome associated to root nodules (Leite et al. 2017). This suggestion is further supported by the direct effect of soil N on the percentage of nodule occupancy by non-rhizobial bacteria ranking from 56 to 87% in low N to less than 50% in high N grown *Dalbergia odorifera* (Lu et al. 2017).

An exhaustive review of the published literature on plant-PAB interactions points out growth and crop yield responses under drought or salinity conditions as the main focus of experimental investigations (i.e., Batista et al. (2018); Etesami (2018); Bounaffaa et al. (2018)). Much less is known about the N pathways and possible N signalings mediating interactions between the plant and its PAB. As reviewed by Baral and Izaguirre-Mayoral (2017), ureides (allantoin and allantoate) enhance the tolerance of legumes and non-legumes to drought and salinity stress, mainly due to the allantoin function as N source and as prime signal for the induction of plant defense mechanisms. Nevertheless, ureides are not an exclusive N product of the purine metabolism in N_2 -fixing plants since many bacteria harbor the full set of genes encoding for the activity of enzymes and purine transporters involved in the synthesis and catabolism of ureides, triggered by stressful conditions like N deficiency (Petridis et al. 2015; Ma et al. 2016). Therefore, we propose that a key role is played by the production of bacterial N ureides. In most bacteria, the purine metabolism covers steps from the deamination of the nucleobase guanine up to its final conversion of the N intermediate into glyoxylate, NH_4^+ , and/or NH_3 , allowing cells to recover C and N. Curiously, while purine metabolism is acknowledged as an important survival trait for microbes grown in stressed environments, its explicit consequences for plants are not addressed in most studies. However, identifying the roles of bacterially produced ureides is complicated by the fact that plants simultaneously produce precisely the same

purine molecules. Thus, this review will present noteworthy progress on understanding the bacterial ureide synthesis and catabolism with the final aim to elaborate possible scenarios to unravel the complex nature of bacterial-plant interactions, at the purine level. Due to the complexity of the microbiome associated with plants, the analyses of the purine metabolism will concentrate mainly on bacteria, with emphasis on the bacterial species or isolates fully identified with 98–100% similarity with reference strains. The names of the bacterial species are mentioned as in the cited references, although we are aware of the recent re-classification of a number of *Pseudomonas* and *Azospirillum* strains into different genospecies (Tran et al. 2017; Maroniche et al. 2017) as well as of the split of the genera *Burkholderia* and *Paraburkholderia* (Martinez-Hidalgo and Hirsch 2017).

Bacterial ureide synthesis

Description of the four metabolic steps for the synthesis of ureides

In a similar way to plants, ureide synthesis in bacteria takes place in four consecutive enzymatic steps (see Fig. 3 in Baral et al. (2016)). The first step, described in *Bacillus subtilis*, is the deamination of guanine to hypoxanthine catalyzed by the enzyme guanine deaminase (Rivas et al. 2018). For this step, guanine riboswitches (Gong et al. 2018) regulate the transcription of *xpt-pbuX* operon in *B. subtilis*, *Staphylococcus aureus* and in the vast majorities of Firmicutes (Kofoed et al. 2016; Laney and Morse 2017; Kirchner and Schneider 2017). The second step is the conversion of hypoxanthine into xanthine and then to uric acid by the enzyme xanthine oxidoreductase (XOR) that occurs in two isoforms: the xanthine dehydrogenase (XDH) and the xanthine oxidase (XO). The third step consists of three major enzymatic reactions: (i) the oxidation of the uric acid to 5-hydroxyisourate (HIU) via a coenzyme-independent enzyme urate oxidase (UOX), also known as uricase, in a two stage—oxidation followed by hydration—in *B. subtilis* and *B. fastidiosus* (Wei et al. 2016); (ii) the conversion of HIU to 5-hydroxy-2-oxo-4-ureido-2,5-dihydro-1H-imidazole-5-carboxylate (OHCU) catalyzed by the putative xanthine upregulated tranthyretin-related proteins 5-hydroxyisourate hydrolase as in *Escherichia coli* (Urano et al. 2015); and, (iii) the stereoselective decarboxylation of OHCU to the

Table 1 Examples of endophytes, besides well-known rhizobia, isolated from root nodules of legumes and actinorhizal plants

Host	Nodule endophytes	References
<i>Abrus precatorius</i>	<i>Ensifer abri</i> , <i>Rhizobium tropici</i>	(Bautista et al. 2017; Suneja et al. 2017)
<i>Acacia abyssinica</i>	<i>Mesorhizobium abyssinicae</i> , <i>M. shonense</i>	(Peix et al. 2015)
<i>Acacia angustissima</i>	<i>Ensifer mexicanus</i>	(Peix et al. 2015)
<i>Acacia salicina</i> , <i>Acacia stenophylla</i>	<i>Achromobacter xylosoxidans</i> , <i>Acinetobacter haemolyticus</i> , <i>Brevibacillus brevis</i> , <i>Caulobacter vibrioides</i> , <i>Chitinophaga sancti</i> , <i>Comamonas testosteroni</i> , <i>Devosia neptuniae</i> , <i>Herbaspirillum frisingense</i> , <i>Microbacterium trichothecenolyticum</i> , <i>Mycobacterium frederiksbergense</i> , <i>Paenibacillus agarexedens</i> , <i>P. amylolyticus</i> , <i>P. glycanilyticus</i> , <i>P. pabuli</i> , <i>Phyllobacterium trifolii</i> , <i>Stenotrophomonas maltophilia</i> , <i>Variovorax paradoxus</i>	(Hoque et al. 2011)
<i>Acacia melanoxylon</i>	<i>Bradyrhizobium ganzhouense</i> , <i>Mesorhizobium acaciae</i>	(Suneja et al. 2017)
<i>Acacia senegal</i>	<i>Ensifer arboris</i> , <i>E. kostiensis</i>	(Peix et al. 2015; Suneja et al. 2017)
<i>Aeschynomene indica</i>	<i>Blastobacter capsulatus</i> , <i>Bradyrhizobium oligotrophicum</i>	(Manju and Prabakaran 2016; Suneja et al. 2017)
<i>Albizia kalkora</i>	<i>Mesorhizobium albiziae</i>	(Suneja et al. 2017)
<i>Alhagi sparsifolia</i>	<i>Mesorhizobium alhagi</i> , <i>M. camelthorni</i>	(Suneja et al. 2017)
<i>Alnus glutinos</i>	<i>Micromonosporae cremea</i> , <i>M. coxensis</i> , <i>M. lupini</i> , <i>M. matsumotoense</i> , <i>M. olivasterospora</i> , <i>M. saelicesensis</i> , <i>M. siamensis</i>	(Trujillo et al. 2015)
<i>Alnus viridis</i>	<i>Micromonosporae chokoriensis</i> , <i>M. coriariae</i> , <i>M. lupini</i> , <i>M. matsumotoense</i> , <i>M. pisi</i> , <i>M. rifamycinica</i> , <i>M. saelicesensis</i>	(Trujillo et al. 2015)
<i>Amorpha fruticosa</i>	<i>Mesorhizobium amorphae</i>	(Suneja et al. 2017)
<i>Alysicarpus nummularifolius</i>	<i>Ensifer mexicanus</i> , <i>Rhizobium etli</i> , <i>Stenotrophomonas maltophilia</i>	(Bautista et al. 2017)
<i>Amphicarpaea trisperm</i>	<i>Rhizobium yanglingense</i>	(Peix et al. 2015)
<i>Anagyris latifolia</i>	<i>Mesorhizobium tamadayense</i>	(Peix et al. 2015)
<i>Anthyllis vulneraria</i>	<i>Aminobacter anthyllidis</i> , <i>Mesorhizobium metallidurans</i> , <i>Rhodococcus strains</i>	(Martinez-Hidalgo and Hirsch 2017; Suneja et al. 2017)
<i>Arachis hypogaea</i>	<i>Bradyrhizobium arachidis</i> , <i>B. guangdongense</i> , <i>B. guangxiense</i> , <i>B. kavangense</i> , <i>B. manausense</i> , <i>B. subterraneum</i> , <i>B. vignae</i> , <i>B. yuanmingense</i> , <i>Inquillinus limosus</i> , <i>Mesorhizobium plurifarum</i> , <i>Rhizobium pakistanensis</i> , <i>R. larrymoorei</i>	(Hossain and Lundquist 2016; Bautista et al. 2017; Suneja et al. 2017; Velázquez et al. 2017a)
<i>Argyrolobium uniflorum</i>	<i>Ensifer garamanticus</i> , <i>E. numidicus</i> , <i>Phyllobacterium leguminum</i>	(Mantelin et al. 2006; Peix et al. 2015)
<i>Astragalus adsurgens</i>	<i>Mesorhizobium septentrionale</i> , <i>M. gobiense</i>	(Suneja et al. 2017)
<i>Astragalus algerianus</i>	<i>Phyllobacterium ifriqiyense</i> , <i>P. leguminum</i>	(Mantelin et al. 2006)
<i>A. chrysopterus</i>	<i>Nocardioides astragali</i>	(Xu et al. 2018)
<i>A. filicaulis</i>	<i>Mesorhizobium gobiense</i>	(Peix et al. 2015)
<i>A. luteolus</i>	<i>Mesorhizobium sangaii</i>	(Suneja et al. 2017)
<i>A. membranaceus</i>		(Yan et al. 2016)

Table 1 (continued)

Host	Nodule endophytes	References
	<i>Mesorhizobium septentrionale</i> , <i>M. tianshanense</i> , <i>Pararhizobium herbae</i>	
<i>A. mongholicus</i>	<i>Mesorhizobium ciceri</i> , <i>M. septentrionale</i> , <i>M. temperatum</i>	(Yan et al. 2016)
<i>A. sinicus</i>	<i>Mesorhizobium huakuii</i> , <i>M. qingshengii</i>	(Suneja et al. 2017)
<i>Biserrula pelecinus</i>	<i>Mesorhizobium australicum</i> , <i>M. opportunistum</i>	(Suneja et al. 2017)
<i>Calliandra grandiflora</i>	<i>Rhizobium calliandrae</i> , <i>R. jaguaris</i> , <i>R. mayense</i>	(Suneja et al. 2017)
<i>Calopogonium mucunoides</i>	<i>Bradyrhizobium elkanii</i> , <i>B. liaoningense</i> , <i>Enterobacter cloacae</i> , <i>Herbaspirillum putei</i>	(Bautista et al. 2017)
<i>Caragana bicolor</i> , <i>C. erinace</i>	<i>Mesorhizobium shangrilense</i>	(Suneja et al. 2017)
<i>Caragana grandiflora</i>	<i>Rhizobium calliandrae</i>	(Suneja et al. 2017)
<i>Caragana intermedia</i>	<i>Neorhizobium alkalisoli</i> , <i>Rhizobium alkalisoli</i>	(Suneja et al. 2017)
<i>Casuarina equisetifolia</i>	<i>Micromonosporae aurantiaca</i>	(Trujillo et al. 2014)
<i>Centrobium paraense</i>	<i>Bradyrhizobium centrolobii</i> , <i>B. macuxiense</i> , <i>B. neotropiale</i>	(Zilli et al. 2014; Michel et al. 2017)
<i>Centrosema macrocarpum</i>	<i>Bradyrhizobium americanum</i>	(Ramírez-Bahena et al. 2016)
<i>Centrosema molle</i>	<i>Bradyrhizobium centrosemae</i>	(Ramírez-Bahena et al. 2016)
<i>Centrosema pubescens</i>	<i>Bradyrhizobium viridifuturi</i>	(Suneja et al. 2017)
<i>Cicer arietinum</i>	<i>Mesorhizobium muleiense</i> , <i>Paenibacillus</i> <i>endophyticus</i> , <i>Serratia marcescens</i>	(Carro et al. 2013; Peix et al. 2015; Zaheer et al. 2016)
<i>Cicer arietinum</i> , <i>Cytisus scoparius</i> , <i>Glycyrrhiza uralensis</i>	<i>Brevibacterium</i> spp., <i>Ochrobactrum</i> spp.	(Martínez-Hidalgo and Hirsch 2017)
<i>Chamaecytisus proliferus</i>	<i>Bradyrhizobium canariense</i>	(Peix et al. 2015)
<i>Clitoria ternatea</i>	<i>Achromobacter xylosoxidans</i> , <i>Bradyrhizobium</i> <i>yuanmingense</i> , <i>Enterobacter cloacae</i> , <i>E. hormaechei</i> , <i>E. turicensis</i> , <i>Rhizobium</i> <i>rhizogenes</i> , <i>Sphingobacterium</i> <i>thalpophilum</i> , <i>Pseudomonas alcaliphila</i> , <i>P. geniculata</i> , <i>Stenotrophomonas</i> <i>maltophilia</i>	(Aeron et al. 2015; Bautista et al. 2017)
<i>Coriaria myrtifolia</i>	<i>Micromonosporae coriariae</i> , <i>M. saelicesensis</i> , <i>M. peucetia</i>	(Trujillo et al. 2014)
<i>Coronilla varia</i>	<i>Rhizobium yanglingense</i>	(Peix et al. 2015)
<i>Crotalaria glaucoides</i> , <i>C. perrottetii</i> , <i>C. podocarpa</i>	<i>Lotononis bainesii</i> , <i>Methylobacterium</i> <i>nodulans</i>	(Jourand et al. 2004)
<i>Crotalaria pallida</i>	<i>Bradyrhizobium elkanii</i> , <i>B. liaoningense</i>	(Bautista et al. 2017)
<i>Cytisus villosus</i>	<i>Bradyrhizobium cytisi</i> , <i>B. rifense</i>	(Peix et al. 2015)
<i>Cytisus scoparius</i>	<i>Ochrobactrum cytisi</i>	(Suneja et al. 2017)
<i>Derris elliptica</i>	<i>Bradyrhizobium yuanmingense</i> , <i>Rhizobium</i> <i>tropici</i>	(Bautista et al. 2017)
<i>Desmodium scorpiurus</i>	<i>Rhizobium etli</i> , <i>R. rhizogenes</i> , <i>Bradyrhizobium liaoningense</i> , <i>B. elkanii</i> , <i>M. plurifarum</i> , <i>Rhizobium tropici</i> , <i>Pseudomonas agglomerans</i>	(Bautista et al. 2017)
<i>Desmodium styracifolium</i>	<i>Rhizobium etli</i> , <i>R. rhizogenes</i>	(Bautista et al. 2017)
<i>Desmodium triflorum</i>	<i>Bradyrhizobium</i> , <i>B. elkanii</i> , <i>B. liaoningense</i> , <i>B. yuanmingense</i> , <i>Rhizobium etli</i> , <i>R. tropici</i> , <i>R. mongolense</i> , <i>R. rhizogenes</i>	(Bautista et al. 2017)

Table 1 (continued)

Host	Nodule endophytes	References
<i>Desmodium heterocarpon</i>	<i>Bradyrhizobium embrapense</i> , <i>B. tropiciagri</i>	(Suneja et al. 2017)
<i>Enterolobium saman</i>	<i>Crabtreeella saccharophila</i> , <i>Ensifer mexicanus</i>	(Bautista et al. 2017)
<i>Erythrophleum fordii</i>	<i>Bradyrhizobium erythrophlei</i> , <i>B. ferriligni</i>	(Suneja et al. 2017)
<i>Galega orientalis</i> , <i>Galega officinalis</i>	<i>Neorhizobium galegae</i> sv. <i>orientalis</i>	(Österman et al. 2014)
<i>Genista saharae</i>	<i>Neorhizobium alkalisoli</i> , <i>N. galegae</i> , <i>N. huautlense</i> , <i>Mesorhizobium camelthorni</i>	(Chaich et al. 2017)
<i>Glycine max</i>	<i>Acinetobacter calcoaceticus</i> , <i>Agrobacterium tumefaciens</i> , <i>Bacillus amyloliquefaciens</i> , <i>B. atrophaeus</i> , <i>B. cereus</i> , <i>B. fastidiosus</i> , <i>B. megaterium</i> , <i>B. mojavensis</i> , <i>B. pumilus</i> , <i>B. subtilis</i> , <i>B. vallismortis</i> , <i>Bradyrhizobium ottawaense</i> , <i>B. daqingense</i> , <i>B. diazoefficiens</i> , <i>B. elkanii</i> , <i>B. huanghuaihaiense</i> , <i>B. liaoningense</i> , <i>Burkholderia cepacia</i> , <i>Deinococcus radiophilus</i> , <i>Diaphorobacter ruginosibacter</i> , <i>Ensifer glycinis</i> , <i>Enterobacter cloacae</i> , <i>Ochrobactrum haematophilum</i> , <i>Pantoea agglomerans</i> , <i>Paenibacillus polymyxa</i> , <i>Pseudomonas putida</i> , <i>Serratia plymuthica</i> , <i>Staphylococcus lentus</i> , <i>Tsakamurella inchenensis</i>	(Sturz et al. 1997; Bai et al. 2002; Hung and Annapurna 2004; Annapurna et al. 2013; Pandya et al. 2013; Peix et al. 2015; Velázquez et al. 2017a; Zhao et al. 2017)
<i>Gueldenstaedtia multijflora</i>	<i>Rhizobium yanglingense</i>	(Peix et al. 2015)
<i>Hedysarum coronarium</i>	<i>Rhizobium sullae</i>	(Peix et al. 2015)
<i>Hedysarum spinosissimum</i> , <i>H. glomeratum</i>	<i>Enterobacter agglomerans</i> , <i>E. kobei</i> , <i>Erwinia persicina</i> , <i>Escherichia vulneris</i> , <i>Lecrercia adecarboxylata</i> , <i>Pantoea agglomerans</i> , <i>Pantoea ananatis</i> , <i>Phyllobacterium myrsinacearum</i> , <i>Pseudomonas corrugata</i> , <i>Staphylococcus pasteurii</i> , <i>Xanthomonas translucens</i>	(Sturz et al. 1997; Muresu et al. 2008; Pandya et al. 2013; Martínez-Hidalgo and Hirsch 2017)
<i>H. multijugum</i>	<i>Rhizobium hedysari</i>	(Xu et al. 2017)
<i>H. polybotrys</i>	<i>Mesorhizobium tianshanense</i> , <i>M. septentrionale</i>	(Yan et al. 2016)
<i>Hedysarum spinosissimum</i>	<i>Xanthomonas maltophilia</i>	(Arone et al. 2014)
<i>Hippophae rhamnoides</i>	<i>Micromonosporae chaiyapumensis</i> , <i>M. chersina</i> , <i>M. coxensis</i> , <i>M. equina</i> , <i>M. lupini</i> , <i>M. narathiwatensis</i> , <i>M. saelicesensis</i> , <i>M. siamensis</i> , <i>M. viridifaciens</i>	(Trujillo et al. 2014)
<i>Indigofera spicata</i>	<i>Rhizobium vallis</i>	(Peix et al. 2015)
<i>Inga edulis</i> , <i>I. laurina</i> , <i>Inga</i> sp.	<i>Bradyrhizobium inga</i> , <i>B. forestalis</i>	(Martins da Costa et al. 2018)
<i>Kummerowia stipulacea</i>	<i>Rhizobium cauense</i> , <i>R. indigoferae</i> , <i>Shinella kummerowiae</i>	(Lin et al. 2008; Peix et al. 2015; Suneja et al. 2017)
<i>Kummerowia striata</i>	<i>Allorhizobium taibaishanense</i> , <i>Rhizobium taibaishanense</i>	(Peix et al. 2015)
<i>Lathyrus maritimus</i>	<i>Rhizobium anhuiense</i>	(Li et al. 2016b)
<i>Lathyrus numidicus</i>	<i>Phyllobacterium ifriqiyense</i>	(Li et al. 2016b)
<i>Lebeckia ambigua</i>	<i>Burkholderia dilworthii</i> , <i>B. sprentiae</i>	(Suneja et al. 2017)
<i>Lens culinaris</i>	<i>Rhizobium bangladeshense</i> , <i>R. binae</i> , <i>R. lentis</i>	(Velázquez et al. 2017a)

Table 1 (continued)

Host	Nodule endophytes	References
<i>Lespedeza cuneata</i>	<i>Bradyrhizobium yuanmingense</i>	(Peix et al. 2015)
<i>Lespedeza</i> sp.	<i>Arthrobacter nitroguaiacolicus</i> , <i>Bacillus megaterium</i> , <i>Burkholderia caledonica</i> , <i>B. glathei</i> , <i>B. phenazinium</i> , <i>B. phytofirmans</i> , <i>B. sediminicola</i> , <i>B. sordidicola</i> , <i>Dyella japonica</i> , <i>D. koreensis</i> , <i>D. marensis</i> , <i>Methylobacterium fujisawaense</i> , <i>Rhizobium miluonense</i> , <i>Staphylococcus warneri</i>	(Gu et al. 2008; Palaniappan et al. 2010; Martínez-Hidalgo and Hirsch 2017)
<i>Leucaena leucocephala</i>	<i>Sinorhizobium morelense</i>	(Suneja et al. 2017)
<i>Listia angolensis</i> , <i>Lupinus texensis</i>	<i>Microvirga lotononidis</i> , <i>M. lupini</i> , <i>M. zambiensis</i>	(Martínez-Hidalgo and Hirsch 2017)
<i>Lotononis bainesii</i>	<i>Methylobacterium nodulans</i>	(Suneja et al. 2017)
<i>Lotus berthelotii</i>	<i>Mesorhizobium tamadayense</i>	(Peix et al. 2015)
<i>Lotus corniculatus</i>	<i>Mesorhizobium erdmanii</i> , <i>M. jarvisii</i> , <i>Rhodococcus</i> strains	(Martínez-Hidalgo and Hirsch 2017; Suneja et al. 2017)
<i>Lotus arabicus</i> , <i>Lotus creticus</i>	<i>Ensifer numidicus</i>	(Suneja et al. 2017)
<i>Lotus frondosus</i>	<i>Mesorhizobium tarimense</i>	(Peix et al. 2015)
<i>Lupinus albus</i>	<i>Cohnella lupini</i> , <i>Paenibacillus lupini</i>	(Flores-Felix et al. 2014)
<i>Lupinus angustifolius</i>	<i>Micromonospora aurantiaca</i> , <i>M. auratinigra</i> , <i>M. chaiyapumensis</i> , <i>M. coriariae</i> , <i>M. coxensis</i> , <i>M. echinospora</i> , <i>M. fulviviridis</i> , <i>M. lupini</i> , <i>M. matsumotoense</i> , <i>M. narathiwatensis</i> , <i>M. olivasterospora</i> , <i>M. sagamiensis</i> , <i>M. saelicesensis</i>	(Trujillo et al. 2014)
<i>L. gredensis</i>	<i>Micromonospora chaiyapumensis</i> , <i>M. chersina</i> , <i>M. coxensis</i> , <i>M. echinofusca</i> , <i>M. echinospora</i> , <i>M. lupini</i> , <i>M. olivasterospora</i> , <i>M. saelicesensis</i> , <i>M. viridifaciens</i>	(Trujillo et al. 2014)
<i>Lupinus hon</i>	<i>Ochrobactrum lupine</i>	(Carro et al. 2014; Suneja et al. 2017)
<i>Lupinus mariae-josephae</i>	<i>Bradyrhizobium valentinum</i>	
<i>Lupinus texensis</i>	<i>Microvirga lupini</i>	(Ardley et al. 2012)
<i>Macroptilium lathyroides</i>	<i>Rhizobium etli</i> , <i>R. rhizogenes</i> , <i>Bradyrhizobium elkanii</i> , <i>B. liaoningense</i> , <i>B. yuanmingense</i> , <i>Pleomorphomonas oryzae</i>	(Bautista et al. 2017)
<i>Medicago hispida</i>	<i>Ensifer medicae</i>	(Arone et al. 2014)
<i>Medicago lupulina</i>	<i>Pseudomonas brassicacearum</i>	(Kong et al. 2017)
<i>Medicago ruthenica</i>	<i>Rhizobium alamii</i> , <i>R. mongolense</i>	(Suneja et al. 2017)
<i>Medicago sativa</i>	<i>Bacillus megaterium</i> , <i>Endobacter medicaginis</i>	(Khalifa and Almalki 2015; Ramírez-Bahena et al. 2016)
<i>Mimosa acutistipula</i> , <i>M. adenocarpa</i> , <i>M. bahamensis</i> , <i>M. blanchetii</i> , <i>M. delicatula</i> , <i>M. diplotricha</i> , <i>M. flocculosa</i> , <i>M. luisana</i> , <i>M. polyantha</i> , <i>M. pigra</i>	<i>Burkholderia phymatum</i> , <i>Cupriavidus taiwanensis</i>	(Elliott et al. 2007)
<i>Mimosa flocculosa</i>	<i>Burkholderia phenoliruptrix</i>	(Zuleta et al. 2014)
<i>Mimosa pudica</i>		

Table 1 (continued)

Host	Nodule endophytes	References
	<i>Burkholderia mimosarum</i> , <i>B. nodosa</i> , <i>B. phymatum</i> , <i>B. tuberum</i> , <i>Cupriavidus</i> <i>taiwanensis</i> , <i>R. vallis</i> , <i>Pseudomonas</i> <i>agglomerans</i>	(Peix et al. 2015; Bautista et al. 2017; Suneja et al. 2017)
<i>Morella pensylvanica</i>	<i>Micromonosporae coriariae</i> , <i>M. cremea</i> , <i>M. olivasteraspora</i> , <i>M. peucetia</i> , <i>M. saelicesensis</i>	(Trujillo et al. 2014)
<i>Myrica gale</i>	<i>Micromonosporae lupini</i> , <i>M. tulbaghia</i>	(Trujillo et al. 2014)
<i>Neonotonia wightii</i>	<i>Bradyrhizobium embrapense</i> , <i>B. tropiciagri</i>	(Suneja et al. 2017)
<i>Neptunia natans</i>	<i>Allorhizobium undicola</i> , <i>Devosia neptuniae</i> , <i>Rhizobium tubonense</i>	(Suneja et al. 2017)
<i>Ononis tridendata</i>	<i>Phyllobacterium trifolii</i>	(Rivas et al. 2002; Martínez-Hidalgo and Hirsch 2017)
<i>Ornithopus pinnatus</i>	<i>Curtobacterium flaccumfaciens</i> , <i>C. herbarum</i> , <i>Enterobacter agglomerans</i>	(Muresu et al. 2008)
<i>Oxytropis glabra</i>	<i>Rhizobium tubonense</i>	(Peix et al. 2015)
<i>Oxytropis cashemiriana</i>	<i>Pararhizobium herbae</i>	(Velázquez et al. 2017a, b)
<i>Oxytropis glabra</i>	<i>Mesorhizobium gobiense</i>	(Peix et al. 2015)
<i>Tetragonolobus purpureus</i>	<i>Staphylococcus epidermidis</i> , <i>Staphylococcus</i> <i>pasteuri</i>	(Sturz et al. 1997; Muresu et al. 2008)
<i>Trifolium pratense</i>	<i>Bacillus brevis</i> , <i>B. insolitus</i> , <i>B. megaterium</i> , <i>B. subtilis</i> , <i>Bortedella avium</i> , <i>Curtobacterium citreum</i> , <i>C. flaccumfaciens</i> , <i>C. luteum</i> , <i>Methylobacterium extorquens</i> , <i>Pseudomonas fragi</i> , <i>Ps. lini</i> , <i>Ps. putida</i> , <i>Ps.</i> <i>viridiflava</i> , <i>Roseateles depolymerans</i>	(Sturz et al. 1997; Muresu et al. 2008)
<i>Pachyrhizus erosus</i>	<i>Bradyrhizobium jicamae</i> , <i>B. pachyrhizi</i>	(Suneja et al. 2017)
<i>Phaseolus lunatus</i>	<i>Bradyrhizobium icense</i> , <i>B. paxllaeri</i> , <i>Rhizobium endophyticum</i> , <i>R. hidalgonense</i>	(Li et al. 2016a; Velázquez et al. 2017a)
<i>Phaseolus vulgaris</i>	<i>Agrobacterium pusense</i> , <i>Bradyrhizobium</i> <i>paxllaeri</i> , <i>Cohnella phaseoli</i> , <i>Cupriavidus</i> <i>necator</i> , <i>Enterobacter hormaechei</i> , <i>Fontibacillus phaseoli</i> , <i>Herbaspirillum</i> <i>lusitanum</i> , <i>Klebsiella pneumoniae</i> , <i>Micromonosporae chaiyapumensis</i> , <i>M. chersina</i> , <i>M. endolithica</i> , <i>Pararhizobium giardinii</i> , <i>Phyllobacterium</i> <i>endophyticum</i> , <i>Providencia rettgeri</i> , <i>Pseudomonas koreensis</i> , <i>Rhizobium</i> <i>azibense</i> , <i>R. ecuadorensis</i> , <i>R. lusitanum</i> , <i>R. paranaense</i> , <i>R. vallis</i> , <i>R. acidisoli</i> , <i>Xiangella phaseoli</i>	(López-López et al. 2010; Trujillo et al. 2015; Peix et al. 2015; Aguilar et al. 2016; Suneja et al. 2017; Velázquez et al. 2017a; Wekesa et al. 2017)
<i>Pisum sativum</i>	<i>Bacillus simplex</i> , <i>Micromonosporae</i> <i>aurantica</i> , <i>M. auratinigra</i> , <i>M. chaiyapumensis</i> , <i>M. chersina</i> , <i>M. coerulea</i> , <i>M. coriariae</i> , <i>M. coxensis</i> , <i>M. fulviviridis</i> , <i>M. lupini</i> , <i>M. matsumotoense</i> , <i>M. pattaloongensis</i> , <i>M. saelicesensis</i> , <i>M. sagamiensis</i> , <i>M. siamensis</i> , <i>M. phytophila</i> , <i>M. luteiviridis</i> , <i>Rhizobium pisi</i>	(Trujillo et al. 2015; Peix et al. 2015; Martínez-Hidalgo and Hirsch 2017; Carro et al. 2017)
<i>Pongamia pinnata</i>	<i>Rhizobium pongamiae</i>	(Suneja et al. 2017)

Table 1 (continued)

Host	Nodule endophytes	References
<i>Prosopis alba</i>	<i>Mesorhizobium chacoense</i>	(Suneja et al. 2017)
<i>Prosopis chilensis</i>	<i>Ensifer arboris</i> , <i>E. kostiensis</i>	(Peix et al. 2015; Suneja et al. 2017)
<i>Prosopis juliflora</i>	<i>Achromobacter xylooxidans</i>	(Arone et al. 2014)
<i>Psophocarpus tetragonolobus</i>	<i>Bradyrhizobium elkanii</i> , <i>B. yuanmingense</i> , <i>Rhizobium rhizogenes</i> , <i>Stenotrophomonas maltophilia</i>	(Bautista et al. 2017)
<i>Psoralea corylifolia</i>	<i>Ensifer psoraleae</i>	(Peix et al. 2015)
<i>Pterocarpus indicus</i>	<i>Bradyrhizobium liaoningense</i> , <i>B. japonicum</i> , <i>Ensifer adhaerens</i> , <i>Labrys neptuniae</i> , <i>Rhizobium lusitanum</i> , <i>R. rhizogenes</i> , <i>R. tropici</i>	(Bautista et al. 2017)
<i>Pueraria candollei</i>	<i>Rhizobium puerariae</i>	(Boonsnongcheep et al. 2016)
<i>Pueraria lobata</i>	<i>Devosia yakushimensis</i>	(Bautista et al. 2010)
<i>Pueraria thunbergiana</i>	<i>Bacillus thuringiensis</i> , <i>Enterobacter asburiae</i> , <i>Serratia marcescens</i>	(Selvakumar et al. 2008)
<i>Retama monosperma</i> , <i>R. sphaerocarpa</i>	<i>Bradyrhizobium rifense</i>	(Suneja et al. 2017)
<i>Robinia pseudoacacia</i>	<i>Mesorhizobium robiniae</i>	(Suneja et al. 2017)
<i>Samanea saman</i>	<i>Bradyrhizobium japonicum</i> , <i>B. liaoningense</i> , <i>Labrys neptuniae</i> , <i>Pantoea</i> sp.	(Bautista et al. 2017)
<i>Scorpiurus muricatus</i>	<i>Phyllobacterium endophyticum</i> , <i>P. ifriqiense</i> , <i>Pseudomonas brenneri</i> , <i>Rhizobium nepotum</i> , <i>R. radiobacter</i> , <i>R. vignae</i> , <i>Starkeya novella</i>	(Bouchiba et al. 2017)
<i>Sophora flavescens</i>	<i>Rhizobium sophorae</i> , <i>R. sophoriradicis</i>	(Velázquez et al. 2017a)
<i>Sophora longicarinata</i>	<i>Mesorhizobium calcicola</i> , <i>M. waimense</i>	(de Meyer et al. 2016)
<i>Sophora microphylla</i>	<i>Mesorhizobium cantuariense</i> , <i>M. kowhahi</i> , <i>M. sophorae</i> , <i>M. waitakense</i>	(de Meyer et al. 2016; Velázquez et al. 2017a)
<i>Sophora prostrata</i>	<i>Mesorhizobium newzealandense</i>	(de Meyer et al. 2016)
<i>Sesbania cannabina</i>	<i>Agrobacterium deltaense</i> , <i>A. salinitolerans</i> , <i>Ensifer psoraleae</i> , <i>Rhizobium radiobacter</i>	(Peix et al. 2015; Martínez-Hidalgo and Hirsch 2017; Yan et al. 2017a, b)
<i>Sesbania herbacea</i>	<i>Neorhizobium huautlense</i>	(Li et al. 2016a)
<i>Sesbania rostrata</i>	<i>Azorhizobium caulinodans</i> , <i>Ensifer indiaense</i>	(Suneja et al. 2017)
<i>Sesbania sesban</i>	<i>Agrobacterium tunefaciens</i> , <i>Pseudomonas geniculata</i> , <i>Pantoea agglomerans</i>	(Hossain and Lundquist 2016)
<i>Sesbania virgata</i>	<i>Azorhizobium doebereineriae</i>	(Suneja et al. 2017)
<i>Sophora alopecuroides</i>	<i>Bacillus cereus</i> , <i>Pseudomonas chlororaphis</i>	(Zhao et al. 2011, 2013)
<i>Sphaerophysa salsula</i>	<i>Bacillus safensi</i> , <i>B. simplex</i> , <i>Brevibacillus borstelensis</i> , <i>Inquilinus limosus</i> , <i>Lysinibacillus fusiformis</i> , <i>Mesorhizobium amorphae</i> , <i>M. gobiense</i> , <i>M. tianshanense</i> , <i>Nocardia uniformis</i> , <i>Paenibacillus amylolyticus</i> , <i>Paracoccus halophilus</i> , <i>Pararhizobium sphaerophysae</i> , <i>Pseudomonas fluorescens</i> , <i>Rhizobium giardinii</i> , <i>R. helanshanense</i> , <i>R. sphaerophysae</i> , <i>Serratia plymuthica</i> , <i>Sphingomonas pruni</i> , <i>Streptomyces bottropensi</i>	(Deng et al. 2011; Peix et al. 2015; Velázquez et al. 2017a)
<i>Sulla capitata</i>	<i>Rhizobium nepotum</i> , <i>Pseudomonas fluorescens</i> , <i>Variovorax paradoxus</i>	(Beghalem et al. 2017)

Table 1 (continued)

Host	Nodule endophytes	References
<i>Sulla pallida</i>	<i>Neorhizobium galegae</i> , <i>Phyllobacterium ifriqiyense</i> , <i>Pseudomonas fluorescens</i> , <i>Rhizobium nepotum</i>	(Beghalem et al. 2017)
<i>Trifolium alexandrinum</i>	<i>Rhizobium aegyptiacum</i>	(Velázquez et al. 2017a)
<i>Trigonella archiducis-nicolai</i>	<i>Rhizobium tibeticum</i>	(Peix et al. 2015)
<i>Vicia alpestris</i>	<i>Microvirga ossetica</i>	(Safronova et al. 2017)
<i>Vicia faba</i> , <i>Pisum sativum</i>	<i>Rhizobium anhuiense</i>	(Velázquez et al. 2017a)
<i>V. faba</i>	<i>Accumulibacter phosphatis</i> , <i>Acinetobacter woffii</i> , <i>Alcaligenes faecalis</i> , <i>Bacillus megaterium</i> , <i>B. muralis</i> , <i>B. subtilis</i> , <i>Brevibacterium luteolum</i> , <i>Burkholderia phytofirmans</i> , <i>B. xenovorans</i> , <i>B. verschuerenii</i> , <i>Calditerrivibrio nitroreducens</i> , <i>Chlorobium leteolum</i> , <i>Dechloromonas aromatica</i> , <i>Deinococcus maricopensis</i> , <i>Desulfovibrio desulfuricans</i> , <i>Enterobacter amnigenus</i> , <i>E. cancerogenus</i> , <i>Geobacater uraniiireducens</i> , <i>Nitrosopira multiformis</i> , <i>Pantoea agglomerans</i> , <i>P. brenneri</i> , <i>P. marginalis</i> , <i>Phyllobacterium trifolii</i> , <i>Pseudomonas aeuroginosa</i> , <i>P. fluorescens</i> , <i>Rhizobium aquatilis</i> , <i>R. grahamii</i> , <i>R. leguminosarum</i> , <i>R. nepotum</i> , <i>R. pusense</i> , <i>R. radiobacter</i> , <i>Serratia maltophilia</i> , <i>S. odorifera</i> , <i>Staphylococcus saprophyticus</i> , <i>Symbiobacterium thermophilum</i> , <i>Synechococcus elongatus</i> , <i>Variovorax paradoxus</i> , <i>Verminephrobacter eiseniae</i> , <i>Xanthomonas campestris</i>	(Saïdi et al. 2013; Trabelsi et al. 2017)
<i>Vigna mungo</i>	<i>Bacillus mycoides</i> , <i>Klebsiella pneumoniae</i>	(Hossain and Lundquist 2016)
<i>V. radiata</i>	<i>Agrobacterium tumefaciens</i> , <i>A. vitis</i> , <i>Bacillus anthracis</i> , <i>B. circulans</i> , <i>B. endophyticus</i> , <i>B. mojavensis</i> , <i>B. safensis</i> , <i>B. sonorensis</i> , <i>B. pumilus</i> , <i>Blastobacter aggregatus</i> , <i>Chitinophaga filiformis</i> , <i>Chryseobacterium indologenes</i> , <i>Cupriavidus necator</i> , <i>Dyadobacter fermentans</i> , <i>Ensifer adhaerens</i> , <i>Klebsiella pneumoniae</i> , <i>Macrophomina phaseolina</i> , <i>Paenibacillus amylolyticus</i> , <i>P. barciconensis</i> , <i>P. circulans</i> , <i>P. kribbensis</i> , <i>P. macquariensis</i> , <i>P. massiliensis</i> , <i>P. pabuli</i> , <i>P. panacisoli</i> , <i>P. taichungensis</i> , <i>P. validus</i> , <i>P. xylanexedens</i> , <i>P. xylanilyticus</i>	(Pandya et al. 2015; Suneja et al. 2017; Harsha Shelat and Panpatte 2017)
<i>V. subterranea</i>	<i>Bradyrhizobium kavangense</i> , <i>B. subterraneum</i> , <i>B. vignae</i> , <i>Burkholderia cenocepacia</i>	(Grönemeyer et al. 2016; Bautista et al. 2017)
<i>V. unguiculata</i>	<i>Bradyrhizobium manausense</i> , <i>B. vignae</i>	(Grönemeyer et al. 2016; Simões-Araújo et al. 2017)
<i>Virgilia oroboides</i>	<i>Paraburkholderia kirstenboschensis</i>	(Steenkamp et al. 2015)

dextrorotatory (*S*)-allantoin catalyzed by the enzyme OHCU decarboxylase in, i.e., *B. subtilis*, *E. coli*, *Herbaspirillum seropedicae*, *Klebsiella* spp., and *Ruegeria pomeroyi* TB-90 (Matiollo et al. 2009; Doniselli et al. 2015; Cunliffe 2016; Hafez et al. 2017). The fourth step underlies the conversion of (*S*)-allantoin into allantoate by the enzyme (*S*)-allantoin amidohydrolase (allantoinase) (Werner and Witte 2011). There is also the possibility of a spontaneous racemization of (*S*)-allantoin to its (*R*)-enantiomer at an estimated rate constant of $\sim 2 \times 10^{-5}$ at neutral pH (Cendron et al. 2016). Therefore, to ensure the overall efficiency of the catabolic pathway, the (*R*)-allantoin enantiomer is converted into (*S*)-allantoin by the enzyme allantoin racemase, as recorded in *K. pneumoniae*, *Pseudomonas fluorescens*, *Ps. putida*, *Ps. testosteroni*, and *Proteus rettgeri* (van der Drift et al. 1975; Cendron et al. 2016; Danchin 2017) to prevent the accumulation of (*R*)-allantoin.

Direct interactions between the purine metabolism and the bacteria IAA production and/or ACCD activity can be extrapolated from (i) the increased ureide content in plants treated with 1-methyl cyclopropene, a known inhibitor of ethylene synthesis (Do Nascimento et al. 2016), and (ii) the upregulation of the nitrogenase activity inside root nodules of drought stressed *Medicago sativa* plants inoculated with the IAA-overproducing *Ensifer meliloti* strain Ms-RD64 (Defez et al. 2017).

Overview of the main enzymes and genes involved in the bacterial synthesis of ureides

The enzyme guanine deaminase belongs to the cytidine (hence a pyrimidine) deaminase superfamily, with marked structural differences with the same enzyme in *E. coli* (Danchin 2017). The enzyme XDH is a NAD⁺ co-factor xanthine FAD/molybdopterin-dependent dehydrogenase as reported in *Acinetobacter baumannii* (Wang et al. 2015), *Rhodobacter capsulatus* (Reschke et al. 2017), *Pseudomonas acidovorans*, *Ps. aeruginosa*, *Ps. aureofaciens*, *Ps. cepacia*, *Ps. putida*, *Ps. testosteroni* (Woolfolk and Downard 1977), and *Streptomyces coelicolor* (Sivapragasam and Grove 2016). In most bacteria, XDH activity diverts the hypoxanthine and xanthine from the purine salvage pathway. However, in *S. coelicolor* as well as in the soil and plant colonizing *Listeria monocytogenes*, the XDH is involved mainly in the purine salvage catabolic pathway needed to generate sufficient GDP and GTP, the substrates for the

phosphorylated nucleosides guanosine 5'(di)triphosphate 3'diphosphate synthetases (Sivapragasam and Grove 2016), via the XDH transcriptional repressor (xdhR) with a binding site to either GTP or ppGpp transcriptional repressor to induce xdhABC expression. As far as we could verify, there is only one publication on the inhibitory effects of plant phenolics and flavonoids from *Juniperus procera* on the XO activity in Gram-positive bacteria (Samaha et al. 2017), contrasting with the large number of clinical reports showing the inhibitor effects of plant isoflavones and flavonol glycosides on the XO and/or UOX activities in bacteria pathogens to animals and humans (Nile et al. 2017; Raziq et al. 2017). Extrapolating from data published by Cantu-Medellin and Kelley (2013), there is a possibility that reduction of NO₃⁻ to peroxynitrite via the XO could take place by PAB in plants grown in low soil pH or in seasonally flooded soils with fluctuating O₂ and NO₃⁻ availability. The detour of xanthine from the ureide synthesis via the purine salvage pathway in *B. subtilis* is catalyzed by the enzyme Mg²⁺-dependent xanthine phosphoribosyl transferase resulting in the synthesis of xanthosine-5'-monophosphate (Del Arco et al. 2017), under the control of the guanine-binding xpt riboswitch (Kirchner and Schneider 2017). In parallel, XDH was reported to actively participate in the stringent (stress) response in the N₂-fixing *S. meliloti* (Krol and Becker 2011). On the other hand, the activity of the enzyme XO, catalyzes in *B. pumilus* (Sharma et al. 2016) and *Arthrobacter* sp. strain MU12 (Li et al. 2017), the oxidation of hypoxanthine to xanthine and uric acid with the concomitant reduction of O₂ to H₂O₂ and O₂⁻ categorized as central redox signaling molecules. On the other hand, the intracellular location of UOX was reported in *B. fastidiosus*, *B. subtilis* RNZ-79, *B. pasteurii*, *P. mirabilis*, and *E. coli*, while extracellular production of UOX was observed in *S. albosriseolus*, *S. graminofaciens*, *S. albidoflavus*, *Microbacterium* sp., and *Ps. aeruginosa* (Zhao et al. 2006; Khade and Srivastava 2016; Kotb 2016; Hafez et al. 2017). Uric acid was shown to be the main inducer of UOX in *B. cereus*, *B. thermocatenuatus*, *S. albosriseolus*, *Sphingobacterium thalpophilum*, *S. exfoliates*, *S. graminofaciens*, and *S. albidoflavus* (Nanda and Jagadeesh Babu 2014). In general, UOX was categorized as a thermosensitive and co-factor-independent enzyme. However, a thermostable Mg²⁺ co-factor UOX was identified in *B. firmus* isolated from soils (Kotb 2016). On the other hand, UOX activity in *Ps. aeruginosa* was triggered by Ca²⁺, but inhibited by

Co²⁺, Mn²⁺, Mg²⁺, Fe²⁺, Zn²⁺, and Cu²⁺ in the growing media (Amirthanathan and Vijayakumar 2011), contrasting with the Ca²⁺, Mn²⁺, Mg²⁺, and Fe²⁺ stimulation of the intracellular UOX in *S. exfoliates* (Aly et al. 2013). While, the extracellular activity of UOX from *S. thalophilum* was enhanced by Cu²⁺ but partially inhibited by Ca²⁺, Fe²⁺, Zn²⁺, and Ni²⁺ (Ravichandran et al. 2015). Details of the conversion of uric acid to HIU by the FAD-dependent UOX in *K. pneumoniae* were described by Hicks et al. (2013). The enzyme allantoinase belongs to the cyclic amidohydrolases family, possesses a binuclear metal center in the active site, and in certain bacterial species, it can be inhibited by the flavonol kaempferol (Peng and Huang 2014). The most effective co-factors of allantoinase are Zn²⁺ and Co²⁺ in *E. coli*, Mn²⁺ in *Streptococcus allantoicus* and *Arthrobacter allantoicus*, and Co²⁺ in *B. licheniformis* CECT 20T that shows an apparent unique inverted enantioselectivity towards (*R*)-allantoin (Martínez-Gómez et al. 2014); while in *E. coli* and *Pseudomonas* species, it is inhibited by Mn²⁺ (Werner and Witte 2011).

Under N-limited availability, *B. subtilis* grown aerobically expresses the full set of genes encoding the synthesis of allantoin (Ma et al. 2016). Similar nutrient conditions trigger the oxidation of hypoxanthine to allantoin in *K. pneumoniae* codified by the hpx cluster of seven genes organized in four transcriptional units: hpxDE, hpxR, hpxO, and hpxPQT (De La Riva et al. 2008). Details on the XDH encoding genes *xdhA*, *xdhB*, and *xdhC* corresponding to the small subunit (XDHA), the large subunit (XDHB), and the chaperone protein (XDHC) were published by Wang et al. (2015). It is interesting to note that the XDH encoding gene in *R. capsulatus* is not under the control of N regulatory network but induced by xanthine (Leimkühler et al. 1998). The genes encoding the enzymes UOX and allantoinase were described in *H. seropedicae* by Matiollo et al. (2009), whereas, the upregulation of genes encoding the enzyme guanine deaminase (msmeg_1298), uricase (msmeg_1296), transthyretin (msmeg_1295), and 2-oxo-4-hydroxy-4-carboxy-5-ureidoimidazole decarboxylase (msmeg_1294) was reported in N-limited *Mycobacterium smegmatis* (Petridis et al. 2015). Divergently oriented genes encoding UOX and the transcriptional regulator HucR were reported in *Deinococcus radiodurans* (Wilkinson and Grove 2005). Interestingly, the *E. coli* K-12 genome encodes the uric acid permease activity (YgfU), in spite of the lack of all enzymes for uric acid catabolism

(Papakostas and Frillingos 2012). As additional information, allantoin is also synthesized in the endophytic fungus *Fusarium* sp. isolated from the roots of *Astragalus membranaceus* and leaves of *Eucommia ulmoides*, in the endophytic fungi *Aspergillus* sp. and *Chaetomium globosum* isolated from *Eucommia ulmoides* and *Ginkgo biloba*, respectively (Zhang et al. 2015), and in a mangrove endophyte fungus ZSU-H19 from the South China Sea (Sharples and Cairney 1997; Zhang et al. 2012), but not in *Aspergillus terreus* from *Artemisia annua* (Sun 2009; Zhang et al. 2015).

Bacterial ureide catabolism

The catabolism of allantoate to NH₃ might proceed via two metabolic routes depending on the bacterial species (Fig. 1). The route 1, i.e., in *Ps. acidovorans*, *R. pomeroyi*, *S. coelicolor*, and in N-limited *M. smegmatis*, starts with the conversion of (*S*)-allantoate to (*S*)-ureidoglycolate by the Mn²⁺-dependent enzyme allantoinase, to be finally hydrolyzed to glyoxylate and NH₄⁺ in a reaction catalyzed by the enzyme ureidoglycolate lyase in *Burkholderia cepacia*, *E. coli*, *Lactobacillus buchneri*, *Methylobacterium nodulans*, *M. radiotolerans*, *Pseudomonas* sp., and *Streptococcus* sp. (Raymond et al. 2005; Liu 2014; Minami et al. 2016), or to glyoxylate and 2NH₃ via the enzymatic reaction catalyzed by the ureidoglycolate amidohydrolase in *E. coli* O157:H7 and *R. pomeroyi* (Serventi et al. 2010; Werner et al. 2010; Cunliffe 2016). The route 2 commences with the conversion of (*S*)-allantoate to (*S*)-ureidoglycine by the enzyme allantoinase and into oxalurate via the reaction catalyzed by the enzyme Mn²⁺-, Co²⁺-, and Ni²⁺-dependent (*S*)-ureidoglycine aminotransferase, concomitantly with the synthesis of α-amino acids from α-keto acids (French and Ealick 2010). The further degradation of oxalurate to carbamoyl phosphate and oxamate is catalyzed by the enzyme oxamate carbamoyl transferase in *E. coli* (Hasegawa et al. 2008; Li et al. 2011) and in *S. allantoicus* (Bojanowski et al. 1964); in contrast to the direct conversion of oxalurate into oxamate and NH₃ described in *K. pneumoniae* (Hicks and Ealick 2016). Oxamate is finally converted to oxalate by the enzyme oxamate amidohydrolase as shown in *K. pneumoniae* (Hicks and Ealick 2016; Danchin 2017). On the other hand, the report of *S. faecalis* ATCC 11700 being capable to metabolize oxalurate but not allantoin

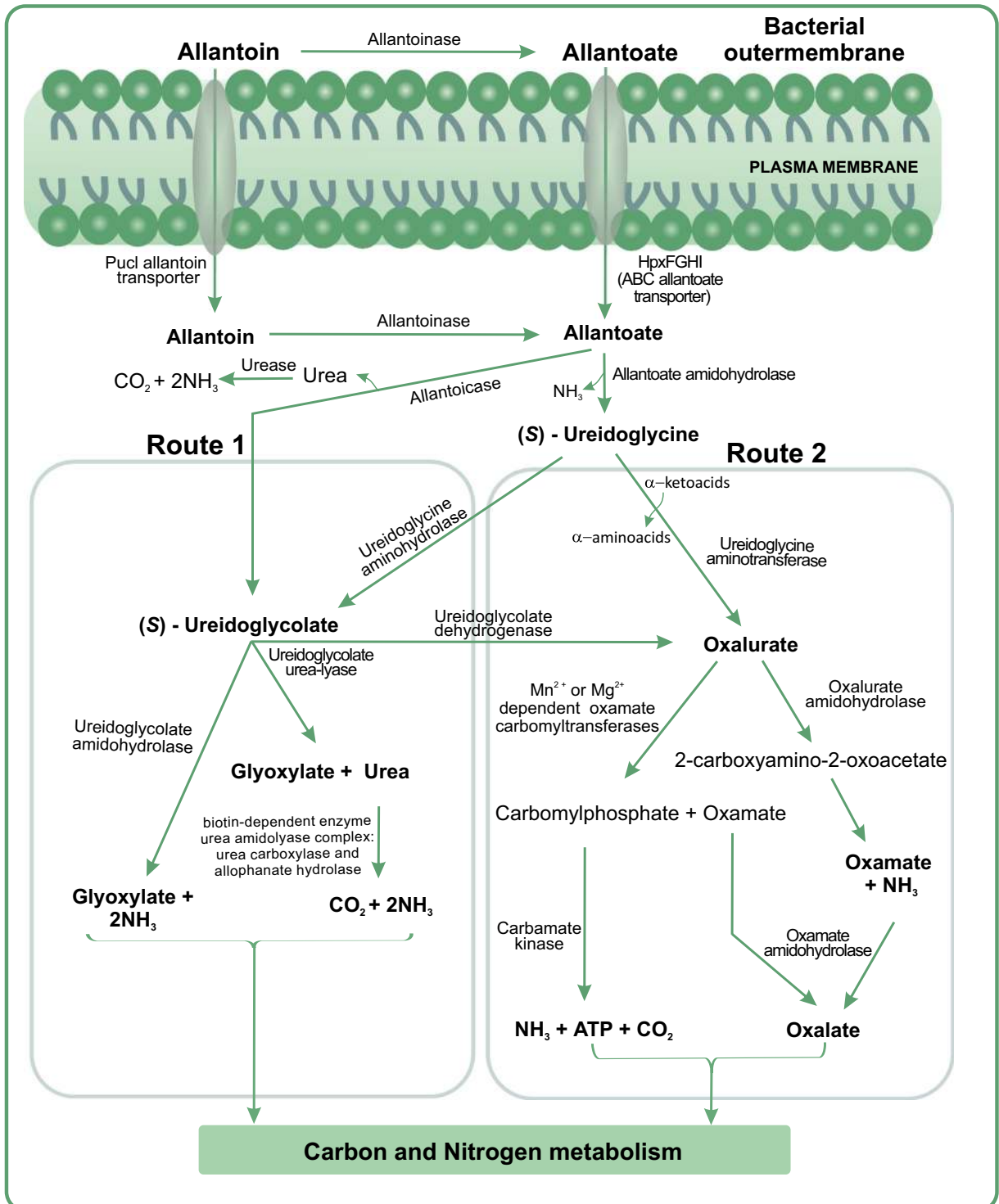


Fig. 1 Metabolic routes for the catabolism of ureides in bacteria. References for each enzymatic pathway are listed in the text. Arrows indicate the enzymatic pathways

for growth (Vander Wauven et al. 1986) suggests the possible existence of interconnections between routes 1 and 2. As shown in *E. coli*, the enzyme NAD(P)⁺-dependent ureidoglycolate dehydrogenase, a member of L-sulfolactate dehydrogenase-like family, may oxidize ureidoglycolate to oxalurate, allowing urease-negative *E. coli* to preserve N and energy resources more efficiently (Werner et al. 2010). Curiously, the microbial purine pathways from allantoin to oxamate have not been a focus of research despite the use of oxamic acid thiohydrazides as precursors for the formation of hydrazones previously inaccessible from traditional hydrazones chemistry (Volkova et al. 2017).

Finally, the NH₄⁺ produced in routes 1 or 2 is broken down to NH₃ in either one-step reaction via urease as described in some rhizobiales bacteria (Neuvonen et al. 2016) or in a two-step reaction catalyzed by the biotin-dependent enzyme urea amidolyase (UAL) complex comprised by the enzymes urea carboxylase and the upregulated gene *msmeg_2189* encoded allophanate hydrolase in *Acetobacter pasteurianus*, *Granulibacter bethesdensis*, *Komagataeibacter nataicola*, *M. extorquens*, *M. mesophilicum*, *M. nodulans*, *M. oryzae*, *M. radiotolerans*, *M. smegmatis*, *Oleomonas sagaranensis*, and *S. avermitilis* (Lin et al. 2016; Minami et al. 2016; Petridis et al. 2016; Zhang et al. 2017a). Genes encoding the enzymes allantoinase, allantoinate aminohydrolase, ureidoglycolate lyase, ureidoglycolate dehydrogenase, and urease as well as for the allantoin proton-coupled symporter (*pucI*, also known as ALLP) and uric acid transporter (*pucJK*) were described in *H. seropedicae* (Matiollo et al. 2009), *B. megaterium*, *B. guano*, *B. brevis*, *B. polymyxa*, and *B. fastidiosus* (except the strain C.4) (Ma et al. 2016). The genes involved in the conversion of allantoin to oxalurate are clustered together forming the *hpxFGHLJK* operon in *K. pneumoniae* (Guzmán et al. 2013). As a curiosity, the micro algae *Chlamydomonas reinhardtii* actively catabolize allantoin as a source of N via the purine catabolic pathway (Pineda et al. 1984). Examples of bacteria with or without the ability to grow on purine derivatives are listed in Table 2.

Putative scenarios for purine-mediated interactions between plant and PAB

In plants, PAB can colonize the apoplastic spaces among cortical, endodermis, and aerenchyma cells of roots, stem parenchyma, and mesophyll leaf cells, as well as

the lumen of the xylem vascular system which becomes the main transport route for the systemic spread of PAB from roots (rhizosphere) to stems (laimosphere and caulosphere), leaves (phylloplane), flowers (anthosphere), fruits (carposphere), and seeds (spermosphere). The xylem not only supplies the aerial parts of the plant with water but also transports inorganic and organic forms of N from the root to the shoot, as in the case of N₂-fixing ureidic legumes, in which ureides are the prevailing form of N transported in the xylem flow (Baral and Izaguirre-Mayoral 2017). Moreover, endophytes such as *Azospirillum brasilense* are known to enlarge the transversal area of xylem vessel in the stems of tomato plants eliciting a better diffusion and storage of substantial amounts of N compounds and of the better upward conduction efficiency of water (Romero et al. 2014). PAB can also colonize the sugar and N-rich phloem vessels mainly via phloem-feeding insects (López-Fernández et al. 2017). Therefore, it can be assumed that bacteria residing in xylem neighboring parenchyma, protoxylem, and/or phloem of underground and aboveground organs will deplete the xylem sap of specific plant-produced purine intermediaries to attenuate bacterial stress as result of seasonal drought or salinity-incited N deficiencies. Greater rates of purine scavenging are expected in rhizospheric and endophytic PABs lacking an active ureide metabolism, but harboring the genes related to the purine pathways modulated by riboswitches (Kirchner and Schneider 2017). In general, microbial populations harboring reversible genotypes of amino acid transporter *Gap1* genes, flanked by two direct repeats that can lead to *GAP1* deletions ($\Delta gap1$) and a self-replicating *GAP1* circle, have a selective advantage as purine or NH₃ scavengers and thus, higher stress tolerance (Møller et al. 2013). In *M. smegmatis*, N deficiency provokes the expression of the genes involved in the uptake of N compounds such as xanthine/uracil permease (*msmeg_2570* and *msmeg_1293*) as well as cytosine/purines/uracil/thiamine/allantoin permease (*msmeg_5730* and *msmeg_6660*) (Petridis et al. 2015). On the contrary, it is possible to assume that PAB with active purine synthesis may benefit stress-challenged plants by supplying purine intermediaries for the synthesis of NH₃ to recycle N. *Massilia albidiflava*, *M. dura*, and *M. plicata* isolated from soils in China are characterized as high NH₃ producers (Zhang et al. 2006). To dissect these possibilities, the purine plant-microbe interactive associations were analyzed in terms of three scenarios (Fig. 2):

Table 2 Examples of bacteria with or without the capacity to actively catabolize purine derivatives as a source of N for colony growth

Bacteria	Xanthine	Hypoxanthine	Uric acid	Allantoin	References
<i>Actinopolyspora erythraea</i>	+				(Duangmal et al. 2016)
<i>A. xinjiangensis</i>	+				(Duangmal et al. 2016)
<i>Alcaligenes denitrificans</i>	–				(Martin et al. 1981)
<i>Aerobacter aerogenes</i>				+	(Rouf 1968)
<i>Aerobacter fecalis</i>	–				(Martin et al. 1981)
<i>Amycolatopsis eurytherma</i> , <i>A. thermoflava</i>				+	(Busarakam et al. 2016)
<i>Angustibacter peucedani</i>	–	–			(Lee 2013)
<i>Aureimonas galii</i>	+	–			(Aydogan et al. 2016)
<i>A. pseudogalii</i>	+	–			(Aydogan et al. 2016)
<i>Bacillus depressus</i>	–	+			(Wei et al. 2016)
<i>B. fastidiosus</i>			+	+#	(Azab et al. 2005)
<i>B. pumilus</i>	+				(Sharma et al. 2016)
<i>Bordetella bronchiseptica</i>	–				(Martin et al. 1981)
<i>Brevundimonas viscosa</i>	–	–			(Wang et al. 2012)
<i>Clostridium aciditurici</i> , <i>C. cylindrosporium</i> , <i>C. purinolyticum</i>	+	+	+		(Durre et al. 1981)
<i>Corynebacterium glyciniphilum</i>				+	(Al-Dilaimi et al. 2015)
<i>Devosia insulae</i>	–	–			(Yoon et al. 2007)
<i>Halobacillus salicampi</i>	–	–			(Kim et al. 2016)
<i>Hydrogenomonas eutropha</i>				+	(Ammann and Reed 1967)
<i>Hyphomicrobium</i> sp. (a denitrifying methylotroph)				+	(van der Drift and de Windt 1983)
<i>Isoptericola cucumi</i>	–	+			(Kämpfer et al. 2016)
<i>I. hypogeus</i>	+	+			(Kämpfer et al. 2016)
<i>I. nanjingensis</i>	+	+			(Kämpfer et al. 2016)
<i>I. variabilis</i>	+	+			(Kämpfer et al. 2016)
<i>Janibacter melonis</i>	–	–			(Yoon et al. 2004)
<i>J. alba</i>	+	+			(Qin et al. 2009)
<i>J. alkaliphila</i>	–	+			(Lee 2008)
<i>J. gansuensis</i>	–	–			(Lee 2008)
<i>Klebisella pneumoniae</i>				+	(Matiasovicova et al. 2011)
<i>Kocuria rosea</i>	+				(Ali et al. 2015)
<i>Kribbella keroonensis</i> , <i>K. shirazensis</i> , <i>K. soli</i>	+			+	(Ozdemir-Kocak et al. 2017)
<i>Methylobacterium aquaticum</i> , <i>M. platani</i> , <i>M. tarhaniae</i>	–			–	(Veyisoglu et al. 2013)
<i>Micromonospora yasonensis</i>				–	(Veyisoglu et al. 2016a)
<i>Microvirga arabica</i>	–			–	(Veyisoglu et al. 2016b)
<i>M. makkahensis</i>	+			–	(Veyisoglu et al. 2016b)
<i>Mucilaginibacter boryungensis</i>	–	–			(Kang et al. 2011)
<i>Nocardia aciditolerans</i>				–	(Golinska et al. 2013)
<i>N. alba</i>				–	(Camas et al. 2017)
<i>N. caishijiensis</i>				–	(Camas et al. 2017)
<i>N. goodfellowii</i>				–	(Camas et al. 2017)

Table 2 (continued)

Bacteria	Xanthine	Hypoxanthine	Uric acid	Allantoin	References
<i>N. sungurluensis</i>				+	(Camas et al. 2017)
<i>Nonomuraea muscovyensis</i>				–	(Ozdemir-Kocak et al. 2014)
<i>Paraburkholderia tropica</i>				+	(Silva et al. 2017b)
<i>Pedobacter sandarakinus</i>	–	–			(Yoon et al. 2006)
<i>Peptococcus prevotii</i>	+				(Reece et al. 1976)
<i>Phenyllobacterium composti</i>	–	–			(Weon et al. 2008)
<i>Pseudomonas acidovorans</i>	+				(Martin et al. 1981)
<i>Ps. alcaligenes</i>	+				(Martin et al. 1981)
<i>Ps. aeruginosa</i>				+	(Rouf 1968)
<i>Ps. diminuta</i>	–				(Martin et al. 1981)
<i>Ps. mesoacidophila</i>				+	(Loveridge et al. 2017)
<i>Ps. pseudoalcaligenes</i>	–				(Martin et al. 1981)
<i>Ps. putida</i>	+	+	+	+	(Fernández et al. 2016)
<i>Ps. putrefaciens</i>	+				(Martin et al. 1981)
<i>Ps. testosteroni</i>	+				(Martin et al. 1981)
<i>Ruania albidiflava</i>	–	–			(Gu et al. 2007)
<i>Salmonella enterica</i>				+	(Matiasovicova et al. 2011)
<i>Serratia kiliensis</i>				+	(Rouf 1968)
<i>Streptomonospora tuzyakensis</i>	–			–	(Tatar et al. 2016)
<i>Staphylococcus flavocyaneus</i>		+			(Aaronsoni 1955)
<i>Streptomyces albidoflavus</i>	–			–	(Gupta et al. 2009)
<i>S. aridus</i>			+	–	(Idris et al. 2017)
<i>S. atroolivaceus</i>	+			+	(Gupta et al. 2009)
<i>S. aurantiacus</i>	–			+	(Gupta et al. 2009)
<i>S. avicennia</i>	–			–	(Saricaoglu et al. 2014)
<i>S. brevispora</i>				+	(Zucchi et al. 2012)
<i>S. burgazadensis</i>	–			–	(Saricaoglu et al. 2014)
<i>S. canus</i>	+			–	(Gupta et al. 2009)
<i>S. chromofuscus</i>	–			–	(Gupta et al. 2009)
<i>S. exfoliatus</i>	–			–	(Gupta et al. 2009)
<i>S. griseoluteus</i>	–			–	(Gupta et al. 2009)
<i>S. hainanensis</i>	–			–	(Saricaoglu et al. 2014)
<i>S. helstedii</i>	+			+	(Gupta et al. 2009)
<i>S. hoynatensis</i>	–			–	(Saricaoglu et al. 2014)
<i>S. karpasiensis</i>				+	(Veyisoglu et al. 2014)
<i>S. laculatispora</i>				+	(Zucchi et al. 2012)
<i>S. lavenduale</i>	+			–	(Gupta et al. 2009)
<i>S. lomondensis</i>	+				(Santhanam et al. 2012)
<i>S. longisporoflavus</i>	–			–	(Gupta et al. 2009)
<i>S. luridus</i>	+			–	(Gupta et al. 2009)
<i>S. lusitanus</i>	+			+	(Zucchi et al. 2012)

Table 2 (continued)

Bacteria	Xanthine	Hypoxanthine	Uric acid	Allantoin	References
<i>S. lydicus</i>	+			–	(Gupta et al. 2009)
<i>S. mayteni</i>	–			–	(Saricaoglu et al. 2014)
<i>S. melanogenes</i>			+	–	(Idris et al. 2017)
<i>S. noboritoensis</i>			+	–	(Idris et al. 2017)
<i>S. nogalator</i>	+			–	(Gupta et al. 2009)
<i>S. pactum</i>	+			–	(Gupta et al. 2009)
<i>S. plumbiresistens</i>				+	(Tatar and Sahin 2015)
<i>S. polyantibioticus</i>			–	+	(Idris et al. 2017)
<i>S. prasinosporus</i>	–			–	(Gupta et al. 2009)
<i>S. pseudovenezuelae</i>				+	(Tatar and Sahin 2015)
<i>S. purpureus</i>	+			–	(Gupta et al. 2009)
<i>S. samsunensis</i>	–	+			(Nalubega et al. 2016)
<i>S. sedi</i>	–			–	(Saricaoglu et al. 2014)
<i>S. seymenliensis</i>				+	(Tatar and Sahin 2015)
<i>S. specialis</i>	–			–	(Saricaoglu et al. 2014)
<i>S. tubercidicus</i>	+			–	(Gupta et al. 2009)
<i>S. varsoviensis</i>	+			–	(Gupta et al. 2009)
<i>S. viridochromogenes</i>	+			–	(Gupta et al. 2009)
<i>S. xanthochromogenes</i>	+			–	(Gupta et al. 2009)
<i>Verrucosipora fiedleri</i>				+	(Xie et al. 2018)
<i>V. gifhornensis</i>				+	(Xie et al. 2018)
<i>V. maris</i>				+	(Xie et al. 2018)
<i>V. rhizosphaerae</i>				–	(Xie et al. 2018)

“+,” catabolized; “–,” not catabolized; empty cells indicate no reports found on the catabolism of the referred N compound; *also allantoin

Scenario 1: xanthine and hypoxanthine

As mentioned previously, most of the PAB studied thus far harbor the complete set of genes for the purine metabolism as well as (i) the functional high-affinity transporters for adenine (PurP and YicO) or hypoxanthine/guanine (YjcD and YgfQ), belonging to cluster COG2252 of the evolutionarily broad family NCS2 in *E. coli* (Papakostas et al. 2013), (ii) the NAT/NCS2 (nucleobase ascorbate transporters or nucleobase cation symporter family 2), (iii) the NCS1 (nucleobase cation symporter family 1) purine transporters (Ma et al. 2016), and (iv) the xanthine permease XanQ in *E. coli* K-12 (Frillingos 2012). Thus, proliferation of PAB with the ability to scavenge xanthine or hypoxanthine from the surrounding media could deplete the plant cells of these substrates for the enzymes XHD and XO. This

situation may result in the plants exhibiting reduced rates of ureide synthesis or with lower effectiveness of the oxidative defense responses. Examples of bacterial species with or without the ability to use xanthine and hypoxanthine as an N source for growth are listed in Table 2. Concomitantly, the presence of high hypoxanthine producer bacteria, as it is the case of *Lysinibacillus fusiformis* (Gallegos-Monterrosa et al. 2016), could increase the bacterial XDH or XO activities (Self 2002). Moreover, in a nutrient-deprived environment, single *S. aureus* (ATCC 25923) and *E. coli* (ATCC 25922) bacterium can release $\sim 10^6$ purine derivative molecules mainly adenine, guanine, hypoxanthine, and xanthine per hour, pointing out changes in their purine salvage process in response to starvation (Chiu et al. 2018). The identification in *Ps. putida* KT2440 of chemoreceptors which specifically recognizes guanine, xanthine,

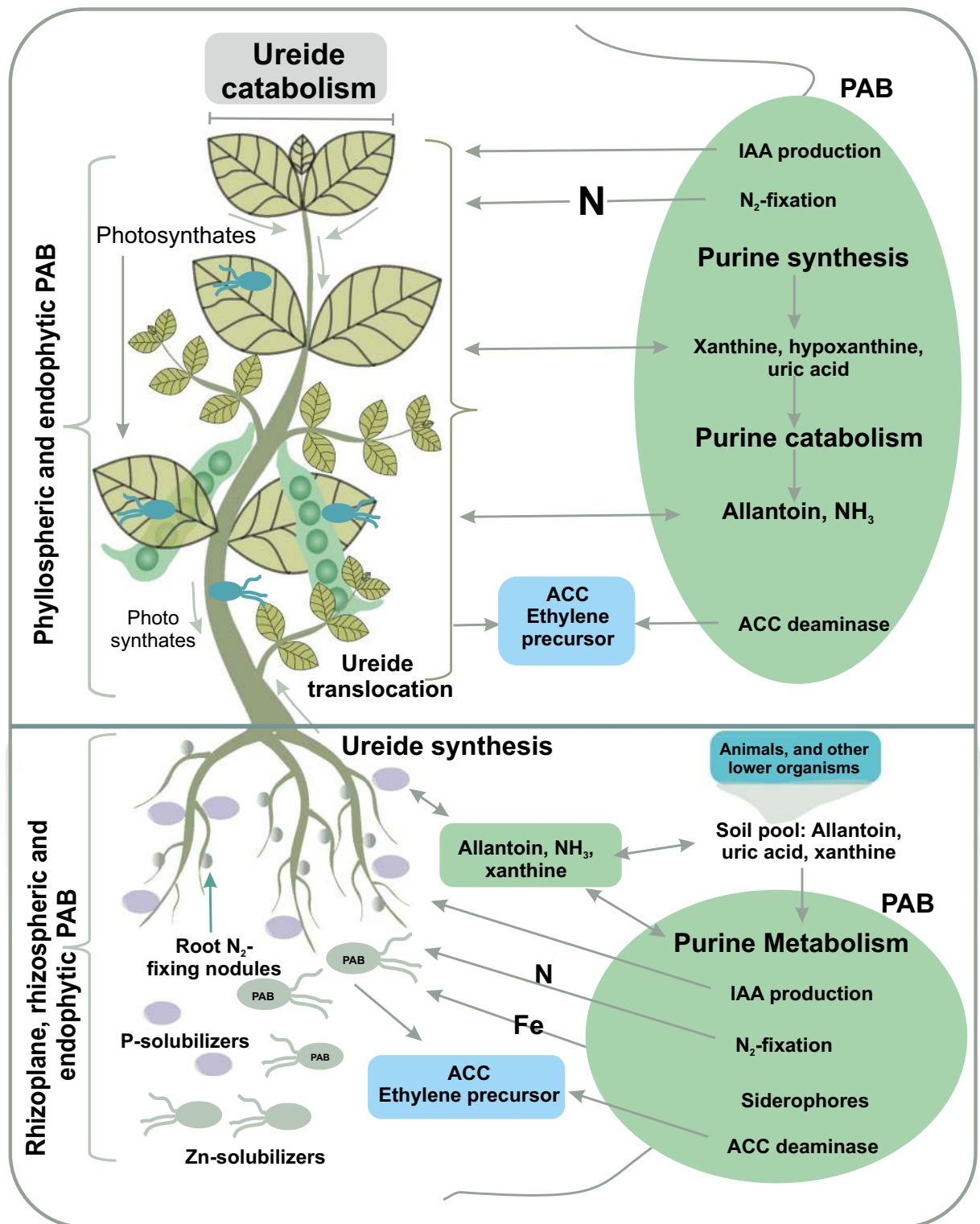


Fig. 2 Purine metabolism interactive scenarios between a plant and its plant-associated bacteria. Details of metabolic pathways and corresponding references are outlined in the text

hypoxanthine, and uric acid could explain the high biodiversity and size of bacterial populations in ureide-enriched rhizospheric soils and N₂-fixing nodules in ureidic legumes (Fernández et al. 2016). A very interesting discovery is the capacity of bacteroids of *Bradyrhizobium elkanii* USDA76 to enzymatically reassimilate 5–16% of the N₂ fixed by the nitrogenase through the purine pathway that includes five isoforms of XDH ending with the synthesis of uric acid, as uricase was not detected (Cooper et al. 2018). The same authors suggested that the recycling of purine intermediates is associated with a higher effectiveness of the symbiosis between *B. elkanii* USDA76 and soybean cv. Peking.

Scenario 2: ureides (allantoin and allantoate)

Shorey (1947) was the first to recognize the relatively high content of allantoin in soils of diverse types and compositions in the USA. In soil, the allantoin pool is sustained by the decomposition of plant tissues, the excretion of ureide-enriched root exudates (Wang et al. 2007), and the ureides released from decaying or active N₂-fixing nodules (24.7 g·N·L⁻¹·day⁻¹) (Ofosu-Budu et al. 1995). Furthermore, the soil allantoin pool can be increased by daily animal urinary excretions containing up to 22.2% allantoin (429 mmol·day⁻¹) (Wang et al. 2007; Nikkhah 2016; Yang et al. 2016), excreted by earthworms (*Lumbricus terrestris*) (Cohen and Lewis 1949), and/or by seasonal fires (Cobo-Díaz et al. 2015). Concomitantly, the soil uric acid, hypoxanthine, and xanthine pools could also be significantly augmented via animal urinary excretions (Zhou et al. 2017). On the contrary, the soil allantoin pool can be depleted by N₂-fixing filamentous cyanobacteria species found colonizing roots of a number of plant species (Prasad 1983; Gantar et al. 1991) and capable of using purine products for growth. Allantoin is also taken up by germinating spores of *B. fasitidiosus* (Salas and Eliar 1985) as well as by populations of soil bacteria and actinomycetes, and is known to stimulate the germination and growth of *Echinochloa crus-galli* (Wang et al. 2007). Examples of bacterial capable to hydrolyze allantoin are listed in Table 2.

Under stressful conditions, many PABs catabolize allantoin to release 4-M equivalents of NH₃ at a low C/N cost. For example, the 22-kb chromosomal *all*-gene locus responsible for ureide catabolism elevates the

capability of *K. pneumoniae* to compete for allantoin as a pivotal N source for growth and replication (Chou et al. 2004; Li et al. 2014). Most methylobacteria do not fix N₂ in the phyllosphere but carry genes for the complete sets of ureide catabolism (allantoinase, allantoate amidohydrolase, and ureidoglycorate urea-lyase) suggesting the possibility that PAB utilize urea and ureide generated by N₂-fixing legumes as an N source (Minami et al. 2016). Under N-limiting conditions, the capacity of *B. cenocepacia* strain H111 to use allantoin as N source depends on the functionality of the response regulator NtrC for N starvation (Liu et al. 2017b). In *B. subtilis*, allantoin from the growing media is transported into the cells by the putative 12-helix PucINCS-1 family of secondary active transporter encoded by the *pucI* gene (Ma et al. 2016). The NCS1 Mhp1 symport located in the cytoplasmic cell membrane promotes the uptake of allantoin into *M. liquefaciens*, serving as part of a salvage purine pathway (Patching 2017). These transporters allow bacteria to scavenge even small concentrations of soil allantoin. Interestingly, soil-occurring purines are toxic to microbial strains lacking allantoinase activity (Darlington and Scazzocchio 1967). On the other hand, the promoted growth of barnyardgrass by the allantoin released from roots of non-allelopathic rice cultivars in paddy soils (Sun et al. 2012) and the promotion of the jasmonic acid responsive genes in *Arabidopsis thaliana* supplied with allantoin (100 mM) (Takagi et al. 2016) are indicators of the capacity of plants to uptake soil allantoin. The possibility exists that not all the soil allantoin enters the root and root nodules due to the capacity of soil microbiota to degrade allantoin to NH₄⁺, to be further taken up and assimilated (Imsande 1986).

For plants grown in low-N soils, a collateral benefit of an active ureide catabolism in PAB is the excessive production of intracellular NH₄⁺ and NH₃ that must be excreted from the bacteria to the surrounding environment as it is the case of *S. coelicolor* fed with allantoin (20 mM) in a minimal N medium (Navone et al. 2014). Although, elevated levels of NH₄⁺ and NH₃ might inhibit the transcription of *MsU2* gene in roots and nodules hindering the N₂ fixation due to inhibition of the nodule UOX activity (Li et al. 2015). In nature, this situation may be counteracted by the urease activity and uric acid transporter (pucJK) present in *B. subtilis* (Bongaerts and Vogels 1976; Ma et al. 2016), as well as by the degradation of urea and the incorporation of the NH₃ into cell material as in *Hydrogenomonas eutropha*

(Ammann and Reed 1967), *K. pneumoniae* (Li et al. 2014), and *Rhodopseudomonas palustris* (Naito et al. 2016). Evidences indicate the capacity of PAB and plants to incorporate the available NH_3 into amino acids via the glutamine synthetase-glutamate synthase pathway (Tian et al. 2017; Zhang et al. 2017c).

Scenario 3: N_2 -fixing ureidic legumes

In N_2 -fixing ureidic legumes, the most relevant impact of soil allantoin can be the inhibition of N_2 fixation as shown in rhizobia-nodulated soybean exogenously supplied with allantoin (5 mM) (Serraj et al. 1999) or allantoate (5–10 mM) (Serraj and Sinclair 2003). Furthermore, the uptake of allantoin (5 $\text{mg}\cdot\text{L}^{-1}$) by 24-h soaked *Phaseolus vulgaris* seeds (Luis Cabrera-Ponce et al. 2015) raises the question of soil allantoin feedback inhibiting nodulation in legumes sown in soils containing elevated allantoin levels. Moreover, allantoin may enter roots and nodules via the UPS family of transporters for its utilization as N source (Lescano et al. 2016). The allantoin transport for endodermis crossing, root xylem loading, and subsequent export to the shoots is mediated by the GmUPS1 in soybean similar to the AtUPS5 (*A. thaliana* Ureide Permease 5) (Lescano et al. 2016). On the other hand, bacterial-excreted xanthine or hypoxanthine could also cause a feedback inhibition of the N_2 fixation in root nodules, or may cause high XO activity rates resulting in toxic levels of ROS in plant cells that, in turn could block, for example, the colonization of root by effective rhizobia (Zipfel and Oldroyd 2017).

Examples of interactive association between plants and associated PAB on plant ureide metabolism are (i) the increased relative ureide index (RUI) measured in the xylem sap of non-nodulated soybean varieties colonized by endophytic *Streptomyces* sp. strain P4, or in the rhizobia-nodulated soybean varieties Hinthada and SJ5 co-inoculated with *Streptomyces* sp. and *B. japonicum* strain USDA110, when compared to the lower RUI measured in the nodulated soybean varieties co-inoculated with *Streptomyces* sp. and the *B. japonicum* strain THA7 (Soe et al. 2012) and (ii) the enhanced leaf ureide content in *B. japonicum* strain 14M2b-nodulated soybean co-inoculated with *A. canadense* strain DS2 (Juge et al. 2012). An interesting discovery was the absence of the genes for the ureidoglycorate urea-lyase that catalyze the last step of ureide degradation in *Methylobacterium* sp. strains 4–46 and WSM2598

nodulating *Lotonosis bainesii*, to avoid the deploy of nodule ureides for colony growth (Minami et al. 2016). Another relevant discovery is the plasticity of the purine catabolism in *M. aquaticum*, *M. platan*, and *M. tarhaniae* that do not catabolize allantoin in soils (Veyisoglu et al. 2013), but express all the genes for the complete sets of enzymes (allantoinase, allantoate amidohydrolase, and ureidoglycorate urea-lyase) for ureide degradation as soybean stem endophytes (Minami et al. 2016). Examples of bacteria capable to hydrolyze allantoin are listed in Table 2.

A myriad of reports has demonstrated the N enrichment of soils by N_2 -fixing legumes (Blesh 2018). Thus, it can be assumed that N released from active or senescence root N_2 -fixing nodules would be mainly in the form of ureide with a known direct impact on microbial species richness and diversity compared with soils with low ureide content (Wang et al. 2010). Despite the relevance of allantoin on soil microbiome, the description of the chemical constitution of the soil total N in terms of purine content is not included in the vast majority of publications. As shown by Wang et al. (2007), exogenous additions of 100 or 500 μg allantoin per gram of soil increase by 3- or 5-fold the number of colony forming bacteria/gram soil, respectively. In the case of N_2 -fixing bacteria different from rhizobia, there are no evidences on ureides being synthesized in the colonized roots to be translocated via the xylem to sink organs. Very low ureide levels were detected in *Paraburkholderia*-root nodulated *Mimosa* spp. native to neotropical savannas (Izaguirre-Mayoral, unpublished data).

Conclusions and final remarks

Knowledge of the underlying physiological mechanisms by which PAB mediate stress tolerance is critical for the effective use of PAB to assure sustained agricultural production in changing environmental conditions. However, the co-selection of microbiota with an efficient purine metabolism according to the plant genome and prevailing abiotic stresses is not an easy task to achieve. For example, the popularization of the use of the lower-cost rock phosphate instead of triple superphosphate by farmers switches the dominance of Proteobacteria to that of Oxalobacteraceae (mainly *Massilia* and *Herbaspirillum*), augmenting the soil populations of *Klebsiella*, *Burkholderia*, and *Bacillus* species

(Silva et al. 2017a). At the soil level, the composition of the microbiota thriving at the root–soil interface is largely determined by the soil pH (Bang-Andreasen et al. 2017; Zhang et al. 2017b), by the soil chemical composition (Canellas and Olivares 2017), and the prevailing agricultural management practices (Hartman et al. 2018). The behavior of the soil microbial communities seems also to be linked to the expression of the bacterial type VI secretion systems, quorum sensing, and biofilm formation (Gallique et al. 2017). At the plant level, rhizospheric and endophytic microbial populations undergo variations in size and biodiversity throughout the plant life cycle and are affected by the selective pressures exerted by crop domestication and plant physiological traits (Senga et al. 2017). Concomitantly, there are complex interactions between the size of the plant aerial mass and the size of the population of soil heterotrophic microorganisms involved in soil-plant N cycling leading to alteration in the ^{15}N values in plant tissues (Jiang et al. 2017). On the other hand, plant genetic traits in terms of cell sensors and receptors to bacteria seem to be the final molecular factors controlling the biodiversity of taxa associated microbiota (Ranf 2017). An example is the reported degree on the specificity of particular bacterial genotypes for particular sugarcane cultivars, depending on geographic origin and level of fertilizers used (Kruasuwan and Thamchaipenet 2016).

The complexity of plant-associated microbiome was recently emphasized by the aerial long-distance transport of microbes from terrestrial habitats and plant surfaces to be ground far away by seasonal rains (Hiraoka et al. 2017). The analysis is further complicated by the great variability among bacterial strains within a determinate genus in terms of N metabolism, N_2 -fixation, IAA production and the ACCD activity (Supplementary Tables 1–6), and pivotal bacterial traits to help plants to survive in abiotically stressed conditions. A breakthrough in breeding for salinity tolerance is the generation of salt-tolerant transgenic *Camelina sativa* expressing the *Ps. putida* UW4 *acdS* gene encoding the ACCD under the control of the root-specific promoter (*rolD*) (Heydarian et al. 2016). It is interesting to speculate that the evolutionary drive for microbes to establish association with plants was to have access to the nutrient resources that plants provide and to maximize this new nutritional niche. Furthermore, there is an estimate of 69,365 genes involved in a wide range of bacterial biological metabolic processes and responses to environmental conditions that are prone to undergo

horizontal transfer (Jeong and Nasir 2017). There is also a new set of multiple functions described for the extracellular soil DNA of microbial origin, the most important being the ensurance of the intraspecific genetic flow, guaranteeing the adaptation and survival of the species and the construction of multicellular communities (Ibáñez de Aldecoa et al. 2017). The communication between plants and soil microbial community represents a bilateral process that goes beyond root exudates and microbial-elaborated signal response molecules.

Given widespread concerns for crop losses due to the drastically changing climate, the understanding of the interactive signaling for the purine metabolisms among PAB as well as between PAB consortia and plants takes on importance, as it may support management decisions necessary to maintain PAB biodiversity and the pivotal roles of agricultural services provided by bacterial consortium to crops. The recent discovery of the *B. megaterium* inducing the expression of the guanine nucleotide-binding protein beta subunit in roots of the ethylene-insensitive tomato *never ripe* (Ibort et al. 2018) further confirms the benefits of PAB on stress-challenged plants. The overexpression of this G-protein β -subunit in transgenic *Nicotiana tabacum* significantly enhanced the plants' drought tolerance (Liu et al. 2017a). A community-level view that considers multiple PAB species interactions provides the best approach to this topic. Available technologies such as the high-resolution tridimensional images of leaf surfaces using taxon-specific fluorescently labeled oligonucleotide probes (Peredo and Simmons 2018) and metagenomic information (Kimura 2018) could help to identify bacterial trait-based mechanisms. An alert on the flaws inherent to the compositional nature of the datasets derived from microbiome studied by high-throughput sequencing (HTS) of 16S rRNA gene amplicons, metagenomes, or metatranscriptomes was issued by Gloor et al. (2017).

To date, however, quantitative metabolic models that can serve as a starting point for generating experimentally testable hypotheses for interactive exchanges of purine derivatives between associated microbiome and plants are not available. Based on the information compiled for this review, it is evident that (i) the way microbes manipulate plant purine intermediates at biotrophic interfaces and finally control the outcome of ureides is still unclear and (ii) the categorization of PAB as growth promoters could not be based exclusively on the bacterial cultural properties, synthesis of

phytohormones, and ACCD activity, as at present. Studies on the functionality of PAB must include the denitrification, cellulolytic, hemicellulolytic, and purine scavenger abilities of bacterial isolates, as well as the interactive plant-bacteria purine exchanges under abiotic challenging conditions.

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