Phytohormone-Producing PGPR for Sustainable Agriculture

Dinesh Kumar Maheshwari, Shrivardhan Dheeman and Mohit Agarwal

Abstract Looking into account, the effective microorganisms (EM) discussed in green revolution are able to enhance plant growth and crop productivity. These act as fertilizers without causing any hazard on edaphic profile and ecological sustainability. In recent scenario, these microorganisms as PGPR are known to produce phytohormones and cover tremendous role in sustainable agriculture. Major six classes of phytohormone including natural, semi-synthetic and synthetic check out seed dormancy of several crop plants and allow to germinate in short period and further induce plant growth in sustainable manner, trigger plant immunity, maintain stress tolerance and aid plant maturity for fruiting and seedling. Under this review, discussion lies on all the aspects covering role and significance of auxin and other phytohormone-producing PGPR important to agriculture in near future.

Keywords PGPR · Phytohormone · Cytokinin · Auxin · Salicylic acid · Plant immunity · Crop productivity

1 Introduction

The ecology of root vicinity is called as rhizosphere, which harbors diversified microorganisms having various interactions, under two broad means as symbiotic (formation of nodule) and non-symbiotic. Based on the mode of interactions in rhizosphere, plant growth promoting rhizobacteria are termed as extracellular PGPR (ePGPR) and intracellular PGPR (iPGPR) as stated by Martinez-Viveros

D.K. Maheshwari (✉) · S. Dheeman · M. Agarwal
Department of Botany and Microbiology, Gurukul Kangri University, Haridwar, UK, India
e-mail: maheshwaridk@gmail.com

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et al. (2010). Due to their importance in agro-ecosystem, these are now established to improve soil health and profile so as to increase crop productivity.

In the beginning of twentieth century, Starling was first to define the term phytohormone as *organic substance which are synthesized in minute quantities in one part of the plant body and transported to another part where these influence specific physiological processes*. Phytohormones are structurally unrelated small molecule in nature, regulating plant growth and development i.e. auxin, abscisic acid, cytokinin, gibberellin and ethylene. However, recently, many semi-synthetic and synthetic phytohormones have been identified: brassinosteroids, jasmonate, salicylic acid, nitric oxide, strigolactones, etc. (Santner and Estelle 2009). Phytohormone producing bacteria are gaining full swing in whole globe under the means of exploitation due to synergy between bacteria and plant led to sustainable agriculture (Narula et al. 2006). Growth and development of plant is predominantly influenced by mineral nutrients, hormones and other secreting metabolites. In fact, almost all the communication in plant cells is brought by plant hormones produced by plant cells or by rhizobacteria.

The most commonly occurring phytohormone is auxin (indole acetic acid). IAA produced in shoot apical meristem of plant and found throughout the plant body. It occurs in the form of free auxins (diffusible auxins), which is released out from plant tissues, released out from tissues only after hydrolysis, autolysis and enzymolysis. Production of IAA is widespread among rhizospheric bacteria (Table 1). Different IAA biosynthesis pathways are used by these bacteria and sometimes a single bacterial strain exhibit more than one pathway (Patten and Glick 1996). There are many chemically synthesized phytohormones such as indole-3-butyric acid (IBA), 2-methyl-4-chlorophenoxy acetic acid (MCPA), indole-3-propionic acid (IPA), 2,4-dichlorophenoxy acetic acid (2,4-D), etc., able to trigger various physiological processes (Table 2).

Plant growth regulatory hormone generally called gibberellins (GAs) forms a large family of plant growth substances with distinct functions during the life cycle of higher plants. Gibberellins are involved in a number of developmental and physiological processes (Crozier et al. 2000) including seed germination, seedling emergence, stem and leaf growth, floral induction and flower or/and fruit growth (King and Evans 2003; Sponsel 2003), regulation of vegetative and reproductive (bud) dormancy and delay of senescence (Bottini and Luna 1993; Fulchieri et al. 1993; Reinoso et al. 2002). Gibberellins in combination with other phytohormones, are directly effective in promotion of shoot elongation in plants (Crozier et al. 2000). Very few bacteria produce GA during their cultivation on artificial culture medium.

Cytokinin mediates the responses to variable extrinsic factors, such as light conditions in the shoot and availability of nutrients and water in the root and also play role in the response to biotic and abiotic stresses. Together, these activities contribute to the fine-tuning of quantitative growth regulation in plants (Werner and Schmülling 2009; Gupta and Rashotte 2012). Cytokinin concentration in plant cells depends on biosynthesis immobilization from extracellular sources,

Table 1 Various indigenous genera-producing IAA and their influence on different crops

Name of genera	Accession number (NCBI)	IAA production (μg/ml)	Yield (%) increase	References
Pseudomonas aeruginosa GRC_1		31.00	42.6 (G/P)	Aeron et al. (2010)
P. aeruginosa PS2		36.00	38.8 (G/P)	Aeron et al. (2010)
P. aeruginosa PSII		30.00	39.2 (G/P)	Aeron et al. (2010)
P. aeruginosa LES4	HQ123431	42.00	41.2 (G/P)	Aeron et al. (2010)
P. aeruginosa PRS4	AB666551	40.00	40.8 (G/P)	Aeron et al. (2010)
P. aeruginosa PS15		41.00	47.3 (G/P)	Aeron et al. (2010)
P. aeruginosa PSI		36.00	45.74	Aeron et al. (2011)
Mesorhizobium loti MP6		24	34.28	Chandra et al. (2007)
Bacillus sp. BPR7	JN208240	17		Kumar et al. (2012)
Bradyrhizobium sp. BMP17	AB665550	40		Maheshwari et al. (2014)
Sinorhizobium meliloti PP3		80		Pandey and Maheshwari (2007)
S. meliloti MSSP		100		Pandey and Maheshwari (2007)

Author's Lab
G/P Growth per plant over control

metabolic inter-conversions, inactivation and degradation. Increased cytokinin concentration results either from their uptake or biosynthesis. Accumulated cytokinins are capable of inducing cytokinin oxidase which consequently decreases cytokinin levels. This seems to be the mechanism of re-establishment and maintenance of cytokinin homeostasis required for further development of physiological events induced by transient cytokinin accumulation (Kaminek et al. 1997).

Abscisic acid (ABA) is produced in a very low concentration which influences physiological processes such as respiration rate, metabolism and root abundance. ABA is involved in protection against drought, salt stress and toxic metals. It also induces stomatal closure of leaf. Rhizospheric bacteria capable of producing ABA are experimentally poorly underpinned. ABA has effective role in synthesis and inhibition of cytokinin (Miernyk 1979), and increases plant growth by managing with cytokinin concentration (Spaepen et al. 2009). It also alleviates plant stress by increasing rhizosphere in terms of root abundance (Maheshwari 2011; Boiero et al. 2007).

Plants use ethylene in gaseous form to regulate myriad developmental processes and stress responses. Ethylene production by infected plants is an early resistance response leading to activation of plant defense pathways. However, plant pathogens are also capable of producing ethylene, which might have an effect not only on the plant but also on the pathogen as well. Therefore, ethylene plays a dual role in plant–pathogen interactions by affecting the plant as well as the pathogen (Chagué et al. 2006). Ethylene regulates seed germination, root

Table 2 Involvement of various genes in biosynthetic pathways of IAA

Bacteria	Gene	Enzymatic activity	Pathway	References
Azospirillum brasilense Yu62	*ald*A	Aldehyde dehydrogenase	IPA	Xie et al. (2005)
A. brasilense Sp245	*ipd*C	Indole pyruvate decarboxylase	IPA	Costacurta et al. (1994)
A. brasilense Sp7	*his*C1	Aromatic amino acid	IPA	Castro-Guerrero et al. (2012)
Rhizobium sp. NGR234	*y4w*E	Aminotransferase	IPA	Kittell et al. (1989)
	*y4w*E			
Enterobacter cloacae FERM BP-1529	*ipd*C	Indole pyruvate decarboxylase	IPA	Koga et al. (1991)
Pseudomonas fluorescens Psd	*iaa*M	Tryptophan monooxygenase	IAM	Kochar et al. (2011)
Ralstonia solanacearum	*iaa*M	Tryptophan monooxygenase	IAM	Salanoubat et al. (2002), Kurosawa et al. (2009)
	*iaa*H	Indole acetamide hydrolase		
Erwinia chrysanthemi 3937	*iaa*M	Tryptophan monooxygenase	IAM	Yang et al. (2007)
	*iaa*H	Indole acetamide hydrolase		
Streptomyces En-1	*iaa*M	Tryptophan monooxygenase	IAM	Lin and Xu (2013)
	*iaa*H	Indole acetamide hydrolase		
P. fluorescens EBC191	*nit*	Indoleacetonitrilase	IAN	Kiziak et al. (2005)
	*nth*AB	Nitrile hydrolase		
Bacillus amyloliquefaciens FZB42	*yhc*X	Indoleacetonitrilase	IAN	Idris et al. (2007)
Bacillus sp. OxB-1	*oxd*	Phenylacetaldoxime dehydratase	IAOX	Kato et al. (2005)
Rhodococcus globerulus A-4	*oxd*RG	Phenylacetaldoxime dehydratase	IAOX	Kato et al. (2005)
	*Nha*1	Nitrile hydratase		
Pseudomonas sp. K-9	*oxd*K	Phenylacetaldoxime dehydratase	IAOX	Kato and Asano (2006)
	*Nha*1	Nitrile hydratase		
Rhodococcus erythropolis JCM 3201	*oxd*K	Phenylacetaldoxime dehydratase	IAOX	Kato et al. (2005)
	*Nha*1	Nitrile hydratase		
Rhodococcus rhodochrous J-1	*oxd*K	Phenylacetaldoxime dehydratase	IAOX	Kato et al. (2005)
	*Nha*1	Nitrile hydratase		
Rhodococcus sp. AK32	*oxd*	Phenylacetonitrilase	IAOX	Kato et al. (2005)

(continued)

Table 2 (continued)

Bacteria	Gene	Enzymatic activity	Pathway	References
Brevibacterium butanicum	*oxd*	Phenylacetaldoxime dehydratase	IAOX	Kato et al. (2005)
	*Nha*1	Nitrile hydratase		
Corynebacterium sp. C5	*oxd*	Phenylacetonitrilase	IAOX	Kato et al. (2005)

IPA Indole-3-pyruvic acid; *IAM* Indole-3-acetamide pathway; *IAN* Indole-3-acetonitrile pathway; *IAOX* Indole acetaldoxime pathway

initiation, flower development, fruit ripening, senescence and responses to biotic and abiotic stresses. It thus plays a key role in responses to the environment that have a direct bearing on a plant's fitness for adaptation and reproduction (Lin et al. 2009).

Beneficial group of bacteria presently dominating by auxin-producing and plant growth promoting rhizobacteria profoundly increases seed germination, root development and water utilization by plants. These rhizobacteria can arouse plant growth directly or indirectly by changing microbial balance in the rhizosphere in service of beneficial microorganisms. They can subdue a broad spectrum of bacterial, fungal and nematode diseases. PGPR can also deliver protection against viral diseases (Siddiqui 2006).

More recently, there has been a resurgence of interest in environmental friendly, sustainable and organic agricultural practices (Esitken et al. 2005). Bio-inoculants or microbial inoculants are agricultural amendments that use beneficial microorganisms to promote plant health by providing phytohormone production in rhizosphere on colonization. Microbial inoculants can induce systemic acquired resistance (SAR) of crop species to several common crop diseases (provides resistance against pathogens).

In this review, present state of knowledge is being discussed for better understanding the nature of beneficial bacterial physiology responsible to deliver phytohormone in root vicinity and interaction with plant for their growth promotion and disease management.

2 Classification, Biochemistry and Biosynthesis of Phytohormones

Phytohormone production by soil bacteria has significant influence on plant growth and performance (Smaill et al. 2010). In fact such hormones are crucial signaling molecules that coordinate all aspects of plant growth, development and defense mechanism. Production of the phytohormone particularly auxin (IAA) is widespread among bacteria that inhabit the rhizosphere of plants.

Phytohormones are commonly classified as semi-synthetic and synthetic hormone including few herbicides. These are grouped into five classes based on structural similarity (biochemistry) and physiological effect on plant (or plant part). Growth regulators of other synthetic hormones are not grouped into these classes; they may occur naturally, chemically synthesized, or organically (biochemically/microbiologically) synthesized in bacterial cells which further may harvest through several criteria and strategies. In each class of phytohormone including chemically synthesized, one have their pragmatic effect on plant for their growth regulation/promotion and health management. Naturally occurring bacteria are able to do such kind of action (production of phytohormone) which signifies their benefits to plant and soil by residing in rhizospheric habitat. Exhaustive information about the biosynthesis of phytohormone auxins, gibberellins, cytokinins, ethylene and abscisic acid, as well as plant growth regulators such as polyamines and nitric oxide in *Azospirillum* spp. have been observed (Cassan et al. 2014). High level of auxin, gibberellins and salicylic acid in chemically defined media was produced by *Bacillus amyloliquefaciens.* Co-inoculation of this strain with *Bradyrhizobium japonicum* enhances soybean nodulation (Masciarelli et al. 2014). Phytohormonal basis for the plant growth promoting action of naturally occurring biostimulators attributed for enhancing the growth of agricultural and horticultural crops (Kurepin et al. 2014). PGPR treatment improves seedling growth and quality of cabbage and increases GA, SA and IAA in plants raised by such group of bacteria (Turan et al. 2014).

2.1 Auxins

Several decades before, the term “Auxin” was introduced into the identification of scientific community (Went and Thirmann 1937). In recent scenario, understanding of IAA in plant growth promotion has been truly spectacular. Undoubtedly, IAA has wide approach in enhancement of plant growth and health promotion. Five bacteria producing IAA in pure culture include members of genera *Bacillus*, *Microbacterium*, *Methylophages*, *Agromyces* and *Paenibacillus* which have considerable impact on root elongation of tropical rice plant (Bal et al. 2013). Rhizospheric halotolerant IAA-producing bacteria *Kocuria turfanensis* were able to promote growth of *A. hypogoea* both in nonsaline and saline soils (Goswami et al. 2014).

Auxins are versatile in nature which exhibit differential physiological action. They belong to five major groups namely indole acids, naphthalene acids, chlorophenoxy acids, benzoic acids and picolinic acids and their derivatives. The first group belongs to indole propionic acids and indole butyric acid; second group comprises Nephthaleneacetic acid and β-naphthoxyacetic acid; third

group has 2,4-dichlorophenoxyacetic acid, 2,4,5-trichlorophenoxyacetic acid and 2-methyl-4-chlorophenoxyacetic acid; whereas, 2,4,6-trichlorobenzoic acid and 2-methoxy-3-6-dichlorobenzoic acid categorized in fourth group and 4-amino-3,5,6-trichloropicoline acid in last group.

It is interesting to note that diverse bacterial genera produce "Auxin." Recently, a number of studies have clearly shown that IAA can be a signaling molecule in microorganisms, in both IAA-producing and IAA-non-producing species. These findings raise new intriguing questions on the role of IAA in bacteria and their interaction with plants. Such phytohormones of bacterial origin directly affect plants physiology particularly in root colonization strategies adopted by bacteria during plant–microbe interaction. IAA acts as signaling molecule in bacteria, therefore, facilitates positive outcome on the plant, which ranges from phytostimulation to plant immunity (Cheynier et al. 2013).

High degree of similarity between IAA biosynthesis pathway in plants and bacteria has been observed. Tryptophan has been identified as a main precursor of IAA biosynthesis pathway in bacteria. Basically, two precursors of IAA formation are presumed, either tryptophan or a tryptophan precursor. Various intermediate products namely indole-3-pyruvate, indole-3-acetaldoxime, indole-3-acetaldehyde (IAAld), indole-3-acetonitrile (IAN), indole-3-acetamide (IAM), or tryptamine (TAM) are involved in IAA biosynthesis.

IAA pathways are usually classified based on these intermittent compounds. Independently, indole-3-acetamide pathways are characterized in bacterial genera *Agrobacterium*, *Pseudomonas*, *Pantoea*, *Rhizobium*, *Bradyrhizobium* (Theunis et al. 2004). Conversion of tryptophan into IAA is accomplished by two steps: first step involved IAM that is produced by enzymatic action (tryptophan-2-monooxygenase) and during second step, IAA is obtained by enzymatic hydrolysis of IAM by IAM hydrolase (Bar and Okon 1993; Prinsen et al. 1993).

The other pathway is named as indole-3-pyruvate (IPyA) pathway which occurs in some pathogenic bacteria including species of *Pantoea* and few beneficial genera such as *Rhizobium* and *Bradyrhizobium*. Initially, tryptophan is converted into IPyA by enzymatic transformation and further decarboxylated into indole-3-acetaldehyde (IAAld) by indole-3-pyruvate decarboxylase (IPDC). In the terminal step, IAAld is oxidized into IAA. In tryptamine (TAM) pathway, TAM is directly converted to IAAld by amine oxidase and further decarboxylation brought about with indole-3-pyruvate decarboxylase lead to the formation of IAA (Hartmann et al. 1983) as identified in *Bacillus* spp. (Perley and Stowe 1966).

In tryptophan side chain oxidase (TSO) pathway, tryptophan is converted into IAAld by IPyA and oxidized to IAA simultaneously as in *Pseudomonas fluorescens* CHA0 (Oberhänsli et al. 1991). Conversion of indole-3-acetamide via nitrilase is another pathway where indole-3-acetonitrile is produced by tryptophan via indole-3-acetaldoxime (Patten and Glick 1996). The diagrammatic representation is shown in Fig. 1.

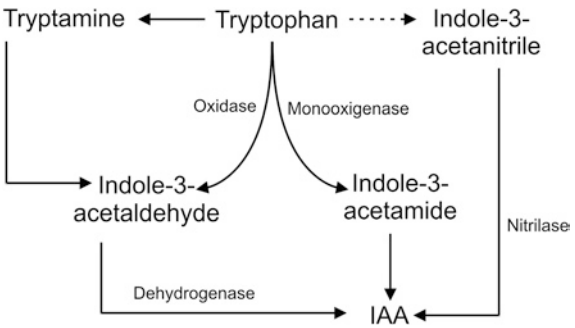

Fig. 1 Auxin (IAA) biosynthesis—an overview via different routes (*Dashed line* represents the unknown pathways and *solid lines* represent the pathways of enzymatic action)

2.2 Gibberellic Acid

The gibberellic acid (GA) production was first noticed in fungal genera *Giberella fujikuroii* and later discovered in higher plant species. The hormone induces stem elongation, early flowering/budding, breaks seed dormancy and delay senescence in plants. Free GAs, conjugated GAs and bound GAs are three major states of GAs. Natural GAs are the conjugates of β-D-glucose. About 76 derivatives of glucosyl esters of GAs are presently identified and more than 6 glucoside derivatives namely GA_1-glucoside, GA_3, GA_8, GA_{26}, GA_{27} and GA_{29} have been characterized. GA is tetracyclic diterpenoid compound and their biosynthetic pathways are quite complex (Richman et al. 1999). Gibberellin biosynthetic pathways comprise three stages according to the nature of the enzymes involved.

During first stage, isopentenyl pyrophosphate (IPP) and ent-kaurene are synthesized from mevalonic acid (Graebe 1987; Macmillan et al. 1997). Synthesized IPP is further converted into dimethylallyl pyrophosphate (DMAPP) which later on converted into geranyl-geranyl pyrophosphate (GGPP), IPP-isomerase and GGPP-synthase, localized in plastids of higher plants (Dogbo and Camara 1987). GGPP is further cyclized into ent-copalyl pyrophosphate (ent-CCP) and finally leads to ent-kaurene by CPP synthase and ent-kaurene synthase (Fig. 2). In second stage, the ent-kaurene so formed is converted into GA12. Ent-kaurene is oxidized into six steps to GA12 via ent-kaurenol, ent-kaurenal, ent-kaurenoic acid, ent-7a-hydroxykaurenoic acid and GA12-aldehyde. Microsomal NADPH-dependent cytochrome P-450 monooxygenases catalyze this intermediate in endoplasmic reticulum (Graebe 1987). 7-oxidation, 12a-hydroxylation and 13-hydroxylation are certain biosynthetic steps catalyzed by both particulate monooxygenases and soluble dioxygenases, which occasionally occur together within the same species or same tissues with few exceptions (Lange and Graebe 1993; Bearder 1983).

The final step involves the oxidation of GA12-aldehyde by 2-oxoglutarate-dependent dioxygenases to form GA12. In fact, GA 20-oxidase catalyzes the whole series of oxidation reactions carried out at carbon-20, leading to either C20-GAs (GA25), or after loss of C20 to form C19-GAs. Later, 3b-hydroxylation activates C19-GAs to plant hormone and subsequently inactivated by

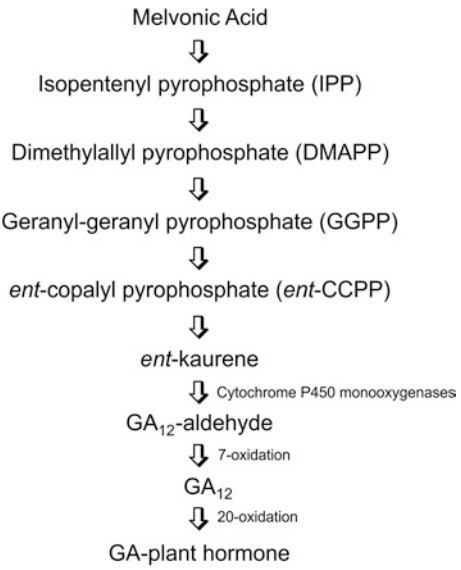

Fig. 2 Gibberellin biosynthesis

2b-hydroxylation. C20-GAs are also 2b and 3b-hydroxylated but the resulting products are GA13 and GA43 (Fig. 2).

Among bacteria, characterization of GA was first reported in *Rhizobium meliloti* (Atzorn et al. 1988). The presence of GA_1, GA_4, GA_9 and GA_{20} was also demonstrated in gnotobiotic cultures. Apart from *Rhizobium* spp., production of gibberellins was also observed in other bacterial genera *Acetobacter diazotrophicus*, *Herbaspirillum seropedicae* (Bastian et al. 1998) and *Bacillus* spp. (Gutiérrez-Mañero et al. 1998). Involvement of GA production in enhanced growth of *Pinus pinea,* is inoculated with *Bacillus licheniformis* and *B. pumilus* was reported by Probanza et al. (2002). Other than *Bacillus,* endophytic *Sphingomonas* is recently reported to enhance growth of tomato (Khan et al. 2014). Kang et al. (2014) reported that *Pseudomonas putida* modulates stress physiology of soybean and enhances its growth under saline conditions.

2.3 Cytokinin

Cytokinins play distinguish role in cell division, leaf expansion, delay senescence and induce seed germination (Mok 1994). Naturally occurring cytokinins, N6-(D2-isopentenyl) adenine (i6Ade) and Zeatin (trans-zeatin), contain hydroxylated side chain. Broadly, direct and indirect pathways have been proposed for cytokinin biosynthesis (Fig. 3).

During direct pathway of cytokinin biosynthesis, N6-isopentenyladenosine monophosphate formed from AMP and dimethylallyl pyrophosphate (DMAPP). Its

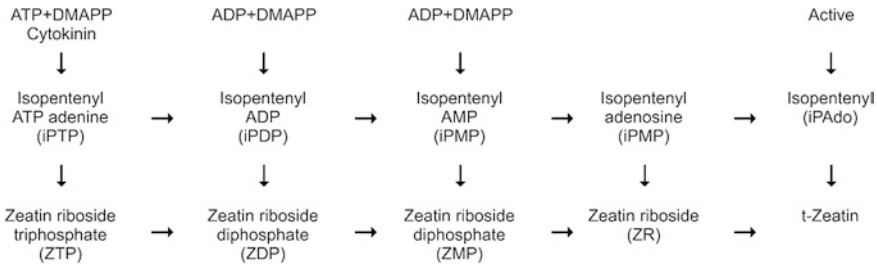

Fig. 3 Cytokinin biosynthesis

side chain hydrolyzed to form zeatin-type compounds, whereas indirect pathway involved release of cytokinin by turnover of tRNA containing cis-zeatin (Chen 1997).

Cytokinin production in *Agrobacterium* and *Pseudomonas* spp. was observed by Akiyoshi et al. (1987). Besides these genera, members of *Methylobacterium* spp. are capable to influence plant growth promotion by production of cytokinin (Lee et al. 2006; Madhaiyan et al. 2006). Earlier, Timmusk et al. (1999) observed that rhizobacteria of wheat produce cytokinin. Different bacterial genera *Proteus*, *Klebsiella*, *Bacillus*, *Escherichia*, *Pseudomonas* and *Xanthomonas* have ability to produce cytokinins (García de Salamone et al. 2001; Karadeniz et al. 2006).

2.4 Ethylene

In general, ethylene is known as hydrocarbon gas (C_2H_4) that acts as plant hormone. Resurgence and current research focus on its role in fruit ripening, inhibition of seedling growth, increase in the membrane permeability and root gravitropism.

For its biosynthesis, S-adenosyl-methionine (S-AdoMet) and ACC are the main precursors. S-AdoMet is used as a substrate for many biochemical pathways including polyamines in plants (Martin-Tanguy 2001). Initially, ethylene biosynthesis occurs by conversion of S-AdoMet to ACC by enzyme ACC synthase (S-adenosyl-L-methionine methylthioadenosine-lyase). In addition to ACC, ACC synthase (ACS) produces 5′-methylthioadenosine (MTA) which later on converted to methionine using a modified methionine cycle (Bleecker and Kende 2000) (Fig. 4).

Ethylene production has been observed in almost all seed-bearing plants. Various plant parameters such as seed germination, tissue differentiation, formation of root and shoots primordial, root elongation, lateral bud formation, flowering initiation, anthocyanin synthesis, flower opening and senescence, fruit ripening and degreening, production of aroma, leaf and fruit abscission and response of plant to biotic and abiotic stresses as the major processes influenced due to ethylene-influenced regulation that affects diverse developmental processes and stress responses (McKeon and Yang 1984; Abeles et al. 2012). Recently, few reports of bacterial species that produce plant growth modulating volatiles have been published. Blom et al. (2011) suggested the effects of bacterial volatiles highly dependent on the

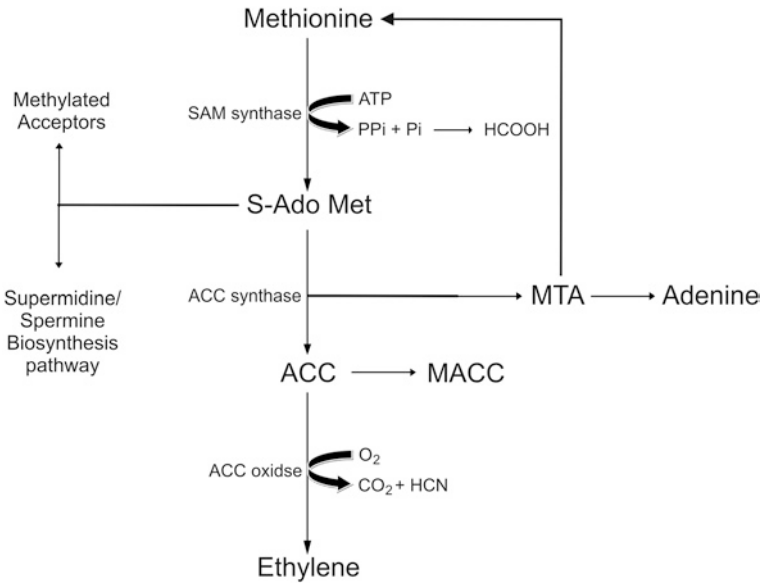

Fig. 4 Ethylene biosynthesis

cultivation medium and the inoculum quantity. However, less bacterial genera are identified to produce ethylene. Long back, Freebairn and Buddenhagen (1964) considered that ethylene might be involved in the apparent early ripening of banana fruits, which is characteristic of infection by *P. solanacearum*. Infected banana fruits indeed produce more ethylene than healthy fruits of comparable age and interestingly, no ethylene was detectable in uninfected green fruit.

On the other hand, IAA can activate the transcription of ACC synthase (Kim et al. 1992; Kende 1993). It may also inhibit IAA transport and signal transduction (Swarup et al. 2007), when ACC deaminase-containing bacteria lower the ethylene concentration in plant roots, relieve the ethylene repression of auxin response synthesis and indirectly increase plant growth. Thus, ACC deaminase-containing bacteria decrease ethylene inhibition, permitting IAA stimulation without the negative effects of increasing ACC synthase and plant ethylene levels. In addition, it acts as signaling molecule in plant protection against pathogens. Ethylene production was reported to act as a virulence factor for bacterial pathogens, e.g. *P. syringae* (Weingart and Volksch 1997; Weingart et al. 2001).

2.5 Abscisic Acid

Abscisic acid (ABA) is a naturally occurring growth inhibitor for leaf abscission and has a significant role in seed dormancy. This hormone is a sesquiterpenoid

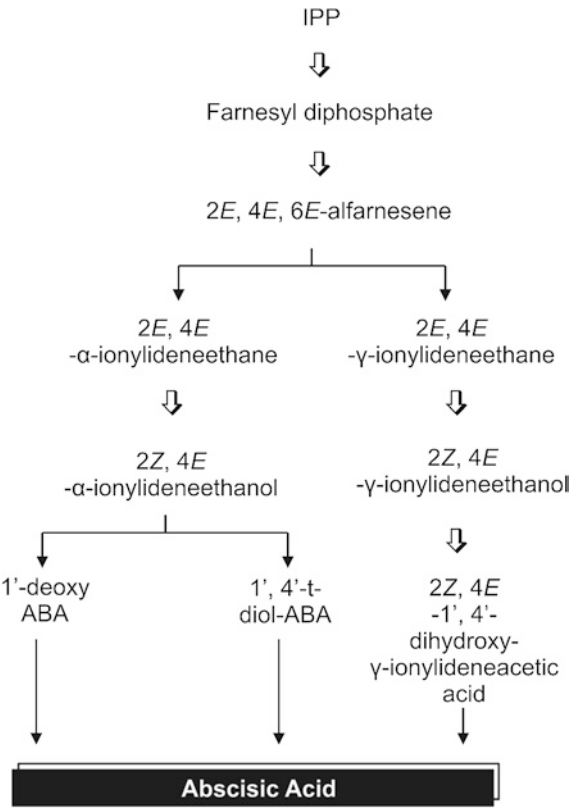

Fig. 5 Abscisic acid biosynthesis

(15-C) compound related to monoterpenes, diterpenes (including GAs), carotenoids and triterpenes. The structural feature of ABA and related compound/molecule contains a free carboxyl group, cyclohexane ring with double bond in α or β- position and C-2 double bond in cis geometry. The hormone regulates physiological processes such as stress adaptation and seed maturation. ABA is synthesized by two distinct pathways (Oritani and Kiyota 2003; Schwartz and Zeevaart 2010). Direct pathway occurs in phytopathogenic fungi in which IPP is synthesized from mevalonate pathway (MVA) (Newman and Chappell 1999), while indirect pathway is present in higher plants wherein Methylerythritol phosphate (MEP) is the source of IPP (Fig. 5).

ABA is produced by bacterial genera *Azospirillum brasilense* (Cohen et al. 2008) and *Bradyrhizobium japonicum* (Boiero et al. 2007). Available literature revealed that the effect of inoculation with ABA-producing bacteria on plant growth is under infancy. Since, ABA inhibits the synthesis of cytokinins (Miernyk 1979), it is therefore speculated that ABA increases plant growth by interfering with the cytokinin pool (Spaepen et al. 2009) and also alleviates plant stress by increasing the root/shoot ratio (Watts et al. 1981). Recent studies have reported regulation of endogenous ABA produced by PGPR of *Oryza sativa* (Belimov et al. 2014).

3 Applications

Phytohormone-producing PGPR are the free-living and associative community of bacteria in rhizosphere which encourage beneficial effects on plant health and growth, suppress disease-causing microbes and accelerate nutrient availability and assimilation. In virtue of metabolite production, survival of disease-causing organisms in its niche (rhizosphere) is quite less. Phytohormone production also corroborates plant immunity to withstand against density-dependent and density-independent stress in rhizosphere. Density-dependent stress includes the parasitic (biotic) mode of interaction brought by pathogenic fungi, bacteria and viruses, while density-independent stress mainly occurs due to abiotic factors such as temperature, pH, water, salinity, etc. Thus, PGPR are the potential candidates to protect plant by colonizing within the rhizosphere and producing antimicrobial metabolites antagonistic in nature. Phytohormones produced by such community of bacteria provide plant health and immunity by regulatory hormones (Pieterse et al. 2012).

3.1 Seed Germination, Seedling Emergence and Elongation

Consideration of phytohormone to maintain seed dormancy is circumstantial evidence and ABA is involved in regulating the onset dormancy and its state. Interaction of abscisic acid (ABA), gibberellins (GA), ethylene (ET), brassinosteroids (BR), auxin and cytokinin influences the regulation of interconnected molecular processes that control dormancy release and seed germination in dicots (Kucera et al. 2005). ABA promotes dormancy induction and maintenance, whereas GA induces progression from release through seed germination. Environmental signals regulate this balance by modifying expression of biosynthetic and catabolic enzymes include both positive and negative regulators that are mainly feedback, regulate to enhance, or attenuate the response. The net result is a slightly heterogeneous response, thereby providing more temporal options for successful seed germination (Finkelstein et al. 2008).

The benefits derived from plant–PGPR interactions are improvements of seed germination rate, root development, shoot and root weights, yield, leaf area, chlorophyll content, hydraulic activity, protein content and nutrient uptake—including phosphorus and nitrogen. PGPRs promote plant growth and development using any one, or more, of these mechanisms as elaborated in Sect. 3.4. Interestingly, PGPR may lower the plants ethylene concentration. Inhibition of seedling root length and lowering of ethylene levels in plants are through the synthesis of the enzyme 1-aminocyclopropane- 1-carboxylate (ACC) deaminase (Glick et al. 2007; Saraf et al. 2011).

Auxins such as indole acetic acid (IAA) and indole acetamide (IAM) influence root development, tissue differentiation and responses to light and gravity

(Adesemoye and Kloepper (2009). Bhatia et al. (2008) reported that IAA containing fluorescent pseudomonads increase seed germination, growth promotion and suppression of charcoal rot disease in oil seed crops. Jagadeesh et al. (2001) tested the influence of deleterious bacteria and PGPR on germination and growth of tomato in vitro. Deleterious bacteria inhibited seed germination, but PGPR (*Pseudomonas* sp. RDV 108) significantly suppressed the growth of deleterious bacteria and increased seed germination, root and shoot length in plants. Çakmakçı et al. (2007) Nitrogen fixing and phytohormone-secreting bacterial inoculant improved growth of spinach (Çakmakçı et al. 2007). Inoculation with PGPR increased shoot fresh weight, leaf area and plant height as compared with the non-inoculated control. Recently, a study done by Singh et al. (2010) showed *P. aeruginosa* PN1, which produce IAA, cyanogen, siderophore and cellulolytic enzymes when inoculated as seed dressing, resulted in increase biomass, root and shoot length in chir-pine seedlings. Increase in length of root and shoot enhanced due to significance of PGPR-mediated IAA which may prominently involve in growth promotion of several pulses and oil seed crop (Maheshwari 2008). Such observation was an agreement for stating that phytohormone-producing PGPRs have positive effect in early and increased seed germination, seed vigor index and increase in biomass with no side effect on plants.

3.2 Somatic Embryogenesis Initiation and Enhancement

Development of somatic cells into zygotic embryos is called somatic embryogenesis (SE). The combination of auxin and cytokinin induces callus formation. Auxin regulates stem cell formation during SE (Su et al. 2009). On the other hand, auxin and cytokinin regulate many processes that are critical to plant growth, development and environmental responsiveness (Jones et al. 2010). Initiation in response to auxins and cytokinins is complex due to strong interactions between these two classes of growth regulators (Hooker and Nabors 1977). Bai et al. (2013) reported that ethylene level decreased progressively during SE initiation, whereas treatment with the metabolic precursor of ethylene, 1-aminocyclopropane-1-carboxylic acid (ACC), or mutation of ethylene-overproduction1 (ETO1) disrupted SE induction. Somatic embryo production was increased more by the presence of exogenous GA_3 in the differentiation than that of induction medium. These results indicate that GA is beneficial for both embryo induction and formation. The level of endogenous gibberellins is presumably sufficient for callus induction and growth. Various PGRs involve in SE/callus induction and development signifies their role in plant development and their early growth. For example, Ruduś et al. (2002) studied the influence of exogenous GA_3 and paclobutrazol, an inhibitor of gibberellin biosynthesis, on growth of callus and SE in petiole-derived tissue cultures of *Medicago sativa* L. resulting increase in the weight of callus and number of somatic embryos. Gutiérrez-Mañero et al. (2001) studied that PGPR *B. pumilus* and *B. licheniformis* isolated from the rhizosphere of alder

(*Alnus glutinosa* [L.] Gaertn.) induce seedlings of *Quercus* species. The promotion and elongation induced by the PGPR could be mediated by bacterial GAs. Earlier, Phillips and Torrey (1970) found hormonal interactions between soybean roots and the *Rhizobium* initiating root nodule proliferation. Recently, Pallai et al. (2012) observed the ability of various strains of *P. fluorescens* that produce cytokinins involved in enhancement of roots elongation and seedling growth.

3.3 Defense Mechanism (Plant Immunity)

Various groups of pathogenic microorganisms such as fungi, bacteria, viruses, nematodes, etc. cause disease in plants. Despite of attack, plants tend to protect themselves against disease. Plant defense mechanisms (immune system) are usually multifaceted and operative against diverse array of pathogens. On the other hand, plants also utilize physical and chemical barriers to avoid pathogen entry and pathogenesis. These consist of molecular, biochemical and morphological changes, such as oxidative burst, expression of defense-related genes, production of antimicrobial compounds and/or programed cell death, lignification of tissues, thickening of cell wall, etc. (van Loon et al. 2006).

Besides other metabolites, phytohormones auxins, gibberellins (GA), abscisic acid (ABA), cytokinins (CK), salicylic acid (SA), ethylene (ET), jasmonates (JA), brassinosteroids (BR) and peptide hormones play important roles in defense mechanisms. Infection of plants with diverse pathogens altered the level of various phytohormones (Robert-Seilaniantz et al. 2006; Adie et al. 2007). Microbial pathogens have also developed the ability to manipulate the defense-related regulatory network mimicking plants by producing phytohormones resulting into hormonal imbalance causing failure of defense responses (Robert-Seilaniantz et al. 2006). Beneficial PGPR able to produce hormones involve in strengthening of induced systemic resistance (ISR) and systemic acquired resistance (SAR) of complex regulatory networks where multiple hormonal pathways interact and influence plant defense responses (van Loon et al. 1998; Pieterse et al. 2014).

In rhizosphere, PGPR antagonize pathogens through competition for nutrients, production of antibiotics and secretion of lytic enzymes (Maheshwari 2013). PGPR reduce the activity of pathogenic microorganisms not only through microbial antagonism, but also by activating the plant to better defend itself. This phenomenon was termed ‘induced systemic resistance’ (ISR). When plant get infected with pathogens, the activation of certain *PR* genes in some, though not all, the systemic resistance is induced by the rhizobacteria, which is similar to pathogen-induced systemic acquired resistance (SAR). In both, exogenous and endogenous productions of plant growth hormone are essential to maintain and develop disease resistance. In fact, plant’s root secretes plethora of organic compounds creating a favorable niche for diverse microbial populations. The means of disease suppression by PGPRs include siderophore-mediated competition for iron, antibiosis,

production of lytic enzymes and ISR, which are added advantages. The signal molecules elicit defense mechanisms in plants by activating quiescent defense genes which are present in healthy plants (Vidhyasekaran 1988a, b).

3.3.1 Induced Systemic Resistance (ISR)

ISR is triggered by PGPR without causing any adverse effect on plant system. Some lipopeptide-producing bacteria induce defense responses in plants. For example, *B. subtilis* S499 produces biosurfactant, viz., fengycins and surfactins, which in turn provide an ISR-mediated protective effect on tomato plant against *Botrytis cinerea* (Ongena et al. 2007). Varnier et al. (2009) also showed that rhamnolipids and other metabolites trigger defense responses in plants.

Bacteria-produced salicylic acid (SA) contributes to the induction of systemic resistance. Involvement of SA as a precursor of pyochelin, its role for pyochelin in ISR cannot be ruled out (Delaney et al. 1994; De Meyer and Hofte 1997). While in initial stage of SA production, it triggers resistance in iron-chelating conditions. JA has also been implicated as a signal in several defensive responses (Wasternack and Parthier 1997).

Several PGPB initiate and carried SA-dependent pathway in rhizosphere exogenously. For example, *Burkholderia phytofirmans* PsJN triggers ISR against *Botrytis cinerea* on grapevine (Ait Barka et al. 2002). Several *Pseudomonas* spp. are able to induce ISR in a wide range of plants against different pathogens (van Loon 2007). ISR is associated with an increase in sensitivity to the related hormone rather than an increase in production. This might lead to the activation of a partially different set of defense gene (Hase et al. 2003). SA, JA and ET, involved in ISR although 2,4-diacetylphloroglucinol (DAPG) are known for its antibiotic property. DAPG has dual nature as hormone and antibiotic-like substance produced by *Pseudomonas* and *Bacillus* spp. leads to physiological changes that subsequently exit ISR (Weller et al. 2012).

3.3.2 Systemic Acquired Resistance (SAR)

Three phytohormones—SA, JA and ET are known to play major role in regulating plant defense responses against various pathogens, pests and abiotic stresses. SA plays a crucial role in plant defense and is generally involved in the activation of defense responses against biotrophic and hemi-biotrophic pathogens as well as the establishment of SAR (Grant and Jones 2002). SAR devised to plant by PGPR and hormones SA, JA and 2,6-dicholoro-isonicotinic acid (INA) or benzo (1,2,3) thiadiazole-7-carbothioic acid *S*-methyl ester (BTH) required for the establishment of SAR coordination through accumulation of SA of JA in whole plant. Any disruption in the plant's ability to accumulate SA resulted in the loss of *PR* gene expression and decrease in SAR response. JA-signaling mutants sgt1b, opr3 and jin1 failed to develop SAR upon leaf infiltration with an avirulent strain of

the pathogen *Pseudomonas syringae* pv. tomato, suggesting that JAs play a role in SAR as well (Cui et al. 2005). SAR is characterized by the increased expression of a large number of PR genes both in local and systemic tissues. Antimicrobial properties of PR proteins function in defense response. SAR results from the corrected effect of many PR proteins rather than specific PR proteins. SAR preceded by an increase in SA concentration which changes in redox status and the induction of defense gene expression (Mou et al. 2003; Durrant and Dong 2004).

The classical form of SAR can be triggered by exposing the plant to virulent, avirulent and non-pathogenic microbes or phytohormones. Depending upon plant and elicitor, a set period of time is required for the establishment of SAR that corresponds to the time required for the coordinated accumulation of PR (Vallad and Goodman 2004).

3.4 Plant Growth Promotion and Crop Productivity

PGPR emerged as biostimulators on account of their ability of efficient phytohormone production, which in turn contributes in plant growth and promotion (Maheshwari 2010). Plant growth and development is regulated by an array of structurally unrelated collection of plant hormones (Santner and Estelle 2009). On the other hand, lowering of plant ethylene levels by the ACC deaminase (Glick et al. 2007) is also a fortifying mechanism to provide drought tolerance to plant or remain healthy in adverse conditions. Other signal molecules are also involved in plant–microbe interactions in the form of nucleic acids, protein, lipid and polysaccharides (Halverson and Stacey 1986). Bacteria interact with plants and bacterial auxins cause interference with plant developmental processes regulated by auxin (Spaepen and Vanderleyden 2011) and affect gene expression in some microorganisms. Therefore, IAA acts as a reciprocal signaling molecule in microbe–plant interactions.

It is interesting to note that plant growth promotion is facilitated by PGPR via diverse mechanisms, due to the production and degradation of the major groups of plant hormones; although plant root exudates have many potential substrates for rhizobacterial growth including plant hormones or their precursors. Rhizobacterial mediation of plant hormone status not only showed local effects on root elongation and architecture, mediating water and nutrient capture, but also affect plant root-to-shoot hormonal signaling that regulates leaf growth and gas exchange. Combining rhizobacterial traits (or species) influences plant hormones and status, thereby, modifying root architecture (to capture existing soil resources) to make additional resources available (e.g. nitrogen fixation, phosphate solubilization) which may enhance the sustainability of crops (Dodd et al. 2010). Hence, the hormones play central role in the ability of plants to adapt to the changing environments, by mediating growth, development, nutrient allocation and source/sink transitions (Mordukhova et al. 1991; Gupta et al. 1999; García et al. 2001; Peleg and Blumwald 2011) leading to sustainable growth and development.

4 Conclusion

Phytohormones produced by PGPR are major signaling molecule employed in enhancement of crops production. IAA in majority and other hormones such as ABA, CK, ET, etc. (natural, semi-synthetic and synthetic) proved beneficial by stabilizing plant immunity, biocontrol and crop productivity. The role of phytohormone in seed dormancy, seedling emergence and elongation as well as somatic embryogenesis, initiation and enhancement bring immense need to manage increasing food production to account sustainable agriculture. Phytohormone is exploiting endogenously and exogenously in the maintenance of several physiological traits of plants. It has been revealed that some PGPR secrete novel signaling molecules that also promote plant growth. The use of rhizobacterial signaling in promoting plant growth offers a new window of opportunity especially to provide novel biological products for enhancing plant growth and development in sustainable manner.

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