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REVIEW
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Plant Growth Promoting Actinobacteria, the Most Promising Candidates as Bioinoculants?

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Plant Growth Promoting Bacteria (PGPBs) are a strong ally for sustainable agriculture. They offer an interesting alternative to chemical fertilizers and pesticides. Many microorganisms have been widely documented for their PGPR traits, but actinobacterial microbes which have been increasingly documented only these two past decades for their ability to promote plant growth. Their action on plant health and yield could be either direct, indirect or both. This review will cover articles that have been published on Actinobacteria PGP traits, highlighting the involved mechanisms to reveal their strong potential as microbial fertilizers. Possible strategies to encourage Actinobacteria use as bioinoculants are also discussed.

Keywords: Actinobacteria, PGPR, PGPB, bioinoculant, biocontrol, sustainability

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INTRODUCTION

Sustainability is a significant challenge currently being faced by human beings. How can we nourish the ever-growing world population and at the same time offer viable soil for future crop production for the next generations? Agricultural ecosystems are fragile and excessive inputs, especially chemicals (nitrogen and phosphate fertilizers) and pesticides, which enable maximal yield, could work for a while, but plant survival is a tributary of soil health, which is, in turn, intimately linked to microbial diversity for nutrient turnover. It has been reported that excessive chemical inputs exert negative impacts on humans and environmental health (Glick, 2012). Moreover, with these incoming chemical inputs, the plant microbiome is modified and in accordance with hologenome theory, which outlines that microorganisms play a role in the evolution of animals and plants (Rosenberg et al., 2009), presumably, the evolution of plants and their associated symbiont microbiota (named holobiont) could be affected.

Plant microbiome are analogous to the gut microbiome: just as the gut microbiome plays a central role in human health (O'Hara and Shanahan, 2006), so too does the plant microbiome present the same properties in plant health. The microbiome is the entire microbial population inhabiting the plant with an extension to the rhizospheric microbiome, as there are important interactions between both (Rosenberg et al., 2009). Among these microbial populations, there are an important group named PGPR "Plant Growth Promoting Rhizobacteria" for those living in the rhizosphere, which ameliorate plant growth both directly and indirectly (Kloepper, 1978) as well as PGPB "Plant Growth Promoting Bacteria" including rhizospheric bacteria and those which are free-living in the soil or associated to plants in rhizoplane, phyllosphere and inside plants as endophytes (Bashan and De-Bashan, 2005). These microbes help plant growth by enhancing soil nutrient availability (Scagliola et al., 2016), the supply of phytohormones, and provide systemic resistance induction against phytopathogens. Thus, the employment of Plant Growth Promoting

Bacteria (PGPB) is considered a promising alternative to conventional agricultural practices, in terms of chemical fertilizer and control of pathogenic agents (Bashan, 1998).

The use of Actinobacteria in agricultural practice has increased in recent years, due to their potential action as PGPR and their ubiquitous repartition in plants (Yadav et al., 2018). Actinobacteria are Gram positive bacteria with a high G+C content in their DNA, ranging from 51 to more than 70% (Ventura et al., 2007), well known for their metabolite production, mainly antibiotics (Saxena, 2014). They are present in the phyllosphere, endosphere (Lopez-Velasco et al., 2013), rhizosphere, and are free living in soil (Bulgarelli et al., 2013). In addition to their PGPB action, some other actinobacterial characteristics could encourage wider use as bioinoculant: many Actinobacteria, which generally represent an abundant proportion of soil microbiota, are particularly effective plant root system colonizers and by forming spores, they are able to endure unfavorable growth conditions (Alexander, 1977) and are more persistent in drought soils (Santos-Medellín et al., 2017). They play a critical role in organic matter recycling (Lacey, 1978) by increasing soil organic matter and nitrogen content along with essential macro and micro-elements, which in turn ameliorate plant growth, carbon metabolism, and allocation, and improve plant yield (AbdElgawad et al., 2020). Finally, their antagonistic and competitive characteristics permit them to colonize the rhizosphere with regards to other soil microorganisms (Bulgarelli et al., 2013). All the characteristics cited above designate Actinobacteria as an auspicious inoculant.

Many studies have proven the PGP action of the plant microbiome, but there is a gap between *in vitro* trials and efficiency in the field, particularly concerning their commercialization as a final bio-input product. The purpose of this review is to demonstrate the beneficial and protective impact of Actinobacterial on plant growth by highlighting the main direct or indirect PGPB traits. All genera of this important taxon were examined to identify their potential PGPB actions. On the other hand, the main impediments and future prospects of their use as biofertilizers are discussed.

ACTINOBACTERIA DIVERSITY AND IMPORTANCE

According to Ludwig et al. (2012), in terms of the number and variety of identified species, the phylum *Actinobacteria* represents one of the largest taxonomic units among the 18 major lineages currently recognized within the domain Bacteria, including 5 subclasses, 6 orders, and 14 suborders. Its genomic diversity reflects its biodiversity which could have great biotechnological applications (Ventura et al., 2007). But an update based on 16S rDNA trees done by Gao and Gupta (2012), eliminated the taxonomic ranks of subclasses and suborders, elevating the former subclasses and suborders to the ranks of classes and orders, respectively. The phylum "*Actinobacteria*" is thus divided into six classes: *Acidimicrobiia* (01 order) (Norris, 2012), *Actinobacteria* (include 20 orders) after the classification based on the whole genome (Nouioui et al., 2018), *Coriobacteriia* (02 order) (Gupta et al., 2013), *Nitriliruptoria* (02 orders) (Ludwig et al., 2012), *Rubrobacteria* (01 order) (Suzuki, 2012), and *Thermoleophilia* (02 orders) (Suzuki and Whitman, 2012). Based on Actinobacteria classification (Parte et al., 2020) (consulted 01/01/2022), the cited classes above include 73 families and 443 genera which are unequally distributed. The majority of them (394) are within the class *Actinobacteria* (**Table 1**).

Actinobacteria present various and different lifestyles including plant pathogens (e.g., *Streptomyces scabiei, S. acidiscabies,* and *S. turgidiscabies)* (Wanner, 2006), mammalian pathogens (e.g., *Mycobacterium* spp., *Nocardia* spp., *Corynebacterium* spp., *Tropheryma* spp., and *Propionibacterium* spp.), plant commensals (*Leifsonia* spp.), soil inhabitants (*Streptomyces* spp.) as reported by Ventura et al. (2007), nitrogen-fixing symbionts (Frankia) (Franche et al., 2009), and gastrointestinal tract (GIT) inhabitants (*Bifidobacterium* spp.) (Ventura et al., 2007; Barka et al., 2016). It should be noticed that members of *Actinobacteria* class are associated with plants growing in different habitats as well as under extreme environments (Goudjal et al., 2013; Singh et al., 2016; Sahay et al., 2017).

Rhizospheric Actinobacteria are predominant in nature, with economic importance to humans because both agricultural and forest fields depend on their contributions to soil systems (Yadav et al., 2017). They possess diverse physiological and metabolic properties, like extracellular enzyme production and the formation of a wide variety of secondary metabolites (Schrempf, 2001). Rhizosphere harbors diverse actinobacterial species which have been further exploited for secondary metabolites (Geetanjali, 2016; Yadav et al., 2018). It has been reported by Berdy (2003), that microorganisms produced about 23,000 bioactive secondary metabolites, over 10,000 of these compounds are produced by Actinobacteria, which represent 45% of all discovered bioactive microbial metabolites and 80% if we only consider those compounds used in a practical way. Among Actinobacteria, *Streptomyces* species produced around 7,600 compounds, and these statistical evaluations should increase, perhaps not in an exponential way, but with the continuous growth of the number of new microbial metabolites.

The genus *Streptomyces* dominated actinobacterial strains isolated from soil, representing over 95% (Williams and Vickers, 1988). These actinobacterial strains are considered *Streptomyces* and Non-*Streptomyces*. Among the bioactive compounds produced by Actinobacteria, antibiotics, which initially confer them competitiveness are the most important in terms of biotechnological application as they produce the majority of the naturally occurring antibiotics (Barka et al., 2016). Other actinobacterial metabolites possess biotechnological applications, including in antifungal (Hoshino et al., 2004), bioherbicide/biopesticide (Waldron et al., 2001), antiparasitic (Burg et al., 1979), antiviral (Farmer and Suhadolnik, 1972), antitumor agent (Igarashi et al., 2007), immunostimulatory (de Reijke et al., 1997), and immunosuppressive (Uyeda et al., 2001) products.

The endophytic trait has been described mostly in the class *Actinobacteria* (Singh and Dubey, 2018), but with the

TABLE 1 | Distribution of some PGP traits among Actinobacteria phylum.

Actinobacterial class	Actinobacterial order	Actinobacterial family (genus number)	Plant growth promotion genus	Associated plants	Mode of action	References
Acidimicrobiia	*Acidimicrobiales*	*Acidimicrobiaceae* (4)	Not found			
		Lamiaceae (4)				
		Microthrixaceae (2)				
Actinobacteria	*Acidothermales*	*Acidothermaceae* (1)	*Acidothermus**	Forest soil	Cellu	Talia et al., 2012
	Actinomycetales	*Actinomycetaceae* (19)	*Actinomyces**	/	Gib, Cyt	Panosyan et al., 1963; Kaunat, 1969
	Actinopolysporales	*Actinopolysporaceae* (3)	*Actinopolyspora**	Wheat	IAA, PS, Sid	Gangwar et al., 2012a
	Bifidobacteriales	*Bifidobacteriaceae (10)*	Not found			
	Catenulisporales	*Actinospicaceae* (1)	Not found			
		Catenulisporaceae (1)	*Catenulispora* *	Soil	Cellu	Anderson et al., 2012
	Cryptosporangiales	*Cryptosporangiaceae* (2)	*Fodinicola**	*Acacia mangium*	IAA, PS, Sid	Ph?m et al., 2020
	Frankiales	*Frankiaceae* (1)	*Frankia**	/	IAA,	Wheeler et al., 1984
				Ochetophila trinervis	IAA, Gib	Solans et al., 2011
		Motilibacteraceae (1)	Not found			
		Vallicoccaceae (1)	Not found			
	Geodermatophilales	*Antricoccaceae* (1)	Not found			
		Geodermatophilaceae (5)	*Modestobacter*	*Salicornia europaea* Linn	PS	Qin et al., 2013
	Glycomycetales	*Glycomycetaceae* (6)	Not found			
	Jiangellales	*Jiangellaceae* (1)	Not found			
	Kineosporiales	*Kineosporiaceae* (6)	*Kineococcus*	Wheat	IAA, NF	Batool et al., 2016
	Micrococcales	*Beutenbergiaceae* (1)	Not found			
		Bogoriellaceae (3)	Not found			
		Brevibacteriaceae (3)	*Brevibacterium*	Aloe vera/*Triticum aestivum*	IAA, PS, Sid	Tara and Saharan, 2017
		Cellulomonadaceae (3)	*Cellulomonas*	Sorghum	IAA, NF	dos Reis Antunes et al., 2019
		Demequinaceae (1)	Not found			
		Dermabacteraceae (4)	*Brachybacterium*	*Salicornia brachiata*	IAA, Sid, ACCD, NF	Gontia et al., 2011
		Dermacoccaceae (11)	*Dermacoccus*	Tomato	IAA, PS, Sid	Rangseekaew et al., 2021
		Dermatophilaceae (8)	Not found			
		Intrasporangiaceae (18)	*Intrasporangium*	Rice	NF	Su et al., 2007
				Alfa	PS, Sid	Guiñaz et al., 2013
			*Knoellia**	/	Sid	Duncan et al., 2021

(Continued)

TABLE 1 | Continued

Actinobacterial class	Actinobacterial order	Actinobacterial family (genus number)	Plant growth promotion genus	Associated plants	Mode of action	References
			Lapillicoccus	Sisal	NF	de Jesus Santos et al., 2019
			*Oryzihumus**	/	Cellu	Kim et al., 2017
		Jonesiaceae (5)	Not found			
		Kytococcaceae (1)	Not found			
		Microbacteriaceae (62)	*Agreia**	*Salicornia europaea* L.	NF	Hrynkiewicz et al., 2019
			Agromyces	*Salix caprea*	IAA, Sid	Kuffner et al., 2008
			Curtobacterium	Paddy	IAA, ACCD, NF	Vimal et al., 2019
			Frigoribacterium	*Nitraria sibirica*	IAA, PS, Sid, ACCD	Zhou et al., 2017
			*Frondihabitans**	Salix caprea	ACCD	Kuffner et al., 2008
			*Herbiconiux**	Ilex *paraguariensis*	PS, NF	Pérez et al., 2016
			*Humibacter**	Rice	IAA	Samson et al., 2021
			*Labedella**	*Salicornia europaea* L.	NF	Hrynkiewicz et al., 2019
			*Lacisediminihabitans**	Lichen	IAA, NF	Noh et al., 2021
			Leifsonia	Tomato	IAA, Gib	Kang et al., 2014
			*Leucobacter**	*Jatropha curcas* L.	IAA, NF	Machado et al., 2020
			Microbacterium	Neem/Tomato	PS, ACCD	Madhaiyan et al., 2010
			*Mycetocola**	*Lepidium draba* L.	IAA	Samad et al., 2017
			Rathayibacter	*Brassica campestris* ssp *pekinensis*	NF	Poonguzhali et al., 2006
			*Subtercola**	*Salix caprea*	IAA	Kuffner et al., 2008
		Micrococcaceae (28)	*Arthrobacter*	Tomato	IAA, Sid Amm	Banerjee et al., 2010
				*Triticum aestivum**	IAA, PS, Sid, NF, Amm	Verma et al., 2014
			Citricoccus	Banana/Onion	IAA, Gib PS, ACCD, Amm	Selvakumar et al., 2015
			Glutamicibacter	*Limonium sinense*	IAA, PS, ACCD, NF	Qin et al., 2018
			Kocuria	*Stipa tenacissima* L.	IAA, PS, ACCD	Dif et al., 2021
			Micrococcus	Maize	IAA, Cyt, Pect, HCN	Raza and Faisal, 2013
				Vigna unguiculata	IAA, PS, Sid, ACCD	Dastager et al., 2010
			Nesterenkonia	Tomato	PS, Prot	Masmoudi et al., 2019
			Paenarthrobacter	Tomato	IAA, ACCD	Riva et al., 2021
			Pseudarthrobacter	*Curcuma longa* L.	IAA, PS, Sid, Amm, Cellu	Kharshandi et al., 2021
			Psychromicrobium	*Arnebia euchroma*	IAA, PS, Sid	Jain et al., 2021
			Rothia	Rice	IAA, PS	Evangelista et al., 2017

(Continued)

TABLE 1 | Continued

Actinobacterial class	Actinobacterial order	Actinobacterial family (genus number)	Plant growth promotion genus	Associated plants	Mode of action	References
			*Sinomonas**	Rice	IAA, PS, NF, Cellu	Susilowatia et al., 2015
			Zhihengliuella	Halophyte plants/Canola	IAA, ACCD, NF Amm, Chit	Siddikee et al., 2010
		Ornithinimicrobiaceae (2)	*Serinicoccus**	*Halimione portulacoides*	IAA, ACCD, Cellu, Prot	Fidalgo, 2017
			Ornithinimicrobium	*Panax ginseng*	IAA, Sid	Huo et al., 2021
		Promicromonospora ceae (13)	*Cellulosimicrobium*	Chili plants	IAA, PS	Chatterjee et al., 2009
				Phaseolus vulgaris	IAA, PS, Amm, Prot	Karthik and Arulselvi, 2017
			Isoptericola	*Limonium sinense*	ACCD, NF	Qin et al., 2014
			Myceligenerans	*Halocnemum strobilaceum*	PS, ACCD	Zhou et al., 2017
			Oerskovia	/*	IAA, PS, Sid, Prot	Yun et al., 2017
			Promicromonospora	*Solanum lycopersicum*	Gib, PS	Kang et al., 2012
			*Xylanimonas**	*Ulmus nigra*	Cellu	Rivas et al., 2003
		Rarobacteraceae (1)	Not found			
		Ruaniaceae (3)	Not found			
	Micromonosporales	*Micromonosporaceae* (29)	*Actinoplanes*	*Cucumis sativus* L.	IAA, Gib Gluc	El-Tarabily et al., 2009
			Micromonospora	*Salicornia bigelovii*	IAA, Sid	El-Tarabily et al., 2019
				Phaseolus vulgaris L.	PS	El-Tarabily et al., 2008
	Mycobacteriales	*Corynebacteriaceae* (1)	*Corynebacterium*	Saline coastal soil and halophytic plants	ACCD, NF, Amm	Siddikee et al., 2010
				Capsicum chinense	PS, Amm, HCN	Chinakwe et al., 2019
		Dietziaceae (1)	*Dietzia*	Wheat	modulating the transcriptional machinery responsible for salinity tolerance in plants	Bharti et al., 2016
				Wheat	Sid	Gusain et al., 2017
		Gordoniaceae (3)	*Gordonia*	*Chenopodium murale*/ Pearl millet	NF	Kayasth et al., 2014
				Zea mays	Sid, ACCD	Hong et al., 2011
			*Gordonia**	Coastal salt marsh plant	PS, Sid, ACCD, NF	Gong et al., 2018
			Williamsia/Gordonia**	Lycium ruthenicum	NF	Liu et al., 2019
			*Williamsia**	*Chenopodium murale*/ Pearl millet	NF	Kayasth et al., 2014
		Lawsonellaceae (1)	Not found			
		Mycobacteriaceae (3)	*Mycobacterium*	Wheat	AF Amyl, Pect	Egamberdieva, 2012
			Mycobacterium	Rice	IAA, PS, ACCD, NF	Karmakar et al., 2021

(Continued)

TABLE 1 | Continued

Actinobacterial class	Actinobacterial order	Actinobacterial family (genus number)	Plant growth promotion genus	Associated plants	Mode of action	References
		Nocardiaceae (9)	*Nocardia*	Coastal salt marsh plant	IAA, PS	Gong et al., 2018
			Nocardia	*Citrus reticulata* L.	IAA	Shutsrirung et al., 2013
			Nocardia	*Aquilaria crassna* Pierre ex Lec	IAA, Sid, Amm, Prot	Nimnoi et al., 2010
			Rhodococcus,	*Brassica juncea* L. Czern	IAA, Sid,	Belimov et al., 2005
			Rhodococcus	*Plectranthus amboinicus* (Lour.) Spreng	IAA, ACCD	Karthikeyan, 2017
		Segniliparaceae (1)	Not found			
		Tsukamurellaceae (1)	*Tsukamurella*	*Zea mays* L.	IAA, PS, Chit, Prot	Marín et al., 2013
				Tea plants/Peanut	IAA, Sid	Zhang et al., 2021
	Nakamurellales	*Nakamurellaceae* (1)	Not found			
	Propionibacteriales	*Actinopolymorphaceae* (4)	Not found			
		Kribbellaceae (1)	Not found			
		Nocardioidaceae (4)	*Aeromicrobium**	/	IAA, Sid, Amm	Yadav et al., 2015
			Nocardioides	*Sorghum bicolor*	IAA, NF, Amm, Prot	Liotti et al., 2018
		Propionibacteriaceae (25)	Not found			
	Pseudonocardiales	*Pseudonocardiaceae* (34)	*Actinokineospora**	*Glycyrrhiza inflata* Bat	IAA	Zhao et al., 2018
			*Amycolata**	/	Cellu, xyl	Br hlmann, 1995
			Amycolatopsis	chickpea and sorghum	IAA, Sid, Cellu, Chit, Prot, Gluc, Pect	Alekhya and Gopalakrishnan, 2016
			*Kibdelosporangium**	*Jatropha curcas* L.	Sid, ACCD	Xing et al., 2012
			*Kutzneria **	/	IAA, PS, Sid, Amm, Prot Amyl, Pect	Devi et al., 2021
			*Prauserella**	/	IAA, PS, Sid	Nafis et al., 2019
			Pseudonocardia	a	IAA, Sid, Amm, Cellu	Borah and Thakur, 2020
			*Saccharomonospora**		IAA, PS, ACCD, Amm, Cellu, Prot	Borah and Thakur, 2020
				Rice	IAA, Sid	Gangwar et al., 2012b
	Sporichthyales	*Sporichthyaceae* (3)	Not found			
	Streptomycetales	*Streptomycetaceae* (6)	*Kitasatospora*	*Trifolium repens* L.	PS, Sid, NF	Franco-Correa et al., 2010
				Yam/*Arabidopsis*	IAA, PS, Sid, ACCD, Cellu, Chit	Arunachalam Palaniyandi et al., 2013
			Streptomyces	Sorgum/Rice	IAA, Sid, Cellu, Prot, Gluc HCN	Gopalakrishnan et al., 2013

(Continued)

TABLE 1 | Continued

Actinobacterial class	**Actinobacterial order**	**Actinobacterial family (genus number)**	**Plant growth promotion genus**	**Associated plants**	**Mode of action**	**References**
				Chickpea	IAA, Sid, Cellu, Prot, HCN, Gluc	Alekhya and Gopalakrishnan, 2017
	Streptosporangiales	*Nocardiopsaceae* Bulgarelli et al., 2013	*Nocardiopsis*	*Pennisetum glaucum*	IAA, PS, Amm, Chit, Gluc	Patel and Thakker, 2019
				Wheat	IAA, PS, Sid, Chit, HCN	Allali et al., 2019
			Thermobifida	*Trifolium repens* L.	PS, Sid, Amm	Franco-Correa et al., 2010
		Streptosporangiaceae (19)	*Microbispora*	/	IAA, PS, NF, Amm, Cellu, Pect	Borah and Thakur, 2020
		Thermomonosporaceae (5)	*Actinomadura*	*Aquilaria crassna* Pierre ex Lec	IAA, Sid, Amm, Prot	Nimnoi et al., 2010
			Spirillospora	*Citrus reticulata* L.	IAA	Shutsrirung et al., 2013
		Treboniaceae (1)	Not found			
Coriobacteriia	*Coriobacteriales*	*Atopobiaceae* (8)	Not found			
		Coriobacteriaceae (4)	Not found			
	Eggerthellales	*Eggerthellaceae* (11)	Not found			
Nitriliruptoria	*Egibacterales*	*Egibacteraceae* (1)	Not found			
	Egicoccales	*Egicoccaceae* (1)	Not found			
	Euzebyales	*Euzebyaceae* (1)	Not found			
	Nitriliruptorales	*Nitriliruptoraceae* (1)	Not found			
Rubrobacteria	*Rubrobacterales*	*Rubrobacteraceae* (1)	Not found			
Thermoleophilia	*Gaiellales*	*Gaiellaceae* (1)	Not found			
	Miltoncostaeales	*Miltoncostaeaceae* (2)	Not found			
	Solirubrobacterales	*Baekduiaceae* (1)	Not found			
		Conexibacteraceae (1)	Not found			
		Paraconexibacteraceae (1)	Not found			
		Parviterribacteraceae (1)	*Parviterribacter**	*Lespedeza*	NF	Padda et al., 2018
		Patulibacteraceae (1)	Not found			
		Solirubrobacteraceae (1)	Not found			
	Thermoleophilales	*Thermoleophilaceae* (1)	Not found			

IAA, IAA production; Gib, Gibberellin production; Cyt, Cytokinin; PS, Phosphate solubilization; Sid, Siderophore production; ACCD, ACCD production; NF, Nitrogen fixation; Amm, Ammonia production; Cellu, Cellulase production; Chit, Chitinase production; Amyl, Amylase production; Xyl, Xylanase production; Prot, Protease production; Gluc, Glucanase; Pect, Pectinase; HCN production.
The actinobacterial strains presenting PGP traits but had not proven their capacity to seedling, growth, or stress alleviation promotion are indicated by an asterisk.

advances of molecular identification tools, other endophytic candidates have been revealed so far, as for *Thermoleophilia* class, e.g., *Solirubrobacter phytolaccae* (*Solirubrobacterales* order) (Wei et al., 2014) and *Patulibacter* (*Solirubrobacterales* order) (Ferrando et al., 2012); for *Rubrobacteria* class e.g., *Rubrobacteria* genus (*Rubrobacterales* order) (Girija et al., 2018) and *Coriobacteria* class (Ren et al., 2018).

The fact that Actinobacteria could survive mesophilic but also for some candidates at thermophilic conditions reaching 60°C is an encouraging trait for its inocula use (Edwards, 1993), a fortiori they are considered as aridity–winners by Marasco et al. (2021) who stated that aridity changes composition and interactions of the plant-microbial community, this by modulating the distribution of aridity-tolerant (winners) and aridity-susceptible (losers) bacterial taxa, which is in favor of the former in a dry environment. There have also been reports that actinobacterial inoculation could not only protect plants from the deleterious effects of drought but also show significant increases in their measured physiological parameters (Chukwuneme et al., 2020). Furthermore, acidophilic Actinobacteria could play a major role in the inoculation of plants living in acidic soil (Bull, 2011). Many halotolerant Actinobacteria have been isolated from saline environments and have proven to be useful crop protective agents to plants in stressful conditions (Siddikee et al., 2010; Zhou et al., 2017; Qin et al., 2018). The extremophile character of some actinobacterial strains could be a valuable tool for rehabilitating degraded areas under extreme environmental conditions and they can enhance crop production under multiple conditions of stress, such as extreme temperatures, pH, salinity, and drought (Qin et al., 2011).

PGP TRAITS OF ACTINOBACTERIA

Bacterial strains are considered as PGPR if they can fulfill at least two of the three following criteria: aggressive colonization, plant growth stimulation, or biocontrol (Vessey, 2003). Globally, plant growth-promoting rhizobacteria (PGPR) are the rhizosphere bacteria that can enhance plant growth by a wide variety of mechanisms like phytohormones production, 1-Aminocyclopropane-1-carboxylate (ACC) deaminase production, induction of systemic resistance (ISR), phosphate solubilization, siderophore production, biological nitrogen fixation (BNF), rhizosphere engineering, quorum sensing (QS) signal interference and inhibition of biofilm formation, exhibiting antifungal activity, production of volatile organic compounds (VOCs), promoting beneficial plant-microbe symbioses, interference with pathogen toxin production, etc. (Bhattacharyya and Jha, 2012; Kumar and Singh, 2020). From a practical point of view, PGP-microbes could be used as biofertilizers by providing macro and micronutrients like biological nitrogen fixation (Vessey, 2003) and utilization of insoluble phosphorous (Chang and Yang, 2009), as biostimulants or phytostimulants by improving nutrient use and efficiency thanks to phytohormones production (Lugtenberg et al., 2002), as biocontronl by controlling plant pathogens using antibiotics or siderophores (Vessey, 2003), for rhizomediation by enhancing heavy metal solubility or decreasing the bioavailability of toxic compounds (Denton, 2007), and as biotisation agents by reducing chemical inputs in *in vitro* plant tissues culture (Diehdhiou et al., 2021). Regarding Actinobacteria, one of the major components of rhizosphere microbial populations, they showed a significant ecological role in soil nutrient cycling (Halder et al., 1991; Elliott and Lynch, 1995) as well as in plant growth-promoting activities (Merzaeva and Shirokikh, 2006), and numerous reports (Gomes et al., 2000; Sousa Cd et al., 2008; Goudjal et al., 2013; Kaur et al., 2013) are available on their potential as plant growth-promoting agents. To illustrate plant promoting ability among *Actinobacteria* phylum, we reviewed the 443 actinobacterial genera by associating each of them to term "plant growth promotion." The most relevant results are reported in **Table 1**.

Among the mechanism of action, we will report below major processes of plant growth promotion related to Actinobacteria. But before, one should wonder if PGP traits, precisely, which one or how many should be accumulated to exert the maximum growth improvement of plants. For example, the most effective strain E108, identified as *Curtobacterium flaccumfaciens*, has increased barley growth up to 300% but has shown only two out of the six investigated plant growth promoting activities comparatively to two other strains, namely the *Microbacterium natoriense* strain E38 and *Pseudomonas brassicacearum* strain E8, which did not promote plant growth even though they showed many PGP traits (Cardinale et al., 2015).

DIRECT ACTION

Biological Nitrogen Fixation

Nitrogen is generally regarded to be one of the major limiting nutrients in plant growth (Franche et al., 2009). It is widely known that *Frankia*, the sole genus of *Frankiales* order fixes atmospheric nitrogen in symbiosis with actinorhizal plants, which play a major role in colonizing nitrogen-poor soils and initiation of ecological successions (Normand et al., 2007). Some studies on nitrogen-fixing properties among the Gram-positive Actinobacteria revealed that some non-symbiotic species of *Agromyces, Arthrobacter, Corynebacterium, Micromonospora, Mycobacterium, Streptomyces,* and *Propionibacteria* have nitrogen fixing capacity (Sellstedt and Richau, 2013). More particularly, the nitrogen fixing *Arthrobacter humicola* (Verma et al., 2014), *Corynebacterium* spp. (Verma et al., 2014), *Microbacterium* FS-01 (Karlidag et al., 2007). To complement these data, **Table 1** summarizes the nitrogen fixation ability among *Actinobacteria* class and some representatives in *Thermoleophilia* class. From the former, *Microbacteriaceae* which is the largest family (62 genus) includes at least seven nitrogen fixers: *Agreia* (Hrynkiewicz et al., 2019), *Curtobacterium* (Vimal et al., 2019), *Herbiconiux* (Pérez et al., 2016), *Labedella* (Hrynkiewicz et al., 2019), *Lacisediminihabitans* (Noh et al., 2021), *Leucobacter* (Machado et al., 2020) and *Rathayibacter* (Poonguzhali et al., 2006).

Producing Phytohormones Like Auxins, Cytokinins, and Gibberellins

Phytohormones are involved in many physiological processes, they include auxins, gibberellins, cytokinins, ethylene, and abscisic acid, which are classified based on their function and structure composition. They are mainly produced by rhizospheric microorganisms, fungi, algae, and Actinobacteria (Mulani et al., 2021).

The auxins are a group of indole ring compounds that have the capacity to ameliorate plant growth by stimulating seed germination, root initiation and elongation, and seedling growth (El-Tarabily et al., 2008). Indole-3-Acetic Acid (IAA) is an auxin that is common and natural and is resulted from L-tryptophan metabolism in microorganisms (Davies, 2004), as we could observe from **Table 1**, IAA is widely produced by Actinobacteria. Even, it was reported a tryptophan- independent pathway operation in *Micrococcus aloeverae* (Ahmad et al., 2020).

Cytokinins are considered the second group of plant hormones biosynthesized by microbes. They mediate signal exchange from roots to shoots under environmental stresses. They also induce cell division, cell enlargement, and increase root surface area with the help of intense proliferation of adventitious and lateral roots (Jackson, 1993). These hormones have been reported for actinobacterial strains, but to a lesser extent than auxins as it was reported for *Leifsonia soli* (Kang et al., 2014) and *Promicromonospora* (Kang et al., 2012).

Gibberellins are plant hormones, that are considered ubiquitous. They generate the diverse metabolic functions necessary during plant growth steps such as seed germination, stem elongation, sex expression, flowering, formation of fruits, and senescence (Hedden, 1997). Gibberellins actinobacterial species production was reported in several studies, as for *Streptomyces olivaceoviridis*, *S. rochei* and *S. rimosus* cultures which were excellent producers of gibberellins-like substances, showing wheat plant growth promotion (Aldesuquy et al., 1998) and for *Arthrobacter globiformis* (Katznelson et al., 1962).

Solubilizing Minerals Like Phosphorus

Phosphorous limitation could prevent plant growth, first because phosphorous is vital and secondly, its bioavailability from the soil is often limited (Feng et al., 2004). Phosphate Solubilizing Bacteria (PSB) including Actinobacteria could increase the availability of soluble phosphate by various mechanisms like production of low molecular weight organic acid, along with the production of hydroxyl and carboxyl groups, serving as a chelating agent to chelate the cations (mainly Ca) bound to phosphate converting them into soluble forms (Kpomblekou-a and Tabatabai, 1994) or by enzymatic actions mostly phosphatase (Solans et al., 2019) and phytase (Sharma et al., 2017), although, it seems that the major action of Actinobacteria was enzymatic (Nimaichand et al., 2016). Phosphate Solubilizing Actinobacteria are often associated with the production of plant growth-promoting regulators, increasing biological nitrogen fixation effectiveness or enhancing the availability of other trace elements such as iron, zinc, etc. (Ponmurugan et al., 2006). This statement is correlated with the reported data in **Table 1**, mainly with IAA production for important crops such wheat (Allali et al., 2019), maize (Marín et al., 2013), rice (Susilowatia et al., 2015), and *Phaseus vulgaris* (Karthik and Arulselvi, 2017).

Production of Siderophores

Iron is often a limiting living growth factor, microorganisms developed siderophore production which relies on chelation phenomena, with a high affinity for iron (Fe^{3+}) chelation and low molecular weight (500–1,000 Da) (Neilands, 1995). After chelation, the available ionic form (Fe^{+2}) is easily absorbed by microorganisms (Kaszubiak, 1998). Microbial siderophores may act as plant promoters by dispensing iron to plants and as a biocontrol agent against phytopathogens by limiting its availability and thus killing pathogens (Anilkumar et al., 2017). In terms of siderophores production, Actinobacteria is one the most important group (Franco-Correa and Chavarro-Anzola, 2016) as illustrated in **Table 1**, which reports many siderophore productions by many species associated with grain crops, such as for *Brevibacterium* associated to *Triticum aestivum* (Tara and Saharan, 2017), *Gordonia* with *Zea mays* (Hong et al., 2011), *Amycolatopsis* with chickpea and sorghum (Alekhya and Gopalakrishnan, 2016), *Kitasatospora* with *Trifolium repens* L. (Franco-Correa et al., 2010), *Streptomyces* with Rice (Gopalakrishnan et al., 2013) and chickpea (Alekhya and Gopalakrishnan, 2017), *Nocardiopsis* with wheat (Allali et al., 2019), *Thermobifida* with *Trifolium repens* L. (Franco-Correa et al., 2010) and *Micrococcus* with *Vigna unguiculata* (Dastager et al., 2010). It has also been reported for halophyte plants as for *Brachybacterium* associated to *Salicornia brachiate* (Gontia et al., 2011), *Micromonospora* with *Salicornia bigelovii* (El-Tarabily et al., 2019); for medicinal plants as for *Frigoribacterium* with *Nitraria sibirica* (Zhou et al., 2017), *Pseudarthrobacter* with *Curcuma longa* L. (Kharshandi et al., 2021), *Psychromicrobium* with *Arnebia euchroma* (Jain et al., 2021), *Ornithinimicrobium* with *Panax ginseng* (Huo et al., 2021), *Pseudonocardia* with *Camellia* spp. (Borah and Thakur, 2020); for metal-accumulating plants as for *Agromyces* with *Salix caprea* (Kuffner et al., 2008), *Nocardia* and *Actinomadura* with *Aquilaria crassna* Pierre ex Lec (Gong et al., 2018; Nimnoi et al., 2010) respectively, *Rhodococcus* with *Brassica juncea* L. Czern (Belimov et al., 2005) and *Dermacoccus* (Rangseekaew et al., 2021) and *Arthrobacter* (Banerjee et al., 2010) associated to tomato.

1-Aminocyclopropane-1- Carboxylate Deaminase (ACC Deaminase)

Ethylene, which are the aging hormones of plants (Patel et al., 2018), are produced as a response to stress "stress ethylene," meaning the development of the plant is slowed, to respond to this stress condition and promote plant growth, PGP bacteria produce 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Glick, 2005). This (ACC) deaminase delivered by PGPR, will metabolize ACC into alpha-ketobutyrate, methionine, and ammonia and thus will regulate ethylene production (Mulani et al., 2021). Inoculation of ACC deaminase-producing bacteria immediately enhances plant root elongation and promotes shoot growth (Onofre-Lemus et al., 2009). It has been reported the presence of ACC deaminase genes among Actinobacteria such as *Actinoplanes, Agreia, Arthrobacter, Austwickia, Brevibacterium, Streptomyces, Amycolatopsis, Mycobacterium, Nocardioidaceae, Rhodococcus,* and others (Nascimento et al., 2014). Some halotolerant Actinobacteria showed ACC deaminase activities such as *Corynebacterium variabile*, *Micrococcus yunnanensis*, and *Arthrobacter nicotianae*, promoting canola plant growth under salt stress conditions (Siddikee et al., 2010).

Production of Hydrolytic Enzymes

Actinobacteria, as a dominant member of the saprophytic community, have been known to secrete a wide array of hydrolytic enzymes in natural conditions (Jog et al., 2016). Actinobacteria are considered as primary decomposers of dead organic matter, especially lignocellulosic biomass (Větrovsk et al., 2014). They show a remarkable ability to produce cellulase, xylanase, lignin peroxidase, and chitinase enzyme cocktail in addition to protease, lipase, pectinase, keratinase, amylase, invertase, and phytase that can trigger as a first step plant biomass degradation, thus processing it into simpler form for a second decomposition step initiated by secondary decomposers (Jog et al., 2016). Finally, complex nutrients are transformed into the simplest mineral forms, which act as natural fertilizers promoting plant health (Jog et al., 2012). These hydrolytic enzymes not only play a role in biomass turnover but also the biocontrol process, as described below.

Induction of Systemic Resistance

Induction of Systemic Resistance (ISR) is activated by non-pathogenic plant-associated microorganisms. Localized infection or treatment with microbial components, products, or a variety of structurally unrelated organic compounds and inorganic compounds caused systemic resistance (ISR) to infectious diseases and herbivorous insects (Ghiasian, 2020). Plant hormones Jasmonic acid (JA) and ethylene provide many contributions to the regulation of the group of inter-related signaling pathways required in ISR induction (Pieterse et al., 1998). Actinobacteria, reported as wheat endophyte, can induce defense pathways in *Arabidopsis* (Conn et al., 2008). Another report (Zhao et al., 2012) showed that culture filtrate from *Streptomyces bikiniensis* HD-087 was able to induce systemic resistance in cucumber against *Fusarium* wilt, caused by *F. oxysporum* f.sp. *cucumerinum*. Furthermore, *Micromonospora* spp. isolated from alfalfa nodules induced ISR through the jasmonate pathway (Martínez-Hidalgo et al., 2015). It seems that Actinobacteria are detected by the plant as "minor" pathogens because they do not have pathogenic determinant, as some endophytic actinobacterial strains possess the faculty to activate the plant defense genes at a low level in the absence of a pathogen (Coombs and Franco, 2003).

INDIRECT ACTION

Biocontrol

Biological control is the use of living organisms to modify the agricultural ecosystem to control a crop disease or prevent the establishment of a pest (Dowling and O'Gara, 1994). Bacteria that are involved in protecting plants are often referred to as biocontrol agents (Beattie, 2007).

Actinobacteria are widely recognized for their potential in biocontrol (El-Tarabily and Sivasithamparam, 2006; Hasegawa et al., 2006) because they are important producers of bioactive compounds (Qin et al., 2011). Over the past 50 years, there have been many studies on the mechanisms by which Actinobacteria might inhibit pathogens in soil, including antibiosis, nutrient competition, production of degradative enzymes (Subramanian et al., 2016), nitrous oxide production (Salwan and Sharma, 2020), and quorum quenching (Vesuna and Nerurkar, 2020).

Antibiosis is defined by the secretion of molecules that kill or reduce the growth of the target pathogen, this could be mediated by the secretion of specific or non-specific metabolites of microbial origin, by lytic agents, enzymes, volatile compounds, or other toxic substances (Fravel, 1988). Antibiotic-mediated inhibition of pathogens is generally the primary focus in efforts to suppress plant diseases. However, the diversity of secondary metabolites produced by *Streptomyces* and other Non- *Streptomyces* species foreshadows an interesting ability for suppressing fungal, bacterial, oomycete, and nematode pathogens (Barka et al., 2016).

Antibiotics are classified into two groups: volatile and non-volatile antibiotics. Volatile antibiotic substances like HCN, ammonia, aldehyde, alcohol, acetone, methane, 2-ethylethyl-1–hexanol, dimethyl sulfide, thioacetate, y-butyrolactones (Cellini et al., 2021) whereas phenazine, phenazine-1-carboxylic acid 2 -hydroxyphenazine, and pyrrolnitrin are some of the non-volatile antibiotic substances (Zhang et al., 2020). As it was reported further, Actinobacteria are widely known for their ability to produce antibiotics that allow them to inhibit pathogens in general and plant pathogens in particular (Berdy, 2005), especially *Streptomyces* genus, which have been the major producer for bioactive metabolites (Alexander, 1978) exhibiting an immense biocontrol action against a range of phytopathogens (Wang et al., 2013). They account for nearly 60% of the production of agriculturally important antibiotics (Ilic et al., 2007). But Non-*Streptomyces* antibiotic producers shouldn't be neglected as there are many reports about their potential antimicrobial production as for *Actinoplanes* sp. producing *Xanthone* (Cooper et al., 1992); *Actinomadura madurae* producing Simaomicin (Maiese et al., 1990); *Micromonospora* spp. producing *Spartanamicins* (Nair et al., 1992); *Saccharothrix* spp. producing Formamicin (Igarashi et al., 1997) and *Streptosporangium albidum* producing Aculeximycin (Ikemoto et al., 1983).

Among volatile compounds considered as antibiosis molecules, Hydrogen Cyanide Nitrogen HCN plays a role in biocontrol, by sequestering iron, thus, competing with phytopathogens (Gu et al., 2020) along with phosphate free for plant assimilation (Rijavec and Lapanje, 2016; Backer et al., 2018) and by inhibiting terminal "cytochrome c oxidase" in the respiratory chain and binding to metalloenzymes which confers it the property of suppressing phytopathogens (Gu et al., 2020). This metabolite production was reported for *Streptomyces* spp., *Microbispora* spp., *Actinomadura* spp., *Micromonospora* spp., *Nocardia* spp. (Dalal and Kulkarni, 2014), for many *Streptomyces* strains (Alekhya and Gopalakrishnan, 2017; Vijayabharathi et al., 2018) and *Nocardiopsis* (Allali et al., 2019). Another volatile compound, nitric oxide produced by *Streptomyces* has been suggested to activate plant defense against pathogen attack (Vaishnav et al., 2018).

In addition to producing antibiotics against a variety of pathogenic diseases in plants, hydrolytic enzymes, which are produced by antagonistic microbes, are capable of degrading fungal and bacterial cell walls, cell membranes, cell membrane proteins, and extracellular virulence factors which have been implicated in the biocontrol of plant diseases (Pal and Gardener, 2006). These hydrolytic enzymes include chitinase, cellulase, glucanase, protease, and phospholipase (Palaniyandi et al., 2013). *Streptomyces* are largely predominant in the suppression of plant disease by the production of chitinase, glucanase (Lee et al., 2012); and protease (Fróes et al., 2012); on another hand, *Actinoplanes campanulatus* was reported as β-glucanase producer (El-Tarabily et al., 2009); *Micromonospora carbonacea* produced chitinase; β-1,3-glucanase (El-Tarabily et al., 2000) and cellulase (El-Tarabily et al., 1996) and finally, *Amycolatopsis* secreted protease, glucanase and pectinase (Alekhya and Gopalakrishnan, 2016).

Quorum sensing (QS) could be defined as bacterial population density regulation and the regulation of their gene expression accordingly (Fuqua et al., 1994). On another hand, quorum quenching covers all processes implicated in (QS) disturbance (Dong and Zhang, 2005), this phenomenon opens many applications in medicine, aquaculture, crop production, and anti-biofouling (Grandclément et al., 2016). Over the last decade, a total of six Actinobacterialgenera: *Arthrobacter* (Flagan et al., 2003), *Microbacterium* (Wang et al., 2009), *Mycobacterium* (Chen and Xie, 2011), *Nocardioid-es* (Yoon et al., 2006), *Rhodococcus* (Latour et al., 2013), and *Streptomyces* (Ooka et al., 2013) have been reported for their quorum quenching activity.

Actinobacteria as Helper Bacteria

The most important symbiotic plant microorganisms namely mycoryzal, actinorhizal, and rhizobial symbiosis establishment are impacted by many biotic and abiotic factors. Several reports have shown the improvement of legume symbiosis and mycorrhizal symbiosis in dual inoculations with diverse PGPR (Barea et al., 2005); however, there is less information on this subject with Actinobacteria. There is a rising belief that Helper Bacteria could promote these symbioses. *Rhodococcus, Streptomyces*, and *Arthrobacter* are considered a Mycorrhizal Helper (Frey-Klett et al., 2007). Moreover, Schrey and Tarkka (2008) showed that the *Streptomyces* genus promotes the formation of symbioses between plant roots and microbes, and this is in part due to their direct positive influence on the symbiotic partner, expressed as, e.g., promotion of hyphal elongation of symbiotic fungi; furthermore, Franco-Correa et al. (2010) showed that co-inoculation of *Streptomyces* spp. MCR9 and MCR24 and *Glomus mosseae* produced synergic benefits on plant growth and P acquisition. The selected actinobacterial strains improved Arbuscular Mycorrhiza (AM) formation in clover plants. Concerning actinorhizal symbiosis, it was observed that saprophytic strains namely *Streptomyces* MM40, *Actinoplanes* ME3, and *Micromonospora* MM18 acted as helper bacteria (Solans, 2007). These actinobacterial strains clearly produced phytohormones (Solans et al., 2011) and had enzymatic activity for cellulose, hemicellulose, pectin, and lignocellulose (Solans and Vobis, 2003), but the real responsible metabolites are still unknown. The same saprophytic Actinobacteria used for actinorhizal symbiosis co-inoculation were co-inoculated to *Medicago sativa–Sinorhizobium meliloti* symbiosis (Solans, 2007). In these assays, the plants co-inoculated with Actinobacteria and rhizobium showed an increase in nodulation and plant growth compared with plants with single inoculations. In addition, *Lotus tenuis* plants co-inoculated with *Mesorhizobium loti* and saprophytic actinobacterial strains (MM40, ME3, and MM18) showed a promoting effect on nodulation and biomass. Another study reported that the combination of *Streptomyces kanamyceticus* and *Bradyrhizobium japonicum* increased nodulation and shoot nitrogen composition of soybeans by up to 55 and 41%, respectively (Gregor et al., 2003). Even if there is still scarce information on the potential of Actinobacteria as Symbiosis Helper, but the studies cited above could encourage this domain of investigation for improving symbiosis under diverse conditions.

COMMERCIAL FORMULATION OF ACTINOBACTERIAL BIOINOCULANTS

From the reviewed information discussed above, it is clear that Actinobacteria possess some interesting characteristics, such as ubiquity, rhizosphere colonization ability (filamentous structure), competitiveness, the capacity to resist harsh conditions, in addition to high strength spores that allow them to survive for prolonged periods in soil and in storage containers in addition to high PGP activity and nutrient cycling capability (Jog et al., 2016). Actinobacteria have proven their value as PGPR and biocontrol agent, but few available commercial actinobacterial products are disposable. Among these commercial products, we could cite an active ingredient, *Strptomyces lydicus* WYEC108, which gave rise to multiple commercial products: "Actinovate® *AG*" (Elliott et al., 2009), "Actinovate® *SP*" and "Micro108® soluble" for biocontrol; "Micro108® Seed" and "Inoculant Action Iron®" (produced by Naturalindustries) for biocontrol and plant growth promotion. *Streptomyces violaceusniger* strain YCED9 microbial agent was named "Thatch Control" for biocontrol (produced by Naturalindustries); *S. griseoviridis* strain K61 "Mycostop®" for biocontrol (Suleman et al., 2002); *Streptomyces saraceticus* KH400 "YAN TEN *Streptomyces saraceticus*" for biocontrol (produced by Yanten). Metabolite Polyoxin D (produced by *Streptomyces cacoi* var. *asoensis*) named AFFIRM$^{\mathrm{WDG}}$ (produced by Chlearychemical) and "PH-D® Fungicide" (produced by Arista-na) both used as a fungicide for turfgrass fungi. Some field trials tested the innocuity of actinobacterial bioinoculation as it was done for "Mycostop®," which was used for the control of Fusarium wilt of carnation and root rot disease of cucumber, and has been used in greenhouse production to protect flowers from pathogens (White et al., 1990). Likewise, Actinovate®, a biocontrol formulation of *Streptomyces lydicus* registered from AgBio in the United States of America, has been suggested for a wide range of environments ranging from greenhouses to field conditions, similarly, for *Streptomyces lydicus* WYEC 108 (MicroPlus®), which has been reported to possess disease suppression against powdery mildew and several root decay fungi (Solanki et al., 2016).

In general terms, "innovation" should include academic research, governmental institutions, industry, and civil society. Overall scientists have made an effort to develop eco-friendly and safe living organisms such as bio-intrant for ameliorating crop yield and protecting plants from pathogens, but these efforts will be infructuous if industry is not interested. Secondly, if governments do not establish legislation supervising the biotechnological application of PGPBs and facilitating interaction between "university" and "industry" (for example spin-off projects from a university or research and development department in industry) and finally if society in general and farmers, in particular, do not adhere to the use of bioinoculation (Etzkowitz and Zhou, 2017).

This assessment being established, much effort should be made before commercializing Actinobacteria or actinobacterial products for the development of sustainable agricultural solutions, beyond laboratory trials, including field assays to evaluate bioinoculant facing plant species, soil nature, and environmental conditions, which are unique for each ecosystem. It is crucial to evaluate bio-input safety and prevent the spread of antibioresistance.

CONCLUSION AND PERSPECTIVES

There are important fields of investigation in developing the use of PGPB for ameliorating plant growth, alleviating plants stress, and enhancing plant resistance to pests. Among these PGPB, Actinobacteria (PGPA) are increasingly studied (Nimaichand et al., 2016). Sustainable agriculture is well integrated in the roadmap of industrialized and developing countries. The former to minimize negative impacts on atmospheric greenhouse gas (GHG) concentrations and water quality caused by N and P losses following high fertilization rates (Haygarth et al., 2013) along with minimizing pesticide impact on environmental and human health (Bernardes et al., 2015). The latter, because they practice low-input agriculture where fertilizers, pesticides, and agro-technical machinery are not widely available (too expensive) and where the application of putative inexpensive bioinoculants is a great challenge (Bashan, 1998). The reviewed literature cited above clearly demonstrates the high potential of Actinobacteria in ameliorating plant growth, whether acting directly or indirectly, and/or as fighting tools against phytopathogens. Furthermore, much valuable research has highlighted the beneficial effects of Actinobacteria PGPB actions on crop yield outlining that these Actinobacterial strains could be candidates as microbial fertilizers. Future studies will deal with the next steps in terms of exploring the effect of these microorganisms on plants under greenhouse conditions (semi-controlled conditions), and then under field conditions (different soil characteristics, environmental conditions, agricultural practices…), and primarily, which formulations of these bioinoculants should be selected: liquid, organic, inorganic, polymeric or encapsulated. This "secret art" formulation will ensure compatibility with routine field practices, should be easy to use, environment-friendly, and have long storage quality (Bashan et al., 2014). In addition to these crucial scientific and bioprocessing stages, registration and regulatory approval of the product should be initiated once the bioinoculant proved its efficacy (Backer et al., 2018). It is obvious that the gap between *in vitro* trials and marketable final products necessitates investment, time, and multidisciplinary skills (Bashan et al., 2014). North America is considered a leader for bioinoculant production in terms of generating revenue, followed by Europe, Asia-Pacific, South America, and finally to a lesser extent Africa (Soumare et al., 2020). Based on the fact that the global biofertilizer market will reach US$1.66 billion by 2022 (Timmusk et al., 2017), government and industries should be confident of a return on any investment. Overall, the major applications of bioinoculation have used BNF bacteria (especially rhizobia of about 79%), followed by phosphate solubilizing bacteria (∼15%) while other inoculants including mycorrhizal products make up the remaining percentage (Research, 2014). Based on the Actinobacteria PGP traits described in this review, which are in addition to their competitiveness, ubiquity, and tremendous potential for metabolite production, this large taxonomic group worth a special attention even if it is not considered as a best candidate presently. Ultimately, it should play a key role in formulating multi-strain inoculants with synergistic actions for promoting sustainable agriculture.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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