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MINI-REVIEW

Bacillus as a source of phytohormones for use in agriculture

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Abstract

Microbial plant biostimulants (MPBs) are capable of improving the productivity and quality of crops by activating plant physiological and molecular processes, representing an efficient tool in sustainable agriculture. Through phytohormone production, MPBs are capable of regulating plant physiological processes, increasing the productivity and quality of crops, in addition to being an efficient alternative in the industrial production of phytohormones. *Bacillus* is a bacterial genus with various species on the market being used as biopesticides, due to their ability to produce antimicrobial, nematicidal and insecticidal compounds. The capability of *Bacillus* species to protect plants against pests and/or pathogens also entails the triggering or increase of plant defense responses. Furthermore, a relevant number of species from the genus *Bacillus* provoke plant growth promotion by different mechanisms such as increasing the tolerance of their host plants under abiotic stress conditions or improving plant nutrition. In several cases, the plant response is mediated by the bacterial production of phytohormones. In the present work, all studies from recent decades where the production of phytohormones by *Bacillus* species are reported, highlighting their role in host plants and the mechanisms by which they are capable of increasing plant growth, promoting their development, and improving their response to different stresses.

Key points

- *Different Bacillus-species are known as agricultural biopesticides.*
- *Bacillus role as biostimulants is being increasingly addressed.*
- *Bacillus represents a good source of phytohormones of agricultural interest.*

Keywords *Bacillus* · Biostimulant · Phytohormone · Auxins · Cytokinins · Gibberellins · Abscisic acid

Introduction

As the United Nations points out in its Sustainable Development Goals, the global development of humanity must be linked to the development and extension of sustainable agriculture, which includes ecological, economic and social aspects (Janker et al. 2018). The world population is constantly growing and it is calculated that it may reach 10 billion people in the year 2050 (Tripathi et al. 2019). To address the demand for food, agricultural productivity must increase globally by 70% (Barea, 2015). In order to feed the future population, it is essential to develop new strategies for sustainable food production (Poveda, 2021), increasing the productive capacity of agricultural crops and reducing the yield losses caused by abiotic and biotic stresses (Poveda, 2020a).

Microorganisms present inside plant tissues and in the rhizospheric soil play a key role in plant growth and development, maintaining the balance of nutrients in the ecosystem. These microorganisms provide important benefits to their host plants, which is why they are valued as an important and promising tool for sustainable agriculture (Yadav et al. 2020). Directly or indirectly, these microorganisms are capable of promoting plant growth, being known as plant growth promoting microbes (PGPMs) (Naik et al. 2019).

PGPMs have received different names depending on their mode of action; in such a way, the term microbial biofertiliser has been used for those microorganisms capable of promoting plant growth, by increasing the supply of nutrients to the host plant, in a direct or indirect manner

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(Mahanty et al. 2017). On the other hand, plant biostimulants have been defined as natural compounds that trigger physiological and molecular processes modulating crop yield and quality, though their primary function is not to supply nutrients (du Jardin 2015). Thus, the formulated products consisting of microorganisms that act in the crop in such a way are, by nature, plant biostimulants (Yakhin et al. 2017; Rouphael and Colla, 2018). The European Union (EU), in the recently released regulation (European Union [EU]) 2019/1009, laying down rules on the making available on the market of EU fertilizing products) coins the term Microbial Plant Biostimulant (MPB), merging the concept of biofertilisers and that of other plant biostimulants, and expressly excluding those microorganisms that act by protecting the crop from pests or disease, either from a direct or indirect point of view (European Council 2019). Thereby, the definition of MPBs encompasses the microorganisms or consortiums of microorganisms that act as fertilizing products independently of the product's nutrient content, provided that they stimulate plant nutrition processes, improving one or more of the following characteristics of the plant or the plant rhizosphere: (a) nutrient use efficiency; (b) tolerance to abiotic stress; (c) quality traits; or (d) availability of confined nutrients in the soil or rhizosphere (European Council 2019). In this work, the EU concept of MPBs has been adopted. The list of taxa accepted by the EU legislation is restricted so far, but it considers a possible extension in the following years. The global market for MPBs in agriculture is estimated to reach 1.95 billion dollars by 2022, reporting an annual growth rate of 14%. Specifically, Europe and Latin America account for 80% of the MPB world market, although the main locations in terms of growth are North America, Europe and Asia–Pacific (Keswani et al. 2019).

Bacillus is a bacterial genus that provides a relevant number of strains belonging to different species for biocontrol in agriculture. However, some species are also very promising as MPBs, but this has received less attention in the scientific literature. The present work analyses the existing information concerning phytohormone production by *Bacillus* strains, and the role that such phytohormones play in the agricultural uses of *Bacillus* species as MPBs. In this sense, there are many reviews so far on *Bacillus* and agriculture. Despite this, the use of *Bacillus* as a biotechnological and industrial tool in the production of phytohormones has never been reviewed. Phytohormones are considered to be very relevant for the crops to thrive with stressing situations, thus, they will be important inputs for future agriculture in the present scenario of increasing biotic or abiotic stresses (Khan et al., 2020). Most of the papers about *Bacillus* show their PGP effect as a complex mix of very different modes of action. This review attempts to unravel the role of *Bacillus* as phytohormone producer, putting on the table what is known about this specific mode of action.

Bacteria as phytohormone producers

Phytohormones regulate all the physiological processes of plants, including their growth, development, nutrient allocation or adaptation to the environment. Therefore, all biological processes that occur in the plant, and in its exogenous interactions, are directly or indirectly affected by phytohormones (Fahad et al. 2015).

In general, auxins, the most important being indole acetic acid (IAA), are key phytohormones in plant growth regulation, including cell elongation, vascular tissue development and apical dominance. Cytokinins (CKs) also regulate growth processes and plant development such as cell division, shoot differentiation or photomorphogenic development. Gibberellins (GAs) are phytohormones involved in the processes of seed germination, flower initiation, leaf expansion, stem elongation, or flower and fruit development. Abscisic acid (ABA) is a phytohormone involved in plant responses of tolerance to abiotic stresses (drought, chilling, heat, salinity, etc.) and in the dormancy process (Fahad et al. 2015). Moreover, there are three phytohormones involved in different physiological processes, which include defense responses to biotic stresses: salicylic acid (SA), mainly against biotrophic pathogens, and jasmonic acid (JA) and ethylene (ET), mainly against necrotrophic pathogens and pests (Poveda, 2020b).

Phytohormones are obtained for several industrial purposes, including application in agriculture. The production process is carried out through plant extraction, chemical synthesis as well as microbial fermentation. Phytohormones are found not only in higher plants, but also in algae, and in plant-associated bacteria and fungi (pathogens and beneficial/symbionts). In plants, the hormone concentration is extremely low, for example, to obtain 9 mg ABA a 200-kg cotton ball is needed. On the other hand, chemical synthesis presents significant disadvantages and difficulties, since phytohormones have a complex chemical structure which complicate operations, causing high cost and low purity. Therefore, microbial production of phytohormones is proposed as a new alternative that overcomes the previous deficiencies, obtaining final products with higher bioactivity and purity, but also at a much lower cost (Tsavkelova et al. 2006; Shi et al. 2017).

In recent decades, different bacterial genera beneficial to plants with the ability to produce phytohormones have been reported. Among them, the genera *Azospirillum*, *Bacillus*, *Paenibacillus*, and *Pseudomonas* stand out, mainly producing IAA, CKs, GAs, and ABA, acting as powerful biostimulants in agriculture (Dodd et al. 2010; Odoh 2017).

Bacillus in agriculture

Bacillus is a gram-positive bacteria genus, rod-shaped, endospore-forming and with the capacity to survive in both aerobic and anaerobic conditions. The complex taxonomy of *Bacillus* has led to the emergence of new genera related to it, some in recent times such as *Paenibacillus*, *Brevibacillus*, *Virdiibacillus*, *Lysinibacillus*, *Geobacillus*, *Virgibacillus*, or *Amphibacillus* (Tiwari et al. 2019). *Bacillus* includes the most abundant bacteria species in the rhizosphere and in the root endosphere (95%) with the ability to promote plant growth and produce antibacterial and antifungal secondary metabolites, being well-known as the main source of strains for registered commercial formulations such as bacterial biocontrollers in agriculture (Nambirajan et al. 2020; Saxena et al. 2020). Indeed, many *Bacillus* species produce a wide range of effective molecules against plant pathogens. They include antimicrobial peptides (such as bacteriocins) or secondary metabolites (such as polyketides). Therewith, species such as *B. subtilis*, *B. amyloliquefaciens*, *B. licheniformis*, *B. cereus*, *B. velezensis* or *B. thuringiensis* have been described as antifungal (against *Fusarium*, *Rhizoctonia*, *Sclerotium*, *Pythium*, *Phytophthora*, etc.), antibacterial (against *Pectobacterium*, *Pseudomonas*, *Xanthomonas*, *Agrobacterium*, etc.), nematicidal and insecticidal (Engelbrecht et al. 2018; Lopes et al. 2018; Ngalimat et al. 2021). Moreover, by interacting with root tissues, *Bacillus* species are able to induce defensive responses in plants against future attacks by pests and/or pathogens by SA, JA or JA/ET pathways, a mechanism called induced systemic resistance (ISR) (Poveda et al. 2020).

However, this genus is also a well-known PGPM; the action mechanisms are diverse, including increased nutrient uptake by the crop mediated by solubilization of insoluble forms, nitrogen fixation, ammonia release from nitrogenous organic matter; also, the synthesis of plant growth phytohormones (IAA, CKs, GAs) or volatile organic compounds' (VOCs) production, which regulate plant physiology. Some of the main *Bacillus* species described with PGP capacity are *B. subtilis*, *B. cereus*, *B. methylotrophicus* or *B. flexus* (Lopes et al. 2018).

Moreover, by interacting and/or colonizing the roots, various species of *Bacillus* are also capable of increasing plant tolerance against abiotic stresses such as drought, salinity or heavy metals, due to mechanisms of action that include increased water transport in plant tissues, uptake and distribution of nutrients, or accumulation of compatible solutes and antioxidants, among others. As inducers of plant tolerance against abiotic stresses, several *Bacillus* species such as *B. megaterium*, *B. thuringiensis*, *B. amyloliquefaciens*, or *B. licheniformis* (Radhakrishnan et al. 2017) have been reported.

Different formulations based on *Bacillus* species are registered as agricultural input for a broad range of crops, e.g., *Solanum lycopersicum* (tomato), *Brassica napus* (canola), *Triticum aestivum* (wheat), *Crocus sativus* (saffron), *Glycine max* (soybean), *Solanum tuberosum* (potato), *Malus domestica* (apple), *Manihot esculenta* (cassava) or *Nicotiana tabacum* (tobacco) (Kashyap et al. 2019). To a lesser extent, *Bacillus* species are also used as bioremediators, and as PGPMs (Islam et al. 2016). Indeed, a large number of agricultural applications of *Bacillus* are related to their use as biopesticides, e.g., *B. thuringiensis* (Bt) has more than 400 Bt-based formulations as a bioinsecticide on the market, and *B. amyloliquefaciens* and *B. subtilis* have also been registered as biofungicides (Sansinenea, 2019), but formulations have also been registered for other uses (MAPA, 2021).

Finally, the use of *Bacillus* in microbial co-inoculants with other bacterial or even fungal strains is increasingly important in agriculture, e.g., the *Bacillus–Rhizobium* application generates an increase in the formation of root nodules in *Phaseolus vulgaris* (common bean) (Petersen et al. 1996) and a reduction in the attack of soil borne pathogens such as *Rhizoctonia solani* and *Fusarium oxysporum* (Jensen et al. 2002). Similarly, the *Bacillus–Pseudomonas* application provokes an increase in the productivity of *Brassica campestris* (Maheshwari et al. 2015), as does the *Bacillus–Bradyrhizobium* application in soybean (Iliäœić et al. 2017).

Phytohormones produced by *Bacillus*

There are numerous studies reporting the ability of various *Bacillus* species to produce phytohormones with beneficial effects for agricultural crops, see Table 1 and the infographic in Fig. 1.

Growth and development phytohormones

The main growth-related phytohormone is IAA auxin, which is biosynthesised by several different *Bacillus* species. Metabolomic and molecular studies carried out in silico have enabled the identification of genes involved in IAA biosynthesis in *B. amyloliquefaciens*, demonstrating that it can occur through multiple pathways (Shao et al. 2015, 2021). The ability to produce IAA in vitro has been reported in *Bacillus* species such as *B. subtilis* (Gerayeli et al. 2018; Wagi and Ahmed, 2019; Chobotarov et al. 2020), *B. cereus* (Karadeniz et al. 2006; Wagi and Ahmed, 2019), *B. thuringiensis* (Gerayeli et al. 2018), *B. amyloliquefaciens* (Gerayeli et al. 2018; Shahzad et al. 2019), *B. megaterium* (Karadeniz et al. 2006; Gerayeli et al. 2018), *B. pumilus* (Gerayeli et al. 2018), *B. anthracis* (Ali et al. 2021) or *B. telluris* (Guo et al. 2020). The use of such strains for the industrial production of IAA in bioreactors has been proposed, and in

Table 1 Phytohormones produced by *Bacillus* species along with their study methodology and effects

Phytohormone		*Bacillus* Species	Productive capacity	Plant used	Plant effect	Reference
Group	Name					
Auxins	Indole acetic acid (IAA)	*B. subtilis*	170-310 µg/ml (without tryptophan addition)	Soybean	Root growth promotion	Araujo et al. 2005
	IAA	*B. cereusB. megaterium*	0.055 µg/ml (without tryptophan addition)	-	-	Karadeniz et al. 2006
	IAA	*B. amyloliquefaciens*	29300 µg/ml (without tryptophan addition)51000-54000 µg/ml (with tryptophan addition)	*Lemna minor*	Fresh weight increment	Idris et al. 2007
	IAA	*B. subtilis*	90000-370000 µg/ml (without tryptophan addition)	*Dioscorea rotundata*	Number of sprouts and roots, shoots length, root and shoot fresh weights increment	Noghabi et al. 2007
	IAA	*B. amyloliquefaciens*	25-32 µg/ml (without tryptophan addition)	Soybean	Roots and shoots length, and fresh and dry weight increment	Buensanteai et al. 2008
	IAA	*B. cereusB. megateriumB. pumilusB. subtilis*	2.7-22.2 µg/ml (without tryptophan addition)	*Vigna radiata*	Shoot length, shoot fresh weight, pods per plant, and weight per seed increment	Ali et al. 2009
	IAAindole-3-propionic acid (IPA)Indole butyric acid (IBA)	*B. licheniforims B. subtilis*	Not indicated	Red-pepper and tomato	Plant growth increase	Lim and Kim, 2009
	IAA	*B. cereusB. licheniformisB. pumilusB. subtilis*	1.2-44.4 µg/ml (without tryptophan addition)	Wheat	Productivity increment	Hussain and Hasnain, 2011
	IAAIBA	*B. aryabhattai*	IAA: 200-470 µg/mlIBA: 100-320 µg/ml(with tryptophan addition)	*Xanthium italicum*	Seed germination, roots and shoots lenght, and dry weight increment	Lee et al. 2012
	IAA	*B. pumilus*	36.7 µg/ml (with tryptophan addition)	*Ocimum sanctum*	Shoots and roots length, and number of leaves increment	Murugappan et al. 2013
	IAA	*B. amyloliquefaciens*	6.25 µg/ml (with tryptophan addition)	Banana	Shoots and roots dry weight increment	Yuan et al. 2013
	IAA	*Bacillus* sp.	4.5-8.3 µg/ml (without tryptophan addition)14.1-16.2 µg/ml (with tryptophan addition)	Wheat	Roots and panicle weight increment.	Baghaee-Ravari and Heidarzadeh, 2014
	IAA	*B. amyloliquefaciens*	Not indicated	Wheat	Limit phosphorus uptake	Talboys et al. 2014

Table 1 (continued)

Phytohormone		*Bacillus* Species	Productive capacity	Plant used	Plant effect	Reference
Group	Name					
	IAA	*B. amyloliquefaciens*	Not indicated	-	-	Shao et al. 2015
	IAA	*B. amyloliquefaciens*	0.0003 µg/ml (without tryptophan addition)0.0004 µg/ml (with tryptophan addition)	Cucumber	Dry weight increment	Liu et al. 2016
	IAA	*B. velezensis*	21.3 µg/ml (with tryptophan addition)	Beet, carrot, cucumber, pepper,potato, radish, squash, tomato, and turnip	Shoots and roots weights increment	Meng et al. 2016
	IAA	*B. amyloliquefaciens*	9-11 µg/ml (with tryptophan addition)	*Arabidopss thaliana*	Root growth increment	Asari et al. 2017
	IAA	*B. altitudinis*	35 pM (without tryptophan addition)	Wheat	Alleviate iron shortage stress	Sun et al. 2017
	IAA	*B. amyloliquefaciensB. megateriumB. pumilusB. subtilisB. thuringiensis*	0.6-8.55 µg/ml (without tryptophan addition)	-	-	Gerayeli et al. 2018
	IAAIndole-3-carboxylic acid (ICA)Indole-3-lactic acid (ILA)	*B. amyloliquefaciensB. muralisB. pumilus B. simplex*	IAA: 12.3-25.9 µg/mlICA: 15.2 µg/mlILA: 8.43-15.2 µg/ml(with tryptophan addition)	Wheat	Increase drought tolerance	Raheem et al. 2018
	IAA	*B. subtilis*	0.1 µg/ml (without tryptophan addition)0.8-1.4 µg/ml (with tryptophan addition)	-	-	do Prado et al. 2019
	IAA	*Bacillus* sp.	12 µg/ml (without tryptophan addition)17 µg/ml (with tryptophan addition)	Canola	Shoots and roots length, dry weights and chlorophyll content increment	Samreen et al. 2019
	IAA	*B. amyloliquefaciens*	12-17 µg/ml (without tryptophan addition)	-	-	Shahzad et al. 2019
	IAA	*B. methylotrophicus*	210 µg/ml (without tryptophan addition)	Strawberry	Shoots and roots fresh weight increment	Vicente-Hernández et al. 2019
	IAA	*B. cereusB. subtilis*	180-300 µg/ml (without tryptophan addition)	-	-	Wagi and Ahmed, 2019
	IAA	*B. subtilis*	0.46 µg/ml	-	-	Chobotarov et al. 2020
	IAA	*B. telluris*	175.94 µg/ml (with tryptophan addition)	-	-	Gou et al. 2020
	IAA	*B. subtilis*	154.53 µg/ml	Wheat	Plant growth increment and increase salt tolerance	Ji et al. 2020

Table 1 (continued)

Phytohormone		*Bacillus* Species	Productive capacity	Plant used	Plant effect	Reference
Group	Name					
	IAA	*B. safensis*	7.51 µg/ml (with tryptophan addition)	-	-	Nazli et al. 2020
	IAA	*B. cereus*	3.8-9.7 µg/ml (with tryptophan addition)	Chinese cabbage	Shoots and roots length and weight increment	Wang et al. 2020a
	IAA	*B. toyonensis*	2-4.2 µg/ml (with tryptophan addition)	Maize	Plant growth increment and enhancementof root development under aluminium toxicity condition	Zerrouk et al. 2020
	IAA	*Bacillus* sp.	0.204 µg/ml	Wheat	Germination percentage and seedling length increment (also under drought stress)	Akhtar et al. 2021a
	IAA	*B. cereus*	81.33 µg/ml	*Brassica nigra*	Dry biomass and phytoextraction increment in Cr contamined soils	Akhtar et al. 2021b
	IAA	*B. subtilis*	0.11 µg/ml (with tryptophan addition)	-	-	Alfonso et al. 2021
	IAA	*B. anthracis*	99 µM/ml	-	-	Ali et al. 2021
	IAA	*B. amyloliquefaciens*	0.23 µg/ml (with tryptophan addition)	-	-	Shao et al. 2021
	IAA	*B. subtilis*	0.0836 µg/ml	Potato	Roots weights increment	Sorokan et al. 2021
Cytokinins	Zeatin mucleotide (ZN) Zeatin riboside (ZR) Izopentyl adenine (iP) Izopentyl adenosine (iPA)	*B. subtilis*	ZN: 0.09-0.1 µg/mlZR: 0.39-0.4 µg/mliP: 0.0007-0.0008 µg/mliPA: 0.0003-0.0004 µg/ml	Lettuce	Shoots and roots weights increment	Arkhipova et al. 2005
	Zeatin (Z)	*B. cereusB. megaterium*	270 µg/ml	-	-	Karadeniz et al. 2006
	-	*Bacillus* sp.	Not indicated	Lettuce	Shoots biomass increments.Roots biomass increments under drought stress	Arkhipova et al. 2007
	ZZR	*B. licheniformisB. subtilis*	Z+ZR: 5.7-20.1 µM	Cucumber	Cotyledons weight and sizes increments	Hussain and Hasnain, 2009
	Cis zeatin (cZ)Trans zeatin (tZ)ZRDihydrozeatin riboside (DHZR)	*B. cereusB. licheniformisB. pumilusB. subtilis*	cZ: 0.0531-0.1271 µg/mltZ: 0.0821-0.1331 µg/mlZR: 0.0586-0.1551 µg/mlDHZR: 0.0258-0.0542 µg/ml	Wheat	Productivity increment	Hussain and Hasnain, 2011

Table 1 (continued)

Phytohormone		*Bacillus* Species	Productive capacity	Plant used	Plant effect	Reference
Group	Name					
	-	*B. subtilis*	Not indicated	*Platycladus orientalis*	Shoots biomass increments under drought stress and well-watered conditions	Liu et al. 2013
	ZZR	*B. subtilis*	Z+ZR: 0.085-0.125 µg/ml	Wheat	Stimulate root exudation of amino acids	Kudoyarova et al. 2014
	ZZRZNZeatin glycoside (ZG)	*B. amyloliquefaciens*	Z: 152.4-205.4 fmol/µlZR: 279.8-300.6 fmol/µlZN: 1.8-3.42 fmol/µlZG: 16.66-17.31 fmol/µl	*A. thaliana*	Root growth increment	Asari et al. 2017
	ZZRZGiPiPA	*B. subtilis*	Z: 0.0539 µg/mlZR: 0.0492 µg/mlZG: 0.1043 µg/mliP: 0.0618 µg/mliPA: 0.0046 µg/ml	-	-	Chobotarov et al. 2020
	Z	*B. subtilis*	0.638 µg/ml	Wheat	Plant growth increment and increase salt tolerance	Ji et al. 2020
	tZcZiP	*B. toyonensis*	tZ: 50 pmol/gcZ: 675 pmol/giP: 140 pmol/g	Maize	Plant growth increment	Zerrouk et al. 2020
	Not identified	*Bacillus* sp.	0.09167 µg/ml	Wheat	Germination percentage and seedling length increment (also under drought stress)	Akhtar et al. 2021a
	Not identified	*B. cereus*	1.55 µg/ml	*Brassica nigra*	Dry biomass and phytoextraction increment in Cr contamined soils	Akhtar et al. 2021b
	ZZR	*B. subtilis*	Z: 0.1038 µg/mlZR: 0.0462 µg/ml	Potato	CK content in shoots increment	Sorokan et al. 2021
Gibberellins	GA$_1$GA$_3$GA$_4$GA$_{20}$	*B. pumilusB. licheniformis*	GA$_1$: 0.13-0.15 µg/mlGA$_3$: 0.05-0.06 µg/mlGA$_4$: 0.008–0.012 µg/mlGA$_{20}$:0.002–0.003 µg/ml	*Alnus glutinosa*	Promotion of stem elongation	Gutiérrez-Mañero et al. 2001

Table 1 (continued)

Phytohormone		*Bacillus* Species	Productive capacity	Plant used	Plant effect	Reference
Group	Name					
	GA$_1$GA$_3$GA$_4$GA$_5$GA$_7$GA$_8$GA$_9$GA$_{12}$GA$_{19}$GA$_{20}$GA$_{24}$GA$_{34}$GA$_{36}$GA$_{44}$GA$_{53}$	*B. cereusB. macrolidesB. pumilus*	GA$_1$: 0.0022-0.0035 µg/mlGA$_3$: 0.0027-0.0145 µg/mlGA$_4$: 0.0042-0.0078 µg/mlGA$_5$: 0.0061 µg/mlGA$_7$: 0.0017-0.0087 µg/mlGA$_8$: 0.0033 µg/mlGA$_9$: 0.0005-0.0011 µg/mlGA$_{12}$: 0.0001-0.0004 µg/mlGA$_{19}$: 0.0005-0.0016 µg/mlGA$_{20}$: 0.0002-0.0003 µg/mlGA$_{24}$: 0.0013-0.0016 µg/mlGA$_{34}$: 0.0011-0.0068 µg/mlGA$_{36}$: 0.0007-0.0046 µg/mlGA$_{44}$: 0.0003-0.0155 µg/mlGA$_{53}$: 0.0001-0.0003 µg/ml	Red pepper	Plant growth increment	Joo et al. 2004
	-	*B. macrolidesB. pumilus*	Not indicated	Red pepper	Increase endogenous gibberellins content and promote growth	Joo et al. 2005
	GA$_3$	*B. cereusB. megaterium*	1200-3510 µg/ml (without tryptophan addition)	-	-	Karadeniz et al. 2006
	-	*B. subtilis*	150 ng/10^9 cells	Radish	Plant growth increment	Malfanova et al. 2011
	GA$_3$	*B. aryabhattai*	53.3-119 µg/mg protein	*Xanthium italicum*	Seed germination, roots and shoots lenght, and dry weight increment	Lee et al. 2012
	-	*B. siamensis*	180-240 µg/ml	-	-	Ambawade and Pathade, 2015
	GA$_3$	*B. cereus*	394.18 µg/ml	-	-	Pandya and Desai, 2013
	GA$_3$	*B. amyloliquefaciens*	3320000 µg/ml	Banana	Shoots and roots dry weight increment	Yuan et al. 2013

Table 1 (continued)

Phytohormone		*Bacillus* Species	Productive capacity	Plant used	Plant effect	Reference
Group	Name					
	$GA_1GA_3GA_7GA_8GA_9GA_{12}GA_{19}GA_{20}GA_{24}GA_{34}GA_{53}$	*B. methylotrophicus*	GA_1: 0.000010 µg/mlGA_3: 0.000026 µg/mlGA_7: 0.000056 µg/mlGA_8: 0.000024 µg/mlGA_9: 0.000017 µg/mlGA_{12}: 0.000266 µg/mlGA_{19}: 0.000008 µg/mlGA_{20}: 0.000015 µg/mlGA_{24}: 0.000009 µg/mlGA_{34}: 0.000113 µg/mlGA_{53}: 0.000004 µg/ml	Lettuce	Enhance plant growth, nutritional metabolites and food values	Radhakrishnan and Lee, 2016
	$GA_4GA_5GA_8GA_9GA_{12}GA_{19}GA_{20}GA_{24}GA_{36}GA_{53}$	*B. amyloliquefaciens*	GA_4: 0.00102 µg/mlGA_5: 0.00008 µg/mlGA_8: 0.000013 µg/mlGA_9: 0.00012 µg/mlGA_{12}: 0.000014 µg/mlGA_{19}: 0.000093 µg/mlGA_{20}: 0.01788 µg/mlGA_{24}: 0.0564 µg/mlGA_{36}: 0.0575 µg/mlGA_{53}: 0.000772 µg/ml	Rice	Enhance plant growth andregulate endogenous phytohormones	Shahzad et al. 2016
	$GA_4GA_8GA_9GA_{19}GA_{20}$	*B. amyloliquefaciens*	GA_4: 0.21 µg/mlGA_8: 0.019 µg/mlGA_9: 0.11 µg/mlGA_{19}: 0.125 µg/mlGA_{20}: 0.013 µg/ml	Radish, tomato and *B. juncea*	Enhance plant growth	Kim et al. 2017
	-	*B. licheniformis*	83.7 µg/ml	-	-	Silpa et al. 2018
	$GA_1GA_4GA_7$	*B. subtilis*	GA_1: 0.00012 µg/mlGA_4: 0.00226 µg/mlGA_7: 0.00008 µg/ml	Chinese cabbage	Enhance plant growth and nutrient uptake	Kang et al. 2019a
	$GA_1GA_3GA_5GA_8GA_{19}GA_{24}GA_{53}$	*B. tequilensis*	GA_1: 0.024 µg/mlGA_3: 0.081 µg/mlGA_5: 0.043 µg/mlGA_8: 0.062 µg/mlGA_{19}: 0.225 µg/mlGA_{24}: 0.128 µg/mlGA_{53}: 0.052 µg/ml	Soybean	Induce thermotolerance	Kang et al. 2019b

Table 1 (continued)

Phytohormone		*Bacillus* Species	Productive capacity	Plant used	Plant effect	Reference
Group	Name					
	$GA_4GA_5GA_8GA_9GA_{12}GA_{19}GA_{20}GA_{24}GA_{36}GA_{53}$	*B. amyloliquefaciens*	GA_4: 0.00109 µg/mlGA_5: 0.000083 µg/mlGA_8: 0.00002 µg/mlGA_9: 0.00014 µg/mlGA_{12}: 0.000015 µg/mlGA_{19}: 0.00009 µg/mlGA_{20}: 10.0767 µg/mlGA_{24}: 0.0057 µg/mlGA_{36}: 0.00585 µg/mlGA_{53}: 0.00077 µg/ml	-	-	Shahzad et al. 2019
	-	*B. methylotrophicus*	6160 µg/ml	Strawberry	Shoots and roots fresh weight increment	Vicente-Hernández et al. 2019
	GA_3	*B. subtilis*	0.103 µg/ml	Wheat	Plant growth increment and increase salt tolerance	Ji et al. 2020
	-	*B. cereus*	12-29 µg/ml	Chinese cabbage	Shoots and roots length and weight increment	Wang et al. 2020a
Abscisic acid	-	*B. subtilis*	010-170 µg/ml	Soybean	Root growth promotion	Araujo et al. 2005
		B. cereusB. megaterium	30-70 µg/ml (without tryptophan addition)	-	-	Karadeniz et al. 2006
		Bacillus sp.	28-45 pmol/ml	-	-	Forchetti et al. 2007
		B. aryabhattai	1.39-1.78 µg/mg protein	*X. italicum*	Seed germination, roots and shoots lenght, and dry weight increment	Lee et al. 2012
		B. amyloliquefaciens	40-50 µg/ml	Soybean	Induce salinity stress tolerance	Kim et al. 2017
		B. amyloliquefaciens	0.00014-0.00032 µg/ml	Rice	Induce salinity stress tolerance	Shahzad et al. 2017
		B. subtilis	Not indicated	*Brassica chinensis*	Induce cadmium stress tolerance	Pan et al. 2019
		B. amyloliquefaciens	0.00012-0.00032 µg/ml	-	-	Shahzad et al. 2019
		B. subtilis	0.0414 µg/ml	-	-	Chobotarov et al. 2020
		B. marisflavi	Not indicated	*Brassica juncea* and barley	Induce drought stress tolerance	Gowtham et al. 2021
		B. subtilis	0.609 µg/ml	Wheat	Plant growth increment and increase salt tolerance	Ji et al. 2020
		Bacillus sp.	0.02567 µg/ml	Wheat	Germination percentage and seedling length increment (also under drought stress)	Akhtar et al. 2021a

Table 1 (continued)

Phytohormone		*Bacillus* Species	Productive capacity	Plant used	Plant effect	Reference
Group	Name					
		B. cereus	2.57 µg/ml	*Brassica nigra*	Dry biomass and phytoextraction increment in Cr contamined soils	Akhtar et al. 2021b
Jasmonic acid	-	*Bacillus* sp.	4-5 pmol/ml	-	-	Forchetti et al. 2007
		B. subtilis	430 µg/ml	Wheat	Plant growth increment and increase salt tolerance	Ji et al. 2020
Salicylic acid	-	*B. licheniformis*	18 µg/ml	-	-	Shanmugam and Narayanasamy, 2009
		Bacillus pumilus	210-230 pmol-ml	-	-	Forchetti et al. 2010
		B. subtilis	0.003865 µg/ml	Wheat	Plant growth increment and increase salt tolerance	Ji et al. 2020

this sense, the highest amounts of IAA are produced by *B. subtilis* growing in substrates with a neutral pH and higher hemicellulose content (do Prado et al. 2019).

As a consequence of its ability to produce IAA, there are numerous examples of increased plant growth in plants inoculated with *Bacillus* species. After root inoculation, an increase in root growth has been observed, as the auxins produced by *Bacillus* act locally; examples include wheat (Baghaee-Ravari and Heidarzadeh 2014) potato (Sorokan et al. 2021) and soybean inoculated with *B. subtilis* (Araujo et al. 2005), while *Arabidopsis thaliana* with *B. amyloliquefaciens* produced an increase of lateral root outgrowth, elongation and root-hair formation (Asari et al. 2017). Consequently, the increase in root development and auxin levels imply an increase in complete plant growth, including shoots and leaves, as has been reported in *Lemna minor*, soybean, *Musa* sp. (banana) and *Cucumis sativus* (cucumber) with *B. amyloliquefaciens* (Idris et al. 2007; Buensanteai et al. 2008; Yuan et al. 2013; Liu et al. 2016); in *Dioscorea rotundata* and *Vigna radiata* with *B. subtilis* (Noghabi et al. 2007; Ali et al. 2009); in *Brassica pekinensis* (Chinese cabbage) with *B. cereus* (Wang et al. 2020a); in *Ocimum sanctum* with *B. pumilus* (Murugappan et al. 2013); in *Fragaria × ananassa* (strawberry) with *B. methylotrophicus* (Vicente-Hernández et al. 2019); and finally, in *Beta vulgaris* (beet), *Daucus carota* subsp. *sativus* (carrot), cucumber, *Capsicum annuum* (pepper), potato, *Raphanus sativus* (radish), *Cucurbita* sp. (squash), tomato and *Brassica rapa* subsp. *rapa* (turnip) with *B. velezensis* (Meng et al. 2016). Increase in plant growth due to the increase in auxin levels also observed in many other PGP rhizobacteria (PGPRs). This plant growth promotion leads to an increase in crop yield, as observed in a wheat crop inoculated with *B. cereus*, *B. licheniformis*, *B. pumilus*, and *B. subtilis* (Hussain and Hasnain, 2011). In addition, due to the production of IAA by *Bacillus*, the foliar content of chlorophyll increased (Samreen et al. 2019). Moreover, inoculation of wheat with *B. amyloliquefaciens* provokes a remodelling of the transporters of inorganic phosphorus (Talboys et al. 2014). Along with IAA, there are species that can produce other auxins, such as indole butyric acid (IBA), that produce an increase in seed germination in *Xanthium italicum* by *B. aryabhattai* (Lee et al. 2012).

As far as responses to abiotic stresses are concerned, the production of IAA has been related to the ability of *Bacillus* to increase plant tolerance against heavy metals, as has been reported for *B. altitudinis* in wheat under iron stress mediated by the upregulation of genes encoding ferritins (Sun et al. 2017). Another example is *Zea mays* (maize) under aluminium toxicity conditions inoculated with *B. toyonensis*, being the necessary plant-auxin transport pathway for the aluminium-induced stress response (Zerrouk et al. 2020). Furthermore, *Bacillus*-IAA has been related to the ability to increase plant tolerance under

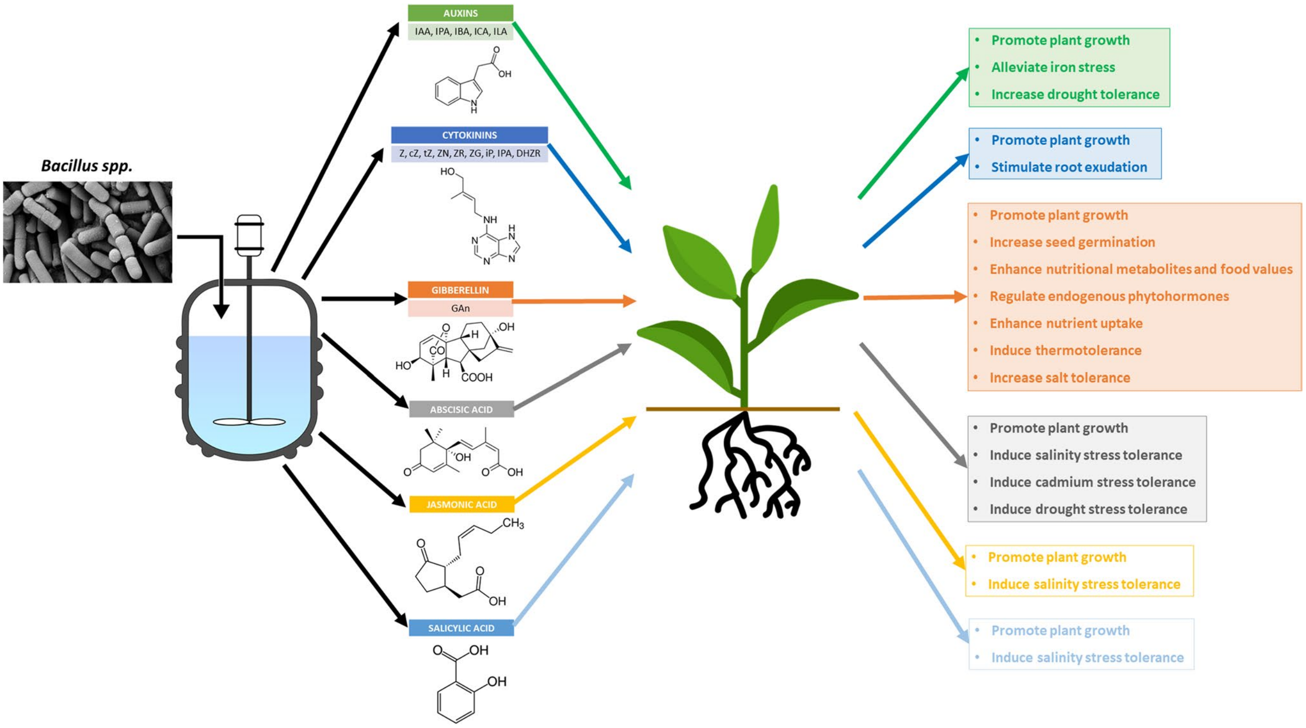

Fig. 1 Infographic showing the variety of phytohormones produced by *Bacillus* and their effect on the plant

salinity conditions in wheat by *B. subtilis* (Ji et al. 2020), and drought by *B. amyloliquefaciens*, *B. muralis*, *B. pumilus*, and *B. simplex*, also due to the production of other auxins such as indole carboxylic acid (ICA) and indole lactic acid (ILA) (Raheem et al. 2018).

Along with auxins, CKs are the main phytohormones involved in plant growth processes. To date, numerous *Bacillus* species capable of producing a wide range of different CKs in vitro have been described. For example, *B. cereus*, *B. megaterium* or *B. subtilis* are capable of producing the CKs zeatin (Z), zeatin riboside (ZR), zeatin glycoside (ZG), izopentyl adenine (iP), and izopentyl adenosine (iPA) in vitro (Karadeniz et al. 2006; Chobotarov et al. 2020). Another study demonstrated that the extracts obtained from cell cultures of *B. licheniformis* and *B. subtilis* are capable of increasing the weight and size of cucumber cotyledons separated from the seedlings, by inducing plant cell division due to the presence of Z and ZR (Hussain and Hasnain, 2009).

As with auxins, the root inoculation with CKs-producing *Bacillus* species increases plant growth, being more pronounced in shoots, as verified in lettuce plants as a consequence of the production of zeatin nucleotide (ZN), ZR, iP and iPA by *B. subtilis* (Arkhipova et al. 2005), or in maize plants by the production of trans-zeatin (tZ), cis-zeatin (cZ) and iP by *B. toyonensis* (Zerrouk et al. 2020). Consequently, the production of CKs by *Bacillus* species supposes an increase in the productivity of crops when they are used as biostimulants, as verified in wheat crops by *B. cereus*, *B. licheniformis*, *B. pumilus*, and *B. subtilis*, capable of producing cZ, tZ, ZR and dihydrozeatin riboside (DHZR) (Hussain and Hasnain, 2011). Furthermore, through the production of Z and ZR, *B. subtilis* is capable of stimulating root exudation of amino acids in wheat, being able to increase the diversity and quantity of beneficial rhizospheric microbiota (Kudoyarova et al. 2014).

Under abiotic stress conditions, CKs production has also been related to the ability of *Bacillus* species, such as *B. subtilis*, to increase plant tolerance to drought in lettuce (Arkhipova et al. 2007) and *Platycladus orientalis* (Liu et al. 2013), or against salinity in wheat, due to the production of Z, promoting plant growth (Ji et al. 2020). Furthermore, by producing CKs and increasing their content in potato stems plants, *B. subtilis* is able to repair shoots growth after Colorado potato beetle damage (Sorokan et al. 2021).

GAs are phytohormones mainly involved in different processes of plant development, although they can also actively regulate other physiological processes (Rizza and Jones, 2019). Various *Bacillus* species have been described has having the ability to produce a wide range of different GAs in vitro, such as GA_3 by *B. cereus* or *B. megaterium* (Karadeniz et al. 2006; Pandya and Desai, 2013), or GA_4, GA_5, GA_8, GA_9, GA_{12}, GA_{19}, GA_{20}, GA_{24}, GA_{36} and GA_{53} by *B. amyloliquefaciens* (Shahzad et al. 2019).

Bacillus species capable of producing GAs promote plant growth mainly by accelerating seed germination (Lee et al. 2012) and increasing stem elongation, as observed in *Alnus glutinosa* through the action of GA_1, GA_3, GA_4, and GA_{20} produced by *B. pumilus* and *B. licheniformis* (Gutiérrez-Mañero et al. 2001). This promotion of plant growth is a direct consequence of GAs' production by *Bacillus*, as reported in red pepper (Joo et al. 2004), radish (Malfanova et al. 2011; Kim et al. 2017), banana (Yuan et al. 2013), strawberry (Vicente-Hernández et al. 2019), tomato, *B. juncea* (Kim et al. 2017) or Chinese cabbage (Wang et al. 2020a), but also by indirect action of these phytohormones in the host plant, increasing the nutrient uptake (Kang et al. 2019a) and increasing the tissue-plant content of phytohormones such as GAs, SA, JA or ABA (Joo et al. 2005; Shahzad et al. 2016). Furthermore, the production of GAs by *Bacillus* species has been related to an increase nutritional metabolites in plant tissues, such as different amino acids, macro and micronutrients, gamma-aminobutyric acid, fructose or carotenoids, increasing the quality of crops, such as lettuce (Radhakrishnan and Lee, 2016).

As far as abiotic stresses are concerned, the production of GA_3 by *B. subtilis* has been related to its ability to increase the tolerance of wheat under salinity (Ji et al. 2020). Moreover, the production of GA_1, GA_3, GA_5, GA_8, GA_{19}, GA_{24}, and GA_{53} by *B. tequilensis* is involved in the induction of thermotolerance in soybean plants due to an increase of endogenous JA and SA contents of the phyllosphere and a downregulation of production of stress-responsive ABA (Kang et al. 2019b).

Stress-related phytohormones

Plants respond to stress situations by modulating their physiological responses, where phytohormones play a key role (Singh et al. 2017). The main phytohormone related to abiotic stresses tolerance is ABA, having reported so far numerous *Bacillus* species with the ability to produce the phytohormone in vitro, such as *B. amyloliquefaciens* (Shahzad et al. 2019), *B cereus*, *B. megaterium* (Karadeniz et al. 2006) or *B. subtilis* (Chobotarov et al. 2020). As a consequence of ABA production, significant benefits have been reported in host plants inoculated with these bacteria. *B. subtilis* can promote soybean root growth (Araujo et al. 2005), in addition to the aerial part in wheat, both in non-stress situations and under saline stress (Ji et al. 2020). Additionally, due to the production of ABA, *B. amyloliquefaciens* can increase tolerance to salinity in rice, although the mechanism involved is still unknown (Shahzad et al. 2017); a similar result was observed in soybean, in this case mediated by increased GA_4 biosynthesis (Kim et al. 2017). Under drought, as a consequence of ABA production by *B. marisflavi* when inoculated in barley and *Brassica juncea*, an increase in plant tolerance occurred due to an induction in stomatal closure and GA_3 induced α-amylase activity in germinating seeds (Gowtham et al. 2021). The same strategy has been reported in *Xanthium italicum* by *B. aryabhattai*, a plant that can be used as a pioneer plant in barren lands (Lee et al. 2012). Regarding the presence of heavy metals, *B. subtilis* has been reported to increase the tolerance of *Brassica chinensis* to cadmium, increasing the production of plant biomass by more than 200%. This is a consequence of the action of ABA produced by the bacteria in the presence of cadmium, reducing the Cd-induced photosynthesis inhibition and the oxidative damage in plant tissues, by increasing plant levels of antioxidant-related compounds (Pan et al. 2019).

On the other hand, although SA and JA are phytohormones directly related to plant defence responses to biotic stresses, their role in tolerance responses to abiotic stresses is increasingly well known (Ahmad et al. 2019; Wang et al. 2020b). The production of these phytohormones has been reported in different *Bacillus* species described as endophytic bacteria (Forchetti et al. 2007; Shanmugam and Narayanasamy, 2009). Specifically, *B. pumilus* can promote the growth of sunflower seedlings under water stress through the production of SA (Forchetti et al. 2010). Due to the production of SA and JA, *B. subtilis* increases the growth of wheat under salinity conditions by inducing specific plant responses (Ji et al. 2020).

Conclusions

The current rates of population growth require the development of new strategies for sustainable agriculture, playing a fundamental role is the use of beneficial microorganisms, for partial and in some cases total replacement of some of the most contaminating chemical inputs. The main mechanism used by MPBs is based on phytohormone production that act directly by regulating plant physiological processes.

Besides the well-known role of biocontrollers of certain species of the bacterial genus *Bacillus*, many species of this genus and allied genera show great potential as MPBs, although their capacity as biostimulants has been less commercially exploited or representing a secondary benefit. However, the potential of *Bacillus* species for use as inoculants in agriculture with expected modes of action different from biocontrol is being increasingly studied. Indeed, the studies carried out with several *Bacillus* species have demonstrated that they act as plant growth promoters in the terms considered by Regulation EU 2019/1009, and that many of such modes of action are mediated by the outstanding production of phytohormones.

Another interesting use of phytohormone-producing *Bacillus* species is to produce phytohormones industrially, using bioreactors. The most reported phytohormones produced by *Bacillus* species belong to the type of growth and development phytohormones, but there is a gap that needs to be bridged regarding stress-related phytohormones. Furthermore, the ability to produce the phytohormones SA and JA by *Bacillus* species has not yet been related to their ability to activate the tolerance responses of plants under abiotic stresses, and thus, there is still a wide field of study in this regard. Moreover, it is worth highlighting the wide variability in the amount of phytohormone produced by each species, and even bacterial strain, both in vitro and in interactions with plant roots, representing a standardization difficulty and a need for more studies.

Author contribution J.P. conceptualized and designed the manuscript. J.P. performed the bibliographic search and analyzed the information. J.P. wrote the first version of the manuscript. F.G.-A. contributed to the manuscript correction and critical reading, as well as to the knowledge on the bacteria and industrial field. All authors have read and agreed to the published version of the manuscript.

Declarations

Ethics approval This article does not contain any studies with human participants or animals performed by any of the authors.

Conflict of interest The authors declare no competing interests.

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