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Microbial volatiles as plant growth inducers

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ABSTRACT

Agricultural practices require novel products that allow sustainable development and commercial production according to the needs of farmers and consumers. Therefore, in the last decade, eco-friendly alternatives have been studied, so volatile organic compounds (VOCs) emitted by microorganisms have emerged as a cheaper, effective, efficient, and an eco-friendly alternative. VOCs are lipophilic compounds derived from microbial metabolic pathways with low molecular weight ($< 300\ g\ mol^{-1}$), low boiling point, and high vapor pressure that allow them to act as signal molecules over short and long distances. Main case studies provide evidence that VOCs released from diverse microorganisms (i.e. *Bacillus*, *Pseudomonas*, *Arthrobacter*, *Fusarium,* and *Alternaria*) can stimulate growth on a specific "target" seedling, such as *Arabidopsis* and tobacco. Some identified compounds, such as 3-hydroxy-2-butanone (acetoin), 2,3-butanediol, 2-pentylfuran, or dimethylhexadecylmine have shown their ability to elicit growth at root or leaf level. Few studies indicate that VOCs act in the regulation at phytohormone, metabolic pathways and nutrition levels according to genetic, proteomic, and metabolic analyses; but action mechanisms associated with growth-inducing activity are poorly understood. In this work, we reviewed case studies regarding identified compounds and action mechanisms for a better understanding of the information collected so far. Additionally, a brief description about the effects of VOCs for induction of resistance and tolerance in plants are presented, where compounds such as acetoin, dimethyl disulfide, 3-pentanol and 6-pentyl-α-pyrone have been reported. Furthermore, we summarized the knowledge to direct future studies that propose microbial VOCs as a technological innovation in agriculture and horticulture.

1. Introduction

Currently, the high demand for food and the need for increasing both performance and quality of agricultural crops have led to the applications of large amounts of chemical products (i.e. mineral fertilizer and commercial phytohormones), which have been used primarily to increase nutrient availability and stimulate the growth of species grown under field and greenhouse conditions, respectively (Zaman et al., 2015). Nevertheless, their applications have caused serious environmental problems, resulting in loss of soil biological activity, erosion derived from runoff, and leaching from spray components of these products (Savci, 2012). In addition, the synthetic compounds applied in greenhouse conditions have caused food contamination associated with toxic substance accumulation (e.g. nitrosamine compounds in lettuce) (Ward, 2009). Therefore, the search for sustainable alternatives has been carried out in order to reduce the input of chemical products in crops and to produce chemical-free food, so rhizosphere microorganisms have emerged as potential growth inducers.

Microorganisms, both bacteria and fungi, are found in high quantity and wide diversity in the rhizosphere zone, defined as "the narrow zone influenced by plant roots and characterized by their intense association with microbial activity" (Mendes et al., 2013; Dessaux et al., 2016; Van Dam and Bouwmeester, 2016). These microorganisms utilize root exudates, which contain ions, oxygen, water, enzymes, mucilage, and primary and secondary metabolites, representing between 20–40% of fixed carbon located in the underground root system (Philippot et al., 2013; Venturi and Keel, 2016). The plant exudates can determine or modify the microbial community along the root system (Badri et al., 2009). Meanwhile, microorganisms secrete diverse non volatile metabolites with beneficial effects to induce plant growth through direct and indirect pathways, which constitutes a traditional mechanisms studied to date (Dotaniya and Meena, 2015). Several studies conducted in the last decades indicate that direct pathways involve the release of phytohormones (i.e auxin, ethylene, and cytokinins) and organic substances (i.e organic acids) that contribute to growth stimulation and nutrient availability, respectively. Indirect pathways comprise

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substances that prevent pathogens attack through the production of hydrolytic enzymes, antibiotics, siderophores, and hydrogen cyanide (Goswami et al., 2016; Vejan et al., 2016). However, a new mechanism mediated by volatile organic compounds (VOCs) was reported for the first time by Ryu et al. (2003), who showed that volatiles released by *Bacillus subtilis* GB03 induced growth on *Arabidopsis thaliana*, being the first evidence that volatile organic compounds can modulate growth, stress, nutrition, and health processes in plants. To date, studies have achieved considerable progress in elucidating the mode of action of this type of compounds; however, it is still poorly understood.

Up to the present, the most studies have been conducted under controlled laboratory conditions using two compartment Petri dishes hermetically sealed with parafilm, which only allows air contact between the microorganism and the tested plant. These experiments have allowed to determine: the exposure time, microorganisms species, plant target, culture medium, amount or concentration of inoculums for the emission of volatiles with growth activity and to identify some bioactive compounds. The experiments have revealed the important role of VOCs as signal molecules in the modulation of physiological processes in the plant, constituting to an important area of unexplored research products (Piechulla and Degenhardt, 2014; Kanchiswamy et al., 2015a).

In summary, the effect of microbial volatiles on the induction of plant growth comprises an interesting field of investigation, so far studied mainly in *A. thaliana*. Studies at cellular, molecular, and metabolic levels have been able to clarify the effect of VOCs in this plant, but further studies are needed to elucidate the mode of action from perception to its concrete action to induce growth. In addition, it is necessary to investigate the effect of VOCs on vegetable, fruit, and forage crops to prospect their application as a sustainable bioproduct and a strategy to reduce the use of chemical products. Therefore, this review focuses on collecting information published since 2003 to date with the purpose of describing (1) the plant – microorganism interactions, (2) the effect of the culture conditions of the microorganism for the emission of volatiles inducing the growth, (3) the chemical nature of the identified VOCs, (4) the mechanisms of action, and (5) the VOCs effects on resistance and tolerance described to date.

2. Microbial VOCs: concept and chemical properties

Microbial VOCs are signal molecules with low molecular weight ($< 300\ g\ mol^{-1}$), low boiling point, high vapor pressure (0.01 kPa at 20 °C) and lipophilic nature that acts as ideal infochemicals for modulating physiological processes and traveling through the air, soil, and water (Kanchiswamy et al., 2015a,b). VOCs released from a determinate microorganism have a specific profile that includes compounds derived from different metabolic pathways depending on the living environment. Some compounds belong to alkanes, alkenes, alcohols, esters, ketones, terpenoids, and sulfur families (Schulz and Dickschat, 2007; Korpi et al., 2009; Audrain et al., 2015). VOCs are produced by microorganisms in a given range of scales, and they play a key role as signaling molecules that can act as a wide range of stimuli giving rise to the activation of a series of signals, which regulate physiological processes involved in plant health (Bailly and Weisskopf, 2012; Bitas et al., 2013; Kai et al., 2016). In the next section, case studies that provide relevant information regarding the role of VOCs as growth inducers are described.

3. Plant growth elicited by microbial VOCs: case studies

Several studies on the inducer effects of bioactive VOCs on plant seedlings have been carried out since 2003 to date (Table 1). The first study was performed by Ryu et al. (2003), who showed that volatiles released by *B. subtilis* GB03 elicited a ~5-fold increase of total leaf area of *A. thaliana* after 10 days of exposition. Subsequently, Banchio et al. (2009) demonstrated that the same bacterial species increased growth on shoot-root biomass of *Ocimum basilicum*, which increased 2-fold respect to control while leaf surface was increased ~2.5-fold. Furthermore, Xie et al. (2009) showed that *A. thaliana* seedlings exposed to volatiles released by GB03 exhibited 58 and 71% increases in fresh and dry weight after 2 weeks of exposition. The same interaction was tested by Zhang et al. (2009), who concluded that chlorophyll concentration in *A. thaliana* had an 84% increase. Afterward, Kwon et al. (2010) demonstrated that GB03 elicited significantly the increase of root and shoot fresh weight on *A. thaliana*, after 6 days of inoculation.

Additionally, others *Bacillus* strains have been tested as growth inducers through the emission of volatiles. Zou et al. (2010) showed that volatiles emitted by *B. megaterium* XTBG-34 exhibited a 1.7-fold increase in fresh weight of *A. thaliana* on day 7. Moreover, the effect of VOCs on root system was demonstrated by Gutiérrez-Luna et al. (2010), who concluded that volatile emitted by *Bacillus* species modified root architecture, eliciting the increase of total fresh weight, primary root length, lateral root number, and lateral root length on *A. thaliana*; and they also evidenced a strong association between fresh weight and lateral root length on day 10 ($r^2 = 0.82$). Subsequently, Santoro et al. (2011) proved that volatiles emitted by *B. subtilis* caused the increase of root dry weight (3.5-fold) and shoot fresh weight (2-fold) on *Mentha piperita*. Afterward, Meldau et al. (2013) reported that *Nicottiana atenuata* exposed to volatiles released from *Bacillus* sp. B55 exhibited 5-fold increase in leaf surface and, true leaves were enhanced in ~200%. In addition, the exposition to B55 increased lateral root for cm^{-1} over 400% compared with control. Furthermore, Ann et al. (2013) indicated that volatiles emitted by *B. vallismortis* EXTN-1 induced the increase ~9-fold in fresh weight of tobacco. Recently, Hao et al. (2016) reported that volatiles released from *B. amyloliquefaciens* FZB42 induced the increase of dry and fresh weight on *A. thaliana*, and a study conducted by Asari et al. (2016) revealed that seedlings of *A. thaliana* exhibited 2-fold increase in fresh and dry weight after 18 days of exposition to volatiles emitted from *B. amyloliquefaciens*.

Other bacterial species that belong to Gram-positive species have been reported for its ability to release volatile organic compounds with growth-inducing activity. A study carried out by Velázquez-Becerra et al. (2011) concluded that *Arthrobacter agilis* UMCV2 had the ability to emit VOCs inducing growth in *Medicago sativa*, enhancing plant fresh weight (~40 mg versus ~60 mg), stem length (~3.0 cm respect to ~1.7 cm), and lateral root density (~2.5 versus ~1.7). Subsequently, Orozco-Mosqueda et al. (2013) demonstrated that seedlings of *Medicago truncatula* exposed to volatiles released from *A. agilis* UMCV2 for 5 days increased shoot fresh weight, root fresh weight, and chlorophyll concentrations in 40%, 35%, and 35%, respectively. Afterward, a study conducted by Castulo-Rubio et al. (2015) showed that the exposition to VOCs of *A. agilis* UMCV2 had a growth-inducing effect on *Sorghum bicolor*, increasing shoot fresh weight in 66% aprox. Besides, Lee et al. (2012) reported that *Paenibacillus polymyxa* E681 emitted a volatile mixture that elicited the increase of surface leaf area foliar (1.6-fold) and fresh weight enhances 2-fold.

Moreover, Gram-negative species have been reported to emit volatile compounds with growth-promoting activity. A study performed by Blom et al. (2011) reported that bacterial species belonging to *Burkholderia*, *Pandoraea*, *Serratia*, and *Chromobacterium* genera increased biomass on *A. thaliana* between ~125–620%. Subsequently, Groenhagen et al. (2013) concluded that exposition of *A. thaliana* to volatiles released from *Burkholderia ambifaria* LMG19182 increased the number of lateral root number around 100% as well as the shoot biomass in 160%. Furthermore, Bailly et al. (2014) indicated that *A. thaliana* exhibited 3-fold increase in plant biomass and number of lateral root after exposition to volatiles released from *Escherichia coli*. Moreover, Bhattacharyya et al. (2015) demonstrated that *A. thaliana* exposed during 14 days to volatiles from *Proteus vulgaris* JBLS202 exhibited a 75–80% increase in fresh weight and induced an increase in primary root length and shoot length by 33.3–37.1% and 24.4–26.7%, respectively. In addition, Park et al. (2015) reported that tobacco seedlings had 8.8 and 9.5-fold increase approximately in fresh weight

Table 1
Study cases of growth induction via volatile organic compounds on different plant-microorganisms interactions.

Microorganism	Genus/Strain	Plant	Culture medium	Exposition (days)	Growth parameter	Reference
Bacteria	*B. subtilis* GB03	*A. thaliana*	MSA	10	Surface leaf area	Ryu et al. (2003)
	B. subtilis GB03	*A. thaliana*	TSA	21	Fresh weight Dry weight	Xie et al. (2009)
	B. subtilis GB03	*O. basilicum*	MSA	14	Leaf area Shoot fresh weight Root fresh weight	Banchio et al. (2009)
	B. subtilis GB03	*A. thaliana*	MSA	14	Chlorophyll content	Zhang et al. (2009)
	B. megaterium XTBG-34	*A. thaliana*	TSA	7	Fresh weight	Zou et al. (2010)
	Bacillus strains	*A. thaliana*	MSA	10	Total fresh weight Primary root length Lateral root number Lateral root length	Gutiérrez-Luna et al. (2010)
	B. pyrrocinia Bcc171 *C. violaceum CV0*	*A. thaliana*	Angle-A MRVPA LBA MSA	14–21	Plant fresh weight	Blom et al. (2011)
	P. fluorecens *B. subtilis* *A. brasilense*	*M. piperita*	MSA	30	Shoot fresh weight Root dry weight	Santoro et al. (2011)
	P. polymyxa *B. subtilis GB03*	*A. thaliana*	MSA	14	Leaf surface area Foliar fresh weight	Lee et al. (2012)
	B. ambifaria	*A. thaliana*	LBA	21	Lateral root number Shoot biomass	Groenhagen et al. (2013)
	Bacillus sp. B55	*N. attenuata*	YPDA	12	Leaf surface True leaf Lateral root cm^{-1} Root length	Meldau et al. (2013)
	B. vallismortis EXT-1	Tobacco	TSA PDA KBA LBA NA WA	7	Fresh weight	Ann et al. (2013)
	A. agilis UMCV2	*M. truncatula*	NA	5	Shoot length Root length Shoot fresh weight Root fresh weight Stem chlorophyll	Orozco-Mosqueda et al. (2013)
	E. coli	*A. thaliana*	MSA	14 and 21	Biomass Secondary roots	Bailly et al. (2014)
	A. agilis UMCV2	*S. bicolor*	NA	2	Shoot fresh weight Root fresh weight	Castulo-Rubio et al. (2015)
	A. agilis UMCV2	*M. sativa*	NA	6	Plant fresh weight Stem length Lateral root density	Velázquez-Becerra et al. (2011)
	P. vulgaris	*A. thaliana*	LBA	14	Fresh weight Root length Shoot length Number of lateral root	Bhattacharyya et al. (2015)
	P. fluorescens SS101	Tobacco	King B	21	Fresh weght Dry weight	Park et al. (2015)
	P. simiae AU	*G. max*	King B	10	Shoot length Root length Fresh weight Number of lateral root Leaf surface area	Vaishnav et al. (2015)
	B. amyloliquefaciens strains	*A. thaliana*	TSA LBA M9A	18	Dry weight Fresh weight	Asari et al. (2016)
	B. amyloliquefaciens FZB42	*A. thaliana*	MSA	16 and 23	Fresh weight Dry weight	Hao et al. (2016)
Fungi	*F. oxysporum* and bacterial consortium	*L. sativa*	CMA	7 and 14	Root length Seedling fresh weight Shoot length Leaf chlorophyll content	Minerdi et al. (2011)
	C. cladosporioides	Tobacco	PDA	30	Fresh weight	Paul and Park (2013)
	Trichoderma	*A. thaliana*	MEA	30	Total biomass Chlorophyll concentration	Hung et al. (2013)
	L. bicolor	*A. thaliana*	PM P20 A	10 days	Lateral root development	Ditengou et al. (2015)
	F. oxysporum strains	*A. thaliana* *Tobacco*	PDA	14 days	Shoot fresh weight Total leaf area Chlorophyll content Root length	Bitas et al. (2015)

(*continued on next page*)

Table 1 (*continued*)

Microorganism	Genus/Strain	Plant	Culture medium	Exposition (days)	Growth parameter	Reference
	A. alternata	*A. thaliana* *Z. mays* *C. annuum*	M9A	12–50 days	Root fresh weight Lateral root density Plant height Total carotenoids Photosynthetic parameters	Sánchez-López et al. (2016)

Abbreviations: MSA: Murashige and Skoog medium agar, Angle-A: Angle agar, MRVPA: Methyl Red Voges Proskauer agar, LBA: Luria Bertani agar, NA: Nutrient agar, PM20 A: Pachlewski medium P20 A, TSA: Tryptic Soy agar, PDA: Potato Dextrose agar, KBA: King's B agar, WA: Water agar, YPDA: Yeast Peptone Dextrose agar. MEA: Malt Extract agar. CMA: Complete Medium agar. M9A: Minimal Medium agar.

and dry weight, respectively, after exposition to volatiles released from *Pseudomonas fluorecens* SS101 during 4 weeks; and Vaishnav et al. (2015) indicated that *Glycine max*. L Merril exposed to volatiles from *Pseudomonas simiae* strain AU exhibited a 58, 86, and 58% of increase in shoot length, root length, and fresh weight, respectively.

Additionally, some fungi species have been reported for emitting bioactive compounds that induce plant growth. Minerdi et al. (2011) indicated that volatiles released from *Fusarium oxysporum* MSA35 induced growth of root length (95.6%), shoot length (75%), fresh weight (85.8%), chlorophyll content (68%), and the number of lateral root (3-fold). Subsequently, Paul and Park (2013) demonstrated that tobacco fresh weight was increased in ~ 10-fold after 4 weeks exposed to VOCs released by *Cladosporum cladospoiodes* CL-1. Besides, Hung et al. (2013) showed that *A. thaliana* exhibited 45% and 58% increase in total biomass and chlorophyll concentration after exposition to VOCs emitted by *Trichoderma viride*. In addition, Ditengou et al. (2015) reported that *A. thaliana* seedlings exposed to volatiles released from *Laccaria bicolor* exhibited 27% increase in lateral root density. Subsequently, Bitas et al. (2015) studied the effects of volatile compounds on 46 *Fusarium oxysporum* strains, but only the isolates NRRL 26379 and NRRL 38335 induced increase in leaf surface area, chlorophyll content, root mass, and root length by 2.7–4.0, 3, 4.8–4.4, 3.6–5.2 fold, respectively. Recently, Sánchez-López et al. (2016) showed that volatiles released from *Alternaria alternata* induced the increase of fresh weight on maize and pepper with a greater percentage (nearly 2-fold). The studies presented above indicated that mediated growth-inducing activity is elicited by diverse microbial species, including fungal and bacterial species. According to the description presented in Table 1, 55% of studies have focused on *A. thaliana* as model plant; whereas 45% of case studies include other species, such as *S. bicolor*, *M. sativa*, *M. piperita*, *O. basilicum*, *L. sativa*, *Z. mays*, *C. annuum*, *M. truncatula*, *N. attenuata*, and *G. max*. The main factors that determine the emission of a specific microbial VOC profile under controlled and field conditions are described in the next section.

4. Conditions involved in the emission of microbial VOCs

The emission of VOCs with specific profile depends strongly on the environment in which the microorganism grows. The experiments performed under controlled conditions have shown that a single bacterial strain may induce or inhibit growth depending on the medium it grows (Asari et al., 2016; Blom et al., 2011; Velázquez-Becerra et al., 2011). Some culture media used for microorganisms growth are MRVPA, MSA, and NA (Bailly and Weisskopf, 2012). MRVPA medium has been used for enhancing the production of 3-hydroxy-2-butanone and 2,3-butanediol, MSA has been used in several previous reports as a medium for bacteria growth and NA has been used in studies that involve *M. sativa* growth (Ryu et al., 2003; Velázquez-Becerra et al., 2011). These culture media are composed differently: MRVPA contains glucose as carbon source and pH 6.9 ± 0.2 and NA is composed of beef extract and peptone with pH 6.8 ± 0.2, while MSA contains mineral nutrients with sucrose as C source and lower pH (pH 5.7). Therefore, different culture medium composition can directly affect the production of volatile organic compounds released by metabolic pathways of microorganisms, so their bioactivity might depend strongly on these factors (Blom et al., 2011). Additionally, a study carried out by Fincheira et al. (2016) showed that some bacterial genus can have a stronger effect to elicit plant growth, that is *Bacillus* species emitted volatile compounds with greater effects to induce growth on *L. sativa* seedlings in comparison with Gram negative genera, such as *Pseudomonas* and *Serratia* species, independently of the used culture media (MRVPA, MSA and NA).

Other parameters that determine the modulator effect on seedlings is the amount or concentration of applied inoculums. Velázquez-Becerra et al. (2011) reported a dose-dependence response of *M. sativa* exposed to VOCs released by *A. agilis* UMCV2, reaching the best increase on root length, root density, stem length, and fresh weight with 50 µl of inoculum grown in NA, compared with doses from 100 to 500 µl. Afterward, Blom et al. (2011) showed that *Burkholderia pyrrocinia* Bcc171 increased dry weight on *A. thaliana* when grown in LBA and MRVPA, reaching the best yield with 10 µl of applied inoculums. Recently, Asari et al. (2016) demonstrated that VOCs released by *B. amyloliquefaciens* UCMB5113 induced a significant increase on dry weight of *A. thaliana* (phyllosphere) when quantities from 20 to 100 µl of inoculum were applied on LBA, minimal medium (M9) or Tryptic Soy agar.

Under field conditions, the profile of VOCs emitted by microorganisms depends on soil properties, microbial community, plant exudates and internal factors that influence the metabolism of each microbial strain (Kai et al., 2016). Soil physicochemical properties such as pH, oxygen, T°, water, inorganic particle size, mineral aggregates, and size and shape of pores determine a microclimate for microbial growth influencing their lifecycle. Additionally, the relation of specific strain with microbial community through intra and inter specific relation can modulate the production and distribution of volatiles, altering the profile in response to external stimuli (Kai et al., 2016). With respect to root exudates, they play a nutritional role for microorganisms present in the rhizosphere (biochemical cycles), whereby plant species, age, and environmental conditions produce different rhizodeposition influencing soil microbial diversity (Bulgarelli et al., 2013). Other important factors are microbial growth rate, the state of development of metabolism, the biofilm formation, and spore generation of a specific strain that can modify the emission and concentration of VOCs (Chen et al., 2015). The VOCs can be adsorbed, desorbed, or reacted with clay surfaces as well as diffuse through soil, water, or air in the rhizosphere (Ramírez et al., 2009; Insam and Seewald, 2010). The bioactive compounds with proven growth inducing activity are described in the next section.

5. Identified bioactive microbial volatiles as growth inducers

Over the last years, diverse chemical compounds emitted by metabolism of bacteria and fungi have been identified by gas chromatography coupled to mass spectrometry (Korpi et al., 2009). These compounds are produced from primary (i.e. derived from aminoacids and fatty acids) and secondary (i.e. derived of side products from primary

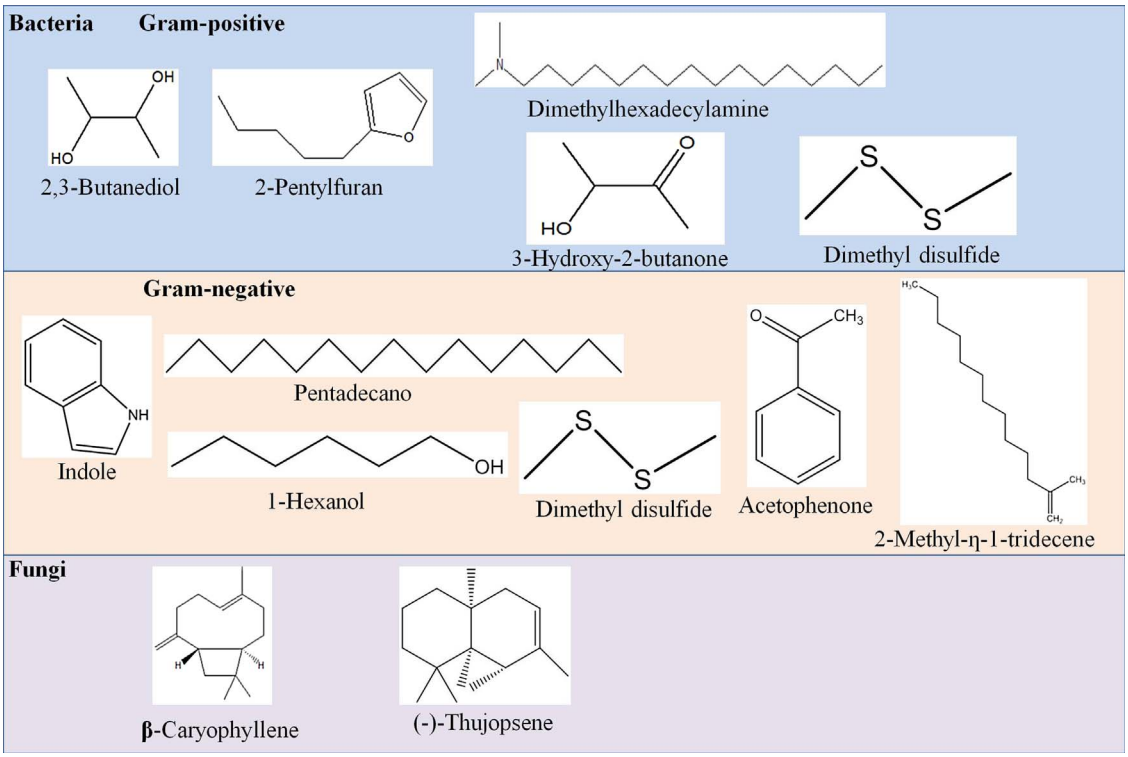

Fig. 1. Chemical structures of microbial VOCs reported for their ability to promote plant growth.

metabolism) metabolisms (Schulz and Dickschat, 2007). The bioactive VOCs identified as growth inducers belong to different chemical natures as alcohols, ketones, sulfur compounds, furans and terpenes, which act at low concentrations (Fig. 1, Table 2). The first identified compound was reported by Ryu et al. (2003), who showed that 2,3-butanediol induced the increase of the surface leaf area in *A. thaliana* when it was applied between 1 and 100 µg. Subsequently, Zou et al. (2010) indicated that 2-pentylfuran elicited the increase of fresh weight in the same plant species at 0.5 µg/µl. Whereas, Velázquez-Becerra et al. (2011) reported that dimethylhexadecylamine (8–32 µM) induced the increase of fresh weight, stem length, root length and root density on *M. sativa.* In addition, β-caryophyllene at doses from 25 to 100 µM induced the enhancement of root length, shoot length, fresh weight, and chlorophyll on *L. sativa* seedlings (Minerdi et al., 2011). Afterwards, Meldau et al. (2013) showed that dimethyl disulfide can act as sulfur source contributing to nutrition on tobacco seedlings with an optime dose of 50 µM. Whereas, Groenhagen et al. (2013) indicated that dimethyl disulfide and acetophenone elicited the increase of biomass in *A. thaliana* at doses of 1 ng/µl and 1 µg/µl. Moreover, Ann et al. (2013) concluded that 3-hydroxy-2-butanone acts as an elicitor of increasing fresh weight at 1 and 10 ppm on tobacco. Subsequently, Bailly et al. (2014) and Bhattacharyya et al. (2015) reported that indole at low doses induced growth on *A. thaliana.*

More recently, studies performed in 2015 showed new compounds as growth inducers. A study carried out by Park et al. (2015) indicated that 13-tetradecadien-1-ol, 2-methyl-η-1-tridecene, and 2-butanone at 5 and 50 ng induced fresh weight on tobacco, and Ditengou et al. (2015) concluded that (−)-thujopsene induced lateral root formation at 100 ppb on *A. thaliana.* Table 2 shows the different solvents used to apply bioactive volatiles on bioassays, highlighting the use of distilled water (i.e 3-hydroxy-2-butanone, dimethyhexadecylamine, and indole) and dichlorometane (i.e 2,3-butanediol, acetophenone and 1-hexanol) in most experiments performed. In the next point, the action mechanisms associated with growth inducer effects of volatiles emitted by microorganisms with a specific plant "target" are discussed.

6. Action mechanisms associated with VOCs effects

Over the last years, some studies have reported physiological and cellular effects on plant seedlings in response to microbial volatile exposition. Studies have shown that VOCs can induce growth principally by four mechanisms: modulation of essential nutrients, hormonal balance, metabolism, and sugar concentrations. It highlights that changes related to genes associated with cellular structures, stress response, and proteins are heavily regulated according to Zhang et al. (2007).

Iron is an intensively studied essential micronutrient due to its importance in photosynthesis process (Kim and Guerinot, 2007; Waldvogel-Abramowski et al., 2015). Two strategies are used by plants to acquire iron from soil. The strategy I consists of proton exudation, reduction Fe^{+3} to Fe^{+2}, and importation of Fe^{+2}. These processes are associated with the following genes: *FIT1* (Fe-deficiency-induced-transcription), *FRO2* (Ferric reductase), and *IRT1* (Iron −regulated transporter 1), where *IRT1* and *FRO2* are regulated by *FIT1*, which codified a protein that regulates the response of plant to iron deficiency. The Strategy II is associated with phytosiderophores, where Fe can be directly transported into root without its reduction due to the presence of specific transporters in plants (Waldvogel-Abramowski et al., 2015). Regarding that matter, Zhang et al. (2009) reported that *B. subtilis* GB03 volatiles induced direct (emission of acid volatile) and indirect (induction of proton release) acidification of rhizosphere of *A. thaliana.* Furthermore, GB03 activated transcriptionally Fe uptake, where the expression of *IRT1* was up-regulated 10–20 fold 2–4 days post exposition. The transcript abundance of *FRO2* increases within 2 days, activating the acquisition of Fe by the strategy I. Based on the above mentioned, strategy is activated to increase Fe content after three days of volatile exposition. Parallel to the induction of expression of *FRO2* and *IRT1* the seedlings exhibited an increase in the accumulation of *FIT1* transcript after exposition to VOCs released by GB03. Therefore, GB03 increased photosynthesis through Fe assimilation, which is supported by the increase of photosynthetic capacity (F_V/F_m) and chlorophyll content. Subsequently, Orozco-Mosqueda et al. (2013) reported

Table 2
Bioactive microbial volatiles identified as growth inducers.

Compound	Solvent	Dose range tested	Optime dose	Seedling target	Parameter	Exposition (days)	Reference
2,3-Butanediol	Dichlorometane	1000 mg 10 mg 100 µg 1 µg 0.01 µg	100 µg 1 µg	*A. thaliana*	Surface leaf area	14	Ryu et al. (2003)
2-Pentylfuran	Dichloromethane or Alcohol	1 mg 20 µl^{-1} 100 µg 20 µl^{-1} 10 µg 20 µl^{-1} 1 µg 20 µl^{-1} 0.1 µg 20 µl^{-1}	10 µg 20 µl^{-1}	*A. thaliana*	Fresh weight	15	Zou et al. (2010)
Indole 1-Hexanol Pentadecano	Dichlorometane	1 ng 10 µl^{-1} 10 ng 10 µl^{-1} 100 ng 10 µl^{-1} 10 µg 10 µl^{-1} 1 mg 10 µl^{-1}	1 mg 10 µl^{-1} 10 µg 10 µl^{-1}	*A. thaliana*	Fresh weight	21	Blom et al. (2011)
β-Caryophyllene	Distilled water	25 µM 50 µM 100 µM	25 µM 50 µM 100 µM	*L. sativa*	Root length Shoot length Fresh weight Chlorophyll	7	Minerdi et al. (2011)
Dimethylhexadecylamine	Distilled water	4 µM 8 µM 16 µM 32 µM 64 µM	8 µM 32 µM	*M. sativa*	Fresh weight Stem length Root length Lateral root density	10	Velázquez-Becerra et al. (2011)
Dimethyl disulfide	Methanol	50 µM 1000 µM	50 µM	*A. thaliana*	Lateral root number	17	Meldau et al. (2013)
3-Hydroxy-2-butanone	Distilled water	0.001 ppm 0.01 ppm 0.1 ppm 1 ppm 10 ppm	1 ppm 10 ppm	Tobacco	Fresh weight	7	Ann et al. (2013)
Dimethyl disulfide Acetophenone	Dichlorometane	1 ng 1 µg 1 mg	1 µg µl^{-1} 1 ng µl^{-1} 1 ng µl^{-1}	*A. thaliana*	Biomass	21	Groenhagen et al. (2013)
Indole	Distillled water	10 nM 100 µM	10 nM	*A. thaliana*	Biomass Secondary roots	14 and 21	Bailly et al. (2014)
Indole	Dichlorometane	0.001 µg µl^{-1} 0.005 µg µl^{-1} 0.01 µg µl^{-1} 0.02 µg µl^{-1} 0.043 µg µl^{-1} 0.080 µg µl^{-1} 0.120 µg µl^{-1} 0.250 µg µl^{-1} 0.500 µg µl^{-1} 1 µg µl^{-1} 10 µg µl^{-1}	0.01 µg µl^{-1} 0.02 µg µl^{-1} 0.043 µg µl^{-1} 0.080 µg µl^{-1} 0.120 µg µl^{-1} 0.250 µg µl^{-1}	*A. thaliana*	Shoot length Primary root length Lateral root number Fresh weight	14	Bhattacharyya et al. (2015)
13-Tetradecadien-1-ol 2-Methyl-η-1-tridecene 2-Butanone	Metanol	5 ng 50 ng 500 ng	50 ng 5 ng	Tobacco	Fresh weight	30	Park et al. (2015)
(−)-Thujopsene	n-Pentadecane	1 p.p.b 10 p.p.b 100 p.p.b 1000 p.p.b	100 p.p.b	*A. thaliana*	Lateral root formation	10	Ditengou et al. (2015)

relevant evidence about Fe acquisition on *M. truncatula* after exposition to volatiles released from *A. agilis* UMCV2, which induced acidification of *M. truncatula* rhizosphere after 24–48 h of Fe stress. Moreover, seedlings exposed to dimethylhexadecylamine exhibited a similar acidification after 48 h. Ferric chelate reductase activity at root level was increased up to 120% after exposition to VOCs released by *A. agilis* under Fe deficiency (after 24 h of stress). In addition, VOCs of UMCV2 induced the increase of chlorophyll content. Recently, Castulo-Rubio et al. (2015) reported that seedlings of *S. bicolor* exposed to VOCs of UMCV2 induced the increase of chlorophyll concentration after deficiency and sufficiency of Fe. The study at molecular level indicated that a relative transcription level of *FRO1* increased after exposition to UMCV2 volatiles (specifically dimethylhexadecylamine) under sufficiency and deficiency of Fe. Furthermore, Wang et al. (2017) reported that *B. amyloliquefaciens* strain BF06 had the ability to emit VOCs with direct activity in some genes encoding for transporters of sulfate and increase Se accumulation, contributing with nutritional constituents (Fig. 2).

A phenomenon strongly associated with the nutritional status of iron is a photosynthesis process, which involves the conversion of light energy into chemical energy through the sugar production. High sugar level induces storage processes and gives feedback inhibition of photosynthesis, where hexokinases play a relevant role acting as glucose sensors. Zhang et al. (2008a) reported that volatiles released by GB03

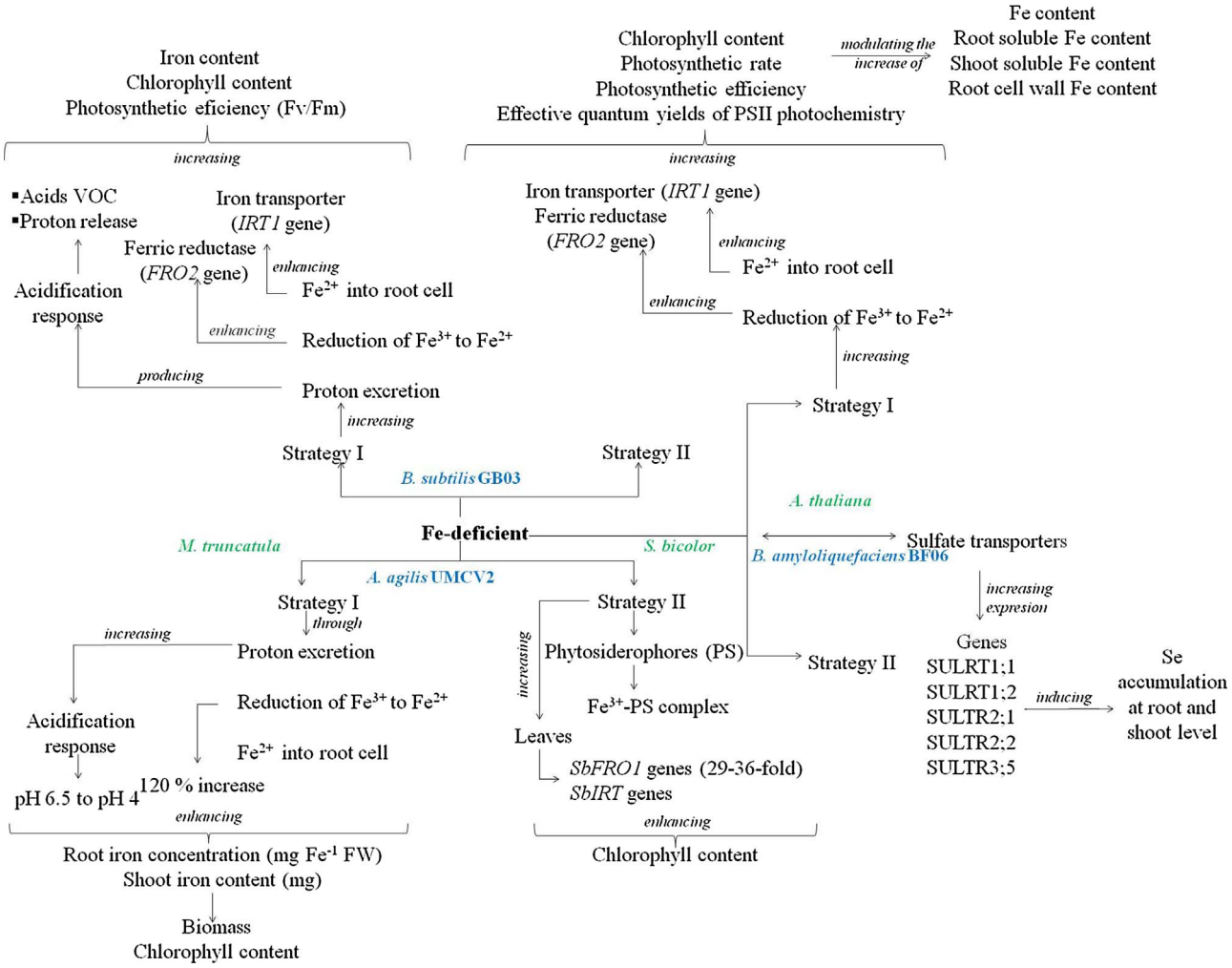

Fig. 2. The implications at physiological and productivity level of VOCs emitted by bacterial species on Fe acquisition. Abbreviations: Phytosiderophores = PS, FIT1 = Fe-deficiency-induced-transcription, FRO2 = Ferric reductase, IRT1 = Iron–regulated transporter 1, and SULRT = Sulfur transporter. Blue color = Bacterial species, Green color = Plant species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

increased photosynthetic activity and chlorophyll content (88%), observing greener plants due to the increase of chloroplast units and the induction of photosynthetic genes as chlorophyll a/b binding protein (CAB2) and Rubisco subunit binding protein. Therefore, photosynthetic activity of photosystem II (PSII) and the maximum and effective quantum yields of PSII (ϕ_{PSII}) were increased, so quantum yield of non-photochemical dissipation in PSII (ϕ_{NPQ}) was reduced. Besides, GB03 VOCs suppress plant sugar sensing as indicated chlorophyll accumulation and the coexistence of increased endogenous photosynthesis and sugar (hexokinase dependent pathway). Signal transduction sugar dependent hexokinase requires abscisic acid (ABA) signaling, but GB03 VOCs reduces its levels through the reduction of expression of genes related to ABA-synthesis and response genes to ABA at foliar level. Recently, Sánchez-López et al. (2016) indicated that VOCs released by *A. alternata* increased photosynthetic parameters in leaves, enhancing total carotenoids and chlorophyll, so net rate of CO_2 assimilation and rate of electron transport. Furthermore, this study indicated that VOCs elicited growth through cytokinin pathway, which is involved in photosynthesis, soluble sugars formation, aerial growth, floral bud appearance, starch accumulation and associated with reactive oxygen species (ROS) scavengers (Fig. 3). However, the induction of increase in fresh weight and starch was carried out only under diurnal conditions.

Some bacterial strains have shown important effects on modulating genetic and proteomic expression in seedlings exposed to VOCs (Fig. 4). The first evidence was reported by Zhang et al. (2007), who performed a transcriptomic analysis in *A. thaliana* seedlings exposed to GB03 VOCs during 48 and 72 h, revealing differential expression of genes associated with metabolism (e.g. asparagine synthetase, chalcone synthase, phospholipase and starch synthase), growth (e.g. nitrilase 1 and β-expansin,), stress (e.g HSP101 and universal stress protein) and cellular signaling (e.g protein kinase and transcription factors). It highlights that genes associated with auxin, including synthesis and responsive genes were up-regulated; whereas genes associated with auxin transport were down-regulated. Furthermore, genes associated with cell wall modification were regulated by GB03 VOCs, covering up regulation of expansins, which promotes cell wall expansion as well as down-regulated pectate lyases and pectinases for reducing cell wall rigidity (Fig. 5). Genes as *EXP5*, *NIT1*, and *NIT2* were strongly up-regulated after 72 h exposition at foliar level. In addition, Minerdi et al. (2011) showed that VOCs released by *F. oxysporum* and its bacterial consortium induced expansin A5 gene expression in lettuce seedlings.

Afterward, Kim et al. (2015) reported that volatiles released by *B. subtilis* strain JS had the ability to modulate gene profile expression in tobacco seedlings during metabolic and cellular processes. The up-regulated genes were chlorophyll a/b binding protein, cellulose synthase, acyl-ACP-thioesterease, succinyl-coA ligase alpha I unit, chloroplast sedoheptulose-1,7-biphosphate, sucrose transporter, MLO-like protein 1,cytosolic NADP-malic enzyme, and P-protein of glycine decarboxylase; while down-regulated genes were glucosyltransferase, nitrate reductase, methionine-R-sulfoxide reductase B4 protein,

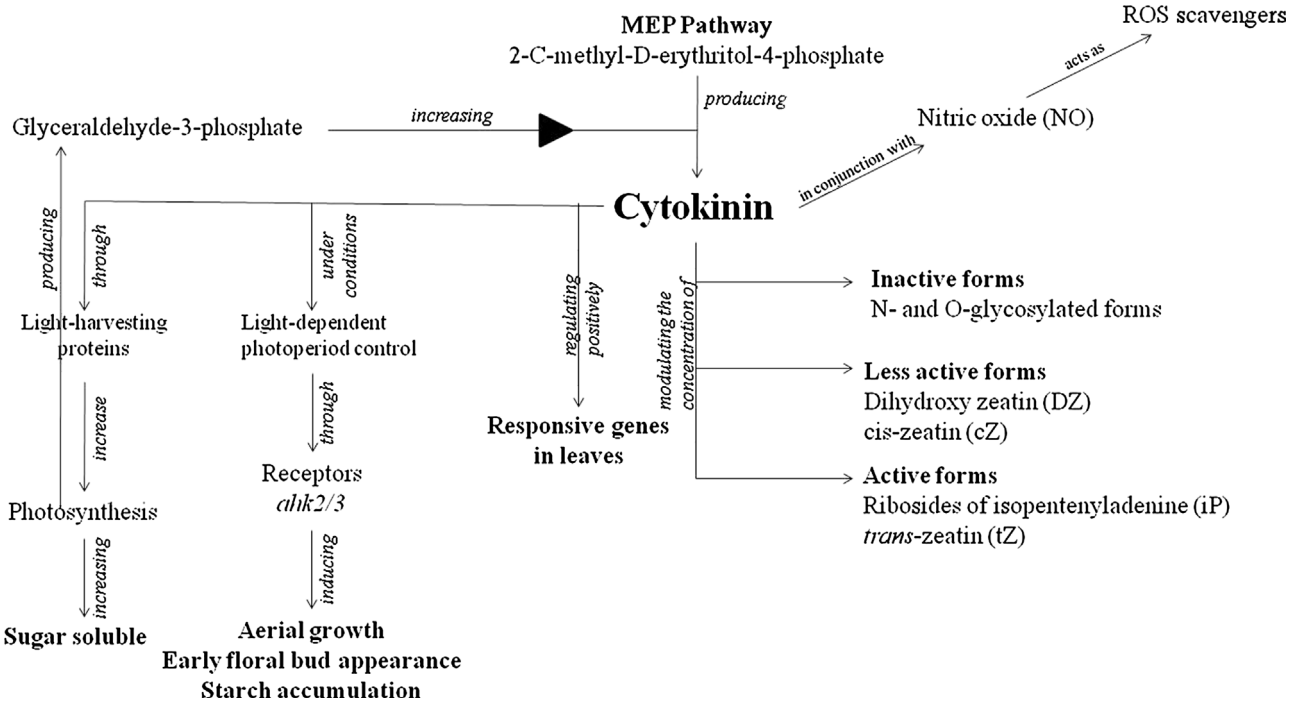

Fig. 3. The forms and physiological effects of cytokinin modulated by VOCs released by *A. alternata* on *A. thaliana* seedlings. Abbreviations: MEP = 2-C-methyl-D-erythritol-4-phosphate, NO = Nitric oxide, ROS = reactive oxygen species.

glutathione S-transferase, and carboxylase. Recently, Hao et al. (2016) indicated that *A. thaliana* exposed to volatiles emitted by *B. amyloliquefaciens* FZB42 induced differential expression in genes associated with plant hormones, cell wall modifications, and protection against stress situations depending on specific (root and leaves) tissue and growth stage (seedlings and mature). It is emphasized that the study conducted at proteomic level by Kwon et al. (2010) showed that GB03 volatiles modulated the expression of proteins related to cellular

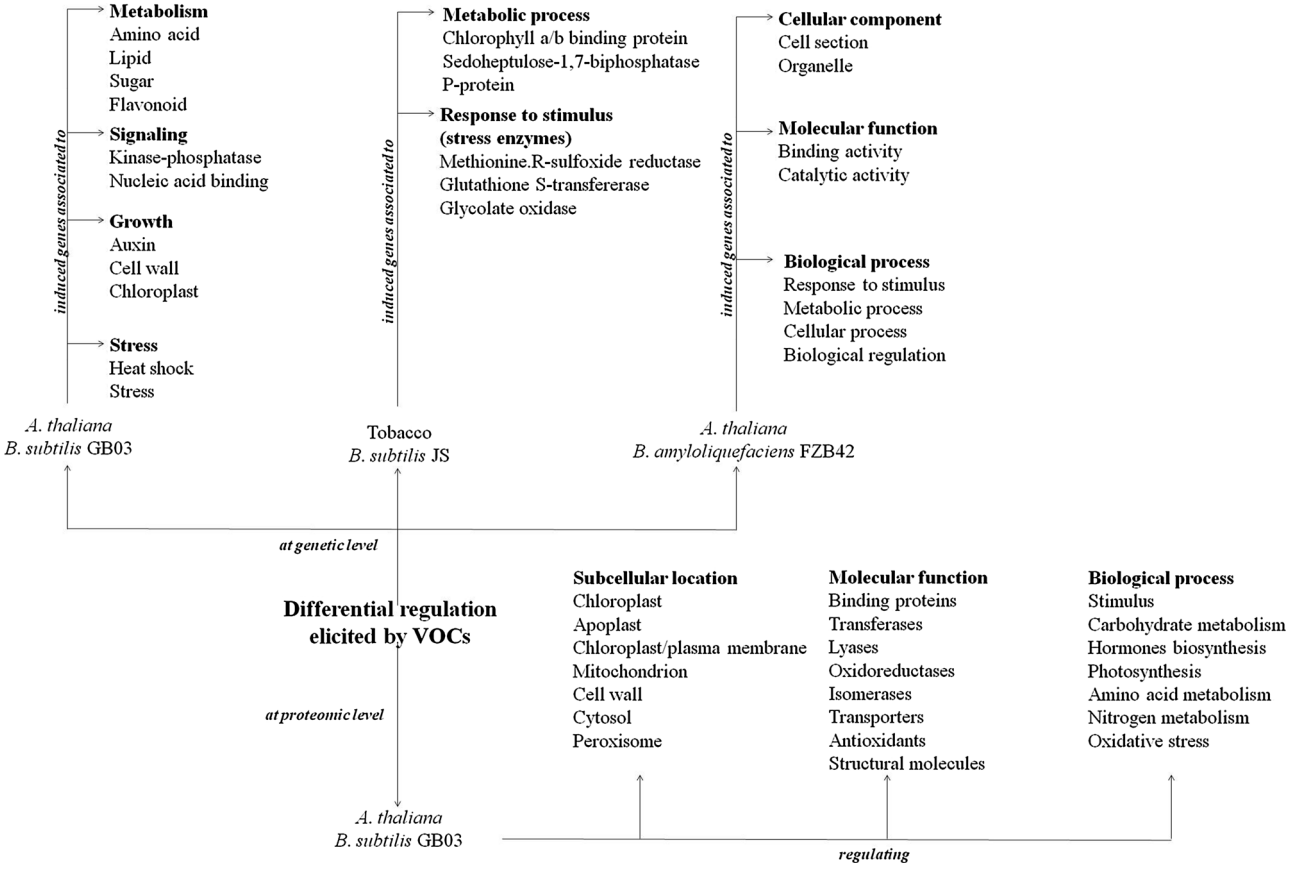

Fig. 4. The differential regulation of genes and proteins modulated by VOCs released from Bacillus species on seedlings.

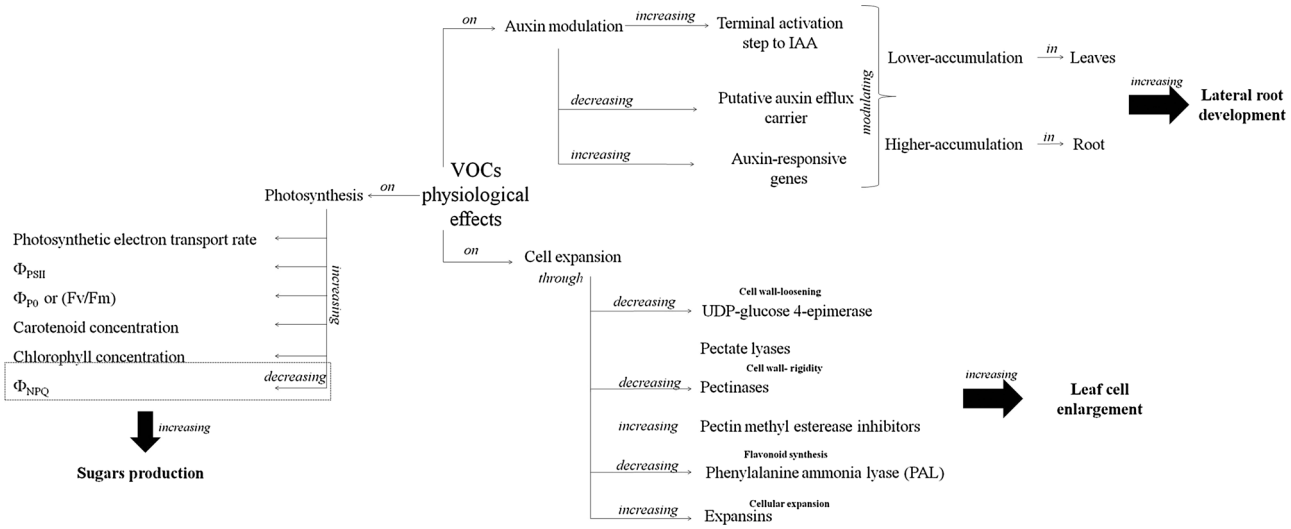

Fig. 5. The physiological effects on auxin modulation, cell expansion and photosynthesis derived from VOCs released by *B. subtilis* GB03.

location, molecular function, and biological processes, highlighting the proteins associated with response to stimulus.

Additionally, some studies have investigated the phytohormones signaling pathways implicated in growth promotion induced by VOCs, where different plant- microorganisms interactions have been reported (Fig. 6). A study conducted by Ryu et al. (2003) showed that *B. subtilis* GB03 increased surface leaf area and the activation of cytokinin signaling pathway. Subsequently, Bailly et al. (2014) reported that indole had a relevant role in modulating secondary root development in *A. thaliana* through auxin signaling. The bioassays showed that indole acts on zones of auxin activity and during its polar transport to induce growth response. The results indicated that indole accumulation

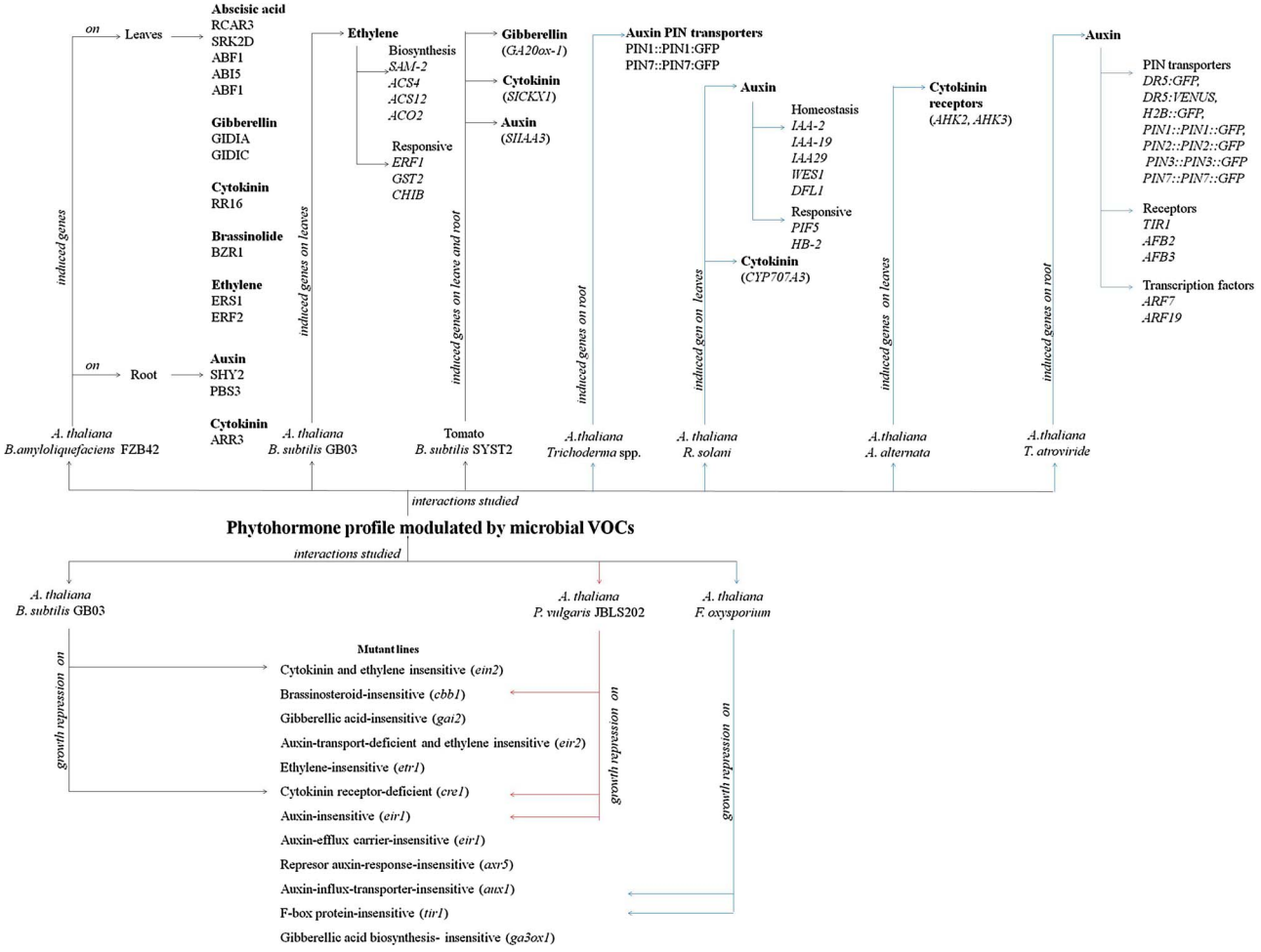

Fig. 6. The mutant lines of A. thaliana and target genes related to phytohormones studied in different microbial-plant interactions. Black line: Gram-positive bacteria, Red line: Gram negative bacteria, Blue line: Fungi. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

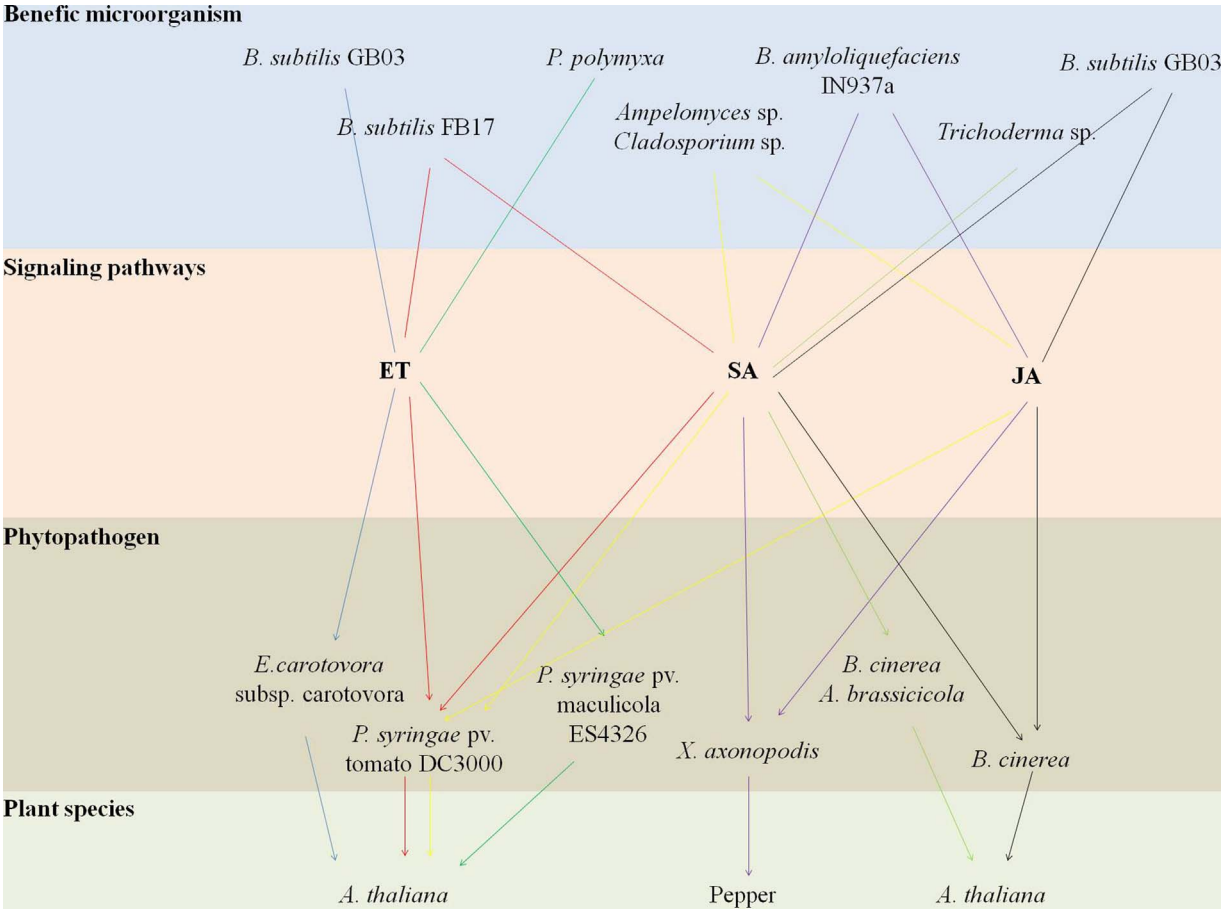

Fig. 7. Benefic microorganisms, signaling pathways and phytopathogens involved in the studies interactions about induced systemic resistance mediated by VOCs.

produced alterations in root physiology for increasing lateral root formation. In addition, this study pointed out that seedlings responded mostly to indole respect to synthetic auxin, suggesting that bioactive compound induces early development of lateral roots controlling the auxin physiology. Afterward, Bhattacharyya et al. (2015) demonstrated through *Arabidopsis* mutants with disruptions in hormone production and signaling of auxin (*eir1*), cytokinin (*cre1*), and brassinosteroid (*cbb1*) their importance for growth induction elicited by VOCs released by *P. vulgaris* JBLS202. Furthermore, bioassays performed at genetic level corroborated the results with seedling mutants, where *SAUR* (auxin response-gene), *AHK1* (induced in response to cytokinin), *CPDA* (associated with biosynthetic pathway of brassinosteroid), and *ERF* (representative of ethylene) were up regulated; while *GA3OX3* (catalyzes conversion of gibberellins precursor in their bioactive compounds) was down-regulated. Additionally, the presence of enzyme inhibitors as aminoethoxyvinylglycine (auxin) and propiconazole (brassinosteroid) supported the results mentioned above. In the same year, Bitas et al. (2015) reported that volatiles released by *F. oxysporum* induced growth on *A. thaliana* through auxin signaling and transport. In contrast, Ditengou et al. (2015) reported changes of sesquiterpenes profile at radical level in *A. thaliana* eliciting the increase on root hair length through ROS-dependent mechanism, associated with the generation of superoxide anion radicals (O_2^-) in roots, independently from auxin signaling. In the next point we summarize different case studies that involve VOCs as resistant and tolerance elicitor have been described

7. Resistance and tolerance mediated by microbial volatiles

The plants are constantly exposed to biotic environmental stresses derived from the attack of phytopathogens, so they have different response survival systems (Pieterse et al., 2014). To date, diverse studies have reported that plant immunity is produced by three main signaling pathways to elicit plant cell defense response, which are: salycilic acid (SA), jasmonic acid (JA) and ethylene (ET) (Farag et al., 2013). Specifically, the induced systemic resistance (ISR) can be elicited by soil microorganisms through the release bioactive compounds that protect aerial plant against diverse phytopathogens, inducing immune responses (Pieterse et al., 2014). In the lasts years, diverse reports have indicated that VOCs released by some microorganisms have the ability to induce ISR through the activation of at least one of the signaling pathways. The first evidence was reported by Ryu et al. (2004), which indicated that VOCs released by *B. subtilis* GB03 and *B. amyloliquefaciens* IN937a reduced the disease severity produced by *Erwinia carotovora* subsp. carotovora through ET signaling-pathway in *A. thaliana*. Later, Rudrappa et al. (2010) reported that *B. subtilis* FB17 emitted VOCs that reduce disease severity in the same plant species against *Pseudomonas syringae* pv. tomato DC3000 through the emission of 3-hydroxy-2-butanone, which requires SA and ET pathways. After, Huang et al. (2011) reported that dimethyl-disulfide emitted by *B. cereus* C1L protects tobacco and corn plants against necrotrophic pathogens as *Botrytis cinerea* and *Cochliobolus heterostrophus* under greenhouse conditions. Afterwards, Lee et al. (2012) indicated that tridecane (C13) emitted by *Paenibacillus polymyxa* induced resistance in *A. thaliana* against *P. syringae* pv. maculicola ES4326 by ET signaling-pathway.

In the last years, some studies have reported different interactions involved in the elicitation of ISR. The study performed by Naznin et al. (2014) showed that m-cresol and methyl benzoate released by *Ampelomyces* sp. and *Cladosporium* sp. reduced the disease severity produced by *P. syringae* pv. tomato DC3000 in *A. thaliana* activating the SA and

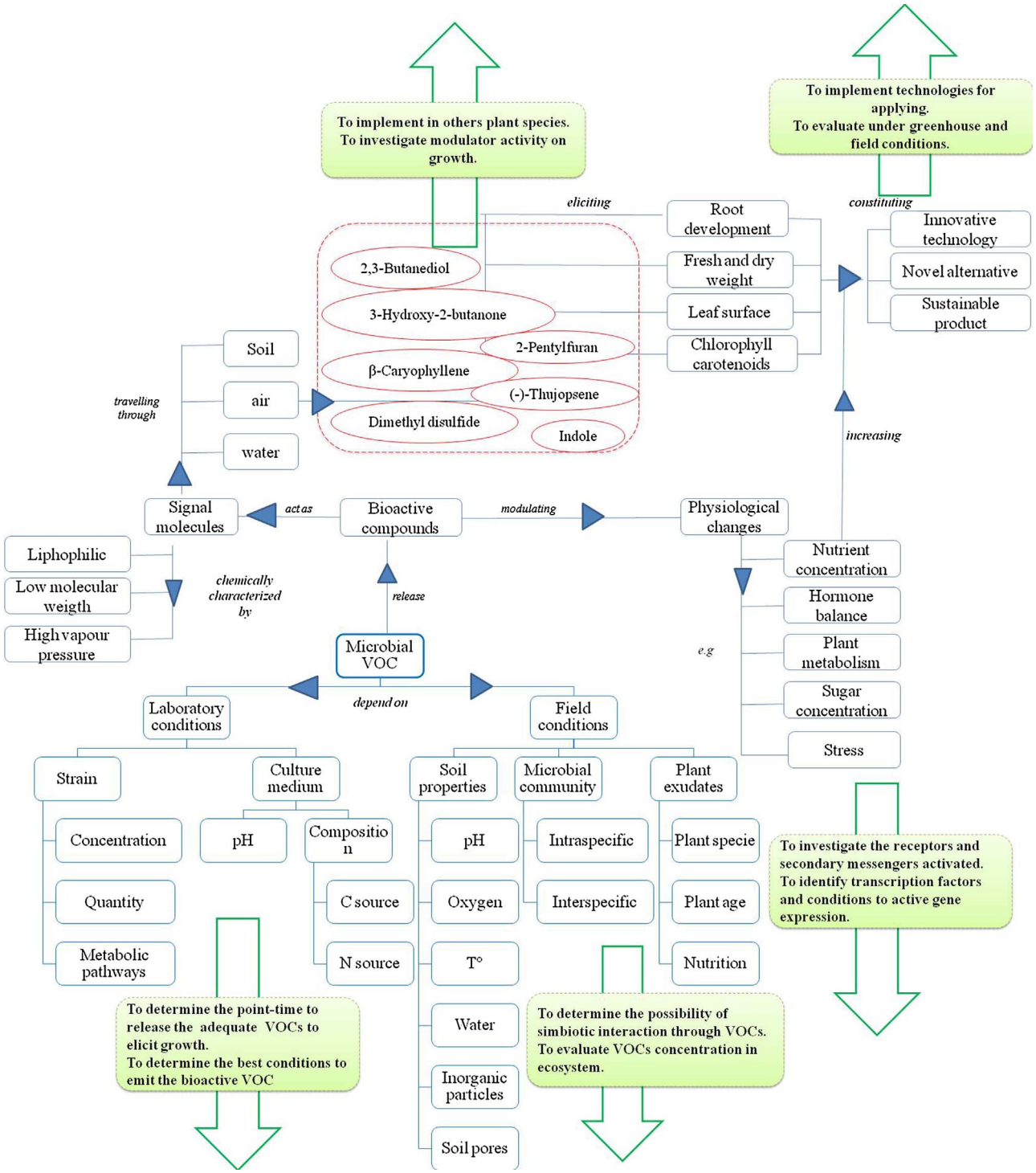

Fig. 8. Summary of the current knowledge about the factors involved in the emission of volatiles and their action in the induction of growth. *Red lines* represent examples of compounds identified as growth inducers and *green arrows* represent prospects for proposed studies at different levels of research. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

JA-signaling pathways. Besides, a field-study performed by Choi et al. (2014) indicated that 3-pentanol released by IN937a triggers the systemic defense response against *Xanthomonas axonopodis* pv. vesicatoria in pepper through JA and SA-signaling pathways after 20–40 days post-transplanting. Afterwards, Kottb et al. (2015) indicated that *Trichoderma* volatiles (specifically 6-pentyl-α-pyrone) reduced the disease symptoms in *A. thaliana* produced by *B. cinerea* and *Alternaria brassicicola* through the activation of SA signaling-pathway. Later, Sharifi and Ryu (2016) reported that volatiles released by GB03 produce ISR against *B. cinerea* in *A. thaliana* through JA and SA signaling-pathways. Recently, Tahir et al. (2017) showed that volatiles released by *B. subtilis* SYST2 reduced the disease severity produced by *Ralstonia solanacerium* on tobacco, where albuterol (1 mM and 0.1 mM) and 1,3-propanediol (10 mM and 1 mM) were the bioactive compounds. It is emphasized that 2,3-butanediol showed an induced defense activity against *R. solani* on creeping bentgrass leaves, where the genes related to JA-signaling pathways, leucine rich repeats (LRR)-transmembrane protein kinase, pathogen-related (PR) gene 5 receptor kinase and nucleotide binding

site-leucine rich repeats (NBS-LRR) domain containing plant resistance gene were up-regulated (Shi et al., 2017) (Fig. 7).

Additionally, induced systemic tolerance (IST) is a term proposed for "rhizobacterial species that induced physical and chemical changes in plants to increase tolerance to abiotic stress" (Farag et al., 2013). The study performed by Cho et al. (2008) indicated that 2R,3R-butanediol induce the systemic tolerance to drought in seedlings of *A. thaliana* by SA-ET and JA signaling-pathways by stomatal closure. Furthermore, Zhang et al. (2008b) showed that *B. subtilis* GB03 increase salt tolerance in *A. thaliana* seedlings through the regulation of sodium transporter *HKT1*, which is up-regulated in shoot and down-regulated in root, eliciting the low accumulation in the plant. Afterwards, Vaishnav et al. (2015) reported that VOCs released by *P. simiae* strain AU elicit the tolerance to salt stress in *Glycine max*. L Merrill, where vegetative storage protein, gamma-glutamyl hydrolase and RuBisco proteins were up-regulated. Moreover, in the same study was found that the concentration of Na^+ is reduced and concentration of K^+ was increase, while the proline was accumulated, evidencing an osmotic protection. Afterwards, Vaishnav et al. (2016) indicated that 4-nitroguaiacol and quinoline induced a seed germination of *G. max* under salt stress (100 mM NaCl) condition, finding that a higher chemotaxis and altered root exudates. Recently, Zhou et al. (2017) demonstrated an important role of volatiles released by *B. amyloliquefaciens* SAY09 to increase *A. thaliana* cadmium tolerance, where the Fe absorption and auxin biosynthesis were increased; moreover, the deposition of Cd was found in cell wall root as mechanism to ameliorating Cd toxicity. In the next section, the principal perspectives respect to VOCs application in agriculture and horticulture are appointed.

8. Perspectives and conclusions

Recent advances have shown that VOCs emitted by microorganisms associated with root plants can be a novel strategy to be applied as growth inducers with potential use in agricultural species. Studies have contributed with relevant evidence that VOCs have the ability to act as signal molecules for eliciting growth, but there is a need to research the emission of volatiles from diverse microorganisms and their ability to act on one or more plant species. Another challenge is the evaluation of the specificity of single or mixture compounds previously identified under laboratory conditions to check their capacity to induce growth, characterizing their action mode. To date, researches on action mode of a specific compound to determine its effect on the regulation of cellular and metabolic processes to elicit growth should be elucidated. Therefore, proteomic, molecular and metabolomic techniques must be carried out to achieve a better understanding of the matter. In addition, a greater progress is required to implement the application of VOCs under field conditions. Therefore, experimental setups should be designed in order to investigate and standardize methodologies and formulations to mimic rhizosphere conditions. New techniques will help to evaluate the effects on plant growth required to prove that microbial VOCs can be an innovative technology to be applied in agricultural crops and a novel alternative to provide sustainable agricultural products that farmers and consumers need. The Fig. 8 represents the summary of knowledge to propose future studies that contribute with to better understand of action mode of VOCs and the possibility to implement as strategy tool.

Conflict of interest

The authors declare they have no conflict of interest in this work.

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