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Current advances in plant-microbe communication via volatile organic compounds as an innovative strategy to improve plant growth

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ABSTRACT

Volatile organic compounds (VOCs) emitted by microorganisms have demonstrated an important role to improve growth and tolerance against abiotic stress on plants. Most studies have used *Arabidopsis thaliana* as a model plant, extending to other plants of commercial interest in the last years. Interestingly, the microbial VOCs are characterized by its biodegradable structure, quick action, absence of toxic substances, and acts at lower concentration to regulate plant physiological changes. These compounds modulate plant physiological processes such as phytohormone pathways, photosynthesis, nutrient acquisition, and metabolisms. Besides, the regulation of gene expression associated with cell components, biological processes, and molecular function are triggered by microbial VOCs. Otherwise, few studies have reported the important role of VOCs for confer plant tolerance to abiotic stress, such as drought and salinity. Although VOCs have shown an efficient action to enhance the plant growth under controlled conditions, there are still great challenges for their greenhouse or field application. Therefore, in this review, we summarize the current knowledge about the technical procedures, study cases, and physiological mechanisms triggered by microbial VOCs to finally discuss the challenges of its application in agriculture.

1. Introduction

Currently, the global demand for sustainable agriculture has important challenges to improve food production, minimizing the harmful effects associated with the application of conventional fertilizers (Moshelion and Altman, 2015; Tyczewska et al., 2018). These problems are intensified due to the increase expected in agricultural demand by at least 70% by 2050 (Hunter et al., 2017). Unfortunately, the use of synthetic plant growth inducers, organic amendments, and genetically modified plants has not solved the problem. Under this context, the scientific approach indicates that microbial communities have an important role in the plant-soil system to improve the health and sustainability of agricultural production (Kanchiswamy et al., 2015a; Arif et al., 2020). Microorganisms have been intensively studied over the years due to their crucial role in the health, nutrition, and growth of their plant host (Phour et al., 2020). Furthermore, it has been reported that they can improve plant performance under biotic and abiotic environmental stress conditions (Mhlongo et al., 2018). Microorganisms interact with plants aboveground in the phyllosphere, inside plant tissues (endophytes), or belowground in the rhizosphere (Compant et al., 2019; Phour et al., 2020). Particularly, the rhizosphere is considered by its relevant role in the interaction with microbial communities.

The rhizosphere is the region of soil surrounding living roots influenced by plant root exudates and associated with the greatest microbial activity (Mohanram and Kumar, 2019). The plant provides nutrients to microorganisms through the rhizodeposits that contain high and low-molecular-weight compounds like sugars, amino acids, vitamins, polysaccharides, organic acids, and secondary metabolites (Mohanram and Kumar, 2019). Rhizodeposition allows the selection of specific microbial communities in the rhizosphere of the plant host (Venturi and Kee, 2016; Hassan et al., 2019). Otherwise, many studies have been performed on non-volatile metabolites emitted by microorganisms that

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provide protection (*i.e.* hydrolytic enzymes, siderophores, and antibiotics) and promote growth by improving nutrient availability (*i.e.,* nitrogen fixation and phosphorus solubilization) and releasing growth inducers (*i.e* auxin, cytokinin, and gibberellins). Also, the study performed by Ryu et al. (2003) showed for the first time the importance of volatile organic compounds (VOCs) emitted by *Bacillus subtilis* GB03 as the growth agent on *Arabidopsis thaliana*, emerging a new line of research in plant-microorganisms communication. In this regard, a series of studies have been conducted to determine its impact on the growth of *A. thaliana* as a model plant (Li et al., 2019a). Furthermore, studies have reported important evidence of VOCs action in other plant species with commercial interests such as *Solanum lycopersicum*, *Zea mays*, *Lactuca sativa*, among others (Sánchez-López et al., 2016; Fincheira et al., 2017; Fincheira and Quiroz, 2018). Studies have identified specific VOCs between certain plant-microorganism interactions. *i.e* 2, 3-butanediol emitted by *B. subtilis* GB03 promotes growth on *A. thaliana*, dimethylhexadecylamine emitted by *Arthrobacter agilis* UMCV2 stimulate growth on *Medicago sativa*, and dimethyl disulfide emitted by *Bacillus* sp. B55 increases growth on *A. thaliana* (Ryu et al., 2003; Velázquez-Becerra et al., 2011; Meldau et al., 2013). Interestingly, the studies suggest that compounds with diverse chemical nature can have the ability to induce growth in plant species.

To date, studies have contributed to significant progress in the knowledge of microorganisms-plant via VOCs communication (Sharifi and Ryu, 2018a). Microbial VOCs can regulate the nutrient acquisition, photosynthesis, phytohormone actions, and metabolic process, leading to the improvement in plant development (Zhang et al., 2008a; Pérez-Flores et al., 2017; Garbeva and Weisskopf, 2019; Martín-Sánchez et al., 2020; Sun et al., 2020). Nevertheless, the action mechanisms modulated by microbial VOCs on the plants have not yet been clarified and there are many questions to answer. Until now, the significant results show that microbial VOCs emerge as an eco-sustainable tool to be established in agriculture. Despite the evidence, there is still study to be carried out to implement VOCs application as an innovative technology in agricultural systems. Based on the above, this review was focused on presenting the current knowledge in the communication of plant-microorganisms via VOCs to improve the plant performance and the challenges for its future implementation in agriculture. For this, the following topics are addressed: (1) VOCs: Concept and properties, (2) technical procedure to evaluate microbial VOCs, (3) study cases of plant-microbial VOC interaction, (4) action mechanisms, (5) challenges for the application of VOCs in agriculture, and (6) conclusions.

2. VOCs: concept and properties

Microbial VOCs are signal molecules characterized by having low-molecular-weight (< 300 g mol^{-1}), low boiling point, high vapor pressure (0.01 kPa at 20 °C), and lipophilic moiety (Schulz and Dickschat, 2007). These physical-chemical properties influence the volatility degree of VOCs, which depends mainly on vapor pressure and molecular weight. For example, a compound with the highest number of carbon atoms and molecular weight present lower volatilization due to its minor vapor pressure. Chemical structures of microbial VOCs can belong to alkanes, alkenes, ketones, alcohols, sulfides, terpenes, among others (Korpi et al., 2009; Kanchiswamy et al., 2015b). Hence, the VOC profile is composed of a wide variety of compounds with specific concentrations, which are emitted as metabolism products depending on the growth conditions.

The VOC profile emission is influenced by environmental factors as a growth substrate, temperature, oxygen, pH, moisture, among others (Schulz-Bohm et al., 2015). For example, *Bacillus* species grown under low-oxygen conditions can produce 2,3-butanediol and 2-hydroxy-2-butanone (Ryu et al., 2003). Furthermore, the perception of inter-kingdom VOCs can regulate the microbial transcriptome, leading to specific VOC profile emission (Sharifi and Ryu, 2018b). For example, it has been revealed that the GacS/GacA two-component regulatory system plays an important role in VOCs production of *Pseudomonas fluorescens* SBW25 (Cheng et al., 2016). In consequence, the physical-chemical properties of microbial VOCs and environmental conditions determine its evaporation and dispersion in the rhizosphere system (Schulz-Bohm et al., 2017). Therefore, microbial VOCs can be accumulated and spread in the rhizosphere to interact with plant roots (Garbeva and Weisskopf, 2019). Diverse studies have been carried out to determine the effectiveness of VOCs to induce plant-growth with similar methodology procedures, which are described below.

3. Technical procedure to evaluate microbial VOCs on plant growth

Diverse techniques have been implemented to elucidate the role of VOCs in the modulation of plant growth (Bailly and Weisskopf, 2012; Kanchiswamy et al., 2015a; Li et al., 2019a). The knowledge about the procedures, techniques, and equipment has great importance to design experiments that allow elucidating and identifying VOCs emitted by microorganisms that promote plant growth. Specific technical procedures from the experimental unit that contains the plant-microorganism sample to the instrumental techniques used for entrapment and identification of VOCs play a relevant role for obtaining results. Most research about the plant response to microbial VOC has been performed under controlled conditions using a Petri dish containing two compartments (I-plate technique) (Farag et al., 2017). The experimental procedure consists mainly on microbial cultivation on the surface of a specific culture medium in one compartment of the Petri dish. In the second compartment, the “target” plant is grown using Murashige and Skoog or Hoagland media as substrate (Bailly and Weisskopf, 2012; Camarena-Pozos et al., 2019; Syed-Ab-Rahman et al., 2019). This system allows only the airborne interaction between plant and microorganism, where a physical barrier is used to prevent the diffusion of non-volatile metabolites emitted by the microorganisms. The Petri dish is sealed with parafilm to prevent microbial VOC leakage (Park et al., 2015).

Furthermore, other experimental designs have been implemented, the review presented by Kai et al. (2016) described the “Systems targeting the roots” as an experimental system introduced by Park et al. (2015), who placed a culture of *P. fluorescens* strain SS101 underneath of plastic container containing on its surface a compartment with seedlings of *A. thaliana* grown in soil substrate. This study showed an increase in fresh weight of *A. thaliana* after three weeks of exposure. Similarly, Tahir et al. (2017) showed that VOC released by *B. subtilis* SYST2 promotes growth on *S. lycopersicum* plants grown in soil substrate, where weight, total leaf surface area, root length, and shoot length were increased. More recently, an experiment performed by Guimaraes Bavaresco et al. (2020) showed that *B. subtilis* AP-3 grown in nutrient agar modulates the root architecture of *Glycine max* cultivated in soil, leading to the increase of shoot (88%) and root (18%) biomass. Otherwise, plastic containers sealed with parafilm have been used to test microbial VOCs on growth induction of plant seedlings grown in vitro conditions (*i.e A. thaliana*) (Xie et al., 2009). A study performed by Li et al. (2019b) reported that tobacco plants grown in Magenta culture vessels containing Murashige and Skoog medium increased its plant biomass (15-fold) after the exposure to VOCs released by *Cladosporium sphaerospermum* TC09. Despite the different experimental designs used to evaluate the growth-inducing effect of VOCs in plants, the headspace component constitutes the microbial VOCs source perceived by plants.

It highlights the importance of headspace analysis, which provides crucial information about the interaction between plant-microorganism via VOCs communication (Farag et al., 2013). Microbial VOC analysis includes four important approaches: entrapment, analysis, identification, and quantification. The collection of VOCs can be performed through two methodologies: dynamic headspace and solid-phase microextraction (SPME). Dynamic headspace is based on the extraction of VOCs from dynamic air-flow provided by microbial culture onto an absorbent filter and diluted in the organic solvent (Ryu et al., 2003).

Otherwise, the SPME fiber technique can extract VOCs in absence of airflow, characterized by being a static headspace sampling, followed by the direct VOCs release into the injector of a gas chromatograph (Timm et al., 2018). Particularly, SPME collects microbial VOCs in a short period (< 30 min), but the fiber coating plays a crucial role to adsorb VOCs of a specific chemical nature based on the polarity and size. Therefore, the identification of VOCs is highly dependent on the SPME fiber or the organic solvent used to collected compounds by dynamic headspace. In general, the identification and quantification of VOCs are performed through gas chromatography coupled to mass spectrometry, which is widely used for its high sensibility and resolution (Farag et al., 2017). At present, the database contains > 600,000 identified microbial VOCs with known mass spectra in libraries, where the Kovats index can help to precise identification (Farag et al., 2017). Otherwise, proton transfer reaction - mass spectrometry (PTR-MS) has emerged as an important tool to identify microbial VOCs without separation stage analysis, minimizing the processing time of samples. PTR-MS can monitor microbial VOC production through real-time procedure with high detection and sensibility (Romano et al., 2015).

There is no particular methodology to carry out VOC analyzes, but the combination of sampling procedures can improve the identification. For example, the collection of VOCs with different fibers of SPME could provide more detailed information about the volatile profile emitted by a microorganism to induce plant growth. In addition, bioassays should be performed to confirm the role of active VOCs in plant growth induction. In general, the application of commercial bioactive VOC in a dose-response experiment is carried out to confirm its role in stimulating plant growth. The experimental design is similar to the previously named, where a filter paper is impregnated with a given concentration of commercial VOC and placed in a compartment of the Petri dish, while the “target” plant is placed in the second compartment. Experimental details of the specific plant-microorganism interactions studied so far are described below.

4. Case studies: Plant growth modulated by microbial VOCs

The important role of microbial VOCs to induce plant growth was first reported by Ryu et al. (2003). Since that date, different studies have focused on the evaluation of plant response to microbial VOCs (Table 1). The reports indicate that VOCs act at low doses from ng to μg scale, increasing the growth in different stages of plant development (Lee et al., 2014; Sánchez-López et al., 2016). Here, we describe in the first instance the study cases associated with *A. thaliana*, which have been widely used as a model seedling to test the VOC effects (Li et al., 2019a). The study conducted by Ryu et al. (2003) showed that VOCs emitted by *B. subtilis* GB03 grown in Murashige and Skoog medium increased the total leaf surface area in *A. thaliana*. Also, the data indicated that 2, 3-butanediol was mostly emitted by *B. subtilis* GB03, reaching ~ 10 μg per 24 h of release. The study confirmed that the doses from 1 to 100 μg of 2,3-butanediol are the more effective concentrations. In addition, it was demonstrated that VOCs emitted by *B. subtilis* GB03 enhanced chlorophyll concentration and improved photosynthetic parameters in *A. thaliana* after 2 weeks of exposure (Zhang et al., 2008a). A longer experiment indicated that the fresh weight, dry weight, and rosette number of *A. thaliana* increased with the exposure to VOCs released by the same bacterial species (Xie et al., 2009). Similarly, an increase in the fresh weight of *A. thaliana* was evidenced after 15 days of exposure to 2-pentylfuran emitted by *B. megaterium* XTBG34 (Zou et al., 2010).

It was evidenced that *Bacillus* species have important effects to induce growth on the root system, *i.e. B. cereus*, *B. simplex*, and *Bacillus* sp. improve the lateral root development in *A. thaliana* (Gutiérrez-Luna et al., 2010). The results showed a strong correlation between fresh weight and lateral root length (r^2 0.82), suggesting the importance of VOCs on growth and root modulation to improve the water and nutrient uptake. The contribution performed by Asari et al. (2016) demonstrated that VOCs emitted by *Bacillus amyloliquefaciens* strains inoculated in different doses (1,5, and 15 drops) on Murashige and Skoog medium (with or without root exudates) promote growth on *A. thaliana*. Further, *B. amyloliquefaciens* BF06 promotes growth on *A. thaliana* via airborne communication (Wang et al., 2017). The results showed an increase in weight, rosette number, total leaf area, and photosynthetic parameters, which suggest that VOCs modulate diverse physiological and biochemical mechanisms at the same time. Interestingly, the study indicated that VOCs improved iron acquisition in plants (Wang et al., 2017). Similarly, the mixture of VOCs emitted by *Bacillus methylotrophicus* M4-96 increased growth on *A. thaliana* (Pérez-Flores et al., 2017). Leaf number per plant, root weight, and shoot weight were highly increased after 6–8 days of interaction. The results highlight the important effect on root development, which since day-4 showed a significant increase in primary root length, lateral root number, and lateral root density (Pérez-Flores et al., 2017). Further, tetrahydrofuran-3-ol, 2-heptanone, and 2-ethyl-1-hexanol emitted by *Bacillus* sp. JC03 increased fresh weight on *A. thaliana* (Jiang et al., 2019). In general, it was observed that different *Bacillus* strains have the capacity to emit VOCs that promote growth on *A. thaliana* by stimulating root development, nutrient availability, and leave parameters (*i.e* chlorophyll).

Interestingly, Blom et al. (2011) reported that different species of rhizosphere bacteria can improve growth on *A. thaliana* depending on culture conditions. In general, *Burkholderia* and *Serratia* species grown on Luria Bertani, Methyl Red Voges Proskauer, and Murashige and Skoog media release VOCs that increase fresh weight. Specifically, *Chromobacterium violaceum* CV0 and *Burkholderia pyrrocinia* Bcc171 had the best results. This study showed the importance of the inoculation method and the amount of bacterium inoculated for the emission of VOCs with plant growth induction activity. Particularly, *Burkholderia ambifaria* can emit highly active VOCs to induce growth on *A. thaliana*, standing out the presence of dimethyl disulfide, acetophenone, and 3-hexanone (Groenhagen et al., 2013). Gram-negative bacteria as *Burkholderia cepacia* and *Staphylococcus epidermidis* released VOCs that increased the fresh weight of *A. thaliana* after 14 days of exposure, but bioactive compounds are unknown (Vespermann et al., 2007). An important study was performed by Bailly et al. (2014), who revealed the crucial role of indole emitted by *Escherichia coli* on the stimulation of lateral root number and biomass of *A. thaliana*. Similarly, *Proteus vulgaris* JBLS202 emitted indole for enhancing shoot length, root length, lateral root number, and fresh weight on *A. thaliana* (Bhattacharyya et al., 2015). The study presented important evidence that indole influences growth through the modulation of plant hormone signaling (auxin, cytokinin, and brassinosteroid). These results suggest that gram-positive and negative bacteria can emit volatiles to induce growth, not being restricted to a limited group of species.

In addition, fungal species have been reported as important VOC sources. For example, *Fusarium oxysporum* released an unknown mixture of VOCs that stimulate growth on *A. thaliana* after two weeks of exposure (Bitas et al., 2015). It was found that shoot weight, total leaf area, and root development improved at a great percentage. Further, Schenkel et al. (2018) presented results about the importance of *Fusarium* strains and growth medium to the emission VOCs with growth-inducing activity. Besides, it was evidenced that the low-abundance of sesquiterpenes (specifically (-)-thujopsene) emitted by *Laccaria bicolor* has an important activity to modulate lateral root development of *A. thaliana* (Ditengou et al., 2015). The number of lateral roots, root hair length, and lateral root density were increased with VOC exposure.

Interestingly, *Trichoderma* species have shown an effective action on *A. thaliana*. For example, Garnica-Vergara et al. (2016) demonstrated that 6-pentyl-2-H-pyran-2-one released from *Trichoderma atroviride* modulates the biomass and root morphogenesis of *A. thaliana*, where at 75 μM increased root length, lateral root number, and emerged lateral roots. Meanwhile, at 200 μM enhance lateral root density. This study showed the important role of auxin signaling to modulate root architecture. Similarly, *Trichoderma virens* Gv29.8, *Trichoderma atroviride* IMI206040, *T. atroviride* BLU132, and *Trichoderma asperellum* LU370

Table 1
Study cases of microbial VOCs as modulating agents of plant growth.

Plant	Microorganism	Microbial growth culture medium	Exposition period	Experimental conditions	VOC	Growth parameter	Reference
Arabidopsis thaliana	*Bacillus subtilis* GB03	Tryptic soy agar (20 μL)	10 days	I-plate	2,3-Butanediol(1 μg, 100 μg)	Total surface area	Ryu et al. (2003)
		Tryptic soy agar (20 μL, 1×10^9 CFU mL^{-1})	14 days	I-plate	ND	Chlorophyll a/b Chlorophyll a + b Photosynthetic parameters	Zhang et al. (2007)
		Tryptic soy agar (50 μL, 1×10^9 CFU mL^{-1})	2–3 weeks	Magenta box	ND	Dry weight Fresh weight Rosette number	Xie et al. (2009)
	Bacillus megaterium XTBG34	Tryptic soy agar (20 μL, 1×10^9 CFU mL^{-1})	15 days	Petri dish	2-Pentylfuran (5 μL, 10 μg)	Fresh weight	Zou et al. (2010)
	Bacillus species	Murashige and Skoo medium (1×10^9 CFU mL^{-1})	10 days	I-plate	ND	Fresh weight Primary root length Lateral root number Lateral root length Lateral root density	Gutiérrez-Luna et al. (2010)
	Bacillus amyloliquefaciens	Tryptic soy agar Luria Broth agar M9A minimal médium (20 μL, OD$_{600}$ = 1.0)	18 days	I-plate	ND	Phylosphere fresh weight	Asari et al. (2016)
	Bacillus amyloliquefaciens BF06	–	10 days	I-plate	ND	Dry weight Fresh weight Rosetter number Total leaf area Chlorophyll content Photosynthetic rate	Wang et al. (2017)
	Bacillus methylotrophicus M4-96	Murashige and Skoo medium (1×10^6 CFU mL^{-1})	10 days	I-plate	Ten ketones (3-hydroxy-2-butanone) Eight alcohols One aldehyde Two hydrocarbons	Root growth Root branching Leaf formation Shoot biomass	Pérez-Flores et al. (2017)
	Bacillus sp. JC03	Luria –Bertani (20 μL, 1×10^9 CFU mL^{-1})	30 days	I-plate	Tetrahydrofuran-3-ol (1 ng/10 μL, 10 ng/10 μL, 100 ng/10 μL, 1 μg/10 μL, 10 μg/10 μL) 2-Heptanone (1 ng/10 μL, 10 ng/10 μL, 100 ng/10 μL) 2-Ethyl-1-hexanol (100 ng/10 μL, 1 μg/10 μL, 10 μg/10 μL)	Fresh weight	Jiang et al. (2019)
	Burkholderia cepacia *Staphylococcus epidermidis*	Nutrient medium (20 or 50 μL)	14 days	Tripartite Petri dish	ND	Fresh weight	Vespermann et al. (2007)
	Burkholderia ambifaria	Luria Bertani (20 μL, OD $_{600}$ of 1)	3 weeks	Square Petri dishes containg stainless steel ring	Dimethyl disulfide (1 ng, 1 μg, 1 mg) Acetophenone (1 ng, 1 μg, 1 mg) 3-Hexanone (1 ng-1 μg)	Biomass	Groenhagen et al. (2013)
	Rhizosphere bacteria	Luria Bertani Methyl Red Vosges Proskauer Murashige and Skoog Angle (20 μL)	21 days	I-plate	Indole (1 ng, 10 ng, 100 ng, 10 μg) Pentadecane (1 ng, 100 ng, 1 mg) 1-Hexanol (10 μg)	Fresh weight	Blom et al. (2011)
	Escherichia coli	Luria Bertani (20 μL, OD $_{600}$ of 0.8)	14–21 days	Petri dishes	Indole (60 μM, 600 μM)	Biomass Lateral root number	Bailly et al. (2014)
	Proteus vulgaris JBLS202	Luria Bertani (10 μL, 1×10^7 CFU mL^{-1})	14 days	I-plate	Indole (0.001, 0.005, 0.01, 0.2,0.043, 0.08, 0.12 μg μL^{-1})	Shoot length Root length Lateral root number Fresh weight	Bhattacharyya et al. (2015)
	Fusarium oxysporum	Potato dextrose medium (0.5 cm-wide strip)	14 days	I-plate	ND	Shoot weight Chlorophyll Root length	Bitas et al. (2015)

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Table 1 (*continued*)

Plant	Microorganism	Microbial growth culture medium	Exposition period	Experimental conditions	VOC	Growth parameter	Reference
	Fusarium species	Soil substrate	11 days	Tripartite Petri dishes	Mixture of VOCs	Root weight Root density Root length Number of lateral roots	Schenkel et al. (2018)
	Laccaria bicolor	Pachlewski médium P20	10 days	I-plate	(-)-Thujopsene (100 ppb)	Root hair length Lateral root density	Ditengou et al. (2015)
	Trichoderma atroviride	Murashige and Skoog medium (1 × 10^6 spores)	10–12 days	Petri dishes	6-Pentyl-2-H-pyran-2-one (75 μM)	Shoot biomass Root biomass Root length Lateral root number	Garnica-Vergara et al. (2016)
	Trichoderma spp. strains	Murashige and Skoog medium (5 μL, 1 × 10^6 spores)	7 days	I-plate	Mixture of VOCs	Shoot biomass Root biomass Total biomass Chlorophyll	Nieto-Jacobo et al. (2017)
	Trichoderma atroviride *Trichoderma virens*	Murashige and Skoog Potato Dextrosa	3–5 days	I-plate	Mixture of VOCs (mainly sesquiterpenes)	Fresh weight Lateral root number	González-Pérez et al. (2018)
	Trichoderma	–	3 days	Glass tissue culture jar	3-Methyl-1-butanol (0.5 μg L^{-1}) 1-Decene (0.5 μg L^{-1}) 2-Heptylfuran (0.5 μg L^{-1})	Fresh weight Chlorophyll Germination	Lee et al. (2019)
	Verticillium dahliae	Potato Dextrosa (5 mm)	14 days	I-plate	ND	Root fresh weight Shoot fresh weight Relative growth rate Leaf surface area	Li et al. (2018)
	Floccularia luteovirens	Murashige and Skoog (3 mycelial plugs)	14 days	Petri dishes	ND	Root length Number of lateral roots Fresh weight Dry weight	Sun et al. (2020)
Mentha piperita	*Pseudomonas fluorescens* *Bacillus subtilis* *Azospirillum brasilense*	Nutrient medium (20 μL, 1 × 10^9 CFU mL^{-1})	30 days	I-plate	ND	Shoot fresh weight Root dry weight Leaf area	Santoro et al. (2011)
Medicago sativa	*Arthrobacter agilis*	Nutrient medium (50–500 μL; 1 × 10^9 CFU mL^{-1})	6 days	I-plate	Dimethylhexadecylamine (0.37 μM, 0.75 μM, 1.5 μM)	Fresh weight Stem length Root length Root density	Velázquez-Becerra et al. (2011)
Lactuca sativa	*Fusarium oxysporium* MSA35	Complete medium (350 μL of 10^9 conidia mL^{-1})	7 days	Petri dish (24 × 24 cm)	β-caryophyllene (25 μM, 50 μM, and 100 μM)	Fresh weight Root length Shoot length Chlorophyll	Minerdi et al. (2011)
	Bacillus sp. BCT9	Murashige and Skoog medium Methyl red Voges Proskauer medium Nutrient medium (OD_{600} = 0.1, 0.2, 0.5, 0.7)	10 days	I-plate	2-Nonanone (0.05 ppm, 50 ppm) 2-Undecanone(0.05 ppm, 50 ppm) 2-Tridecanone (0.05 ppm, 50 ppm) 3-Hydroxy-2-butanone (0.05 ppm, 50 ppm) 2,3-Butanediol(0.05 ppm, 50 ppm)		Fincheira et al. (2017)
	Trichoderma asperellum T1	Potato dextrose	14 days	6-well cell culture plates 3.3 cm	6-Pentyl-2H-pyran-2-one (25 μL mL^{-1})	Number of leaf Number of root Fresh weight Dry weight chlorophyll	Wonglom et al. (2020)
Medicago truncatula	*Arthrobacter agilis* UMCV2	Nutrient medium (1 × 10^6 CFU)	5 days	Glass flask	Dimethylhexadecylamine (5 μL to 100 μM)	Shoot length Root length Fresh weight on root	Orozco-Mosqueda et al. (2013)

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Table 1 (*continued*)

Plant	Microorganism	Microbial growth culture medium	Exposition period	Experimental conditions	VOC	Growth parameter	Reference
						Fresh weight on shoot Chlorophyll Iron	
	Pseudomonas fluorescens strains UM16, UM240, UM256, UM270	Nutrient medium (1 × 10^6 CFU mL^{-1})	20 days	Flask	Mixture containing sulfur compounds volatiles	Root fresh weight Shoot fresh weight Chlorophyll	Hernández-León et al. (2015)
Nicotiana tabacum	*Pseudomonas fluorescens* SS101	King B medium (20 µL, 1 × 10^7 CFU mL^{-1})	3 weeks	I-plate	13-Tetradecadien-1-ol (50 ng) 2-Butanone (50 ng, 500 ng)	Fresh weight	Park et al. (2015)
Sorghum bicolor	*Arthrobacter agilis* UMCV2	Nutrient medium (100 µL, 1 × 10^1CFU mL^{-1})	2 days	Flask I-plate	Dimethylhexadecylamine (8 µM)	Fresh weight Root length Shoot length Chlorophyll Lateral root number Iron	Castulo-Rubio et al. (2015)
Solanum lycopersicum	*Trichoderma viride* BBA 70239	Malt extract medium (sporulating *Trichoderma*)	14 and 21 days	Culture vessel	It was suggested the role of terpenes	Plant biomass Plant length Lateral root development Chlorophyll content	Lee et al. (2016)
	Bacillus subtilis SYST2	Murashige and Skoog medium (20 µL, 1 × 10^7 CFU mL^{-1})	14 days	Tissue culture jars Pot experiment	Albuterol (100 ng) 1,3-Propanediole (200 ng)	Fresh weight Dry weight Total leaf area Length	Tahir et al. (2017)
Zea mays *Capsicum annum*	*Alternaria alternata*	Murashige and Skoog medium	20–50 days	Soil-potting	ND	Plant height	Sánchez-López et al. (2016)
Cucumis sativus	*Bacillus subtilis* GB03	Tryptic soy ($OD_{600} = 1$)	7–14 days	Soil-potting	2,3-butanediol	Shoot fresh weight Leaf area Root fresh weight	Song et al. (2019)
Zea mays	*Serratia plymuthica* PRI-2C *Fusarium culmorum* PV	Potato dextrose Water agar supplied with artificial root exudates	14 days	Pot-in-jar system	ND	Nutrients at root and shoot levels	Martín-Sánchez et al. (2020)

released a mixture of VOC with great activity on root development and biomass of *A. thaliana* with 7 days of exposure (Nieto-Jacobo et al., 2017). Further, *T. atroviride* and *T. virens* grew in Potato Dextrose agar improved growth fresh weight and number of lateral roots at 3 and 5 days post-inoculation (González-Pérez et al., 2018). It notes that VOCs emitted by *Trichoderma* strains grown on Potato Dextrose Agar and Murashige and Skoog media promote the tolerance of seedlings exposed to low temperature (12 °C) by stimulating the increase of fresh weight, lateral root number, and primary root length. More recently, Lee et al. (2019) demonstrated that 2-methyl-1-butanol, 1-decene, 2-heptylfuran at 0.5 μg L^{-1} stimulates the fresh weight and chlorophyll on the same plant species. Until now, studies carried out on the interaction of *A. thaliana* and *Trichoderma* via VOC communication show positive results in plant growth induction, but more studies are needed for future applications.

Further, mycelia and sclerotia of fungal root-pathogen *Rhizoctonia solani* released VOCs that increased shoot weight on *A. thaliana* (Cordovez et al., 2017). Priming-treatment with VOCs released by *R. solani* improved seed and seedlings performance grown in soil potting after 1 and 2 weeks, which was reflected in the increase of shoot fresh weight, length of the flower stem, and the number of flowers (Cordovez et al., 2017). Otherwise, *Verticillium dahlia* strains emitted VOCs with great growth-inducing activity on *A. thaliana* (Li et al., 2018). The results indicated that *V. dahlia* PD322 and PD413 increased weight, leaf surface area, and root length; where a strong relationship was found between the root and shoot fresh weight (r^2 0.9). This suggests the importance of fungal VOCs in the root development to improve the plant nutrient acquisition, which can be reflected in the increase of fresh weight. More recently, it was reported that VOCs released by *Floccularia luteovirens* modulate the root development of *A. thaliana* grown after 14 days of exposure (Sun et al., 2020). The results showed an increase in root length, the number of lateral roots, and primordium, which were modulated by auxin-signaling.

Interestingly, the studies about the impact of microbial VOCs o plant response have been expanded to species with commercial interest. Unknown VOCs emitted by *P. fluorecens*, *B. subtilis*, and *Azospirillum brasilense* stimulated the growth on *Mentha piperita* L. (peppermint) by increasing weight, leaf area, and essential oil yield. It notes that (+)-pulegone, (-)-menthone, (-)-menthol, and (+)-menthofuran were major essential oil found with the VOCs exposure (Santoro et al., 2011). In the same year, it was reported that dimethylhexadecylamine released by *Arthrobacter agilis* promotes growth on *Medicago sativa* (alfalfa) by improving fresh weight, stem length, and root density (Velázquez-Becerra et al., 2011). Likewise, the study presented important evidence about the impact of the exposure period and microbial cell density applied in the experiment, where a minor concentration of bacterium applied was more efficient to promote plant growth (Velázquez-Becerra et al., 2011). The role of dimethylhexadecylamine was also reported to increase growth on *Medicago truncatula* by improving the length and fresh weight on root and shoot (Orozco-Mosqueda et al., 2013). It notes that the concentration of dimethylhexadecylamine increased 12-fold during *M. truncatula*- *A. agilis* UMCV2 interaction. Similarly, dimethylhexadecylamine emitted by the same bacterium stimulates the growth on *Sorghum bicolor*, increasing fresh weight, length of shoot and root, and chlorophyll content (Castulo-Rubio et al., 2015). Besides, it was presented relevant evidence that dimethylhexadecylamine modulates the iron acquisition by Strategy II through the production of phytosiderophores and regulating the transcription of *SbFRO1*. These results suggested that the same VOC can be applied in different plant species to stimulate growth.

Further, Song et al. (2019) reported that VOCs emitted by *B. subtilis* GB03 have an important role to increase growth on *Cucumber sativus* grown under soil conditions, where 2,3-butanediol at doses from 0.1–1000 μM improved fresh weight. Besides, VOC emitted by soil bacterial diversity was study by Fincheira et al. (2016), who showed that *Bacillus*, *Pseudomonas*, and *Serratia* species can stimulate growth on *Lactuca sativa* with differential impact. Principally, *Bacillus* species have the greatest ability to induce shoot length and root development. After that, it was shown that *Bacillus* sp. BCT9 grown in different culture media (Murashige and Skoog, Nutrient, and Methyl red Vosges Porskauer media) emitted VOC with great activity on root length, shoot length, dry weight, and root development of L. *sativa* (Fincheira et al., 2017). Specifically, 2-nonanone, 2-undecanone, and 2-tridecanone were identified as compounds with a crucial role to modulate growth on L. *sativa*. Otherwise, some Gram-negative bacteria species can induce plant growth, for example, Park et al. (2015) reported that *Pseudomonas fluorescens* SS101 enhanced the fresh weight of *Nicotiana tabacum*, where 13-tetradecadien-1-ol and 2-butanone had a crucial role. In addition, Hernández-León et al. (2015) reported that VOCs emitted by different *P. fluorescens* strains stimulate growth on *M. truncatula* by improving fresh weight and chlorophyll content, where the results suggest a role of sulfur compounds emitted as part of the volatiles mix. These studies indicated that VOCs provided by different bacterial species can improve the growth status of different plant species.

VOCs emitted by fungal species have shown significant activity in different plant species. Volatiles from *Fusarium oxysporum* MSA 35 stimulates growth on L. *sativa* seedlings by enhancing root length, fresh weight, leaf chlorophyll, and shoot length (Minerdi et al., 2011). It was confirmed that β-caryophyllene played an important role in growth promotion (Minerdi et al., 2011). The same plant species was studied by Wonglom et al. (2020), who indicated that 6-pentyl-2H-pyran-2-one emitted by *Trichoderma asperellum* T1 promotes strongly the growth in L. *sativa*. These studies showed that VOCs emitted by different fungal species can improve the growth of the same plant. Furthermore, an important contribution was performed by Lee et al. (2016), who reported that VOCs provided by *Trichoderma* species stimulate growth on *S. lycopersicum* by enhancing shoot fresh weight and chlorophyll content after 14 and 21 days of exposure. Likewise, *Alternaria alternata* releases an unknown mixture of VOCs that improve growth on *Zea mays* and *Capsicum annum* on days 20−45 (Sánchez-López et al., 2016). Interestingly, a study performed by Martín-Sánchez et al. (2020) demonstrated that VOCs emitted by *Fusarium* modulate the concentration of macro and micro-nutrients of *Zea mays* grown in soil, showing important evidence that soil microorganisms via volatiles communication can have a crucial role to modulate plant nutrient content. The study cases indicated that different VOCs emitted by fungal and bacterial species can improve growth in plants with commercial interest, potentiating its application in agriculture.

The studies described above show the chemical diversity of VOCs compounds emitted by bacteria and fungi that stimulate plant growth. Interesting, dimethyl disulfide released by *Bacillus* sp. B55 (Gram-positive) improved the growth and sulfur nutrition on *Nicotiana attenuate* and the same VOC released from *B. ambifaria* (Gram-negative) stimulated the growth on *A. thaliana* (Groenhagen et al., 2013; Meldau et al., 2013). Both bacterial species differ in that one is beneficial and the other pathogenic. This suggests that dimethyl disulfide has an important ecological role and can be emitted by various bacterial genera found in the rhizosphere. Also, it supports that pathogenic bacteria can release the same compounds that benefic bacterial species to improve plant growth, playing an important role to interact with plant species. Probably, environmental conditions can modulate the pathogenicity, potentiating the release of metabolites (i.e.VOCs) that stimulate plant growth. In addition to the above, these results suggest that pathogenic microorganisms can stimulate plant growth at long-distance as a consequence of its diffusion through the soil pores. Furthermore, it was evidenced that 3-hydroxy-2-butanone (acetoin) and 2,3-butanediol emitted by *Bacillus* species have an important role for inducing growth on *A. thaliana* and L. *sativa* (Ryu t al., 2003; Fincheira et al., 2017;). 3-Hydroxy-2-butanone (acetoin) and 2,3-butanediol are products of pyruvate fermentation, which is a metabolic pathway present in Gram-positive and negative bacterial species. These compounds can also be emitted by other bacterial species as *Klebsiella oxytoca*, *Paenibacillus* *polymyxa*, *Klebsiella pneumonia*, *Bacillus licheniformis*, *Enterobacter cloacae*, and *Serratia marcescens*, among others (Yang et al., 2017; Novak et al., 2020). Consequently, a VOC with the ability to induce plant growth can be emitted by a wide range of bacterial species, suggesting that this action can be modulated by various rhizospheric microorganisms, enhancing its beneficial ecological action.

5. Physiological mechanisms of plants activated by VOCs

The research performed in the last years has demonstrated the ability of microbial VOCs to trigger a series of physiological changes that allow stimulating plant growth (Zhang et al., 2007; Fincheira and Quiroz, 2018). Many studies about the bacterial-plant interaction via VOC emissions have been conducted to achieve a better understanding of the dynamic effect (Sharifi and Ryu, 2018ab). Consequently, studies to elucidate the action mechanisms allow increasing our knowledge about the mechanisms elicited by VOCs (Li et al., 2019a). Nevertheless, the plant signaling process induced by microbial VOCs is little known, where perception, intracellular signals, signal cascades, and cellular responses are unknown. In general, it's known that VOCs can diffuse through the air to reach plant perception, producing the depolarization of the cell membrane. In the case of green leaf volatiles (GLV), an increase in the Ca^{2+} influx into the cytosol via reactive oxygen species (ROS) production has been detected in *A. thaliana* (Asai et al., 2009). However, Zebelo et al. (2012) reported that β-caryophyllene induced strong depolarization and did not exert action on the homeostasis of Ca^{2+}, suggesting that response depends on volatile and plant species. It was found that microbial VOCs can induce ROS production, which can be associated with the signaling pathway of mitogen-activated protein kinase (MAPK), but future studies about the influence of Ca^{2+} and ROS should be performed for a better understanding (Sharifi and Ryu, 2018a). Additionally, Wang et al. (2017) reported the importance of nitric oxide (NO) in the sulfur and selenium acquisition, suggesting the role of NO signaling as plant response to microbial VOCs. Therefore, a series of studies at the cellular signaling level must be carried out to elucidate the mechanism of perception of microbial VOCs.

Until now, research performed at genetic, proteomic, transcriptional, and metabolomic areas has allowed understanding of the principal physiological mechanisms triggered in plants after exposure to microbial VOCs. The main effects are the modulation of photosynthesis, nutrient balance, modulating hormone cross-talk, and metabolisms, which are summarized and described below.

5.1. *Modulation of photosynthesis*

Photosynthesis is the process by which plants capture solar energy to fix carbon dioxide (CO_2) into carbohydrates, releasing O_2 as a byproduct, through a series of reactions that occur in the chloroplast (Batista-Silva et al., 2020). The photochemical reaction occurs in thylakoid membranes, meanwhile the carbon-fixing and reducing reactions in the stroma of chloroplast (Batista-Silva et al., 2020; Khorobrykh et al., 2020). The sugar produced during photosynthesis is the principal energy source for plant growth and development. A mixture of the unknown VOCs emitted by *B. subtilis* GB03 showed an important role to modulate the photosynthesis process in *A. thaliana* (Zhang et al., 2008a). The results indicated that the number of chloroplasts and chlorophyll content

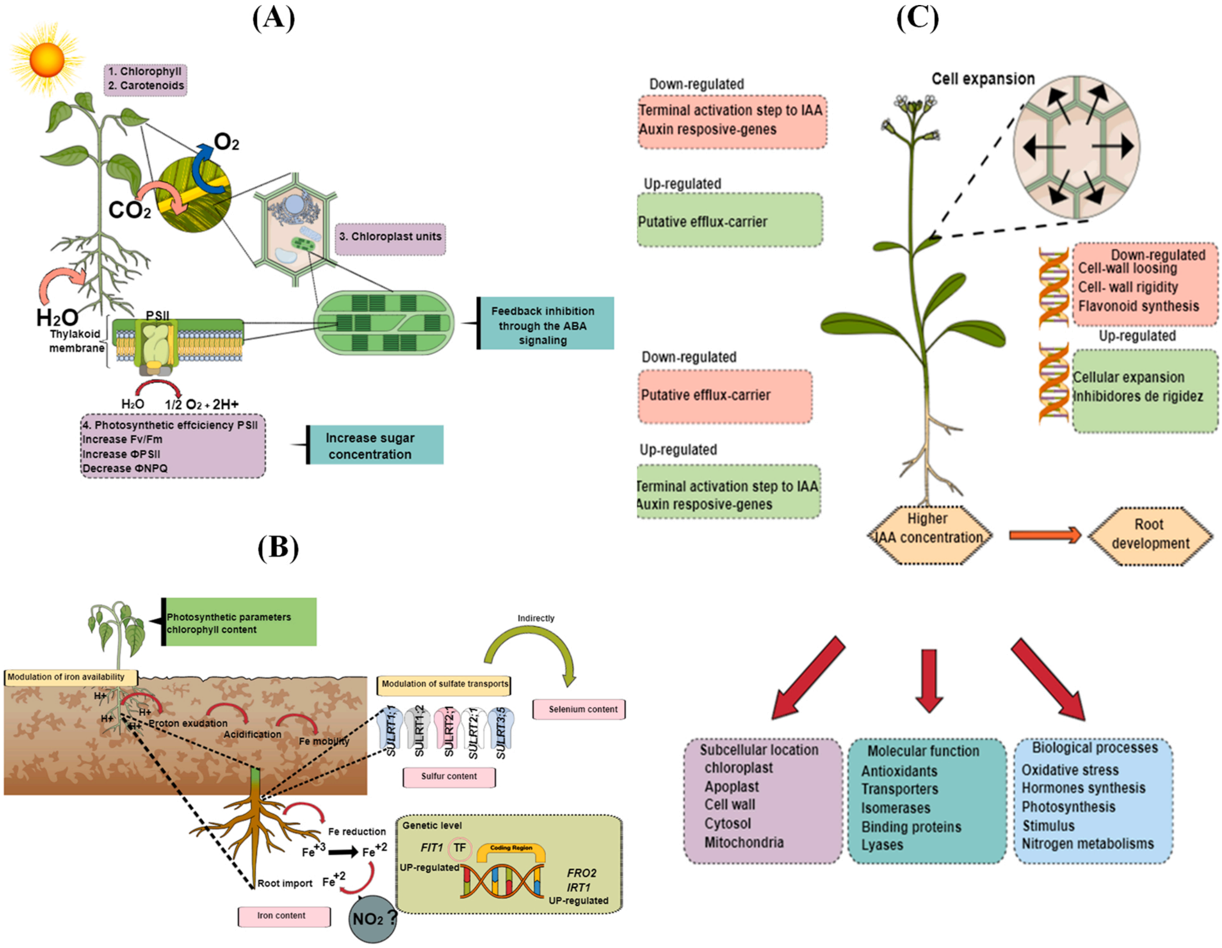

Fig. 1. Plant response to microbial VOCs in physiological processes. (A) Modulation in photosynthesis, (B) regulation in nutrient availability, and (C) genetic process involved in action mechanisms.

(Chl. a + b) were increased after two weeks of exposition, not altering the radius (chlorophyll *a/b*). It is worth mentioning that the chlorophyll complex captures the sunlight and transmits to the reaction center of both photosystems, so this pigment is essential to carry out photosynthesis (Pavlović et al., 2014). Besides, the data indicated that the maximum quantum efficiency (Fv/Fm), photosynthetic efficiency of complex II (PSII), and effective quantum yield (Φ_{PSII}) were increased, meanwhile photochemical dissipation in PSII decreases (Zhang et al., 2008a). VOCs suppressed the feedback inhibition in seedlings of *A. thaliana* through the ABA signaling. Consequently, the photosynthesis process can be carried out independently of endogenous sugar concentration. Likewise, long-term exposure of *A. thaliana* to VOCs of *B. subtilis* GB03 improved effective quantum yield and chlorophyll content (Xie et al., 2009). These studies indicated that *B. subtilis* GB03 has a strong effect to improve the photosynthesis process at the short and long term of exposure, suggesting great effectiveness of VOCs.

Moreover, it was reported that other *Bacillus* strains can influence the photosynthesis process. An analysis performed through the gene ontology (GO) functional indicated that genes-related to the photosynthesis process were differentially expressed in *A. thaliana* seedlings after the exposure to VOCs released by *B. amyloliquefaciens* FZB42 (Hao et al., 2016). Similarly, VOCs emitted by *B. amyloliquefaciens* BF06 improved photosynthetic rate, Fv/Fm, and Φ_{PSII} on *A. thaliana* after 10 days of exposure. More recently, VOCs emitted by *B. subtilis* SYST2 increased the photosynthesis rate and stomatal conductance on *S. lycopersicum* plants after 14, 21, and 28 days of exposure (Tahir et al., 2017). Likewise, VOCs emitted by fungi can modulate the photosynthesis process, for example, a study conducted by Sánchez-López et al. (2016) revealed the importance of VOCs emitted by *A. alternata* to increase the photosynthetic efficiency of *A. thaliana*. Under the light phase condition, VOCs increased parameters as Fv/Fm and Φ_{PSII}, and decrease the Φ_{NPQ}, leading to improve the efficiency of captured light. The net rate of CO_2 assimilated (A_n) and photosynthetic electron transport (ETR) increased after VOCs exposition. Besides, chlorophyll and carotenoids contents increased on leaves after 18 days of the exposition (Sánchez-López et al., 2016). It is worth mentioning that carotenoids are plant pigments with an essential role in photosynthesis and photoprotection (Maoka, 2020). These studies indicated that VOCs released by microorganisms both bacterium and fungal species played an important function to increase the efficiency of photosynthesis (Fig. 1A).

5.2. Nutrient balance

Adequate nutrition allows the optimal growth and development of plants (White and Brown, 2010). It notes that plant performance is highly dependent on adequate nutrient concentration. In this regard, some reports point out that microbial VOCs play a crucial role in the modulation of nutrient acquisition (Fig. 1B). VOCs emitted by *B. subtilis* GB03 increased copper content on leaves, meanwhile, sulfur, iron, and copper were increased on the root of *A. thaliana* (Kwon et al., 2010). Recently, it was reported that VOCs blends released by *S. plymuthica* and *F. cumorum* influenced the macro and micronutrient concentration in the shoot and root of maize, suggesting that soil microorganisms can modulate the nutrient status (Martín-Sánchez et al., 2020).

Particularly, iron (Fe) constitutes one of the most limiting essential microelements for plant development because it participates in photosynthetic complex functioning, biosynthesis of chlorophyll, and protection of thylakoid membrane against reactive oxygen species (Morrissey and Guerinot, 2009).VOCs emitted from *B. subtilis* GB03 improve Fe acquisition through strategy I, which consists of three stages: (1) proton exudation to improve iron mobility, (2) reduction of Fe^{+3} to Fe^{+2}, and (3) the root import of Fe^{+2} (Zhang et al., 2009). As the first mechanism, VOCs emitted by *B. subtilis* GB03 reduce the pH in the rhizosphere of *A. thaliana* by stimulating the production of organic acids and proton releases from the root. Subsequently, VOCs activate the Fe acquisition by enhancing transcript regulation of the iron transporter (*IRT1*) and ferric reductase (*FRO2*) in response to the strong regulation of Fe-deficiency-induced transcription factor (*FIT1*). Consequently, the iron content, chlorophyll, and photosynthetic activity were improved in *A. thaliana* after VOCs exposition (Zhang et al., 2009). Specifically, dimethylhexadecylamine emitted by *A. agilis* UMCV2 shows an important effect to improve iron availability in *M. truncatula* (Orozco-Mosqueda et al., 2013). Dimethylhexadecylamine induces acidification in the root environment, promoting proton extrusion under iron deficiency conditions. Next, it was confirmed an increase in ferric reductase activity under deficiency and sufficiency of iron. Nonetheless, root and shoot iron content was increased only under Fe-sufficiency conditions (Orozco-Mosqueda et al., 2013). Furthermore, dimethylhexadecylamine stimulated the expression of ferric reductase activity (*SbFRO1K*) in *Sorghum bicolor* (Castulo-Rubio et al., 2015). More recently, it was demonstrated that VOCs released by *B. amyloliquefaciens* BF06 increased the Fe uptake in *A. thaliana* grown under Fe deficiency conditions and enhanced the genes encoding for sulfate transporters (*SULRT1;1, SULRT1;2, SULRT2;1, SULRT2;2, and SULRT3;5*) leading to the increase of selenium content (Wang et al., 2017).

Other studies have also been carried out on the acquisition of nutrients, for example, it was reported that dimethyl disulfide emitted by *Bacillus* sp B55 increases the S-nutrition on *N. attenuate* by improving the concentration of SO_4^{-2} due to the regulation of genes associated with S-assimilation and methionine biosynthesis (Meldau et al., 2013). Finally, a study performed by Morcillo et al. (2020) shows that diacetyl plays an important role to modulate the physiological process in seedlings of *A. thaliana* grown under P-deficiency. Therefore, microbial VOCs play an important role to improve nutrients acquisition through the modulation of action mechanisms induced physiologically in plants.

5.3. Modulating hormone cross-talk

Phytohormones are organic molecules synthesized by plants that act at low concentrations ($<10^{-6}$ M) to regulate cellular processes associated with growth, development, and stress (Wani et al., 2016). Auxins, gibberellins, cytokinin, abscisic acid, ethylene, and brassinosteroids constitute the principal phytohormones that modulate plant development. Several studies with *A. thaliana* mutants have shown important evidence that microbial VOCs can modulate phytohormone pathways in seedlings. It was reported that VOCs released by *B. subtilis* GB03 activated cytokinin pathways in *A. thaliana*, playing an important role in the increase of the surface leaf. Mutant strain seedlings *ein2* (cytokinin- and ethylene-insensitive) and *cre1* (cytokinin receptor insensitive) supported the importance of cytokinin production (Ryu et al., 2003). Besides, VOCs emitted by *B. subtilis* GB03 have shown an important role to modulate auxin homeostasis in *A. thaliana*, where genes of auxin synthesis (*NIT1* and *NIT2*) and responsive genes were up-regulated (Zhang et al., 2007). This study showed that VOCs promote the auxin accumulation in roots through the activation of basipetal auxin transport in *A. thaliana*. Moreover, VOCs emitted from *B. methylotrophicus* M4-96 increased the auxin content in *A. thaliana*, which was evidenced by the high activity of *DR5:: GUS* reporter in lateral root primordia and meristems (Pérez-Flores et al., 2017). Further, VOCs emitted by *B. subtilis* SYST2 increased the concentration of auxin and cytokinin in *S. lycopersicum* seedlings, which was supported by the up-regulation of *SlIAA3* and other genes related to cytokinin synthesis (Tahir et al., 2017). The mixture of VOCs released by *B. methylotrophicus* M4-96 promotes the enhanced concentration of indole acetic acid in the shoot and root of *A. thaliana*, indicating the activation of the auxin pathway (Pérez-Flores et al., 2017). More recently, it was reported that VOCs released from *Bacillus* sp. JC03 modulates growth through auxin and strigolactone action (Jiang et al., 2019).

It was evidenced that Gram-negative species can have an important role in the modulation of phytohormones pathways, for example, indole emitted by *E. coli* regulates lateral root development in *A. thaliana* by modulating auxin-signaling to regulate root tip elongation, number of adventitious roots, and lateral root length (Bailly et al., 2014). VOCs released from *P. vulgaris* JBLS202 elicited the growth of *A. thaliana* through the activation of cytokinin, brassinosteroid, and auxin pathways (Bhattacharyya et al., 2015). Mutant lines of *A. thaliana* defective in cytokinin (*cre1*) and brassinosteroid (*cbb1*), auxin transport (*eir1*), ethylene (*etr1*), and gibberellins (*gai1*) were used to investigate the phytohormone pathways involved. Moreover, inhibitors of biosynthesis of auxin and brassinosteroid were applied in seedlings of *A. thaliana* to confirm the role of these phytohormones (Bhattacharyya et al., 2015).

In addition, fungal VOCs have shown an important activity to regulate phytohormone pathways, for example, VOCs emitted by *F. oxysporium* regulate the auxin transport and signaling in *A. thaliana* (Bitas et al., 2015). Mutant seedlings that encode the repressor of auxin response (*AUX1*) and F-box protein that degrades the AUX/IAA transcriptional repressor (*TIR1*) showed no growth activity. Reporter *DR5::GUS* showed a pattern response of auxin in lateral root primordial and root tips (Bitas et al., 2015). *Trichoderma* spp. release 6-pentyl-2H-pyran-2-one (6-PP), which modulated the root architecture of *A. thaliana* by auxin signaling pathways through the modulation of PIN-auxin transport proteins in specific root tissue. 6-PP modulate the function of auxin receptors (*TIR1*, *AFB2*, and *AFB3*), influencing the lateral root development (Garnica-Vergara et al., 2016). Moreover, it was reported that VOCs emitted by *A. Alternata* stimulated the accumulation of cytokinin, which played an important role in the growth of *A. thaliana* (Sánchez-López et al., 2016). This result was supported by the arrest of growth in mutants with CK-deficiency (35S: AtCKX1) or receptor sensibility (*ahk2/3*). Moreover, VOCs emitted by *R. solani* up-regulated genes associated with auxin (*IAA-2*, *IAA-19*, *IAA-29*, *PIF5*, and *HB-2*) and abscisic acid (*CYP707A43*) pathways in *A. thaliana* (Cordovez et al., 2017). Interestingly, VOCs emitted by *Verticillium* spp. regulated the auxin-signaling to promote growth in *A. thaliana*, which was confirmed using mutants in *AUX1*, *TIR1*, and *AXR1* (Li et al., 2018). Finally, it notes that VOCs emitted by *F. luteovirens* increased the lateral root number in *A. thaliana* and reduce the auxin accumulation in primary root length through the repression of auxin efflux carrier PIN-FORMED 2 (*PIN2*) (Sun et al., 2020).

In addition to the phytohormones widely reported as growth regulators, polyamines have been described for their important role in growth modulation and stress tolerance in plants (Pál et al., 2018; Paschalidis et al., 2019). Polyamines are involved in many cellular processes as photoprotection in chloroplasts, protein regulation, and membrane fluidity. Besides, it was evidenced that polyamines improved plant development during embryo development, flowering, and senescence (Chen et al., 2019; Wang et al., 2019). Interestingly, the levels of polyamines are regulated during plant-microorganism, depending on microbial strains and growing conditions (Jiménez-Bremont et al., 2014). In this regard, Salazar-Badillo et al. (2015) reported that the airborne interaction between *A. thaliana* and Trichoderma strains promotes more increase in fresh weight, primary root length, and lateral roots compared to direct contact between both species. Furthermore, this study revealed that polyamine levels are regulated by Trichoderma strain, interaction type, and exposure time. This study strongly suggests that not only phytohormones as growth regulators are modulated by volatiles, but also other metabolites involved in plant growth and development processes may be involved.

5.4. *Other physiological mechanism actions*

A. thaliana has been widely used to understand the principal mechanisms associated with the response to microbial VOCs (Fig. 1C). In this regard, it was demonstrated that VOCs emitted by *B. subtilis* GB03 modulated the gene related to cell expansion in the leaves of *A. thaliana*, where genes that regulate cell-wall losing (UDP-glucose-4-epimerase), cell-wall rigidity (pectinases), and flavonoid synthesis (phenylalanine lyase) were down-regulated (Zhang et al., 2007). Meanwhile, genes of cellular expansion (expansin) and to reduce cell wall rigidity (pectate lyase) were up-regulated. Another study performed by Kim et al. (2015) evidenced that VOCs emitted by *B. subtilis* JS modulate the gene expression on tobacco seedlings, which are associated with metabolisms (92%), cellular process (87%), and response to the stimulus (31%). Moreover, VOCs released by *B. amyloliquefaciens* FZB42 on *A. thaliana* regulated genes associated with the cellular component (i.e organelle, cell), molecular function (i.e binding and catalytic process), and biological processes (i.e response to the stimulus, metabolisms, cellular processes, and biological regulation) (Hao et al., 2016). At the proteomic level, it was demonstrated a differential protein expression in seedlings of *A. thaliana* exposed to VOCs emitted by *B. subtilis* GB03, where proteins related to subcellular location, molecular functions, and biological processes were regulated (Kwon et al., 2010).

Other microbial species have been studied to a lesser degree, for example, VOCs emitted by *S. plymutica* and *Stenotrophomonas maltophilia* regulated genes related to biological processes (i.e response to biotic and abiotic stimulus, response to stress, transcription, and transport), cellular component (i.e intracellular components) and molecular function (i.e transporter activity, transcription factor, and nucleotide-binding) (Wenke et al., 2012). Moreover, important evidence support that VOCs emitted by *Trichoderma* modulate gene related with the response to stress, stimulus (chemical, hormone, jasmonic acid), and defense response (Lee et al., 2019).

6. Microbial VOCs improves the tolerance to abiotic stress

In addition to the increased plant growth, microbial VOCs can induce tolerance against abiotic stress, but few studies have been performed (Liu and Zhang, 2015). Studies reported that microbial VOCs trigger plant tolerance to drought and salt, principally. Dehydration is commonly found in plants caused by drought, salinity, and osmotic conditions. This stress is naturally prevented by osmoprotectants, which modulate the osmotic pressure and physiological changes (Zulfiqar et al., 2020). It was reported that 2R,3R-butanediol emitted by *Pseudomonas chlororaphis* O6 increased the tolerance to drought in *A. thaliana* by increasing the percentage of closed stomata (Cho et al., 2008). Also, 2R,3R-butanediol required salicylic acid, ethylene, and jasmonic acid signaling pathways to exert its action.

Other studies about the effects of VOCs in plants are focused on salt stress tolerance. Salinity is considered the greatest abiotic stress-causing great agricultural loss (Almeida et al., 2017). The higher concentration of sodium (Na^+) produces osmotic and ionic stress in plant cells, affecting the plant growth. A study indicated that seedlings of *A. thaliana* have higher growth and lower accumulation of Na^+ after exposition to VOCs emitted by *B. subtilis* GB03 (Zhang et al., 2008b). The expression of *HKT1K* transporter was down and up-regulated in root and shoot of *A. thaliana*, respectively. In consequence, Na^+ accumulation is lower due to the “shoot to root” recirculation, revealing that the organ-specific regulation allows the Na^+ homeostasis (Zhang et al., 2008b). Similarly, it was evidenced that VOCs released by *Paraburkholderia phytofirmans* PsJN confer salt tolerance in *A. thaliana*, where it was observed that primary root length, rosette area, and total fresh weight were increased under salt stress (150 mM NaCl) (Ledger et al., 2016). Interestingly, Zhou et al. (2017) reported that VOCs emitted by *B. amyloliquefaciens* strain SAY09 allowed that seedlings of *A. thaliana* alleviate the cadmium toxicity through the increase of auxin biosynthesis. The results indicated a Cd deposition in the cell wall of roots and the enhancement of Fe absorption in plants.

Also, soybean plants have been studied, for example, VOCs released by *Pseudomonas simiae* strain AU provided salt tolerance in soybean plants by reducing Na^+. Oppositely, potassium, and phosphorus content increased under salt stress (100 mM NaCl) conditions (Vaishnav et al., 2015). This study showed that proline and other vegetative storage proteins that confer salt tolerance increased in the root of plants exposed to VOCs. Further, VOCs emitted by *P. simiae* in conjunction with a donor of nitric oxide (sodium nitroprusside) improved salt tolerance (100 mM

NaCl) in soybean plants (Vaishnav et al., 2016). The results indicated that an up-regulated gene expression of peroxidase, catalase, nitrite reductase, and vegetative storage protein, whereas *HKT1* transporter, pyrroline-5-carboxylate synthase (P5CS), polyphenol oxidase were down-regulated (Vaishnav et al., 2016). These studies showed that microbial VOCs have great potential to be applied in plants to lessen the effects of abiotic stress; however, researches must be carried out for their scalability and a better understanding of the mechanisms of action.

7. The main challenges of applying VOCs in agriculture

The studies performed since 2003 to date support that microbial VOCs have shown an efficient activity to improve plant health through the growth induction and the increase of tolerance to abiotic stress in plants (Chung et al., 2015; Brilli et al., 2019). The results support the potential application of VOCs to minimize the use of synthetic phytohormones or chemical products (Datta, 2013; Kanchiswamy et al., 2015a). The positive effects of microbial VOCs during the different stages of plant development are one of its main advantages (Hung et al., 2014; Sánchez-López et al., 2016). Therefore, microbial VOCs constitute a promising tool to be applied in plants grown under greenhouse or field conditions (Sharifi and Ryu, 2018b). In consequence, its implementation to plants under real growing conditions constitutes an area of agronomic interest with future challenges (Bailly and Weisskopf, 2012; Farag et al., 2017). Technical progress and experiments must be performed to overcome current limitations for scaling the VOC implementation from controlled conditions to agricultural systems.

The knowledge of the chemical nature of microbial VOC is essential to develop an effective application system. Some VOCs can present a high degree of lipophilicity due to a long carbon structure, which difficult their application due to the low solubility in water (Schulz and Dickschat, 2007; Korpi et al., 2009; Kanchiswamy et al., 2015b). Moreover, the high vapor pressure and low boiling points of the VOCs produce high volatility, which can trigger a large loss of VOCs under field conditions (Farag et al., 2013). Interestingly, high biodegradability may minimize VOC persistence in the environment. It is worth mentioning that VOCs can quickly disappear in polluted environments due to their reactivity with ozone, NOx, and OH- radicals, among others. Therefore, the effectiveness of microbial VOCs in open-systems is influenced by its volatilization and a series of environmental conditions. In consequence, it is necessary to implement an application system of VOCs that allow increasing the efficiency to promote plant growth, reducing the environmental risks that interfere in the action.

It stands out that microbial VOCs at low concentrations (from the ng to μg range) can stimulate plant growth (Fincheira and Quiroz, 2018). It is considered that commercial VOCs have a low-moderate cost, increasing the possibility to scale to agricultural systems (Kanchiswamy et al., 2015a). Hence, the dose plays an important role to optimize the application cost and plant performance. However, it is worth considering that the dose to apply in cropping systems must not produce harmful effects in the ecosystem. The concentration of microbial VOCs tested in Petri dishes under laboratory conditions has a highly controlled condition, so a series of experiments must be carried to determine its impact on other organisms. In this respect, research articles reported that microbial VOCs can modulate the interaction in soil microbial communities with positive and negative effects, and it can produce adverse effects on pathogenic bacteria (Schulz-Bohm et al., 2015; Samad Tahir et al., 2017). Furthermore, strong interactions between fungal and bacterial species via VOC communication have been reported (Werner et al., 2016; Weisskopf et al., 2016). In consequence, the secondary effects according to the doses of bioactive VOCs should be evaluated to avoid problems toxicity effects in biological systems (*i.e* insects, fungi, bacteria, and nematodes) (Hacquard, 2016).

Additionally, biological mechanisms activated by microbial VOCs must be studied to obtain a better result in the application. The perception of microbial VOCs by plant hosts has not been elucidated, being one of the main research challenges. There are many plant mechanisms associated with cellular signaling that clarify to have a better understanding of the mechanisms triggered by microbial VOCs to induce plant growth. There is no knowledge about the ability of VOCs to travel through the vegetal tissue to trigger their action or that endogenous signal in plants can be transported (Farag et al., 2013). Consequently, biological tests about the perception should be studied to improve the effectiveness through the application of VOCs in the plant "target" organ. Further insight about VOCs effects in plants as molecular mechanisms related to the perception, signal pathways, or the assimilation of plants must be elucidated.

Based on the above, a great study process is required to extrapolate the experiments from the laboratory to open-field conditions. Besides, technical strategies should be designed to resolve the problems associated with the implementation of microbial VOCs in agricultural systems. The development of an effective carrier that allows the encapsulation and controlled release of VOCs under greenhouse or field conditions must be done. The encapsulation techniques have been developed to protect a compound against degradation, leaching, or evaporation through a wall material, which can contain one or the mixture of materials that allow making a cover (Madene et al., 2006). The encapsulation of active compounds allows the controlled release and prevents losses as a consequence of environmental factors like water, temperature, oxygen, pH changes, and light (Jatin Chawda et al., 2017). Some encapsulation techniques have been tested to encapsulate conventional agricultural products (i.e herbicides and conventional fertilizers) (Sopeña et al., 2009; Morgan et al., 2009; Dubey et al., 2011; Ibahati Sempeho et al., 2014). Nevertheless, the development of techniques to encapsulate VOCs should be tested to determine its effectiveness, due to the different chemical nature compared to conventional products.

Techniques to encapsulate VOCs have been developed for increasing product stability to control the release, prolong the half-life, and increase the stability against oxidation or reactions produced in the environment (Celebioglu et al., 2016; Chan et al., 2017). VOCs encapsulated must retain-release the appropriate concentration to ensure satisfactory biological result for plants grown in an open space. More recently, few studies have been performed to design a carrier with sustainable properties that allow the controlled release of VOCs to apply in species with commercial interest. For example, a recent work reported that 2-nonanone and 2-undecanone can be released from oil-in-water (O/W) multilayer emulsions composed of oil phase and layers of chitosan and sodium alginate that confer stability and protection against environmental stress (Fincheira et al., 2019). The results indicated that O/W multilayer emulsions provide a controlled release of VOCs for inducing the growth in L. *sativa* and *S. lycopersicum* seedlings in experiments performed under controlled conditions. More recently, it was demonstrated the efficient action of 2-nonanone, 2-undecanone, and 2-tridecanone released by solid lipid nanoparticles and nanostructured lipid carriers to stimulate growth induction on L. *sativa* and *S. lycopersicum* by improving shoot length and root development (Fincheira et al., 2020). These studies show that encapsulation systems are efficient tools to encapsulate microbial VOCs to reach the implementation under real growing conditions, but a series of experiments on plants must be carried out from in vitro to greenhouse or field tests. Also, the concentration of VOC encapsulated should be standardized to demonstrate its effectiveness in plants grown on diverse substrates (i.e hydroponic, soil, vermiculite, among others.).

8. Future prospects

Microbial VOCs have emerged as an innovative strategy to improve agricultural production and mitigate environmental problems of ecosystems derived from chemical fertilization. However, further studies must be carried out to reach microbial VOC application under greenhouse or field conditions. As discussed above, research focused on the chemical nature of VOC, toxicity, action mechanisms, and the design of carrier are relevant challenges that must be overcome before scaling tests for their application in agricultural systems. Studies should answer some questions like, Which VOC is more effective? Is a VOC or a mixture of VOCs better? Does the same VOC similar effectiveness for several species of plants? What are the optimal doses to apply to plants?. In a like manner, it should be considered that the application of microbial VOCs may be subject to effects produced on non-target organisms, being a principal limiting factor. Consequently, studies of toxicity on organisms present in the ecosystem should be performed before bioassay scaling in agricultural systems. Interesting studies can be carried out in model organisms of different lineages in insects, nematodes, bacteria, fungi, among others. Besides, the environmental impact of the application of different doses of microbial volatiles must be studied to provide scientifically proven information as a strategy for future commercialization.

On other hand, comprehensive studies in plants should be performed to determine all the implications of the application of microbial volatiles, *i.e.* stress. Thus, studies at genomic, proteomic, metabolomic, and other "omics" levels should be considered to provide a clear vision of plant response to microbial VOC and its implications. Specifically, the elucidation of the VOC perception mechanism by plants plays a key role in the specificity and effectiveness of the VOCs application because the dose-response relationship could be optimized. Nevertheless, it would be interesting to study these parameters on plants grown at the laboratory and field level to assess whether there are similar or divergent responses. There are few studies about the action mechanisms induced by microbial volatiles on plants grown under greenhouse or field conditions. Therefore, it should be designed experiments under open-conditions to evaluate the efficiency of microbial VOCs on plant growth and the triggered mechanisms as a strategy to overcome the current limited knowledge about its effect under agricultural systems.

Nowadays, the development of microbial VOCs carrier is a limitation for its application. Although there are several studies that evaluate the effect of VOCs on plants, there is little research on carrier design that allows its controlled release under environmental conditions. The development of carriers with sustainable characteristics to the controlled release of VOCs is one of the main challenges to achieve its application in agricultural systems. Current encapsulation systems of compounds related to the food and pharmaceutical area may be an important search strategy due to their low toxicity and biocompatibility. Consequently, it's should be design experiments to evaluate the effect and efficiency of VOCs released from carriers to improve plant growth. Until now, studies are focused on evaluating the effects associated with the direct release of the pure compound. Nevertheless, it should be performed bioassays to determine the effective dose released from the carrier to induce plant growth. For this reason, it is recommended to perform dose-response tests to determine stimulation and toxicity effects of VOCs released from carriers to continue with its scaling of application to agricultural systems. According to recently described, extensive research to scale VOC application to field and greenhouse conditions must be performed before commercial application of these products, covering the knowledge of various areas such as biology, microbiology, plant physiology, engineering, and agronomy.

9. Conclusions

Important scientific evidence support that microbial VOCs have a crucial role to increase plant growth and to confer plant tolerance to abiotic stress. The researches have contributed with significant results that potentiate the prospection of microbial VOCs implementation in agricultural systems. Interestingly, VOCs modulate physiological changes carried out naturally to stimulate plant growth. These results support that microbial VOCs are an efficient tool to induce plant growth with quick action at the foliar and radical level. Also, the biodegradable, organic, and non-toxic nature of VOCs, allows that it constitutes a friendly strategy that exerts action on plants. Therefore, an efficient system should be formulated for the controlled release of VOC on plants, which allows a long-term exposition under environmental conditions. In summary, according to our knowledge, we propose microbial VOCs as a novel strategy to implement in agriculture due to its efficient action on plant growth and tolerance to stress. Currently, these issues are topics widely studied due to the necessity to decrease the environmental problems derived from the chemical application and mitigate the effects associated with climate change.

CRediT authorship contribution statement

Paola Fincheira: Conceptualization, Investigation, Writing - original draft, Writing - review & editing. **Andrés Quiroz:** Writing - review & editing. **Gonzalo Tortella:** Conceptualization, Investigation, Writing - review & editing. **María Cristina Diez:** Writing - review & editing. **Olga Rubilar:** Writing - review & editing, Supervision, Visualization.

Declaration of competing interest

The authors report no declarations of interest.

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