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# Cell-free microbial culture filtrates as candidate biostimulants to enhance plant growth and yield and activate soil- and plant-associated beneficial microbiota

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In this work we compiled information on current and emerging microbial-based fertilization practices, especially the use of cell-free microbial culture filtrates (CFs), to promote plant growth, yield and stress tolerance, and their effects on plant-associated beneficial microbiota. In addition, we identified limitations to bring microbial CFs to the market as biostimulants. In nature, plants act as metaorganisms, hosting microorganisms that communicate with the plants by exchanging semiochemicals through the phytosphere. Such symbiotic interactions are of high importance not only for plant yield and quality, but also for functioning of the soil microbiota. One environmentally sustainable practice to increasing crop productivity and/or protecting plants from (a)biotic stresses while reducing the excessive and inappropriate application of agrochemicals is based on the use of inoculants of beneficial microorganisms. However, this technology has a number of limitations, including inconsistencies in the field, specific growth requirements and host compatibility. Beneficial microorganisms release diffusible substances that promote plant growth and enhance yield and stress tolerance. Recently, evidence has been provided that this capacity also extends to phytopathogens. Consistently, soil application of microbial cell-free culture filtrates (CFs) has been found to promote growth and enhance the yield of horticultural crops. Recent studies have shown that the response of plants to soil application of microbial CFs is associated with strong proliferation of the resident beneficial soil microbiota. Therefore, the use of microbial CFs to enhance both crop yield and stress tolerance, and to activate beneficial soil microbiota could be a safe, efficient and environmentally friendly approach to minimize shortfalls related to the technology of microbial inoculation. In this review, we compile information on microbial CFs and the main constituents (especially volatile compounds) that promote plant growth, yield and stress tolerance, and their effects on plant-associated beneficial microbiota. In addition, we identify challenges and limitations for their use as biostimulants to bring them to the market and we propose remedial actions and give suggestions for future work.

KEYWORDS

**plant-microbe interaction, biostimulants, crop yield, stress tolerance, volatile organic compounds, soil- and plant-associated microbiota**

## Introduction

Plant' growth and development are influenced by microorganisms occurring in the phytosphere that communicate with plants by exchanging chemical signals (Hartmann et al., 2014). Some of these microorganisms can benefit host plants in a variety of ways, a scenario of utmost interest when searching for new and efficient agricultural approaches based on manipulation of plant-associated microbiota. Beneficial microorganisms can directly promote plant growth through mechanisms involving production of bioactive compounds (e.g. phytohormones, volatile compounds, peptides, etc.), dinitrogen fixation, solubilization of minerals and organic material and enhancement of water and nutrient uptake and use (Tsavkelova et al., 2006a; Rodríguez et al., 2007; Francis et al., 2010). These microorganisms can also indirectly promote plant growth by antagonism/antibiosis against pathogens, alleviation of stress caused by environmental pollutants or other stressful abiotic conditions (e.g. drought and salinity), or by triggering in the host plant enhanced defense capacities against pathogen attack.

A decline in natural resources and the environmental damage caused by practices relying on the excessive and inappropriate application of fertilizers and depletion of soil and water resources have become major limitations in conventional agriculture. A more sustainable and eco-friendly agriculture requires increases in product yield quality, while reducing the negative environmental impact of agrochemicals on soil fertility and biodiversity; potential solutions may be fostered by microbial-based approaches (Calvo et al., 2014). The aim of this review was to compile information on current and emerging microbial-based fertilization practices, particularly the use of microbial inoculants, microbial-derived compounds and microbial culture filtrates (CFs), to promote plant growth, yield and stress tolerance, and their effects on plant-associated beneficial microbiota. In addition, we identify challenges and limitations to bring microbial CFs to the market as biostimulants compliant with scientific requirements of the official regulations for fertilizer products.

## Soil inoculation of beneficial microorganisms: limitations of a widely used practice to enhance crop yield and/or protect plants from (a)biotic stresses in an eco-friendly manner

One environmentally safe and sustainable practice to promote plant growth, increase crop yield and/or enhance stress tolerance is based on the inoculation of soil with plant growth promoting microorganisms (PGPM) (Miransari, 2011; Calvo et al., 2014; Ahmad et al., 2018; Backer et al., 2018; Fiorentino et al., 2018; Zhong et al., 2019; Noceto et al., 2021). Microbial inoculants consist of one or a reduced number of microbial strains which are grown separately or in mixed culture fermentation, concentrated and then formulated with an appropriate carrier into the final product form. Despite its undisputable success (Li et al., 2022), the technology based on PGPM inoculation has faced a number of limitations and inconsistences that are summarized in Table 1. First, the efficiency of inoculation depends on soil pH, temperature and nutrient content, interaction with the crop species (host specificity), competition with native strains and compatibility between the microbial inoculants (Svenningsen et al., 2018; Emmanuel and Babalola, 2020). Second, development of multi-strain bioinoculants on a large-scale level is difficult since each co-inoculant requires specific culture media and physical-chemical conditions (Reddy and Saravanan, 2013). Third, inoculation with beneficial microorganisms without a proper carrier or formulation may result in a rapid decline in the applied microbial population, as the inoculated microbes must compete with the often better-adapted native microbial community (Bashan et al., 2014; Cardinale et al., 2015; Parnell et al., 2016). For instance, the abundance in soil of some well-known beneficial microbes such as *Bacillus amyloliquefaciens* FZB42 and *Trichoderma harzianum* falls below detection limits just a few weeks after application (Papavizas, 1982; Kröber et al., 2014; Oskiera et al., 2017). Although seed coating with beneficial

TABLE 1 Limitations of soil inoculation of PGPM and application of microbial-derived compounds and microbial culture filtrates.

| | PGPM inoculation | Application of microbial-derived compounds | Application of microbial culture filtrates |
|---|---|---|---|
| Efficiency depends on environmental factors, host compatibility and competition with native microbes | x | | |
| Efficiency depends on microbial culture composition and age | x | x | x |
| Difficulty to develop multi-strain bioinoculants | x | | |
| Manner of application: necessity for a proper carrier or formulation | x | x | x |
| Pathogenicity risk to indigenous microbial communities and/or plants | x | | |
| Biostimulant effect depends on plant nutritional status | x | | |
| Scaling-up: difficulty to culture plant-associated microbes in reactors | x | x | x |
| Long and difficult process to isolate, identify and purify the beneficial compound | | x | |
| Dose-dependence response | | x | x |
| Complex synergic and cooperative interactions between different compounds to promote plant growth | | x | |
| Contradictory effect on different plant species | | x | |
| Antagonistic effects on native microbiota | | x | |
| High production cost | | x | x |

"X" highlights the limitation of each microbial-derived method.

microorganisms may be a suitable option to maintain microbial survival in soil over a longer period, an appropriate coating requires a delicate balance between coating materials, microbe and compatible chemistry, which is not always easy to obtain (Glare et al., 2012; Parnell et al., 2016). Moreover, an adequate delivery system for microorganisms in the soil is also required, which represents a major challenge to industry since it involves mass production, formulation, and application of the beneficial microbes (Ravensberg, 2011; Glare et al., 2012; Vassilev et al., 2020). Fourth, some PGPM including some *Pseudomonas* spp. are opportunistic pathogens (Belimov et al., 2007; Sitaraman, 2015) and thus their use is associated with a pathogenicity risk. Fifth, the growth-promoting effect of inoculating beneficial microorganisms strongly depends on the nutritional status of the plant in relation to the extent that they can be rendered ineffective in promoting plant growth (Hoeksema et al., 2010; Pineda et al., 2013). Thus, plants respond better to mycorrhizal inoculation when grown in soils with high microbial diversity and when subjected to phosphorous limitation (Hoeksema et al., 2010). For instance, *Colletotrichum tofieldiae* promotes growth in *Arabidopsis thaliana* only under phosphorus deficiency conditions (Hiruma et al., 2016). Inoculation with the growth-promoting rhizobacterium *B. amyloliquefaciens* GB03 can have deleterious effects on plant growth under phosphate deficiency conditions, due to an activation of the phytohormone-mediated immune response modulated by a phosphate-starvation response (Morcillo et al., 2020). Sixth, the PGPM inoculation efficiency largely depends upon production of bioactive compounds by the inoculated microbes, which in turn strongly depends on abiotic and biotic environmental contexts. Therefore, it can never be guaranteed that inoculation of a particular microbe will result in the production of compounds with plant growth-promoting or stress tolerance-conferring properties. Seventh, most of soil and plant-associated microorganisms cannot be cultured in reactors. Eighth, inoculation of non-native, allochthonous microorganisms is known to produce strong shifts in microbial communities (Schmidt et al., 2014; Diagne et al., 2018; Berg et al., 2021), with unpredictable and unwanted effects (Hart et al., 2018). For instance, non-native mycorrhizal fungal commercial inoculants may lead to undesirable promotion of exotic over native plant species (Burkle and Belote, 2015; Middleton et al., 2015; Hart et al., 2018).

Some of the constraints of the classic single and multi-strain bioinoculation approach can be circumvented by holistic approaches based on the use of SynComs (for **Syn**thetic microbial **Com**munities), which has emerged as a new paradigm not only to better understand plant-microbe interactions, but also to benefit from them

(Castrillo et al., 2017; Durán et al., 2018; Kwak et al., 2018; Carrión et al., 2019; Marin et al., 2021). SynComs are based on the use of metagenomic tools to determine the structure and potential function of plant-associated microbial communities, followed by the isolation and co-culturing of multiple locally adapted native microorganisms. Establishment and survival of inoculated SynComs in the field are higher than that of single or multi-strain bioinoculations, as SynComs are capable of competing with the pre-existing microbiota present in the plant or soil (Liu et al., 2022; Shayanthan et al., 2022). However, despite the obvious theoretical advantages of application of SynComs designed "à la carte" to mimic the role of a particular microbiome, this technology still has some constraints, including technical limitations in the correct metagenomic identification of the isolated microorganisms (Liu et al., 2020), development of SynComs inoculants at a large-scale industrial level, dependence upon the nutritional status of the plant, maintenance of the stability and function of SynComs over time under changing environmental conditions in open field, etc.

## Application of microbial-derived compounds: A step to minimize shortfalls related to PGPM inoculation technology

Depending on environmental conditions, microorganisms can release diffusible compounds including phytohormones, siderophores, proteins, peptides, sugar-derived molecules, amino acids, exopolysaccharides, organic acids and volatile compounds that alter metabolism, enhance photosynthesis, promote plant growth, confer resistance to (a)biotic stresses and cause massive lateral root formation, thus improving the root´s exploratory capacity for nutrients and predisposing plants for colonization and infection by microbes (Ryu et al., 2003; Arkhipova et al., 2005; Tsavkelova et al., 2006b; Spaepen et al., 2007; Berg, 2009; Contreras-Cornejo et al., 2009; Ortíz-Castro et al., 2009; Chanclud and Morel, 2016; Saha et al, 2016; Sánchez-López et al, 2016; Egamberdieva et al., 2017; García-Gómez et al., 2019; Morcillo and Manzanera, 2021). Some of these compounds are capable of activating soil microbial activity (Rodríguez-Morgado et al., 2017; Macias-Benitez et al, 2020). To address limitations related to PGPM inoculation technology, the application of small quantities of microbial bioactive compounds in pure form, either as alternatives, supplements or complements to microbial cells, has been proposed as a possible approach for improving crop productivity and stress tolerance while reducing agrochemical use (Kanchiswamy et al., 2015; Naamala and Smith, 2021). This approach offers reliability and the easy control of the quantity and quality of a compound of interest (Table 1). Furthermore, compared with the PGPM inoculation technology, the use of pure microbial compounds can benefit a broader range of crops and minimize pathogenicity risk (Table 1). Although the stability of many of these compounds depends on abiotic environmental factors (temperature, salt concentration in soil, pH, etc.) and biotic factors (they could be used by native microorganisms as nutrient source), their rapid perception by plants can prime them for growth promotion. However, there are quite a number of limitations associated with the use of microbe-derived compounds including time-consuming processes of isolation, identification and purification of bioactive compounds, dose-dependence of the response, complex synergic and cooperative interactions between different compounds to promote plant growth, contradictory effects of the same compound on different plants, antagonistic effects on beneficial microbiota, etc. (Naamala and Smith, 2021) (Table 1).

## Application of cell-free microbial culture filtrates: A sustainable and environmentally friendly approach to activate the soil- and plant-associated beneficial microbiota and cope with constraints related to PGPM inoculation and application of microbial-derived compounds?

Some of the limitations related to the use of microbe-derived compounds could be circumvented by the use of cell-free filtrates of beneficial bacterial and fungal cultures, which are mixtures of phytohormones, siderophores, proteins, peptides, amino acids, exopolysaccharides, organic acids, volatile compounds, etc. derived from broth cultures processed through centrifugation or filtration (i.e. micro/ultra/nanofiltration and inverse osmosis) for cell removal (Pellegrini et al., 2020). Agronomic studies have provided evidence that application of these complex cocktails is an efficient approach to promote plant growth and enhance yield and stress tolerance in a wide range of crops while reducing the use of agrochemicals. Notably, recent studies have shown that cell-free CFs of phytopathogens can also be used to enhance yield and stress tolerance (Baroja-Fernández et al., 2021 and unpublished results). Table 2 summarizes details of the studies on effects of microbial CF application. Most of these studies indicated that phytohormones occurring in the microbial CFs (especially indole acetic acid (IAA)) are major determinants of the response of plants to these extracts. However, some studies indicated that microbial amino acids, peptides, extracellular proteins, lipopeptides and siderophores could also play important roles in the response of plants to fungal CFs. For instance, Buensateai et al. (2013) showed that application of *Bacillus* sp. strain CaSUT007 CFs enriched in extracellular proteins increased root and shoot

TABLE 2 Studies on effects of microbial CF application on plant.

| Microbial species | | Culture medium | Plant species | Application manner | Effect on plant | Mechanism/ mode of action | Reference |
|---|---|---|---|---|---|---|---|
| *Bacterial species* | | | | | | | |
| ***Azotobacter vinelandii*** | Beneficial | Specific medium | *Solanum lycopersicum* | Root irrigation with culture supernatants | Increase shoot dry weight and fruit production | CFs contain auxins, gibberellins and cytokinin-like substances | Azcón and Barea (1975) |
| ***Azotobacter beijerinckii*** | | | | | | | |
| ***Streptomyces olivaceoviridis*** | Beneficial | Starch-casein medium | *Triticum aestivum* | Pretreatment of wheat grain with CFs | Enhance growth vigor and crop yield | CFs contain auxins, gibberellins and cytokinin-like substances | Aldesuquy et al. (1998) |
| ***Streptomyces rimosus*** | | | | | | | |
| ***Streptomyces rochei*** | | | | | | | |
| ***Streptomyces atroolivaceus*** | Beneficial | MBGM | *Triticum aestivum* | Pretreatment of wheat grain with CFs | Increases the shoot length, fresh and dry mass, root fresh and dry mass but suppresses the depth of the root system | Effects probably caused by activity of plant growth regulators | El-Shanshoury (1989) |
| ***Azospirillum brasilense*** | Beneficial | NFb | *Oryza sativa* | CFs applied in hydroponic medium | Enhance root growth and development | CFs contain IAA | El-Khawas and Adachi (1999) |
| ***Klebsiella pneumoniae*** | | NFDM | | | | | |
| ***Bacillus amyloliquefaciens (FZB24, FZB42, FZB45)*** | Beneficial | GNB | *Zea mays* | Coleoptiles incubated with CFs | Enhance length growth | CFs contain IAA | Idris et al. (2004) |
| ***Bacillus subtilis FZB37*** | | | | | | | |
| ***Bacillus amyloliquefaciens* KPS46** | Beneficial | GNB | *Glycine max* | Pretreatment of seeds with CFs | Increases root and shoot length and plant biomass | IAA and extracellular proteins | Buensanteai et al (2008) |
| ***Streptomyces coelicolor*** | Beneficial | GYMA broth | *Triticum aestivum* | Seed coating with CFs | Improve plant growth under water-stress conditions | CFs contain IAA | Yandigeri et al. (2012) |
| ***Streptomyces olivaceus*** | | | | | | | |
| ***Streptomyces geysiriensis*** | | | | | | | |
| ***Methylobacterium* spp.** | Beneficial | AMS | *Triticum aestivum* | Pretreatment of seeds with CFs | Enhances seed germination and seedling growth | CFs contain CKs | Meena et al. (2012) |
| ***Bacillus* sp. CaSUT007** | Beneficial | GNB | *Manihot esculenta* | Preteatment of stakes with CFs | Increases root and shoot lengths | IAA and extracellular proteins | Bulgarelli et al. (2013) |
| ***Bacillus subtilis* EA-CB0575** | Beneficial | TSB, SBM | *Musa* spp. | Pretreatment of germinated seeds with CFs | Increases shoot length and dry weight | CFs contain Lipopeptides and siderophores | Posada et al. (2016) |
| ***Burkholderia seminalis*** | Beneficial | Specific medium | *Solanum lycopersicum* | *In vitro* application of CFs | Increases seed germination | CFs contain IAA | Tallapragada et al. (2015) |

*(Continued)*

TABLE 2 Continued

| Microbial species | | Culture medium | Plant species | Application manner | Effect on plant | Mechanism/ mode of action | Reference |
|---|---|---|---|---|---|---|---|
| ***Enterococcus faecium*** | Neutral | LB | *Cucumis melo* | Soil irrigation with CFs | Increases shoot and root lengths, plant fresh weight, and chlorophyll content | CFs contain IAA and GAs | Lee et al. (2015) |
| ***Streptomyces* sp.** | Beneficial | TYB | *Solanum lycopersicum* | Soil irrigation with CFs | Enhances plant growth | Effects probably caused by IAA production | Kaur et al. (2019) |
| ***Azospirillum brasilense* (*Ab–V5, Ab–V6*)** | Beneficial | DYGS | *Glycine max* | Spraying of leaves or seeds | Increase root nodulation and root development | Indolic compounds | Rondina et al. (2020) |
| ***Pectobacterium carotovorum***<br>***Pseudomonas syringa*** | Pathogenic | LB | *Arabidopsis thaliana* | Soil irrigation with CFs | Increase shoot and root biomass but not production | Unkwnon | Ávila and Poveda (2022) |
| *Fungal species* | | | | | | | |
| ***Piriformospora indica*** | Beneficial | Specific medium | *Zea mays* | Root irrigation with CFs | Enhances shoot but not root growth | Unknown | Varma et al. (1999) |
| ***Piriformospora indica*** | Beneficial | M+ medium | *Arabidopsis thaliana* | *In vitro* application of CFs | Induces root branching | Production of a diffusible factor that is probably IAA | Sirrenberg et al. (2007) |
| ***Sebacina vermifera*** | Beneficial | MYP | *Panicum virgatum* | Pretreatment of seeds with CFs | Enhances seed germination and biomass production | Unknown | Ghimire et al. (2009) |
| ***Cladosporium* sp. MH-6** | Beneficial | Czapek's broth | *Cucumis sativus* | *In vitro* application of CFs | Increases shoot and root lengths and plant dry and fresh weight | CFs contain GAs | Hamayun et al. (2010) |
| ***Penicillium minioluteum* LHL09** | Beneficial | Czapek's broth | *Oryza sativa (waito-C)/ Glycine max* | *In vitro* application of CFs | Promotes plant growth and nitrogen assimilation, with and without sodium chloride-induced salinity | CFs contain GAs | Khan et al. (2011) |
| ***Piriformospora indica*** | Beneficial | *Aspergillus*minimal medium | *Helianthus annus L* | Root irrigation with CFs | Increases plant growth and seed production. Increases oil content in seeds | Unknown | Bagde et al. (2011) |
| ***Shimizuomyces paradoxus*** | Pathogenic | PDB | *Brassica napus* | Pretreatment of seeds with CF and foliar spray | Increases seed germination and seedling growth | Unknown | Sung et al. (2011) |
| ***Penicillium citrinum* KACC43900** | Beneficial | Czapek's broth | *Carex kobomugi* | Injection/foliar spray with CFs | Increases leaf blade length, chlorophyll and carotenoids contents and photosynthesis | Unknown | Hwang et al. (2011) |
| ***Fusarium oxysporum*** | Pathogenic | CYA | *Cajanus cajan* | Pretreatment of seeds with CF | Increases seed germination and promotes plant growth | Unknown | Jalander and Gachande (2012) |
| ***Penicillium* sp.** | Beneficial | Czapek's broth | *Suaeda japonica* | *In vitro* application of CFs | Increases plant lenght | CFs contain GAs | You (2012) |
| ***Trichoderma virens***<br>***Trichoderma pseudokoningii*** | Beneficial | Richard's solution | *Capsicum annuum* | Seed coating with CFs | Enhance seed germination and plant vigor | Unknown | Rahman et al. (2012) |

*(Continued)*

TABLE 2 Continued

| Microbial species | | Culture medium | Plant species | Application manner | Effect on plant | Mechanism/ mode of action | Reference |
|---|---|---|---|---|---|---|---|
| ***Trichoderma harzianum*** | | | | | | | |
| ***Penicillium* sp. PNF2** | Beneficial | PDB | *Sesamum indicum* | Pretreatment of seeds with CFs | Increases shoot length and fresh weight | CFs contain IAA | Radhakrishnan et al. (2013) |
| ***Fusarium oxysporum*** | Pathogenic | LGN | *Solanum lycopersicum* | Pretreatment of seeds with CFs | Inhibit seed germination and plant growth | CFs contain toxins | Raithak and Gachande (2013) |
| ***Alternaria solani*** | | | | | | | |
| ***Penicillium* spp.** | Beneficial/ Pathogenic | ME | *Triticum aestivum* | Pretreatment of seeds with CFs | Increases seed germination and plant biomass | Unknown | Khokhar et al. (2013) |
| ***Piriformospora indica*** | Beneficial | *Aspergillus*minimal medium | *Aristolochia elegans* | Soil irrigation with CFs | Increases shoot and root length and fresh and dry weight | Unknown | Bagde et al. (2013) |
| ***Trichoderma* spp.** | Beneficial | ME | *Cicer arietinum* | Pretreatment of seeds with CFs | Increases seed germination and promote plant growth | Unknown | Ali et al. (2014) |
| ***Penicillium* spp. (*NICS01, DFC01*)** | Beneficial | PDB | *Sesamum indicum* | Pretreatment of seeds with CFs | Increase shoot and root length and fresh and dry weight | Amino acids | Radhakrishnan et al., 2014 |
| ***Pseudomonas* sp.** | Beneficial | King´s B medium | *Coriandrum sativum* | Pretreatment of seeds with CF and foliar spray | Increases fresh and dry weight and oil production | Unknown | Hegazi et al. (2015) |
| ***Alternaria alternata*** | Pathogenic | Czapek's broth | *Triticum aestivum* | Pretreatment of seeds with CF and foliar spray | Increase seed germination and plant growth | Unknown | Bhajbhuje (2015) |
| ***Alternaria solani*** | | | | | | | |
| ***Penicillium nordicum*** | Pathogenic | CYA | *Sorghum bicolor* | Pretreatment of seeds with CFs | Inhibit seed germination | CFs contain mycotoxin | Vankudoth et al. (2015) |
| ***Penicillium citrinum,*** | | | | | | | |
| ***Penicillium chrysogenum*** | | | | | | | |
| ***Penicillium commune*** | | | | | | | |
| ***Penicillium verrucosum*** | | | | | | | |
| ***Penicillium camemberti*** | | | | | | | |
| ***Penicillium digitatum*** | | | | | | | |
| ***Penicillium oxalicum*** | Beneficial | PDB | *Pennisetum glaucum* | Pretreatment of seeds with CFs | Increases seed germination and seedling vigor | Unknown | Murali and Amruthesh (2015) |
| ***Fusarium tricinctum RSF-4L*** | Pathogenic | Czapek's broth | *Oryza sativa L.* cv. *Dongjin* | *In vitro* application of CFs | Increase shoot and root lengths, plant fresh weight, and chlorophyll content | CFs contain IAA | Khan et al. (2015) |
| ***Alternaria alternata RSF-6L*** | | | | | | | |

*(Continued)*

TABLE 2 Continued

| Microbial species | | Culture medium | Plant species | Application manner | Effect on plant | Mechanism/ mode of action | Reference |
|---|---|---|---|---|---|---|---|
| **_Purpureocillium lilacinum_** | Beneficial | Specific medium | *Solanum lycopersicum* | Pretreatment of seeds with CFs/ Soil irrigation with CFs | Increases seed germination and promotes plant growth | CFs contain IAA | Cavello et al. (2015) |
| **_Fusarium oxysporum_** | Pathogenic | Czapek's broth | *Triticum aestivum*<br>*Hordeum vulgare*<br>*Solanum tuberosum* | Pretreatment of seeds with CFs | Inhibit seed germination and plant growth | Unknown | Ogórek (2016) |
| **_Fusarium sulphureum_** | | | | | | | |
| **_Gibberella avenacea_** | | | | | | | |
| **_Gibberella intrincans_** | | | | | | | |
| **_Trichoderma harzianum_ WKY1** | Beneficial | Czapek's broth | *Shorgum* | Soil irrigation with CFs | Increase shoot and root lengths, plant fresh weight, and total phenol content | CFs contain IAA | Saber et al. (2017) |
| **_Aspergillus fumigatus_ TS1** | Beneficial | Czapek's broth | *Oryza sativa (waito-C)* | Application to the apical meristem | Enhance chlorophyll content, root-shoot length, and biomass production | CFs contain IAA and GAs | Bilal et al. (2018) |
| **_Fusarium proliferatum_ BRL1** | | | | | | | |
| **_Fusarium solani_** | Pathogenic | Richard's solution | *Solanum lycopersicum*<br>*Brassica rapa*<br>*Raphanus sativus*<br>*Trigonella melongena* | Pretreatment of seeds with CFs | Enhances seed germination | Unknown | Parveen et al. (2019) |
| **_Trichothecium roseum_** | | | | | Inhibit seed germination | CFs contain mycotoxins | |
| **_Aspergillus niger_** | | | | | | | |
| **_Cladoporium herbarum_** | | | | | | | |
| **_Alternaria alternata_** | | | | | | | |
| **_Penicillium chrysogenum_** | | | | | | | |
| **_Penicillium expansum_** | | | | | | | |
| **_Trichoderma_ spp.** | Beneficial | | | | Enhance seed germination | Unknown | |
| **_Trichoderma asperellum_** | | | | | | | |
| **_Trichoderma harzianum_** | | | | | | | |
| **_Piriformospora indica_** | Beneficial | CM | *Cichorium intybus* | Foliar spray | Enhances growth and morpho-physiological traits | Unknown | Rashnoo et al. (2020) |
| **_Trichoderma harzianum,_** | Beneficial | MS | *Capsicum annuum* | Soil irrigation with CFs and DEs | Stimulate root growth and enhance fruit yield | CFs produce changes in plant-associated microbiota | Baroja-Fernández et al. (2021) |
| **_Alternaria alternata_** | Pathogenic | | | | | | |
| **_Penicilium aurantiogriseum_** | | | | | | | |

*(Continued)*

TABLE 2 Continued

| Microbial species | | Culture medium | Plant species | Application manner | Effect on plant | Mechanism/ mode of action | Reference |
|---|---|---|---|---|---|---|---|
| ***Gibberella intermedia*** | Beneficial | Czapek's broth | *Oryza sativa (waito-C)* | Application to the apical meristem | Increases shoot growth | CFs contain GAs | Khalmuratova et al. (2021) |
| ***Fusarium oxysporum*** | Pathogenic | PDB | *Arabidopsis thaliana* | Soil irrigation with CFs | Increase shoot and root biomass but not production | Unkwnon | Ávila and Poveda (2022) |
| ***Pythium irregulare*** | | | | | | | |
| ***Rhizoctonia solani*** | | | | | | | |
| ***Chaetomium globosum*** | Beneficial | ME | *Cichorium intybus* | Soil irrigation with CFs | Increase of biomass, shoots and roots length, and leaf area | Increases phenylalanine pathway and chicoric acid | Spinelli et al. (2022) |
| ***Minimedusa polyspora*** | | | | | | Increases phenylalanine pathway and 4-OH-benzoate | |
| ***Geotrichum candidum*** | Neutral | PDB | *Vigna radiata* | Pretreatment of seeds with CFs | Increases seed germination and promotes plant growth | CFs contain IAA | George et al. (2019) |
| ***Saccharomyces cerevisiae*** | Beneficial | Sucrose | *Coreandrum sativum* | Pretreatment of seeds with CF and foliar spray | Increases fresh and dry weight and oil production | Unknown | Hegazi et al. (2015) |

IAA, Indole-3-acetic acid; GAs, Gibberellins; AMS, Ammonium mineral salt medium supplemented with methanol; CM, Complex medium; CYA, Czapek yeast medium; GNB, Glucose-enriched nutrient broth; GYMA broth, Glucose, yeast extract, malt extract; LB, Luria-Bertani broth; LGN, Liquid glucose nitrate medium; MBGM, Modified bouillon glycerol medium; ME, Malt extract broth; MS, Murashige and Skoog medium; MYP broth, Malta Yeast Peptone broth; PDB, Potato Dextrose Broth; NFb, Nitrogen-free malate; NFDM, Nitrogen-free dextrose; SBM, Sporulation Bacillus Medium; TSB, Trypticase Soy Broth; TYB, Tryptone-Yeast Extract Broth. Specific medium, see publication for details.

lengths and total biomass of cassava stalks. Furthermore, Posada et al. (2016) showed that application of *B. subtilis* EA-CB0575 CFs enhanced dry weight of banana plants by the action of lipopeptides and siderophores. Moreover, Buensanteai et al. (2008) showed that extracts of *B. amyloliquefaciens* strain KPS46 promoted soybean growth through the actions of the antibiotic surfactin and proteins secreted by the bacterium, including auxin biosynthetic enzymes, proteins related to phosphate solubilization and nitrogen metabolism, antifungal lipopeptides and proteins related to protection against oxidative stress. Also, CFs enriched in amino acids secreted by several *Penicillium* spp. enhanced shoot and root length as well as the biomass of sesame plants under well-irrigated and drought conditions (Radhakrishnan et al., 2014).

Baroja-Fernández et al. (2021) have recently shown that soil application of CFs of beneficial and phytopathogenic fungi cultured in Murashige & Skoog (MS) medium promoted root growth, enhanced fruit yield and altered composition of fruits of pepper plants. In the same study, the authors found that CFs of the different fungal species possessed volatile organic compounds (VOCs) that, once distilled and applied to soil, promoted responses similar to those triggered by direct application of the fungal CFs. These findings indicated that (i) CFs of both beneficial and phytopathogenic fungi can be used to improve crop yield and (ii) VOCs mediate the crops' responses to fungal CF application. Some bioactive VOCs present in the fungal CFs are shown in Table 3. As further discussed below, it is conceivable that some these compounds (particularly acetic acid) are involved in the crop response to soil application of CFs. Notably, high-throughput sequencing analyses revealed that soil application of fungal CFs and distillates (DEs) promoted similar changes in the soil microbiota, and promoted the proliferation of the same beneficial microbial taxa (Baroja-Fernández et al., 2021) (Table 4). Collectively, the findings of Baroja-Fernández et al. (2021) indicated that (i) CFs of both beneficial and fungal phytopathogens can be used to activate the soil and plant-associated beneficial microbiota, and (ii) microbial VOCs mediate the plants' responses to soil application of fungal CFs through mechanisms involving stimulation of the beneficial soil microbiota as schematically illustrated in Figure 1.

TABLE 3 List of potentially relevant bioactive VOCs present in at least one of the fungal CFs used by Baroja-Fernández et al. (2021) and their effects on plant.

| VOCs | Effect on plant | Reference |
|---|---|---|
| **1-butanol-3-methyl** | Enhances fresh shoot and root biomass and chlorophyll content in Arabidopsis and increases both root length and thickness in *Agave salmiana*. | Camarena-Pozos et al. (2019) |
| | Increases size, fresh weight and total chlorophyll content in Arabidopsis | Lee et al. (2019a) |
| **1-butanol-2-methyl** | Increases size, fresh weight and total chlorophyll content in Arabidopsis | Lee et al. (2019a) |
| **1-hexanol** | Promotes growth of Arabidopsis | Blom et al. (2011) |
| **benzaldehyde** | Increases the volatile oil accumulation in *Atractylodes lancea* | Zhou et al. (2016) |
| **2-phenylethyl alcohol** | Enhances fresh shoot and root biomass, chlorophyll content, in Arabidopsis and increases both root length and thickness in *A. salmiana* | Camarena-Pozos et al. (2019) |
| **acetic acid** | Enhances drought tolerance in Arabidopsis, rapeseed, maize, rice and wheat plants | Kim et al. (2017) |
| | Increases root biomass and photosynthesis in mung bean | Rahman et al. (2019) |
| **acetoin** | Increases root length, shoot length and dry weight in *L. sativa* seedlings | Fincheira et al. (2017) |
| | Induces stomatal closure in Arabidopsis and *Nicotiana benthamiana* | Wu et al. (2018) |
| **2,3-butanediol** | Promotes growth of Arabidopsis | Ryu et al. (2003) |
| | Induces stomatal closure in Arabidopsis and *N. benthamiana* | Wu et al. (2018) |
| | Increases root length, shoot length and dry weight in *L. sativa* seedlings | Fincheira et al. (2017) |
| **2-heptanone** | Promotes the growth of Arabidopsis seedlings | Jiang et al. (2019) |
| **2-nonanone** | Increases root length, shoot length and dry weight in *L. sativa* seedlings | Fincheira et al. (2017) |
| **acetophenone** | Elicits the increase of biomass in Arabidopsis | Camarena-Pozos et al. (2019) |
| **cis-thujopsene** | Induces lateral root formation of Arabidopsis seedlings and poplar plantlets | Ditengou et al. (2015) |

## Challenges and limitations of the microbial CF technology

Despite having great potential as a strategy for improving productivity in a sustainable and eco-friendly manner, the technology based on microbial CF application is still at its infancy and faces important challenges and limitations before it can be widely used (Table 1). First, one challenging aspect of the microbial CF-based technology is the manner of application of the extracts, especially in cases in which bioactivity of CFs is based on compounds with high evaporation rates such as VOCs. Most studies on the effect of application of microbial CFs on plants are based on seed coating and soil applications of CFs (Table 2), but other means of delivery, should be explored to develop appropriate and durable methods that can be used in the field. Second, another challenging aspect of the microbial CF-based technology is the scaling up from lab-scale shake flasks to stirred tanks-based pilot-scale production (Figure 2). This also applies to the technologies of soil inoculation of beneficial microorganisms and application of microbial-derived compounds. Overcoming this limitation is not an easy task due to marked differences in hydromechanical properties and nutrients/oxygen gradients between flasks and large fermentors. For successful scaling up, key parameters affecting heat, momentum and mass transfer should be considered (Trujillo-Roldán et al., 2013). Moreover, some physical parameters should be combined to obtain dimensionless numbers intended to be kept constant during the scaling up process. Third, there are no studies on techno-economic viability of large-scale production of microbial CFs involving (1) propagation of the microbial strain until desired inoculum concentration is reached, (2) fermentation of the microbial strains in large, industrial size fermentors until desired cell concentration is reached and (3) microbial cell removal. For the first two steps, some techno-economic models have been developed for typical liquid biofertilizer production plants (Pérez-Sánchez et al., 2018). These models can be used to investigate the main factors that affect the production process, in order to optimize plant productivity and reliability, and also to reduce costs. Fourth, the limitations to microbial CF use are closely related to the downstream processes for production. However, there are no studies on the formulation and shelf life of microbial CFs and on allocation of fitness costs for resources for the large-scale synthesis of these extracts. Clearly, the formulation of new products ready to be commercialized requires further scientific and industrial up-scaling studies. Fifth, the effects

TABLE 4 List of microbial species whose populations are enriched by the soil application of fungal CFs and DEs used by Baroja-Fernández et al. (2021).

| Microbial species | Mechanism/mode of action | Reference |
|---|---|---|
| Bacterial species | | |
| ***Burkholderia arboris*** | Solubilizes phosphate and produces IAA and siderophores | Zhang et al. (2022) |
| ***Burkholderia silvatlantica*** | Has ACC deaminase activity<br>Fixes $N_2$ | Onofre-Lemus et al. (2009)<br>Perin et al. (2006) |
| ***Caballeronia udeis*** | Solubilizes phosphate and produces siderophores | Puri et al. (2020) |
| ***Duganella ginsengisoli*** | Produces IAA | Goodwin (2022) |
| ***Pseudomonas brassicacearum*** | Has ACC deaminase activity | Belimov et al. (2007) |
| ***Pseudomonas mediterranea*** | Solubilizes organic phosphate and produces siderophores, proteases, ammonia and IAA | Gu et al. (2020) |
| ***Pseudomonas Knackmussii*** | Solubilizes phosphate and produces IAA and siderophores | Rabhi et al. (2018) |
| ***Rhodanobacter glycinis*** | Synthesizes osmolytes and biocontrol-related substances | Lee et al. (2019b) |
| Fungal species | | |
| ***Candida subhashii*** | Biological control of plant pathogenic fungi | Hilber-Bodmer et al. (2017) |
| ***Geotrichum candidum*** | Produces phytohormones and reactive oxygen species | Waqas et al. (2017) |
| | Solubilizes phosphate | Wu et al. (2012) |
| | Produces IAA, ammonia and polyamines | Fu et al. (2016) |
| | Produces IAA and siderophores and has ACC deaminase activity | George et al. (2019) |
| ***Pseudogymnoascus* spp.** | Solubilizes phosphate | Abdel-Ghany et al. (2019) |

of CFs on plants and associated microbiota may vary depending on the plant and microbial species and ecotypes as well as on media composition, age and growth conditions of the microbial culture. Thus, whereas Khokhar et al. (2013) reported that application of CFs of several *Penicillium* spp. cultured for 15 days at 20 °C in malt extract broth exerted a positive effect on wheat germination and growth, Vankudoth et al. (2015) reported that application of CFs of the same fungal species cultured for 12 days at 27 °C in CYA broth exerted a negative effect on sorghum germination. CFs of the phytopathogen *Fusarium oxysporum* grown in Czapek-Dox and potato dextrose liquid media exerted a negative effect on seed germination and growth of cucumber and garden cress (*Lepidium sativum* L.) plants (Melo and Piccinin, 1999; Ogórek, 2016), whereas application of CFs of *F. oxysporum* cultured for 5 days at 25 °C in CYA broth enhanced pigeonpea (*Cajanus cajan* L.) seed germination and growth (Jalander and Gachande, 2012). Application of CFs of the fungal phytopathogen *A. alternata* cultured in Czapek broth and MS media promoted growth of rice and wheat plants and enhanced pepper fruit yield (Bhajbhuje, 2015; Khan et al., 2015; Baroja-Fernández et al., 2021), whereas application of CFs of the same species cultured in Richard´s solution exerted a negative effect on germination of seeds of several crop plants (Parveen et al., 2019). In many instances, the growth inhibitory effect of the CFs of phytopathogens was due to toxins released by the microorganism to the culture medium (Raithak and Gachande, 2013; Vankudoth et al., 2015; Parveen et al., 2019). Sixth, above threshold levels, many microbial compounds are toxic to plants. Therefore, excess application of microbial CFs has the potential to exert a negative effect on plants. However, after due assessment of the dose-response effect on specific crops, microbial CFs can be safely managed. Seventh, although Baroja-Fernández et al. (2021) showed that application of CFs of diverse microorganisms resulted in activation of beneficial soil and plant-associated microbiota without significant changes in the relative abundance of populations of pathogenic microbial species, it is important to ensure that these results can be extrapolated to other CFs in different soil types and environmental scenarios. Eighth, CFs based on co-cultivation of various microorganisms might be an efficient approach to obtain widely range of bioactive compounds. Nevertheless, this practice faces similar problems to those of multi-microbial bioinoculants, since each co-inoculant requires specific culture conditions (Reddy and Saravanan, 2013). Nineth, there are few studies on the mechanisms and modes of action of microbial CFs on plants.

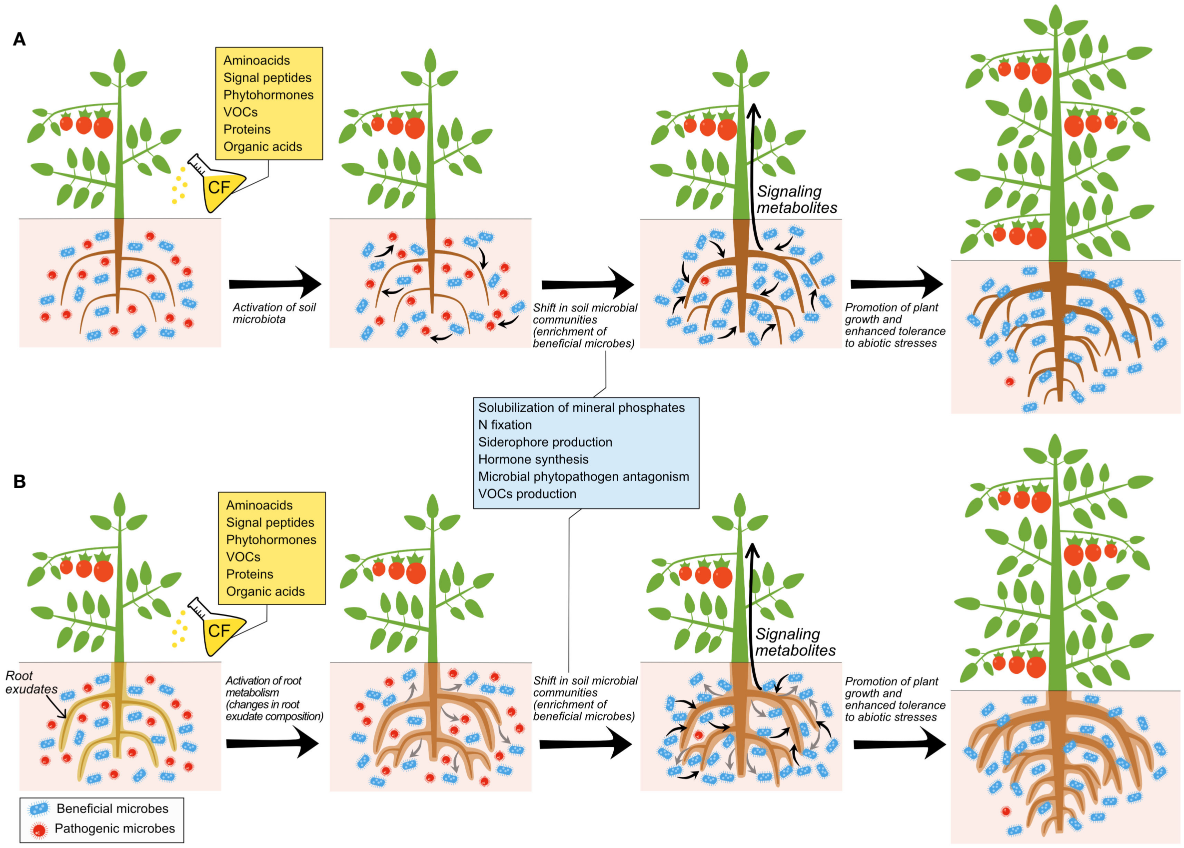

FIGURE 1
Different scenarios of responses of plants and microbiota to soil application of cell-free microbial CFs. **(A)** illustrates direct action of microbial CF compounds on roots and/or on beneficial microorganisms, which release compounds that exert antagonistic effects on pathogenic microorganisms and/or promote plant growth. **(B)** illustrates direct action of microbial CF compounds on the root exudate composition, which modulates rhizosphere microbiota by impoverishing populations of pathogenic microorganisms and enriching those of beneficial microorganisms, which in turn promote plant growth and enhance the capacity of plants to adapt to their environment.

## The necessity of identifying the mechanisms and modes of action of cell-free microbial CFs for their use as biostimulants

In our opinion, the exploitation of microbial CFs as biostimulants (defined by the European Biostimulant Industry Council (https://biostimulants.eu/) as "*substances and/or microorganisms whose function when applied to plants or to soil is to stimulate natural processes to enhance or benefit nutrient uptake, nutrient efficiency, tolerance to abiotic stress and crop quality*" (du Jardin, 2015)) is only just evolving and its broad potential is now beginning to be demonstrated. The majority of studies describing the positive effect(s) of the application of microbial CFs on plant growth and yield did not identify modes or mechanisms of action of these extracts (Table 1). At most, some of these studies proposed that phytohormones and other growth promoting compounds released by microbes in their culture media are involved in the response of plants to microbial CFs. This may result in the assumption by many that these complex, multicomponent mixtures are "magic potions" or "snake oil" not compliant with scientific requirements of the official regulations for fertilizer products (Yakhin et al., 2017). The identification of mechanisms and modes of action of microbial CFs on plants and the characterization of the biological functions and ecological roles of their bioactive components, based on reasonable scientific hypotheses rather than a try-it-and-see approach, could be important not only to develop novel products able to increase yields in crops in a sustainable and environmentally benign manner, but also to obtain clues for the biotechnological design of more productive and efficient crops.

Baroja-Fernández et al. (2021) showed that VOCs are important mediators in the response of plants and plant-associated microbiota to soil application of microbial CFs. However, the bioactive VOCs produced by fungal cultures and

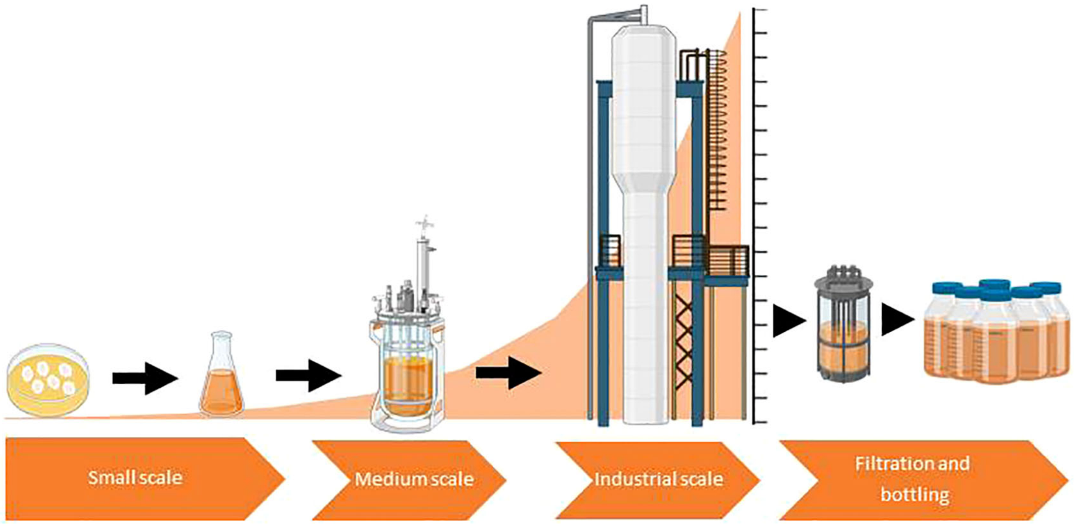

FIGURE 2
Scheme illustrating the scaling-up process of cell-free microbial culture filtrates (CFs) production to industrial level. Figure was created using BioRender.com.

their mechanisms and modes of action remain unverified. Furthermore, whether the effect exerted by soil application of VOCs on plants is direct or mediated by changes induced in the composition of the soil microbiota (or both) still needs to be determined, as does whether the effect exerted by soil application of VOCs on the plant-associated microbiota is direct or mediated by changes induced in the root metabolism (Figure 1). That VOCs isolated from CFs of diverse beneficial and phytopathogenic microorganisms promoted similar growth and fruit yield and quality responses in crops indicate that plants respond similarly to a wide range of bioactive microbial VOCs. Alternatively, it is likely that many microorganisms produce the same growth promoting VOCs. One of such compounds could be acetic acid, which is present in soils, where microorganisms produce it in response to biotic and abiotic stresses (Adeleke et al., 2017). Recent studies have shown that soil application of acetic acid, but not other organic acids, enhances drought tolerance in Arabidopsis and important crops including maize, wheat, rice and cassava (Kim et al., 2017; Utsumi et al., 2019) and tolerance to bacterial wilt disease (Wang et al., 2021). In Arabidopsis, the enhancement of drought resistance promoted by soil application of acetic acid involves JA signaling and an ON/OFF switching epigenetic mechanism dependent on histone deacetylase HDA6 (Kim et al., 2017). However, the biochemical and molecular mechanisms underlying the enhancement of drought tolerance promoted by soil application of acetic acid in crops remain to be elucidated.

Several lines of evidence indicate that the manner of application of microbial volatile compounds and/or plant growth conditions are important determinants of the biochemical and molecular mechanisms triggered in plants. Application of these compounds *via* the air promotes plant growth and metabolic and developmental changes, enhances photosynthesis and improves nutrient and water acquisition (Ryu et al., 2003; Zhang et al., 2008; Zhang et al., 2009; Ezquer et al., 2010; Gutiérrez-Luna et al, 2010; Garnica-Vergara et al., 2016; Sánchez-López et al., 2016; García-Gómez et al., 2019; García-Gómez et al., 2020). In *Arabidopsis*, these responses are associated with changes in the transcriptome, proteome, metabolome, hormonome and redox-proteome through mechanisms involving long-distance communication between roots and the aerial part of the plant and proteostatic regulation of central metabolic pathways in the plastidial compartment (Zhang et al., 2007; Zhang et al., 2008; Zhang et al., 2009; Sánchez-López et al., 2016; Ameztoy et al., 2019; García-Gómez et al., 2020; Ameztoy et al., 2021; Gámez-Arcas et al., 2022). However, Baroja-Fernández et al. (2021) showed that no such mechanisms operate in crops irrigated with VOC-containing microbial CFs and DEs. Needless to say, further work will be necessary to understand how plants respond to microbial volatiles.

The discovery that soil application of VOCs from diverse microorganisms can enhance crop yield and promote similar changes in the soil microbiota extends knowledge on the mechanisms modulating the physiology of the plant and their interaction with plant-associated microbes, raising questions on their ecological significance and biotechnological applications. Because microbes respond to microbial VOCs, it is likely that the fungal VOC-promoted enrichment of the soil beneficial microbiota is due to direct action of these compounds on the microorganisms, which in turn determine plant growth and metabolism through emission of semiochemicals. These compounds trigger the production of molecules by roots that, once transported to the aerial part of the plant, act as long-distance signals that promote growth and enhance yield (Figure 1A). In line with this presumption, Yuan et al. (2017) showed that exposure of soil to VOCs of *B. amyloliquefaciens* NJN-6 altered the composition of soil microbial communities. Compounds secreted by roots in their exudates attract beneficial microorganisms which, in turn, strongly influence plant fitness and enhance the capacity of plants to adapt to environmental changes and stress (Baudoin and Benizri, 2003; Badri and Vivanco, 2009; Badri et al., 2013; Bulgarelli et al., 2013; Schulz-Bohm et al., 2017; Sasse et al., 2018; Zhalnina et al., 2018; Huang et al., 2019; Chen et al., 2020; Vílchez et al., 2020; He et al., 2022). Therefore, it is conceivable that enrichment in the plant-associated beneficial microbiota triggered by application of fungal CFs and DEs is due to an alteration of composition of root exudates (Figure 1B). This capacity of root exudates to influence the soil microbiota is not static since the composition of root exudates is not uniform over time (Zhalnina et al., 2018) and depends on the plant species or genotype (Bulgarelli et al., 2012; Bodenhausen et al., 2014; Bouffaud et al., 2014; Zhong et al., 2019). For instance, it has been shown that soybean genotype significantly influences the structure and composition of its associated rhizosphere and affects connections in rhizobacterial networks (Zhong et al., 2019).

## Additional remarks

According to the Regulation (EU) 2019/1009 of the European Parliament and of the Council of 5 June 2019 laying down rules on the making available on the market of EU fertilising products, a microbial plant biostimulant may contain micro-organisms belonging to the *Azotobacter Rhizobium*, *Azospirillum* genera and mycorrhizal fungi, including dead or empty-cell micro-organisms and non-harmful residual elements of the media on which the microorganisms were cultured (https://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:32019R1009). Although regulations are of great importance for guaranteeing food security and preserving environmental integrity, the stringency and exclusivity of the list of microorganisms that can be used for the production of biostimulants may strongly limit the potential benefits of these products. As shown in the review, growing evidence has been compiled demonstrating that application of cell-free CFs of beneficial and phytopathogenic microorganisms is an efficient approach to promote plant growth and enhance yield and stress tolerance in a wide range of crops while reducing the use of agrochemicals. Therefore, it may be appropriate to enlarge the list of microorganisms that can be used for the production of cell-free CF-based biostimulants according to EU regulation on fertilising products, assuming scientific evidence can demonstrate that these products are safe for both the environment and consumers.

## Authors contributions

RL, EB-F and J-PR conceptualized the topic and wrote the manuscript. All authors contributed in the literature search and discussions, and reviewed and approved the final manuscript.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## Publisher's note

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