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Bioprospecting bacterial and fungal volatiles for sustainable agriculture

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Current agricultural practice depends on a wide use of pesticides, bactericides, and fungicides. Increased demand for organic products indicates consumer preference for reduced chemical use. Therefore, there is a need to develop novel sustainable strategies for crop protection and enhancement that do not rely on genetic modification and/or harmful chemicals. An increasing body of evidence indicates that bacterial and fungal microbial volatile organic compounds (MVOCs) might provide an alternative to the use of chemicals to protect plants from pathogens and provide a setting for better crop welfare. It is well known that MVOCs can modulate the physiology of plants and microorganisms and in this Opinion we propose that MVOCs can be exploited as an eco-friendly, cost-effective, and sustainable strategy for agricultural practices.

MVOCs

Bacteria and fungi are the major inhabitants of the soil rhizosphere, the narrow zone of soil that surrounds and is influenced by plant roots and which is considered to be one of the most dynamic interfaces on Earth. In agroecosystems, the rhizosphere microbiotas have been shown to have a profound influence on plant growth, nutrition, and health [1,2]. Numerous organisms are responsible for these processes, partaking in innumerable interactions between plants, antagonists, and mutualistic symbionts both below and above ground [3–5]. To help plants defend against attack from multiple pathogens, sophisticated alternative interactions involving plant growth-promoting rhizobacteria (PGPRs) and fungi (PGPFs) occur, through the activation of induced systemic resistance (ISR) [6]. Many of the current insights into these interactions and processes have originated from direct physical contact between interacting partners. However, in the past decade considerable progress has also been made in understanding the role that microbial signals and MVOCs play in below- and above-ground multitrophic interactions and MVOC functions in modulating the growth, nutrition, and health of interacting partners [7–13].

Microorganisms produce a plethora of intriguingly complex and dynamic MVOCs, which are defined as compounds that have high enough vapor pressures under normal conditions to significantly vaporize and enter the atmosphere [1]. Despite increasing attention on the importance of MVOCs in both atmospheric ('above ground') and soil ('below ground') ecosystems [7,14–17], their functional

Glossary

Above ground: a position measured with respect to the underlying ground surface.
Agrochemicals: a generic term for the various chemical products used in agriculture. In most cases, 'agrochemical' refers to the broad range of pesticides, including insecticides, herbicides, and fungicides. It may also include synthetic fertilizers, hormones, and other chemical growth agents and concentrated stores of raw animal manure.
Below ground: a position measured with respect to the upper ground surface.
Biofertilizer: a substance containing living microorganisms that when applied to seed, plant surfaces, or soil colonize the rhizosphere or the interior of the plant and promote growth by increasing the supply or availability of primary nutrients to the host plant.
Biofilm: any group of microorganisms in which cells stick to each other on a surface.
Biopesticides: include several types of pest management intervention through predatory, parasitic, or chemical relationships. The term has been associated historically with biological control and the manipulation of living organisms.
Bioprospecting: the search for new natural and sustainable molecules in the hope of finding novel biotechnological applications.
Crop welfare: the provision of a minimal level of well-being and social support for all crops.
Infochemical: information-conveying chemicals including kairomones, allelochemicals, and pheromones that play a crucial role in food web interactions.
Microorganism: a diverse group that includes all Bacteria and Archaea and almost all Protozoa. It also includes some members of the Fungi and algae and animals such as rotifers.
Multitrophic interactions: the incorporation of species from different trophic or nutritional levels interacting in the same system.
Microbial volatile organic compounds (MVOCs): compounds that have high enough vapor pressures under normal conditions to significantly vaporize and enter the atmosphere.
Mycofumigation: the use of gas-producing fungi to kill other microorganisms via production of MVOCs.
Plant growth inhibition: reduction of plant growth determined by environmental factors such as temperature, available water, available light, carbon dioxide, and available nutrients in the soil or by the actions of pathogenic and saprophytic organisms and herbivores.
Priming: exposure to conditions by which the processing of a target stimulus is aided or altered by the presentation of a previously presented stimulus.
Rhizobacteria: root-colonizing bacteria that form symbiotic relationships with many plants. Although parasitic varieties of rhizobacteria exist, the term usually refers to bacteria that form a relationship that is beneficial for both parties (mutualism).
Rhizosphere: a narrow region of soil that is directly influenced by root secretions and associated soil microorganisms. It contains many bacteria that feed on sloughed-off plant cells, termed rhizodeposition, and the proteins and sugars released by roots.
Sustainable agriculture: an integrated system of plant and animal production practices having a site-specific application that will last long term.

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role remains elusive. Only recently, a small number of studies have shown the wealth of MVOCs for the modulation of crop growth, development, defense, and inter- and intraspecific communication [2]. Surprisingly, only 400 of the 10 000 described microbial species have been shown to produce MVOCs [10].

At the plant–microbe community level, substantial progress has been made in studying the multifaceted role in agroecosystems of MVOCs produced by PGPFs, phytopathogens, and various strains of PGPR. Chemical ecologists consider MVOCs as potential semiochemicals that function as attractants and repellants to insects and other invertebrates. For agriculture scientists, MVOCs are seen as biocontrol agents to control various phytopathogens and as biofertilizers for plant growth promotion. In the food industries, MVOCs' biocontrol properties are used to prevent postharvest plant diseases. Most recently, MVOCs have been considered as a potential source of biofuel [18,19].

Because many recent reviews have considered the multifaceted importance of MVOCs, including the regulation of VOC emissions, the role of VOCs in plant rhizosphere processes (i.e., competence, pathogenesis, symbiosis), and their potential functions as quorum-sensing signals for both microbial growth and the regulation of root development [8–10,20], we do not repeat this in detail here. Instead, this Opinion focuses on the role of MVOCs in plant growth, nutrient uptake, and pathogen defense. Here we suggest that a conceptual framework is needed to stimulate the adoption of MVOCs under open-field conditions as a possible substitute for hazardous chemical pesticides and fertilizer.

MVOCs in the field for crop welfare

Under highly competitive but symbiotic conditions, MVOCs are particularly important for antibiosis and signaling and may serve as regulators of plant growth and development. The ecological functions of microbial volatiles are not understood in detail, but several functions such as inter- and intraspecies communication, defense against other microorganisms, and plant growth promotion/priming have been suggested. Research over the past 10 years has led to an increasingly clear conceptual understanding of the role that MVOCs play in the welfare of crops. These studies have demonstrated modulation of the metabolome, genome, and proteome of crop plants on MVOC treatment [21–24]. MVOCs' influence on the modulation of phytohormones, induction of systemic acquired resistance, the defense and priming response, multiple pathogen resistance, and change in plant biomass, growth, and development has been extensively studied and reviewed elsewhere [7,9,14,15,17,25–29]. Here we emphasize selected examples of how microbial MVOCs modulate the abovementioned multifaceted interactions.

Exposure of *Arabidopsis thaliana* plants to MVOCs from rhizosphere strains of *Bacillus subtilis* and *Bacillus amyloliquefaciens* resulted in significant growth promotion. Further investigation of the volatile profile revealed that 2,3-butanediol is the major volatile compound contributing to this phenotypic response [13,30]. Similarly, exposure of tobacco (*Nicotiana tabacum*) plants to *Pseudomonas chlororaphis* MVOCs promoted growth via GacS kinase-dependent production of 2,3-butanediol [31]. These GacS kinases also regulate the synthesis of signal molecules such as acyl-homoserine lactones (AHLs), suggesting that 2,3-butanediol and other MVOCs may belong to a novel class of chemical signal that bacteria utilize to communicate with neighboring organisms [31]. *B. subtilis* emitting 2,3-butanediol contributes in *Arabidopsis* to salt tolerance and ISR, whereas the same compound produced by *P. chlororaphis* resulted in drought tolerance and enhanced disease resistance against *Erwinia carratovora* but not against *Pseudomonas syringae* pv. *tabaci* [12,24,31,32]. Many other bacterial volatiles from species that are present in the plant rhizosphere, such as *Burkholderia cepaci* and *Staphylococcus*, show growth-promoting features, although their chemical structures remain to be determined [27]. There are certain bacterial genera, including *Burkholderia*, *Chromobacterium*, *Pseudomonas*, *Serratia*, and *Stenotrophomans*, whose volatile profiles have been shown to have adverse effects on plant growth and development [25,28]. Transcriptional and molecular analysis of *Arabidopsis* exposed to growth-inhibiting volatile profiles of *Serratia plymuthica* and *Stenotrophomnas maltophilia* suggests an important role of the WRKY18 transcription factor in volatile-mediated plant growth inhibition [33]. The growth modulation, ISR, and drought tolerance observed in plants after microbial volatile exposure depend on genomic, metabolomic, and proteomic changes that are largely attributed to alterations of phytohormone levels. The influence of 2,3-butanediol from *B. subtilis* on plant growth and ISR is due to the modulation of ethylene and auxin homeostasis. Similarly, drought tolerance induced by 2,3-butanediol from *P. chlororaphis* depends on jasmonic and salicylic acids, although the involvement of other phytohormones and cross-talk between them could not be excluded [12,13,24,34]. Transcriptomic, proteomic, and metabolomic analyses of *Arabidopsis* exposed to *B. subtilis* suggests the involvement of various signaling pathways for enhanced plant growth, involving cell wall modification, stress responses, hormone regulation, antioxidant enzyme activity, and photosynthesis [23,34,35].

Similar studies were conducted to understand the role of fungal volatile profiles in plant growth, nutrients, and health. *Trichoderma viride* volatiles induce significant changes in *Arabidopsis*, including increased lateral roots and taller, larger, and early-flowering phenotypic changes [36]. 1-Octen-3-ol is produced by many fungi and contributes to enhanced plant resistance to the necrotropic fungal pathogen *Botrytis cinerea* by inducing defense signaling cascades [37,38]. The volatile profiles of *Alternaria alternata*, *Penicillium charlesii*, and *Penicillium aurantiogriseum* promote growth and starch accumulation in several plant species [39]. Interestingly, volatiles from a nonpathogenic strain of *Fusarium oxysporum*, MSA35, associated with a group of ectosymbiotic bacteria promote growth in lettuce (*Lactuca sativa*) [40,41]. Further studies on this strain revealed that sequiterpenes such as β-caryophyllene produced by the ectosymbiotic bacterial species are the major volatile compounds responsible for the enhanced growth [41]. Ectomycorrhizal truffles such as *Tuber borchii*, *Tuber indicum*,