

## REVIEW

## Root symbionts: Powerful drivers of plant above- and belowground indirect defenses

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**Abstract** Soil microbial mutualists of plants, including mycorrhizal fungi, non-mycorrhizal fungi and plant growth promoting rhizobacteria, have been typically characterized for increasing nutrient acquisition and plant growth. More recently, soil microbes have also been shown to increase direct plant defense against above- and belowground herbivores. Plants, however, do not only rely on direct defenses when attacked, but they can also recruit pest antagonists such as predators and parasitoids, both above and belowground, mainly via the release of volatile organic compounds (i.e., indirect defenses). In this review, we illustrate the main features and effects of soil microbial mutualists of plants on plant indirect defenses and discuss possible applications within the framework of sustainable crop protection against root- and shoot-feeding arthropod pests. We indicate the main knowledge gaps and the future challenges to be addressed in the study and application of these multifaceted interactions.

**Key words** arbuscular mycorrhizal fungi; crop protection; entomopathogenic nematodes; plant growth promoting rhizobacteria; *Trichoderma*

## Introduction

Global crop losses due to the combined detrimental effects of weeds, pests and diseases can be high (up to 40%, estimated by Oerke & Dehne, 2004). Animal pests alone account for 18% of crop yield losses globally (Oerke, 2006), and it has been estimated that the amount of crop consumed by insect pests could feed 1 billion people (Birch *et al.*, 2011). Farmers are thus required to increase production to feed the growing human population (Ray *et al.*, 2013), while at the same time minimizing the environmental impacts of pest control (Kiers *et al.*, 2008; Gomiero *et al.*, 2011). Consequently, agriculture is currently facing a significant challenge to maintain or increase crop yields with fewer chemical inputs and more

sustainable approaches using biofertilizers and biological control strategies (Godfray *et al.*, 2010).

Soil microbial mutualists, including root endophytic fungi, mycorrhizal fungi, plant growth-promoting fungi and rhizobacteria and rhizobia, have been long studied for their positive effects on plant nutrition, growth and yield (Vessey, 2003; Rodriguez & Sanders, 2015; Bender *et al.*, 2016). Recent evidence has also highlighted the role that root and/or rhizosphere-associated microbes can play in plant resistance against arthropod pests (Ramamoorthy *et al.*, 2001; Pineda *et al.*, 2010; Pineda *et al.*, 2015), either through changes in plant vigor, or through changes in plant endogenous regulators, and ultimately plant defenses (Poza & Azcon-Aguilar, 2007; Van Wees *et al.*, 2008; Van der Ent *et al.*, 2009; Vannette & Hunter, 2009; Pineda *et al.*, 2010; Pieterse *et al.*, 2014).

Herbivore feeding damage provokes the release of several types of elicitors in plant tissues (Kessler & Baldwin, 2002; Heil *et al.*, 2012), which activate the immune

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system of the plants (Howe & Jander, 2008; Schmelz *et al.*, 2009; Schmelz, 2015). Subsequently, plants can reduce herbivore fitness via the production of direct defenses, often through chemical or physical changes in plant tissues that have a direct impact on herbivore growth and/or reproduction (Schoonhoven *et al.*, 2005), or indirectly, via the attraction of the natural enemies of the invading herbivore (Stenberg *et al.*, 2015). Nearly 4 decades ago, Price *et al.* (1980) showed that plants could defend themselves against herbivores by recruiting natural enemies through the constitutive or inducible production/release of rewards (e.g., extrafloral nectar, EFN), shelter (e.g., domatia), or 'signals' in the form of volatile organic compounds (hereafter referred to as VOCs), a mechanism defined as indirect defense (Kessler & Heil, 2011). Since then, the identity, specificity and the metabolic pathways involved in the production (and release) of biogenic molecules mediating indirect defenses have been assessed in a number of multitrophic systems (Dicke & Baldwin, 2010). Both VOCs and EFN production by a plant following herbivore attack depends on a number of physical parameters such as temperature, relative humidity, atmospheric pressure and photoperiod, and biological parameters including the identity of the herbivore, plant age and phenology (Dudareva *et al.*, 2013; Heil, 2015).

While most of the work on multitrophic systems has centered its focus aboveground (Dicke & Baldwin, 2010; Kessler & Heil, 2011; Stam *et al.*, 2014), belowground plant organs of wild and cultivated plants are also constantly surrounded by complex communities of herbivores and predators (Blossey & Hunt-Joshi, 2003; Wardle *et al.*, 2004; Rasmann & Agrawal, 2008; Johnson & Rasmann, 2015), and it is clear that belowground herbivory can rival that aboveground in terms of effects on plant fitness (Brown & Gange, 1989; Brown & Gange, 1990; Maron, 1998).

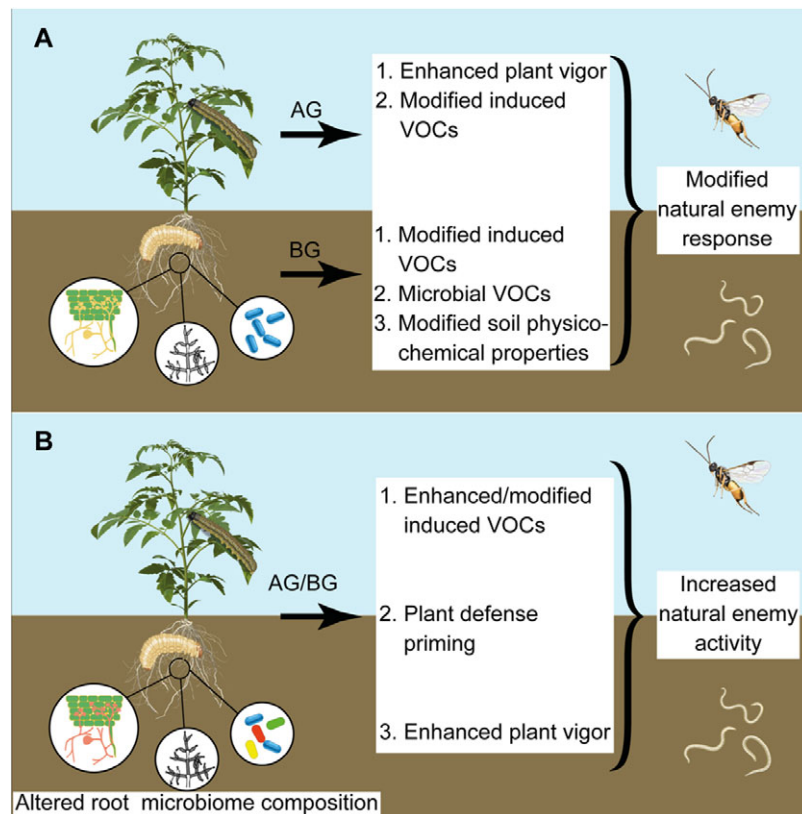
Plant-associated microbes are capable of influencing indirect plant defenses and recruitment of natural enemies of plant pests (Guerrieri *et al.*, 2004; Katayama *et al.*, 2011; Babikova *et al.*, 2013; Battaglia *et al.*, 2013; Kautz *et al.*, 2014; Godschalx *et al.*, 2015). Further, microbes are known to prime, or alter plant defense pathways (Van Wees *et al.*, 2008), which can influence the release of VOCs (Kim & Felton, 2013; Stenberg *et al.*, 2015). In this paper, we review current knowledge of the effect of soil microbial mutualists of plants on plant indirect defenses against insect herbivores above- and belowground. We will indicate how these interactions could be deployed for improved crop protection and identify gaps in our knowledge that need to be addressed to utilize these multifaceted interactions in sustainable agriculture.

## Soil microbe effects on aboveground indirect defenses of plants

Variation in indirect defense predominantly results from changes in plant quality for herbivores and/or herbivore quality as prey that alters the fitness and success of natural enemies of the herbivore. This can occur through several mechanisms, for example by attracting/repelling the natural enemy, altering its searching efficiency for prey/host or influencing herbivore quality for natural enemy consumption or parasitism. Beneficial soil microbes can mediate the expression of plant traits that contribute to these effects on natural enemies. We propose 3 ways by which plant-microbial interactions could alter and enhance plant indirect defense aboveground (Fig. 1A): (i) by changing plant size/vigor, (ii) by altering plant primary and secondary metabolism, and (iii) through microbial release of VOCs that interfere with plant signaling.

### *Soil microbes influence plant vigor*

Plant beneficial microbes can strongly influence plant growth rate, size, architecture, and vigor (Smith & Read, 2008), which could have negative or positive effects on indirect defenses. For instance, mycorrhizal fungi can increase leaf trichome density (Vannette & Hunter, 2013), which may not only affect herbivore performance, but also reduce the searching efficiency of predators and parasitoids (e.g., Romeis *et al.*, 1998; Krips *et al.*, 1999). Changes in plant size, particularly leaf density, can also influence the ability of parasitoids to find their host (Hassell & Southwood, 1978; Andow & Prokrym, 1990). Notably, if beneficial microbes increase the plant surface area per herbivore host, this can result in decreased parasitism rates, since a larger surface area per host is often associated with an increase in the searching time of parasitoids and predators (Need & Burbutis, 1979; Burbutis & Koepke, 1981). Gange *et al.* (2003) speculated that this mechanism might be one of the explanations for their observation that the number of parasitized leaf miners in *Leucanthemum vulgare* decreases with an arbuscular mycorrhizal (AM) fungi by increase in the number of leaves and height on the infested plants. Nonetheless, the authors did not study other potential factors that could drive the observed phenomenon, as for example changes in the chemistry of the leaves (Gange *et al.*, 2003). Thus, in the absence of other potential influences on indirect defense, it is possible that beneficial soil microbes that promote plant growth can impair herbivore enemy searching efficiency and thereby reduce the efficacy of plant indirect defenses (Cloyd & Sadof, 2000; Gingras & Boivin, 2002). However, microbially mediated increases in plant



**Fig. 1** (A) Mechanisms by which different soil microbial mutualists can enhance plant indirect defense toward invertebrate above or below ground (AG or BG, respectively) herbivores (here represented by a generalist chewing caterpillar and a chafer grub, respectively) through increased activity or abundance of herbivores' natural enemies (represented by a parasitoid wasp aboveground and entomopathogenic nematodes belowground). These include increased plant size/vigor and VOCs emission, altered plant metabolism and VOCs composition, microbial release of VOCs, and microbial modification of soil physicochemical properties. (B) Microbial mutualists' effects on plant indirect defense could be optimized through crop breeding and/or crop manipulation to tailor the composition of the soil microbial community, enhance or modify VOCs production, or prime the plant defense response.

size do not necessarily result in reduced parasitism rates. In the above leaf miner example, increases in leaf area did not result in a concomitant increase in prey density. By contrast, several studies have shown that, more vigorous plants support larger and more vigorous pest populations (Cornelissen *et al.*, 2008), which in turn promote larger parasitoid or predator populations (e.g., Kher *et al.*, 2014) that facilitate natural enemy searching efficiency by being more physically and chemically apparent (Hassell & Southwood, 1978; Andow & Prokrym, 1990; Aslam *et al.*, 2013). For instance, AM fungi enhanced population growth rates of both a spider mite and its predatory mite on common bean plants (Hoffmann *et al.*, 2011b), negating negative effects of increased herbivory on mycorrhizal plants. In general, such cascading effects on natural enemy populations could be mediated by a functional response to enhanced prey density as well as by an increase in shoot VOC production related to the increased

herbivore pressure, shoot volume or surface area of the host plant. The consequences of changes in herbivore population sizes induced by AM fungi for attack rates of the herbivores can vary. For instance, AM fungi increased the densities of 3 herbivore species on *Baccharis halimifolia*, and resulted in decreased parasitism on all of 3 species (Moon *et al.*, 2013). The effects may also depend on mycorrhizal species. Aphids feeding on *Phleum pratense* colonized by *Rhizophagus irregularis* (previously known as *Glomus intraradices*) experienced 140% greater parasitism than aphids feeding on plants colonized by *Funniformis mosseae* (previously known as *Glomus mossae*), or uncolonized plants (Hempel *et al.*, 2009). These latter results highlight the species-specificity of microbial effects on parasitism rates and the outcome of these 3-way interactions. Understanding this variation is extremely important in order to assess the suitability to exploit these interactions for arthropod pest control.

### Soil microbes influence plant metabolites

Aside from influences on plant growth, beneficial soil microbes can also cause massive changes in primary and secondary plant metabolites in their host plants (e.g., Schweiger *et al.*, 2014). For instance, AM fungi can increase leaf phosphorus and nitrogen concentrations and can prime plants for the production of defense metabolites such as proteinase inhibitors in response to feeding by generalist chewing insect herbivores (Jung *et al.*, 2012; Song *et al.*, 2013). These metabolic changes not only affect the performance of the insect herbivores themselves, but also their interactions with natural enemies (Minton *et al.*, 2016). The effects of beneficial plant microbes on these interactions may qualitatively vary, as the quality of herbivore hosts for their natural enemies can be either enhanced or reduced by plant-associated beneficial microbes. Enhanced indirect defense may result from 3 mechanisms. First, enhanced levels of primary metabolites that increase plant tissue quality for the herbivore can result in increased herbivore size, providing a larger resource for natural enemies and increasing for instance brood size of gregarious endoparasitoids, or enhance other aspects of prey quality, as was stressed above. For instance, predatory mites preferentially oviposit next to spider mites that have fed on mycorrhizal common bean plants as compared to spider mites that fed on nonmycorrhizal plants (Hoffmann *et al.*, 2011a), a response that is mediated by egg-derived cues indicating enhanced prey quality. Second, increased levels of defense metabolites in plant tissues may increase larval development time of nonadapted herbivores and hence the time available for successful attack by natural enemies (i.e., the “slow-growth-high-mortality” hypothesis, Clancy & Price, 1987). Third, increased levels of defense metabolites in plant tissues can also reduce the immune capacity of herbivore hosts, enhancing the chances of successful parasitization (Vinson, 1990; Schmid-Hempel, 2009; Smilanich *et al.*, 2011), if the effects of elevated plant defenses on herbivore survival and availability are not too severe. On the other hand, plant beneficial microbes could also impede indirect defenses. Enhanced plant tissue quality can enhance the herbivore’s immune system and hence reduce successful attack, whereas enhanced levels of defense metabolites can be sequestered by specialist herbivores, contributing to their immune response to parasitoid attack (Richards *et al.*, 2012).

By contrast with the paucity of work for testing the mechanisms outlined above, several studies have evaluated the effect of plant beneficial microbes on VOCs production by plants, which can serve as cues for foraging predators or parasitoids. AM fungi, for instance, have

been shown to significantly enhance the attraction of an aphid parasitoid, *Aphidius ervi*, to AM fungal colonized tomato plants in the absence of aphids when compared to uncolonized control plants (Guerrieri *et al.*, 2004); the attractiveness of AM fungal colonized plants to *A. ervi* was comparable to uncolonized tomato plants infested with aphids. Therefore, it appears that the changes in VOC profiles induced by aphids and AM fungi elicit a similar parasitoid response in tomato plants (Guerrieri *et al.*, 2004). These results are supported by a study on *Plantago lanceolata*, in which the increase in (*Z*)-3-hexenyl acetate production observed after herbivore feeding was similar to that observed in plants colonized by *R. irregularis* in the absence of herbivore feeding (Fontana *et al.*, 2009). A number of additional studies have similarly reported alteration of plant VOC profiles by mycorrhizal plants compared to nonmycorrhizal plants, although for those plants it was not tested whether the observed alterations resulted in changes in the attraction of natural enemies or not. For example, tomato plants colonized by AM fungi released larger quantities of camphene, sabinene, delta-3-carene, and *p*-cymene (Asensio *et al.*, 2012). Similarly, in *Artemisia annua*, mycorrhizal colonization enhanced the emission of limonene and artemisia ketone along with an accumulation of specific sesquiterpenes (Rapparini *et al.*, 2008). On the other hand, in broad bean, AM fungi suppressed the emission of the sesquiterpenes (*E*)-caryophyllene and (*E*)-farnesene, which was associated with enhanced attraction of aphids (Babikova *et al.*, 2014). Finally, in the absence of herbivore activity, in the model plant *Medicago truncatula*, AM fungal colonization enhanced the release of an unknown compound (named RI 1038 = C<sub>9</sub>H<sub>14</sub>O<sub>3</sub>), while reducing that of another one (named RI 1112 = C<sub>11</sub>H<sub>18</sub>O<sub>3</sub>), although a possible role of nitrogen fixing bacteria could not be excluded (Leitner *et al.*, 2010). Such soil microbe effects on constitutive plant VOCs release might result in unexpected physiological and ecological costs for the plants (Kessler & Heil, 2011). Specifically, an increase in VOCs emissions in nonattacked plants would impose physiological costs for the plants, if of course VOCs production is energetically costly. Second, enhanced VOCs emissions could decrease the efficiency of predator recruitment on plants that are effectively being under herbivore attack, therefore impose ecological costs.

In addition to changing VOC emission per se, AM fungi can also affect the release of volatiles by plants in response to herbivory. For instance, in broad bean, aphid-induced emissions of (*Z*)-3-hexenyl acetate, naphthalene and (*R*)-germacrene-D were modified when AM fungi were present on the plants (Babikova *et al.*, 2014). Recent studies show that such microbial modulation of



herbivore-induced VOCs can result in enhanced or decreased attraction of herbivore natural enemies. For example, the colonization of *Phaseolus vulgaris* roots with the mycorrhizal fungus *F. mosseae* enhanced the production of 2 sesquiterpenes ( $\beta$ -ocimene and  $\beta$ -caryophyllene) induced by the 2-spotted spider mite *Tetranychus urticae*, resulting in an enhanced attraction of the predatory mite *Phytoseiulus persimilis* (Schausberger *et al.*, 2012). Conversely, the presence of *R. irregularis* decreased the release of herbivore induced VOCs in *P. lanceolata* (Fontana *et al.*, 2009). Thus, while there are some examples where AM fungi increase the attractiveness of their host plants to herbivore enemies, their effects on VOC release after aboveground herbivory are not always consistent, and are highly context dependent.

Plant colonization with *Trichoderma* species, another genus that includes some fungal symbionts that promote plant growth and defense, especially against soil borne pathogens (Vinale *et al.*, 2008), has also been shown to affect volatile release and the attraction of natural enemies of herbivorous insects. For example, *T. longibrachiatum* MK1 altered VOCs release by tomato plants resulting in increased attractiveness to both a parasitoid and a predator of the aphid *Macrosiphum euphorbiae* (Battaglia *et al.*, 2013). The compounds potentially contributing to this natural enemy attraction included (*Z*)-3-hexenol, methyl salicylate, and  $\beta$ -caryophyllene, which elicit antennal responses by the parasitoid *A. ervi* at low concentrations (Sasso *et al.*, 2009).

Although as with *Trichoderma*, we found a similar paucity of data, evidence suggests that plant growth-promoting rhizobacteria (PGPR) can have variable effects on the attraction of natural enemies to herbivore-infested plants. For example, a common parasitoid of *Chloridea virescens* was significantly more attracted to plants colonized by a specific blend of bacterial strains compared with plants colonized by *Bacillus pumilis* strain INR-7, or untreated (control) plants (Ngumbi, 2011). Similarly, *Pseudomonas fluorescens* WCS417r colonization of *Arabidopsis thaliana* resulted in increased attraction of the parasitoid *Microplitis mediator*, a natural enemy of the leaf-chewing insect *Mamestra brassicae* (Pangesti *et al.*, 2015). VOCs analysis indicated that this attraction was related to decreased emission of the terpene (*E*)- $\alpha$ -bergamotene and the aromatics methyl salicylate and linal (Pangesti *et al.*, 2015).

By contrast, PGPR have also been shown to interfere with plant indirect defense through their effect on the production and/or release of herbivore-induced plant volatiles. For example, the attraction of *A. thaliana* infested by the aphid *Myzus persicae* towards the

parasitoid *Diaeretiella rapae* decreased when the roots of the plant were colonized by *P. fluorescens* WCS417r (Pineda *et al.*, 2012). The outcome of indirect interactions between PGPR and parasitoids or predators of pests is likely to depend on a complex interplay between plant species, bacterial strain, herbivore and natural enemy identity as well as the local biotic and abiotic environment (Pineda *et al.*, 2013).

Finally, also rhizobia can alter traits involved in indirect defense, including VOCs emissions. In lima bean plants, rhizobia decreased the emission of terpenoids and products of the octadecanoid pathway, while enhancing those of the shikimic acid pathway (Ballhorn *et al.*, 2013). The effects on attraction of herbivore natural enemies were not studied. Conversely, several studies show effects of rhizobia on predators, but have not assessed the involvement of altered VOCs profiles in the responses. For instance, in soybean rhizobia enhanced the abundances of both chewing insects and of their predators (Katayama *et al.*, 2011), while in lima bean they reduced the attractiveness of EFN for ants (Godschalx *et al.*, 2015).

#### VOCs released by soil microbes

Soil can be a significant source of microbial VOCs (Insam & Seewald, 2010), with the potential for ecological roles through their effects on plant and microbial growth, soil function and plant health (Bitas *et al.*, 2013). Research effort to date has focused on the effects of bacterial VOCs on plant growth and induced resistance towards plant pathogens (e.g., Chung *et al.*, 2016). While there are few studies of VOCs production by soil bacterial and fungal mutualists of plants in relation to plant indirect defenses, the potential for an effect on the behavior of beneficial insects is recognized (Davis *et al.*, 2013). One study provides evidence for this phenomenon. In maize plants, infection with the endophytic bacterium *Enterobacter aerogenes* promoted feeding and growth of the caterpillar *Spodoptera littoralis* and also increased the attraction of its parasitoid *Cotesia marginiventris*; these effects on insect fitness were linked to production of a major bacterial VOC, 2,3-butanediol by *E. aerogenes*, although the precise mechanisms remain to be uncovered (D'Alessandro *et al.*, 2014).

Exploiting VOCs production by plant-associated microbes is considered a potential method for enhancing plant indirect defense, as metabolic engineering of soil bacteria to enhance VOCs production is feasible (Chung *et al.*, 2016). In addition, effects of microbial VOCs have been demonstrated in field conditions, for example, soil application of 2 volatiles commonly produced by soil microbes, 2-butanone and 3-pentanol, to field-grown

cucumber seedlings was associated with reduced infestation by the aphid *M. persicae* and elevated abundance of predatory coccinellids (Song & Ryu, 2013). Greater research effort in this area might identify further examples of VOCs emitted by plant-associated microbes that have direct effects on repellence of arthropod pests and/or attraction of their natural enemies.

### Soil microbial effect on belowground indirect defenses

Root-associated microbes have been shown to affect root exudate and root volatile production, and can thereby affect plant indirect defenses belowground as described in the introduction. Specifically, we propose that soil microbes that benefit plant growth and plant resistance (Pineda *et al.*, 2010) can interfere with or promote natural enemy recruitment by plants in several ways (Fig. 1A): (1) Soil microbes increase plant vigor, and therefore change the emission of VOCs in the soil; (2) soil microbes can change plant phytohormonal-mediated induced responses and plant herbivore-predator interactions; (3) soil microbes produce a highly complex blend of VOCs that might disrupt the foraging behavior of herbivore natural enemies, and (4) soil microbes can change the physicochemical structure of the soil, therefore directly affecting predator searching behavior. Below, we discuss each point and provide directions for future research venues.

#### *Soil microbes increase plant vigor*

Plants can enhance the rhizosphere environment (e.g., Peters *et al.*, 1986; Besserer *et al.*, 2006; Neal *et al.*, 2012; Poloni & Schirawski, 2014), in order to attract soil microbes that can enhance plant growth by providing soluble inorganic nutrients and producing growth-promoting factors (Vanrhijn & Vanderleyden, 1995; Arshad & Frankenberger, 1998; Compant *et al.*, 2005; Weisskopf *et al.*, 2005; Bulgarelli *et al.*, 2013). As for aboveground parts of plant system, we can, therefore, speculate that mutualistic interactions favoring plant vigor could also indirectly enhance the production of root exudates, including root-derived VOCs released after herbivore damage, and thus attracting more herbivore natural enemies. Indeed, *Heterorhabditis bacteriophora* EPNs increased their movement toward damaged roots in response to higher levels of (*E*)-caryophyllene production (Rasmann & Turlings, 2008). Similarly, higher inducibility of VOCs in roots of *Asclepias syriaca* correlated positively with higher infection rates of EPNs near damaged roots (Rasmann *et al.*, 2011). Nonetheless,

whether a general enhancement of root VOCs production is mediated by microbe-induced plant vigor still remains to be demonstrated.

It might also be that increased plant vigor enhances the fitness of the herbivores attacking the roots, in turn negatively impacting the efficacy of soil-dwelling predators (Schmid-Hempel, 2009), but this, to our knowledge has never been tested belowground.

#### *Soil microbes influence plant defense regulation*

As for aboveground tissues, following herbivore attack, plants reconfigure their metabolism and activate genes related to defense through changes in phytohormonal networks, but nuanced differences exist between roots and shoots (Johnson *et al.*, 2016). For example, the jasmonates have been considered master regulators of counter-herbivore defenses (Howe & Jander, 2008), both in roots and shoots (Erb *et al.*, 2008), although jasmonates are less inducible in the roots than in the shoots (Erb *et al.*, 2012). Other hormones, such as abscisic acid, ethylene, or salicylic acid might also be involved in orchestrating anti-herbivore defenses in roots, but this remains to be fully elucidated (Johnson *et al.*, 2016). What is clear, however, is that soil microbes can influence plant hormonal pathways (e.g., Cameron *et al.*, 2013; de Zelicourt *et al.*, 2013; Großkinsky *et al.*, 2016), therefore likely influencing belowground tritrophic interactions, since induction of root exudates is also controlled by hormonal signaling (Pierre *et al.*, 2012; Johnson *et al.*, 2016). For example, soil fungi of the genus *Trichoderma*, which are highly abundant in the rhizosphere, produce a wide array of secondary metabolites (Contreras-Cornejo *et al.*, 2016), including plant hormones such as auxins (Contreras-Cornejo *et al.*, 2009), which can change defense induction and plant immunity (Contreras-Cornejo *et al.*, 2016). Similarly, mitogen-activated protein kinases (MAPK), which modulate the expression of the genes LOX1 (Lipoxygenase 1), a component of the jasmonic acid (JA) biosynthetic pathway (Schweizer *et al.*, 2013), were activated with the inoculation of the biocontrol agent *T. asperellum* in the roots (Shoresh *et al.*, 2006). Therefore, the application of *Trichoderma* in soils might occasionally have unintended effects on predator recruitment through gene expression changes in plants. Also root colonization by AM fungi may involve priming of the plant defense system (Cameron *et al.*, 2013; Pozo & Azcon-Aguilar, 2007). It is therefore likely that AM fungi can alter root exudates and VOCs production (as has been shown for shoot VOCs production), and subsequent recruitment of herbivore natural enemies, but this has yet to be tested.

### *Soil microbes produce VOCs that might interfere with indirect defenses*

As discussed for the aboveground system, several plant-growth promoting bacteria, or root-associated bacteria, can be responsible for producing a significant quantity and diversity of VOCs in the rhizosphere (e.g., Kai *et al.*, 2016). Soil microbe-derived VOCs in soil, besides having positive effects on plant fitness (Blom *et al.*, 2011; Bailly & Weiskopf, 2012), and reducing pathogen infectivity in the soil (Hunziker *et al.*, 2015), may also influence predator attraction. To our knowledge, there are no examples to demonstrate the impact of emission of VOCs by soil microbes on recruitment of natural enemies belowground, the interplay of these factors on plant-herbivore interactions belowground merits further elucidation.

### *Soil microbes influence soil properties*

Inoculation of beneficial microbes near the root surface can have the indirect and unintended effect of altering the native microbial community near the roots of plants (Philippot *et al.*, 2013), which in turn alters soil physicochemical properties and plant performance (Schnitzer *et al.*, 2011; Lau & Lennon, 2012; Bever *et al.*, 2013). Variation in soil properties has been shown to alter the efficacy of EPNs (Kawaka *et al.*, 2001; Toepfer *et al.*, 2010; Campos-Herrera *et al.*, 2013). Therefore, the indirect effect of soil microbes on soil properties might influence plant recruitment of foraging EPNs, either through modification of the soil physicochemical structure that directly affects nematode movement and behavior, but also indirectly by altering the ways that VOCs propagate through the soil (Hiltpold & Turlings, 2008; Rasmann *et al.*, 2012). In addition, whether the physical presence of AM fungi, or other beneficial soil microbes, interferes with nematode searching behavior is unclear. For example, the presence of AM fungi in roots of *Asclepias* plants strongly reduced the survival of fungus gnat larvae (Diptera: Sciaridae) independently of chemical defense induction in the plant (Vannette & Rasmann, 2012), suggesting that AM fungi can have direct physical effects on root herbivores, and potentially, their natural enemies.

### **Potential applications for crop protection**

Currently, there is a strong interest in optimizing crops and crop management for biocontrol of pests and diseases (Stenberg *et al.*, 2015). Although there is no general consensus about whether plant breeding has led to a loss of indirect defense traits (Benrey *et al.*, 1998; Chen *et al.*, 2015), a steady decline in herbivore-induced plant VOCs

production has been observed in several crop species when compared to their wild ancestors (Koellner *et al.*, 2008; Rodriguez-Saona *et al.*, 2011; Tamiru *et al.*, 2011; Tamiru *et al.*, 2015). Therefore, using breeding and management practices to recreate and enhance the opportunities for indirect defense is regarded as a promising way to contribute to environmentally friendly and sustainable agriculture, although this is currently severely underexploited (Kaplan, 2012; Stenberg *et al.*, 2015).

Above we have outlined the potential of soil beneficial microbes to enhance indirect plant defenses through modulation of the expression of plant traits involved in the attraction, survival and performance of the natural enemies of plant herbivores, and below we posit 2 potential means for promoting the use of soil beneficial microbes in indirect plant defense in agriculture. To date, to our knowledge, no products, applications or practices have been developed that are specifically based on the use of live beneficial soil microbes to enhance plant indirect defenses. Current applications of beneficial soil microbes are primarily based on their effects on plant growth promotion through enhanced nutrient acquisition (biofertilizers) or phytohormone production (biostimulants), enhanced tolerance to abiotic stresses such as drought and heavy metals (used in phytoremediation), and disease suppression (bioprotectants) (Bhardwaj *et al.*, 2014). This does not rule out the possibility that the growth-promoting effects of soil beneficial microbes used in current applications arises, in part, from their enhancement of plant indirect defenses; it just means that no specific effort has been devoted to select microbes for this effect.

First, to promote the use of beneficial microbes in plant indirect defense we propose that strains of beneficial microbes should be screened for consistent effects on plant indirect defense. Second, we propose that crops should be bred for traits that enhance interactions with such beneficial soil microbes. As explained in the sections above, this will require careful selection of microbial strain-crop variety combinations, as soil microbial effects can range from strong enhancement to strong reduction of predator or parasitoid attraction to the host crop. Developing such applications will not be an easy task. Below we outline some of the challenges shared with more traditional approaches to enhance plant indirect defenses that do not involve the use of beneficial soil microbes, and some of the specific advantages and disadvantages associated with an approach involving beneficial soil microbes.

There are a number of different approaches to enhance the attraction of naturally occurring or augmented biocontrol agents, including via the application of soil-dwelling microbes. At the crop level, these are summarized in Fig. 1(B) and include: (1) direct breeding, selection

or engineering of crops for enhanced VOCs emission (Dudareva & Pichersky, 2008; Stenberg *et al.*, 2015); (2) breeding crops for traits that affect the composition of the rhizosphere microbiome (Lakshmanan *et al.*, 2014; Quiza *et al.*, 2015), specifically to enhance plant colonization by beneficial microbes that contribute to indirect defense (Hiltbold & Turlings, 2012); (3) application of volatile or nonvolatile chemical elicitors to crops to induce or prime them for indirect defense (Thaler, 1999; Bektas & Eulgem, 2015); or (4) using microbial mutualists to induce or prime crops for indirect defense (Saravanakumar *et al.*, 2008; Song & Ryu, 2013; D'Alessandro *et al.*, 2014); At the crop management level, there are cultivation practices that allow for better attraction, survival or performance of pest natural enemies and antagonists, such as specific habitat provisioning (Pickett & Bugg, 1998), intercropping with natural enemy pull crops (Khan *et al.*, 2008), or placement of synthetic semiochemical or kairomone emitter release stations (Mallinger *et al.*, 2011).

Breeding or engineering crops for enhanced constitutive release of specific herbivore-induced VOCs or pest sex pheromones that attract pest natural enemies is considered to hold great promise (Degenhardt *et al.*, 2003; Kappers *et al.*, 2005; Turlings & Ton, 2006; Dudareva & Pichersky, 2008), but has yielded mixed reviews. One major concern of breeding or engineering for constitutive VOCs release is that natural enemies will quickly cease to respond to these volatiles, because volatile production is essentially decoupled from a reward, that is, is no longer strictly associated with the presence of prey, the “boy who cries wolf” scenario (Simpson *et al.*, 2011; Kaplan, 2012; Schuman *et al.*, 2012). In this regard, an important advantage of augmenting crops with beneficial soil microbes to prime crops for herbivore-induced VOCs emissions involved in indirect defense is that this approach is unlikely to suffer from the potential risk of such natural enemy adaptation, as these microbes would only enhance plant VOCs production when plants are actually attacked by the pest.

On the other hand, there are at least 2 additional challenges for increasing pest biocontrol based on the use of augmentation of beneficial soil microbes compared to more traditional approaches. One is the general challenge to develop effective microbial formulation methods that guarantee successful root colonization by the beneficial soil microbes in the competitive rhizosphere. The second is that effects of beneficial soil microbes on plant direct and indirect defense show strong context-dependency. One of the reasons for this is that there are interactions (i.e., cross-talk) between plant hormone signaling pathways that allow plants to fine-tune their responses to multiple signals from the environment. As a result, the induction of defense pathways that results in downstream

activation of VOCs biosynthesis genes can strongly depend on plant responses to other biotic and abiotic stresses in the environment such as drought (Pozo *et al.*, 2015). In addition, while we know that the performance of herbivores is influenced by an interaction between pests' life-history traits and beneficial microbes (e.g., specialist and sucking herbivores benefit whilst chewing and generalist herbivores tend not to benefit), to our knowledge no one has ever tested whether beneficial microbes influence VOCs biosynthesis based on herbivore life history or whether they promote VOCs blends that favor herbivore enemies (i.e., parasitoids and predators) with different life histories. A more thorough understanding of the synergistic and antagonistic interactions between signaling pathways in response to different types of environmental stresses will be necessary to optimize cultivation practices that reduce interference with signaling responses necessary for enhanced indirect defense. Another way to overcome such dependence on other environmental stresses might be to engineer (Chung *et al.*, 2016), or to use combinations of microbial strains that differ in their modes of triggering host plant defenses, which has been suggested as a means to overcome poor consistency in the effects of beneficial soil microbes on disease suppression (direct defense) (Gadhav *et al.*, 2016). Thus, while soil beneficial microbes can prime indirect defenses, it is unclear whether this priming occurs through multiple signaling pathways, differs from priming of direct defenses, or changes with combinations of soil microbial inoculants (Gadhav *et al.*, 2016).

Recently, engineering of the rhizosphere microbiome has been advocated as a promising approach to boost crop protection (Lakshmanan *et al.*, 2014; Quiza *et al.*, 2015). One way to achieve this is to use soil legacies in which the soil microbiome is modulated by previous crops in a way that alters the soil microbe-mediated resistance of following crops (Lapsansky *et al.*, 2016), a principle that has been demonstrated for modulation of plant direct defense (Kostenko *et al.*, 2012). Soils could thus be amended by inoculum from legacy-bearing soils.

Another approach is to design management practices or breeding crops for traits that enable crops to make more efficient use of the soil microbiome, such as root architectural traits, traits affecting specific root exudation, or traits governing communication with beneficial microbes in the rhizosphere (Lakshmanan *et al.*, 2014). While in its infancy, such attempts to engineer the rhizosphere microbiome, including their effects on below-ground and above-ground biocontrol, could contribute significantly to sustainable agricultural practices.

In conclusion, there are promising examples of beneficial effects of plant-associated soil microbes on plant



indirect defenses and arthropod pest control. However, research in this area is in its infancy and greater effort is required to understand the mechanisms underpinning the regulation of plant indirect defenses and the resulting efficacy of pest biocontrol. Promising areas of focus involve enhanced priming of plant defense, whether through crop breeding or by tailoring soil microbial composition and soil management. These approaches should be considered as a key component of integrated methods for sustainable pest and disease management in crop systems of the future.

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## Disclosure

All authors have no conflict of interest to declare.

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