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Linking aboveground and belowground interactions via induced plant defenses

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Plants have a variety of chemical defenses that often increase in concentration following attack by herbivores. Such induced plant responses can occur aboveground, in the leaves, and also belowground in the roots. We show here that belowground organisms can also induce defense responses aboveground and vice versa. Indirect defenses are particularly sensitive to interference by induced feeding activities in the other compartment, and this can disrupt multitrophic interactions. Unravelling the involvement of induced plant responses in the interactions between aboveground and belowground communities associated with plants is likely to benefit from comprehensive metabolomic analyses. Such analyses are likely to contribute to a better understanding of the costs and benefits involved in the selection for induced responses in plants.

Despite being separated in space, aboveground and belowground organisms influence each other, either directly, for example via predation of soil insects by predators that live aboveground, or indirectly, via changes in biomass and the nutritional quality of host plants [1–3]. As primary producers that have belowground (roots) and aboveground (leaves, stems and flowers) organs, plants are an important link between most life above and below ground [4]. In response to the many organisms that feed on them, such as arthropods, nematodes, and pathogenic microorganisms [5], plants have evolved a variety of chemical defenses to repel, deter or kill their enemies [6]. These defense strategies can be divided into direct defenses (directly impacting the enemy; e.g. trichomes and toxins; see Glossary) and indirect defenses (which include compounds that enable plants to recruit carnivores or enhance their effectiveness; e.g. extrafloral nectar and volatiles) (Box 1). Rather than maintaining high (constitutive) levels of these indirect defense chemicals, many plants increase their levels of defense only when they are attacked. Such 'induced defenses' (Box 1) have been studied intensively, primarily in an aboveground context [6,7]. Roots, however, also have direct and indirect induced defenses [8,9]. Because many induced defenses are not restricted to the site of attack, but result instead in

systemic defense induction throughout the plant, root feeders can change shoot defense levels, and vice versa.

In this themed issue of *TREE*, Bardgett *et al.* [10] review the temporal dynamics of soil communities and the implications for ecosystem functioning, whereas De Deyn and Van der Putten [11] discuss linkages between aboveground and belowground biodiversity. Here, we focus on the individual interactions that occur between plants and higher trophic levels and evaluate how induced plant defense responses can mediate interactions between aboveground and belowground organisms.

Recently published studies that explicitly analyzed root- and shoot-induced responses in different plant species show that root-induced responses in particular affect the effectiveness of shoot-induced defense responses and that this can disrupt aboveground multitrophic interactions. Directly, because changes in plant quality can influence, via the herbivore, organisms at higher trophic levels [12], and indirectly via the efficiency of predation or parasitization. Although studies thus far have focused specifically on changes in well-known plant defense compounds, such as terpenoids or glucosinolates, induced responses can also affect the levels of nutritional compounds (e.g. sugars and amino acids) or other compounds (e.g. hormones) that are involved in induced defense. A new technology, 'metabolomics', has recently emerged that enables a comprehensive analysis of all the

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Glossary

Constitutive defenses: plant defenses that are always expressed, independent of herbivore or pathogen attack.
Direct defenses: plant structures, such as trichomes, or compounds, such as toxins, deterrents or digestibility reducers, that directly reduce the preference or performance of a herbivore or pathogen.
Indirect defenses: enable the plant to recruit carnivores or enhance the efficiency with which carnivores attack herbivores; can be plant-induced compounds for attraction (e.g. volatiles), plant-provided food supplements for facilitation (e.g. extra-floral nectar), or plant structures for providing shelter to carnivores (e.g. domatia).
Induced defenses: changes in the plant following herbivore damage or pathogen infestation that benefit the plant by decreasing herbivore or pathogen performance or preference.
Parasitoids: insects that lay their eggs in or near other invertebrates, usually other insects, and whose larvae feed on the host and eventually kill it. Only larval stages are parasitic, whereas adults are free living.
Systemic induction: herbivore- or pathogen-induced changes in plant defense levels in unchallenged plant parts.

Box 1. What are induced plant defenses?

Induced plant responses occur in most studied plant species and are produced in response to a wide variety of organisms, such as bacteria, viruses, nematodes, insects and mammalian herbivores [6,7]. The defense response can be limited to the site of attack ('local induction'), or can be expressed in remote, undamaged plant parts ('systemic induction'). The defenses range from structural defences, such as thorns and trichomes, to toxic chemical compounds, such as nicotine and terpenoids [6,7].

The compounds that are produced in response to herbivory can either have a direct effect on the attacker itself (e.g. toxins or digestibility reducers), or serve as indirect defenses by attracting the natural enemies of the herbivores [59]. Natural enemies of herbivores, such as parasitoids or predators, can be attracted to the plant by providing sugar (Box 3) or by specific volatile organic compounds (VOC) that plants emit in response to herbivore feeding. The volatile bouquet depends not only on the plant species involved, but also on the species of herbivore that is causing the damage [60]. Components in the excretions or saliva of the herbivore, such as enzymes or amino acid conjugates, can trigger specific signaling cascades in the plant, resulting in the emission of a specific VOC blend that can attract a specific enemy to the herbivore [61,62].

Plant hormones have an important role in shaping induced responses. Jasmonic acid (JA or its methylated form, MeJA), salicylic acid (SA or MeSA), ethylene (ET), and abscisic acid (ABA), are all involved in induced responses against insects or pathogens, and can change in response to other stresses, such as drought and competition for nutrients [25,63]. Although JA is generally associated with induced responses against chewing herbivores, and SA with responses against pathogens and spider mites [60,64], the pathways that are triggered by these hormones are not independent. In some species, such as *Rumex* spp., JA and SA-induced responses overlap [65], whereas in *Lycopersicon esculentum* tomato plants, SA-induced responses counteract the expression of JA-induced responses [64]. ET and ABA are thought to act as modulators, thus enabling the plant to fine-tune its response to its attacker [66,67]. Transport of hormones or signaling molecules via the vascular system (e.g. JA and SA), or via the air (e.g. MeJA, MeSA and ET), can cause the systemic induction of defenses in undamaged parts of the plant [35].

Box 2. Metabolomics as a tool for ecologists?

Metabolomics has been defined as an unbiased way to identify and quantify comprehensively all metabolites of an organism [68], and is closely related to other fields in functional genomics, such as proteomics (the comprehensive analysis of all proteins in an organism) and transcriptomics (analysis of the entire gene expression profile of an organism) [13,69].

Metabolomics enables the simultaneous analysis of primary compounds (such as amino acids and sugars, which are of nutritional importance to herbivores), and secondary plant compounds (such as phenolics or glucosinolates, which have a defensive function in the plant) [13,69]. The potency of certain defensive compounds is contingent on the nutritional quality of the plant. Together with multivariate statistical analysis techniques such as principal component analysis and hierarchical cluster analysis, metabolomics has been used to differentiate between different genotypes or cultivars of one species [70], diseased and healthy plants [71], and plants under different nutrient regimes [72]. Although much effort has been put in to analyzing gene expression profiles of plants, metabolomics is a more valuable technique to ecologists than is transcriptomics, because differences in gene expression profiles do not automatically translate in metabolic differences (i.e. on the phenotype level) [69]. The disadvantage of metabolomic analyses is that it requires expensive high-throughput equipment, for example for nuclear magnetic resonance and gas-chromatography time-of-flight mass spectrometry, which is not readily available to evolutionary and ecologically oriented research groups. We are confident, however, that metabolomics will prove to be an important tool for the advancement of ecological studies of the multitrophic interactions associated with plants.

metabolites of a plant [13] (Box 2). Future aboveground–belowground studies should take advantage of this technology, which could significantly improve our understanding of the role of induced defenses in the complex multitrophic interactions associated with plants.

Effects of belowground organisms on aboveground plant defense

When exposed to belowground organisms, plants can show several direct (e.g. production of toxins) and indirect (e.g. release of volatiles) defense responses in the foliage that can affect aboveground herbivores and disrupt multitrophic interactions.

Direct defense

A range of belowground organisms that are directly associated with plant roots (e.g. insects, nematodes, root pathogens and mycorrhizal fungi) influence the concentration of plant defense compounds, such as terpenoids, glucosinolates or phenolics, in aboveground plant tissues [14–21]. Because these compounds frequently have a negative effect on aboveground herbivores, the action of belowground organisms can influence the performance of aboveground organisms via changes in plant defense levels. Increases and decreases in aboveground defense

as a result of belowground herbivory have been reported, suggesting that there is a range of interactions between aboveground and belowground herbivores. We argue here that these differences in responses of the plant to root-associated soil organisms are related to the differences in their feeding habits.

Several studies have shown that root chewing by belowground insects causes an increase in plant defense compounds in aboveground plant parts that is similar to that observed for foliar-feeding chewing insect larvae [14,15,19,20]. Studies that use artificial root damage or hormone applications as a substitute for root feeding show similar induction patterns [14,17,18]. Root and shoot chewers thus elicit similar induction pathways. Interestingly, the distribution of defense compounds between leaves in response to damage by root chewers can differ from that observed after foliar feeding [14]. Such spatial changes in plant defense can have major implications for aboveground organisms feeding from the plant and, thus, for plant fitness (Box 3).

Plant responses to root-feeding nematodes are more variable, and decreases and increases in concentrations of aboveground defense compounds have both been observed [16,22]. The response depends not only on the susceptibility of the plant to nematodes, but also on the type of feeding behaviour [16,23]. For example, endoparasitic sedentary root-knot and cyst nematode species, such as *Meloidogyne* and *Heterodera* spp., establish a feeding cell, which elicits hormonal regulatory responses in the host plant; endoparasitic migratory and ectoparasitic plant-feeding nematodes, such as *Pratylenchus* and *Tylenchorynchus*, do not form a cell and are likely to influence the host plant to a lesser extent [23,24].

Box 3. Case study: aboveground–belowground interactions via plant defense

In *Gossypium herbaceum* cotton plants that are exposed to root-chewing insect larvae, concentrations of non-volatile terpenoid compounds (known to deter insect feeding) in the leaves increase. Terpenoid concentrations also increase after foliar feeding by insects, but only in the youngest leaves. By contrast, older leaves also show increases in terpenoid concentrations following root damage, but the level of increase per leaf is lower than after foliar feeding (Figure I, [14]). Interestingly, this more-even distribution of defense compounds between leaves after root herbivory rather than after foliar herbivory is detrimental to insects feeding on the foliage. If the plant had been damaged previously by foliar feeders, insects preferentially feed on older leaves and avoid the young leaves with high terpenoid levels, with little consequences for larval growth rates. However, if the plant had been previously damaged by root feeders, foliar-feeding insects feed less and have reduced growth rates [15].

Cotton plants also show an aboveground indirect defense response to root herbivory and the spatial distribution also differs from the response observed after aboveground herbivory. Extrafloral nectar production (Figure II) of leaf glands increases following root herbivory. Extrafloral nectaries have an indirect defensive function because they attract ants that subsequently feed on herbivores present on the plant. Following foliar herbivory, the production of extrafloral nectar increases specifically on the leaf that is under attack, possibly to direct ants to the source of that attack. After root herbivory, however, the increase is more evenly distributed among leaves [37].
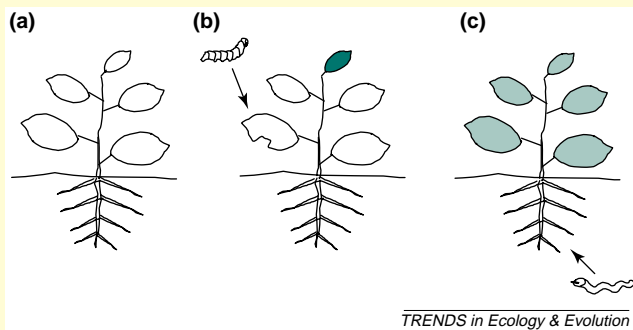

Figure I. Spatial differences in the induction of aboveground direct defense in cotton plants experiencing no herbivory (a), and after aboveground (b) and belowground (c) herbivory. Shading of leaves indicates the level of induction (white, no induction; light green, low induction; dark green, high induction).

Figure II. Extrafloral nectar gland with nectar droplet (arrow) on a cotton leaf. The production of extrafloral nectar is an indirect defense response of the plant.

Plants that are infested by bacterial or fungal root pathogens can also increase their defenses against shoot pathogens, even though the shoots are not yet infected, so-called 'systemic acquired resistance' (SAR) [20]. The presence of non-pathogenic soil bacteria, however, can cause the faster accumulation of aboveground defenses once the shoots become infested with pathogenic bacteria or fungi. The enhanced responsiveness of induced responses aboveground by non-pathogenic root bacteria has been called 'induced systemic resistance' (ISR) [25]. Induction of SAR by pathogenic root-bacteria involves the salicylic (SA) signaling pathway, whereas induction of ISR by non-pathogenic soil bacteria is SA independent and requires functional jasmonic acid (JA) and ethylene (ET) pathways [20]. SAR and ISR act independently and in an additive way: plants in which there is simultaneous activation of both pathways experience enhanced levels of shoot protection against pathogens compared with plants with only SAR or ISR [20].

Mycorrhizal fungi also form associations with plant roots. There are various types of such fungi (i.e. ectomycorrhiza and arbuscular mycorrhiza) and, although they are commonly considered beneficial, they can also have negative or neutral effects on the growth of the host plant [26,27]. Even closely related arbuscular mycorrhizal species can cause different effects within the host plant. A comparison of infection of roots of *Medicago truncatula* by two different arbuscular mycorrhizal species (*Glomus*

spp.), for example, showed that, within the plant, several hundred genes are up-regulated specifically by only one of the two mycorrhizal species [28]. Arbuscular mycorrhizal infection can cause an increase in aboveground defense compounds [29], whereas ectomycorrhizal infection can cause a decrease [30]. Other studies, using different plant species, have shown that plant defense does not change following infection with arbuscular mycorrhiza or ectomycorrhiza [21,31]. The variety of the effects of different types and species of mycorrhiza on plants could explain the variation in aboveground direct defenses (from a decrease, to none, to an increase in direct defense) in response to mycorrhizal infection [32].

Although earthworms and other decomposers are not directly associated with plant roots, they can influence aboveground plant defense levels and shoot herbivore performance [31,33,34]. A decline in foliar iridoid glucosides was observed, for example, in the presence of earthworms [31] and probably occurs as a result of differences in the availability of nutrients to the plant. Via decomposition, earthworms can increase nitrogen availability in the soil, resulting in the plant investing more in growth and less in direct defense compounds. A recent study has shown that earthworms can increase lipoxygenase (*lox*) gene expression in the leaves [34]. *Lox* is the first enzyme in the pathway that results in the signaling hormone JA, which is responsible for systemic defense induction [35]. Thus, the increase in *lox* expression caused by earthworm

activity belowground can influence aboveground plant defense responses directly.

Indirect defense

Recent studies have shown that soil organisms also influence aboveground indirect defense responses, such as the emission of volatiles. Indirect defenses enable the plant to attract carnivores or enhance the effectiveness with which those carnivores attack herbivores. *Brassica rapa* turnips that are infested with root fly larvae, for example, emit a specific shoot-produced volatile blend that attracts parasitoids of root flies [36]. Similar induction processes have been found in maize [9]. We can thus assume that parasitoids that live aboveground as adults, but attack soil-dwelling hosts, have evolved the ability to detect shoot-emitted plant cues that indicate the presence of their hosts. However, predators and parasitoids of aboveground herbivores can also be influenced by belowground organisms. Extrafloral nectar production is an indirect defense response that is found in many plant species. By producing extrafloral nectar in response to foliar herbivory, plants attract ants that subsequently feed on the insect herbivore [37]. *Gossypium herbaceum* cotton plants exposed to root-feeding insects also show increased production of extrafloral nectar in the leaves (Box 3). Other studies have shown that plants exposed to root herbivory by chewing herbivores experience increased visits from parasitoids of their aboveground herbivores [38,39]. Although these studies did not explicitly measure induced responses, such as volatiles, the results indicate that aboveground volatile production is likely to increase after root herbivory given that parasitoids are known to use plant-emitted volatiles to locate their hosts.

Similar effects on aboveground indirect defenses were found for symbiotic root interactions. The volatile blends released by plants with arbuscular mycorrhizal fungi were more attractive to aphid parasitoids than were the blends from plants without mycorrhiza [40]. The herbivore (aphids), however, performed significantly worse on plants with mycorrhizal fungi. Parasitoids were thus attracted to the plants with the fewest hosts. The so-called 'cry for help' response of the plant is thought to be a reliable defense response of plants against aboveground herbivores [41], but these results suggest that belowground organisms confuse this system, because carnivores are attracted to the least-infested plants. An important question is how these indirect defense responses have evolved under natural conditions in which plants constantly interact with different types of organisms belowground (Box 4).

Effects of aboveground organisms on belowground plant defense

Similar to belowground organisms, foliar-feeding organisms can influence belowground direct and indirect plant defense responses. Although the effects of aboveground organisms on plant defense levels in roots are less well studied, the data suggest that the influence of aboveground organisms on direct belowground plant defense is less severe, but that the composition of the soil community can be altered by changes in indirect root defenses induced by aboveground herbivores.

Direct defense

Aboveground herbivory can influence the concentration of defense compounds in the roots. Foliar feeding by caterpillars, for example, caused a decrease in alkaloid concentrations in ragwort roots; these alkaloids are known to reduce the growth of pathogenic root fungi [18]. One study reported an increase in hydroxamic acids in root exudates of rice, but only after repetitive defoliation [42]. This result is of relevance, however, because hydroxamic acids are used by the plant to defend itself against herbivores and pathogens. Other studies using foliar-feeding insects [14], shoot hormone applications [17] or moderate artificial defoliation [43] showed no significant change in the levels of defense compounds in roots. The lack of induction of root defenses by shoot feeders might be due to the source–sink relationships within a plant, with plants increasing the amount of carbon allocated to root tissues after foliar damage [2,4], and thus investing more in root growth than in root defense.

There are also several studies providing evidence, without identifying the defense compounds involved, that aboveground-induced responses influence root-associated organisms. Foliar application of JA to grape vine reduced the number of root-feeding grape phylloxera to about half the numbers on control plants [44]. Application of SA to leaves of okra plants also halved the numbers of root-knot nematode that established on treated compared with control plants [45]. However, shoot induction of SA pathways tripled the root infestation rate by endoparasitic migratory nematodes in barley [46].

In addition to changes in internal defense levels, aboveground feeding, particularly by foliar-feeding insects, might also alter the quantity and quality of root exudates. Root exudates contain various organic substances, such as sugars, amino acids and plant defense compounds [47], and attract root-feeding insects, bacteria, fungi and nematodes. Given that these exudates are released into the soil, they also influence soil organisms that live in the vicinity of the roots, but are not directly associated with them, such as decomposers [5]. Root exudation can increase in response to foliar herbivory or defoliation [42,47,48], thus having a detrimental effect on the roots themselves (if root herbivores are attracted). Moreover, after severe defoliation, the concentration of defense compounds in root exudates can increase, possibly as a result of passive leakage from the roots [42,47].

Indirect defense

Root-feeding organisms are exposed to different types of predators and parasites, such as carnivorous nematodes, mites, fungi and insects [5,49]. Carnivorous nematodes of insects (i.e. entomopathogenic nematodes), as well as insect parasitoids, are attracted to root exudates and volatile organic compounds (VOC) that are excreted by plant roots when they are damaged by root-chewing herbivores [8,9,36]. Similar results have been found for predatory mites that are attracted to volatiles that are

Box 4. Spatial–temporal model for aboveground–belowground interactions

Figure I details a conceptual model of how aboveground- and belowground-induced responses might mediate interactions between root and shoot herbivores and higher trophic levels in time. Solid arrows (e.g. between herbivores and plants) indicate trophic inter-actions and dashed arrows (e.g. between plant and other organisms) indicate effects of induced responses on aboveground and below-ground organisms. Red stars indicate interactions between root- and shoot-induced responses.

Seeds that germinate in the soil first produce a root, with which root-associated soil organisms will begin to interact even before the shoots have emerged. These root-induced responses not only affect root-associated organisms, but also entomopathogenic nematodes and other non-root-associated organisms [9,18]. Moreover, root-induced responses can cause changes in shoot defense levels. The likelihood of the shoot being detected and attacked by aboveground herbivores increases with shoot size. The response induced by aboveground feeders can be affected by the root-induced responses that are already occurring. This interaction can directly affect the shoot- and root-induced responses, and thus indirectly influence the second (herbivores) and higher trophic levels (e.g. predators and parasitoids) associated with plants.
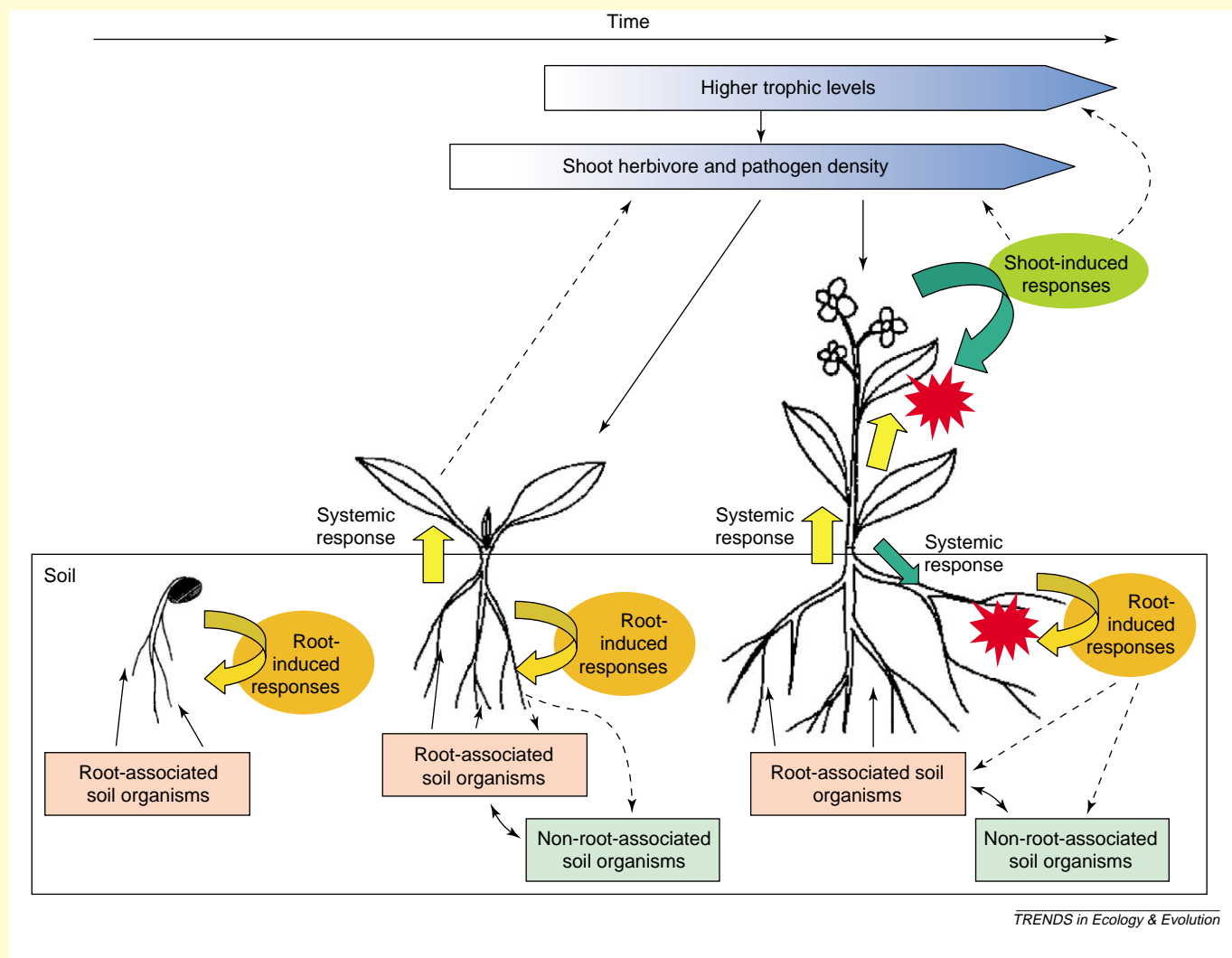

Figure I.

emitted by mite-infested tulip bulbs [50]. Because above-ground herbivory can change the quantity and composition of root exudates, it is likely that the attraction of entomopathogenic nematodes and other predators can also be altered by aboveground foliar feeders. We are not aware of any published work on such aboveground–belowground interactions affecting belowground induced indirect defense. Such interactions, however, could have far-reaching consequences for belowground multitrophic interactions. For example, they could result in a 'mis-match', whereby predators are attracted to plants where their prey are not present; alternatively, root-feeding insects and other organisms that are not directly associated with the root, such as collembola or mites, can also be attracted by root exudates [47]. Different types of organism can thus be attracted to roots of plants that sustain aboveground damage, resulting in more complex soil food webs associated with damaged than with undamaged plants. Because the stability of soil food webs is often related to the diversity of organisms that the food web consists of [51], aboveground organisms could affect the stability of belowground food webs.

Several studies have shown that adult parasitoids of root-feeding insects are also attracted to plants that are damaged by aboveground herbivores as a result of shoot-produced VOC that shoot-damaged plants emit [36,52]. These parasitoids live aboveground as adults but their larvae develop in soil-dwelling larvae or pupae. Thus, although belowground indirect plant defense efficacy appears to be affected by feeding activities of aboveground organisms, further empirical studies are needed to confirm these patterns.

Additional aboveground–belowground effects of plant defense compounds

Plant defense compounds can also influence aboveground–belowground interactions in ways that, strictly speaking, are not plant defense responses. For example, if foliar herbivory increases levels of defense compounds in leaves, these compounds can remain in dead leaf material and thus influence the decomposition behaviour and performance of belowground decomposers [3,53]. Moreover, compositional changes in leaf VOCs or root exudates might trigger neighbouring plants to induce their defenses [54,55]. This 'eaves-dropping' can result in either an increase in direct resistance against herbivores in neighbouring plants [54], or in enhanced attractiveness of these plants to aboveground parasitoids or predatory mites [55,56]. Predators might also be attracted to the 'wrong' host plant (i.e. the undamaged one), and thus aboveground–belowground interactions via plant–plant communication could disrupt the reliability of indirect defense responses of the plant. Alternatively, this type of communication could lead to a collective odour plume and, thus, to a more effective attraction of small predators or parasitoids. Given that damaged plants appear to produce more VOC than do undamaged ones [57], differences in the odour gradient within the plume would lead the natural enemy to the correct plant.

Conclusions and future directions

There is increasing evidence that induced plant defense responses have a significant role in interactions between aboveground and belowground organisms. Both direct and indirect plant defenses are affected; for example, the interactions between root- and shoot-induced defenses can reduce the effectiveness of multitrophic relationships that are mediated by indirect defense responses.

Based on this evidence, we identified three areas for future research on aboveground–belowground interactions. First, a substantial research effort has been expended on identifying which herbivores switch on particular signaling pathways and how this affects defense compounds that are often part of well-characterized metabolic pathways. However, plants contain thousands of metabolites; many of these are important for organisms feeding on the plant, and can change following herbivory. Until recently, it was difficult to study these metabolites simultaneously; however, novel analytical and statistical techniques now enable researchers to study comprehensively the chemical phenotype (i.e. metabolome) of a plant (Box 2). Such metabolomics studies have been predominantly descriptive, but this technique offers unprecedented possibilities for understanding the interactions between plants and aboveground and belowground organisms. Recently, for the legume *Lotus japonicus*, the level of hundreds of known and unknown metabolites was described in nodules, roots, leaves and flowers [58]. Similar studies at the transcriptional level are underway for symbioses with mycorrhizal fungi [28]. Future studies should address how metabolites in aboveground and belowground plant organs change after aboveground or belowground herbivory, and what the consequences are of changes in these metabolites for other associated organisms. There is great potential for studies that link complex changes in induction patterns to changes in multitrophic complexes, as well as to differences in whole-plant fitness.

Second, the spatial and temporal aspects of induced defenses of plants to aboveground and belowground organisms need to be considered in more detail. The spatial distribution of defense compounds, for example among leaves, might differ depending on the compartment (aboveground or belowground) in which the induction is triggered. Additionally, there are temporal aspects of aboveground and belowground induced responses that must be considered when evaluating the ecological and evolutionary aspects of these interactions (Box 4).

Third, studies should go beyond individual interactions between single species pairs of aboveground and belowground plant feeders and analyse the effects of soil and shoot multitrophic communities associated with plants. Indirect defense responses, both aboveground and belowground, could become disrupted, with consequences for multitrophic interactions. Future work should address the question of whether the composition of indirect plant defense compounds differs following aboveground and belowground damage. For example, how do volatile blends that are released aboveground change when plants are damaged belowground, and what are the consequences for herbivores, their natural enemies, and the plant? These 'side' effects might be ecologically important and, consequently, could be a significant selective force.

Thus, the comprehensive analysis of metabolomic changes in roots and shoots in a multitrophic context is likely to contribute to a better understanding of the costs and benefits involved in the selection for induced responses in plants. In nature, plants are exposed almost constantly to aboveground and belowground herbivores. Given that such herbivores can influence each other via changes in the shared host plant, a better understanding of those changes will also help to disentangle the relationships that occur between plants and their enemies. In agricultural systems, such knowledge could enhance the effectiveness of biological control programmes and might explain why some biological control programmes are successful whereas others fail.

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