Multitrophic interactions below and above ground: *en route* to the next level

Nicole M. van Dam[1] and Martin Heil[2]*

[1]*Radboud University Nijmegen, Institute for Water and Wetland Research (IWWR), PO Box 9010, 6500 GL Nijmegen, The Netherlands; and* [2]*Departamento de Ingeniería Genética, CINVESTAV – Irapuato, Km. 9.6 Libramiento Norte, 36821 Irapuato, Guanajuato, México*

Summary

1. Plants mediate multiple interactions between below-ground (BG) and above-ground (AG) heterotrophic communities that have no direct physical contact. These interactions can be positive or negative from the perspective of each player, can go from the BG to the AG community or vice versa, and comprise representatives of different phyla. Here we highlight emerging general patterns and discuss future research directions.

2. Ecologists initially postulated that root herbivores induce general stress responses, which increase the levels of primary (nutritional) compounds in the undamaged plant compartment and thereby facilitate future attack by AG herbivores. However, damage can also reduce the levels of primary compounds or increase contents of secondary (defensive) metabolites. Both effects may cause resistance phenotypes that play an important role in mediating BG–AG interactions. Systemically induced resistance does not only affect other herbivores but also pathogens in the AG and BG compartment and may inhibit beneficial organisms such as natural enemies of herbivores, microbial root symbionts and pollinators. Conversely, symbiotic mutualists such as mycorrhiza and rhizobia may affect AG and BG defence levels. Finally, BG–AG interactions may be costly if they impede optimal defence strategies in the undamaged compartment.

3. *Synthesis.* In order to better understand the adaptive value of BG–AG induced responses for the players involved and to identify the driving evolutionary forces, we need a better integration of studies at the community level with experiments on model systems that allow unravelling the genetic and physiological mechanisms of BG–AG interactions. Experiments preferably should be carried out at realistic densities and using the natural temporal sequence at which the various associations are established, because we can expect plants to be adapted only to events that are common over evolutionary time spans. Detailed mechanistic knowledge will help to reproduce relevant interactions in experiments that study multiple species in the field. This step will ultimately allow us to evaluate the importance of plant-mediated interactions between BG and AG communities for the fitness of the species involved and for the structuring of natural communities.

Key-words: food webs, induced defence, induced resistance, plant–herbivore interactions, plant–insect interactions, plant–microbe interactions, soil communities, systemic induction, tritrophic interactions

Introduction

Typically, higher plants root firmly in the soil, which enables them to acquire resources such as water and mineral nutrients that the aerial parts require for carbon assimilation. In spite of this obvious anatomical integration of roots and shoots, scientists only recently have started to realize that plants are also mediators of interactions between above-ground (AG) and below-ground (BG) communities (Bardgett & Wardle 2003). Most soil organisms are physically separated from AG organisms, which may be the reason that both communities have mainly been studied independently. However, plants play a key role in a multitude of specific interactions that exist between AG and BG biota (Masters & Brown 1997; van der

*Correspondence author. E-mail: mheil@ira.cinvestav.mx

Putten *et al.* 2001; Blossey & Hunt-Joshi 2003; Bezemer *et al.* 2004). In addition, soil biota affect chemical composition of soil, and the capacity of roots to absorb mineral nutrients, thereby having species-specific effects on plant growth rates, which determine the species composition of plant communities as well as of the communities at higher trophic levels. These large-scale effects can occur from the BG to the AG compartment and vice versa, and we begin to identify the first general patterns (Wardle *et al.* 2004; van der Putten *et al.* 2009).

By contrast, mechanistic studies at the level of individual plants and on the effects of certain interactions at higher trophic levels have revealed a large variety of different outcomes. BG–AG interactions that are mediated by plants occur between members of many different species, feeding guilds and phyla and can be of antagonistic, synergistic or neutral nature for one, several or all members of the complex communities that are associated with a single plant species (Bezemer *et al.* 2005; Poveda *et al.* 2005; Hol *et al.* 2010). Figure 1 illustrates some of the most commonly described interactions among BG and AG phyla and their outcomes from the perspective of both the plant and the interacting organisms. In this dazzling diversity of possible interactions, the most difficult aspect is to assess whether a response is of adaptive value for the plant or the attacker, or whether the observed phenomena represent accidental by-products of mechanisms that have evolved to serve different functions, for example, repair and tolerance responses or responses that serve to cope with abiotic stress (Núñez-Farfán, Fornoni & Valverde 2007; Kaplan *et al.* 2008c; Erb *et al.* 2011a).

As ecologists, our aim is to identify the general concepts underlying BG–AG interactions, to assess their effects on the fitness of the involved partners, and to understand their role in structuring ecosystems. In our opinion, reaching this goal requires a detailed knowledge of mechanistic aspects, such as the timing of the induced plant responses and the chemical nature of the underlying signals, combined with ecological studies analysing the effect of BG–AG interactions in a community context (see Fig. 2). To date, most studies have focussed on interactions between single (insect) species. These have been extremely valuable for assessing the role of plant compounds, and the concomitant signalling pathways involved in BG–AG interactions, but they do not provide the necessary insight into the ecological relevance of the responses. Based on papers in this special feature and the literature, we propose a conceptual ecological and evolutionary framework that will carry the research on BG–AG interactions into the future.

Interactions between BG and AG herbivores

Interactions between BG and AG herbivores have first been reported from ecological studies that experimentally manipulated the numbers of herbivores on wild plant species (Blossey & Hunt-Joshi 2003). The global pattern emerging from these studies was that BG herbivores facilitate feeding by AG herbivores such as aphids on the same plant (Moran & Whitham 1990; Masters 1995), a phenomenon that among gardeners is well known as a 'weakening' of the resistance of the aerial parts of the plant. By contrast, AG herbivores often reduced the performance of BG herbivores on roots (Fig. 1a).

RESISTANCE PHENOTYPES RESULT FROM CHANGED PRIMARY OR SECONDARY METABOLISM

At the time it was postulated that these effects were mainly driven by physiological changes in the plant that altered
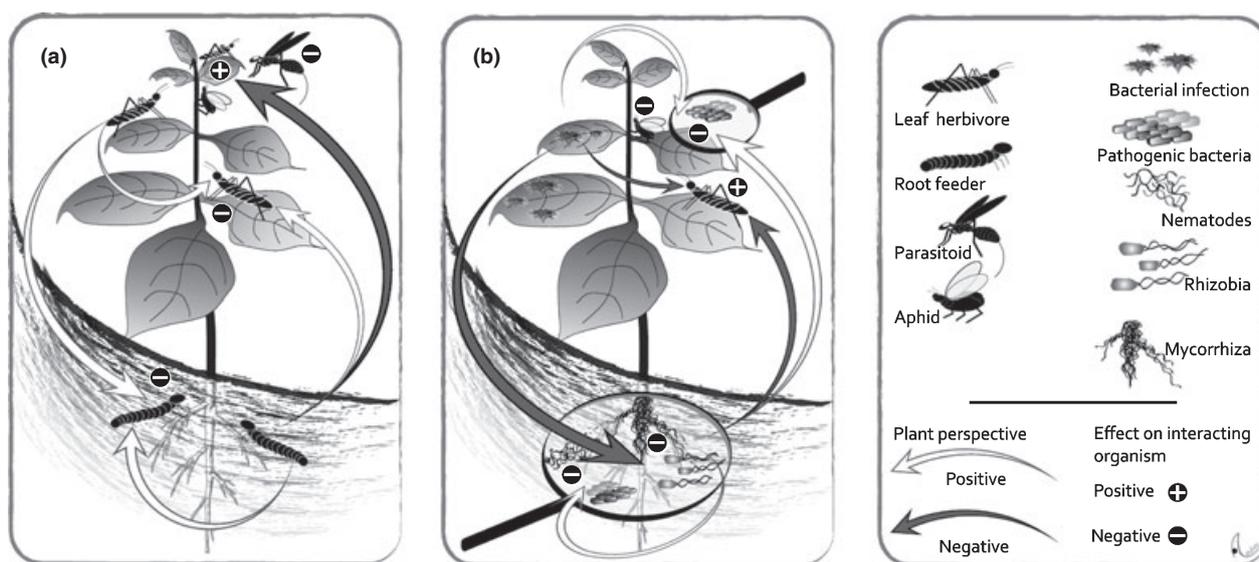

Fig. 1. Multiple interactions between below-ground (BG) and above-ground (AG) communities. Induced plant responses mediate a diverse array of interactions among AG and BG herbivores (a) and among AG herbivores and BG micro-organisms (b). These interactions can be positive (white arrows) or negative (grey arrows) from the plant's perspective and can have positive (+) or negative (−) effects on the interacting organisms. For example, root-feeding herbivores can induce resistance to AG folivores (hence, a white BG–AG arrow in (a) but commonly increase susceptibility to AG herbivores (folivores as well as sap-suckers) and negatively affect the interaction of the aerial plant parts with the third trophic level (grey BG–AG arrow in (a)). See text for details.

resource availability to herbivores in the 'other' compartment (Blossey & Hunt-Joshi 2003). Feeding by BG herbivores causes root damage, which may trigger drought stress responses (Masters, Brown & Gange 1993). Because of drought stress, the levels of primary metabolites, such as sugars and amino acids, may increase in the shoot, especially in the phloem where aphids are feeding. As most plants contain relatively low amounts of nitrogen and insect herbivore performance is mostly limited by this nutrient (Cole 1997; Schoonhoven, Jermy & van Loon 1998), it is likely that increases in nutrient levels will boost AG insect herbivore performance.

From the perspective of the herbivore, such positive effects could be termed 'facilitation' (see Table 1 for definitions of central terms as used in this contribution), because the presence of one herbivore has a beneficial effect on the performance of the other herbivore and because this effect does not depend on direct interactions between both animals (Bronstein 2009; van der Putten 2009). From the plant's perspective, facilitation of one herbivore by the other would, however, be called 'induced susceptibility' and cause a negative rather than a positive outcome of the interaction (Fig. 1a). Feeding by AG herbivores, on the contrary, was postulated to reduce the photosynthetic potential of the plant and, consequently, the allocation of resources to the roots and the resource availability to root herbivores.

However, it was also noted that other studies did not always support these general concepts (Blossey & Hunt-Joshi 2003), which called for a different or additional mechanism to explain BG–AG interactions. The early studies focused on nutritional quality of the plant, as defined by the content of primary metabolites whose increase will augment the preference for or performance of a herbivore on a plant (Table 1). Consecutive researchers identified induced defence responses as a potential mechanism underlying plant-mediated interactions between BG and AG herbivores. 'Defence' here is defined as the expression of traits, such as secondary compounds or morphological defences, which negatively affect the preference for, or performance on, a plant of an herbivore (Table 1).

A resistance phenotype can, thus, result from an increase in the defensive compounds or from a decrease in the nutritional quality of the plant. Although both phenomena cause a similar or identical phenotype with respect to the interactions between the plant and the feeding insect, the underlying physiological mechanisms are different. Understanding these differences will be essential for identifying the selective forces that guide the evolution of these responses and their interactions. For example, Erb and colleagues recently showed how phenotypic resistance responses to root herbivory in the above-ground compartment of maize are directly caused by abscisic acid (ABA)-mediated responses to water stress that results from the damage inflicted on roots, and not by increases in defensive compounds (Erb *et al.* 2011a). We therefore will always have to consider carefully whether a resistance phenotype is truly adaptive in the context of plant defence, or rather a by-product of adaptive responses to other stresses.

BG–AG INDUCED DEFENCES

Herbivore-induced responses can trigger the production of several signalling molecules that are transported throughout the plant and then cause increases in the content of defensive compounds *sensu strictu* in as yet undamaged parts of the plant (Staswick & Tiryaki 2004; Heil & Ton 2008). Systemically induced resistance responses often cross the BG–AG border. Indeed, it has been experimentally assessed that herbivore damage to the roots improves the defensive status of the aerial compartments, and vice versa (van Dam *et al.* 2003; Bezemer *et al.* 2004; Bezemer & van Dam 2005; Kaplan *et al.* 2008a; van Dam 2009). For example, the aerial parts of *Brassica nigra* plants whose roots were infested by larvae of the cabbage root fly (*Delia radicum*) had higher levels of glucosinolates, which are chemical defence compounds commonly found in Brassicaceae, and were less infested by AG herbivores than uninfested controls (Soler *et al.* 2009). Similarly, attack by root-feeding larvae of *Diabrotica virgifera* induced resistance to caterpillars in the aerial parts of maize plants due to increased levels of 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA: Erb *et al.* 2009a). Sometimes the effects of root herbivores were found to be less direct: feeding on maize roots may also cause priming of chlorogenic acid induction in the shoots upon subsequent infestation by *Spodoptera littoralis* (Erb *et al.* 2009a). These findings support the general pattern that feeding on roots, mechanical root damage or the application of defence-related hormones to the BG compartment usually enhances the defensive status of the aerial compartment (Erb *et al.* 2008; Kaplan *et al.* 2008a; Rasmann *et al.* 2009).

These more recent studies are in contrast to the earlier ones that have convincingly demonstrated facilitation of AG feeding after root damage (Masters & Brown 1992; Masters 1995). However, these earlier studies mainly used aphids as the AG herbivores whereas the others assessed the effects on lepidopteran larvae. Therefore, the effect of root damage on AG herbivores depends on their feeding strategy (Fig. 1a). The effect of shoot feeding on the resistance to root herbivores has been less studied. So far, caterpillars feeding on aerial parts have been found to increase the levels of root defence compounds and resistance to root-feeding herbivores (Soler *et al.* 2007a; Erb *et al.* 2011b) (Fig. 1a).

EFFECTS ON HIGHER TROPHIC LEVELS

Damage by BG or AG herbivores has also been found to affect pollinators and higher trophic levels, such as the natural enemies of root and shoot herbivores in the food web (Masters, Jones & Rogers 2001; Rasmann *et al.* 2005; Soler *et al.* 2005; Qiu *et al.* 2009; Ali, Alborn & Stelinski 2010; Ali, Alborn & Stelinski 2011; Johnson *et al.* 2011). Where studied, these interactions also crossed the border between roots and aerial parts. Such interactive effects may be caused by changes in herbivore quality or quantity due to systemically induced resistance in infested plants, which may directly affect the abundance and performance of parasitoids feeding on these inferior hosts (Poveda *et al.* 2005; Soler *et al.* 2005; Jansen *et al.* 2009; Qiu

Table 1. Definitions of concepts as used in this paper

Term/concept	Definition	References
Defence	Defensive traits negatively affect the enemies of the plant. Examples are thorns and other mechanical defences and toxic secondary compounds, defensive proteins, etc. as chemical defences. Karban & Baldwin (1997) defined defence responses as traits whose induction increases plant fitness by reducing damage. Here, defensive responses or compounds *sensu strictu* refer to traits such as secondary compounds, which increasingly diminish the preference for or performance on a plant of herbivores when their contents increase and which affect the fitness of the plant only in the presence of enemies.	Karban & Baldwin (1997)
Defence, indirect	A defence against plant enemies that is mediated by interactions among a plant and a third species. Most commonly, plants attract members of the third trophic level to reduce herbivore pressure	Dicke (1999), Heil (2008)
Facilitation	A positive effect of the presence of one species on the performance of another species (can, but does not need to be mutualistic)	Bronstein (2009)
Mutualism	An interaction between members of two or more different species that have a beneficial effect on all species involved	Bronstein (1994)
Nutritional quality	In the context of the present article, the sum of all compounds (usually primary metabolites) that have beneficial effects on the feeding insect. Increases in the content of these compounds increase the preference for or performance on a plant of a feeding insect.	
Priming	A process whereby the plants gets into a state of enhanced ability to express induced defence responses	Conrath, Pieterse & Mauch-Mani (2002)
Resistance	In the context of this article, any trait that negatively affects the preference for – or performance on – the plant of a herbivore or pathogen, regardless of the underlying mechanism	Karban & Baldwin (1997)
Susceptibility, induced	The induced vulnerability of a plant to attack by herbivores or pathogens. Can physiologically result from a decrease in defensive traits or an increase in compounds that are beneficial for the enemy, usually primary metabolites	Karban & Niiho (1995)
Tolerance	A fitness increase of a plant in the presence of enemies that is based on reducing the negative effects of damage caused by these enemies rather than the encounters with them	Núñez-Farfán, Fornoni & Valverde (2007)

et al. 2009). Additionally, it has been found that effects on higher trophic levels may be caused by changes in the quantity or quality of volatile emissions induced by herbivores. For example, parasitoids use shifts in volatiles as cues to identify plants without root herbivores (Rasmann & Turlings 2007; Soler *et al.* 2007b) and *Vicia faba* plants with mycorrhized roots produced lower numbers of extrafloral nectaries (Laird & Addicott 2007).

These two examples illustrate how two AG responses to very different BG events reduce the indirect defensive potential of the aerial parts of the plant. The aerial parts of BG-induced plants may emit lower quantities of volatiles or produce different volatile profiles than plants with only an AG herbivore (Rasmann & Turlings 2007; Soler *et al.* 2007b). In this case, the defence potential of the plant seems to be reduced when there are BG herbivores, as parasitoids avoid plants that usually support low-quality hosts. The density and the developmental stage of the BG herbivores, which both are related to the amount of damage that is done, are crucial factors determining the nature of the response. Parasitoid wasps foraging for AG hosts, for example, only avoided *B. nigra* plants infested by large root fly larvae, not those with small larvae (Soler *et al.* 2007b).

Another often-overlooked aspect in these studies is the timing of the AG and BG infestation (van Dam & Bezemer 2006). In this issue, Erb *et al.* (2011b) show that the sequence of arrival on the plant seems to be an essential determinant of the outcome of the interaction. The natural sequence of events is usually not considered in studies performed under controlled conditions. It seems reasonable, although, that roots associate with small, ubiquitous soil organisms such as nematodes and mycorrhiza before shoot herbivores localize the plants (van Dam & Bezemer 2006). As we explain in the following sections, soil micro-organisms can therefore play crucial roles in the interactions between BG and AG herbivores or higher trophic levels.

Interactions among AG pathogens and mutualistic BG micro-organisms

Plant roots are the central source of water and mineral nutrients and also the site of synthesis of many defensive secondary compounds. It does, therefore, not appear surprising that interactions among roots and soil-borne micro-organisms are often leading to changes in the AG resistance to microbial pathogens, just as has been described above for herbivores.

Interactions among BG and AG micro-organisms appear as diverse as those among BG and AG herbivores (Fig. 1b), because resistance that has been induced in the aerial compartment can spread to the roots and affect mutualistic micro-organisms such as rhizobia, mycorrhizal fungi and non-symbiotic bacteria in the rhizosphere (de Román *et al.* 2011; Yang *et al.* 2011). Hundreds of studies have demonstrated that the colonization of plant roots with plant-growth promoting rhizobacteria (PGPR) can elicit an induced systemic resistance (ISR) to pathogens (Pieterse *et al.* 2001; Zehnder *et al.* 2001; de Vleeschauwer & Höfte 2009), which usually does not come with the normal costs of reduced growth rates and reproductive outcomes in resistance-expressing plants (Spaepen, Vanderleyden & Okon 2009). Whereas the positive effects of PGPR for plant growth rates and resistance are well established, much less is known on the multiple effects of non-PGPR microbial root mutualists (Pineda *et al.* 2010).

AG DISEASE RESISTANCE INDUCED BY BG MICROBIAL MUTUALISTS

How can root symbioses with non-PGPR micro-organisms such as mycorrhizal fungi and nodulating rhizobia affect the resistance status of the aerial parts of the plants? Resistance expression often appears to be limited by nutrient supply (Heil & Baldwin 2002), and we would therefore generally expect a positive effect of BG mutualisms with micro-organisms on resistance expression in the entire plant that should be independent of the detailed nature of the attacker (Heil & Walters 2009). However, mycorrhized or nodulated plants grow better, contain in general more primary nutrients and may therefore be more attractive to many AG enemies of the plant (Pineda *et al.* 2010).

In general, arbuscular mycorrhizal fungi increase plant resistance to soil-borne pathogens, but the effects on AG pathogens appear to depend largely on the lifestyle and infection strategy of the pathogen (Pozo & Azcón-Aguilar 2007). For example, mycorrhization improved the resistance of banana (*Musa*) roots to nematodes (Elsen *et al.* 2008) and improved the resistance of the aerial parts of tomato (*Solanum lycopersicum*) to early blight caused by the necrotrophic fungus *Alternaria solani* (Fritz *et al.* 2006). By contrast, mycorrhization decreased the capacity of barley to express chemically induced resistance to powdery mildew caused by the biotrophic fungus *Blumeria graminis* f. sp. *hordei* (Sonnemann, Streicher & Wolters 2005). These two examples appear to be representative of the general pattern: mycorrhiza usually improves resistance to necrotrophic pathogens (white BG–AG arrow in Fig. 1b) whereas it can increase the susceptibility to biotrophic pathogens (Pozo & Azcón-Aguilar 2007).

AG PATHOGEN RESISTANCE AFFECTS BG MICROBIAL MUTUALISMS

Below-ground mutualistic micro-organisms can render their host plant more resistant to certain groups of AG pathogens, but how do AG pathogens affect the capacity of a plant to establish these beneficial interactions? The induction of salicylic acid (SA)-dependent resistance to pathogens can transiently inhibit the mycorrhization and the nodulation of soybean roots (Faessel *et al.* 2010; de Román *et al.* 2011; and references therein), whereas a treatment of the aerial parts with low concentrations of jasmonic acid (JA) increased the mycorrhization of cucumber roots (Kiers *et al.* 2010). Both observations are in line with the interpretation that a broad-spectrum resistance expression to pathogens negatively interacts with the plant's mutualistic interactions with microbes that use similar infection strategies (Heil 2001).

Plant responses to microbial infection and herbivore damage are mainly regulated by two hormones. In most species, SA controls multiple responses to biotrophic pathogens, whereas JA and its precursors and derivates control responses to herbivores and necrotrophic pathogens (Métraux 2001; Shah 2003; Heidel & Baldwin 2004; Wasternack 2007; Heil & Ton 2008). Although based on different hormones and acting against different classes of enemies, both pathways are highly interconnected (Pieterse *et al.* 2006, 2009). For example, SA can inhibit the synthesis of JA and the expression of JA-responsive genes. This situation commonly leads to a trade-off, that is, an impaired capacity of a plant to respond to insect damage when the SA-signalling pathway is already active or vice versa (Heil & Bostock 2002; Thaler, Fidantsef & Bostock 2002; Bostock 2005). In consequence, jasmonates may have positive effects on plant infections with biotrophic micro-organisms, likewise mutualistic and pathogenic ones, simply by reducing the capacity of the plant to mount a full SA-dependent response. In fact, Pozo & Azcón-Aguilar (2007) suggested that the inducing effects of mycorrhiza on AG resistance to necrotrophs and the increased susceptibility to biotrophs may result from this trade-off. The (essentially biotrophic) mycorrhizal fungus needs to suppress the (usually SA-dependent) resistance to biotrophs and thereby increases the ability of the plant to mount JA-dependent defences to necrotrophic pathogens.

Timing again appears important in the interplay among the multiple plant responses to mutualistic and pathogenic micro-organisms (see de Román *et al.* 2011) as it is in the case of interactions with herbivores (Erb *et al.* 2011b). Several studies found a negative effect of AG resistance induction by biotrophic pathogens or SA or its mimics on mutualisms of plant roots with mycorrhizal fungi or rhizobia (Faessel *et al.* 2010; de Román *et al.* 2011 and references therein). The other way round, the general effect of mycorrhiza appears to be an increased susceptibility to biotrophic pathogens. Thus, an already established mycorrhiza generally facilitates the infection of the aerial compartment by biotrophs, whereas an active systemic disease resistance to AG biotrophs impairs the potential of plant roots to establish their interaction with mycorrhiza or rhizobia.

BG–AG interactions across phyla

Although plant responses to pathogens and herbivore damage usually are dominated by either the SA or the JA pathway,

cross-talk between both signalling pathways causes various interactive effects in plants under multiple attacks (Pozo, Van Loon & Pieterse 2005; Pieterse & Dicke 2007; Korneef & Pieterse 2008; Pieterse *et al.* 2009). We would thus expect that BG–AG interactions can also occur among members of different phyla.

Indeed, plant resistance to AG herbivores can be affected by mutualisms of roots with BG micro-organisms. Plants of several herbaceous species (grasses and several annual or biennial weeds) exhibited significantly increased growth rates when being mycorrhized, but they also increased herbivore performance (Kempel *et al.* 2010). Consequently, mycorrhization in this case led to an induced susceptibility to herbivores of the aerial compartment (grey BG–AG arrow in Fig. 1b). This example likely represents only a part of the general pattern, and feeding strategy again plays an important role, as exemplified above for the lifestyles of leaf pathogens. In their meta-analysis, Koricheva *et al.* (1998) found that mycorrhization in most cases benefited mono- and oligophagous folivores, whereas the performance of polyphagous folivores was lower. Among sucking insects, phloem feeders benefited from mycorrhizal infection (grey BG–AG arrow in Fig. 1b) whereas the performance of mesophyll feeders was lower. Thus, the net outcome of a certain interaction depends both on the feeding mode and the degree of specialization of the herbivore. As a likely reason, specialists have a higher potential than generalists to adapt to the increased content of defensive compounds in the mycorrhized plant, whereas phloem feeders are less exposed to leaf secondary chemistry than are mesophyll feeders. In both cases, these feeding guilds can make better use of the increased content of the plant in primary nutritive compounds that results from the mycorrhizal interaction.

Mycorrhiza and rhizobia do not necessarily cause the same effects in this context. An infection with rhizobia induced resistance of soybean to aphids (white BG–AG arrow in Fig. 1b) and this effect depended on the genetic identity of the rhizobial strains: wild strains elicited stronger resistance than commercial ones, although leaf nitrogen contents were similar (Dean, Mescher & De Moraes 2009). In a study that quantified the costs of resistance induction by comparing growth responses to insect-mediated induction of several plant species (Kempel *et al.* 2010), mycorrhization significantly increased the costs of resistance induction, which appears contradictory to the general expectation that resistance expression reduces growth due to allocation costs (Heil & Baldwin 2002; Heil & Walters 2009). The results obtained by Kempel *et al.* (2010) are, however, in line with the observation of a reduced production of extrafloral nectaries in mycorrhized *V. faba* plants (Laird & Addicott 2007). Likewise, the capacity of *Plantago lanceolata* plants to re-grow after defoliation was compromised by mycorrhization, and leaves of mycorrhized plants contained lower amounts of iridoid glycosides than non-mycorrhized plants (Dean, Mescher & De Moraes 2009).

When searching for general patterns, we must consider that quantitative effects also play a crucial role and that the individual outcome of the interaction can be affected by shifts in the resource demands of the plant. Resistance expression is costly and uses potentially limiting resources. Whether or not a plant allocates assimilates to its rhizobia or mycorrhizal partners depends on its current need of nitrogen and phosphorous. For example, the positive effect on the mycorrhization of cucumber disappeared at high (5 mM) concentrations of JA, and a biological induction of JA-dependent responses by herbivore feeding increased the mycorrhization of the grass *Deschampsia flexusa* but not of other species (Kempel *et al.* 2010). Again, this observation likely represents the general case because the effects of mycorrhization on plant performance are nonlinear, which may be a result of increasing costs and saturating benefits within the symbiosis.

Vannette & Hunter (2011) propose a general model to explain such nonlinear outcomes. In their study, rhizome cuttings of *Asclepias syriaca* grown with different densities of mycorrhizal fungi contained different amounts of latex and cardenolides in the AG compartment and exhibited nonlinear relations among the defensive traits and the densities of mycorrhizal inoculum. This latter study and the one by Kempel *et al.* (2010) have been conducted in the context of resistance to insect feeding. Surprisingly, comparable studies in the context of disease resistance are apparently missing and would be urgently needed to determine the importance of the intensity of mycorrhization on disease resistance in the aerial parts of the plant.

Ecological and evolutionary considerations

As reviewed above, interactions between AG and BG organisms via systemically induced plant responses are common. These interactions occur in many plant species and connect AG herbivores and pathogens with BG herbivores and other ubiquitous soil organisms such as nematodes, pathogens and mutualistic micro-organisms. Both AG- and BG-induced responses may have systemic effects on the interactions of the other plant compartment with organisms that can belong to the same, or different, guilds or phyla. Adding to the puzzling diversity of possible outcomes, not all of the responses that can be seen in one compartment after the other compartment has been attacked by herbivores or infected by pathogens have necessarily evolved in a defensive context. Phenotypic resistance responses or facilitation phenomena might also result from a re-allocation of primary compounds that serve to increase the tolerance of the plant against the biotic or abiotic stress that is caused by the first attack.

PLANT-WIDE PHENOMENA: ADAPTATIONS OR SIDE-EFFECTS?

Are any general conclusions possible by now and what do we have to do in the future to predict likely general patterns? One pattern that seems to emerge is that induced responses generally appear adaptive for the affected compartment itself (white AG–AG and BG–BG arrows in Fig. 1), but may negatively affect responses in the other compartment, at least from the

perspective of the plant (grey AG–BG and BG–AG arrows in Fig. 1). This observation raises the question whether and under which conditions AG defences induced by BG organisms – or vice versa – are adaptive from the plant's perspective.

On the one hand, the benefits of resistance responses crossing the BG–AG boundary can be very obvious, as in the case of folivorous adult beetles whose larvae feed on plant roots of the same species (Johnson & Gregory 2006). Here, the AG stage and the BG stage of the herbivore belong to the same species and both may have negative effects on the host plant, which in some cases may be more than additive. An attack by the root-feeding larvae under these circumstances has a direct predictive value for the future appearance of the folivorous adults, and vice versa, depending on the life cycle of the species. Therefore it is likely that inducing shoot defences upon root damage has an adaptive value for the plant, because it provides resistance against the next developmental stage of the same herbivore (Kaplan *et al.* 2008a). Similarly, it is conceivable that plants infested with one herbivore may suffer more than proportional fitness losses when infested by another, unrelated, herbivore, be it AG or BG. Under these conditions, it may be beneficial to increase defence levels in the entire plant, especially when infestation by one herbivore is an indicator for the risk of attracting another herbivore, for example, in highly productive environments that contain many generalist herbivores (Karban 1997).

Systemically induced resistance responses, however, might be negative for the plant when causing investments in resistance of the unaffected compartment against future enemies, which then never arrive. In both cases, it may be more advantageous to systemically prime defences, as priming may be a cost-saving strategy compared with an immediate full induction of defences in the undamaged compartment (van Hulten *et al.* 2006). So far, priming of AG defence responses by BG organisms has been mainly studied with PGPR, but there are also indications for AG priming effects in nematode-infested plants (van Dam, Raaijmakers & van der Putten 2005).

On the contrary, there are numerous examples where BG–AG interactions constrain optimal defence strategies in the undamaged compartment, resulting in apparently antagonistic interactions for the plant. For example, root herbivores can alter the allocation of plant chemical defences to the leaves. Ecological theory predicts that the distribution of defences over plant organs reflects optimal defence allocation patterns: plant organs that are highly vulnerable to herbivores and have a high value in terms of future fitness should have the highest levels of defences (McKey 1974, 1979; Zangerl & Rutledge 1996). Young leaves and flowers indeed have been found to invest much more in (constitutive or induced) direct and indirect defences than mature leaves (van Dam *et al.* 1995, 2001; Iwasa *et al.* 1996; Orians, Pomerleau & Ricco 2000; Bezemer *et al.* 2004; Radhika *et al.* 2008; Rostás & Eggert 2008; Holland, Chamberlain & Horn 2009). Below-ground herbivores feeding on cotton roots, however, induced the defence levels in young leaves much less than AG feeding and increased the levels of defences in older leaves as well (Bezemer *et al.* 2004). The ecological consequences of these altered allocation patterns in the aerial parts were not extensively assessed, but it is possible that BG damage renders younger leaves less well defended compared with older leaves. The most parsimonious explanation may be that systemic induction simply follows source–sink relations and is constrained by the vascular architecture.

Indeed, both AG and BG herbivory have been found to elicit induced responses specifically in orthostichous leaves that are directly connected via vascular bundles to the induced organ (Orians, Pomerleau & Ricco 2000; Kaplan *et al.* 2008b). Moreover, it was shown that shading of the younger leaves on a ramet, which reverses the phloem flow, also reverses the direction of induction towards the older leaves in white clover (Gomez & Stuefer 2006). Unfortunately, the overall effects of source–sink constraints on plant defences have not been assessed on the plant fitness level yet. As many induced responses change the phenotype only temporally, we cannot exclude that the (long-term) positive effect of local responses in the affected compartment outweighs the transiently negative effects on the other compartment. To understand the proximal and ultimate causes of these defence induction patterns, we need more data on the underlying mechanisms and on the fitness effects of BG–AG interactions.

The most difficult situation from a scientific perspective arises, however, when the re-allocation of resources has evolved in the context of coping with abiotic stress, but also causes resistance to future biological attackers as a side-effect. Erb *et al.* (2011a) demonstrate nicely how an ABA-mediated response to water stress that results from root damage leads to resistance in the aerial parts of the plant. It is likely that the major selective force is the abiotic stress rather than a putative future biological attack. In the last section, we discuss how the major driving forces in these complex interactions could be identified and how we can determine the relative importance for the fitness of the involved partners and, finally, ecosystem functioning.

Understanding BG–AG interactions: steps towards the future

So far, our understanding of plants mediating the interactions among AG and BG communities has been based either on studies manipulating (sub-)communities with little or no control over the organisms that were removed or added (Masters, Brown & Gange 1993; de Deyn *et al.* 2003; Bezemer *et al.* 2005; Hol *et al.* 2010), or highly controlled studies with model systems that consisted of limited sets of herbivores and other species associated with the plant (Bezemer *et al.* 2004; van Dam, Raaijmakers & van der Putten 2005; Rasmann *et al.* 2005; Soler *et al.* 2005; Wurst & van der Putten 2007; Erb *et al.* 2009b). Whereas studies of the first type provide insight into the ecological relevance of BG–AG interactions for plants and their associated food webs, they yield little information about the importance of individual species in the food web, or the physiological and molecular mechanisms that drive these interactions. By contrast, studies of the second type are always in danger of losing ecological realism when using combinations of species that do not, or only rarely, occur in nature. Soil

micro-organisms in particular are often excluded from controlled experiments, whereas they can significantly affect the outcome of the interactions between BG and AG communities (see above). By contrast, the strong benefit of studies under highly controlled conditions is that they allow the elucidation of the underlying physiological and genetic mechanisms. Only when this mechanistic knowledge is combined with data on the fitness consequences will it be possible to evaluate whether particular BG–AG interactions are indeed adaptive responses, by-products of physiological restrictions or adaptations to other challenges.

DETERMINING ADAPTIVENESS

In order to determine the adaptiveness of – or driving selective forces behind – any induced response, the effect of this response on plant fitness must be studied in the presence and absence of the putatively important interacting species. For example, a phenotypic resistance against a folivore attack that is caused by root damage might result from a re-allocation of primary metabolites and might primarily represent an adaptation to drought stress that is caused by the damaging effects of root-feeding. In this case, resistance represents only a side effect and the response will positively affect plant fitness also in the absence of a second herbivore attack. Truly adaptive systemic defensive responses, by contrast, will exhibit their positive effect on plant fitness only when the second attacker enters the system.

INTEGRATING MECHANISTIC AND HOLISTIC PERSPECTIVES

In our opinion, both the global ecological approaches at the community level and the detailed experimental (physiological and genetic) studies on model systems are indispensable to obtain a comprehensive view on BG–AG interactions. The integration of the holistic – but necessarily descriptive – and the physiological – more causal, but necessarily reductionistic – approaches may be facilitated when supported by adequate theoretical modelling (Meyer *et al.* 2009a,b), or by using adequate comparative approaches under semi-field conditions.

Figure 2 illustrates how we envision the integration of these various approaches. The cycles – or rather the upward spirals – aim at increasing our level of knowledge with every shift from the community level to the model system and back. For example, observations at the community level can serve to identify the presumably important players and their role in the ecosystem. This information can be used to design simplified model systems that allow experimental manipulations. Particularly, this step can gain important support from individual-based simulation models. A prime example of such an approach is given by Meyer and colleagues, who designed an individual-based simulation to analyse the ecological consequence of BG–AG interactions including BG and AG food webs and decomposer communities (Meyer *et al.* 2009b). This first attempt was mainly based on glasshouse data obtained from a few plants species with a defined set of organisms, but like any other theoretical model it can be extended to include other parameters.

A second promising approach to study the evolutionary and ecological importance of various traits is the use of genetic families of plants that differ in the intensity at which they express the traits in question. Using genetic families of milkweed that in their roots exhibit different levels of constitutive and inducible cardenolides (as direct defence) and volatiles (attractants of entomopathogenic nematodes as indirect defence), Rasmann *et al.* (2011) demonstrate that both traits are partly redundant in their effect but combine to obtain maximum defensive effects under specific conditions of defence intensity and enemy density (Rasmann *et al.* 2011).
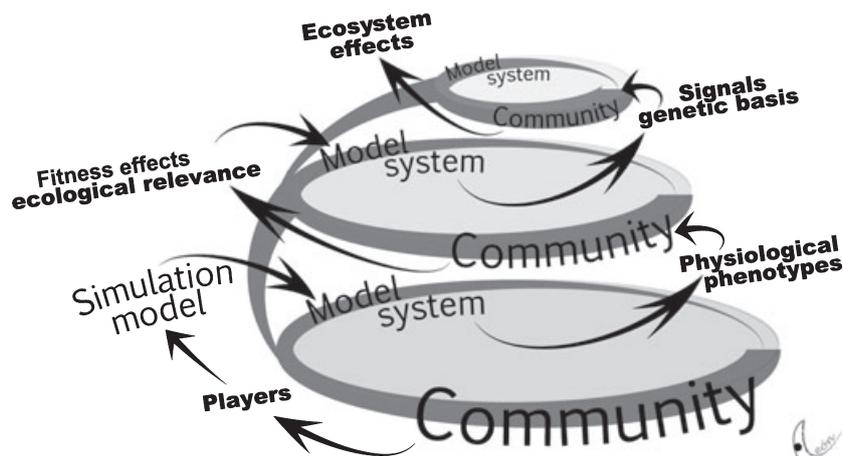

Fig. 2. Workflow diagram depicting the processes required for a more complete understanding of below-ground (BG)–above-ground (AG) interactions. Multiple transitions from analyses at the community level to studies of simplified model systems under controlled conditions are required to increase our understanding of the underlying mechanisms and the consequences of BG–AG interactions in nature. Simulation models can help to identify the most important players, which need to be included in the experimental model systems. Only the combination of these two types of approaches will yield relevant information regarding the effects of BG–AG interactions on the fitness of the interacting species and community structure.

KEYSTONE PLAYERS

A major contribution of including modelling simulations can be the identification of putatively important (combinations of) keystone players in the interactions. This information helps to design truly relevant experiments with simplified model systems under controlled conditions. Both field and semi-field data on BG–AG interactions are direly needed to parameterize mathematical models, as the interactive effects may differ from those obtained from potted plants (Hunt-Joshi & Blossey 2005).

Combining data on the net outcomes of these experiments for the involved species with measurements of their physiological phenotypes can reveal the most prominent phenomena that characterize the responses in the interacting organisms. These responses should then be experimentally reproduced under semi-field or field conditions to verify their ecological relevance. The second round of field experiments can also make use of this information to experimentally impose certain interactions, in order to estimate their fitness consequences for the partners involved. Mechanistic understanding on the regulating hormonal signals and the genetic basis of the observed responses can then be refined by further experiments under controlled conditions with those organisms that showed the greatest responses. Finally, the system is ready for the study of effects of certain interactions on the structuring of communities as soon as the current state of mechanistic understanding allows the reproducible production of certain interactions in the field.

MECHANISTIC ASPECTS OF THE RESPONSES

Our understanding of BG–AG interactions will particularly benefit from a better understanding of root–shoot integration and the communication between roots and shoots in plants (Kaplan *et al*. 2008c) as well as from additional knowledge on the timing of the appearance of important players in nature. On the one hand, the physiological integration of roots and shoots limits the spectrum of systemically induced responses that may occur. This means that certain response patterns, which would seem optimal to ecologists, may simply be physiologically impossible in the light of vascular tissue architecture and prevailing source–sink interactions (Orians, Pomerleau & Ricco 2000; Kaplan *et al*. 2008b,c). Moreover, there is too little knowledge about the regulatory mechanisms that signal root herbivory to other plant compartments as to predict how similar these are to shoot-induced responses (van Dam 2009).

These aspects may also be of importance when tolerance responses are taken into account (Núñez-Farfán, Fornoni & Valverde 2007; Kaplan *et al*. 2008c). Plants under attack by shoot herbivores may allocate primary metabolites to the roots, possibly to store resources in the undamaged compartment or to support defence production in the root (Schwachtje & Baldwin 2008). In order to assess the relative importance of tolerance vs. defence responses in a plant species, semi-field experiments are essential as they provide a better insight in the adaptive value of BG–AG interactions in the light of other

strategies to survive herbivore attacks (Núñez-Farfán, Fornoni & Valverde 2007). As mentioned above, considering the timing of the AG and BG interactions and the density of root herbivores or soil microbes are important if one wants to assess the adaptiveness of AG–BG interactions via induced resistance for the plant (van Dam & Bezemer 2006). If plants do not respond as expected to experimental treatments it may simply be a consequence of applying a sequence of events to which plants are not adapted based on their evolutionary history.

Conclusions

In this essay review we have tried to extract general patterns from the growing number of publications reporting BG–AG interactions that are mediated by inducible plant responses. We also suggest experimental strategies that will help to better understand the underlying mechanisms, to study fitness effects in order to reveal which of the observed responses are adaptive for whom, and to quantify the importance of these interactions for the structuring of communities. One pattern that is emerging is that most induced responses in the aerial parts of the plant caused by feeding on roots, or by root associations with beneficial micro-organisms, increase resistance in the shoots. As responses to root damage may also arise to reduce drought stress, it is not clear whether this form of systemically induced resistance represents an adaptive response *per se*. By contrast, the reduced capacity of roots to establish mutualisms with micro-organisms when the aerial compartment express resistance to biotrophic pathogens likely represents an unavoidable side effect of resisting the pathogens. In the end, plants, herbivores, pathogens, pollinators and members of the third trophic level all exert their own – and usually contrasting – selective pressures on plant traits. We simply cannot expect the plant to be optimally adapted to all these different threats and situations, especially not when they occur at the same time.

For the future, we suggest to apply a systematic cycle that combines controlled, mechanistic studies with studies at the community level (Fig. 2). Crucial aspects to consider in the design of these experiments are identity, density and sequence. First, it is well known from other systems that only a few keystone species can drive ecosystem function and the evolution of other species, whereas the 'passenger' species – although being intensively affected themselves – do not represent important ecological or evolutionary forces from the perspective of the other species (Agrawal 2005). The processes have been well known for AG ecosystems and these ideas need to be integrated into the study on BG–AG interactions as well. Second, we can only expect plants to be adapted to realistic densities of the most commonly interacting partners. Integrating mechanistic studies with experiments in complex systems and fulfilling the prerequisite of natural densities will help to identify the quantitatively important (i.e. most common) organisms and distinguish among drivers and passengers of plant-mediated BG–AG interactions. Third, it will be especially important to include temporal aspects in these studies: BG–AG systemically induced responses are only likely to be adaptive when the ini-

tial damage inflicted on one compartment has a predictive value for future attack of the other compartment, and when the particular order of events is sufficiently common over evolutionary time-scales.

Finally, studies analysing the physiological mechanisms will help to get crucial information on whether a particular BG–AG interaction represents an adaptive response or rather is a by-product of another mechanism, and to facilitate controlled experiments under natural conditions. Understanding whether an observed response may be adaptive is only possible when we quantify its fitness effects for the entire plant in a realistic setting. By manipulating interactions and combinations of species in the field, we will also gain a better understanding of the importance of BG–AG interactions for the structuring of ecosystems.

Acknowledgements

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