

SPECIAL FEATURE – EDITORIAL

PLANT-MEDIATED INTERACTIONS BETWEEN ABOVE- AND BELOW-GROUND COMMUNITIES

Plant-mediated interactions between above- and below-ground communities at multiple trophic levels

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Summary

1. Above-ground (AG) and below-ground (BG) biota show little overlap and are usually investigated independently. However, both communities are connected by a group of organisms that intrinsically belong to both worlds: plants. The responses of plants to environmental stresses often move from the aerial compartments to the roots and *vice versa* and thereby enable interactions among species that never come into direct physical contact.

2. Plant-mediated AG–BG interactions can have positive or negative effects on organisms from all phyla. For example, damage inflicted on roots or root symbioses with mycorrhizal fungi and rhizobia can affect the interactions between the aerial compartment and herbivores, pollinators, predators and parasitoids, whereas resistance expression in leaves can affect root herbivores as well as mutualistic or parasitic soil microorganisms. Given the tremendous diversity in the interacting organisms and also in the outcomes of the interactions, we are only just beginning to identify general patterns in the net effects of plant-mediated interactions between AG and BG communities.

3. *Synthesis*. The papers in this Special Feature reveal an important problem that remains to be solved: for most AG–BG interactions, the driving evolutionary forces remain to be identified. Because several plant responses in the context of AG–BG interactions ultimately result in negative effects on the plant itself, it appears obvious that in some cases the interacting partners manipulate the plant for their own benefit. In the future we will need to combine knowledge on the underlying physiological mechanisms with data on fitness effects. ‘Negative’ results, which demonstrate that the other compartment does NOT respond to a certain stress, or which demonstrate no or negative fitness effects on the involved species, are as important as reports on successful systemic resistance responses. Integrating knowledge on the physiological and genetic mechanisms with data on the fitness effects on all interacting partners will help to determine whether a certain AG–BG interaction is adaptive from the perspective of the plant, or the interacting organism, or both.

Key-words: herbivory, induced resistance, multitrophic interactions, mutualism, mycorrhiza, plant defence, plant pathogens, rhizobia, soil biota, systemic resistance

Introduction

Plants respond to changing abiotic conditions and attack by herbivores or pathogens with multiple responses that increase their tolerance or resistance to future stress (Karban & Baldwin 1997; Agrawal 2005; Heil 2010). Many of these responses are systemic and cross the border between the roots and the aerial plant compartments, and not all of them yield positive

outcomes from the perspective of the plant. Plants are, however, also engaged in numerous mutualisms in which they provide nutritional or structural resources to their partners (Bronstein 1994).

Because most systemic plant responses to environmental stresses are associated with changes in the resistance to the inducing or other stresses, or in the nutritional status of roots and shoots, these responses usually affect numerous other species, which directly or indirectly depend on the plant as a source of nutrients and energy. Plants thereby mediate

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interactions between two communities that hardly ever come into direct physical contact: above-ground (AG) and below-ground (BG) animals and microorganisms (Blossey & Hunt-Joshi 2003; Bezemer & van Dam 2005). These interactions are highly diverse, occur among members of different phyla and can have positive or negative effects on the plant as well as on each of the interacting organisms.

The articles in this Special Feature on 'Plant-mediated interactions between above- and below-ground communities' cover various experimental approaches and study systems and demonstrate that all types of organisms can be involved in plant-mediated AG–BG interactions. We hope that the combination of these approaches will lead us to the future: the integrated investigation of AG–BG interactions at multiple trophic levels, considering both the underlying mechanisms and the effects on the fitness of the interacting organisms and, ultimately, the structure of ecosystems.

Sequences in the establishment of interactions

Many plant responses to leaf damage also change the phenotype of roots and *vice versa*, for multiple reasons. For example, plants use roots for the synthesis of compounds that serve their resistance to AG herbivores (Erb *et al.* 2009a). Second, insects which act as folivores in their adult stage may possess larvae that feed on roots. In this case, the attack on roots predicts future danger for the leaves and a BG–AG induced systemic resistance appears highly adaptive. Plants may, however, also use the roots to 'hide' valuable resources from folivores. Although this mechanism can enhance the tolerance to folivory (Núñez-Farfán, Fornoni & Valverde 2007) it can make the roots more attractive to soil herbivores (Kaplan *et al.* 2008). Alternatively, a re-allocation of resources from roots to increase leaf resistance may consecutively limit the capacity of roots to establish or maintain costly mutualisms with microorganisms.

In all these interactions, the sequence in which the various interactions are established represents a crucial factor, which is usually not considered. In this issue, Erb and colleagues use leaf caterpillar-induced resistance responses in maize (*Zea mays*) roots to demonstrate that the sequence of arrival of different herbivores on the plant is an essential determinant of the outcome of the interaction (Erb *et al.* 2011). Similarly, induction of resistance to bacterial pathogens in leaves transiently impaired the capacity of soy bean (*Glycine max*) roots to become mycorrhizal (de Román *et al.* 2011), whereas an already established mutualism with mycorrhiza or rhizobia is usually not affected by a consecutive induction of plant resistance to pathogens (Heil 2001; de Román *et al.* 2011).

The other way round, mycorrhization in many cases exerts positive effects on the resistance state of the plant, although this effect is subject to delicate dose–response relationships and dependent on the detailed biology of the mycorrhizal fungus (Vanette & Hunter 2011). The plant has to invest costly resources in the maintenance of this mutualism and we can expect these costs to increase linearly with the degree of mycorrhization. By contrast, the potential benefits likely follow a

saturation curve. Thus, the relation of the degree of colonization by a mycorrhizal fungus with its benefits on plant fitness is nonlinear. Vanette & Hunter (2011) investigated the effect of mycorrhiza on plant defence levels and found quadratic responses in latex exudation and the content of cardenolides in *Asclepias syriaca* plants to increasing levels of mycorrhization by *Scutellospora pellucida*. They propose a general model to explain such nonlinear outcomes and thereby also underline the importance to consider nutritional mutualisms in plant defence theory. Nonlinear relations also apply to the combination of different defence strategies. As illustrated by Rasmann and colleagues, plant roots might benefit from attracting entomopathogenic nematodes only when they contain a low concentration of directly acting defence compounds (Rasmann *et al.* 2011).

Whereas cost–benefit ratios must be considered to quantitatively predict the influence of mycorrhizal associations or of multiple resistance traits on plant defence, we can expect that any effect requires the establishment of the defence-enhancing interaction before the plant is attacked, whereas active resistance expression might dramatically impair the capacity of the plant to establish mutualisms *de novo*. In the future, we should carefully study – and control for – the sequence in which plants establish their interactions with the numerous other organisms in their environment, whether these are AG or BG.

AG–BG interactions between different phyla

The resistance-mediating effects of mycorrhizal fungi demonstrate that AG–BG interactions can also occur between members of different phyla. In fact, induced resistance responses to herbivores and pathogens are highly interconnected (Pieterse *et al.* 2006, 2009) and due to the systemic nature of both responses (Heil & Ton 2008) these interactions can also cross the AG–BG border. Using foliar infestation with whitefly (*Trialeurodes vaporariorum*) of red pepper (*Capsicum annuum*), Yang and colleagues found an increased resistance to both foliar and root-infecting bacteria and also observed positive effects on probably beneficial soil microorganisms (Yang *et al.* 2011).

How complex such interactions can become is nicely demonstrated in the study by Johnson and colleagues, who demonstrate how soil biota affect the composition of experimental plant communities as well as the AG herbivores and parasitoids that depend on these plants, and how all these interactions further depend on abiotic conditions (in this case, summer drought) (Johnson *et al.* 2011). The studies by Johnson *et al.* and Yang *et al.* illustrate how local interactions between a plant and one type of organism can impact the entire AG and BG communities with which it is associated.

Costs and benefits of AG–BG interactions

Plant defence can be costly and plant responses that cross the AG–BG border add further complexity to this issue. For example, plant tolerance mechanisms to AG herbivores can be 'abused' by root herbivores (Kaplan *et al.* 2008). Volatile-

mediated indirect defence strategies depend on openly presented information and therefore are particularly prone to cause ecological costs (Heil 2008). For example, roots can gain a significant defensive benefit from the release of volatiles that attract entomopathogenic nematodes (Rasmann *et al.* 2005; Ali, Alborn & Stelinski 2010; Hiltbold *et al.* 2010). However, root volatiles may attract nematodes that cover a wide range of feeding modes and thereby also attract plant parasitic species. In this issue, Ali and colleagues demonstrate how plants can reduce the resulting ecological costs. The release of nematode-attracting cues from roots of various *Citrus* cultivars was found to be constitutive in the case of nematode-resistant cultivars but induced in the case of susceptible ones (Ali, Alborn & Stelinski 2011). Probably, susceptible cultivars take this risk only when under attack, because then the potential benefit of attracting beneficial nematodes can outweigh the potential costs. Although it is difficult to draw evolutionary conclusions from traits of cultivated plants, we must assume that the capacity of the plant roots to release these volatiles has not been considered during the breeding process. It appears, thus, likely that similar relationships between the susceptibility of a plant to certain enemies and the release of defensive traits that come at the risk to attract these enemies also exist in wild plants.

Conclusions: Research on AG–BG interactions in the need for both positive and negative results

We are only just beginning to realize the importance of plant-mediated AG–BG interactions in the structuring of multitrophic AG and BG communities. Multiple induced responses cross the border between the aerial plant compartment and the roots and also affect other species, and only a proportion of these effects are adaptive from the perspective of the plant (van Dam & Heil 2011). We must therefore expect that plants can gain benefits from avoiding non-adaptive systemic AG–BG signalling. In fact, Ali, Alborn & Stelinski (2011) searched for systemic responses of Sour orange (*Citrus aurantium*) and found no release of nematode-attracting volatiles from roots in response to weevil feeding on leaves. That plant responses to stresses that are inflicted upon one compartment must not necessarily spread to the other compartment in an uncontrolled manner was also demonstrated by genetic studies on the systemic response of maize to local attack, which revealed little overlap between AG- and BG-induced genes (Erb *et al.* 2009a,b).

Unfortunately, we must assume a severe bias in the published data towards reports on responses that do cross the AG–BG border. Researchers have only recently begun to search for responses that cross the AG–BG border. Much more remains to be discovered and recognizing the importance of 'negative' results, which clearly demonstrate that the other compartment does NOT respond to a certain stress, will be as important as reports on systemic effects. Hopefully, researchers will follow the example of Ali, Alborn & Stelinski (2011) and also report cases where no systemic responses have been found. Only more complete knowledge about the

existence – and the absence – of phenotypic changes in the different plant compartments and on the consecutive responses of other organisms will yield the complete picture. Having this information will then allow researchers to decide which species has the evolutionary control over particular plant-mediated AG–BG interaction between different organisms.

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