PLANT-MEDIATED ABOVEGROUND-BELOWGROUND INTERACTIONS: THE SPIDER MITE PERSPECTIVE

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ABSTRACT — Research on aboveground-belowground interactions has recently experienced a boost. In spite of the relative prosperity of scientific literature featuring aboveground herbivorous arthropods involved in aboveground-belowground interactions, mites have so far been under-represented. To stimulate work with mites in this area, we summarize existing research on plant-mediated interactions of aboveground herbivorous mites and belowground plant-associated organisms. A literature search revealed 17 studies dealing with plant-inhabiting mites, all of which involve the two-spotted spider mite *Tetranychus urticae*. We categorize the studies according to the belowground biota associated with the mite's host plants, summarize the observed effects of the belowground biota on the aboveground mites and discuss possible interaction mechanisms. The paucity of existing studies does not yet allow to draw general conclusions but it is apparent that these aboveground-belowground interactions are strongly context-dependent and vary among plant species and species of belowground biota. In conclusion, we argue that the wealth of knowledge on the behavior, ecology, physiology, and genetic make-up of *T. urticae* and its natural enemies, and their suitability for laboratory rearing and experimental studies at various spatial scales and organizational levels, make these plant-inhabiting mites perfectly-suited model organisms for future research on aboveground-belowground interactions.

KEYWORDS — Pathogen; symbiont; rhizosphere; *Tetranychus urticae*; predator; plant response; mycorrhiza; *Phytoseiulus persimilis*

INTRODUCTION

In recent years, research concerned with plant-associated organisms proceeded from regarding the belowground and aboveground spheres in isolation to a more integrated view of multi-trophic interactions crossing the below-aboveground boundary. The below- and aboveground each harbor a plentitude of different species and functional groups, which interact with each other and their abiotic environment at various temporal and spatial scales.

The resulting ecological complexity is enormous and mirrored in the increasing wealth and diversity of scientific output on aboveground-belowground interactions (for review see Wardle *et al.*, 2004; van der Putten *et al.* 2001, 2009). For facilitation and promotion of scientific discussion, the published studies may be classified according to various properties, e.g. theoretical versus empirical studies (although according to van der Putten *et al.* (2009) the vast majority of scientific literature on this topic deals with empirically produced data), according

to organizational level (individual, population or community effects) or experimental scale (laboratory, semi-field or field). Most existing reviews and syntheses, however, chose to classify the original literature according to the species or functional groups involved, e.g. interactions between decomposers and aboveground vertebrate (Bardgett and Wardle, 2003) or invertebrate (Scheu, 2001) herbivores, mycorrhizal fungi and insects (Gange and Brown, 2002; Koricheva *et al.*, 2009), soil microbes and aboveground insects (Pineda *et al.*, 2010), aboveground and belowground insect herbivores (Masters *et al.*, 1993) or aboveground-belowground interactions of various trophic levels occurring in each sphere (van der Putten *et al.*, 2001).

Here, we focused on aboveground-belowground interactions involving plant-inhabiting mites. The first qualifying property for scientific literature to be included in this review was mites (Acari) associated with plants being part of the studied system. Yet, arthropods of the arachnid subclass Acari are not specific to any particular terrestrial habitat (Krantz and Walter, 2009). The Acari are an extremely diverse group and may participate in aboveground-belowground interactions in various ways. Soil mites, for example, may be saprophytic and be part of the nutrient cycling complex; they may also be fungivorous and thus limiting growth and spread of plant-pathogenic and/or symbiotic fungi in the soil; they may help to disperse certain fungi by transporting the fungi's propagules or they may live as carnivorous predators and exert top down forces on the soil's microfauna (Coleman *et al.*, 2004). This list is far from being exhaustive but every function possibly affects interactions of plants with other organisms. Consequently, studies featuring mites as protagonists in aboveground-belowground interactions differ greatly in types and outcome (e.g. Scheu, 2001; Coleman, 2008) and are difficult to cover in a single review. We therefore decided to further narrow the focus of this paper to herbivorous mites feeding on aboveground plant parts, partaking in plant-mediated interactions between above- and belowground plant-associated organisms.

Arthropod herbivores are important compo-

nents of agro-ecosystems. As crop pests they have been and are thoroughly investigated. Accordingly, insect herbivore-green plant systems have been one of the first aboveground systems to be linked to belowground interactions. Many reviews have been published on the interactions between herbivorous arthropods and the belowground (e.g. Bardgett and Wardle, 2010) but studies featuring herbivorous mites are underrepresented. Interestingly, all currently published studies concerning aboveground herbivorous mites and their role in aboveground-belowground interactions feature the two-spotted spider mite *Tetranychus urticae* Koch as a model herbivore. *Tetranychus urticae* is an ubiquitous polyphagous plant pest, occurring on every continent and exploiting up to 900 different host plant species (Bolland *et al.*, 1998; Navajas, 1998). Due to its importance as a crop pest, its biology, ecology and role in aboveground trophic interactions have been thoroughly investigated (e.g. Helle and Sabelis, 1985a,b). In this review, we give an overview of empirical studies describing plant-mediated interactions between plant-associated soil biota and *T. urticae* and its predators living on aboveground plant parts. We report the outcomes of these studies, discuss possible mechanisms, look for common principles in the observed interactions, and make a case for featuring plant-inhabiting mites in future belowground-aboveground research.

Going belowground

As a starting point, we surveyed the Science Citation Index Expanded, CAB Abstracts and Google Scholar databases (all accessed October 2011) for publications reporting interactions between mites living on aboveground plant parts and belowground plant-associated organisms. The survey yielded 17 studies, all of them concerned with *T. urticae* (Table 1). The studies represent three different functional groups of plant-associated soil biota. Most studies were performed with either arbuscular mycorrhizal (7) or pathogenic (3) fungi. Five publications dealt with bacteria as soil organisms, one of which being the plant symbiont rhizobia. There are no studies on the interactions between

herbivores feeding on roots and mites living on aboveground plant parts. The study by Apriyanto and Potter (1990) on the Tobacco Necrosis Virus (TNV) is a borderline case regarding the scope of this paper because TNV *per se* is not a soil-borne organism, but is usually transmitted by soil-borne zoospores of the plant-pathogenic fungus *Olpidium brassicae* (Wor.) Dang. (Teakle and Gold, 1963). The effects of two different soil biota, an endophytic plant-pathogenic nematode and arbuscular mycorrhiza are reported in a single publication (Bonte *et al.*, 2010) and are thus represented as two entries in table 1. Here, the performance of *T. urticae* in different soil biota treatments was assessed as a consequence of local adaptation, therefore the study will be discussed separately. In addition to the studies found in the literature databases, we included our recently published study on arbuscular mycorrhiza adaptively changing spider mite induced plant volatiles (Schausberger *et al.*, 2012). We did not include the study by Findlay *et al.* (1996) showing that spider mite damage had a negative effect on leaf litter decomposition. As leaf litter is no longer part of a living plant, the described interaction is not considered plant-mediated.

Spider mites and soil-borne pathogens

The first study on plant-mediated interactions between a plant associated soil organism and *T. urticae* was performed by Karban *et al.* (1987) using the soil-borne pathogen *Verticillium dalhiae* Kleb. Previous studies had shown that aboveground microorganisms such as plant-pathogenic fungi, bacteria and viruses were able to induce resistance to similar and other microorganisms in host plants, a phenomenon often referred to as systemic acquired resistance (SAR). Similar effects had been shown for temporally or spatially separated herbivores, dubbed induced resistance (IR) (for review of both SAR and IR see Agrawal *et al.*, 1999). Karban *et al.* (1987) were however amongst the first to report plant-mediated interactions between microorganisms and herbivores, namely fungi and arthropods, thereby connecting the hitherto separated concepts of SAR and IR. Cotton plants, *Gossypium hirsutum* L., were less susceptible to the root pathogen *V.*

dalhiae if subjected to feeding by *T. urticae* prior to inoculation with the fungus. As the herbivore and the pathogen were not present at the same time, the authors concluded that these effects had been induced by the spider mites and mediated by the shared host plant (Karban *et al.*, 1987). In the same study, plants infested with *V. dalhiae* and spider mites simultaneously, carried less spider mites. However, because plant biomass was negatively affected by *V. dalhiae*, the negative effect of *V. dalhiae* on spider mite reproduction could not be unambiguously ascribed to pathogen-induced resistance to the herbivore. The proximate mechanisms of the interaction could not be determined, yet for the first time a clear link between the aboveground herbivore *T. urticae* and a soil dwelling organism was established (Karban *et al.*, 1987).

Subsequent studies addressed the effects of the athracnosis causing fungus *Colletotrichum lagenarium* (Pass.) Ell. et Halst. (Ajlan and Potter, 1991) and infection with TNV, which is usually transmitted by a soil-borne fungus (Apriyanto and Potter, 1990), on the performance of *T. urticae* on cucumber plants. Neither study revealed an observable effect of the soil borne pathogens on *T. urticae*. On tomato plants, oviposition of *T. urticae* was decreased by 20–25% in the simultaneous presence of the fungus *Fusarium oxysporum* Schltdl. (Jongebloed *et al.*, 1992). However, reduced oviposition of the spider mites was not necessarily due to the fungus because an effect of similar quality and magnitude was triggered by water stress (Jongebloed *et al.*, 1992). Pathogens as well as herbivore attacks may influence a plethora of plant quality parameters such as the qualitative and quantitative content of nutrients, primary and secondary metabolites, plant biomass, morphological features, water content, etc. and their relation to each other (van Dam *et al.*, 2003). A clear characterization of the underlying mechanisms of plant-mediated interactions between the pathogens and the mites was not undertaken in any of the above-mentioned studies (Karban *et al.*, 1987; Ajlan and Potter, 1991; Apriyanto and Potter, 1990; Jongebloed *et al.*, 1992). Stout *et al.* (2006) thoroughly reviewed the variability of plant-mediated pathogen-herbivore interactions, but did

not provide explanations for the lack of a common trend in the above cited studies, which appear to be fairly similar in their experimental setups.

Spider mites and belowground symbionts

Most terrestrial plants live in association with arbuscular mycorrhizal (AM) fungi (Smith and Read, 2008). The association of plant roots and such fungi, commonly called mycorrhiza or mycorrhizal symbiosis, alters morphological and physiological plant attributes and may thereby influence aboveground plant-associated organisms such as pathogens, herbivores and their natural enemies (Gehring and Whitham, 2002). Studies on direct effects of AM symbiosis on host plants are numerous whereas research on indirect interactions between AM and aboveground bi- and tritrophic systems have just recently gained popularity. Hoffmann *et al.* (2009, 2011a,b,c) scrutinized aboveground-belowground interactions using a model system consisting of the AM fungus *Glomus mosseae* Nicol. and Gerd., common bean plants *Phaseolus vulgaris* L., the herbivo-

rous spider mite *T. urticae* and its specialized natural enemy, the predatory mite *Phytoseiulus persimilis* Athias-Henriot, or subsystems thereof. The spider mites thrived better on mycorrhizal plants and, in a choice situation, preferred the more nutritious and phosphorous-rich mycorrhizal host plants to their non-colonized counterparts (Hoffmann *et al.*, 2009). In general, the effect of AM on insect herbivores may be highly variable (e.g. Gehring and Whitham, 2002). This variability has been attributed to the herbivores' mode of feeding and specialization, plant and fungal species or genotype and the abiotic environment (e.g. Bennett *et al.*, 2006; Koricheva *et al.*, 2009; Gange, 2007; Hartley and Gange, 2009). As known from insect herbivores (Bennett and Bever, 2007; Bennett *et al.*, 2009), also the effects of AM on spider mite performance and plant response are highly variable and depend on the AM fungus species involved (Nishida *et al.*, 2010). In an outdoor glass chamber experiment, *Lotus japonicus* (Regel) Larsen was inoculated with four different AM fungus species, namely *Gigas-*

TABLE 1: Studies investigating plant-mediated interactions between *Tetranychus urticae* and belowground plant-associated organisms and viruses.

Soil-borne functional group	Soil-borne species	Host plant species	Effects[1,2] on *T. urticae*	Effects[1,2] on host plant	Effects[1,2] on soil borne species	Remarks	References
Pathogenic fungi	*Verticillium dahliae*	*Gossypium hirsutum*	–	n.a.	–		Karban *et al.*, 1987
Pathogenic fungi	*Colletrichum lagenarium*	*Cucumis sativus*	No effect	n.a.	n.a.		Ajlan and Potter, 1991
Pathogenic fungi	*Fusarium oxysporum*	*Solanum lycopersicum*	–	n.a.	n.a.		Jongebloed *et al.*, 1992
Pathogenic viruses	Tobacco necrosis virus[3]	*C. sativus*	No effect	n.a.	n.a.		Apriyanto and Potter, 1990
Rhizobacteria	*Pseudomonas* spp., *Pseudomonas fluorescens*	*C. sativus*	–	n.a.	n.a.	Increase in phenol and cucurbitacin	Tomczyk, 1999, 2002, 2006; Tomczyk and Kielkiewicz, 2000
N-fixing bacteria	*Bradyrhizobium japonicum*, *Bradyrhizobium elkani*, *Rhizobium fredii*	*Glycine max*	+	+ (w/o herbivore)	n.a.		Katayama *et al.*, 2010
Mycorrhizal fungi	*Glomus mosseae*	*Phaseolus vulgaris*	+	+	–	Multitrophic effects	Hoffmann *et al.*, 2009, 2011a,b,c; Schausberger *et al.*, 2012
Mycorrhizal fungi	*Gigaspora margarita*	*Lotus japonicus*	n.a.	n.a.	– (short term)		Nishida *et al.*, 2009
Mycorrhizal fungi	*Glomus margarita, Glomus etunicatum, Glomus intraradices, Acaulospora longula*	*L. japonicus*	+/–	+/–	n.a.		Nishida *et al.*, 2010
Mycorrhizal fungi	*Glomus mosseae*	*P. vulgaris*	+/–	–	n.a.	Plant P increased	Bonte *et al.*, 2010
Parasitic nematodes	*Pratylenchus penetrans*	*P. vulgaris*	+/–	–	n.a.	Plant N and P increased	Bonte *et al.*, 2010

[1] + and - indicate positive and negative effects, respectively

[2] n.a.: not assessed

[3] TNV *per se* is not soil-borne but transmitted by a soil-borne pathogen; infection was performed manually on leaves

pora margarita Becker and Hall, *Glomus etunicatum* Becker and Gerd, *Glomus intraradices* Schenk and Smith or *Acaulospora longula* Spain and Schenck. Not only did the AM fungal species differentially affect the performance of *T. urticae*, but also the chemical response of *L. japonicus* upon spider mite attack. Compounds associated with induced resistance to herbivores in general and spider mites in particular were differentially altered, depending on the AM fungus species (Nishida *et al.*, 2010).

Glomus mosseae-Leguminosae associations are predominantly, albeit not always, mutualistic, resulting in a net benefit for the host plant (e.g. Ibijbijen *et al.*, 1996). For the system AM-bean-spider mite, Hoffmann *et al.* (2011c) hypothesized that for evolutionary stability of the symbiosis between the plant and the AM fungus, the AM-mediated benefit for the plants should not vanish or even turn into a cost in the presence of the herbivores. Positive effects of AM on herbivore performance, possibly threatening plant fitness, should be compensated for by AM-induced increase of plant tolerance and/or AM-induced enhancement of third trophic level natural enemies of the herbivores. Accordingly, Hoffmann *et al.* (2011c) showed that plant tolerance, the plant's capacity to re-grow and reproduce after herbivore damage, was positively affected by AM symbiosis. Both increased plant tolerance and enhanced predation by *P. persimilis* resulted in higher lifetime seed production of mycorrhizal plants as compared to non-mycorrhizal plants (Hoffmann *et al.*, 2011c). Positive effects of AM symbiosis on the predatory mites could be traced back to bottom-up trophic cascades (Hoffmann *et al.*, 2011a) and altered foraging and oviposition behaviors (Hoffmann *et al.*, 2011b; Schausberger *et al.*, 2012). In fact, *T. urticae* feeding on mycorrhizal bean plants was a more favorable prey for *P. persimilis* than *T. urticae* feeding on non-mycorrhizal plants. Thus, the positive effects of AM on the spider mites cascaded up to the next trophic level via changing the nutritional quality of the prey (Hoffmann *et al.*, 2011a). *P. persimilis*' preference for AM spider mite prey (Hoffmann *et al.*, 2011b) and stronger attraction to volatiles of spider mite-infested mycorrhizal plants than those of non-mycorrhizal plants (Schausberger *et al.*, 2012) is therefore adaptive for the predatory mites.

When AM plants are attacked by herbivores, also the belowground symbiotic fungus is affected (see Gehring and Bennett, 2009). On common bean plants, the reduction of plant damaging spider mite populations by predatory mites led to an increase in the percentage of root length colonized by the AM fungus (Hoffmann *et al.*, 2011c). Nishida *et al.* (2009) observed that spider mites feeding on *Lotus* plants (*L. japonicus*) for 3 days resulted in a short term increase of AM colonization, which was then however followed by a long term decrease. In spite of the decrease in the level of root colonization, mycorrhizal activity, measured as succinate dehydrogenase activity rate in live root tissue, was lastingly increased in plants attacked by *T. urticae* (Nishida *et al.*, 2009). If AM fungal colonization levels increase in response to herbivory, these increases typically occur early after herbivore attack (Wamberg *et al.*, 2003; Nishida *et al.*, 2009) or under intermediate levels of herbivory (Kula *et al.*, 2005). This may be attributed to elevated root exudation shortly after herbivore attack to the benefit of the AM fungus (Wamberg *et al.*, 2003; Gange, 2007). Nonetheless, in the majority of cases, herbivory on aboveground plant parts led to a decrease in root colonization levels by the AM fungus, most likely due to decreased carbon allocation to the roots (Gehring and Whitham, 2002; Barto and Rillig, 2010).

As with AM symbiosis, plant-mediated effects of nitrogen-fixing bacteria, rhizobia, on aboveground plant-associated organisms are documented in several publications (e.g. Kempel *et al.*, 2009). Similar to mycorrhizal fungi, nitrogen-fixing bacteria live in obligate symbiosis with plant roots. They live in root nodules of legumes and synthesize plant accessible nitrogen (N) compounds from atmospheric N_2. Increased levels of N can therefore be observed in tissue of plants associated with rhizobia (Lambers *et al.*, 2008). N is thought to be a limiting factor in herbivore performance (Mattson, 1980). Apart from an increase in N content, several other changes in plant chemistry take place in the process of nodulation and throughout the symbiosis. *T. urticae* feeding on nodulating soybean plants (*Glycine max*) laid

significantly more eggs than on a non-nodulating mutant (Katayama *et al.*, 2010). This effect, however, was not exclusively attributable to increased N. In soil with increasing N levels, ureid-N, an indicator of N provided by rhizobia, was found to decrease as compared to soil with low N. The positive effect on mite reproduction persisted, indicating more complex rhizobia-induced effects than a mere increase in plant-accessible N.

Bacteria of the genus *Pseudomonas* are non-obligate symbionts of plants and commonly encountered in the rhizosphere of terrestrial plants. Some *Pseudomonas* species and strains are considered favorable for plant growth (Vessey, 2003) and were thus dubbed plant growth promoting rhizobacteria (PGPR), following the pioneering work by van Peer *et al.* (1991). In greenhouses, the inoculation of cucumber (*Cucumis sativus*) plants with PGPRs (*Pseudomonas* spp) hampered spider mite performance. Population growth was decreased by approximately 40% on an otherwise spider mite-susceptible cucumber cultivar (Tomczyk, 1999). Feeding on PGPR-inoculated cucumber resulted in reduced fecundity of *T. urticae* females. Feeding damage observed on spider mite infested leaves was less severe if PGPRs were present (Tomczyk and Kielkiewicz, 2000). In a follow-up study with the same cucumber cultivar, Tomczyk (2002) observed an increase in phenols and cucurbitacins upon infestation with PGPRs and spider mites. Phenols as well as cucurbitacins are thought to play important roles in plant defense against herbivore attack. Changes in those secondary metabolites, however, seemed to depend on the plant cultivar and mite densities (Tomczyk, 2002). Moreover, *Pseudomonas fluorescens* (Trev.) Mig. changed the foraging behavior of the spider mites. Previous inoculation with the bacteria decreased host-plant acceptance of *T. urticae* in a choice experiment (Tomzcyk, 2006).

Spider mite adaptation and belowground biota

As plants interact with belowground biota, their phenotype and consequently their quality as host plants to herbivores may be altered. Plant genotypic variation has formerly been investigated for its po-

tential to influence local adaption of aboveground herbivores, herbivore performance and communities (e.g. Egan and Ott, 2007; Zovi *et al.*, 2008), but little attention has been granted to the host plant's phenotypic variation as a driver of local adaptation of herbivores. Spider mites proved to be highly adaptable to different plant species (e.g. Agrawal, 2000; Magalhães *et al.*, 2007) and are therefore well suited study organisms to investigate all kinds of selective processes. Bonte *et al.* (2010) showed that *T. urticae* can quickly adapt to phenotypic changes induced by belowground biota. Spider mites were reared for 15 generations on plants that were either infested with AM fungi, nematodes or free of plant-associated soil biota. The spider mite performance on either plant group was then assessed in a reciprocal selection experiment. Spider mites performed best on the plant phenotype of their provenance. This effect was most marked in the AM and control-adapted mites. Bonte *et al.* (2010) concluded that belowground biota may be an important yet hitherto overlooked driver of aboveground speciation.

Complex interactions, variable effects

The relatively small number of studies on plant-mediated interactions between soil biota and spider mites limits the value of generalizations from current literature. Existing studies are biased towards interactions with soil microorganisms and lack other possibly important soil biota, e.g. belowground herbivores. Most studies were concerned with the performance of individual spider mites and besides Hoffmann *et al.* (2011a,b,c) and Schausberger *et al.* (2012) none of the studies dealt with multi-trophic interactions. Proximately, the observed changes in spider mite performance were ascribed to induced direct resistance (e.g. Karban *et al.*, 1987) via an increase in plant secondary compounds (Tomczyk 1999, 2002, 2006; Tomczyk and Kielkiewicz, 2000), water stress (Jongebloed *et al.*, 1992), change in plant primary nutrient composition (Hoffmann *et al.*, 2009; Katayama *et al.*, 2010), or combinations thereof (Nishida *et al.*, 2010). Although all studies were performed with the same species of aboveground herbivore, no predictions can be made regarding the outcome of the interac-

tion or possible mechanisms to be triggered. Beneficial belowground organisms resulted in positive (Hoffmann *et al.*, 2009; Nishida *et al.*, 2009) as well as negative (Tomczyk, 1999, 2002, 2006; Tomczyk and Kielkiewicz, 2000) outcomes for the spider mites. By adding another trophic level, namely predatory mites, the spider mite density decreased, turning the originally beneficial interaction between AM fungi and spider mites into a disadvantage for the herbivore (Hoffmann *et al.*, 2011c). As a result, the only conclusion that can be drawn from the presented studies is that plant-mediated interactions between plant-mutualistic soil biota and spider mites are dependent on the abiotic and biotic context, the plant species and the species of the associated soil biota.

The scientific literature on the effect of belowground biota on insect herbivores is far more numerous than that for mites and mirrors a greater diversity in functional groups of soil organisms (see van der Putten *et al.*, 2009; Stout *et al.*, 2006). However, despite the comparable wealth of studies with insects, the deduction of general trends in the interaction with soil biota is hampered by strong interspecific variation between the insects tested, possibly correlated with the insect's mode of feeding and feeding specialization (Koricheva *et al.*, 2009; Stout *et al.*, 2006; Walling, 2000). Studies using insects are also more diverse in scale than studies using mites, featuring field experiments and a growing yet still small number of multi-trophic aboveground-belowground interactions (Bardgett and Wardle, 2010).

A case for *T. urticae* and other plant-inhabiting mites

The understanding of aboveground-belowground interactions is considered essential for the prediction and management of the ecological impacts of climate change, loss of biodiversity and the expansion of invasive species (Wardle *et al.*, 2004; Bardgett and Wardle, 2010; van der Putten *et al.*, 2004). Yet, for research to live up to these expectations, the hitherto assessed variability and context dependency will have to be succeeded by the development and formulation of more general theories

and predictions. Future studies will hence need to encompass interactions at various organizational levels and utilize the whole array of experimental scales (van der Putten *et al.*, 2009; van Dam and Heil, 2011). *T. urticae* appears to be especially apt to serve as a model protagonist for several reasons.

Any attack on or symbiosis with a plant triggers a complex cascade of plant responses. Gene-expression may be altered, resources may be translocated and secondary plant compounds may be synthesized *de novo* or in different quantities than in undisturbed plants (Bezemer and van Dam, 2005). In future studies, the employment of genomic and metabolomic tools will be indispensable in order to better understand the molecular mechanisms of aboveground-belowground interactions. Here, *T. urticae* may prove to be a perfect model organism: primarily, because great progress has been made to understand spider mite-induced plant defense at the molecular level (e.g. Kant *et al.*, 2008) and, secondly, the whole genome of *T. urticae* has recently been published (Grbic *et al.*, 2011).

Moreover, the spider mite's ecology is relatively well understood and its aboveground interactions have been excessively studied (e.g. Janssen *et al.*, 1998). This knowledge base facilitates future excursions into plant-mediated interactions between belowground organisms and aboveground multi-trophic interactions involving spider mites. Due to its ubiquitous occurrence and high agricultural relevance, bio-monitoring and field studies linking spider mites and plant-associated soil biota, may prove fruitful.

Our *status quo* assessment revealed various knowledge gaps and hence ideas for future studies. Thus far, no study on the plant-mediated interaction between spider mites and belowground herbivores has been performed. The addition of other herbivores aboveground has already been shown to have an effect on the emitted volatile blend and the response of *P. persimilis* submitted to the volatiles, suggesting antagonistic and synergistic effects (De Boer *et al.*, 2008). Clearly, multitrophic interactions above- and belowground, and if they are altered by plant-mediated interactions in the corresponding subsystem, will need further scrutiny. Scherber

et al. (2010) determined in a highly complex field monitoring study that the effect of primary producers diminishes the higher the trophic level. Although in this case only plant diversity had been investigated, similar effects may be expected for phenotypic variation of plant communities, which may be induced by soil-borne biota.

Behavioral alterations in organisms involved in aboveground-belowground interaction have scarcely been investigated. Some of the above summarized studies report changes in herbivore host acceptance and even higher trophic levels may be affected, as was shown for *P. persimilis* (Hoffmann *et al.*, 2011b,c; Schausberger *et al.*, 2012). Similarly, Aratchige *et al.* (2004) showed that tulip bulbs upon attack by *Aceria tulipae* Keifer (Acari: Eriophydae) may emit volatiles, which attract a litter- and plant-inhabiting predatory mite in a y-tube olfactometer experiment. If this effect persists under more natural conditions remains unclear. Apart from spider mites, eriophyoid mites, most of which are highly host specific and agronomically important, should be considered for future research on aboveground-belowground interactions. As many eriophyoids induce gall formation in their host plants, molecular crosstalk and hence repercussions of compartmental effects may be quite different from other more polyphagous and less host-adapted herbivores (Lillo and Skoracka, 2009).

Investigations of effects of belowground interactions on aboveground biological control have high agronomical relevance. PGPRs and mycorrhizal fungi are widely used as plant strengtheners in commercial crop production. Yet, the scientific fundament required to understand their complex effects on aboveground plant-herbivore-carnivore interactions, and thus natural and biological control, are largely lacking. Due to their agricultural and scientific relevance, plant-inhabiting mites are ideal study organisms for such research.

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