Interactions between Arthropod-Induced Aboveground and Belowground Defenses in Plants[1]

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Plants can be attacked by arthropods both above and below ground. The ensuing systemic defense response of the plant can affect even the most distant tissues. Both primary and secondary metabolic profiles of shoots can be altered upon root herbivory and vice versa (Gange and Brown, 1989; Bezemer et al., 2003; Hol et al., 2004; Schwachtje et al., 2006), making plants powerful mediators of interactions between otherwise loosely connected food webs (van der Putten et al., 2001; Bardgett and Wardle, 2003). Whereas the ecological relevance of such processes has been recognized and the role of primary and secondary metabolites acknowledged (for review, see Blossey and Hunt-Joshi, 2003; van Dam et al., 2003; Bezemer and van Dam, 2005), it remains to be explored exactly how plants coordinate their root and shoot responses against herbivores.

We propose that results from current research into the mechanisms governing plant stress responses might provide several starting points to explore the physiological basis of plant-mediated aboveground and belowground interactions. Priming (Ryals et al., 1996; van Wees et al., 1999; Ton et al., 2005; Conrath et al., 2006; Frost et al., 2008) and plant volatile signaling (Engelberth et al., 2004; Heil and Kost, 2006; Ton et al., 2007) may be particularly relevant, and we attempt to place these novel insights in the context of interactions between aboveground and belowground plant defense responses.

Because of the scope of this *Focus Issue*, we limit our review to arthropod-induced plant defense responses. We do not discuss induced changes in primary metabolites, which can be of substantial importance (Mattson, 1980; Gange and Brown, 1989; Babst et al., 2005; Schwachtje et al., 2006; Schwachtje and Baldwin, 2008). We also acknowledge the importance of putting the current findings in an appropriate ecological context (Rasmann and Agrawal, 2008) and the necessity of including microorganisms as important players in both rhizosphere and phyllosphere interactions. Several excellent reviews cover these and other intricacies of aboveground and belowground interactions (van der Putten et al., 2001; Blossey and Hunt-Joshi, 2003; van Dam et al., 2003; Bonkowski, 2004; Wardle et al., 2004).

PLANT DEFENSE RESPONSES UPON ABOVEGROUND AND BELOWGROUND HERBIVORY

Changes of Defenses in Nonattacked Tissues

Various studies on interactions between aboveground and belowground plant responses have found an increase in basal levels of shoot defenses (defined here as the level of shoot defenses in the absence of aboveground herbivores) following root herbivory, artificial damage, and plant defense hormone application (Table I). Root treatments have been shown to increase shoot concentrations of terpenoids in *Gossypium herbaceum* and maize (*Zea mays*; Bezemer et al., 2003, 2004; Rasmann et al., 2005), phenolics in *Brassica nigra* (van Dam et al., 2005), pyrrolizidine alkaloids in *Senecio jacobea* (Hol et al., 2004), certain glucosinolates in *Brassica* spp. (Birch et al., 1992; van Dam et al., 2004; Soler et al., 2005, 2007; van Dam and Raaijmakers, 2006), phytoectosteroids in spinach (*Spinacia oleracea*; Schmelz et al., 1998), proteinase inhibitors in *Nicotiana attenuata* (van Dam et al., 2001), and extrafloral nectar in *G. herbaceum* (Wäckers and Bezemer, 2003). Within this wide array of defensive metabolites, negative effects of root herbivory on basal levels of shoot defenses are also possible in some plant genotypes (Hol et al., 2004) and under certain experimental conditions (van Dam et al., 2005). Current results are as yet inconclusive about whether the generally observed increase of shoot defensive compounds is a result of active defense signaling and de novo synthesis in the shoot or whether the metabolites are translocated from the root to the shoot. We discuss both possibilities below.

In the reverse direction, effects of shoot herbivores on basal levels of root defenses have been observed (Table I). Shoot herbivory or treatment with jasmonic acid can increase root concentrations of nicotine and proteinase inhibitors in *N. attenuata* (Baldwin et al.,

Table I. *Summary of the literature on effects of root treatments (herbivory, mechanical damage, or defense hormone application) on shoot defenses and vice versa*

MD, Mechanical damage; ST, shoot treatment; RT, root treatment; AB, above ground; BG, below ground; n.a., not applicable. For a complementary table, see Rasmann and Agrawal (2008).

Plant	Root Treatment	Induced Root Defense	Altered Basal Shoot Defense	Shoot Treatment	Altered ST-Induced Shoot Defense	Influences on Herbivore AG	Reference
Effects of root treatments on shoot defenses							
G. herbaceum	*Agriotes lineatus*	Terpenoids	+ Increase of terpenoids	*S. exigua*	0 None	Reduced growth	Bezemer et al. (2003)
G. herbaceum	*A. lineatus,* MD	Terpenoid aldehydes	+ Higher terpenoid aldehyde levels	*S. exigua*	0 None	n.a.	Bezemer et al. (2004)
B. oleracea, Brassica napus	*Delia floralis*	Glucosinolates, indole-based compounds	+/− Higher glucosinolate contents, lower indole- based compounds	n.a	n.a.	n.a.	Birch et al. (1992)
S. jacobea	MD	Pyrrolizidine alkaloids	+ Partially increased pyrrolizidine alkaloids (genotype)	*M. brassicae*	0 None	Partially reduced survival	Hol et al. (2004)
B. campestris	*D. radicum*	Unknown volatiles	+ Induced volatiles	n.a.	n.a.	n.a.	Neveu et al. (2002)
Maize	*D. virgifera*	(E)-β-caryophyllene	+ Increased (E)-β-caryophyllene (foliage)	n.a.	n.a	n.a.	Rasmann et al. (2005)
Maize	*D. virgifera*	(E)-β-caryophyllene	0 None (headspace)	*S. littoralis*	− Reduced volatiles (trend)	n.a.	Rasmann and Turlings (2007)
Spinach	MD, MeJA	20-Hydroxyecdysone	+ Small induction of 20E	*S. exigua,* MD, MeJA	0 None	n.a	Schmelz et al. (1998)
Spinach	*Otiorhynchus sulcatus*	20-Hydroxyecdysone	0 None	n.a.	n.a.	n.a.	Schmelz et al. (1999)
B. nigra	*D. radicum*	n.a.	+ Higher sinigrin levels	*P. brassicae*	0/+ None/trend for increased sinigrin levels (young leaves)	Reduced growth	Soler et al. (2005)
B. nigra	*D. radicum*	n.a.	+ More volatile sulfides (headspace)	*P. brassicae*	−/+ Altered volatile profile	n.a.	Soler et al. (2007)
N. attenuata	MeJA	Proteinase inhibitors	+ Higher proteinase inhibitor levels	n.a.	n.a.	n.a.	van Dam et al. (2001)
B. oleracea, B. nigra	JA/SA	Glucosinolates (JA)	+ Induced glucosinolates (JA)	JA, SA	+ More total glucosinolates (JA/JA)	n.a.	van Dam et al. (2004)
B. nigra	*D. radicum*	n.a.	−/+ Less total glucosinolates, more phenolics	*P. rapae*	+ More total phenolics	Reduced growth and survival	van Dam et al. (2005)
B. oleracea, B. nigra	*D. radicum*	Indole glucosinolates	0/+ None/higher glucosinolate levels (plant species)	n.a.	n.a.	n.a.	van Dam and Raaijmakers (2006)
G. herbaceum	*A. lineatus,* MD	n.a.	+ Induced extrafloral nectar	n.a.	n.a.	n.a.	Wäckers and Bezemer (2003)
Plant	Shoot Treatment	Induced Shoot Defense	Altered Basal Root Defense	Root Treatment	Altered RT-Induced Root Defense	Influences on Herbivore BG	References
Effects of shoot treatments on root defenses							
N. attenuata	MD	Nicotine	+ Nicotine	n.a.	n.a.	n.a.	Baldwin et al. (1994)
G. herbaceum	*S. exigua*	Terpenoids	0 None	*A. lineatus*	− Nonsignificant reduction of terpenoids	None	Bezemer et al. (2003)
G. herbaceum	*S. exigua*	Terpenoid aldehydes	0 None	*A. lineatus,* MD	− Reduced terpenoid aldehyde levels	n.a.	Bezemer et al. (2004)

(Table continues on following page.)

Table I. (*Continued from previous page.*)

Plant	Shoot Treatment	Induced Shoot Defense		Altered Basal Root Defense	Root Treatment		Altered RH-Induced Root Defense	Influences on Herbivore BG	References
S. jacobea	*Mamestra brassicae*	None (pyrrolizidine alkaloids)	−	Reduced pyrrolizidine alkaloids	MD	0/−	Partially reduced pyrrolizidine alkaloids (genotype)	n.a.	Hol et al. (2004)
B. campestris	JA, SA	Glucosinolates	+	Higher level of glucosinolates	n.a.		n.a.	n.a.	Ludwig-Müller et al. (1997)
Maize	*S. littoralis*	(E)-β-caryophyllene	0	None	*D. virgifera*	−	Reduced (E)-β-caryophyllene	n.a.	Rasmann and Turlings (2007)
Spinach	*S. exigua*, MD, MeJA	None (20E)	0	None	n.a.		n.a.	n.a.	Schmelz et al. (1998)
B. nigra	*P. brassicae*	n.a.	+	Higher indole glucosinolate levels	*D. radicum*		n.a.	Reduced survival and size	Soler et al. (2007)
N. attenuata	MJ, MD	Proteinase inhibitors	+	Higher level of trypsin proteinase inhibitors	n.a.		n.a.	n.a.	van Dam et al. (2001)
B. oleracea, *B. nigra*	JA, SA	Glucosinolates	0	None	JA, SA	0	None discussed	n.a.	van Dam et al. (2004)
C. officinale	MD	Pyrrolizidine alkaloids	+/−	Higher/lower level of pyrrolizidine alkaloids (genotype)	n.a.		n.a.	n.a.	van Dam and Vrieling (1994)

1994; van Dam et al., 2001), as well as glucosinolates in *Brassica campestris* and *B. nigra* (Ludwig-Müller et al., 1997; Soler et al., 2007). In contrast, reduced concentrations of other defense-related compounds can also be observed, such as in the case of pyrrolizidine alkaloids in the roots of *S. jacobea* after herbivory on shoots (Hol et al., 2004). Other studies found no clear effects of shoot treatments on basal levels of root defensive compounds, including terpenoids in *G. herbaceum* and maize (Bezemer et al., 2003, 2004; Rasmann and Turlings, 2007), phytoectosteroids in spinach (Schmelz et al., 1998), pyrrolizidine alkaloids in *Cynoglossum officinale* (van Dam and Vrieling, 1994), and glucosinolates in *Brassica oleracea* and *B. nigra* (van Dam et al., 2004). Various patterns can be found, even for different genotypes of the same species (van Dam and Vrieling, 1994), making it difficult to draw general conclusions on how shoot treatments affect basal levels of root defenses.

Aboveground and Belowground Changes of Induced Defenses

The above examples deal with single challenges of plant tissue that affect nonattacked parts of the plant. However, recent studies show that effects of herbivory on distant tissues do not always result in changes of defense substances, but rather in how these tissues respond when they themselves are subsequently attacked (Table I). This is the principle of priming for

defense, a cost-effective way of "getting ready for battle" that results in faster and stronger defense responses upon attack (Conrath et al., 2006; van Hulten et al., 2006; Frost et al., 2008). Whereas several studies indicate that root herbivory results in enhanced resistance against aboveground attackers (Bezemer et al., 2003; Hol et al., 2004; Soler et al., 2005; van Dam et al., 2005), the importance of priming has not been thoroughly investigated in this context. van Dam et al. (2005) found that *Delia radicum* attack of the roots resulted in lower initial glucosinolate levels in the shoot of *B. nigra*. Upon leaf damage by *Pieris rapae*, however, aboveground glucosinolate levels increased more strongly in these plants, suggesting that *B. nigra* leaves were primed for defense. In contrast, Soler et al. (2005) found no clear effect of belowground herbivory on glucosinolate levels in *B. nigra* leaves attacked by *Pieris brassicae*, implying that aboveground and belowground responses may depend on the herbivore combination. Because priming often merely involves a faster defense reaction upon attack, its occurrence can easily be missed if measurements are taken only at one time point. Intensity and timing of direct defenses might be most easily observed by measuring the expression of defense marker genes and hormone levels (Engelberth et al., 2004; Ton et al., 2007) rather than a small subsample of defense-related secondary metabolites present in a plant. It has also been found that root herbivory can reduce herbivore-induced defense responses in the shoot, specifically the production of volatile terpenoids as shown

for *B. nigra* (Soler et al., 2007) and maize (Rasmann and Turlings, 2007). Suppression of inducible plant defenses could be of benefit if the plant has to "set priorities" in cases of resource limitations and differential effects on fitness.

The effects of shoot herbivory on belowground herbivore-induced root defenses have received little attention. Bezemer et al. (2003, 2004) found that shoot attack leads to a reduction of root treatment-induced terpenoids and terpenoid aldehydes in *G. herbaceum*. A similar phenomenon was observed for terpenoid volatiles in maize (Rasmann and Turlings, 2007). We are not aware of any study that reports an increase of belowground herbivore-induced root defenses upon shoot herbivory, and it has been speculated that when attacked by both aboveground and belowground herbivores simultaneously, plants preferentially allocate their defenses to the shoot (Bezemer et al., 2004; Rasmann and Turlings, 2007). This hypothesis awaits further testing. Another exciting possibility is that herbivores themselves manipulate plant defenses in their favor, which could also result in changes in distant tissues. This could simply be suppression of defense responses (Musser et al., 2002) or activation of defenses that are ineffective against the herbivore itself, but might affect other attackers. Such "decoy strategies" could be of major ecological significance and should be kept in mind when investigating aboveground and belowground interactions.

THE PHYSIOLOGICAL BASIS OF ROOT-SHOOT INTERACTIONS

The findings discussed in the previous section strongly suggest that signals are exchanged between roots and shoot upon herbivore attack. Root-shoot communication likely follows either the internal vascular network of the plant (i.e. phloem and xylem bundles; Orians, 2005; Atkins and Smith, 2007) or the external route via volatile signaling. These possible routes and preferential flows are depicted in Figure 1. It remains largely unclear which signals and/or compounds are mediating the interactions between root
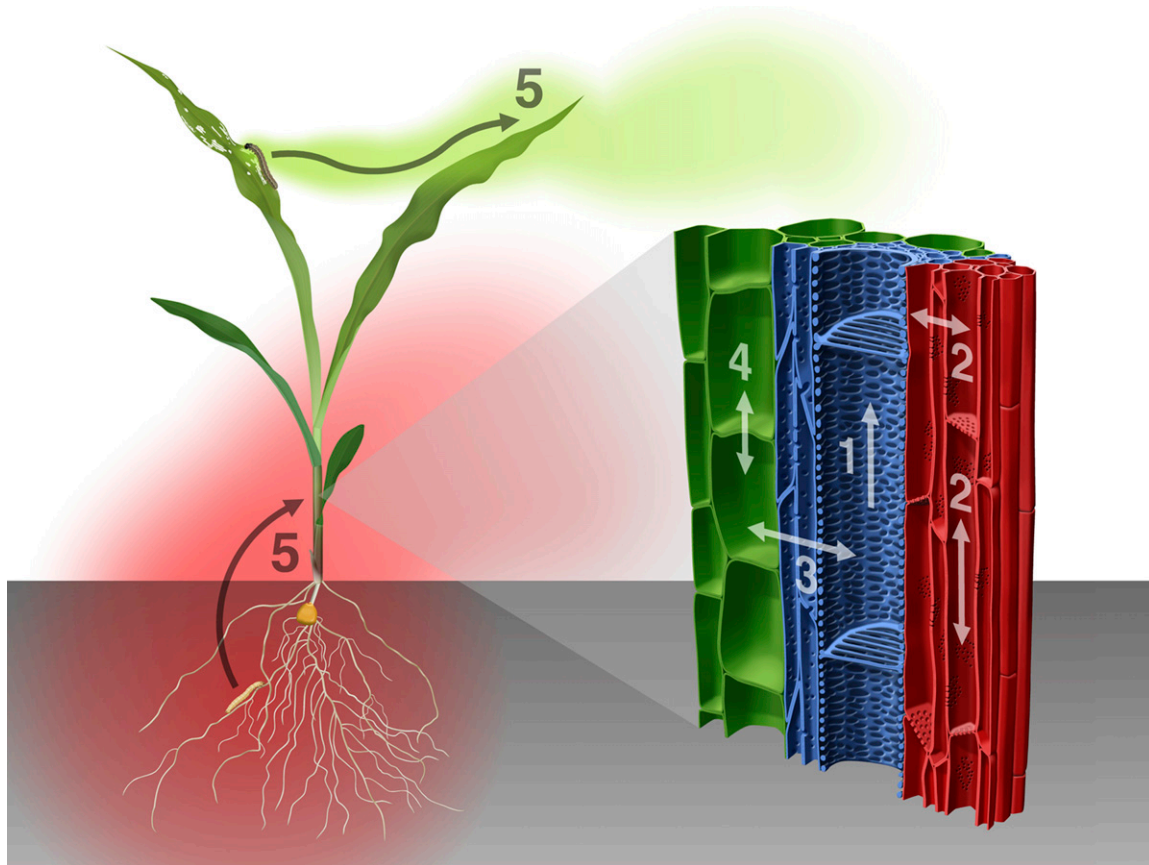

Figure 1. Model of the signaling processes behind plant-mediated aboveground and belowground interactions. Herbivores attack roots and shoot of a plant, resulting in the production of various stress-related signals. As depicted in the enlarged section of a monocotyledonous vascular bundle (right), aboveground and belowground signaling will most probably involve root-to-shoot transport via xylem vessels (1), bidirectional translocation via the phloem (2), exchange between the vascular tissue and the surrounding cells (3), and nonvascular cell-to-cell signaling (4). External communication with volatile compounds that can reach distant parts of the plant is also possible (5), as illustrated for a maize seedling (left). Possible mediators of the interactions are typical stress signals such as plant hormones and volatiles, as well as bioactive nonhormonal metabolites.

and shoot. The extremely variable effects of root herbivores on shoot responses and vice versa make it unlikely that one specific signal or process is involved. We discuss three classes of compounds that could be of major importance in this context: plant hormones, volatile organic compounds, and nonhormonal secondary metabolites.

Plant Hormones

Plant hormones are crucial components of the regulatory network underlying plant growth, development, and defense reactions. Several hormones have been implicated in root-shoot communication and might therefore mediate aboveground and belowground interactions in response to herbivory.

Auxin is readily translocated from the shoot to the roots (Reed et al., 1998), where it promotes root cell proliferation and elongation (Hager et al., 1971). Belowground attack can result in compensatory root growth (Steinger and Müller-Schärer, 1992), thereby likely affecting the auxin-cytokinin balance (Woodward and Bartel, 2005), which is of major importance in regulating aboveground and belowground metabolic states. Application of synthetic auxin (1-naphtaleneaic acid) to spinach roots has been found to enhance levels of root phytoecdysteroids (Schmelz et al., 1999) and causes root to shoot dry mass ratios to shift. This shift indicates higher resource allocation to the roots (Schmelz et al., 1999) and implicates auxin's role as a possible regulator of aboveground and belowground feedback. Indeed, transcriptional up-regulation of the auxin marker gene *ZmSAUR2* in the roots of maize upon belowground feeding by *Diabrotica virgifera* was found (M. Erb, J. Ton, and T.C.J. Turlings, unpublished data), indicative of increased auxin shoot-root translocation or biosynthesis in the roots.

Abscisic acid (ABA) represents a classic example of a xylem-translocated root-shoot hormone (Davies and Zhang, 1991; Jackson, 1997; see also Christmann et al., 2005, 2007). Whereas ABA is traditionally associated with responses to drought stress (Davies and Zhang, 1991), it is becoming evident that it may also have an important role in herbivore defense (Anderson et al., 2004). Schmelz et al. (1999) found that application of ABA to the roots of spinach decreased the concentration of the defensive phytoecdysteroid 20E in the shoot. ABA deficiency has been shown to enhance the performance of both *Spodoptera exigua* on *Solanum lycopersicum* and *Spodoptera littoralis* on Arabidopsis (*Arabidopsis thaliana*; Thaler and Bostock, 2004; Bodenhausen and Reymond, 2007). Furthermore, root herbivory can elicit drought-like responses in plants (Gange and Brown, 1989), which may represent an additional link between ABA and aboveground and belowground interactions. This is expected to be especially important when herbivores severely damage root systems, as is the case for various chewing insects. Hence, further research into the role of ABA in plant-mediated interactions between root and shoot herbivores is certainly warranted.

Jasmonic acid (JA) is often considered to be the central hormone governing systemic plant responses to herbivory above ground (Farmer and Ryan, 1992; Howe et al., 1996; McConn et al., 1997) and probably has a similar role below ground (McConn et al., 1997; Schmelz et al., 1999; Puthoff and Smigocki, 2007). Compounds of the JA family are suggested to be responsible for long-distance wound signaling (Stratmann, 2003; Wasternack et al., 2006), a fact supported by the ability of methyl jasmonate (MeJA) to move readily along both xylem and phloem pathways (Thorpe et al., 2007), as well as through the air (Farmer and Ryan, 1990). The potential of JA as an aboveground and belowground regulator is indicated by the fact that, when applied to the leaves of *Nicotiana sylvestris*, it seems to be transported to the roots, where it induces nicotine synthesis (Zhang and Baldwin, 1997). Furthermore, application of JA (or MeJA) to roots induces shoot defenses (Baldwin, 1996; van Dam et al., 2001, 2004), providing additional evidence for its key role in root-shoot interactions.

Salicylic acid (SA) is usually implicated in defense responses to pathogens, but can also be involved in plant responses upon herbivore attack (Zarate et al., 2007). It is not clear, however, in what respect SA functions as a systemic signal. It is unlikely that SA is the translocated signal inducing resistance in plant-pathogen interactions (Ryals et al., 1996), and van Dam et al. (2004) found no systemic effects of SA applied to either roots or shoots on glucosinolate levels in two *Brassica* species. However, the methylated form of SA (MeSA) is a mobile signal that is required for systemic resistance induction in tobacco (*Nicotiana tabacum*) plants (Park et al., 2007). MeSA and may also function as an airborne signal (Shulaev et al., 1997). Root systems damaged by herbivores can be assumed to have an increased risk of colonization by microorganisms, be it from the oral secretions of the attacker itself or from the rhizosphere. Hence, SA-related defenses induced in response to herbivory could be adaptive and also modulate aboveground defenses, for example, via SA/JA cross talk (Niki et al., 1998).

Finally, ethylene and its precursor 1-amino-cyclopropane-1-carboxylic acid have a well-known function in positive root-shoot signaling (Bradford and Yang, 1980; Jackson, 1997). Research focusing on plant hormonal cross talk has shown the importance of ethylene in modulating responses to biotic stress above ground (Xu et al., 1994; Odonnell et al., 1996; van Loon et al., 2006), which includes activity upon attack by arthropod herbivores (Kendall and Bjostad, 1990; von Dahl and Baldwin, 2007). Puthoff and Smigocki (2007) found an up-regulation of genes responsive to root herbivory in *Beta vulgaris* upon ethylene treatment, a first indication that ethylene is also involved in root defenses. Because of its volatility, ethylene can either diffuse through the vascular tissue directly into the shoot (Jackson and Campbell, 1975) or travel externally, diffusing from the rhizosphere (Jackson and Campbell, 1975) to the phyllosphere. Because it is

likely that ethylene is involved in volatile defense signaling within and between plants (Ruther and Kleier, 2005; J. Ton, unpublished data), it is imperative to study this compound as a possible root-shoot signal in plant-arthropod interactions.

Volatile Organic Compounds as Root-Shoot Signals

Apart from ethylene, a wide range of other volatile organic compounds are synthesized and released after herbivore attack above and below ground (e.g. Rasmann et al., 2005; D'Alessandro et al., 2006). Plant volatiles, in particular induced volatiles, have long been implicated in plant-plant communication. The benefit of such communication for the emitting plant is questionable, unless the information is passed on to a closely related plant. Moreover, volatile signals can be exploited by herbivores (Carroll et al., 2006; Halitschke et al., 2008) and even parasitic plants (Runyon et al., 2006). A more adaptive functioning of volatiles is in overcoming the plant's vascular constraints and communicating between parts of the same plant (Frost et al., 2007; Heil and Silva Bueno, 2007). There is increasing evidence that green-leaf volatiles (GLVs) play an important role in this context (Arimura et al., 2001; Engelberth et al., 2004; Ruther and Furstenau, 2005). Some GLVs belong to the family of reactive electrophile species, which have recently been implicated as stress and defense signals (Farmer and Davoine, 2007). Several reactive electrophile species are very short-lived and therefore could be ideal short-range signals. We have found evidence that GLVs, despite their name, are also released from crushed roots of maize (M. Erb and T.C.J. Turlings, unpublished data). In the only study that looked for belowground GLVs, Steeghs et al. (2004) did not detect any emission from artificially damaged Arabidopsis roots, possibly because the ecotype they used (Columbia-0) carries a mutation severely affecting hydroperoxide lyase activity and C_6 volatile synthesis (Duan et al., 2005). GLVs, if indeed produced by the roots, and other volatiles are likely to diffuse into the phyllosphere and change the physiological state of plants above ground (Fig. 1). Research on the biochemistry of GLVs and other volatile organic compounds is progressing rapidly (Matsui, 2006; Schnee et al., 2006; D'Auria et al., 2007), revealing new experimental approaches to test for their effects.

Translocation of Nonhormonal Secondary Metabolites

Secondary metabolites with defensive properties are by no means bound to either the roots or the shoot of a plant, and their translocation could account for many of the observed effects of cross-resistance and interactions between aboveground and belowground plant defenses. Nicotine is the prime example of a secondary metabolite that it synthesized in the roots of *Nicotiana* spp. and then translocated to the shoots to unleash its antiherbivore properties (Shoji et al., 2000, and refs. therein). van Dam and Vrieling (1994) report a negative

relationship between changes in wound-induced pyrrolizidine alkaloid content in the roots and shoots of *C. officinale*, which can be seen as an indication for within-plant transport of this class of compounds. Rasmann et al. (2005) found increased levels of (E)-β-caryophyllene in maize shoots upon root feeding by *D. virgifera*. Koellner et al. (2008) found no indication of higher transcriptional activity of the corresponding terpene synthase in the shoot upon *D. virgifera* feeding on the roots, indicating that it is the compound itself that is translocated from the roots to the shoot. A recent study on terpenoid synthesis in carrots (*Daucus carota*) found (E)-β-caryophyllene to be independently synthesized in the roots and shoots (Hampel et al., 2005). These indicative results underpin the possibility that it is not necessarily only the activation of aboveground defenses that leads to higher concentrations of secondary compounds in the shoot upon root herbivory, but also simple translocation, be it active transport or passive diffusion.

CONCLUSION

Plant-mediated interactions between aboveground and belowground arthropod herbivores can have profound effects on natural and agricultural food webs. Although only few studies have specifically looked at defense responses of plants that have been subjected to both root and shoot herbivory, it is clear that there is considerable complexity, which depends on a variety of biotic and abiotic factors. Even with our limited knowledge, we can conclude that it is unlikely that all effects are the result of the same physiological processes. Research into the mechanisms as well as the ecological significance of root-shoot feedback effects is sorely needed, and current progress in plant biochemistry and targeted molecular manipulation is likely to reveal which genes and pathways are involved. Recent discoveries focusing on priming for defense and the role of volatiles as external cues involved in plant defense responses show great promise for better understanding of within-plant signaling. Applying this knowledge for comprehensive insight into the ecological relevance of cross-effects between aboveground and belowground interactions requires close collaboration between plant physiologists and ecologists.

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