

1 Running head: Interactions between Above- and Belowground Plant Defenses

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1 Interactions between Arthropod-Induced Above- and  
2 Belowground Defenses in Plants

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1 This work was supported by the Swiss National Science Foundation (grant 31-058865.99) and  
2 the Swiss National Centre of Competence in Research “Plant Survival”. J.T. receives funding  
3 from a BBSRC Institute Career Path Fellowship (no. BB/E023959/1).

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# 1 INTRODUCTION

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

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

20           Because of the scope of this special issue, we limit our review to arthropod-induced  
21 plant defense responses. We do not discuss induced changes in primary metabolites, which  
22 can be of substantial importance (Mattson, 1980; Gange and Brown, 1989; Babst et al., 2005;  
23 Schwachtje et al., 2006; [Schwachtje and Baldwin, this issue](#)). We also acknowledge the  
24 importance of putting the current findings in an appropriate ecological context (see Rasmann  
25 and Agrawal, this issue) and the necessity to include micro-organisms as important players in  
26 both rhizosphere and phyllosphere interactions. Several excellent reviews cover these and  
27 other intricacies of above-belowground interactions (van der Putten et al., 2001; Blossey and  
28 Hunt-Joshi, 2003; van Dam et al., 2003; Bonkowski, 2004; Wardle et al., 2004).

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3 **Changes of defenses in non-attacked tissues**

4 Various studies on interactions between above- and belowground plant responses have  
5 found an increase in basal levels of shoot defenses (defined here as the level of shoot defenses  
6 in absence of aboveground herbivores) following root herbivory, artificial damage and plant  
7 defense hormone application (Table I). Root treatments have been shown to increase shoot  
8 concentrations of terpenoids in *Gossypium herbaceum* and *Zea mays* (Bezemer et al., 2003;  
9 Bezemer et al., 2004; Rasmann et al., 2005), phenolics in *Brassica nigra* (van Dam et al.,  
10 2005), pyrrolizidine alkaloids in *Senecio jacobea* (Hol et al., 2004), certain glucosinolates in  
11 *Brassica spp.* (Birch et al., 1992; van Dam et al., 2004; Soler et al., 2005; van Dam and  
12 Raaijmakers, 2006; Soler et al., 2007), phytoectosteroids in *Spinacia oleracea* (Schmelz et al.,  
13 1998), proteinase inhibitors in *Nicotiana attenuata* (van Dam et al., 2001) and extrafloral  
14 nectar in *G. herbaceum* (Wäckers and Bezemer, 2003). Within this wide array of defensive  
15 metabolites, negative effects of root herbivory on basal levels of shoot defenses are also  
16 possible in some plant genotypes (Hol et al., 2004) and under certain experimental conditions  
17 (van Dam et al., 2005). Current results are as yet inconclusive about whether the generally  
18 observed increase of shoot defensive compounds is a result of active defense signaling and *de*  
19 *novo* synthesis in the shoot or if the metabolites are translocated from the roots to the shoot.  
20 We discuss both possibilities below.

21 In the reverse direction, effects of shoot herbivores on basal levels of root defenses  
22 have been observed (Table I). Shoot herbivory or treatment with jasmonic acid can increase  
23 root concentrations of nicotine and proteinase inhibitors in *N. attenuata* (Baldwin et al., 1994;  
24 van Dam et al., 2001) as well as glucosinolates in *Brassica campestris* and *B. nigra* (Ludwig-  
25 Müller et al., 1997; Soler et al., 2007). In contrast, reduced concentrations of other defense-  
26 related compounds can also be observed, such as in the case of pyrrolizidine alkaloids in the  
27 roots of *S. jacobea* after herbivory on shoots (Hol et al., 2004). Other studies found no clear  
28 effects of shoot treatments on basal levels of root defensive compounds including terpenoids  
29 in *G. herbaceum* and *Z. mays* (Bezemer et al., 2003; Bezemer et al., 2004; Rasmann and  
30 Turlings, 2007) phytoectosteroids in *S. oleracea* (Schmelz et al., 1998), **pyrrolizidine**  
31 **alkaloids** in *Cynoglossum officinale* (van Dam and Vrieling, 1994) and **glucosinolates in**  
32 ***Brassica oleracea* and *B. nigra*** (van Dam et al., 2004). Various patterns can be found, even  
33 for different genotypes of the same species (van Dam and Vrieling, 1994), making it difficult  
34 to draw general conclusions on how shoot treatments affect basal levels of root defenses.

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**Above-belowground changes of induced defenses**

The above examples deal with single challenges of plant tissue that affect non-attacked 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., this issue). While 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 above-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 sub-sample 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 *Z. mays* (Rasmann and Turlings, 2007, own research). A suppression of inducible plant defences 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 *Z. mays* (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 above- and belowground herbivores simultaneously, plants preferentially allocate their

1 defenses to the shoot (Bezemer et al., 2004; Rasmann and Turlings, 2007). This hypothesis  
2 awaits further testing. Another exciting possibility is that herbivores themselves manipulate  
3 plant defenses in their favor, which could also result in changes in distant tissues. This could  
4 simply be suppression of defense responses (Musser et al., 2002) or the activation of defenses  
5 that are ineffective against the herbivore itself, but might affect other attackers. Such “decoy  
6 strategies” could be of major ecological significance and should be kept in mind when  
7 investigating above- belowground interactions.

## 9 THE PHYSIOLOGICAL BASIS OF ROOT-SHOOT INTERACTIONS

11 The findings discussed in the previous section strongly suggest that signals are  
12 exchanged between roots and shoot upon herbivore attack. Root-shoot communication likely  
13 follows either the internal vascular network of the plant (i.e. phloem and xylem bundles,  
14 Orians, 2005; Atkins and Smith, 2007) or the external route via volatile signaling. These  
15 possible routes and preferential flows are depicted in Figure 1. It remains largely unclear  
16 which signals and/or compounds are mediating the interactions between root and shoot. The  
17 extremely variable effects of root herbivores on shoot responses and *vice versa* make it  
18 unlikely that one specific signal or process is involved. We discuss three classes of  
19 compounds that could be of major importance in this context: plant hormones, volatile  
20 organic compounds and non-hormonal secondary metabolites.

### 22 **Plant hormones**

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

27 Auxin is readily translocated from the shoot to the roots (Reed et al., 1998), where it  
28 promotes root cell proliferation and elongation (Hager et al., 1971). Belowground attack can  
29 result in compensatory root growth (Steinger and Müller-Schärer, 1992), thereby likely  
30 affecting the auxin-cytokinin balance (Woodward and Bartel, 2005), which is of major  
31 importance in regulating above- and belowground metabolic states. Application of synthetic  
32 auxin (1-naphthaleneic acid) to spinach roots has been found to enhance levels of root  
33 phytoecdysteroids (Schmelz et al., 1999) and causes root/shoot dry mass ratios to shift. This  
34 shift indicates higher resource allocation to the roots (Schmelz et al., 1999) and implicates

1 auxin's role as a possible regulator of above-belowground feedback. Indeed, transcriptional  
2 upregulation of the auxin-marker gene *Zm-SAUR2* in the roots of maize upon belowground  
3 feeding by *Diabrotica virgifera* was found (own results, unpublished), indicative of increased  
4 auxin shoot-root translocation or biosynthesis in the roots.

5 Abiscisic acid (ABA) represents a classical example of a xylem-translocated root-  
6 shoot hormone (Davies and Zhang, 1991; Jackson, 1997; but see Christmann et al., 2005;  
7 Christmann et al., 2007). While ABA is traditionally associated with responses to drought  
8 stress (Davies and Zhang, 1991), it is becoming evident that it may also have an important  
9 role in herbivore defense (Anderson et al., 2004). Schmelz et al. (1999) found that application  
10 of ABA to the roots of spinach decreased the concentration of the defensive phytoecdysteroid  
11 20E in the shoot. ABA-deficiency has been shown to enhance the performance of both  
12 *Spodoptera exigua* on *Solanum lycopersicum* and *Spodoptera littoralis* on *A. thaliana* (Thaler  
13 and Bostock, 2004; Bodenhausen and Reymond, 2007). Furthermore, root herbivory can elicit  
14 drought-like responses in plants (Gange and Brown, 1989, own observations), which may  
15 represent an additional link between ABA and above-belowground interactions. This is  
16 expected to be especially important when herbivores severely damage root systems, as is the  
17 case for various chewing insects. Hence, further research into the role of ABA in plant  
18 mediated-interactions between root and shoot herbivores is certainly warranted.

19 Jasmonic acid (JA) is often considered to be the central hormone governing systemic  
20 plant responses to herbivory aboveground (Farmer and Ryan, 1992; Howe et al., 1996;  
21 McConn et al., 1997) and probably has a similar role belowground (McConn et al., 1997;  
22 Schmelz et al., 1999; Puthoff and Smigocki, 2007). Compounds of the jasmonic acid family  
23 are suggested to be responsible for long distance wound signaling (Stratmann, 2003;  
24 Wasternack et al., 2006), a fact supported by the ability of methyl jasmonate (MJ) to move  
25 readily along both xylem and phloem pathways (Thorpe et al., 2007) as well as through the air  
26 (Farmer and Ryan, 1990). The potential of JA as an above-belowground regulator is indicated  
27 by the fact that when applied to the leaves of *Nicotiana sylvestris*, it seems to be transported  
28 to the roots, where it induces nicotine synthesis (Zhang and Baldwin, 1997). Furthermore,  
29 application of JA (or MJ) to roots induces shoot defenses (Baldwin, 1996; van Dam et al.,  
30 2001; van Dam et al., 2004), providing additional evidence for its key role in root-shoot  
31 interactions.

32 Salicylic acid (SA) is usually implicated in defence responses to pathogens, but can  
33 also be involved in plant responses upon herbivore attack (Zarate et al., 2007). It is not clear,  
34 however, in what respect SA functions as a systemic signal. It is unlikely that SA is the

1 translocated signal inducing resistance in plant-pathogen interactions (Ryals et al., 1996), and  
2 van Dam et al. (2004) found no systemic effects of SA applied to either roots or shoots on  
3 glucosinolate levels in two *Brassica* species. However, the methylated form of SA (MeSA) is  
4 a mobile signal that is required for systemic resistance induction in tobacco plants (Park et al.,  
5 2007). MeSA and may also function as an airborne signal (Shulaev et al., 1997). Root systems  
6 damaged by herbivores can be assumed to have an increased risk of colonization by  
7 microorganisms, be it from the oral secretions of the attacker itself or from the rhizosphere.  
8 Hence, SA-related defenses induced in response to herbivory could be adaptive and also  
9 modulate aboveground defenses, for example via SA/JA crosstalk (Niki et al., 1998).

10 Finally, ethylene and its precursor 1-amino-cyclopropane-1-carboxylic acid (ACC)  
11 have a well known function in positive root-shoot signaling (Bradford and Yang, 1980;  
12 Jackson, 1997). Research focusing on plant hormonal cross-talk has shown the importance of  
13 ethylene in modulating responses to biotic stress aboveground (Xu et al., 1994; Odonnell et  
14 al., 1996; van Loon et al., 2006), which includes activity upon attack by arthropod herbivores  
15 (Kendall and Bjostad, 1990; von Dahl and Baldwin, 2007). Puthoff and Smigocki (2007)  
16 found an upregulation of genes responsive to root herbivory in *Beta vulgaris* upon ethylene  
17 treatment, a first indication that ethylene is also involved in root defenses. Because of its  
18 volatility, ethylene can either diffuse through the vascular tissue directly into the shoot  
19 (Jackson and Campbell, 1975) or travel externally, diffusing from the rhizosphere (Jackson  
20 and Campbell, 1975) to the phyllosphere. Since it is likely that ethylene is involved in volatile  
21 defense signaling within and between plants (Ruther and Kleier, 2005; Ton, unpublished), it is  
22 imperative to study this compound as a possible root-shoot signal in plant-arthropod  
23 interactions.

24

### 25 **Volatile organic compounds as root-shoot signals**

26 Apart from ethylene, a wide range of other volatile organic compounds (VOCs) are  
27 synthesized and released after herbivore attack above- and belowground (see for example  
28 Rasmann et al., 2005; D'Alessandro et al., 2006). Plant volatiles, in particular induced  
29 volatiles, have long been implicated in plant-plant communication. The benefit of such  
30 communication for the emitting plant is questionable, unless the information is passed on to a  
31 closely related plant. Moreover, volatile signals can be exploited by herbivores (Carroll et al.,  
32 2006) and even parasitic plants (Runyon et al., 2006). A more adaptive functioning of  
33 volatiles is in overcoming the plant's vascular constraints and communicating between parts  
34 of the same plant (Frost et al., 2007; Heil and Silva Bueno, 2007). There is increasing

1 evidence that green leaf volatiles (GLVs) play an important role in this context (Arimura et  
2 al., 2001; Engelberth et al., 2004; Ruther and Furstenu, 2005). Some GLVs belong to the  
3 family of reactive electrophile species (RES), which have recently been implicated as stress  
4 and defense signals (Farmer and Davoine, 2007). Several RES are very short-lived and  
5 therefore could be ideal short-range signals. We have found evidence that GLVs, despite their  
6 name, are also released from crushed roots of *Z. mays* (unpublished). In the only study that  
7 looked for belowground GLVs, Steeghs et al. (2004) did not detect any emission from  
8 artificially damaged *A. thaliana* roots, possibly because the ecotype they used (Col-0) carries  
9 a mutation severely affecting HPL activity and C<sub>6</sub> volatile synthesis (Duan et al., 2005).  
10 GLVs, if indeed produced by the roots, and other volatiles are likely to diffuse into the  
11 phyllosphere and change the physiological state of plants aboveground (Fig 1). Research on  
12 the biochemistry of GLVs and other VOCs is progressing rapidly (Matsui, 2006; Schnee et  
13 al., 2006; D'Auria et al., 2007), revealing new experimental approaches to test for their  
14 effects.

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## 16 **Translocation of non-hormonal secondary metabolites**

17 Secondary metabolites with defensive properties are by no means bound to either the  
18 roots or the shoot of a plant, and their translocation could account for many of the observed  
19 effects of cross-resistance and interactions between above- and belowground plant defenses.  
20 Nicotine for example is the prime example of a secondary metabolite that it synthesized in the  
21 roots of *Nicotiana spp.* and then translocated to the shoots to unleash its anti-herbivore  
22 properties (Shoji et al., 2000 and references therein). Van Dam and Vrieling (1994) report a  
23 negative relationship between changes in wound-induced pyrrolizidine alkaloid contents in  
24 the roots and the shoots of *Cynoglossum officinale*, which can be seen as an indication for  
25 within-plant transport of this class of compounds. Rasmann et al. (2005) found increased  
26 levels of (E)- $\beta$ -caryophyllene in maize shoots upon root feeding by *Diabrotica virgifera*  
27 *virgifera*. Koellner et al. (in preparation) found no indication of higher transcriptional activity  
28 of the corresponding terpene synthase in the shoot upon *D. virgifera* feeding on the roots,  
29 indicating that it is the compound itself that is translocated from the roots to the shoot. A  
30 recent study on terpenoid synthesis in carrots found (E)- $\beta$ -caryophyllene to be independently  
31 synthesized in the roots and the shoot (Hampel et al., 2005). These indicative results underpin  
32 the possibility that it is not necessarily only the activation of aboveground defenses that leads  
33 to higher concentrations of secondary compounds in the shoot upon root herbivory, but also  
34 simple translocation, be it active transport or passive diffusion.

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### CONCLUSIONS

Plant-mediated interactions between above- 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 a better understanding of within-plant signaling. Applying this knowledge for a comprehensive insight into the ecological relevance of cross-effects between above and belowground interactions requires close collaboration between plant physiologists and ecologists.

### ACKNOWLEDGMENTS

We thank Gregg Howe and Georg Jander for the invitation to contribute to this special issue. Sarah Kenyon, Marco D'Alessandro and Claudia Zwahlen provided valuable comments on an earlier version of the manuscript. *We are grateful to two anonymous reviewers that helped to improve this review.* Figure 1 was created by Thomas Degen ([www.thomas-degen.ch](http://www.thomas-degen.ch)).

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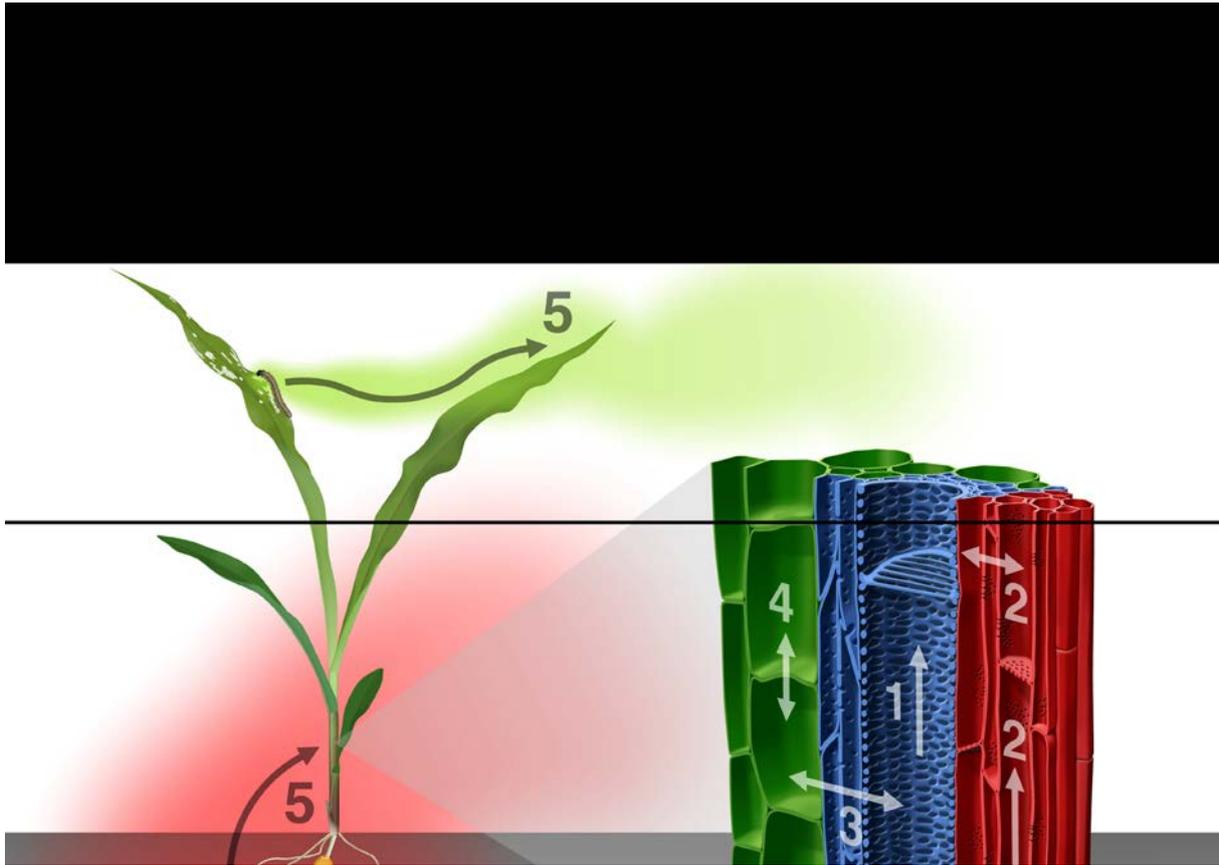
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Figure 1: Model of the signaling processes behind plant-mediated above belowground interactions. Herbivores attack roots and shoot of a plant resulting in the production of various stress-related signals. As depicted in the enlarged section of a monocotyledonous vascular bundle (right), above-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 non-vascular 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 non-hormonal metabolites.

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, MJ= Methyl jasmonate, JA= Jasmonic acid, SA= Salicylic acid, ST= Shoot treatment, RT= Root treatment, AB= Aboveground, BG= Belowground, n.a.=Not applicable. For a complementary table, see also Rasmann and Agrawal (this issue).

Effects of root treatments on shoot defenses							
Plant	Root treatment	Induced root defense	Altered basal shoot defense	Shoot treatment	Altered ST induced shoot defense	Influences on herbivore AG	Reference
<i>Gossypium herbaceum</i>	<i>Agriotes lineatus</i>	Terpenoids	+ Increase of terpenoids	<i>Spodoptera exigua</i>	0 None	Reduced growth	Bezemer et al., 2003
<i>Gossypium herbaceum</i>	<i>Agriotes lineatus</i> , MD	Terpenoid aldehydes	+ Higher terpenoid aldehyde levels	<i>Spodoptera exigua</i>	0 None	n.a.	Bezemer et al., 2004
<i>Brassica oleracea</i> , <i>Brassica napus</i> <i>Senecio jacobea</i>	<i>Delia floralis</i> MD	Glucosinolates, indole-based compounds Pyrrolizidine alkaloids	+/- Higher glucosinolate contents, lower indole-based compounds + Partially increased pyrrolizidine alkaloids (genotype)	n.a. <i>Mamestra brassicae</i>	n.a. 0 None	n.a. Partially reduced survival	Birch et al., 1992 Hol et al., 2004
<i>Brassica campestris</i>	<i>Delia radicum</i>	Unknown volatiles	+ Induced volatiles	n.a.	n.a.	n.a.	Neveu et al., 2002
<i>Zea mays</i>	<i>Diabrotica virgifera</i>	(E)- $\beta$ -caryophyllene	+ Increased (E)- $\beta$ -caryophyllene (foilage)	n.a.	n.a.	n.a.	Rasmann et al., 2005
<i>Zea mays</i>	<i>Diabrotica virgifera</i>	(E)- $\beta$ -caryophyllene	0 None (headspace)	<i>Spodoptera littoralis</i>	- Reduced volatiles (Trend)	n.a.	Rasmann & Turlings, 2007
<i>Spinacia oleracea</i>	MD, MJ	20-hydroxyecdysone	+ Small induction of 20E	<i>Spodoptera exigua</i> , MD, MJ	0 None	n.a.	Schmelz et al., 1998
<i>Spinacia oleracea</i>	<i>Otiorynchus sulcatus</i>	20-hydroxyecdysone	0 None	n.a.	n.a.	n.a.	Schmelz et al., 1999
<i>Brassica nigra</i>	<i>Delia radicum</i>	n.a.	+ Higher sinigrin levels	<i>Pieris brassicae</i>	0/+ None/ Trend for increased sinigrin levels (young leaves)	Reduced growth	Soler et al., 2005
<i>Brassica nigra</i>	<i>Delia radicum</i>	n.a.	+ More volatile sulfides (headspace)	<i>Pieris brassicae</i>	-/+ Altered volatile profile	n.a.	Soler et al., 2007
<i>Nicotiana attenuata</i>	MJ	Proteinase inhibitors	+ Higher proteinase inhibitor levels	n.a.	n.a.	n.a.	van Dam et al., 2001
<i>Brassica oleracea</i> , <i>Brassica nigra</i>	JA/ SA	Glucosinolates (JA)	+ Induced glucosinolates (JA)	JA, SA	+ More total glucosinolates (JA/JA)	n.a.	van Dam et al., 2004
<i>Brassica nigra</i>	<i>Delia radicum</i>	n.a.	-/+ Less total glucosinolates, more phenolics	<i>Pieris Rapae</i>	+ More total phenolics	Reduced growth and survival	van Dam et al., 2005
<i>Brassica oleracea</i> , <i>Brassica nigra</i>	<i>Delia radicum</i>	Indole glucosinolates	0/+ None/ Higher glucosinolate levels (plant species)	n.a.	n.a.	n.a.	van Dam & Raaijmakers, 2006
<i>Gossypium herbaceum</i>	<i>Agriotes lineatus</i> , MD	n.a.	+ Induced extrafloral nectar	n.a.	n.a.	n.a.	Wäckers & Bezemer, 2003
Effects of shoot treatments on root defenses							
Plant	Shoot treatment	Induced shoot defense	Altered basal root defense	Root treatment	Altered RH induced root defence	Influences on herbivore BG	Reference
<i>Nicotiana attenuata</i>	MD	Nicotine	+ Nicotine	n.a.	n.a.	n.a.	Baldwin et al., 1994
<i>Gossypium herbaceum</i>	<i>Spodoptera exigua</i>	Terpenoids	0 None	<i>Agriotes lineatus</i>	- Non-significant reduction of terpenoids	None	Bezemer et al., 2003
<i>Gossypium herbaceum</i>	<i>Spodoptera exigua</i>	Terpenoid aldehydes	0 None	<i>Agriotes lineatus</i> , MD	- Reduced terpenoid aldehyde levels	n.a.	Bezemer et al., 2004
<i>Senecio jacobea</i>	<i>Mamestra brassicae</i>	None (Pyrrolizidine alkaloids)	- Reduced pyrrolizidine alkaloids	MD	0/- Partially reduced pyrrolizidine alkaloids (genotype)	n.a.	Hol et al., 2004
<i>Brassica campestris</i>	JA, SA	Glucosinolates	+ Higher level of glucosinolates	n.a.	n.a.	n.a.	Ludwig-Müller et al., 1997
<i>Zea mays</i>	<i>Spodoptera littoralis</i>	(E)- $\beta$ -caryophyllene	0 None	<i>Diabrotica virgifera</i>	- Reduced (E)- $\beta$ -caryophyllene	n.a.	Rasmann & Turlings, 2007
<i>Spinacia oleracea</i>	<i>Spodoptera exigua</i> , MD, MJ	None (20E)	0 None	n.a.	n.a.	n.a.	Schmelz et al., 1998
<i>Brassica bigra</i>	<i>Pieris brassicae</i>	n.a.	+ Higher indole glucosinolate levels	<i>Delia radicum</i>	n.a.	Reduced survival & size	Soler et al., 2007
<i>Nicotiana attenuata</i>	MJ, MD	Proteinase inhibitors	+ Higher level of trypsin proteinase inhibitors	n.a.	n.a.	n.a.	van Dam et al., 2001
<i>Brassica oleracea</i> , <i>Brassica nigra</i>	JA, SA	Glucosinolates	0 None	JA, SA	0 None discussed	n.a.	van Dam et al., 2004
<i>Cynoglossum officinale</i>	MD	Pyrrolizidine alkaloids	+/- Higher/lower level of pyrrolizidine alkaloids (genotype)	n.a.	n.a.	n.a.	van Dam & Vrieling, 1994