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Mechanisms and ecological implications of plant-mediated interactions between belowground and aboveground insect herbivores

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Abstract Plant-mediated interactions between belowground (BG) and aboveground (AG) herbivores have received increasing interest recently. However, the molecular mechanisms underlying ecological consequences of BG–AG interactions are not fully clear yet. Herbivore-induced plant defenses are complex and comprise phytohormonal signaling, gene expression and production of defensive compounds (defined here as response levels), each with their own temporal dynamics. Jointly they shape the response that will be expressed. However, because different induction methods are used in different plant-herbivore systems, and only one or two response levels are measured in each study, our ability to construct a general framework for BG–AG interactions remains limited. Here we aim to link the mechanisms to the ecological consequences of plant-mediated interactions between BG and AG insect herbivores. We first outline the molecular mechanisms of herbivore-induced responses involved in BG–AG interactions. Then we synthesize the literature on BG–AG interactions in two well-studied plant-herbivore systems, *Brassica* spp. and *Zea mays*, to identify general patterns and specific differences. Based on this comprehensive review, we conclude that phytohormones can only partially mimic induction by real herbivores. BG herbivory induces resistance to AG herbivores in both systems, but only in maize this involves drought stress responses. This may be due to morphological and physiological differences

between monocotyledonous (maize) and dicotyledonous (*Brassica*) species, and differences in the feeding strategies of the herbivores used. Therefore, we strongly recommend that future studies explicitly account for these basic differences in plant morphology and include additional herbivores while investigating all response levels involved in BG–AG interactions.

Keywords Root herbivory · Herbivore-induced defenses · Plant–insect interactions · Glucosinolates · Defense signaling

Introduction

About half of the 3–6 million insect species use plants as a food source, thus constituting the most diverse taxon of plant attackers (Schoonhoven et al. 2005). Most of these phytophagous insects are specialized on a narrow range of plant species belonging to the same genus or family, contrary to generalists which feed on plant species from different plant families (Bernays and Chapman 1994). To cope with their enemies, plants possess an arsenal of chemical weapons, the so-called plant secondary metabolites (Schoonhoven et al. 1998). Some plant secondary metabolites are characteristic of specific plant families. For example, glucosinolates are typical secondary metabolites serving as defensive compounds in Brassicaceae plants (Halkier and Gershenson 2006), benzoxazinoids in Poaceae (Gierl and Frey 2001) and alkaloids in Solanaceae (Wink 2003).

Some defensive compounds are constitutively expressed in plants, while others are induced only in response to a herbivore attack (Wu and Baldwin 2010). Many defensive compounds (i.e. glucosinolates) can be constitutively present in plants and be induced to even higher levels in response to herbivore feeding (Wittstock and Halkier 2002). Inducible defenses can directly affect the development or behavior of the attacker (direct defenses), or attract natural enemies of the attacking herbivore, known as indirect defenses (Turlings et al. 2002;

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Schoonhoven et al. 2005; Gols et al. 2008a; Dicke and Baldwin 2010). Inducible defenses are especially intriguing, as in general, it has been postulated that they reduce production costs and provide a regulatory mechanism that allows plants to trade-off between defense and growth (Herms and Mattson 1992; Karban and Baldwin 1997; Heil and Baldwin 2002). Furthermore, specific signals, such as volatile organic compounds (VOCs) released by neighboring plants in response to herbivore attack, can prime plant inducible defenses. The primed plant does not activate defenses immediately, but is prepared for faster and stronger defense responses after subsequent herbivore attack (Conrath et al. 2006; Frost et al. 2007).

Herbivore attack can induce plant defenses locally in damaged tissues or systemically in undamaged plant parts (Heil and Ton 2008). Thus, plant defenses induced in response to one attacker may affect plant defenses against another attacker that feeds sequentially or simultaneously on distal parts of the same plant (Karbon and Baldwin 1997; Soler et al. 2007; Vos et al. 2013). In nature, attack by a single herbivore species is unusual and inducible defenses against multiple attackers have been extensively studied (Rodríguez-Saona et al. 2005; Poelman et al. 2008; Ali and Agrawal 2014). Although most of these studies were constrained to aboveground herbivores, plant-mediated interactions occur also between belowground (BG) and aboveground (AG) herbivores (Hol et al. 2004; Bezemer and van Dam 2005; van Dam et al. 2005; Soler et al. 2007; Erb et al. 2009b). Interactions between BG–AG herbivores affect the preference or performance not only of the herbivores that share the same plant, but also of organisms at higher trophic levels (Masters et al. 2001; Soler et al. 2005; Rasmann and Turlings 2007) affecting composition and dynamics of plant-associated communities (van der Putten et al. 2001; Bezemer et al. 2004; Wardle et al. 2004).

The main aim of this review is to link the molecular and chemical mechanisms driving BG–AG plant–insect interactions with the ecological implications for the AG herbivores. We first discuss the key aspects of the molecular mechanisms governing inducible defenses, such as the role of phytohormones, in the context of BG–AG interactions. Furthermore, we synthesize the current knowledge on different response levels, such as gene expression, phytohormonal signaling and metabolomics. Additionally, we discuss the effect of plant morphology and physiology on BG induced plant defenses and the ecological consequences on AG herbivores. Although AG herbivory can also affect BG plant defenses as well as the performance of BG herbivores (Erb et al. 2008), the focus of this review is on how BG herbivory affects AG inducible defenses and herbivore performance as there are currently more data available for a comprehensive analysis. Moreover, as the mechanisms and the ecological consequences of BG–AG interactions are complex and vary depending on many different factors, we primarily focus on direct defenses.

We also limit our review to interactions between plants and insect herbivores, though we acknowledge the interconnection of signaling pathways underlying plant–microbe and plant–insect interactions, as well as interactive effects on higher trophic levels (Pieterse et al. 2012; Pangesti et al. 2013). We compared two of the best-studied plant–herbivore systems with regards to BG–AG interactions between herbivore induced direct defenses, i.e. maize (*Zea mays*) and *Brassica* spp. The former species is a monocotyledon whereas the latter belong to the dicotyledons. So far, this aspect has never been explicitly considered in comparative studies or reviews on BG–AG interactions, making our synthesis even more relevant. In general, BG induction of defenses increases AG resistance against herbivores in both *Brassica* spp. and maize. However, the molecular mechanisms underlying BG–AG interactions differ significantly between the two systems. Differences in leaf, stem and root morphology and physiology of monocotyledonous and dicotyledonous plants likely are key factors responsible for the different mechanisms of BG–AG interactions in *Brassica* spp. and maize plants. Including such basic aspects may help us to better understand differences and generalities of BG–AG interactions via herbivore-induced plant responses.

Aboveground and belowground inducible defenses—the role of phytohormones

The activation of plant inducible defenses by herbivores consists of different consecutive steps. The first step is the recognition of herbivore- (herbivore-associated molecular patterns; HAMPs) or plant-derived signals (damage-associated molecular patterns; DAMPs), serving as elicitors (Felton and Tumlinson 2008; Heil 2009). Second, herbivore detection activates a network of signaling pathways consisting of different phytohormones (Pieterse et al. 2012). Eventually, this signal transduction cascade results in the upregulation of defense-related genes and the production of defensive compounds (Berenbaum and Zangerl 2008; Wu and Baldwin 2010).

Apart from their role in plant growth and development, phytohormones are important regulators of plant inducible defenses after an herbivore has been perceived by a plant. It is well known that jasmonic acid (JA) and salicylic acid (SA) are the main regulators of plant inducible defenses, while ethylene (ET), abscisic acid (ABA), auxins and cytokinins (CKs) play an important modulatory role. Moreover, antagonistic and synergistic interactions (crosstalk) between different signaling pathways, provide plants with another layer of plasticity and allow them to fine-tune their defenses (Jaillais and Chory 2010; Pieterse et al. 2012; Thaler et al. 2012).

JA is a key player in plant inducible defenses against chewing insects from a wide range of taxa, such as Lepidoptera, Diptera, Coleoptera, Thysanoptera, Homoptera and Heteroptera (Kessler and Baldwin 2002;

Bostock 2005; Howe and Jander 2008; Verhage et al. 2011; Erb et al. 2012). Several studies have shown the important role of JA in BG–AG interactions (Erb et al. 2008; Soler et al. 2013; Fragoso et al. 2014). For example, JA application on roots of *Brassica* spp. (van Dam et al. 2001, 2004) and methyl-JA (Me-JA) application on *Nicotiana attenuata* roots induces AG plant defenses (Baldwin 1996). Thus, jasmonate application on one organ affects plant defenses in the other organ. Interestingly, only local increases in jasmonate levels have been observed in maize plants (*Zea mays*) after BG herbivory by western corn rootworm (*Diabrotica virgifera virgifera*) or AG herbivory by cotton leafworm *Spodoptera littoralis*. However, JA levels remained unchanged in systemic tissues of the same plants after BG or AG herbivory, suggesting the importance of other long-distance signals, at least in some plant-herbivores systems (Erb et al. 2009a). Alternatively, induced defense compounds may be produced locally and then be transported into the shoots (Baldwin et al. 1994; Morita et al. 2009; Andersen et al. 2013).

In *Arabidopsis* the phytohormones ABA and ET are known to act as modulators of two distinct and antagonistic branches of the JA signaling pathway, the MYC- and the ERF-branch, respectively (Fig. 1) (Anderson et al. 2004; Lorenzo and Solano 2005; Pré et al. 2008). Moreover, interactions of both ABA and ET with other molecular players of the signaling network have been reported and thus these phytohormones may affect plant defenses against insect herbivores (de Torres-Zabala et al. 2009; Jiang et al. 2010; Kazan and Manners 2012; Pieterse et al. 2012). The role of ABA and ET in BG–AG interactions has been shown (Jackson 1997; Erb et al. 2009a). For example, ABA levels were increased systemically after BG herbivory in maize plants (Erb et al. 2011). It is known that ABA plays a role in plant responses to both wounding and abiotic stresses including drought (Christmann et al. 2006; Hauser et al. 2011; Nguyen et al. 2016). Since herbivory by BG or AG chewing insects is accompanied by wounding and water loss (Aldea et al. 2005; Erb et al. 2009a; Conales et al. 2011), it seems likely that root herbivore-mediated abiotic stress may result in systemic induction of AG ABA levels, which may affect AG induced defenses (Erb et al. 2011).

SA regulates plant defenses against pathogens, phloem-sucking insects and plant responses to insect oviposition (de Vos et al. 2005; Zarate et al. 2007; Vlot et al. 2009; Bruessow et al. 2010). SA alone does not seem to play a signaling role, neither in plant defenses induced by BG insect herbivores (Erb et al. 2009a; Pierre et al. 2012), nor in BG–AG interactions in *Brassica* spp. (van Dam et al. 2004). Nonetheless, SA application could activate some root maggot-induced genes in the roots of *Beta vulgaris* (Puthoff and Smigocki 2007). Interactions of SA with JA, ET and ABA are well known (Pieterse et al. 2012) and thus SA could affect BG and/or BG–AG plant defenses via interactions with other phytohormones.

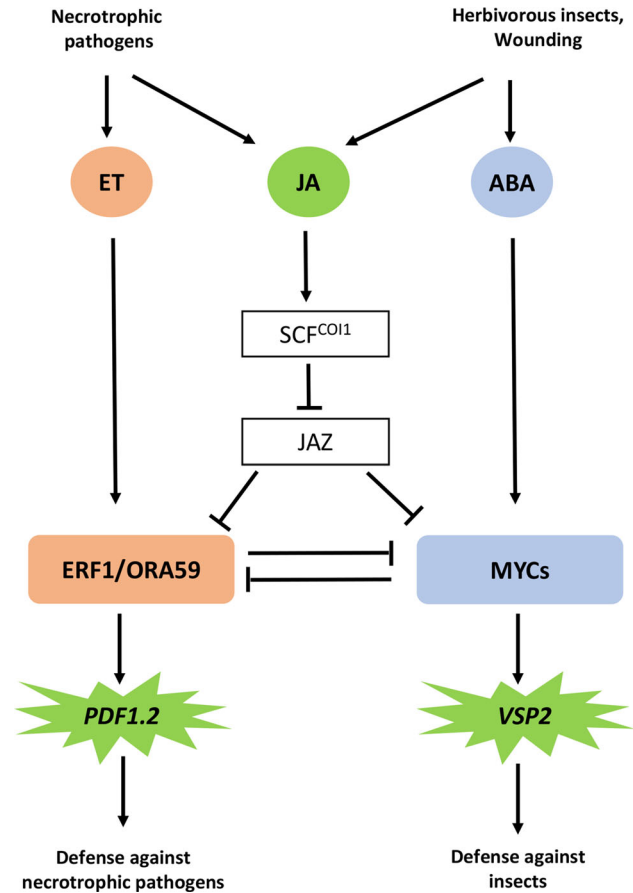


Fig. 1 Schematic representation of interactions between the most relevant signaling pathways in plants. Necrotrophic pathogens induce the ET-regulated ERF-branch (ERF1/ORA59), while herbivorous insects and wounding induce the ABA-regulated MYC branch (MYCs) of JA signaling pathway. The two branches of the JA pathway are mutually antagonistic. Arrows represent positive effects, blocked lines represent negative effects. ET ethylene, JA jasmonic acid, ABA abscisic acid, *SCF^{COI1}* E3 ubiquitin ligase SKP1-Cullin-F-box complex, JAZ JASMONATE ZIM transcriptional repressor proteins, VSP2: VEGETATIVE STORAGE PROTEIN2, PDF1.2 PLANT DEFENSIN1.2 Modified from Pieterse et al. 2012)

In addition, auxins and cytokinins (CKs) seem to play an important role in BG–AG interactions. Auxins have been shown to be translocated from AG to BG plant parts where they regulate root growth and BG plant defenses (Shi et al. 2006; Benjamins and Scheres 2008). The biosynthesis of the auxin indole-3-acetic acid (IAA) is closely connected to that of indole glucosinolates, providing a direct link between the two metabolic pathways, those of phytohormones and plant defensive compounds in Brassicaceae (Bak et al. 2001; Radojčić Redovniković et al. 2008). Changes in CKs levels and CKs-regulated gene expression in response to herbivory have been found not only locally but also systemically (Schäfer et al. 2015). Schäfer et al. (2015) have shown that AG simulated herbivory by wounding and application of oral secretions, resulted in changes in CKs levels in systemic leaves as well as in roots of *N. attenuata*

and *Arabidopsis thaliana* plants (Schäfer et al. 2015). Mobility of both auxins and CKs between leaves and roots has been reported (Reed et al. 1998; Kudo et al. 2010). Therefore it is imperative to further investigate the role of these phytohormones as mobile signals or as modulators of interactions between BG–AG plant inducible defenses.

Integrating different response levels of inducible defenses

Despite the extensive knowledge on the different response levels of inducible defenses and many observations of ecological effects, the exact molecular mechanisms driving BG–AG plant-herbivore interactions are not fully understood. One main reason is that different plant-herbivore systems are used for experiments. It is generally accepted that plant defenses are attacker-specific (Howe and Jander 2008; Erb et al. 2012), and even closely related, congeneric, plant species differ in their defenses against the same herbivore (van Dam and Raaijmakers 2006; Agrawal et al. 2014). In addition, individual genotypes of the same species were shown to differ in the allocation of defensive compounds to AG or BG tissues when exposed to herbivory (Birch et al. 1992, 1996; Hol et al. 2004).

Even studies on the same or similar plant-herbivore systems can yield different emerging patterns. For a part, this may be due to different experimental approaches used, such as application of phytohormones to simulate herbivory versus real herbivory. Although phytohormones are commonly used to simulate herbivory and the defense responses they elicit are broadly similar to those induced by real herbivory (Baldwin 1990; Dicke and Vet 1999; Loivamäki et al. 2004; Bruinsma et al. 2008), some differences may still occur (Bruinsma et al. 2009; van Dam et al. 2010). Moreover, as there are differences in the temporal dynamics between response levels within a plant, the link between the mechanisms and the ecological consequences of BG–AG interactions may be missed when focusing only on one response level or one time point. To gain a more comprehensive overview of general patterns that may emerge, we conducted an extensive literature review on inducible defenses in response to BG and AG herbivores in two well studied systems, *Brassica* spp. and *Zea mays*. By doing so, we could overcome some of the limitations related to single studies and reveal general as well as species-specific patterns emerging from these study systems. Furthermore, it enabled us to discuss the possible link between the mechanisms and the consequences of BG–AG interactions on the performance of AG herbivores in a broader ecological context. The relevant literature (see Tables 1 and 2) was searched on the Web of Science platform with search terms such as roots, shoots, belowground, aboveground, herbivory, defense, defence, maize, *Brassica*, in different combinations.

Below- and aboveground interactions of inducible defenses in *Brassica* spp. plants

Different *Brassica* species have been exposed to herbivores or phytohormone applications BG and/or AG (Table 1). We investigated studies where AG inducible defenses were analyzed after BG induction only, or BG as well as AG herbivory/phytohormone application. A literature search revealed that the vast majority of studies focused on changes in GLS levels, which are characteristic defensive compounds of Brassicaceae plants. Much less attention has been paid to other response levels, such as gene expression and metabolomics (Table 1). Surprisingly, we are not aware of any study measuring changes in BG and/or AG phytohormone levels in *Brassica* spp. in the context of BG–AG interactions, though it is well-known that they play an important role in the regulation of plant inducible defenses (Fig. 2).

The first pattern that is observed among *Brassica* spp. is that BG insect herbivory or JA application increases total GLS levels in shoots (Griffiths et al. 1994; van Dam et al. 2004; Soler et al. 2005; van Dam and Raaijmakers 2006; van Dam and Oomen 2008; Qiu et al. 2009; Pierre et al. 2012). In the few studies showing that BG induction results in a decrease (van Dam et al. 2005) or has a no effect (van Dam and Raaijmakers 2006; Pierre et al. 2012; Tytgat et al. 2013), GLS were either measured at earlier time points (less than 3 days) after BG induction or show a trend for an increase that is not statistically significant (yet). Thus, the observed differences may be mostly attributed to the timing of induction, at least for the different *Brassica* species that have been tested so far. Interestingly, although BG JA application has been shown to increase total GLS levels in *B. oleracea* shoots under greenhouse conditions (van Dam et al. 2004; van Dam and Oomen 2008; Qiu et al. 2009; Pierre et al. 2012), no effect was found under field conditions when the same plant species and phytohormone application methods were used (Pierre et al. 2013). Therefore, patterns observed under controlled greenhouse conditions cannot be directly translated to the effect under field conditions without further testing.

The second observed pattern is that inducible defenses in *Brassica* spp. show organ-specificity for both the induction and the response. Interestingly, this organ-specificity was observed for different response levels, such as transcriptome profiles of defense-related genes, specific classes of GLS and VOCs, that were induced after JA application or insect herbivory (van Dam et al. 2004; Soler et al. 2007; van Dam and Oomen 2008; Jansen et al. 2009; van Dam et al. 2010; Pierre et al. 2011a; Tytgat et al. 2013). Regarding GLS profiles, for example, BG JA application increased the expression of genes involved in the aliphatic GLS pathway and the levels of aliphatic GLS in *B. oleracea* shoots (van Dam et al. 2004; van Dam and Oomen 2008; Tytgat et al. 2013). In contrast, AG application increased mainly indole GLS levels and the expression of related genes in

Table 1 Summary of a literature review on different inducible response levels (gene expression, phytohormones, glucosinolates (GLS), metabolome, volatile organic compounds (VOCs) and other) studied in belowground (BG) and aboveground (AG) tissues of different Brassica species after BG and/or AG treatments (insect herbivory or phytohormone application) and changes in the performance of AG herbivores

Plant species	BG plant treatment	AG plant treatment	Gene expression	Chemistry						Other						Performance	References
				Phytohormones		GLS		Metabolomics		VOCs		Other					
				AG	BG	AG	BG	AG	BG	AG	BG	AG	BG	AG	BG		
<i>Brassica nigra</i>	JA, SA	JA, SA		V	V										van Dam et al. (2004)		
	<i>D. radicum</i>	<i>P. rapae</i>		V	V					Phenolics, proteins					van Dam et al. (2005)		
	<i>D. radicum</i>	<i>P. brassicae</i>		V			V								Soler et al. (2005)		
	<i>D. radicum</i>	<i>P. brassicae</i>		V			V								Soler et al. (2007)		
<i>Brassica rapa</i>	<i>D. radicum</i>	<i>P. brassicae</i>		V	V										van Dam and Raaijmakers (2006)		
	<i>D. radicum</i>	<i>P. brassicae</i>					V								Dammer et al. (2015)		
	<i>D. radicum</i> , JA, SA			V	V		V								Pierre et al. (2011a)		
	SA			V	V		V								Pierre et al. (2012)		
<i>Brassica napus</i>	JA	JA		V											Tytgat et al. (2013)		
	<i>D. floralis</i>			V	V										Birch et al. (1992)		
	<i>D. floralis</i>			V	V					Sulfur					Birch et al. (1996)		
<i>Brassica oleracea</i>	<i>D. floralis</i>			V	V										Griffiths et al. (1994)		
	JA, SA	JA, SA		V	V										van Dam et al. (2004)		
	JA	<i>P. brassicae</i>		V											Qiu et al. (2009)		
	JA	JA, <i>P. brassicae</i> , <i>P. rapae</i>		V						Sugars, a.a					van Dam et al. (2010)		
<i>Brassica oleracea</i>	JA	JA		V	V										Tytgat et al. (2013)		
	JA	JA, <i>P. brassicae</i> , <i>P. rapae</i>		V	V										Jansen et al. (2009)		
	JA	JA, <i>P. brassicae</i> , <i>P. rapae</i>		V	V										Pierre et al. (2012)		
	<i>D. radicum</i> , JA, SA			V	V										van Dam and Raaijmakers (2006)		
<i>Brassica oleracea</i>	<i>D. radicum</i>			V	V										van Dam and Raaijmakers (2006)		
	JA	JA, <i>M. brassicae</i> , <i>P. rapae</i>		V											van Dam and Raaijmakers (2006)		
	<i>D. radicum</i> , JA, SA			V											Oomen (2008)		
	<i>D. floralis</i>			V											Pierre et al. (2013)		

↓ some of the performance parameters were negatively affected, *V* studied response levels in a particular system, *JA* jasmonic acid, *SA* salicylic acid, *C* carbon, *N* nitrogen; *P* (in "Other") phosphorus, *K* potassium, *a.a* amino acids, *D* Delia, *P* (in "AG plant treatment") *Pteris*, *M* Mamestra

Table 2 Summary of a literature review on different inducible response levels (gene expression, phytohormones, 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA), metabolome, volatile organic compounds (VOCs) and other) studied in belowground (BG) and aboveground (AG) tissues of maize (*Zea mays*) plants after BG and/or AG treatments (insect herbivory or phytohormone application) and changes in the performance of AG herbivores

BG plant treatment	AG plant treatment	Gene expression	Chemistry						Other			Performance	Reference	
			Phytohormones		DIM-BOA		Metabolites		VOCs					
			AG	BG	AG	BG	AG	BG	AG	BG	AG			BG
<i>D. v. virgifera</i> , ABA, JA, ACC	<i>S. littoralis</i> , BTH	V	V	V	V	V	V					Phenolics	↓ after <i>D. v. virgifera</i> , None after ABA	Erb et al. (2009a)
<i>D. v. virgifera</i> , water stress	<i>S. littoralis</i>	V	V									Phenolics C/N, a.a	↓	Erb et al. (2009c) Erb et al. (2011)
<i>D. v. virgifera</i> , water stress												Sucrose, C		Dunn and Frommelt (1998)
<i>D. v. virgifera</i>											V	V		Rasmann et al. (2005)
<i>D. v. virgifera</i>	<i>S. littoralis</i>										V	V	Attractiveness of natural enemies	Rasmann and Turlings (2007)
<i>D. undecimpunctata howardi</i> , JA, SA		V	V											(Lawrence et al. 2012)

↓ some of the performance parameters were negatively affected, V studied response levels in a particular system, ABA abscisic acid, JA jasmonic acid, ACC 1-aminocyclopropane-1-carboxylate (ethylene precursor), SA salicylic acid, BTH benzo(1,2,4)thiazole (functional homologue of SA), C carbon, N nitrogen, a.a amino acids, D *Diabrotica*, D. v *Diabrotica virgifera*, S *Spodoptera*

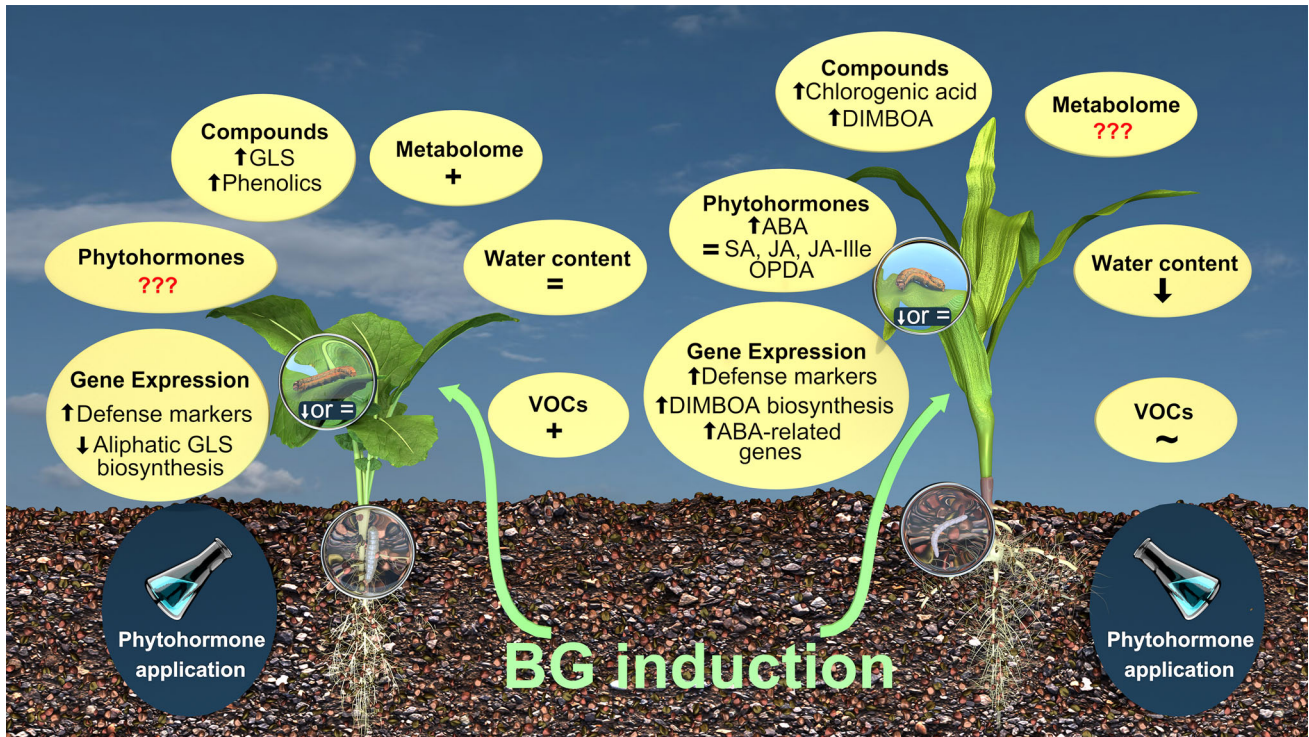


Fig. 2 Overview of the different levels of inducible defense responses studied in *Brassica* spp. (left) and maize (right) plants and their effects on aboveground (AG) insect herbivores. Response levels were measured in AG tissues after belowground (BG) or BG and subsequent AG induction by insect herbivores or phytohormone application. ↑ increase, ↓ decrease, = symbol no effect; ? not

studied, unknown; ~ the effect on the particular response level is not clear; + changes in a response level have been observed but not in a uniform direction, *GLS* glucosinolates, *VOCs* volatile organic compounds. The position of the BG herbivores shows their preferred feeding sites. See text and tables for details

shoots (van Dam et al. 2004; van Dam and Oomen 2008; Tytgat et al. 2013). This pattern was also observed in *B. rapa* plants, where only AG and not BG JA application increased indole GLS in shoots (Tytgat et al. 2013). Contrasting responses of aliphatic GLS (increase) and indole GLS (decrease) were also found in *B. oleracea* and *B. napus* leaves in response to BG herbivory by the turnip root fly *Delia floralis* (Birch et al. 1992). It is important to mention that the two classes of GLS (aliphatic and indole) are produced from different amino acids in two independently regulated biosynthetic pathways (Gigolashvili et al. 2007; Beekwilder et al. 2008). These results indicate that plant defense profiles in *Brassica* shoots are highly dependent on the initial side of induction.

However, whether or not specific GLS are induced is also species dependent. In *B. nigra* shoots, which GLS consists for > 98% of aliphatic GLS, both BG and AG JA application increased AG aliphatic GLS levels (van Dam et al. 2004). Moreover, BG herbivory by the cabbage root fly *Delia radicum* increased AG aliphatic as well as indole GLS levels in *B. nigra*, underscoring once more the difference between phytohormone applications and real herbivory (van Dam and Raaijmakers 2006). In contrast to the abovementioned studies on feral *B. oleracea*, a study using cultivated *B. oleracea* has shown that BG JA application resulted in much stronger AG

induction of indole, and not of aliphatic GLS (Pierre et al. 2012). Although these studies have used similar induction methods (i.e. same concentrations of phytohormones), the differences in the GLS induction patterns observed may be attributed to the different plant accessions that were used. Therefore, whether organ-specificity for the induction of different classes of GLS is a general phenomenon among *Brassica* spp. needs further investigation.

Interestingly, organ-specificity in *B. oleracea*, *B. nigra* and *B. rapa* also occurs for some classes of VOCs after JA application or insect herbivory (Soler et al. 2007; van Dam et al. 2010; Pierre et al. 2011a). For example, *B. nigra* plants exposed only to BG and not to AG insect herbivory emit volatile blends containing high levels of sulfur compounds and low levels of terpenes (Soler et al. 2007). Similarly, AG JA application on *B. oleracea* increased AG emissions of sesqui- and homoterpenes, whereas BG application did not (van Dam et al. 2010). These results show that different VOC biosynthetic pathways are activated in plants induced in BG and AG organs. Therefore, even when organ-specificity is not observed for one type of defense (i.e. the GLS profile), another type of defense in the same system may still show organ specificity.

So far, data from gene expression, GLS and VOCs analyses have shown that BG induction of defenses

generally affect AG induced defenses in *Brassica* species (Fig. 2). These changes are likely to affect defenses induced by AG herbivores as well as AG herbivore performance. As discussed before, BG induction increases total, and particularly aliphatic GLS levels in the shoots of different *Brassica* spp.. Aliphatic GLS are found to be more toxic than indole GLS as they produce isothiocyanates (ITC), which are more toxic than the breakdown products of indole GLS (Bones and Rossiter 2006). This matches with the general observation that BG-induced changes in AG GLS profiles negatively affect the performance of AG generalist herbivorous insects, as generalists are more sensitive to GLS and their ITCs (Hopkins et al. 2009). For example, the performance of the generalist cabbage moth *Mamestra brassicae* was negatively affected by BG JA-induced increase in AG aliphatic GLS levels of *B. oleracea* plants (van Dam and Oomen 2008). However, BG induced increases in shoot aliphatic GLS had no effect on the performance of the specialist small white butterfly *Pieris rapae* reared on *B. oleracea* plants subjected to BG JA application (van Dam and Oomen 2008). On the other hand, *P. rapae* performed worse when reared on *B. nigra* plants previously exposed to *D. radicum* herbivory (van Dam et al. 2005). Although specialist herbivores, such as *P. rapae*, are known to use GLS as feeding stimulants (Schoonhoven et al. 1998) and to be able to deal with this major defense weapon of Brassicaceae plants (Wittstock et al. 2004), negative effects of GLS and their hydrolysis product on the performance of specialist herbivores have also been reported (Agrawal and Kurashige 2003). Interestingly, it was shown that the initial GLS levels in *B. nigra* shoots were lower after *D. radicum* attack but were strongly induced after subsequent *P. rapae* herbivory (van Dam et al. 2005). Moreover, other defenses, such as phenolic compounds, to which the specialists are not well adapted may be induced by BG induction as well (Jansen et al. 2009). This may explain why the performance of another specialist large cabbage white butterfly *Pieris brassicae* was also negatively affected when developing on *B. nigra* plants previously exposed to BG *D. radicum* herbivory. In this system GLS levels were reduced to that of plants without previous BG herbivory, ruling out a role for GLS as the causal agent (Soler et al. 2005). Moreover, when *P. brassicae* developed on *B. oleracea* plants previously exposed to BG JA application, the performance was not affected, despite the increased AG aliphatic GLS levels (Qiu et al. 2009). These studies show that the performance of the two closely related specialists, *P. rapae* and *P. brassicae*, was differentially affected when grown on two different *Brassica* species exposed to different BG induction methods. Although it is hard to discriminate whether these differences were due to differences between plant species or induction methods, it can be concluded that the consequences of BG induction on the performance of both AG specialist herbivores cannot solely be attributed to changes in GLS levels and profiles.

Induction of BG plant tissues has been also shown to change AG levels of plant primary compounds, such as amino acids, proteins, sugars or N (Soler et al. 2005; van Dam and Oomen 2008; Qiu et al. 2009). In *Brassica*, BG herbivory did not affect the water content in AG tissues, even though root herbivory may reduce the capacity for water uptake (van Dam et al. 2005). Whether and how BG herbivory affects AG levels of defensive compounds other than GLS (i.e. protease inhibitors) in *Brassica* spp. plants has not been extensively studied. Increased total phenolic levels were found in *B. nigra* plants exposed to *D. radicum* and subsequent *P. rapae* feeding (van Dam et al. 2005). Phenolics are not as toxic as hydrolysis products of GLS; nevertheless, they are known to have anti-feedant properties and to reduce protein digestibility by herbivorous insects (Duffey and Stout 1996; Schoonhoven et al. 1998). Therefore, BG herbivorous insects may also affect food quality for the AG feeders via more global changes in plant chemistry. A more comprehensive analysis of these changes is required in order to link the physiological mechanisms with the ecological consequences of plant-mediated interactions between BG and AG insect herbivores.

Below- and aboveground interactions of inducible defenses in maize plants

A similar literature review on maize (*Zea mays*) revealed that the same response levels have been studied in maize plants as in *Brassica* spp., with the exception of an untargeted metabolomics approach (Table 2). Although metabolomics has been used to assess changes in AG and BG maize tissues in response to AG herbivory by *Spodoptera littoralis* (Marti et al. 2013), we are not aware of any study using metabolomic approach to investigate AG changes in response to BG herbivory (Fig. 2).

Laboratory and field experiments have shown that BG herbivory by larvae of *Diabrotica virgifera virgifera* induces resistance against AG herbivores (Erb et al. 2009a, 2011). Field observations revealed that leaf damage was reduced on plants that were exposed to BG herbivory compared to uninfested plants (Erb et al. 2011). Moreover, under laboratory conditions, the performance of *S. littoralis* was reduced when developed on plants previously infested with *D. v. virgifera* (Erb et al. 2009a; 2011). In an attempt to understand the mechanisms governing this interaction, different response levels have been studied in *D. v. virgifera*-maize-*S. littoralis* system (Table 2; Fig. 2). Phytohormone analysis has shown that *D. v. virgifera* feeding increases AG ABA levels, while the levels of SA, JA, JA-Ile and 12-oxo-phytodienoic acid (OPDA, a biosynthetic precursor of JA) are not affected (Erb et al. 2009a, 2011). Not only did BG herbivory increase these levels, but also it primed the AG ABA levels induced by *S. littoralis* feeding. Moreover, BG ABA application as well as *D. v. virgifera* feeding primed the AG production of the

defensive phenolic compound chlorogenic acid in response to *S. littoralis* feeding (Erb et al. 2009a, c). Therefore, ABA is a good candidate for a systemic signal governing BG–AG interactions. Eventually, it was shown that *D. v. virgifera* causes AG responses similar to drought stress, such as reduced water content, increased ABA levels and increased levels of defensive compounds that were also found in response to water stress (Richardson and Bacon 1993; Hura et al. 2008; Erb et al. 2009a, c). It was concluded that *D. v. virgifera*-mediated induction of AG defenses results from a combination of drought-stress dependent and independent mechanisms. First, *D. v. virgifera*-mediated water stress induces some of the AG defense markers, including ABA biosynthetic gene transcription and ABA levels. Second, increases in ABA levels caused by *D. v. virgifera*-induced water stress, activated some, but not all of the AG defense markers, such as the anti-feedant secondary metabolite 2, 4-dihydroxy-7-methoxy-1, 4-benzoxazin-3-one (DIMBOA). Third, some of the defense markers, such as putative cystatin protease genes, were induced by ABA, but not by water stress. This comprehensive analysis of different response levels shows that water stress and the ABA signaling pathway are important, but not the only players in *D. v. virgifera*-mediated changes in AG defenses (Erb et al. 2011).

Interestingly, *D. v. virgifera* feeding activates ABA signaling in AG tissues; nevertheless, *D. v. virgifera*-induced resistance against *S. littoralis* seems to occur irrespective of ABA signaling (Erb et al. 2009a, 2011). Although AG ABA levels and gene expression profiles in plants exposed to *D. v. virgifera* and BG ABA application were similar, BG ABA treatment did not affect the performance of *S. littoralis* (Erb et al. 2009a). Furthermore, *D. v. virgifera* reduced *S. littoralis* performance even more strongly in plants inhibited in ABA signaling. Thus it was suggested that ABA-independent changes in AG water content also contribute to resistance against *S. littoralis* (Erb et al. 2011).

In maize plants, the effect of BG induced AG resistance studies has been mainly studied using *S. littoralis* (Table 2). However, a field experiment has shown that *D. v. virgifera* infestation resulted in an overall increase in resistance, including to other AG herbivores such as European corn borer *Ostrinia nubilalis* and fall armyworm *Spodoptera frugiperda* (Erb et al. 2011). Therefore, it would be interesting to investigate whether BG-induced changes in water content affects resistance against these other AG herbivores directly or via changes in AG plant inducible defenses.

Mechanisms and ecological implications of below- and aboveground interactions in *Brassica* spp. and maize

When comparing *Brassica* and maize as the most comprehensively studied systems for the BG–AG interactions to date, both differences and general patterns

emerge. In both systems, induction with phytohormones cannot fully mimic the responses induced by real herbivory. Phytohormone application is an important tool in studies on plant inducible defenses, for example when investigating the role of the specific phytohormonal signals in plant defense responses. In studies on BG–AG interactions, phytohormone application is particularly useful in understanding, for instance, the organ specificity of inducible defenses. In nature, the same insect species usually do not feed on both BG and AG plant tissues, at least not in the same developmental stage. However, single phytohormones can only partly mimic the responses induced by real root herbivores and the effect they may have on AG herbivore performance (Erb et al. 2009a; van Dam et al. 2010). This highlights the involvement of multiple signaling pathways in BG–AG interactions. The contributions of these pathways and their interactions, can be best investigated by infesting plants with—different species of—real insect herbivores, after which changes in phytohormone levels and marker gene expression levels in the plants are assessed at different time points after onset of herbivory.

Studies using real insect herbivores as inducers of BG plant defenses have identified some consistent differences between *Brassica* and maize plants regarding the mechanisms governing BG–AG interactions. While in *Brassica* spp. BG-induced changes in AG plant responses do not seem to be related to drought stress, BG herbivory on maize plants changes AG water content. This discrepancy may be attributed to elementary morphological and physiological differences in leaves, stems and root of monocotyledonous (maize) and dicotyledonous (*Brassica*) plants (Fig. 3). In monocotyledonous plants the vascular system is scattered throughout the stem, while the vascular system of dicotyledonous plants is neatly organized in vascular bundles arranged in a ring around the edge of the stem. In roots of monocotyledonous plants, the xylem and phloem are interspersed and arranged in a wide ring around a central non-vascular pith, while in dicotyledonous plants the xylem is located in the center of the vascular bundle with the phloem surrounding the xylem (Purves et al. 1994). Studies on different plant species have shown that the systemic induction of defenses in AG tissues is controlled by vascular architecture (Davis et al. 1991; Rhodes et al. 1999; Schittko and Baldwin 2003; Ferrieri et al. 2015). For example, phyllotactic arrangements and vascular connectivity was shown to affect the among and within leaf variation of systemic induction of defensive compounds proteinase inhibitors (PIs) in tomato and *Solanum dulcamara* (Orians et al. 2000; Viswanathan and Thaler 2004). Vascular anatomy was also shown to affect the movement or accumulation of signals required for the systemic induction of defenses in leaves, such as SA in tobacco *Nicotiana tabacum* (Shulaev et al. 1995). Stronger systemic induction of defenses has been found in leaves directly connected via the vasculature to the damaged leaves than leaves without vascular connections.

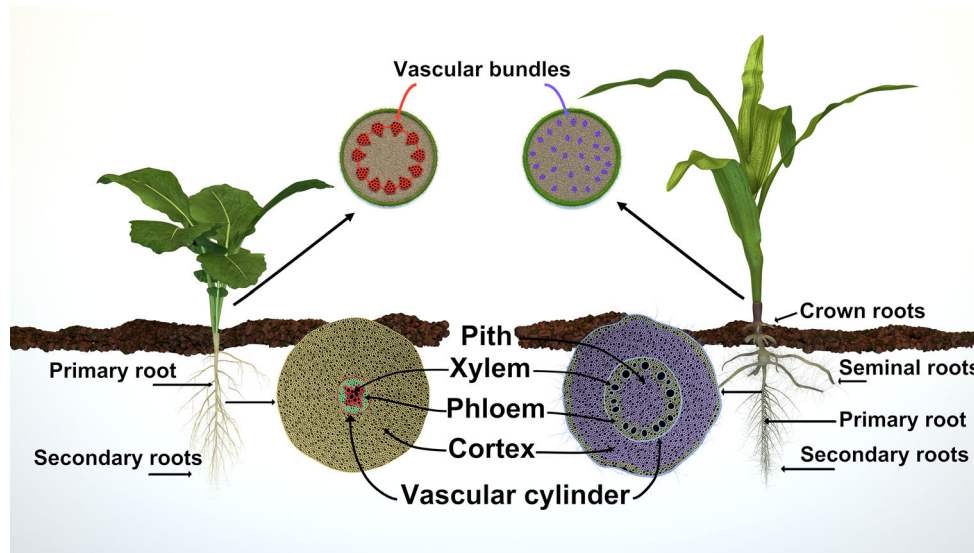


Fig. 3 Schematic representation of morphological differences in root and shoots/stems of *Brassica* (left) and maize (right) plants. The elementary morphological and physiological differences between the two most studied systems might be responsible for the drought-independent (in *Brassica*) and drought-dependent (in maize) belowground (BG)-induced changes in aboveground (AG) plant responses. In contrast to *Brassica*, the root system of maize

plants possess crown roots. The most studied root herbivore of maize plants *Diabrotica virgifera virgifera* usually feeds on crown roots that morphologically originate directly from the stem. The different arrangements of *Brassica* and maize stem and root vascular bundles may also partially explain differences in the mechanisms governing BG–AG interactions between the two plant-herbivore systems. See text for details

While the importance of vascular architecture for the systemic induction of defenses in AG tissues has been studied (Orians 2005), to date the effect of vascular architecture on the systemic induction of defenses between BG and AG plant tissues has received little or no attention. The correlation of BG-induced changes in AG plant responses with drought stress in maize but not in *Brassica* spp. suggest that differences in morphology and physiology play an important role in BG–AG interactions. In contrast to *Brassica*, the root system of maize plants possess crown roots, also known as adventitious or post-embryonic roots, in addition to primary and secondary roots (Fig. 3) (Hochholdinger and Tuberosa 2009). The BG herbivore *D. v. virgifera* which has been used in the majority of studies reviewed here, shows a strong preference and performs better when feeding on crown roots than on primary or secondary roots (Fig. 2) (Robert et al. 2012). As the crown roots morphologically directly originate from the stem, their vascular system is directly connected to the main central cylinder of the stem (Hochholdinger and Tuberosa 2009). Damage caused during *D. v. virgifera* feeding thus is likely to directly affect water status in AG plant tissues. *Brassica* plants do not possess crown roots and the larvae of the root fly *Delia*, the commonly used BG insect herbivore to induce *Brassica* species, preferably feed on the primary root (Fig. 2). In addition, different feeding strategies of the BG herbivores could also be responsible for the drought-dependent (maize) and drought-independent (*Brassica*) BG-induced resistance against AG herbivores. The larvae of *D. v. virgifera* are chewers that may feed on the entire crown root of maize plants, while

root fly larvae are mining into the cortex of *Brassica* (tap) roots (Gratwick 1992). This rather superficial mining feeding behavior of the root fly larvae prevents them from reaching the central cylinder of the root immediately and thus interfering with water transport to the AG tissues.

Despite these differences between maize and *Brassica* plants and their respective herbivores, in the majority of the cases induction of BG tissues increases AG resistance leading to root herbivore-induced shoot resistance, (RISR—Erb et al. 2011) in both systems. Two hypotheses have been discussed regarding the possible ecological reasons underlying RISR (van Dam 2009). First, RISR could simply be a consequence of the morphological and physiological integration of BG and AG plant tissues. According to this hypothesis the signals or defensive compounds produced in response to BG herbivory are passively transferred from the BG to AG tissues following water transportation via the xylem. In maize plants, BG-induced changes in water content of AG tissues are likely to be a result of such morphological constraints (Erb et al. 2011). The second hypothesis states that RISR could have an adaptive value for plants when the BG and AG herbivory have an additive negative effect on plant fitness (van Dam 2009). Thus it would be crucial for plants to increase the response levels or to prepare AG tissues for an herbivore attack directly or via priming after BG herbivory. This hypothesis could apply to *Brassica* plants, where the two mostly studied insect herbivores *D. radicum* (BG) and *P. brassicae* (AG) often co-occur in the field (Pierre et al. 2011b). BG herbivore feeding may have a severe impact

on plant growth, depending on which part of the roots is damaged (Tsunoda et al. 2014). However, whether the presence of BG and AG herbivores has a more than additive negative effect on plant fitness remains to be investigated.

Conclusion and future directions

In conclusion, our understanding of the mechanisms and the ecological consequences of BG–AG interactions is currently constrained due to the limited amount of data that is available. Moreover, different response levels are studied in different systems using different plant species, induction methods and herbivores. The morphology and physiology of plants belonging to different phylogenetic groups affects the mechanisms underlying BG–AG interactions and thus these aspect should be considered, or even specifically studied. As plant responses vary depending on the system, future studies should preferably integrate several response levels in the same plant-herbivore system. A good example are maize plants, where the mechanisms underlying BG–AG interactions are better (although not completely) understood as many response levels were studied using the exact same plant-herbivore complex. The next step then would be to explore what the discrepancies in plant responses to different herbivorous insects (such as AG insects from different taxa, specialists, generalists, etc.) are. Furthermore, it would be interesting to explore the differences in responses of plant species belonging to the same genera or family against the same insect herbivores. In this perspective, *Brassica* provides a good study system as several of its defenses have been deeply investigated in different species within the family. Moreover, higher trophic level interactions and the herbivore communities associated with *Brassica* species have been charted out very well (Gols et al. 2008b; Poelman et al. 2008; Ahuja et al. 2010; Kugimiya et al. 2010). With such a global model system it may be more likely to gain a much deeper understanding of interactions between plants (as a whole organism) and their BG–AG insect communities.

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