CHAPTER 9

CHEMICAL COMMUNICATION BETWEEN ROOTS AND SHOOTS

Towards an integration of aboveground and belowground induced responses in plants

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Abstract. Induced responses in plants occur in response to both aboveground (AG) and belowground (BG) herbivores and pathogens. So far, the majority of studies have focused on AG induced responses. Possible interactions between AG and BG induced responses have only recently received scientific attention. On the one hand, induction in one plant part may result in systemically induced responses in other parts. On the other hand, simultaneously occurring AG and BG induced responses may interfere, for example, when the activities of root feeders alter the effectiveness of induced responses against leaf feeders. In both cases, AG–BG interactions between induced responses may affect the amount of damage to a plant and therefore constitute an important selection pressure in the evolution of optimal plant-defence strategies.

Here we present a new concept for the integration of AG and BG induced responses in current optimal-defence theory. First, we will consider differences in physiology and morphology between roots and shoots, which relate to their different roles in resource acquisition and which are important in interactions with their environment. Then, we will evaluate how general principles emerging from current theories and mathematical models of optimal AG induced plant defences can be applied to BG induced responses, as well as to their interactions with AG responses. Finally, we argue that plants integrate the information that is communicated by roots and shoots to optimize plant fitness in a multitrophic context..
Keywords: aboveground–belowground interactions; herbivores; inducible defences; nematodes; optimal-defence theory; pathogens; plants; root-induced responses; shoot-induced responses; tolerance

INDUCED RESPONSES IN PLANTS

As the main primary producers on this planet, plants serve as food to a large diversity of aboveground and belowground heterotrophic organisms. To protect themselves against this multitude of enemies, plants have evolved a large arsenal of defences, such as trichomes, toxins and digestibility reducers. Many of these defences are inducible, i.e., their production increases when the plant is under attack of herbivores or pathogens. These changes in plants following damage or stress are called 'induced responses' (Karban and Baldwin 1997). They have been found to occur in over 100 plant species and can be elicited by organisms as different in size and feeding strategy as viruses and giraffes (Karban and Baldwin 1997; Agrawal et al. 1999). The compounds or morphological structures, such as trichomes, that are produced in response to an attack may either directly affect the fitness or behaviour of the herbivore, or indirectly affect its survival by attracting or augmenting natural enemies (Vet and Dicke 1992). Generally, induced responses are thought to act as induced defences, i.e., to increase resistance against herbivores and to reduce the negative fitness consequences of herbivory (Karban and Baldwin 1997).

Induced defences are thought to have several advantages over constantly produced constitutive defences. First, it is assumed that induced defences are cost-saving in comparison to constitutive defences, because they are produced only when plants are under attack. When herbivory is absent, the resources that are not used to produce defences may be allocated to growth and reproduction. This is especially beneficial when plants are in competition for limited resources such as light and nutrients (Van Dam and Baldwin 2001). Moreover, high levels of constitutive defences may deter mutualists, such as pollinators and mycorrhizal fungi, which may positively contribute to plant growth and reproduction (Strauss et al. 2002). Inducible defences may allow the plant to decrease defence-compound levels temporarily during mutualistic interactions (Euler and Baldwin 1996). Finally, induced defences are known to be very specific because the plant can obtain 'information' about the herbivore or pathogen that is present before producing defences. Pathogens and herbivores are known to trigger signalling pathways in plants differentially. The plant hormones, jasmonic acid (JA or its methylated form MeJA), salicylic acid (SA or MeSA), ethylene and abscisic acid (ABA), are the best-known compounds for their role in induced responses against insects and other environmental stresses. JA is a product of the lipoxygenase (LOX) signalling pathway that is specifically triggered by herbivore damage (Reymond and Farmer 1998). SA is involved in the signalling pathway that is activated upon pathogen infestation (Hammerschmidt and Smith-Becker 1999; Pieterse et al. 2002). Ethylene and ABA are thought to act mainly as modulators of JA and SA responses, thus enabling the plant to fine-tune its response (Reymond and Farmer 1998; Kahl et al. 2000). This signalling specificity may not only provide information about future risk of herbivory, but also enable the plant to tailor the nature and magnitude of the response to the enemy that is attacking (Karban et al. 1999).

Because defence-related signalling hormones are transported via the vascular system (Zhang and Baldwin 1997) or travel via the air (MeJA, MeSA and ethylene, Kahl et al. 2000; Karban et al. 2004), induced responses are not restricted to the site

of attack. In many cases there is a systemically induced response in undamaged plant parts as well. Within shoots, systemic induction patterns generally match source–sink relations and the vascular anatomy of the plant (Davis et al. 1991; Orians et al. 2000; Van Dam et al. 2001). When mature leaves are damaged, undamaged younger – sink – leaves show increased levels of defences as well, whereas undamaged older – source – leaves do not. This may be a functional response of the plant to protect its more valuable photosynthetically active leaves, reflecting an optimal allocation of defence products within the plant (Iwasa et al. 1996; Van Dam et al. 1996; Bezemer et al. 2003).

INTERACTIONS BETWEEN ABOVEGROUND AND BELOWGROUND INDUCED RESPONSES

Although induced plant responses have been studied intensively for over three decades now, induction by belowground (BG) feeding herbivores and how this may affect above ground (AG) herbivores, or AG induced responses and vice-versa, has only recently received scientific attention (Van der Putten et al. 2001; Van Dam et al. 2003). A number of studies have shown that roots employ directly as well as indirectly induced chemical defences against soil pathogens, nematodes and insects (Neori et al. 2000; Van Tol et al. 2001; Walker et al. 2003a; Bauer and Mathesius 2004; Bais et al. 2005). Similar to AG induced responses, the induction by BG herbivores and pathogens may readily result in systemic responses in the leaves. However, with the exception of induced systemic resistance (ISR) and systemic acquired resistance (SAR) by soil bacteria (Pieterse et al. 2002), AG and BG induced responses have rarely been considered in conjunction.

Systemic induction between roots and shoots

Interactions between AG and BG induced defences may occur at different levels. The simplest form of AG–BG interactions is that an induction event in one plant organ alters defence levels in the other organ as well. A review of the literature shows that there are many examples that this may be the case (Table 1). This systemic effect may involve an active up- or down-regulation of genes involved in defence production. Alternatively, the observed changes in defensive chemicals may be a side-effect of reallocation processes after damage. For example, the direction of pyrrolizidine alkaloid induction in artificially shoot-damaged *Cynoglossum officinale* plants appeared to be determined by the genetic strain the plant belonged to. Since the changes in root and shoot alkaloid levels were negatively correlated with each other within half-sib families, the observed changes were assumed to reflect resource reallocation patterns triggered by the damage (Van Dam and Vrieling 1994). Simultaneous reallocation of resources and defence compounds may especially occur when severe artificial damage is applied, which disturbs the shoot–root balance of plants and triggers regrowth responses (Iwasa and Kubo 1997).

Table 1 shows that shoot defence levels may be affected by root-feeding organisms or by root cutting, as well as by decomposers that have no direct

Table 1. *Studies that explicitly measure changes in defence levels in the untreated organ after aboveground or belowground induction. Abbreviations: AG = aboveground, BG = belowground, PI = protease inhibitor, PR protein = pathogen-related protein, suscept. = susceptible genotype, JA = jasmonic acid, SA = salicylic acid*

	Induction by	Plant	Defence	Effect	Reference
BG to AG	*Root-invading organisms*				
	Arbuscular mycorrhiza	Plantain	Catalpol	0	Wurst et al., 2004a
		Plantain	Catalpol	+	Gange and West, 1994
	Ectomycorrhiza	Chestnut	Tannins	-	Rieske et al., 2003
		Scots pine	Phenolics	0	Manninen et al., 1998, Manninen et al., 2000
		Scots pine	Terpenes	0	Manninen et al., 1998
	Non-pathogenic bacteria	Arabidopsis	PR gene priming	+	Pieterse et al., 2002
	Plant-feeding nematodes	Black mustard	Glucosinolates	-	Van Dam et al. 2005
		Black mustard	Phenolics	0	Van Dam et al. 2005
		Tobacco resistant	Nicotine	+	Hanounik and Osborne, 1977
		Tobacco suscept.	Nicotine	-	Hanounik and Osborne, 1977
		Rice	Defence genes	+	Blouin et al., 2005
		Potato	PR proteins	+	Rahimi et al., 1996
		Sweet vernal grass	Total phenolics	-	Bezemer et al., 2005
	Root-chewing insects	Black mustard	Glucosinolates	0/+	Van Dam et al. 2005, van Dam et al. unpublished
		Cabbage	Glucosinolates	+	Birch et al., 1992
		Cotton	Terpenoids	+	Bezemer et al. 2004

(cont.)

Table 1 (cont.)

	Induction by	Plant	Defence	Effect	Reference
BG to AG	*Induction mimics*				
	Artificial damage	Ragworth	Alkaloids	0	Hol et al., 2004
		Potato	PI gene	+	Peña-Cortes et al., 1988, Dammann et al., 1997
	JA/SA application	Potato	PI gene	JA +	Dammann et al., 1997
		Black mustard Wild cabbage	Glucosinolates	JA + SA 0/-	Van Dam et al. 2004
		Wild tobacco	PI activity, nicotine	JA +	Baldwin, 1996, van Dam et al., 2001
	Decomposers				
	Earthworms	Plantain	Aucubin	0	Wurst et al., 2004b
		Plantain	Catalpol	-/0	Wurst et al., 2004a, Wurst et al., 2004b
		Plantain	Phytosterols	+	Wurst et al., 2004b
		Rice	Defence genes	+/-	Blouin et al. 2005
AG to BG	*Foliar feeders*				
	Leaf-chewing insects	Cotton	Terpenoids	0	Bezemer et al. 2004
		Ragwort	Alkaloids	-	Hol et al. 2004
	Induction mimics				
	Hormone application	Black mustard Wild cabbage	Glucosinolates	JA 0 SA 0	Van Dam et al. 2004
		Chinese cabbage	Glucosinolates	SA + JA +	Ludwig-Müller et al., 1997
		Okra	PR protein	SA+	Nandi et al., 2003
		Wild tobacco	PI activity	JA +	Van Dam et al. 2001
	Artificial damage	Maize	Hydroxamic acids	0	Collantes et al., 1998
		Rye	Hydroxamic acids	+	Collantes et al., 1999
		Hound's tongue	Alkaloids	+/-	van Dam and Vrieling, 1994

organisms or by root cutting, as well as by decomposers that have no direct interaction with the plant. Based on the data in Table 1, we may conclude that root-chewing insects and application of JA generally increase defence levels in the shoots. This suggests that the JA signalling pathway is involved similarly in the systemic induction from roots to shoots by root-chewing insects, as it is in AG systemic induction by shoot chewers. Even though it has been hypothesized that associations with arbuscular myccorhizal fungi are involved in shoot herbivore specialization (Gange et al. 2002) we found no clear evidence in the literature that this is due to increased levels of defence compounds (Table 1, Wurst et al. 2004a; 2004b). Nematode infestations did not show a clear pattern of changes in shoot defence levels, which may be explained by the different feeding types of the nematode species that were used in the different experiments (Williamson and Gleason 2003).

In contrast to root chewers, neither leaf-chewing insects nor JA application uniformly increased defence levels in roots (Table 1). This suggests that systemic induction from the shoot to the root is not as common as the reverse. A thorough comparison between induction patterns from roots to shoots and the reverse is hampered, however, because we found many more examples of BG induction to affect AG defence levels than the reverse. Possibly, this is due to the practical difficulties involved in quantitatively extracting roots from the soil.

Negative interactions between aboveground and belowground induced responses

AG and BG induced responses may also indirectly affect each other. This may happen when BG and AG herbivores are feeding on the plant at the same time, which is a common situation in natural environments (Van der Putten et al. 2001). As shown above, feeding on one organ may affect defence levels in the other, and when both organs are induced simultaneously, AG and BG induced responses may negatively affect each other. In AG studies it has been shown, for example, that (SA-mediated) pathogen-induced responses may reduce or even inhibit (JA-mediated) herbivore-induced responses (Hammerschmidt and Schultz 1996). Signalling compounds transported from infested roots to the shoot may interact similarly with locally induced hormones triggered by shoot-feeding organisms. In *Brassica nigra* or *B. oleracea* plants, however, we found no evidence that SA application suppresses JA-induced systemic responses when these hormones were applied simultaneously, but spatially separated, to roots and shoots (Van Dam et al. 2004). An experiment that used actual herbivory, however, showed that infestation of *B. nigra* with nematodes or root-fly larvae altered the course of induction in response to shoot-chewing herbivores (Van Dam et al. 2005). Plants increased their shoot defence levels faster when they were infested with nematodes, which suggests that nematodes may prime plants in a way similar to non-pathogenic soil bacteria (Pieterse et al. 2002). Clearly more studies are needed to investigate the generality of this phenomenon.

BG induced responses may also alter 'optimal' defence allocation within the shoot. Cotton plants induced with root-chewing herbivores had a more even

distribution of defence compounds among leaves than plants with an AG herbivore (Bezemer et al. 2004). Due to this more even distribution, generalist shoot feeding insects fed less and had reduced growth rates compared to herbivores on plants without root herbivores (Bezemer et al. 2003). Moreover, on cotton plants with root herbivores, extrafloral nectar production was also more evenly distributed among leaves, whereas foliar herbivory caused an increase of extra-floral nectar production specifically for the leaf that was under attack (Wäckers and Bezemer 2003). Because extra-floral nectar serves as an indirect defence by guiding ants to the herbivores, root herbivory thus has the potential to constrain optimal induction of indirect defences in the shoot.

INTEGRATING INTERACTIONS BETWEEN ABOVEGROUND AND BELOWGROUND INDUCED RESPONSES

Both systemically induced responses and negative interactions between simultaneously induced AG and BG induced responses can affect the performance of herbivores and their natural enemies. Consequently, these interactions may affect the amount of damage, and thereby fitness loss, that the plant will suffer. Therefore, interactions between AG and BG induced responses may constitute a significant selection pressure in the evolution of optimal plant-defence strategies. If we want to understand the evolutionary process that has shaped induced responses, BG induced responses must be included (Van der Putten et al. 2001; Van Dam et al. 2003).

In the remainder of this chapter we will present a new conceptual approach to integrate interactions between AG and BG induced responses by focusing on physiological and morphological differences between roots and shoots that are important for their ecological interactions with the environment. Subsequently, we will consider current theories and mathematical models on optimal AG induced plant defences in order to find general principles that may be used to structure new concepts that include BG induced responses.

Differences and similarities between roots and shoots

The differences between roots and shoots in terrestrial plants, of course, are mainly related to the differences in their primary roles in resource acquisition for the plant. Whereas roots primarily acquire water and mineral nutrients from the soil, the primary function of the shoot is to fix carbon via photosynthesis (Hutchings and De Kroon 1994; Taiz and Zeiger 1998). The distinct differences in morphology and physiology of roots and shoots not only reflect the different functions but also the different media in which they forage. The soil in which roots grow is a dense and patchy medium (Crawford et al. 2005). Roots show a high morphological and physiological plasticity in response to the physical and chemical properties of soil. They are able to avoid obstacles, toxins and roots of other plants by guiding the direction of root-tip growth and by controlled withering of tips that grow towards an obstacle (Falik et al. 2005). Moreover, plants can quickly respond to nutrient-rich patches by specifically proliferating into the patch and by increasing local nutrient

uptake rates in newly formed root tips (Hutchings and De Kroon 1994; De Kroon et al. 2005). Because the location of nutrient patches in the soil is *a priori* unpredictable, roots forage in many different directions with many different root tips growing simultaneously (Drew 1990).

Other than nutrients in the soil, the distribution of the main AG resource, light, is more homogeneous and unidirectional. Nevertheless, light distribution may also be patchy due to shading by other plants or plant parts. As a consequence, shoots also show several plastic adaptations in response to light availability. In dense populations, for example, shoots are less branched than in open habitats, which is a plastic adaptation to competition with neighbouring plants. Moreover, plants may increase leaf area and reduce leaf thickness when shaded by other plants (Hutchings and De Kroon 1994; De Kroon et al. 2005). As a consequence of the different distributions of AG and BG resources, roots have many more actively growing root tips than shoots have shoot apices, especially in non-clonal herbaceous dicots. Roots also have higher turnover rates than leaves. Damage to a root tip by herbivory or pathogen infection therefore is probably less dramatic for plant growth than the removal of a shoot apical meristem.

Another important difference between roots and shoots is that they grow in environments that are physically very different, which affects the chemical communication with their environment. Roots are constantly and actively excreting a wide array of compounds into the soil, which mainly affect their direct environment, called the rhizophere (Campbell and Greaves 1990; Neori et al. 2000). Root exudation plays a major role in maintaining root–soil contact and in guiding root growth and, thus, in plant survival (Walker et al. 2003a; Bais et al. 2005). The compounds in root exudates may selectively attract and support different micro-organisms that benefit the plant, such as nitrogen-fixing bacteria and mycorrhiza (Walker et al. 2003a). On the other hand, they may also contain defensive compounds that deter pathogenic micro-organisms, fungi and nematodes (Walker et al. 2003b; Bais et al. 2005), or volatile organic compounds that attract natural enemies of root feeders (Van Tol et al. 2001; Rasmann et al. 2005). Root exudates thus may have similar functions as volatile emissions by shoots, for example the attraction of natural enemies of herbivores (Dicke and Van Loon 2000). However, the physical differences between air and soil are responsible for great differences in transport distances and catabolic rates of AG and BG emitted volatiles, for example because UV radiation does not penetrate into the soil (Walker et al. 2003a). There is some evidence that severe artificial shoot damage can increase levels of defensive compounds in root exudates (Collantes et al. 1999). Due to a lack of knowledge on the exact mechanism underlying secretion of phytochemicals by roots, it remains unclear whether this is an active process or a concomitant effect of resource reallocation for regrowth processes (Walker et al. 2003a).

Neither roots nor shoots can survive in isolation but constantly have to exchange their acquired resources as well as coordinate their foraging activities by hormonal signalling (Hutchings and De Kroon 1994). Changes in internal hormone levels also regulate root–shoot regrowth processes after severe damage, especially when the sites of hormone production – root growth tips or shoot apical meristems – are lost (Taiz and Zeiger 1998). Interestingly, the hormones that coordinate root–shoot

regrowth after damage, such as auxins, cytokinins, ethylene and ABA, are also involved in modulating induced responses after herbivore damage (Baldwin 1989; Rojo et al. 1998). This emphasizes the importance of considering repair and reallocation processes when studying induced responses.

Optimal plant-defence theory

Central to all theories on optimal defence allocation is that the evolution of plant defences is driven by a cost–benefit balance (Coley et al. 1985; Fagerstrom et al. 1987; Herms and Mattson 1992; Simms 1992; De Jong 1995; Jokela et al. 2000; Shudo and Iwasa 2001; Strauss et al. 2002). In all theories, the benefit is the reduction in damage to the plant, resulting in increased fitness compared to a sub-optimally defended plant. The concept of costs has been debated more intensely. Originally, direct resource investments needed for construction of the defence molecules were considered the principal costs of defence (Gershenzon 1994). However, in many instances, these production costs *per se* were not found to reduce fitness in plants that had higher defence levels than their conspecifics (Bergelson and Purrington 1996). More recently, it has been generally acknowledged that the main costs of defence induction are ecological costs, which occur for example when high defence levels reduce attractiveness to mutualists or competitive strength (Strauss et al. 2002).

Optimal-defence theory also emphasises the value of individual plant parts. If the loss of a certain plant part is reducing plant fitness more than the loss of another plant part, the plant should preferably allocate defence compounds to the former, more valuable part (Van Dam et al. 1995a; Iwasa et al. 1996; Van Dam et al. 2001). The valuation of plant parts has been used as a basis to predict optimal defence allocation as well as optimal defence strategies (Table 2). For example, flowers and seeds, whose survival is highly correlated with plant fitness, often contain very high constitutive levels of defence compounds (Hartmann et al. 1989; Van Dam et al. 1995b; Van Dam et al. 2001). High defence levels are also found in young leaves but, in contrast to flowers, they are still able to increase defence levels after damage (Van Dam et al. 2001; Bezemer et al. 2004). Removing young leaves from a plant significantly reduces future biomass production, whereas removal of old leaves frequently does not (Van Dam et al. 1995b). This again indicates that the high – inducible – defence levels generally found in young leaves reflect optimal defence allocation to more valuable plant parts (McKey 1979; Iwasa et al. 1996).

Several theories include tolerance as an alternative strategy to reduce fitness loss to herbivory (Strauss and Agrawal 1999; Jokela et al. 2000; Fornoni et al. 2004). Originally, defence and tolerance were thought to be mutually exclusive strategies (Van der Meijden et al. 1988), but more recent analyses have revealed that individual plants may use both tolerance and defence to reduce fitness losses (Mauricio et al. 1997; Fornoni et al. 2004).

As for shoots, root parts may differ both in value and vulnerability. Consequently we may expect that different root parts have different optimal strategies when they are damaged (Table 2). Whereas several studies have evaluated

the value of different AG plant parts, there is only one study we know of that uses a similar approach for roots (Yanai and Eissenstat 2002). These authors developed a mathematical model and used physiological data on respiration and uptake rates of apple and citrus roots as parameters (Bouma et al. 2001). The model predicted that under high herbivore and pathogen pressure, root life span – and return on investment – could be increased by allocating moderate levels of defences to roots (Yanai and Eissenstat 2002). Under low herbivore pressure, allocation to root defence did not increase root life span. Because this model considers cohorts of roots of the same age, they could not predict differences in defence levels among root parts. However, as stated by the authors, data on the exact costs and benefits of optimal root defence are currently lacking.

Table 2. Expected values of different shoot and root parts for plant survival and plant fitness and the predicted local optimal defence strategies after pathogen or herbivore damage

	Damage to plant if lost	**Predicted defence strategy**
Shoot		
Old leaves	-	Tolerance
Young leaves and apical meristem	++	Constitutive and induced defence
Stems	++	Constitutive defence
Flowers/seeds	+++	Constitutive defence
Root		
Tap/main root	++	Constitutive and induced defence
Lateral roots	+	Induced defence
Root tips	-	Tolerance

Another important aspect that is frequently considered in optimal-defence theories, is the likelihood of being attacked. This is especially so for theories that evaluate the costs and benefits of induced vs. constitutive defences. If the likelihood of being attacked is low, induced-defence strategies may be preferred over constitutive defences (Jokela et al. 2000; Shudo and Iwasa 2001). The risk for roots to be attacked by insect herbivores may be much lower than for leaves because roots are less accessible and less nutritious for insects (Hunter 2001). However, roots may have a much higher risk of being attacked by bacteria, fungi and plant-feeding nematodes, with the highest diversity and abundance in the soil (Bongers 1994; Crawford et al. 2005). In response to these abundant root feeders, tolerance may be the preferred strategy (Jokela et al. 2000).

TOWARDS AN INTEGRATION OF ABOVEGROUND AND BELOWGROUND INDUCED RESPONSES IN OPTIMAL-DEFENCE THEORY

The few studies published to date clearly indicate that BG induced defences are important in shaping AG induced responses. In natural environments, plants start to

interact with BG organisms as soon as a root has been formed, which usually precedes the onset of shoot emergence (Bezemer and Van Dam in press), and as a consequence, BG induced responses may be very common. Therefore, we argue that BG induced responses must be integrated in optimal plant-defence theory before we can understand the evolution of induced plant responses.
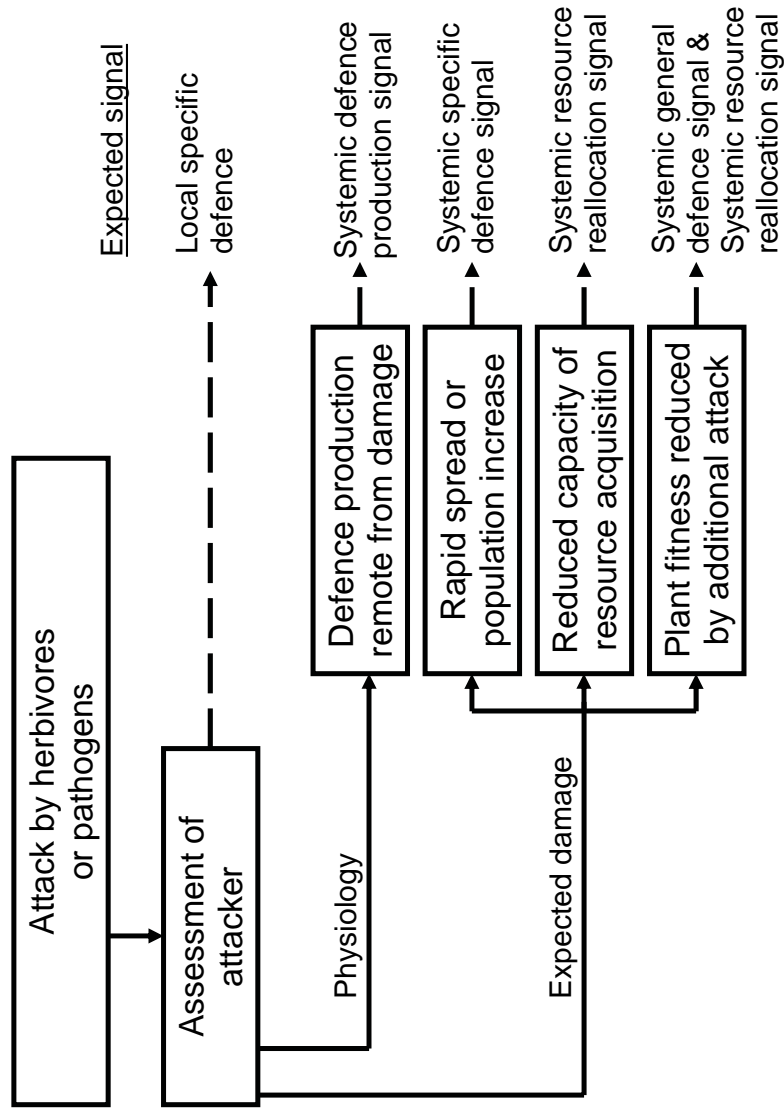
To include AG–BG induced responses in optimal plant-defence theory we need to keep in mind that plants are an integrated system in which roots and shoots *together* contribute to plant fitness. This – trivial, but often ignored – concept also considers the fact that roots and shoots constantly exchange, via hormones, information about their current status and that optimal integration of this information is used to maximize plant fitness in unpredictable AG and BG environments. AG or BG attacks by herbivores or pathogens may affect the status of the roots or the shoots, and as a consequence determine the type of signals that will be produced.

Following attack, plants may first acquire information about the type of organism that is attacking. Based on, for example, bacterial excretions or salivary compounds, plants are able to recognize their attacker (Boland et al. 1995; Mattiacci et al. 1995). After recognition, the plant may produce a specific local signal, for example to initiate localized and rapid death of a few host-plant cells, known as the hypersensitive response, to isolate the site of pathogen infection or oviposition from the rest of the plant (Meiners and Hilker 1997; Hammerschmidt and Nicholson 1999). The locally produced signal or a secondary messenger, however, may also be rapidly transported from the site of damage to other plant parts (Schittko et al. 2000). In some plant species, the systemic signal may simply be required because the site of defence production is remote from the site of damage. Defence compounds that are produced exclusively in the roots, such as nicotine in tobacco or terpenoids in cotton, can only increase in the shoot if there is a systemic signal to trigger defence production in the roots (Zhang and Baldwin 1997). In such plants, the systemic signal results from the physiological organization of the plant species.

Alternatively, the type of the signal may depend on the kind of damage that may be expected. If the attacker is mobile, increases rapidly in population size or is known to spread quickly throughout the whole plant, the plant may benefit by triggering defences in all undamaged plant parts to prepare for the upcoming invasion.

On the other hand, if the organ under attack is damaged to the point at which it will soon lose capacity to acquire its specific resource, it may be more advantageous to signal for reallocation of resources for regrowth and repair (Figure 1). Such a signal may consist of, for example, a decline in auxin production rates after severe damage of the apical shoot meristem (Taiz and Zeiger 1998).

Finally, the plant may be able to compensate for fitness loss after a single attack, but not if another enemy will attack it. In that case, a general systemic defence response may be beneficial to reduce the chance of an additional attack. The latter may be especially beneficial if the plant species has an evolutionary history with several different herbivores that occur sequentially over the growth season (English-Loeb et al. 1993; Viswanathan et al. 2005). The above processes are not mutually exclusive and several signals may be produced at the same time. Possibly there is a

Expected signal

Attack by herbivores or pathogens

Assessment of attacker

Local specific defence

Physiology

Expected damage

Defence production remote from damage → Systemic defence production signal

Rapid spread or population increase → Systemic specific defence signal

Reduced capacity of resource acquisition → Systemic resource reallocation signal

Plant fitness reduced by additional attack → Systemic general defence signal & Systemic resource reallocation signal

Figure 1. Conceptual scheme of the types of local and systemic signals that may be produced after an attack by aboveground or belowground herbivores and pathogens. Solid arrows indicate the path of subsequent and parallel processes that may occur in plants that are subject to an attack. Dashed arrows indicate signalling that may result from the process in the box

hierarchy among these signalling events and the resulting responses, depending on the prevailing environmental conditions in which the plant species has evolved (De Kroon et al. 2005). We therefore cannot speak of a single induced response, but rather of a *suite* of induced responses in roots and shoots that minimizes damage to the plant and optimizes plant fitness as a whole (after Shudo and Iwasa 2001).

It is still unclear how this suite of responses, which may occur in sequence or all at the same time, are integrated to optimize AG and BG induced responses. It may help to consider the temporal aspects of AG and BG induced responses when evaluating the ecological and evolutionary aspects of these interactions (see also Viswanathan et al. 2005). In most natural environments, soil organisms will begin to interact with roots even before the shoots have emerged from the seed coat. The frequency of interactions with AG herbivores and pathogens will increase with shoot size and thus will occur later in time. We therefore argue to focus first on how BG root–soil-organism interactions can affect shoot defence levels and how this can interact with subsequent responses induced by AG feeders (Bezemer and Van Dam in press).

In conclusion, data on interactions between AG and BG induced responses are scarce. More information is especially needed on how these interactions are integrated towards an optimal defence response in plants. In order to raise future experiments above the level of descriptive studies, we need to consider plants as integrated systems and analyse the integration of AG–BG induced responses at different organizational levels, ranging from genes to multitrophic ecological interactions. Only then may we be able to gain a more comprehensive insight into how AG–BG interactions have affected the evolution of induced defences in plants.

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