

Chapter 17

The Role of Roots in Plant Defense Responses to Aboveground Herbivores

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17.1 Introduction

Roots are integral to a plant's growth and survival. In addition to anchoring plants to the soil, they absorb water and nutrients from the surrounding soil, serve as sites of storage for valuable photoassimilates, and also act as sites of synthesis for several plant hormones and secondary metabolites. As a consequence, plants invest heavily in the development and establishment of their root system with some plants investing substantially more than 50 % of their body weight in roots (Taiz and Zeiger 2002). Belowground herbivores (BGH) such as insects and nematodes have evolved to take advantage of the tremendous amount of organic matter that the roots represent (Blossey and Hunt-Joshi 2003; Raaijmakers et al. 2009). To protect themselves against BGH, roots also utilize both direct and indirect defenses similar to those found in the aboveground parts of a plant (van Dam 2009; Kandath and Mitchum 2013). However, the experimental limitations posed by the general inaccessibility of roots and the "hidden" nature of belowground herbivores have resulted in a paucity of data. Given the importance of roots to any plant, interest in the role of roots in plant defenses has surged, and literature comparing root and shoot defense has been on the rise in the past decade (Bezemer and van Dam 2005; Kaplan et al. 2008; Rasmann and Agrawal 2008; van Dam 2009; Soler et al. 2012b).

Previously, plant–insect interactions have been largely studied by only focusing on the response in the aboveground tissue, i.e., the leaves of plants, leading to a skewed and unbalanced understanding. Plants counter insect herbivory by utilizing a wide variety of strategies comprising of constitutive and inducible defenses (Howe and Jander 2008; Walling 2008; Fürstenberg-Hägg et al. 2013). In some cases, the plants' traits affect insect preferences, such as morphological features that affect host plant selection and feeding behavior. Preformed barriers such as

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waxes on leaf surface, leaf toughness, trichomes, accumulation of chemicals in reproductive tissues, etc., are hardwired into developmental programs and are constitutively present (Howe and Jander 2008; Walling 2009). In other cases, the plants' traits influence insect performance, such as the production of secondary metabolites in response to herbivory that either deters or kills the insect. Inducible defenses are initiated at the site of attack and also transported systemically through the entire plant (Karban and Baldwin 1997). These highly dynamic induced defenses not only offer the advantage of reduced cost in terms of resource allocation but also increase the phenotypic variability in the plant phenotype resulting in higher efficiency (Karban et al. 1997; Karban and Baldwin 1997; Cipollini et al. 2004).

In this chapter, we would like focus on the contribution of roots to aboveground herbivory (Fig. 17.1). A growing body of evidence supports an integral role for roots in aboveground plant defense strategies. Roots serve as (1) sites of synthesis for several secondary metabolites that are not only actively synthesized to protect roots against BGH but are also transported aboveground to increase foliar resistance to AGH, (2) act as dynamic storage organs for valuable photoassimilates which can be reallocated aboveground after the threat has passed, and, finally, (3) also actively recruit beneficial soil microbes to help deal with aboveground herbivory.

17.2 Root-Derived Defenses to Aboveground Herbivory

17.2.1 AGH Induced Changes in Root Transcriptome

Plants resist insect herbivory by rapidly and accurately inducing defenses. Large-scale gene expression profiling has provided researchers with an insight into the transcriptional changes that occur in response to herbivory (Smith 2005; Chen 2008). The induction of defenses occurs at the site of insect attack and also systemically in undamaged tissue (Bostock 2005). In recent years, the physiological and transcriptional changes occurring in roots due to AGH is also being investigated (Erb 2009; Erb et al. 2009b; Ankala et al. 2013; Tytgat et al. 2013). Erb (2009) found that in maize (*Zea mays*), AGH by cotton leafworm (*Spodoptera littoralis*) resulted in the differential regulation of a larger proportion of genes in roots as compared to changes in the shoot tissue. In shoots, genes involved in plant defense were upregulated after *S. littoralis* attack including those involved in the biosynthesis and signaling of two critical plant defense hormones, jasmonic acid (JA) and salicylic acid (SA). Functional analyses of transcripts showing differential regulation in roots, however, did not display any overlap with changes that occurred in the shoot tissue. Further, transcripts implicated in protein metabolism were found to be preferentially upregulated in roots suggesting a specific function of root metabolism in response to shoot attack. Ankala et al. (2013) studied transcriptional

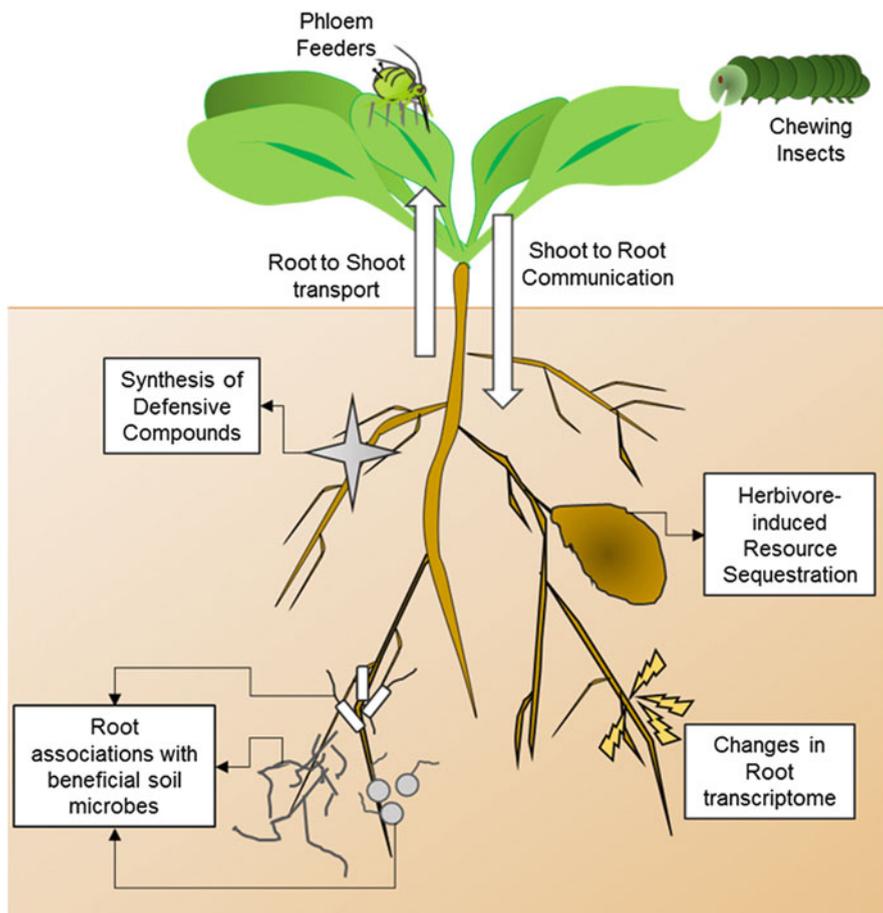


Fig. 17.1 The contribution of roots in plant defense strategies against aboveground herbivory

changes occurring in roots and shoots of a maize inbred line resistant to the fall armyworm (*S. frugiperda*). Interestingly, in this case, although genes involved in JA biosynthesis and signaling were upregulated in the roots, genes involved in the signaling and perception of another plant defense hormone, ethylene (ET), were also upregulated in roots in response to AGH. Further, transcript levels of genes encoding proteins involved in direct defenses were enhanced in roots. However, whether these transcriptional changes that occur in roots in response to AGH have an impact on the performance of the insect herbivore is not clear and warrants further research. Tytgat et al. (2013) studied the transcriptional responses that occur in shoots and roots of *Brassica oleracea* plants by mimicking herbivory by JA application. Specific responses in primary metabolism, development, and defense were observed depending on whether JA was applied to the shoots or the roots. These differential responses observed in these studies suggest that plants are able to

respond differently to signals coming from the shoots or from the roots. As a result plants are able to fine-tune their responses specifically to only the plant part that is under attack. Taken together, these studies indicate that distinct transcriptional changes occur in roots during AGH and further highlight the need to include roots to develop a comprehensive understanding of plant response to AGH.

17.2.2 *Synthesis of Shoot Defensive Compounds*

Plants have evolved a wide variety of defensive compounds to ward off, inhibit, or kill insect herbivores. These defensive compounds are usually secondary metabolites or plant proteins that are either constitutively present or induced in response to insect herbivory. A large body of evidence supports the role of secondary metabolites such as alkaloids, terpenoids, glucosinolates, furanocoumarins, etc., in plant defense, and several of these are synthesized in the roots of plants and transported to the shoots where they act on AGH [reviewed in Van der Putten et al. (2001), Kaplan et al. (2008), Rasmann and Agrawal (2008), Erb et al. (2009a), Erb (2012) and Nalam et al. (2013)]. The reasons why plants have adopted to synthesize defensive compounds in roots are uncertain. One reason may be that by separating the site of synthesis and the site of action, plants can guarantee delivery of the defensive compounds in situations where extensive defoliation occurs making roots safer areas for synthesis. The earliest example for a root-derived secondary metabolite providing resistance against AGH comes from studies in tobacco (*Nicotiana sp.*) plants (Dawson 1941). Nicotine, an alkaloid that is constitutively present in the leaves of plants belonging to the genus *Nicotiana*, is synthesized in the roots of the plant. Simulated insect herbivory by the application of methyl jasmonate (a derivative of jasmonic acid) on the leaves of the plant results in an increase in root nicotine synthesis and transport to the shoots providing increased protection against the herbivore (Baldwin et al. 1994; Morita et al. 2009). Another class of alkaloids, the tropane alkaloids are also synthesized in the roots of plants of the genus *Solanaceae* and transported to the shoots (Bais et al. 2001; Ziegler and Facchini 2008).

Glucosinolates are a class of secondary metabolites that are mainly found in plants belonging to the genus *Brassicaceae*. Their role in plant defense against not only insect herbivores but also pathogens has been well documented (Bednarek et al. 2009; Hopkins et al. 2009). An increase in the levels of glucosinolates is observed in the shoots and roots of plants under attack by an AGH (Ludwig-Müller et al. 1997; Soler et al. 2009). Although the site of synthesis of these compounds has not been identified, the presence of these compounds in roots of plants under attack by AGH raises the possibility that they may be synthesized in roots. In certain other instances, the final version of a bioactive secondary metabolite is not completely synthesized in the roots; rather precursors are synthesized and transported to the shoots where they undergo further modifications. A prime example comes for a group of secondary metabolites known as furanocoumarins. Umbelliferone is a precursor for several bioactive furanocoumarins that act as feeding deterrents and

also have antifungal and antibacterial properties (Berenbaum 1978; Yamane et al. 2010). The site of synthesis for this precursor has been localized to the roots in bishop-weed (*Ammi majus*) plants from where it is transported to the rest of the plant for further modifications (Sidwa-Gorycka et al. 2003). In addition to secondary metabolites, plants also produce defensive proteins (arthropod-inducible proteins, AIPs) that protect the plant against insect herbivory by interfering with the insect digestive system [reviewed in Zhu-Salzman and Liu (2011)]. In maize lines that are genetically resistant to a wide variety of insect pathogens, a unique AIP termed Mir1-CP accumulates in the foliar tissue during insect herbivory (Lopez et al. 2007). The site of synthesis of this protein was found to be in the root and in maize plants, where the roots were removed just prior to insect feeding, and the same accumulation was not observed suggesting strongly that Mir1-CP is synthesized in roots. With the advent of genomics and an increased interest in root biochemistry, it is quite plausible that other examples of AIPs synthesized in roots will be uncovered.

Secondary metabolites and AIPs synthesized in the roots for shoot defenses are probably transported to the roots via the vasculature of the plant. Evidence for transport through both the xylem and phloem exists. For instance, the immunohistochemical localization of enzymes involved in nicotine biosynthesis indicates that the synthesis of nicotine occurs in the cortex and endodermis of roots from where it diffuses into the upward-flowing stream of the xylem (Shoji et al. 2000). Although the site(s) of synthesis of tropane alkaloids within the roots is unknown, the xylem serves as the mode of transport for several of them (Ziegler and Facchini 2008). Mir1-CP synthesis was also shown to occur in roots specifically in xylem parenchyma and from where it moves to the xylem for upward transport to the foliar tissue. Interestingly, in the foliar tissue, Mir1-CP is also found in the phloem of both minor and intermediate veins (Lopez et al. 2007). The transport of secondary metabolites may also occur through the phloem. Pyrrolizidine alkaloids are another class of secondary metabolites that provide protection against insect herbivores (Lindigkeit et al. 1997). The transport to shoots of the precursor of pyrrolizidine alkaloids, senecione N-oxide, which is synthesized in roots has also been shown to occur via the phloem. The use of girdling experiments and the localization of biosynthetic enzymes for senecione N-oxide in root cortex parenchyma and endodermis across the phloem confirm that roots are the sites for synthesis and the phloem is the mode of transport (Moll et al. 2002; Ober and Kaltenecker 2009).

17.2.3 Signal(s) in Shoot-to-Root Communication

The synthesis of shoot defensive compounds in the roots suggests that upon perception of an AGH, a signal is sent to the roots resulting in the synthesis and subsequent transport of the compounds aboveground (Fig. 17.1). This shoot-root-shoot communication and transport likely follows the internal vascular network of the plant, i.e., phloem and xylem. Plant- and insect-derived molecules have the

potential of acting as signal molecules. However, to be considered as signal, the molecule must be found at the site of attack and be capable of inducing plant responses both locally and systemically.

Among the plant-derived candidates, the defense hormone, jasmonic acid (JA), is a likely candidate for a mobile element. JA and associated compounds, collectively termed jasmonates, are critical for long-distance wound signaling and the activation of defenses against necrotrophic pathogens and chewing insects (Heil and Ton 2008; Wu and Baldwin 2009; Woldemariam et al. 2011). There is strong evidence that methyl jasmonate moves in the phloem along with photoassimilates and also in the xylem as a result of vigorous exchange allowing the movement to regions which are the sources of the photoassimilates (Thorpe et al. 2007). Support for jasmonates as mobile elements comes from studies in several plants. Simulated foliar herbivory of tobacco (*N. sylvestris*) results in an increase in JA concentration immediately in the leaves and subsequently in the roots stimulating the synthesis of nicotine (Baldwin et al. 1994; Winz and Baldwin 2001). A similar pattern is observed in poplar (*Populus nigra*), where mechanical wounding or foliar JA application results in the induction of defense marker genes in the roots (Major and Constabel 2007). In maize plants, Mir1-CP accumulation is observed in response to foliar methyl jasmonate treatment (Ankala et al. 2009). Evidence for the role of other plant hormones involved in defenses, SA, ethylene (ET), and ABA as mobile elements in shoot-to-root communication, is however less clear and warrants further research (Soler et al. 2012a; Nalam et al. 2013). For instance, SA is critical for the activation of systemic acquired resistance that occurs in response to pathogen attack. Although it is clear that SA itself is not the mobile element, the activation of SA signaling at the site of attack results in the transmission of long-distance signal(s) through the whole plant (Shah 2009; Dempsey and Klessig 2012). With respect to insect herbivory, feeding by phloem-feeders such as aphids and whiteflies induces the activation of SA-mediated signaling and defenses (Moran and Thompson 2001; Zarate et al. 2007) which raises the possibility of a SA-derived signal being a mobile element involved in shoot-to-root communication. In several plant species, small RNAs molecules such as short-interfering RNAs and micro-RNAs play an important role in plant defense (Padmanabhan et al. 2009). These small RNAs have been identified in the phloem sap of several plant species and could quite possibly function as mobile elements (Kehr and Buhtz 2008, 2012). However, evidence supporting their role as mobile elements performing shoot-to-root communication during AGH is lacking and requires further research.

Insect-derived candidates can also potentially function as mobile elements in shoot-to-root communication. The saliva of phloem-feeders and chewing insects contains effector proteins that are introduced into plants during feeding. These effector proteins modulate plant defenses by interfering with or eliciting plant defense responses (Tjallingii 2006; Will et al. 2007; Harmel et al. 2008; Mutti et al. 2008; Carolan et al. 2009; Bos et al. 2010). For instance, a peptide in the 3–10 kDa range in the saliva of the green peach aphid (*Myzus persicae*) induces defense responses in *Arabidopsis* resulting in reduced aphid performance (De Vos

and Jander 2009). On the other hand, a secreted protein product of the salivary gland gene, *C002*, is delivered into plant tissue and aids in the enhancement of aphid fecundity (Mutti et al. 2008; Bos et al. 2010). Furthermore, foliar feeding by *M. persicae* results in the induction of *LOX5* expression in roots of *Arabidopsis* (Nalam et al. 2012). Although the identity of the component responsible for root-specific induction is unknown, it is conceivable that aphid salivary proteins secreted into the phloem are capable of eliciting plant responses in the roots.

17.3 Herbivore Induced Resource Sequestration

Roots in many plants are modified to serve as storage organs for water and nutrients. Many of these modified roots like cassava, sweet potato, ginger, etc., are edible and form an important part of the human diet. In some perennial species, photoassimilates are often reallocated to roots to help tide over unfavorable periods serving as buffers against abiotic and biotic stresses (Palacio et al. 2007; Kobe et al. 2010). It is however clear that in several species, roots can aid in the ability of plants to tolerate AGH (Orians et al. 2011; Schultz et al. 2013). This phenomenon termed induced resource sequestration involves the rapid transport of nutrients/photoassimilates from the aboveground parts to the roots, making them temporarily inaccessible to the aboveground attacker. These nutrients/photoassimilates can then be reallocated back aboveground for regrowth after the herbivore has passed (Mauricio et al. 1997). In several herbaceous species, this reallocation from roots to shoots is the most common mechanism of tolerance (Welter and Steggall 1993; De Jong and Van Der Meijden 2000).

Herbivore induced short-term resource allocation has been shown to occur in several species. AGH by a generalist grasshopper (*Romalea guttata*) on maize plants growing in a $^{14}\text{CO}_2$ -rich environment showed that a significant amount of ^{14}C is recovered from not only the roots but also root exudates (Holland et al. 1996). In poplar, leaf feeding by gypsy moth (*Lymantria dispar*) larvae resulted in an immediate increase in the export speed of carbon to the stem and roots (Babst et al. 2008). Similarly, AGH by tobacco hornworm (*Manduca sexta*) caterpillars on tobacco plant growing a $^{13}\text{CO}_2$ -enriched chamber resulted in increased ^{13}C allocation to roots (Kaplan et al. 2008). In common milkweed (*Asclepias syriaca*), AGH by monarch caterpillars (*Danaus plexippus*) induced significant changes in the allocation of carbon to the roots (Tao and Hunter 2013). In addition to feeding by an insect herbivore, simulated herbivory by either mechanical damage, application of defense hormones, or insect salivary regurgitant has also been shown to result in resource reallocation. For instance, in poplar, tomato (*Solanum lycopersicum*), and *Arabidopsis*, the application of JA also resulted in resource allocation to the roots (Babst et al. 2005; Gómez et al. 2010; Ferrieri et al. 2013). Interestingly, in addition to mechanical damage caused due to insect feeding, the presence of insect-derived elicitors present in the insect salivary regurgitant is required to induce resource allocation. In tobacco and tomato plants, regurgitant from *M. sexta* larvae applied to

damaged leaves but not mechanical damage alone resulted in a 75 % increase in carbon transport to roots (Schwachtje et al. 2006; Gómez et al. 2012). Taken together, these studies show that plants can transport some resources away from the AGH. However, relatively little is known about the long-term consequence of induced resource sequestration. In wild tobacco, herbivore induced sequestration results in an extended flowering time and increase in seed production suggesting an increase in fitness (Schwachtje et al. 2006) although whether this occurs due to resource remobilization from the roots was not demonstrated.

The mechanisms that initiate and control reallocation to the roots are not fully understood. Photoassimilates are normally transported in the plant via the phloem. It is therefore plausible that by either increasing the loading into the phloem in the leaves or increasing unloading from the phloem at the roots can help achieve the rapid sequestration that is observed (Turgeon and Wolf 2009). The observation that the activity of sugar cleaving enzymes such as invertases increases in tobacco roots after herbivory (*M. sexta*) (Kaplan et al. 2008) or simulated herbivory (*M. sexta* regurgitant) (Hermesmeier et al. 2001) suggests that during AGH, the “sink” strength of roots increases. The molecular basis of this phenomenon has been studied in tobacco plants where it was found that sucrose non-fermenting-related kinase1 (SnRK1) plays an important role in this process. SnRK1 plays a central role in the energy metabolism of the cell (Halford and Hey 2009). The transcripts of SnRK1 are downregulated in the leaves within hours of simulated herbivory by *M. sexta* resulting in an increase of 10 % more photoassimilate allocation to the roots (Schwachtje et al. 2006). The initiation of sequestration by the application of JA suggests that this plant defense hormone is involved in the process. And indeed, leaf-derived jasmonates are major regulators of this process. However, tobacco plants which lack a fully functional JA pathway still exhibit resource reallocation (Schwachtje et al. 2006; Machado et al. 2013), suggesting that other signaling pathways may be involved. A recent study in tobacco plants shows that the levels of indole-3-acetic acid (IAA), a precursor of the hormone auxin, increase in roots after AGH and application of IAA resulted in the root sequestration in a JA-independent manner (Machado et al. 2013). A complete picture of the mechanisms of initiation and control of reallocation in response AGH is however far from complete.

17.4 Recruitment of Beneficial Soil Microbes

The environment in which roots exist, the rhizosphere, supports a diverse array of soil-borne microbes. Plant roots produce copious amounts of exudates that are mainly comprised of an enormous range of small molecular weight compounds which serve as a major source of carbon to soil microbes (Walker et al. 2003; Bais et al. 2006). As a result, the composition of the rhizosphere is strongly influenced by the plant itself, and interactions mediated by these exudates can exert a strong positive or negative effect on plant growth and health (Van Der Heijden et al. 2008;

Raaijmakers et al. 2009). Soil microbes such as pathogenic fungi, oomycetes, bacteria, and nematodes negatively impact plant growth. On the other hand, arbuscular mycorrhizal fungi (AMF), nitrogen-fixing bacteria, plant growth-promoting rhizobacteria (PGPR), and plant growth-promoting endophytic fungi (PGPF) exert a positive influence directly by promoting plant growth and indirectly through induced systemic resistance (ISR) (Bezemer and van Dam 2005; Van Loon 2007). ISR refers to the systemic induction of plant defenses in the whole plant as result of the association of roots with certain beneficial soil microbes. ISR provides the plant with broad spectrum protection against a wide range of insect herbivores and pathogens including those that occur only on aboveground plant tissue (Bent 2006; Pozo and Azcon-Aguilar 2007; Van Oosten et al. 2008; Doornbos et al. 2010).

The mechanism of induction of ISR shares several similarities with defenses that are initiated against AGH (Pieterse and Dicke 2007; Pieterse et al. 2009). The defense hormone, JA, plays a central role in ISR and also negatively impacts chewing insects. For example, the larvae of the diamondback moth (*Plutella xylostella*) feeding on cabbage plants associated with an endophytic fungus (*Acremonium alternatum* Gams) suffered from reduced growth and increased mortality (Raps and Vidal 1998). With respect to phloem-feeders, the result of ISR can be either a negative or neutral effect on herbivore performance and seems to depend on the plant, microbe, and the AGH. Phloem-feeding insects, aphids and whiteflies, mainly activate salicylic acid (SA)-mediated defenses that can negatively affect JA-mediated defenses via crosstalk (Kunkel and Brooks 2002). Although, JA-mediated defenses have also been shown to be involved in defense against phloem-feeders (Kunkel and Brooks 2002; Zhu-Salzman et al. 2005; Zarate et al. 2007). Examples of negative effects occur in the case of the phloem-feeders such as the green peach aphid and silverleaf whitefly (*Bemisia argentifolii*) which perform poorly on tomato or sweet pepper (*Capsicum annuum*) plants, respectively, whose roots have formed an association with a PGPR (*Bacillus amyloliquefaciens*) (Murphy et al. 2000; Herman et al. 2008). The association of another PGPR, *B. subtilis*, with tomato leaves also retards the development of silverleaf whitefly (Valenzuela-Soto et al. 2010). An example of neutral effect on a phloem-feeder, green peach aphid, occurs in white leaf clover (*Trifolium repens*) plants associated with rhizobia (*Rhizobium leguminosarum*) (Kempel et al. 2009). Additional biotic factors like the degree of specialization of the insect, microbe identity, plant developmental stage, and genotype have also been known to modulate ISR and as a result influence the AGH (Pineda et al. 2010). Abiotic factors like drought stress also seem to influence the effect of beneficial microorganisms. For example, in tomato plants associated with an endophytic fungus (*A. strictum*), whitefly mortality was higher only in plants that were undergoing drought stress (Vidal 1996). Altogether, these examples demonstrate that roots can act as important modulators of aboveground defenses.

Arbuscular mycorrhizal fungi (AMF) form intricate associations with roots of plant and aid the plant in the uptake of nutrients and water by effectively increasing the surface area occupied by the roots in the soil. By a mechanism that is similar to

but not the same as ISR, AMF can impact AGH (Fritz et al. 2006; Hempel et al. 2009; Pozo et al. 2010). It has been shown that resistance against a bacterial pathogen (*Xanthomonas campestris*) in *Medicago truncatula* and a fungal pathogen in tomato is induced by the association of AMF with the roots of these plants (Fritz et al. 2006; Liu et al. 2007). With respect to insect herbivores, factors such as degree of specialization and feeding guild impact the outcome of the interaction [reviewed in Jung et al. (2012)]. For example, root colonization of tomato plants with AMF was recently shown to affect the performance of cotton bollworm (*Helicoverpa armigera*) caterpillars with the JA pathway playing a crucial role in defense mediated by the mycorrhiza (Song et al. 2013). Mycorrhizal mycelia also form long interconnected networks known as common mycorrhizal networks (CMNs) that can connect multiple plants via their roots. In addition, to acting as conduits for the exchange of water and nutrients like nitrogen and phosphorous, they act as information “superhighways” between them (He et al. 2003; Selsosse et al. 2006; Mikkelsen et al. 2008; Barto et al. 2012). Pathogen-infected tomato plants transmit defense signals to healthy plants via CMNs resulting in the induction of defense genes resulting in induced resistance to future attacks (Song et al. 2010). In bean (*Vicia faba*) plants, infestation by the pea aphid (*Acyrtosiphon pisum*) results in the activation of SA-mediated defenses, and the induction of these defenses also occurs in uninfested plants only when the plants are connected by CMNs (Babikova et al. 2013b). Additionally, the transmission of a defense signal to healthy plants occurs rapidly within 0–24 h resulting in the production of volatiles that make the healthy plant unattractive to aphids (Babikova et al. 2013a). The nature of the signal that is transmitted is unknown; however sufficient evidence now exists to show that plants communicate the presence of AGH with each other’s CMNs.

17.5 Conclusion

Plants have developed sophisticated strategies to protect themselves against insect herbivores. The impact insect herbivores cause on world agriculture has resulted in intense research on plant defense mechanisms against insect herbivory. Roots are increasingly being recognized as important contributors to plant defenses not only against belowground insect herbivores but also against aboveground herbivores (AGH). Transcriptional profiling of roots during AGH has revealed that plants are capable of fine-tuning their response depending on which part of the plant, the root or the shoot, is under attack. Roots also serve as the sites of synthesis of numerous defensive compounds that exert anti-herbivore effects in the shoots. Roots act as sites of storage during herbivore induced resource sequestration. The interactions of roots with a wide variety of soil microbes also influence the outcome of plant-insect interactions. This chapter summarizes the current status of research on roots as important contributors to plant defense against AGH. In addition to possessing a potent defense system against BGH, roots also contribute significantly to plant defense strategies to AGH. Although there are several questions that yet remain to

be answered, a survey of current literature highlights the importance of roots in plant response to AGH. It is evident that a comprehensive understanding of plant-insect interactions can only be achieved by including the role of roots in the conservation. Far away and safe from the AGH, roots serve as sites for the synthesis of defensive compounds and as sites for the storage of valuable photoassimilates and recruit the help of beneficial soil microbes for protection.

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