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Van der Putten, W.H.

published in

Ecology

2003

DOI (link to publisher)

[10.1890/02-0284](https://doi.org/10.1890/02-0284)

document version

Publisher's PDF, also known as Version of record

[Link to publication in KNAW Research Portal](#)

citation for published version (APA)

Van der Putten, W. H. (2003). Plant defense below ground and spatiotemporal processes in natural vegetation. *Ecology*, 84(9), 2269-2280. <https://doi.org/10.1890/02-0284>

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PLANT DEFENSE BELOWGROUND AND SPATIOTEMPORAL PROCESSES IN NATURAL VEGETATION

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Abstract. Root herbivores and pathogens play an important role in driving plant abundance, species diversity, and succession in natural vegetation. Subterranean plant feeders and pathogenic microorganisms interfere with basic functions of plant roots, such as resource uptake, storage of reserves, and anchoring of plants in the soil, but concepts and theories on control of herbivores and pathogens, such as the Green World Hypothesis, have been developed and applied almost exclusively for the aboveground subsystem. Root herbivores and pathogens affect spatial and temporal patterns in natural plant communities, and whether these patterns are cyclic or irreversible depends on characteristics of the root feeders, interactions with other soil or aboveground organisms, and the rate of changes in the abiotic environment. Established plants can tolerate root herbivores and pathogens at densities that are lethal to their offspring. Dispersal by seeds or rhizomes allows new cohorts to become established before root herbivores or root pathogens colonize and develop, but it provides only temporal release of plants from their natural enemies. Permanent release from root herbivores and pathogens contributes to plant invasiveness. I propose to expand the concept of plant–soil feedback by including plant defense belowground. Many plant secondary compounds are synthesized in the roots, and these chemicals could affect root herbivores, root pathogens, and their natural enemies. Plants may exert direct and indirect defense, resistance, tolerance, or dispersal to move away from the herbivores and pathogens belowground, and I propose that acknowledging trade-offs and life history strategies will enhance our capacity to predict spatiotemporal patterns in natural vegetation. Further studies in this area will enhance our understanding of plant abundance, succession, and invasions in natural communities, as well as the evolution of plant dispersal and other defensive strategies against root herbivores and pathogens in natural communities.

Key words: *direct and indirect defense; dispersal; diversity; enemy release; invasiveness; multitrophic; nematode; plant community; resistance; root pathogen; subterranean herbivore; succession.*

INTRODUCTION

Many soil organisms have the potential to influence the composition of plant communities in space and time, either through changing the availability of resources, or by direct feeding on plant roots (Wardle 2002). Plants affect soil organisms and soil organisms reciprocally affect plants, leading to a feedback that drives changes in plant communities over space and time (Bever et al. 1997). The feedback between plants and soil organisms can be positive, neutral, or negative for the plants involved, for their offspring, and for other plant species in the community (Reynolds et al. 2003). In order to enhance our understanding of plant–soil feedback in relation to plant life histories and plant community processes, interactions between plants and the various functional groups of organisms inhabiting the root zone need to be explored in more detail.

I will focus mainly on interactions between plant roots, invertebrate herbivores, microbial pathogens,

mutualistic symbionts, and natural enemies of the herbivores and pathogens. These interactions below ground may contribute to the relative abundance of plant species (Gange et al. 1993, Klironomos 2002), plant species diversity (Bever 1994, Holah and Alexander 1999, Packer and Clay 2000, De Deyn et al. 2003), primary succession (Van der Putten et al. 1993), secondary succession (Brown and Gange 1992, Holah and Alexander 1999, Callaway et al. 2000, Verschoor et al. 2001, De Deyn et al. 2003), and possibly also to plant invasiveness (Klironomos 2002). I propose that these plant community processes are strongly affected by plant defense belowground.

In general, plant defensive strategies may include tolerance, resistance, direct and indirect defense, or moving away from their above- and belowground herbivores or pathogens (Burdon 1987, Karban and Baldwin 1997). Plant defense theory that includes the natural enemies of herbivores (Price et al. 1980), has been almost solely developed and tested for aboveground interactions (Van der Putten et al. 2001). In soil, most studies have focused on plant–herbivore or plant–pathogen interactions, and in spite of a vast amount of biocontrol research on belowground invertebrate her-

Manuscript received 8 May 2002; revised 4 October 2002; accepted 12 October 2002; final version received 11 November 2002. Corresponding Editor: A. A. Agrawal. For reprints of this Special Feature, see footnote 1, p. 2256.

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bivores and pathogens in crop systems, very little is known on the role of natural enemies of root herbivores and pathogens in the feedback between plant and soil communities. Since the number of examples of root herbivores and pathogens in natural plant communities is steadily increasing, we now can start examining plant defense from a belowground perspective in order to further understand spatiotemporal processes in natural vegetation and plant life history evolution.

Here, I focus on direct and indirect interactions between living plant roots and soil organisms, explore examples of plant–herbivore/pathogen interactions in natural ecosystems, and discuss current ideas investigating how plants may avoid, tolerate or resist, or defend themselves against root herbivores and root pathogens.

ROOT HERBIVORES, ROOT PATHOGENS, AND HOST SPECIFICITY

Most root herbivores are invertebrates (insects, micro-arthropods, and nematodes), though vertebrates, mainly small mammals, also feed on plant roots (Mortimer et al. 1999). As far as microorganisms are concerned, the majority of the examples of soil pathogens in natural vegetation concern fungal diseases (Jarosz and Davelos 1995). Detailed reviews have highlighted the effects of root-feeding insects (Andersen 1987, Brown and Gange 1990), root-feeding nematodes (Stanton 1988, Mortimer et al. 1999), and root pathogens (Jarosz and Davelos 1995), and how these affect the productivity and composition of natural plant communities. I will focus on host specificity and, briefly, on dispersal of root herbivores and root pathogens, since these are important features for plant defense belowground.

Host specificity varies widely between belowground insect herbivores (Mortimer et al. 1999). The larval stages of root herbivorous insects, as well as the other root herbivores and pathogens have limited active dispersal capacity, usually ranging from a few centimeters up to a meter per year (Mortimer et al. 1999, Gormsen 2001). However, active dispersal, such as of the aboveground stages of some root-feeding insect larvae, may facilitate host location (Nordenhem and Eidmann 1991). Microarthropods, nematodes and soil microorganisms are dispersed passively by wind (Orr and Newton 1971, Griffin et al. 2001), which does not favor the development of host specificity. Specific root feeding nematodes are mainly known in agricultural ecosystems, where crop rotation leads to the predictable presence of host plants. Specificity also occurs in temperate coastal foredunes, where natural plant species typically occur in monospecific stands. Some nematode species, such as *Meloidogyne duytisi* on *Elymus farctus* (sand twitch) and *M. maritima* on *Ammophila arenaria* (mar-ram grass) occur on a single host-plant species (Van der Putten and Van der Stoel 1998). Probably, the predictability and reliability of the presence of host plant

roots favors selection for specialization in root-feeding nematodes in sand dunes.

Microorganisms have poorer active dispersal abilities, for example, through hyphal growth, than most invertebrates (De Boer et al. 1998b). Specialists might also develop in the case of facultative saprotrophic growth of soil pathogens, such as oömycete fungi, which survive the absence of their host plants by feeding on dead organic matter (Jarosz and Davelos 1995). An example of this group of facultative saprotrophs is *Pythium* sp., which kills seedlings of *Prunus serotina* (black cherry) in North American forests (Packer and Clay 2000). However, facultative saprotrophic species are inferior competitors for dead organic matter and will, sooner or later, be outcompeted by obligatory saprophytes unless host plants become re-established. Other strategies that might favor the development of host specificity of nematodes and soil microorganisms are the formation of survival structures (cysts, dauer larvae, spores) which enables these organisms to survive periodic absence of the hosts.

PLANT DEFENSE STRATEGIES AGAINST ROOT HERBIVORES AND ROOT PATHOGENS

After publication of the Green World Hypothesis (Hairston et al. 1960), a major debate arose as to whether herbivores were controlled more effectively by resources or predators. Alternatively, it was argued that there is an arms race between plants and herbivores leading to the evolution of plant chemical defense (Ehrlich and Raven 1964). Nowadays, it is generally accepted that evolutionary processes and resulting adaptation from interactions between plants and herbivores cannot be fully understood without including the antagonists of the herbivores in a multitrophic framework (Price et al. 1980), although such approach has rarely been applied to belowground interactions. Interestingly, studies on aboveground plant pathogens have typically focused on disease resistance and co-evolution of plants and pathogens (Burdon 1987), whereas studies examining control of natural plant pathogens by their natural enemies are rare (Yang et al. 1993). Studies on aboveground plant–herbivore and plant–pathogen interactions have pointed to a number of defense responses by plants and possible trade-offs. I will apply and develop these ideas for belowground defense in relation to plant life history strategies and plant community processes.

Avoidance and escape

Avoidance and escape have been studied in relation to both aboveground and belowground herbivores and pathogens. Plants may avoid their herbivores or pathogens through processes known as phenological escape, whereby they flower early (or late) in the growth season, or exhibit spatiotemporal unpredictability (Van der Meijden et al. 1988). Phenological escape also includes the postponement of, for example, flowering un-

til a reliable cue has indicated low risk of future attack (Agrawal 2000).

The capacity of plants to produce roots in late autumn and early spring is an example of avoiding root herbivores and soil pathogens, as growth continues when the herbivores and pathogens may be relatively inactive. Seed dispersal (Packer and Clay 2000), clonal growth (De Rooij-Van der Goes et al. 1995), and dormancy enable plants to avoid or escape from root herbivores and pathogens. Similar to some plants that respond positively to aboveground herbivores (Agrawal 2000), exposure to mycorrhizal fungi increases the intensity of rhizome branching (Streitwolf-Engel et al. 1997), whereas pathogens stimulate unidirectional rhizome growth (D'Hertefeldt and Van der Putten 1998).

Tolerance and resistance

The capacity of plants to regrow and reproduce following herbivory is called tolerance (Strauss and Agrawal 1999). Similarly, tolerance for diseases is expressed as the performance of individuals in the presence compared to their performance in the absence of pathogens (Burdon 1987). Herbivory may even lead to overcompensation, which can increase fitness (Agrawal 2000). Overcompensation occurs especially at low densities of the grazers (Crutchfield and Potter 1995), and it also expressed by fungal hyphae in soil when exposed to low densities of enchytraeids (Hedlund and Augustsson 1995). Plant roots may also exert such a compensatory response at low nematode densities.

Whereas tolerant plants allow herbivores and pathogens to develop and reproduce, resistant plants reduce the performance of their enemies (Karban and Baldwin 1997). In agricultural systems, tolerance and resistance have been studied for above- and belowground herbivores, as well as for shoot and root pathogens. For natural systems, on the other hand, tolerance and resistance have been mainly studied in relation to aboveground herbivores and pathogens.

Tolerance and other defense mechanisms, such as resistance, are considered alternative plant traits in plant-herbivore interactions (Van der Meijden et al. 1988). High growth rates enhance the competitive ability of plants, but it may come at the expense of their capacity to defend against herbivores (Herms and Mattson 1992). Tolerance might be favored when resistance is not possible, or very costly (Agrawal 2000). Empirical support to trade-offs between tolerance and defense are idiosyncratic (Strauss and Agrawal 1999). Probably, experimental conditions are crucial for the results obtained. In controlled conditions, a large fraction of plant root systems can be removed without negatively affecting plant production (Van der Veen 2000), however, selective root feeding reduces production of susceptible plants when competing with resistant species (Van der Putten and Peters 1997).

Tolerance may evolve when, for example, plant attack by multispecies communities of pathogens is in-

evitable. In this case, avirulence is less likely to develop (Roy et al. 2000). Soil communities will usually consist of multispecies communities, so that root pathogens can be expected to be moderately aggressive. Some soil pathogens, however, are so aggressive that they kill all establishing plants (Packer and Clay 2000). There is no evolutionary penalty for such aggressiveness, as the pathogens concerned are facultative saprophytes, which enables feeding on organic matter and dead plant parts (Jarosz and Davelos 1995). Tolerance, therefore, might not be the ideal solution for plant defense against facultatively saprotrophic root pathogens.

In model calculations, resistant species should often coexist with other, less resistant competing species (Chase et al. 2000). In the same models, tolerant species could not coexist with other, less tolerant competitors. According to these models, species-rich plant communities are expected to be mixtures of plant species that resist root herbivores and soil pathogens, and others that are tolerant.

Direct defense

A number of secondary plant compounds are produced, or presynthesized, in roots and then transported to other plant organs (Karban and Baldwin 1997). Examples are pyrrolizidine alkaloids of *Senecio jacobea* (Vrieling and Van Wijk 1994). Host plant secondary defense chemicals are able to affect the performance of root-feeding insect larvae (Brust and Barbercheck 1992), as well as entomopathogenic nematodes that feed on the insect larvae (Jaworska and Ropek 1994). These effects might be positive or negative for second- and third-trophic-level organisms, although studies on effects of plant chemicals on natural enemies of the belowground herbivores or pathogens are scarce and causal effects are difficult to establish. Root chemicals that affect root-sucking insects have been rarely reported (Brown and Gange 1990). There is also little information on direct effects of secondary plant chemicals on root-feeding nematodes.

There is very little information on the effects of plant defensive compounds on root pathogens and their natural enemies. Fungal pathogens (*Fusarium oxysporum*) collected from roots of *Senecio jacobea* (common ragwort) performed better on alkaloids from *S. jacobea* than the same fungi which had been collected from other plant species (Hol and Van Veen 2002). Possibly, plant defense compounds select for certain rhizosphere microorganisms, but the feedback effects to plant performance and consequences for plant community processes have not yet been studied.

Indirect defense

A main question in relation to indirect defense is whether plants may be actively involved in recruiting the enemies of their enemies (Dicke and Vet 1999, Thaler et al. 1999). Entomopathogenic nematodes can be recruited by plant roots through unknown attractants

that are released from the roots upon larval feeding (Van Tol et al. 2001, Boff et al. 2002). However, there are comparatively few other examples of active recruitment of third-level soil organisms by plants. Belowground signals will operate over much smaller scales than is the case above ground, because poor diffusion and transport rates of volatiles and soluble chemicals inhibit the spread of these compounds.

Antagonists of root herbivores and pathogens are well known in agriculture, but the development of effective population densities lags behind their hosts, sometimes requiring years of monocropping before effective control levels have been achieved (Weller et al. 1995, Kerry and Crump 1998). In natural systems, therefore, short-lived plants might experience little benefit from such antagonists, because they will be replaced by more resistant plant species before antagonists have even developed an effective population density. Nevertheless, antagonists of soil pathogens have been observed in natural soils (Holah and Alexander 1999), but these also directly affect root pathogens without any involvement of plant roots (De Boer et al. 1998a, b).

Arbuscular mycorrhizal fungi have been reported to act as antagonists of root pathogens (Carey et al. 1992, Newsham et al. 1994, 1995), plant-feeding nematodes (Little and Maun 1996, Roncadori 1997), and root-feeding insects (Gange 2000). Similarly, endophytic fungi are able to reduce plant sensitivity to herbivorous nematodes (Clay 1991).

Pathogenic rhizobacteria can induced systemic acquired resistance (SAR) and nonpathogenic rhizobacteria can induce systemic resistance (ISR) against plant pathogens (Van Loon et al. 1998). The rhizosphere bacteria that induce resistance, for example fluorescent *Pseudomonas* spp., need to be present in sufficiently high densities in order to be effective (Van Loon et al. 1998). Most of this work has been done on crop plants and *Arabidopsis thaliana*. Theoretically, indirect defenses against root herbivores and pathogens might be operating in many natural systems, but their importance for spatiotemporal processes in natural plant communities has received little attention.

PLANT COMMUNITY PROCESSES IN RELATION TO BELOWGROUND DEFENSE STRATEGIES

The question of what drives changes in the composition of natural plant communities has been a recurrent theme in ecology, but it has only recently been acknowledged that root herbivores and root pathogens can influence these processes. Root herbivores and pathogens affect primary (Van der Putten et al. 1993) and secondary succession (Brown and Gange 1992, Verschoor et al. 2001, De Deyn et al. 2003), as well as plant dispersal (Packer and Clay 2000), plant species diversity (Bever 1994, De Deyn et al. 2003), and abundance or invasiveness of alien plant species (Klironomos 2002). I propose that there is a relationship be-

tween plant defense belowground and the plant community processes that are observed in the field.

Primary succession

In coastal dunes of Europe, the nitrogen-fixing shrub *Hippophaë rhamnoides* (sea buckthorn) is highly vigorous in outer dunes, whereas, along a transect from foredunes towards the inland, the shrubs die back and gradually disappear from the vegetation. Initially, it was supposed that root-feeding nematodes, such as *Tylenchorhynchus microphasmis*, were causing the die-back patterns (Oremus and Otten 1981). Subsequent studies, however, have shown that nematodes alone cannot cause the observed growth reduction (Maas et al. 1983), and that plant pathogenic fungi may be involved as well (Zoon et al. 1993). The precise mode of interaction still needs to be resolved. Similarly, both root-feeding nematodes and root pathogens are able to reduce vegetative growth of a pioneer dune grass *Ammophila arenaria* (Marram grass; Van der Putten et al. 1988). Single nematode or root pathogen species cannot account for the growth reduction observed in the field soil, so it has been proposed that degeneration of *A. arenaria* is facilitated through a complex of root-feeders and root pathogens (De Rooij-Van der Goes 1995).

Colonizing *A. arenaria* produces new roots in spite of a negative feed-back from the soil community, which develops with a time lag of less than one month (Van der Stoel et al. 2002). Avoidance may, therefore, only partially explain vigorous plant growth in mobile sand dunes. Specialist nematodes can be controlled by the plant (Van der Stoel 2001), whereas generalist nematodes are limited by unknown factors (De Rooij-Van der Goes 1995). Plant defense against root-feeding nematodes, therefore, appears to depend on the type of nematode (generalist or specialist). In the field, a range of direct and indirect effects such as mycorrhizal fungi and natural enemies of the nematodes appear to be involved in the belowground defense of *A. arenaria* (Fig. 1). It is difficult to establish how tolerance acts as a defense of *A. arenaria* against root-feeding nematodes. Root formation in mature plants continues in soil where seedlings are severely growth reduced (Van der Stoel et al. 2002), but this might be due to indirect defense, for example caused by mycorrhizal fungi (Little and Maun 1996). These symbiotic mutualists are prominent in zones with vigorous *A. arenaria*, whereas they are less significant in degenerate stands (Kowalchuk et al. 2002).

Later successional plant species are less susceptible to the soil community of *A. arenaria* than their predecessors (Van der Putten et al. 1993). Specialist root-feeding nematodes of *A. arenaria* have not been found in roots of later succession plant species suggesting that successors are resistant against the nematodes of their predecessors (Van der Putten and Peters 1997). Therefore, avoidance and resistance are important be-

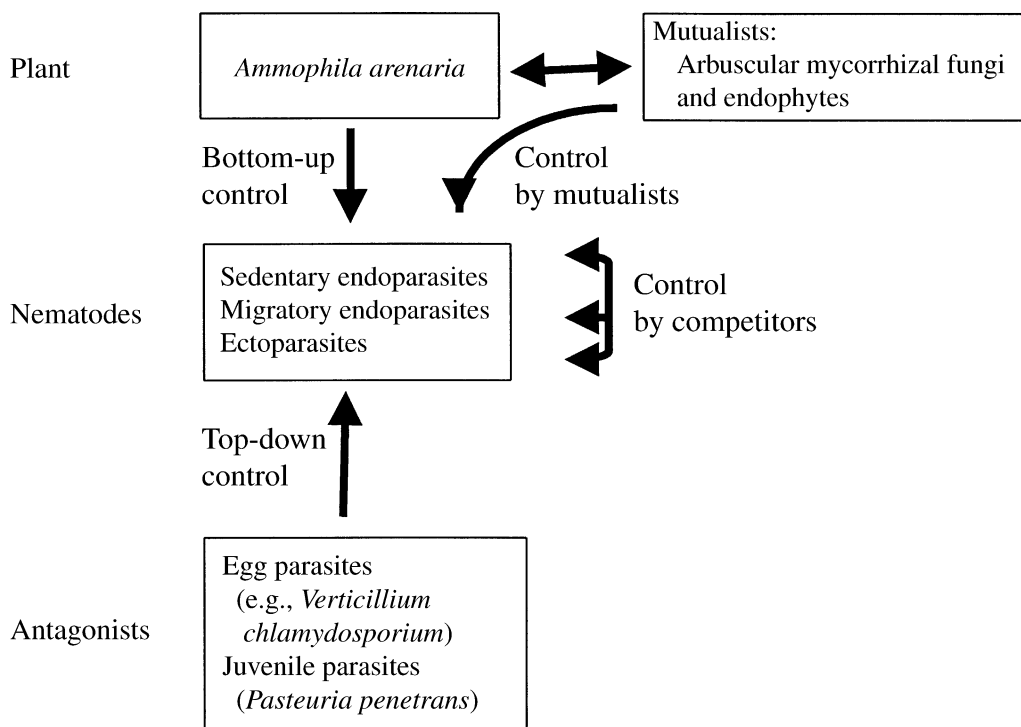


FIG. 1. Factors that may control nematodes in the root zone of *Ammophila arenaria* (marram grass) in coastal sand dunes. Specialist nematodes (coinciding with endoparasitic feeding types) can be controlled by the plant, whereas generalists (coinciding with ectoparasites) are controlled by other factors. Arbuscular mycorrhizal fungi and endophytes, as well as rhizosphere fungi (*Verticillium chlamydosporium*) and bacteria (*Pasteuria penetrans*), may act as predators of nematode eggs and juveniles, respectively. The arrows point in the assumed direction of control. This scheme is used by the EU-EcoTrain project in order to determine the relative contribution of the various nematode control mechanisms.

lowground defense mechanisms that drive succession. Probably, tolerance, direct and indirect defense may counteract, or slow down succession. Both primary and secondary succession proceed in an environment where biotic and abiotic conditions change rapidly (Fig. 2).

SECONDARY SUCCESSION

In early secondary succession on previously cultivated land, soil insects are a major cause of seed predation and seedling mortality of annual and perennial forb species (Gange et al. 1991). Based on insecticide experiments (Brown and Gange 1989b), it was concluded that soil-dwelling insects negatively influence the survival and competitiveness of early successional forbs in these secondary succession gradients and that these insects enhance the rate of succession (Gange et al. 1993). Foliar insecticides, on the other hand, increased the dominance of grasses, so that aboveground insects increase plant species diversity within succession stages (Brown and Gange 1989a). Aboveground plant-feeding insects indirectly reduce the performance of root-feeding insects due to limitation of carbohydrate investments into the roots following defoliation (Masters and Brown 1992). Arbuscular mycorrhizal fungi also affect aboveground plant-feeding insects, which leads to complex aboveground–belowground tri-

trophic interactions (Brown and Gange 2002). With successional age, the root-feeding insect community contains more specialized insects (Mortimer et al. 1999), which will influence plant defense strategies belowground throughout a successional sequence.

Root-feeding nematodes might affect secondary succession, but it has been proposed that their effects are most obvious in local “hot spots” where the nematodes are abundant (Verschoor 2002). Outside these hot spots, nematode abundance seems too low to affect plant species interactions (Verschoor et al. 2002). High local abundance of nematodes might reflect stochasticity of colonization and multiplication. Alternatively, it could be that nematode abundance increases when released from control by predators. There are no clear patterns of specialist and generalist root-feeding nematodes in relation to secondary successional stages in grasslands (Verschoor et al. 2001).

Soil pathogens are involved in the secondary succession of Douglas fir (*Pseudotsuga menziesii*) and true firs in western Oregon. These trees experience extensive root rot caused by the native fungal pathogen *Phellinus weirii*, which spreads from one tree to another via root contacts. The subsequent death of the trees may lead to the increased cover of herbaceous species and therefore enhances species diversity. At some sites,

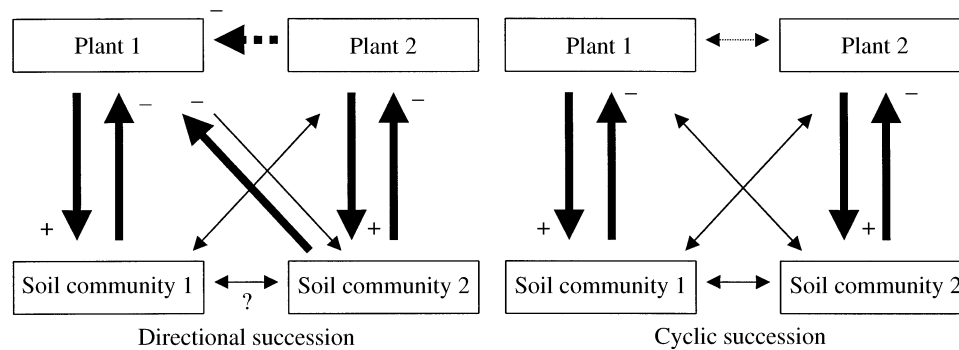


FIG. 2. Plant-soil feedback patterns according to Bever et al. (1997): every plant develops a soil community that may have a neutral (\pm), negative ($-$), or positive ($+$) net effect on the productivity and fitness of the plant or its offspring. Depending on the effects of the soil community of one plant species on the performance of other plant species, the vegetation development may be directed, leading to primary or secondary succession (left; redrawn from Van der Putten and Van der Stoel 1998), or cyclic (right). The thicknesses of the arrows indicate the strengths of interactions; arrows point in the direction of the effect, and straight lines indicate direct effects whereas dashed lines indicate indirect effects. However, these plant-soil feedback schemes lack a temporal component, and they also do not elucidate the role of competitive and top-down components within the soil community. They also do not elucidate possible aboveground-belowground interactions (see also Bardgett and Wardle 2003).

the reduction of Douglas fir due to pathogenic activity enhances forest succession by the western hemlock (*Tsuga heterophylla*) (Holah et al. 1997). The presence of dead trees also leads to aggregate fire incidence after which succession may be reset. The cycles of forest succession indicate at avoidance, but other defense types may be active as well, albeit not yet recognized.

Plant abundance and species diversity

Forces that drive plant abundance or plant species diversity and the possible consequences of species loss for the functioning of natural ecosystems are major issues in ecology (Schulze and Mooney 1993, Gaston 1994). Root herbivores and root pathogens undoubtedly contribute to plant species abundance and species diversity. In coastal dunes of the western USA, the abundance of the coastal shrub lupine (*Lupinus arboreus*) depends on the root-boring larvae of ghost moths (*Hepialus californicus*) (Strong 1999). The insect larvae cause large temporal and spatial changes in the shrub cover due to patchy dieback of *L. arboreus* (Strong et al. 1995, 1999) and they can reduce cumulative seed production over three years by up to 31% (Maron 1998). Shrub lupine is indirectly defended against the ghost moth larvae by entomopathogenic nematodes (Jaffee 1996). The nematodes are in turn subjected to predators, such as nematophagous fungi and predaceous nematodes (Koppenhoffer et al. 1997). Indirect defense does not prevent the local disappearance of lupine, so that herbaceous vegetation may take over until shrubs become reestablished (Maron and Jefferies 1999). The presence and abundance of shrub lupine, therefore, depends on a combination of indirect defense and avoidance.

In seminatural grasslands, the ground cover of dominant plant species (*Festuca rubra* and *Carex arenaria*) oscillates over time. These oscillations coin-

cide with the occurrence of root herbivorous nematodes and other plant growth-reducing inhabitants of the root zone (Olf et al. 2000). In these grasslands, aboveground vertebrate herbivores (cows) affect the activity of yellow ants (*Lasius flavus*), which use fresh subsoil to produce mounds. This subsoil contains less plant-growth-reducing biota than the original top soil and therefore favors the ability of formerly dominant clonal plants to regrow. Because of its rapid vegetative expansion rate, *C. arenaria* is the first to recolonize ant mounds, whereas *F. rubra* is the subsequent colonizer (Blomqvist et al. 2000). Ants therefore create patches where plants may avoid root-feeding nematodes and root pathogens.

Mills and Bever (1998) observed that the accumulation rate of fungal soil pathogens of the genus *Pythium* was faster on roots of plant species that were sensitive to the pathogen than on less sensitive plants. Klironomos (2002) related plant abundance in a grassland community to the development rate of a negative feedback with the soil community and found that rare species accumulated root pathogens at a faster rate than dominant plant species. Fungi that were most abundant on the roots of rare plants contributed to this negative feedback. Both studies suggest that resistant plants may become dominant, whereas susceptible plants remain rare. Dominant and rare plants may coexist when there are ample potential regeneration sites acting as enemy-free spaces for rare plants. Moreover, the abiotic conditions of the system need to be relatively invariable in order to enable re-establishment of the rare species (Fig. 3). Coexistence may also be due to one-sided effects, which is illustrated by the pathogenic root fungi of the annual legume *Chamaecrista fasciculata*, that have a negative effect on the perennial prairie grass *Andropogon gerardii* (Holah and Alexander 1999).

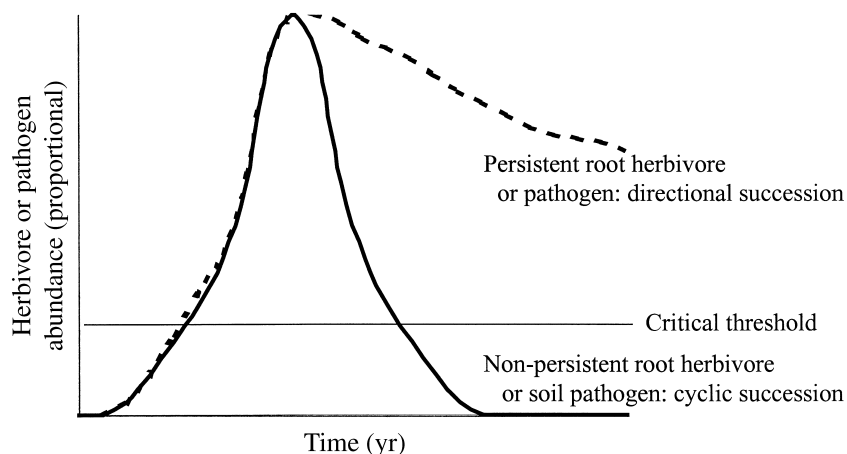


FIG. 3. Two theoretical examples of root herbivore or soil pathogen persistence. The persistent type (dashed line) may lead to directional succession, especially when the environment changes fast, so that after some time, conditions for plants have changed unfavorably (as in coastal dunes; Van der Putten et al. 1993). The non-persistent type (solid line) may allow cyclic succession and such type may contribute to plant species diversity in natural vegetation (as suggested by Bever [1994] and shown by Olf et al. [2000], Blomqvist et al. [2000] and Klironomos [2002]). The horizontal line represents the threshold herbivore or pathogen density that determines whether or not plants may become established.

In summary, dominant plants appear to control their root herbivores and pathogens whereas rare plants fail to do so. Most studies examining the relationship between plant abundance and species diversity, however, provide inconclusive evidence on the relative importance of tolerance, direct defense, and indirect defense.

Plant dispersal and vegetative expansion

According to the Janzen-Connell hypothesis, tree species diversity in neotropical rain forests depends on the presence of specialist herbivores (Janzen 1970, Connell 1978). New tree seedlings can establish only at a distance from parent trees, where the seedlings are out of reach of specialist herbivorous insects (Janzen 1970). This hypothesis has also been tested for soil pathogens in tropical rain forests (Augspurger 1983, Augspurger and Kelly 1984) and in a temperate forest (Packer and Clay 2000). In all cases, soil pathogens accumulating in the root zone of parent trees caused seedling mortality of the tree offspring. In the temperate forest, *Pythium* species caused the mortality of saplings of *Prunus serotina*, whereas other tree species did not appear to be affected with equal severity (Packer and Clay 2000). *Prunus* seedlings need effective dispersal at sufficient distance from older trees of the same species in order to establish. The mature trees appear to tolerate the root pathogen, whereas the seedlings cannot establish because of pathogen accumulation under the trees. Other tree species can establish underneath *P. serotina*, which indicates that coexisting forest species are resistant against *Pythium* of *Prunus* trees.

Many clonal plants disperse mainly through the vegetative growth of rhizomes or stolons. In the case of *A. arenaria* (Van der Putten et al. 1988, De Rooij-Van der Goes et al. 1995), *Carex arenaria* (D'Hertefeldt

and Van der Putten 1998), and *Trifolium repens* (Ennik et al. 1965), clonal expansion leads to avoidance. However, in some cases the escape "window" seems so narrow (Van der Stoel et al. 2002) that other factors, such as tolerance, direct defense, or indirect defense may play an important role in maintaining plant growth when the newly formed roots are colonized by herbivores and pathogens. Exposure of *A. arenaria* to pathogen-infested patches reduced root development (De Rooij-Van der Goes et al. 1995). Root pathogens reduced local patch exploitation of *C. arenaria* because apical rhizome buds developed while lateral buds, from which lateral rhizomes develop, remained dormant (D'Hertefeldt and Van der Putten 1998). These examples, as well as the example showing an effect of mycorrhizal fungi on rhizome branching patterns (Streitwolf-Engel et al. 1997) reveal that plant defense belowground needs to be incorporated in studies on clonal growth.

INVASIONS OF EXOTIC PLANTS

Plant invasions are among a suite of major factors worldwide that threaten ecosystem integrity and ecosystem functioning (Dukes and Mooney 1999). In their new territories, invasive plants might have escaped from their specific root herbivores and soil pathogens (Keane and Crawley 2002). Alternatively, local root herbivores, root pathogens, and other parasites provide biotic resistance against the invaders, which is one of the explanations why so few exotics become pests.

Thus far, few studies have focused on how soil communities respond to invasive plant species. The invaders may cause major changes in the soil, especially when these plants have specific attributes such as the ability to fix atmospheric nitrogen (Vitousek et al. 1987). Some invading plant species affect soil quality

for native species, e.g., by changing the soil microbial composition (Callaway et al. 2000), whereas the mycorrhizal fungi will allow the invader to establish symbiotic relationships, because these symbiotic mutualists are relatively nonspecific (Richardson et al. 2000).

In a study by Klironomos (2002), five plant species that have invaded North America and Canada from Eurasia were compared with five rare native species in their rate of developing a negative feedback to the soil community. Overall, the invaders had a neutral or positive feedback, whereas the rare native species developed a negative feedback. Isolation of spores of arbuscular mycorrhizal fungi and of the remaining microbial component of the soil and reinoculation of those fungal species showed that all ten plant species responded either neutrally or positively to the presence of mycorrhizal fungi. Although none of the invasive plant species were negatively affected by the addition of the remaining microbial component collected from pots with cultures from their own species, all of the rare species performed worse under these conditions (Klironomos 2002). This result suggests that the invasive species are free of soil pathogens from their native ecosystems while benefiting from the (aspecific) mycorrhizal symbionts in their new territory. However, we need comparisons of the response of invasive plants to their soil communities in both their native and new territories in order to determine in which cases escape from native soil pathogens indeed might explain plant invasiveness as the dominant native species also had a neutral to positive soil feedback.

DISCUSSION AND CONCLUSIONS

Plant defense belowground strongly affects spatio-temporal processes in natural vegetation. Dispersal through seeds or rhizomes enables plants to avoid root herbivores and pathogens that develop in the root zone of established plants. Plant dispersal has a number of functions, such as colonizing new resources and encountering new mating partners, but root herbivores and soil pathogens could be a major factor selecting for plant dispersal. A dilemma of plant dispersal, however, may be that plants escape from their belowground "bodyguards" as well. I assume that there are trade-offs belowground similar to above ground between dispersal and defense (Van der Meijden et al. 1988) and fast growth and defense (Herms and Mattson 1992). Plants that develop clonally have a distinct disadvantage in that they cannot easily escape from their root feeders, although a benefit is that their resistance might remain systemically induced and that both root feeders and their predators keep track of the newly formed roots.

The ultimate escape from root herbivores and pathogens is achieved when plants reach new territories where no similar root feeders occur. Both *P. serotina* and *A. arenaria* have been introduced in new areas where they have become important pests. Studies that

examine the presence and sensitivity of invasive plant species to root feeders in their original and new territories will elucidate to what extent escape from belowground enemies may contribute to invasiveness. By contrast, the "biotic resistance hypothesis" argues that native plant enemies present in the new territories may switch over to the introduced species thereby suppressing their invasive capacity (Keane and Crawley 2002). Biotic resistance may be due to absence of plant resistance, but the exotics might also miss effective secondary chemicals, or fail to recruit the natural enemies of the plant feeders in the new territories.

Soil pathogens or root herbivores can also be introduced into new territories. *Phytophthora cinnamomi* that has been introduced into Australia causes the dieback of many native species thereby changing the species composition of native forest ecosystems (West et al. 2002). The native plants were obviously not resistant against the introduced soil pathogens, but it might also be (partly) due to the escape of the introduced pathogen from its own natural enemies.

The consequence of avoidance depends on the rate of changes in the environment. In coastal foredunes, where strong gradients occur in the abiotic environment (sand deposition, salt spray, leaching of calcium carbonate, and accumulation of organic matter), avoidance results in directional succession. Plants that have accumulated root herbivores and pathogens are replaced by resistant plants (Van der Putten and Van der Stoel 1988). By the time that the abundance of root feeders of the predecessor has dropped below threshold densities the abiotic environment has changed, so that the predecessors cannot return (Fig. 3). This is in contrast with cyclic succession (Fig. 2), which can only occur in an environment that is maintained in a relatively constant state by, for example, mowing or grazing, or that is reset by, for example, soil disturbance (Blomqvist et al. 2000) or fire (Holah et al. 1997).

In the field, many plants will be protected by mycorrhizal fungi, rhizosphere bacteria, or other defensive organisms, so that it will be very difficult to provide evidence for tolerance. Nevertheless, whether tolerance for root feeders is directly or indirectly achieved, it may largely affect plant community structure, for example, because seedlings cannot establish when exposed to the density of root herbivores or pathogens as supported by the roots of their parents (Packer and Clay 2000). Therefore, tolerance of mature plants for root feeders will contribute to plant species diversity in a similar way as predicted by the Janzen-Connell hypothesis (Janzen 1970, Connell 1978) for aboveground specialist insect herbivores.

Resistance is an important mechanism driving directional or cyclic succession. Later succession plants are resistant against the root feeders of their predecessors which provides an indirect advantage in competition (Van der Putten and Peters 1997). In a mixed vegetation, resistant plants may also become dominant,

TABLE 1. Summary of proposed consequences of plant defense strategies against belowground herbivores and pathogens for spatiotemporal processes in natural plant communities.

Plant defense	Spatiotemporal process in natural vegetation			
	Succession	Abundance and diversity	Dispersal and vegetative expansion	Invasion
Avoidance	Leads to directional succession in a fast-changing environment and to cyclic succession in a relatively stable environment.	Abundance is only temporal; spatiotemporal diversity is stimulated.	Avoidance selects for dispersal and vegetative expansion.	Plant life histories selected for avoidance might not be as effective in new territories, because of no or different natural enemies.
Escape	Ultimate escape is not possible in a successional sequence.	Plants remain local, so that there is no long-term escape possible.	Duration of escape depends on dispersal capacity and unpredictability of newly founded populations.	Escape from natural enemies to new territories without their enemies, and no native enemies present, contributes to invasiveness of exotics.
Tolerance	Slows down succession, albeit that it may constrain the establishment of offspring, when susceptible in germination and establishment phase.	May increase abundance, but on the other hand, tolerance of parents and susceptibility of offspring increases diversity (e.g., <i>P. serotina</i>).	Tolerance of parents enforces the need of dispersal for establishment of offspring (e.g., <i>P. serotina</i>).	Tolerance patterns in native and new territories may differ due to exposure to new communities of root feeders.
Resistance	Later successional plants resist root feeders of their predecessors. Resistant plants may be more persistent (also their offspring), so that they could slow down succession.	Resistant plants can become abundant, which might negatively affect plant species diversity.	Resistant plants have lower need for dispersal because there is no real need to escape from their enemies.	Resistance patterns in native area may not be indicative of resistance in new territories. Therefore, susceptible plants may become as invasive as resistant plants when released from exposure to native root feeders.
Direct defense	Increases plant persistence; effectiveness might depend on early (less defended plants) vs. late successional (well defended plants) stage.	Stimulates abundance, but acts against diversity. Information on direct defense against belowground root is rare.	Dispersal does not affect direct defense, and vice versa, since defense mechanism is intrinsic.	Direct defense may evolve in the new territories, especially when they provide costs and no benefits. Data are lacking.
Indirect defense	May increase plant vigor (e.g. of <i>A. arenaria</i> by mycorrhizal fungi). Effects on successional process have not been investigated.	Abundance may be enhanced, but also species diversity (depending on which species [the rare or abundant ones] the indirect defense is responding to).	There is a possible trade-off between dispersal and indirect defense. This may be less of a problem for clonal plants, since they remain connected to the established plant, which might lead to, for example, induced defense.	Mycorrhizal fungi may provide indirect defense in new territories, since they are fairly nonspecific. Other indirect defenses have not yet been properly explored.

whereas susceptible plants remain relatively rare (Klironomos 2002). Therefore, plant species diversity and the consequences of biodiversity loss need to be examined from the perspective of belowground interactions as well (see also Reynolds et al. 2003).

Root feeders are susceptible for secondary plant compounds (Van Dam et al. 2003), but almost all studies on the evolution of this type of plant defense concerned aboveground plant–herbivore interactions (Van der Putten et al. 2001). Root feeders may affect the distribution of plant defense compounds, and therefore

herbivore damage, over the entire plant (Bezemer et al. 2003), but it remains to be studied to what extent direct defense is under selection from belowground herbivores.

There is compelling evidence that indirect defense belowground does exist, although very little information exists on the consequence of this defense trait for spatiotemporal processes in natural plant communities. Mycorrhizal fungi may protect plants against root feeders, as well as aboveground herbivores (Newsham et al. 1995, Brown and Gange 2002) and plant roots pro-

duce unknown signals that attract entomopathogenic nematodes (Van Tol et al. 2001). However, the reliability of these defense strategies needs to be further explored.

I conclude that avoidance and resistance as plant defense strategies against belowground herbivores and pathogens are major drivers of change in the species composition of natural plant communities (Table 1). The type of changes (directional vs. cyclic) depends on other abiotic and biotic environmental factors (Fig. 3). On the other hand, the persistence of plants in a community may depend on their defense belowground (Table 1). Effective defense (or resistance) will increase the capacity of plants to become dominant, and it may increase the length of the successional trajectory in which certain plant species can maintain themselves. Future studies on plant ecology, plant population dynamics, and plant community ecology need to include plant defense belowground in order to get a better understanding of plant community processes and trade-offs between plant life history strategies.

ACKNOWLEDGMENTS

I thank Jeffrey A. Harvey, Arjen Biere, Wietse de Boer, Nicole M. van Dam, T. Martijn Bezemer, Anurag A. Agrawal, and two anonymous referees for their useful comments on previous versions of the manuscript. Ideas for the manuscript emerged from discussions with the members of the Multi-trophic Interactions Department and the EU-EcoTrain project team (contract HPRN-CT-2002-00210 with the European Commission). This is NIOO 3157.

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