

Microbes as Targets and Mediators of Allelopathy in Plants

Don Cipollini · Chad M. Rigsby · E. Kathryn Barto

Received: 2 February 2012 / Revised: 27 April 2012 / Accepted: 1 May 2012 / Published online: 15 May 2012
© Springer Science+Business Media, LLC 2012

Abstract Studies of allelopathy in terrestrial systems have experienced tremendous growth as interest has risen in describing biochemical mechanisms responsible for structuring plant communities, determining agricultural and forest productivity, and explaining invasive behaviors in introduced organisms. While early criticisms of allelopathy involved issues with allelochemical production, stability, and degradation in soils, an understanding of the chemical ecology of soils and its microbial inhabitants has been increasingly incorporated in studies of allelopathy, and recognized as an essential predictor of the outcome of allelopathic interactions between plants. Microbes can mediate interactions in a number of ways with both positive and negative outcomes for surrounding plants and plant communities. In this review, we examine cases where soil microbes are the target of allelopathic plants leading to indirect effects on competing plants, provide examples where microbes play either a protective effect on plants against allelopathic competitors or enhance allelopathic effects, and we provide examples where soil microbial communities have changed through time in response to allelopathic plants with known or potential effects on plant communities. We focus primarily on interactions involving wild plants in natural systems, using case studies of some of the world's most notorious invasive plants, but we also provide selected examples from

agriculturally managed systems. Allelopathic interactions between plants cannot be fully understood without considering microbial participants, and we conclude with suggestions for future research.

Keywords *Alliaria petiolata* · Glucosinolates · Microbial degradation · Mycorrhizae · Phenolics · Rhizobia · Invasive plants

Allelopathy and Soil Microbes

Allelopathy, generally, is considered as a form of negative chemical communication between organisms, whereby one participant (the donor) in an interaction produces a compound(s) that is released in the environment in ecologically relevant quantities that negatively impacts the fitness of other participants (the receivers); the effect presumably benefits fitness of the donor. While the concept of allelopathy extends back to at least Theophrastus in the third century B.C., who invoked this phenomenon as an explanatory mechanism of plant growth, abundance, or community structure in natural systems, the concept has fluctuated in popularity over time (see Willis, 2007 for review). Allelopathy often has been subjected to criticisms of ecological relevance that other phenomena, such as resource competition, have not, thus explaining why it has fallen out of favor during certain time periods. However, studies of allelopathy in terrestrial systems have experienced a tremendous “re-birth” in the last 20 years as interest has risen in describing biochemical mechanisms responsible for structuring plant communities, determining agricultural and forest productivity, and explaining invasive behaviors in introduced organisms. More rigorous observational and experimental approaches, along with better analytical techniques, have

D. Cipollini (✉) · C. M. Rigsby
Department of Biological Sciences, Environmental Sciences PhD
Program, Wright State University,
Dayton, OH, USA
e-mail: don.cipollini@wright.edu

E. K. Barto
Institut für Biologie, Dahlem Center of Plant Sciences,
Freie Universität,
Berlin, Germany

been brought to bear on this issue yielding better data. As a result, allelopathy as a significant ecological phenomenon has now become firmly entrenched in the literature, with entire books and journals devoted to the topic (e.g., Reigosa et al., 2006).

In terrestrial systems, much emphasis has been placed on allelopathic interactions that have focused on direct effects (e.g., toxicity) of putative allelochemicals on plant growth. In addition to agriculturally-focused studies with plants like wheat, rye, and sorghum (e.g., Belz, 2007), one of the more famous examples of a wild plant with direct allelopathic effects is walnut, *Juglans nigra*, which produces the allelopathic compound juglone (Jose, 2002). This compound is released into the soil in measureable quantities and is believed to be largely responsible for the depauperate plant community around walnut trees. The emphasis of many recent studies has been on allelopathic invasive plants, including the herbs *Centaurea stoebe* (aka *C. maculosa*) (Callaway and Ridenour, 2004), *Solidago canadensis* (Abhilasha et al., 2008), and *Alliaria petiolata* (Prati and Bossdorf, 2004), the shrubs *Lonicera maackii* (Dorning and Cipollini, 2006) and *Artemisia* spp. (Lydon et al., 1997), and the trees *Ailanthus altissima* (Small et al., 2010) and *Eucalyptus* spp. (Sasikumar et al., 2001). While debate continues for some of these species (e.g., Duke et al., 2009; Bais and Kaushik, 2010), field or laboratory studies that use growing plants, field- or laboratory-conditioned soils, and tissue extracts have revealed that these plants and the compounds that they produce can have direct biochemical effects on other plants in some situations. Early criticisms of the ecological relevance of allelopathy, however, involving issues with allelochemical production, stability, and degradation in soils, lead to the contention that allelochemicals rarely reach concentrations with meaningful direct effects in the field due to microbial degradation (Willis, 2007). To understand these dynamics, an understanding of the chemical ecology of soils and the organisms it contains is of paramount importance (Romeo, 2000; Inderjit, 2005). This concern has been increasingly incorporated in studies of allelopathy (Kaur et al., 2009), and is being increasingly appreciated as an essential predictor of the outcome of allelopathic interactions.

The soil microbial community is diverse, and its composition varies greatly in space and time. Among the more important types of soil biota with relevance to allelopathy are the many free-living and symbiotic bacteria and fungi that are found in the plant rhizo- and mycorrhizosphere (Johansson et al., 2004, Fig. 1). The presence of a live soil microbial community can greatly modify allelopathic effects of some plants, and sometimes beneficial microbes themselves appear to be directly negatively affected by allelopathic compounds (Table 1). It is widely known that plant species will culture somewhat specific microbial populations in their rhizospheres

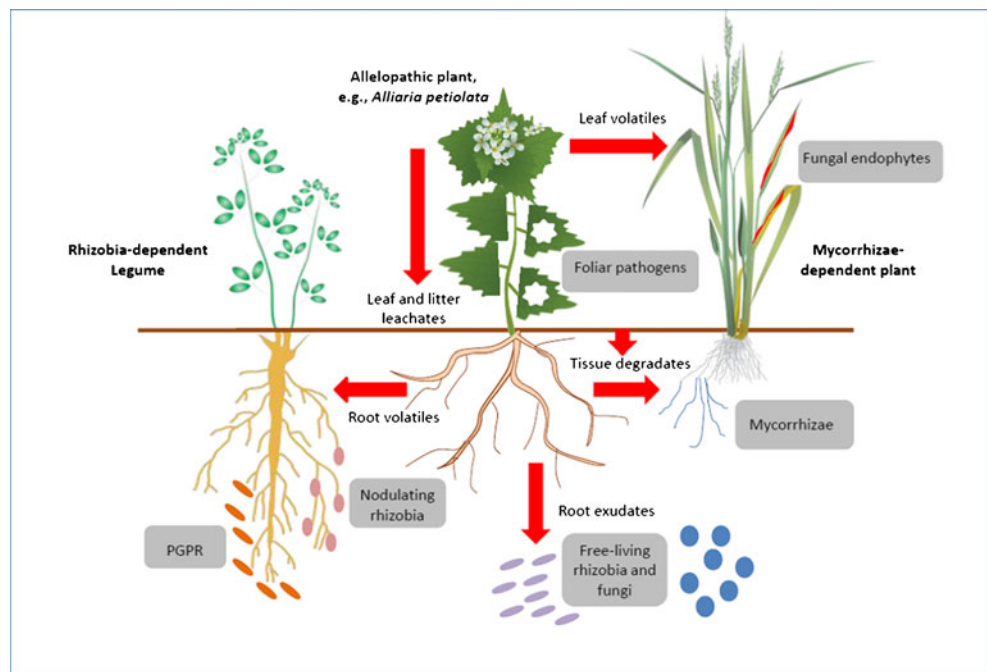
that have subsequent feedbacks on conspecific and heterospecific individuals grown in the same soil. This effect can be due to such factors as the amount and form of carbon and other nutrients that the plant provides to the soil, but is also due to allelochemicals with direct positive and negative effects on microbes (Reinhardt and Callaway, 2006). In this review, we examine cases where microbes are directly affected by allelopathic plants leading to indirect effects on competing plants, provide examples where microbes either protect plants from allelopathic competitors or enhance allelopathic effects, and provide examples where soil microbial communities have changed through time in response to allelopathic plants with potential effects on plant communities. We focus primarily on interactions involving wild plants in natural systems, exploiting the emerging literature on invasive plants, while providing selected examples from studies on agricultural plants in managed systems. We use the term “microbe” throughout to refer to both bacteria and fungi.

Allelopathic Effects on Beneficial Microbes

From an ecological and evolutionary perspective, allelopathic effects of plants on soil microbes may have indirect effects on competing plants that are just as important as direct effects. Such effects on soil microbes could arise from direct selection for this effect, or could be a side-effect of allelochemicals selected for their phytotoxic effects. Either way, effects on the microbial community on which competing plants rely for nutrient and water uptake, nutrient cycling, and other services, could promote fitness of an allelopathic plant as long as it does not harm itself in the process. This possibility is exemplified by allelopathic plants that inhibit mutualistic bacteria or fungi that other plants require for optimal growth, but that the donor plant does not require. It is also likely most apparent in environments lacking an evolutionary history with the allelopathic plant and the allelochemicals that it produces (Callaway and Ridenour, 2004).

Mycorrhizal Fungi as Targets of Allelopathic Effects One well-studied example of the effect of an allelopathic plant on mutualistic microbes is that of the widespread Eurasian invader, *Alliaria petiolata* (*Alliaria*), on arbuscular and ectomycorrhizal fungi (AMF and EMF; Fig. 1). This plant belongs to the family (Brassicaceae) well-known for its lack of association with mycorrhizal fungi (Shreiner and Koide, 1993). This may contribute to the ability of plants from this family to be rapid colonizers of disturbed habitats worldwide where depauperate mycorrhizal communities could limit colonization by mycorrhizal-dependent plants. However, it also permits plants from this family to inhibit mycorrhizal fungi of neighboring plants without the possibility

Fig. 1 Sources of alleochemical inputs and routes of transport (red arrows) and microbes that are targets and mediators of allelopathy in plants (grey boxes)



of harming themselves in the process, which might provide them with a competitive advantage. Studies of the biochemical basis of the effect have focused historically on the glucosinolates, a class of compounds produced by Brassicaceous plants that have been proposed as a mechanism of resistance to either pathogenic or beneficial fungi (Shreiner and Koide, 1993). Vaughn and Berhow (1999) first raised the possibility that allyl isothiocyanate (AITC) and benzyl isothiocyanate (BzITC), toxic degradation products of the two major glucosinolates that *Alliaria* produces, sinigrin and glucotropaeolin, respectively, could have effects on mycorrhizal fungi. Roberts and Anderson (2001) revealed this potential when they showed that aqueous leaf extracts of *Alliaria* could inhibit spore germination of AMF in addition to having some direct effects on plant performance in laboratory studies. *Alliaria* density in the field also negatively correlated to mycorrhizal inoculum potential of field soils. Stinson et al. (2006) followed these studies by showing that tree seedlings exposed to aqueous *Alliaria* extracts or *Alliaria*-conditioned soils had reduced AMF infection rates, with indirect negative effects on growth. Wolfe et al. (2008) later showed similar effects of *Alliaria* on EMF of pine trees in the field. Callaway et al. (2008) demonstrated that the extent of allelopathic effects of *Alliaria* depended on the degree of mycorrhizal dependence of target plant species, and that the allelopathic effects of *Alliaria* on AMF spore germination and infection rates had a biogeographical basis. Specifically, AMF from soils lacking an evolutionary history with *Alliaria* were more susceptible to allelopathic effects of its extracts, supporting predictions of the “Novel Weapons Hypothesis” (Callaway and Ridenour, 2004). Moreover, they showed that both glucosinolate and flavonoid-enriched extracts of *Alliaria*

leaves were partly responsible for allelopathic effects on AMF spores, and that this mixture worked synergistically to inhibit spore germination in *Alliaria*-naïve soils. Koch et al. (2011) later showed that this combination of allelochemicals from leaves could inhibit colony growth of a single AMF species *in vitro*. Lankau et al. (2009) showed that allelopathic potential of *Alliaria* appeared to decline with the age of the population, which correlated with declining root glucosinolate levels with population age. In turn, Barto et al. (2012) showed that AMF infection rates of sugar maple were reduced and AMF community composition was affected by the presence of *Alliaria* in the field, an effect most noticeable in an area with a presumably younger population of *Alliaria*. Lankau (2011a) showed that effects of *Alliaria* populations on mycorrhizal richness and community structure in the rhizosphere of *Quercus rubra* were correlated with concentrations of glucosinolates and the hydroxynitrile glucoside, alliarinoside, in their roots. Importantly, as *Alliaria* pushed mycorrhizal community structure increasingly away from the native condition, growth of *Q. rubra* and another native tree increasingly declined. However, correlations with *Alliaria* population age were not as apparent.

While studies like Callaway et al. (2008) attempted to expose AMF to ecologically realistic concentrations of putative allelochemicals from *Alliaria* through soil conditioning or extract dilution, one missing link from these studies was the assessment of field concentrations of putative allelochemicals. Barto and Cipollini (2009b) were unable to extract glucosinolates from field soils under *Alliaria*, but did detect some potentially bioactive flavonoid derivatives through biomimetic extraction that were related to those that showed negative effects on AMF. However, half lives of

Table 1 Examples of cases where microbes of different taxonomic groups are the target of allelopathic effects, experience community shifts, and degrade or enhance allelopathic effects of plants

Plants involved	Type of microbe	Identity	Reference
Targets of Allelopathy			
<i>Centaurea stoebe</i>	PGPR ^a	mixed ^b	Pollock et al., 2011
<i>Polygynum avuncular</i>	PGPR	<i>Azotobacter</i> spp.	Alsaadawi and Rice, 1982
<i>Polygynum avuncular</i>	Rhizobacteria	<i>Rhizobium</i> spp.	Alsaadawi and Rice, 1982
Several weed species	Rhizobacteria	<i>Bradyrhizaobium japonicum</i>	Mallik and Tesfai, 1988
<i>Sysimbrium loeselii</i>	AMF ^c	mixed	Bainard et al., 2009
<i>Alliaria petiolata</i>	AMF, EMF ^d	mixed; <i>Glomus intraradices</i>	e.g., Stinson et al., 2006; Wolfe et al., 2008; Callaway et al., 2008; Koch et al., 2011
<i>Brassica nigra</i>	AMF	mixed	Lankau et al., 2011
Allelochemicals Cause Microbial Community Shifts			
<i>Alliaria petiolata</i>	AMF	mixed	Barto et al., 2012
<i>Alliaria petiolata</i>	AMF and soil bacteria	mixed	Lankau, 2011b
<i>Cunninghamia lanceolata</i>	Pathogenic fungi	mixed	Zhang, 1997
<i>Oryza sativa</i>	mixed	mixed	Kong et al., 2008
Degraders of Allelopathic Compounds			
<i>Cucumis sativus</i>	Fungus	<i>Trichoderma harzianum</i> SQR-T037	Chen et al., 2011
<i>Bambusa chungii</i> , <i>Pinus massoniana</i> , <i>Oryza sativa</i>	Gram negative bacteria	<i>Pseudomonas putida</i> 4CD1 <i>Pseudomonas nitroreducens</i> <i>Pseudomonas putida</i> 4CD3	Zhang et al., 2010
	Fungus	<i>Rhodotorula glutinis</i>	
Enhancers of Allelopathy			
<i>Secale cereale</i>	Gram negative bacteria	<i>Actinobacter calcoaceticus</i>	Chase et al. 1991
Herbaceous Plants	AMF CMN ^e	mixed	Barto et al., 2011
<i>Festuca rubra</i>	Endophytic fungi	<i>Epichloe festucae</i>	Vásquez-de-aldana et al., 2011
<i>Lolium arundinaceum</i>	Endophytic fungi	<i>Neotyphodium coenophialum</i>	Rudgers and Orr, 2009

^a PGPR plant growth promoting rhizobacteria, ^b mixed mixture of species, ^c AMF arbuscular mycorrhizal fungi, ^d EMF ectomycorrhizal fungi, ^e CMN common mycorrhizal network

most of these compounds were exceedingly short in non-sterile field soils. In contrast, Cantor et al. (2011) were able to detect AITC in field soils at levels that were sufficient to inhibit a single AMF species in laboratory bioassays. This was an important find, as *Alliaria* produces lower levels of glucosinolates than many of its weedy relatives, and levels also vary in concentration in leaves and roots through the season (Vaughn and Berhow, 1999). If glucosinolates or their degradation products are partly responsible for its allelopathic effects, then they must generally work in low concentrations and would be expected to vary in importance throughout the season.

Despite the evidence that *Alliaria* or its extracts can affect AMF spore germination, growth, infection rates, and community structure, some studies have not found major allelopathic effects of *Alliaria* on these variables. For example,

Burke (2008) found little effect of *Alliaria* presence on either AMF infection rates of three forest herbs or AMF community structure in a field study. Barto and Cipollini (2009a) and Barto et al. (2010a) showed direct effects of *Alliaria* extracts on germination and growth of *Impatiens pallida* in pots or in glass chambers, but no effect on AMF infection rates if the *I. pallida* plants were colonized before exposure to *Alliaria* extracts (Barto et al., 2010a). Despite finding direct effects of *Alliaria* extracts on AMF colony growth, Koch et al. (2011) found little effect of *Alliaria* on AMF species richness or community structure in a pot study with field soils. Lankau (2011b) showed that effects of *Alliaria* on AMF community composition in the field appear to change with the age of *Alliaria* populations, showing declines in AMF species richness and shifts in community structure as you move from young to medium-aged

populations, followed by a rebound in richness and in the number of *Alliaria*-sensitive AMF species in older populations of *Alliaria*. Thus, different conclusions about the effect of *Alliaria* on mycorrhizae and subsequent indirect effects on plant competitors can be reached at different field sites that could be related to variation in “toxicity” of particular *Alliaria* populations (Lankau, 2011b).

From these studies, ecologically important effects of *Alliaria* on AMF (and possibly EMF) in the field seem clearly possible, but the magnitude of these effects depends on plant density, age, and allelopathic potential of the *Alliaria* population, the evolutionary history of the soils and its AMF community with *Alliaria*, the dependence of target plants on AMF, and the timing of exposure to *Alliaria* during the development of mycorrhizal symbioses. While declines in AMF infection rates of native species would seemingly have negative fitness effects, it is not always clear that changes in AMF community composition, when seen, will necessarily have negative effects on competing plants (but see Lankau, 2011a). Providing additional support for potentially important allelopathic effects are reports of the impact of other weedy Brassicaceous species on mycorrhizae, including that of *Brassica nigra* (Lankau et al., 2011) and *Sysimbrium loeselii* (Bainard et al., 2009), but none of these cases have been as fully developed as that of *Alliaria*, and may be subject to the same limitations that intensive study of this species has revealed. The role of glucosinolates in effects of Brassicaceous species on mycorrhizae also remains to be fully elucidated. By taking advantage of several glucosinolate-containing, but mycorrhizal species, along with several non-mycorrhizal Brassicaceous species, Vierheilig et al. (2000) found that gluconasturtin (2-phenylethylglucosinolate) was the only glucosinolate that could consistently be associated with non-mycorrhizal status in these plants. Glucotropaeolin, a major glucosinolate in *Alliaria*, was found in mycorrhizal species, was induced to increase in both non-hosts and hosts by mycorrhizal inoculation, and variation in its concentration in roots was unrelated to variation in mycorrhizal status (Ludwig-Muller et al., 2002). Since *Alliaria* produces insignificant quantities of gluconasturtin, if any, that seems to leave sinigrin and AITC as the leading candidates if glucosinolates are involved in allelopathic suppression of AMF by *Alliaria*. However, a mechanism involving other chemical weapons of *Alliaria* could be important, including flavonoids and their glycoside derivatives, alliarinoside and other hydroxynitrile glucosides, and cyanide (Callaway et al., 2008; Barto et al., 2010b; Lankau, 2011b; Frisch and Moller, 2012). Phenolics common in litter and humus, for example, have been shown to have both direct effects on plants and to affect mycorrhizal physiology (e.g., Boufalas and Pellissier, 1994). While certain flavonoids can be stimulatory to AMF, some isolated flavonoids that *Alliaria* contains, such as apigenin, inhibit

AMF spore germination and hyphal growth (Beard et al., 1992), in addition to having some direct phytotoxic effects (Cipollini et al., 2008). When it occurs, allelopathic inhibition of mycorrhizae is likely multifaceted, and is not yet fully understood even in a system as well studied as *Alliaria*.

Beneficial Bacteria as Targets of Allelopathy Other types of mutualistic microbes, including free living and symbiotic rhizobial bacteria, can differentially benefit plants and be affected by allelopathic plants (Fig. 1). As for mycorrhizal fungi, the ability to inhibit symbiotic rhizobia could provide allelopathic plants an advantage when in competition with plants that benefit strongly from these mutualists. This possibility has been studied extensively in weedy plants of agricultural systems because of the importance of nitrogen-fixing nodulating rhizobia to the success of Leguminous crop species. Using one such system, Mallik and Tesfai (1988) showed that shoot extracts of several weed species, including *Chenopodium album*, *Cyperus esculentus*, and *Helianthus annuus*, not only had direct effects on soybean (*Glycine max*) seed germination and seedling growth, but also severely reduced or eliminated nodulation by *Bradyrhizobium japonicum*. Effects of extracts were dose dependent, however, being stimulatory at lower concentrations in some cases. In that study, *Polygynum pennsylvanicum* was found to have little effect on *B. japonicum*, but Alsaadawi and Rice (1982) found that extracts containing phenolic glycosides of *Polygynum avuncular* had direct effects on germination and growth of *Chenopodium album*, and inhibited some nitrogen-fixing strains of *Rhizobium* in both the lab and the field. Sasikumar et al. (2001) showed that phenolic-containing extracts of several *Eucalyptus* species used in agroforestry inhibited seed germination and growth of *Cajanus cajan*, and could also inhibit nitrogenase activity in already nodulated roots of this legume. In a rare study on a wild system, Larson and Schwartz (1980) exposed black locust (*Robinia pseudoacacia*) and red clover (*Trifolium pratense*) seedlings to litter from several old field species, including *Solidago altissima*, and found that nodulation and nitrogen fixation rates generally declined at high litter exposures in parallel with declines in growth of these species. On the other hand, *R. pseudoacacia* (like some other legumes) has been examined for its own direct allelopathic effects (Nasir et al., 2005) and for its ability to associate with a wide variety of nodulating rhizobia across its native and invasive range (Callaway et al., 2011). This suggests that some nodulating bacteria are susceptible to allelochemicals from some plants, but either evade or suppress those of its host. This appears to be true for mutualistic fungi, like *Piriformaspora indica*, that act as beneficial endophytes in roots of a wide variety of plants including those of the Brassicaceae that do not form mycorrhizal associations (Jacobs et al., 2011). In summary, while the potential ecological effects

of a variety of weedy plants on nodulating rhizobia have been documented, most of the studies have involved plants in managed systems. No cases of the inhibition of nodulating rhizobia by allelopathic plants have been as thoroughly examined as the interaction of some allelopathic plants, like *Alliaria*, with mycorrhizae.

Other beneficial soil bacteria, like the Plant Growth Promoting Rhizobacteria (PGPR), also may be affected by allelopathic plants (Fig. 1). The PGPRs include strains of many species of free-living bacteria, such as *Pseudomonas fluorescens*, *Bacillus subtilis*, and other species, that associate with the roots of plants providing benefits to some of them in the form of enhanced growth and disease resistance (Kloepper et al., 2004). Although much less studied in this regard than nodulating rhizobia, Alsaadawi and Rice (1982) found that extracts containing phenolic glycosides of *Polygonum avuncular* that affected nodulating *Rhizobium* strains could also negatively affect free living nitrogen fixing strains of *Azotobacter*, a PGPR. A range of free living bacterial species, some of them possibly PGPRs, were inhibited at both the population and community level by (\pm) catechin, a putative allelochemical from *Centaurea stoebe* (Pollock et al., 2011). In some cases involving free living bacteria, allelopathic effects have been reported at the community or ecosystem level, with often unknown consequences. Like its effect on mycorrhizal species richness and community structure, Lankau (2011a, b) showed that species richness and structure of the bacterial communities associated with *Alliaria* populations varied with the age and allelopathic potential of the invasive population, with unknown consequences for competing plant performance. Often, a known microbially-associated ecological function, like nitrogen mineralization rate or decomposition rate, has been shown to respond to an allelopathic plant without an examination of the microbial community itself (Ehrenfeld, 2003). Even some microfauna with important ecosystem functions can be affected by allelochemicals. When incorporated into soils, benzyl isothiocyanate (BzITC) from Brassicaceous cover crops not only has a pest and pathogen-resistance function (Brown and Morra, 1997), but also deleteriously affects the springtail (*Folsomia fimetaria*), a beneficial soil-dwelling micro-arthropod that plays a significant role in soil organic carbon and nutrient cycling (Jensen et al., 2010). For free-living bacteria and other soil biota that perform important ecological functions and lack a tight association with particular species, however, it is more difficult to argue that negative allelopathic effects on them could occur without harm to the allelopathic plant itself. Species vary, however, in their response to PGPRs and other organisms, including, presumably, the allelopathic plants themselves. Furthermore, some species of free living bacteria that have growth-promoting properties can also exhibit allelopathic effects (Barazani and Friedman, 2001), thus

indicating why it is sometimes difficult to determine the identity of the allelochemical donor in allelopathic interactions.

In summary, evidence is accumulating that microbial mutualists in soils, such as mycorrhizal fungi or nodulating bacteria, can be the target of allelopathic effects by plants. Such effects may give allelopathic plants a competitive advantage when competing with sensitive species, especially those highly dependent on symbiotic microbes. While free living microbes that confer either fitness-enhancing effects on individual plants or play broader ecological roles also may be subjected to allelopathic effects, these effects are less likely to be the result of specific targeting, and are less clearly beneficial for the allelopathic plant that would also benefit from ecosystem services of such microbes.

Microbial Protection from Allelopathy

Microbial Degradation of Allelochemicals Microbes play an important role in limiting allelopathic effects in natural environments, as has been demonstrated in numerous studies that compare effects in sterile and non-sterile environments. One of the first demonstrations of this phenomenon used an indirect approach, incubating leaves of *Gmelina arborea* for varying times before adding corn seeds to conduct a germination bioassay (Hauser, 1993). When microbial degradation of leaf material was allowed to occur for 14 days before bioassays took place, the germination rates were significantly higher, suggesting that microbes degraded the allelopathic compounds. More direct demonstrations followed with Heisey (1996) showing that aianthone from *Ailanthus altissima* inhibited cress radicle growth more in sterile soil than in non-sterile soil. More recent work has demonstrated this phenomenon for other trees, as well as herbaceous plants and grasses producing a range of allelopathic compounds (Fernandez et al., 2008; Kaur et al., 2009; Rudgers and Orr, 2009; Zhu et al., 2011). Mechanisms by which microbes reduce allelopathic effects include degradation of allelochemicals, increasing tolerance of target plants to allelopathic effects, and altering phytochemical profiles of allelopathic plants to reduce production of allelochemicals.

Microbial degradation is the reason most often given to explain microbial reductions of allelopathic effects, and it has been demonstrated in studies that have found increased growth of bioassay plants along with reduced recovery of allelochemicals under non-sterile conditions (Inderjit and Foy, 1999; Chiapusio and Pellissier, 2001; Inderjit et al., 2010). As expected, recovery of many allelochemicals such as phenolic acids, saponins, isothiocyanates, and flavonoid glycosides spiked into soils is greater in sterile than non-sterile soils (Blum et al., 1994; Okumura et al., 1999; Weidenhamer and Romeo, 2004; Furubayashi et al., 2005;

Barto and Cipollini, 2009b; Chen et al., 2011). More surprising is the range of half-lives found for specific compounds in non-sterile soils. Measured half-lives of benzylglucosinolate range from 6 hours to 9 days (Gimsing et al., 2006, 2007); for 2-benzoxazolinone from 12 h to 30 days (Macías et al., 2004; Understrup et al., 2005); and for *p*-coumaric acid from 5 to 30 days (Blum et al., 1994; Pue et al., 1995). Factors that contribute to this variation include different degradation capabilities of microbial communities in different soil samples, abiotic soil characteristics such as pH (Gimsing et al., 2007; Johansen et al., 2007), the starting concentration of the allelochemical (Understrup et al., 2005; Kong et al., 2007; Gimsing et al., 2009), and the identities and concentrations of other organic compounds present in the soil (Blum et al., 1993; Pue et al., 1995; Blum, 1998; Macías et al., 2004). Half-lives are often modeled by using first-order kinetics, which implicitly states that the half-life is independent of starting concentration. This holds true for the portion of degradation driven by microbial enzymes, but the regular deviation of actual data from this model shows that microbial degradation sometimes operates under very limited conditions. Below a lower threshold, there may not be enough of the allelochemical to induce production of enzymes necessary for degradation, while toxicity of the compounds may limit microbial growth above an upper threshold (Macías et al., 2004). Further complicating matters is the fact that the lower threshold can increase if other organic compounds that are easier to digest are also present in the soil. The half-life of *p*-coumaric acid increased in the presence of glucose, thus demonstrating sequential carbon utilization where the energy rich glucose was degraded before *p*-coumaric acid (Pue et al., 1995). Phenylalanine and *p*-hydroxybenzoic acid also increased the half-life of *p*-coumaric acid, presumably through sequential carbon utilization as well (Pue et al., 1995). Allelochemical half-lives also can be increased by competition for degradative enzymes, and this was suggested as the mechanism behind the increased half-lives of two benzoxazinoids added to soil simultaneously (Macías et al., 2004). The importance of microbes in the degradation of allelochemicals is clear, and amazing progress is being made in understanding how interactions between allelochemicals and biotic and abiotic components of the soil matrix affect degradation.

Microbial Enhancement of Plant Tolerance to Allelochemicals Much of the reduction in allelopathic effects by microbes appears to be due to degradation of allelochemicals, but microbes also may increase plant tolerance of allelochemicals without actively degrading the offending compounds. Extracts of *Empetrum hermaphroditum* reduced nitrogen uptake in *Paxillus involutus* and *Pinus sylvestris* plants colonized by ectomycorrhizal fungi to one

third that seen in controls, but nitrogen uptake in uncolonized plants was reduced to a tenth of the level seen in controls (Nilsson et al., 1993). Arbuscular mycorrhizal fungi also appear able to increase tolerance of plants to allelochemicals such as benzoxazinoids (Džafić et al., 2010) and glucosinolates and flavonoid glycosides (Barto et al., 2010a, b). Arbuscular mycorrhizal fungal spores are sensitive to allelochemicals produced by *Alliaria* (Callaway et al., 2008), as are AMF cultures *in vitro* (Koch et al., 2011), demonstrating that the fungus is not broadly tolerant of these allelochemicals. The North American native herbaceous plant, *Impatiens pallida*, also is sensitive to *Alliaria* allelochemicals, suffering reduced germination and growth when not associated with AMF. However, plants colonized by AMF grew similarly to controls, and had similar colonization levels when AMF were added to the system before allelochemicals (Barto et al., 2010a, b). Since the fungi were sensitive when not associated with the plant, it seems unlikely that they can degrade these allelochemicals on their own. It remains unclear whether the fungus increases plant tolerance, or whether both partners provide enzymes necessary for the degradation of these allelochemicals and that the complete pathway only exists in mycorrhizal plants. Symbiotic degradation of an allelochemical has been demonstrated by the degradation of the benzoxazinoid BOA by *Zea mays* only when colonized by a *Fusarium* endophyte (Knop et al., 2007). Interestingly, *Fusarium* growing in pure culture can initiate BOA breakdown (Yue et al., 1998), but when growing as an endophyte it will only produce enzymes for the later stages of BOA degradation, and it relies on its plant host to perform the first step (Knop et al., 2007). The increased tolerance of allelochemicals by plants colonized with AMF is less likely to be due to degradation of the allelochemicals by the fungus because the only carbon used by these fungi is provided by their plant hosts in the form of hexoses; the fungi are not thought to take up other carbon sources from the environment (Smith and Read, 2008). These fungi often improve plant nutrition and most likely increase tolerance of the plant to stresses such as exposure to allelochemicals by making it easier for stressed plants to recover.

Microbial Effects on Plant Allelochemical Production Microbes, such as foliar fungal pathogens (Fig. 1), also can reduce allelopathic effects by modifying the phytochemical profile of the allelopathic plant to reduce production of allelochemicals. *Ageratum conyzoides* infected with *Erysiphe cichoracearum* (powdery mildew) was less allelopathic on other herbaceous plants than uninfected plants, despite the fact that production of many volatiles was induced by infection (Kong et al., 2002). This result highlights the complexity of synergistic reactions among allelochemicals because many of the volatiles that were induced by *E.*

cichoracearum infection were allelopathic when applied alone (Kong et al., 1999). Although higher total amounts of volatile compounds were produced in infected plants, the mix of compounds was altered, and the concentration of precocene I declined significantly (Kong et al., 2002), suggesting that this compound may be especially important in the allelopathic effect of *A. conyzoides*. Infection by *Erysiphe cruciferarum*, a powdery mildew fungus that infects *Alliaria*, reduced the belowground competitive effects of *Alliaria* on a native herbaceous plant (Cipollini and Enright, 2009). Virulent strains of this fungus induce some generalized defense responses in leaves of *Alliaria* (Enright and Cipollini, 2011), but the profiles of putative phytochemicals involved in allelopathy belowground have not been compared between infected and uninfected individuals.

In summary, allelopathic effects can be greatly reduced by free-living soil bacteria and fungi, as well as by symbiotic and endophytic bacteria and fungi. These microbes act directly by degrading the allelopathic compound, and indirectly by increasing target plant tolerance of allelopathic effects and reducing production of allelochemicals by allelopathic plants. Going forward, future work should incorporate realistic microbial communities into experimental tests of allelopathy in order to better understand how microbes modify allelopathic effects. Important allelopathic effects in the field would appear to require that microbial protection mechanisms be overcome, and are perhaps restricted to areas with a limited history with the allelopathic plant.

Microbial Enhancement of Allelopathy

While the importance of abiotic soil factors with respect to the alteration and influence of allelochemicals cannot be stressed enough (Inderjit et al., 2010), microbial transformations and the general role of microbes with respect to allelochemicals clearly plays a major role in influencing allelopathic effects (Inderjit, 2005). In addition to detoxifying allelochemicals through degradation, however, soil microbial communities also have been shown to degrade toxic compounds into more toxic products (e.g., Gagliardo and Chilton, 1992) and to degrade relatively innocuous substances into toxic products. Allelopathic plants can modify plant-microbe interactions, resulting in increased allelopathic effects through increasing the sensitivity of target plants to pathogens and favoring growth of pathogenic or parasitic microbes. In addition, microbial communities can affect the allelopathic potential of a species or system in a more indirect way, such as the case of endophytic fungi that can stimulate allelochemical production by their host plants. Finally, networks of mycorrhizal fungi can distribute the toxic allelochemicals throughout plant communities, broadening their sphere of influence (Barto et al., 2011).

Increases in Allelochemical Toxicity through Microbial Degradation One of the more well-studied examples of the phytotoxicity of an allelochemical increasing through microbial modification comes from cereals in the Gramineae with consequences in agriculture, but also from plants in the Acanthaceae, Ranunculaceae, and Scrophulariaceae families. Many cereals produce the hydroxamic acids 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3(4*H*)-one (DIMBOA) and 2,4-dihydroxy-1,4-benzoxazin-3(4*H*)-one (DIBOA) (Niemeyer, 1988; Baumeler et al., 2000). The benzoxazolinones 6-methoxy-2-benzoxazolinone (MBOA) and 2-benzoxazolinone (BOA), interestingly enough, are the degradation products of DIMBOA and DIBOA, respectively (Fomsgaard et al., 2006). MBOA and BOA have been shown to be further transformed into 2-amino-7-methoxy-3*H*-phenoxazin-3-one (AMPO) and 2-amino-3*H*-phenoxazin-3-one (APO), respectively (Understrup et al., 2005). Gents et al. (2005) were able to demonstrate that the degradation of BOA to APO was concentration-dependent with low soil concentrations ($400 \mu\text{g kg}^{-1}$) yielding only one unidentified transformation product, while higher soil concentrations (400mg kg^{-1}) yielded eight distinct transformation products, one of which was confirmed as APO in accordance with Gagliardo and Chilton (1992). APO has been shown to be more biologically active than BOA (Gagliardo and Chilton, 1992) including higher phytotoxicity and increased toxicity towards beneficial soil organisms and fungi (Gents et al., 2005). Gents et al. (2005) suggest that BOA is only toxic to microorganisms at higher concentrations and, therefore, microbes may convert BOA into APO and several other products thus ameliorating toxic conditions, thereby increasing phytotoxicity.

Allelopathic effects can be enhanced by microbial modification even when the parent compound is otherwise innocuous, with implications for plant invasions. Bains et al. (2009) found that exotic populations of *Phragmites australis* contained higher concentrations of the non-toxic gallotannin in their rhizospheres than native populations. These authors concluded that the invasiveness of the exotic *P. australis* can be partly explained by the increased levels of gallotannin that are degraded by native microbial and native plant communities into gallic acid, a much more biologically active and phytotoxic compound. Native plant and soil communities produce greater amounts of tannase, the enzyme responsible for hydrolyzing gallic acid from gallotannin, with greater activity than exotic *P. australis* plants. Therefore, it appears that *P. australis* exudes a relatively benign substance and relies on the surrounding microbial and plant communities to degrade it into a noxious compound, effectively freeing space (Bains et al., 2009) for further *P. australis* colonization. It is likely that gallic acid is further broken down to form even more phytotoxic products (Weidenhamer and Romeo, 2004), although it is

unknown what role soil microbes play in this process. The findings reported by Bains et al. (2009) offer an interesting perspective on the Novel Weapons Hypothesis (Callaway and Ridenour, 2004; Callaway et al., 2008) in that a common compound that is produced at higher levels by an invasive plant genotype is “weaponized” by native soil microbial communities.

Microbial Infection and Realized Allelopathic Effects Indirect effects of allelopathic compounds include effects on microbial resistance of competitors. Voll et al. (2004) reported that extracts of *Brachiaria plantaginea* inhibited seed germination and root lengths of the two weed species, *Commelina benghalensis* and *Acanthospermum hispidum*. Interestingly, addition of *B. plantaginea* extracts to *C. benghalensis* seeds elevated levels of endophytic fungal infections and lowered germination rates. This study reveals the possible indirect allelopathic interaction that results when exposure to noxious chemicals enhances susceptibility of competing plants to microbial pathogens. Allelopathic plants in the Brassicaceae, especially *Brassica napus*, may also stimulate soil populations of plant pathogens like *Pythium* (Hoagland et al., 2008), which are expected to reduce the growth of surrounding plants. Mycorrhizal associations also can be modified by allelopathic plants, as shown for *Molinia caerulea*, which appears to limit growth of an efficient ectomycorrhizal symbiont in *Picea abies* roots while stimulating growth of a more parasitic symbiont instead (Timbal et al., 1990). It remains to be seen how the spread of invasive plants is enhanced by the allelopathic modification of microbial interactions with native plants.

Endophytic fungi also have been shown to enhance the allelopathic potential of plants, possibly by producing allelochemicals for their plant hosts or by stimulating allelochemical production (Fig. 1). Pyrrolizidine alkaloids were produced by *Festuca* only when infected by an endophyte (Malinowski et al., 1999), and are likely produced by the endophytes and provided to the plants. A similar mechanism may be behind the results of Vásquez-de-Aldana et al. (2011), who showed that root exudates of red fescue (*Festuca rubra*) had a greater inhibitory effect on the germination and seedling growth of four target species when infected with a fungal endophyte, *Epichloë festucae*. Endophyte infection can be beneficial to the host plant with respect to many factors including increased resistance to drought, salt stress, nematodes, mammalian and insect herbivores, and bacterial and fungal pathogens (Kimmons et al., 1990; Li et al., 2009; Ownley et al., 2010; Sabzalain and Mirlohi, 2010; Miranda et al., 2011; Rocha et al., 2011). Rudgers and Orr (2009), however, were able to show that soils conditioned by non-native tall fescue (*Lolium arundinaceum*) that was infected by the fungal endophyte, *Neotyphodium coenophialum*, were able to reduce the biomass of *Elaeagnus umbellata*, *Fraxinus pennsylvanica*, and

Platanus occidentalis. This reduction in biomass was apparent only in live soil treatments suggesting that above and below-ground microbial interactions are important in this system.

Microbial Enhancement of Allelochemical Distribution The existence of mycorrhizal networks may enhance allelopathic effects of plants, especially if the mycorrhizae themselves are insensitive to the allelochemicals. Despite early evidence that the invasive forb *Centaurea stoebe* was more allelopathic towards *Festuca idahoensis* when mycorrhizal than when un-colonized (Marler et al., 1999), it does not appear that *C. stoebe* was parasitizing *F. idahoensis* by drawing carbon through the mycorrhizal network (Zabinski et al., 2002). In this specific case, Zabinski and coworkers attributed the invasiveness of *C. stoebe* to its ability to outcompete native grasses with respect to exploiting mycorrhizal relationships more effectively, and, therefore, being better able to capture resources from soil. More broadly, Barto et al. (2011), suggest that common mycorrhizal networks facilitate the transfer of allelochemicals from donor to target plants. In two separate experiments, these authors showed enhanced accumulation of an herbicide, imazamox (representing a hydrophilic allelopathic compound), in tissues of target plants (*Zea mays*) connected to the dosing site by a common mycorrhizal network. In order to eliminate concerns about the application of compounds in unrealistic amounts as well as simulating a natural donor-target plant system, these authors also used the allelopathic *Tagetes tenuifolia* which exudes hydrophobic phytotoxic thiophenes from its roots. Again, allelochemical concentrations in soils were significantly greater and target plant biomass lower with common mycorrhizal networks present. Transfer of plant available P was not a factor in these experiments (Barto et al., 2011), in contrast to the results found by Zabinski et al. (2002). Barto et al. (2011) was the first study to clearly demonstrate the role that soil communities can have with respect to the amplification and expansion of plant-plant allelopathic effects and in light of these findings, future allelopathy studies must incorporate these principles and control for the effects of common mycorrhizal networks.

Though not the specific subject matter of this review, it is worth mentioning studies such as Meier and Bowman (2008) that showed that certain allelochemical fractions of *Acomastylis rossii* increased soil respiration, reduced *Deschampsia caespitosa* growth, and reduced *D. caespitosa* N concentrations. The explanation these authors offered was that the availability of labile sources of C stimulated microbial activity, which, therefore, reduced the availability of N to *D. caespitosa*. This is an indirect way in which microbial processing of soil C sources can indirectly mimic allelopathic effects, but does not necessarily require “toxic” allelochemicals to be present. For a review of the ecosystem function and biogeochemistry in plant invasions, see Weidenhamer and Callaway (2010).

Mechanisms by which microbes can enhance allelopathic effects may be at least as important in community dynamics (i.e., plant invasions), as the mechanisms described above where microbes reduce allelopathic effects. The importance of these alternative mechanisms likely varies in different systems, and specific research is needed to understand how these opposing mechanisms interact in the field.

Conclusions and Outlook

Allelopathy has been an increasingly popular topic of study for the past 50 years, with almost 4000 articles indexed by ISI. Microbes have been included in these studies only in the past 30 years, and fewer than 300 publications have been indexed by ISI in that time. Within this short period, much progress has been made towards understanding how microbes act as targets and mediators of allelopathy in plants. Allelopathic inhibition of beneficial microbes such as mycorrhizal fungi, rhizobia, and plant growth promoting rhizobacteria also indirectly limits growth of the plants hosting those microbes. Microbes whose growth is not directly affected by allelochemicals still often mediate effects of those compounds on other plants, both reducing and increasing allelopathic effects. Reductions in allelopathic effects occur through several mechanisms that include microbial degradation of allelochemicals, an increasing tolerance of colonized plants to the stress of exposure to allelochemicals, and the modification of the phytochemical profiles of allelopathic plants that reduces allelochemical production. Increases in allelopathic effects also can be driven by microbial degradation of natural products when the products of degradation are more toxic than the parent compounds, through modifications of plant microbe interactions, and by microbial induction of allelochemical production by plants. Furthermore, bioactive zones of allelochemicals are increased in soils with intact arbuscular mycorrhizal fungal networks, which seem to serve as ‘highways’ for allelochemical movement directly from donor to target plants.

It is becoming increasingly apparent that the degree and direction of microbial mediation of allelopathy will not remain constant through time. Much of the research on allelopathy in natural systems is focused on invasive plants, which are usually non-native species. The Novel Weapons Hypothesis posits that non-native invasive plants are more able to exert allelopathic effects on naïve plants in the invaded range because the invader and the native plants do not share a co-evolutionary history (Callaway and Ridenour, 2004). This same logic can be applied to naïve microbes in invaded ranges because they are less likely to have evolved mechanisms to degrade allelochemicals or affect allelochemical production than microbes in the native range of invaders. As microbes become more adapted to both

the novel weapons and the non-native plants producing them, allelopathic effects are likely to decrease in some cases, but increase in others. Beneficial microbes that are sensitive to allelochemicals will likely develop resistance over time, and the indirect inhibitory effects on the plants associating with them will, therefore, decline. Likewise, microbes that act to reduce allelopathic effects by degrading allelochemicals will likely become more efficient as they adapt to the novel allelochemicals (Blum and Shafer, 1988; Walker and Welch, 1991). Conversely, microbial enhancement of allelopathic effects through increased toxicity of microbial degradation products is predicted to increase as the time since invasion increases. Microbial reduction of allelopathic effects through increased tolerance of the target plant is unlikely to change through time if the microbes are not sensitive to the allelochemicals, but could increase as native microbes develop resistance to any inhibitory effects of the allelochemicals.

Effects of time since invasion on microbial modification of the phytochemical profile of non-native allelopathic plants are more difficult to predict. Production of allelochemicals by *Alliaria* appears to decline with time since invasion (Lankau et al., 2009), but it is unclear what role microbes play in this reduction. Arbuscular mycorrhizal fungal communities in areas invaded by *Alliaria* are beginning to shift away from those found in uninvaded areas (Burke, 2008; Lankau, 2011b; Barto et al., 2012). Bacterial communities are not always affected by *A. petiolata* invasion (Burke and Chan, 2010), but where microbial communities are affected, resistance to *Alliaria* allelochemicals has begun to develop in only 50 years since the invader was introduced (Lankau, 2011b). Another allelopathic invasive plant, *C. stoebe*, also modifies microbial communities, including effects on rhizosphere bacteria and arbuscular mycorrhizal fungi associating with neighboring plants (Batten et al., 2006; Mummey and Rillig, 2006; Broz et al., 2009). This modification of the microbial community is not short term (Kulmatiski and Beard, 2011) and likely takes years to develop, as has been shown for *Alliaria*.

Microbes can serve as targets and mediators of allelopathic effects in plants, with both strong positive and negative effects being possible. More effort should be made in the future to include microbes in allelopathy research to improve ecological realism. Ecological realism is attained partly by using non-sterile soils in assays of allelopathic effects, using natural inputs of allelochemicals, followed by examination of microbial community changes. In addition, soil sterilization followed by substitutions of different portions of the microbial community could be used to identify important classes or specific species of microbes that modify allelopathic effects. These studies also could be enhanced by using

representatives of plant species that are differentially dependent on specific microbes, and done in different soil types to examine abiotic influences. Selection experiments could also be performed to evaluate evolutionary responses of microbes to allelochemicals, and more work on adaptation of specific microbes or microbial populations to allelopathic plants is needed in the field. Further exploration of microbial communities in the native range of invasive plants could aid predictions of microbial adaptation, community shifts, and the “longevity” of allelopathic effects in invasive ranges. Knowing the extent of departure of the microbial communities from the native range of an invasive plant from that found in a “preinvaded” range, coupled with the extent of departure of allelochemistry in the invasive plant from relatives in the preinvaded range (e.g., Barto et al., 2010b), may aid predictions of the potential allelopathic effects of invasive species. All of this work should be coupled with improvements in sampling and analytical techniques for allelochemicals and microbes in the environment.

In an applied sense, research is needed to explore the potential of reintroducing microbes to areas where allelopathic plants have taken hold as a part of restoration plans. In turn, potentially negative effects of microbial reintroduction (or controlled inoculations in agricultural systems) on allelochemical modification should also be explored. Much additional research is needed on how allelochemical degradation is affected by the presence of other plant-derived compounds, since this can both increase and decrease allelopathic effects. Understanding how seemingly disparate mechanisms interact in the field will become increasingly important. In situations where allelopathic effects are seen in natural environments, microbial protection mechanisms are apparently being overcome by other, often undefined, mechanisms. A deeper understanding of the factors that control the balance between reducing and enhancing effects could allow development of management schemes targeted for specific areas that could reduce the impact of allelopathic plants without actively removing them. Likely candidates for these controlling factors include microbial species identities and abundances, neighboring plant species identities and abundances, along with abiotic factors such as soil organic matter content, nutrient levels, and water holding capacity. Additionally, the contribution of allelopathic effects to the phenomenon of plant-microbe feedback is still unclear, even for plants with known effects on soil biota. Finally, the movement of allelochemicals through common mycorrhizal networks provides a mechanism for greatly enhanced delivery of bioactive doses of allelochemicals to target plants, but it is still unclear how important this mechanism is in the field. Interest in microbial mediation of allelopathic effects is only expected to increase in the future, and the field is ripe with questions.

Acknowledgments We acknowledge financial support from the Ohio Plant Biotechnology Consortium, USDA-APHIS, and Wright State University (DC and CR), as well as the Freie Universität—Berlin (EKB) during the preparation of this manuscript. Comments by two anonymous reviewers substantially improved this manuscript.

References

- ABHILASHA, D., QUINTANA, N., VIVANCO, J., and JOSHI, J. 2008. Do allelopathic compounds in invasive *Solidago canadensis* s.l. restrain the native European flora. *J. Ecol.* 96:993Y1001.
- ALSAADAWI, I. S. and RICE, E. L. 1982. Allelopathic effects of *Polygonum aviculare* L. II. Isolation, characterization, and biological activities of phytotoxins. *J. Chem. Ecol.* 8:1011Y122.
- BAINARD, L. D., BROWN, P. D., and UPADHYAYA, M. K. 2009. Inhibitory effect of tall hedge mustard (*Sysymbrium loeselii*) allelochemicals on rangeland plants and arbuscular mycorrhizal fungi. *Weed Sci.* 57:386Y393.
- BAINS, G., KUMAR, A. S., RUDRAPPA, T., ALFF, E., HANSON, T. E., and BAIS, H. P. 2009. Native plant and microbial contributions to a negative plant-plant interaction. *Plant Physiol.* 151:214Y–2151Y.
- BAIS, H. P. and KAUSHIK, S. 2010. Catechin secretion and phytotoxicity Fact not fiction. *Comm. Integ. Biol.* 3:46Y–470Y.
- BARAZANI, O. and FRIEDMAN, J. 2001. Allelopathic bacteria and their impact on higher plants. *Crit. Rev. Micro.* 27:4Y–55Y.
- BARTO, E. K. and CIPOLLINI, D. 2009a. Density dependent phytotoxicity of *Impatiens pallida* plants exposed to extracts of *Alliaria petiolata*. *J. Chem. Ecol.* 35:495Y504.
- BARTO, E. K. and CIPOLLINI, D. 2009b. Half-lives and field soil concentrations of *Alliaria petiolata* secondary metabolites. *Chemosphere* 76:71Y75.
- BARTO, E. K., FRIESE, C. F., and CIPOLLINI, D. 2010a. Arbuscular mycorrhizal fungi protect a native plant from allelopathic effects of an invader. *J. Chem. Ecol.* 36:351Y360.
- BARTO, E. K., POWELL, J., and CIPOLLINI, D. 2010b. How novel are the chemical weapons of garlic mustard in North American forest understories? *Biol. Inv.* 12:3465Y3471.
- BARTO, K. E., HILKER, M., MÜLLER, F., MOHNEY, B. K., WEIDENHAMER, J. D., and RILLIG, M. C. 2011. The fungal fast lane: Common mycorrhizal networks extend bioactive zones of allelochemicals in soils. *PLoS One* 6:e27195.
- BARTO, E. K., ANTUNES, P. M., STINSON, K., KOCH, A. M., KLIRONOMOS, J. N., and CIPOLLINI, D. 2012. Differences in arbuscular mycorrhizal fungal communities associated with sugar maple seedlings in and outside of invaded garlic mustard forest patches. *Biol. Inv.* doi:10.1007/s10530-011-9945-6.
- BATTEN, K. M., SCOW, K. M., DAVIES, K. F., and HARRISON, S. P. 2006. Two invasive plants alter soil microbial community composition in serpentine grasslands. *Biol. Inv.* 8:217Y230.
- BAUMELER, A., HESSE, M., and WERNER, C. 2000. Benzoxazinoid-cyclic hydroxamic acids, lactams and their corresponding glucosides in the genus *Aphelandra* (Acanthaceae). *Phytochemistry* 53:213Y222.
- BECARD, G., DOUDS, D. D., and PFEFFER, P. E. 1992. Extensive in vitro hyphal growth of vesicular-arbuscular mycorrhizal fungi in the presence of CO² and flavonols. *Appl. Env. Micro.* 1992:821Y825.
- BELZ, R. G. 2007. Allelopathy in crop/weed interactions—an update. *Pest Manag. Sci.* 63:308Y326.
- BLUM, U. 1998. Effects of microbial utilization of phenolic acids and their phenolic acid breakdown products on allelopathic interactions. *J. Chem. Ecol.* 24:685Y708.
- BLUM, U. and SHAFER, S. R. 1988. Microbial populations and phenolic acids in soil. *Soil Biol. Biochem.* 20:793Y800.

- BLUM, U., GERIG, T. M., WORSHAM, A. D., and KING, L. D. 1993. Modification of allelopathic effects of *p*-coumaric acid on morning-glory seedling biomass by glucose, methionine, and nitrate. *J. Chem. Ecol.* 19:2791Y2811.
- BLUM, U., WORSHAM, A. D., KING, L. D., and GERIG, T. M. 1994. Use of water and EDTA extractions to estimate available (free and reversibly bound) phenolic acids in Cecil soil. *J. Chem. Ecol.* 20:341Y359.
- BOUFALIS, A. and PELLISIER, F. 1994. Allelopathic effects of phenolic mixtures on respiration of two spruce mycorrhizal fungi. *J. Chem. Ecol.* 20:2283–2289.
- BROWN, P. D. and MORRA, J. M. 1997. Control of soil-borne plant pests using glucosinolate-containing plants. *Adv. Agron.* 61:167Y231.
- BROZ, A. K., MANTER, D. K., BOWMAN, G., MÜLLER-SCHÄRER, H., and VIVANCO, J. M. 2009. Plant origin and ploidy influence gene expression and life cycle characteristics in an invasive weed. *BMC Plant Biol.* 9:33.
- BURKE, D. J. 2008. Effects of *Alliaria petiolata* (garlic mustard; Brassicaceae) on mycorrhizal colonization and community structure in three herbaceous plants in a mixed deciduous forest. *Am. J. Bot.* 95:1416Y1425.
- BURKE, D. J. and CHAN, C. R. 2010. Effects of the invasive plant garlic mustard (*Alliaria petiolata*) on bacterial communities in a northern hardwood forest soil. *Can. J. Microbiol./Rev. Can. Microbiol.* 56:81Y86.
- CALLAWAY, R. M. and RIDENOUR, W. M. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. *Front. Ecol. Environ.* 2:436Y443.
- CALLAWAY, R. M., CIPOLLINI, D., BARTO, K., THELEN, G. C., HALLETT, S. G., PRATI, D., STINSON, K., and KLIRONOMOS, J. 2008. Novel weapons: Invasive plant suppresses fungal mutualists in America but not in its native Europe. *Ecology* 89:1043Y1055.
- CALLAWAY, R. M., BEDMAR, E. J., REINHART, K. O., SILVAN, C. G., and KLIRONOMOS, J. 2011. Effects of soil biota from different ranges on *Robinia* invasion: acquiring mutualists and escaping pathogens. *Ecology* 92:1027Y1035.
- CANTOR, A., HALE, A., AARON, J., TRAW, M. B., and KALISZ, S. 2011. Low allelochemical concentrations detected in garlic-mustard invaded forest soils inhibit fungal growth and AMF spore germination. *Biol. Inv.* 13:3015Y3025.
- CHASE, W. R., M. G. NAIR, A. R. PUTNAM, and S. K. MISHRA. 1991. 2,2'-oxo-1,1'-azobenzene: Microbial transformation of rye (*Secale cereale* L.) allelochemical in field soils by *Acinetobacter calcoaceticus*: III. *Journal of Chemical Ecology*, 17:1575-1584.
- CHEN, L., YANG, X., RAZA, W., LI, J., LIU, Y., QIU, M., ZHANG, F., and SHEN, Q. 2011. *Trichoderma harzianum* SQR-T037 rapidly degrades allelochemicals in rhizospheres of continuously cropped cucumbers. *Appl. Micro. Biotech.* 89:1653Y1663.
- CHIAPUSIO, G. and PELLISIER, F. 2001. Methodological setup to study allelochemical translocation in radish seedlings. *J. Chem. Ecol.* 27:1701Y1712.
- CIPOLLINI, D. and ENRIGHT, S. 2009. A powdery mildew fungus levels the playing field for garlic mustard (*Alliaria petiolata*) and a North American native plant. *Inv. Plant Sci. Man.* 2:253Y259.
- CIPOLLINI, D., STEVENSON, R., ENRIGHT, S., EYLES, A., and BONELLO, P. 2008. Phenolic metabolites in leaves of the invasive shrub, *Lonicera maackii*, and their potential phytotoxic and anti-herbivore effects. *J. Chem. Ecol.* 34:144Y152.
- DORNING, M. and CIPOLLINI, D. 2006. Leaf and root extracts of the invasive shrub, *Lonicera maackii*, inhibit seed germination of three herbs with no autotoxic effects. *Plant Ecol.* 184:287Y296.
- DUKE, S. O., BLAIR, A. C., DAYAN, F. E., JOHNSON, R. D., MEEPAGALA, K. M., COOK, D., and BAJSA, J. 2009. Is (–) catechin a “novel weapon” of spotted knapweed (*Centaurea stoebe*)? *J. Chem. Ecol.* 35:141Y153.
- DŽAFIĆ, E., PONGRAC, P., LIKAR, M., VOGEL-MIKUŠ, K., and REGVAR, M. 2010. Colonization of maize (*Zea mays* L.) with the arbuscular mycorrhizal fungus *Glomus mosseae* alleviates negative effects of *Festuca pratensis* and *Zea mays* root extracts. *Allelopath. J.* 25:249Y258.
- EHRENFELD, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6:503Y523.
- ENRIGHT, S. and CIPOLLINI, D. 2011. Overlapping defense responses to water limitation and pathogen attack and their consequences for resistance to powdery mildew disease in garlic mustard. *Alliaria petiolata* *Chemoecology* 21:89–98.
- FERNANDEZ, C., VOIRIOT, S., MÉVY, J.-P., VILA, B., ORMEÑO, E., DUPOUYET, S., AND BOUSQUET-MÉLOU, A. 2008. Regeneration failure of *Pinus halepensis* Mill.: The role of autotoxicity and some abiotic environmental parameters. *For. Ecol. Manag.* 255:2928Y2936.
- FOMSGAARD, I. S., MORTENSEN, A. G., IDINGER, J., COJA, T., and BLÜMEL, S. 2006. Transformation of benzoxazinones and derivatives and microbial activity in the test environment of soil ecotoxicological tests on *Poecilus cupreus* and *Folsomia candida*. *J. Ag. Food Chem.* 54:1086Y1092.
- FRISCH, T. and MOLLER, B. L. 2012. Possible evolution of alliarinoside from the glucosinolate pathway in *Alliaria petiolata*. *FEBS J.* 279:1545–1562. doi:10.1111/j.1742-4658.2011.08469.x.
- FURUBAYASHI, A., HIRADATE, S., and FUJII, Y. 2005. Adsorption and transformation reactions of L-DOPA in soils. *Soil Sci. Plant Nutr.* 51:819Y825.
- GAGLIARDO, R. W. and CHILTON, W. S. 1992. Soil transformation of 2 (3H)-Benzoxazolone of rye into phytotoxic 2-amino-3H-phenoxazin-3-one. *J. Chem. Ecol.* 18:1683Y1691.
- GENTS, M. B., NIELSEN, S. T., MORTENSEN, A. G., CHRISTOPHERSEN, C., and FOMSGAARD, I. S. 2005. Transformation products of 2-benzoxazolinone (BOA) in soil. *Chemosphere* 61:74Y84.
- GIMSING, A. L., SØRENSEN, J. C., TOVGAARD, L., JØRGENSEN, A. M. F., and HANSEN, H. C. B. 2006. Degradation kinetics of glucosinolates in soil. *Environ. Toxicol. Chem.* 25:2038–2044.
- GIMSING, A. L., POULSEN, J. L., PEDERSEN, H. L., and HANSEN, H. C. B. 2007. Formation and degradation kinetics of the biofumigant benzyl isothiocyanate in soil. *Environ. Sci. Technol.* 41:4271Y4276.
- GIMSING, A. L., BÆLUM, J., DAYAN, F. E., LOCKE, M. A., SEJERØ, L. H., and JACOBSEN, C. S. 2009. Mineralization of the allelochemical sorgoleone in soil. *Chemosphere* 76:1041Y1047.
- HAUSER, S. 1993. Effect of *Acioa barberi*, *Cassia siamea*, *Flemingia macrophylla* and *Gmelina arborea* leaves on germination and early development of maize and cassava. *Agric. Ecosyst. Environ.* 45:263Y273.
- HEISEY, R. M. 1996. Identification of an allelopathic compound from *Ailanthus altissima* (Simaroubaceae) and characterization of its herbicidal activity. *Am. J. Bot.* 83:192Y200.
- HOAGLAND, L., CARPENTER-BOGGS, L., REGANOLD, J. P., AND MAZZOLA, M. 2008. Role of native soil biology in Brassicaceous seed meal-induced weed suppression. *Soil Biol. Biochem.* 40:1689Y1697.
- INDERJIT 2005. Soil microorganisms: An important determinant of allelopathic activity. *Plant Soil* 274:227–236.
- INDERJIT and FOY, C. L. 1999. Nature of the interference mechanism of mugwort (*Artemisia vulgaris*). *Weed Tech.* 13:176Y182.
- INDERJIT, BAJPAI, D., and RAJESWARI, M. S. 2010. Interaction of 8-hydroxyquinoline with soil environment mediates its ecological function. *PLoS One* 5:e12852.
- JACOBS, S., ZECHMANN, B., MOLITOR, A., TRUJILL, M., PETUTSCHNIG, E., LIPKA, V., KOGEL, K. H., and SCHAEFER, P. 2011. Broad-spectrum suppression of innate immunity is required for colonization of Arabidopsis roots by the fungus *Piriformospora indica*. *Plant Phys.* 156:726Y740.

- JENSEN, J., STYRISHAVE, B., GIMSING, A. L., and HANSEN, H. C. B. 2010. The toxic effects of benzyl glucosinolate and its hydrolysis product, the biofumigant benzyl isothiocyanate, to *Folsomia fimetaria*. *Environ. Tox. Chem.* 29:359Y364.
- JOHANSSON, J. F., PAUL, L. R., and FINLAY, R. D. 2004. Microbial interactions in the mycorrhizosphere and their significance for sustainable agriculture. *FEMS Micro. Ecol.* 48:1Y13.
- JOHANSEN, H., RASMUSSEN, L. H., OLSEN, C. E., and HANSEN, H. C. B. 2007. Rate of hydrolysis and degradation of the cyanogenic glycoside—dhurrin—in soil. *Chemosphere* 67:259Y266.
- JOSE, S. 2002. Black walnut allelopathy: current state of the science, pp. 149–172, in A. U. Mallik and Inderjit (eds.), *Chemical Ecology of Plants: Allelopathy in Aquatic and Terrestrial Ecosystems*. Birkhäuser Verlag, Basel.
- KAUR, H., KAUR, R., KAUR, S., BALDWIN, I. T., and Inderjit 2009. Taking ecological function seriously: soil microbial communities can obviate allelopathic effects of released metabolites. *PLoS Biol.* 4:e4700.
- KIMMONS, C. A., GWINN, K. D., and BERNARD, E. C. 1990. Nematode reproduction on endophyte-infected and endophyte-free tall fescue. *Plant Dis.* 74:75Y761.
- KLOPPER, J. W., RYU, C.-M., and ZHANG, S. 2004. Induced systemic resistance and promotion of plant growth by *Bacillus* spp. *Phytopathology* 94:1259Y1266.
- KNOP, M., PACYNA, S., VOLOSHCHUK, N., KANT, S., MÜLLENBORN, C., STEINER, U., KIRCHMAYER, M., WCHERER, H. W., and SCHULZ, M. 2007. *Zea mays*: Benzoxazinone detoxification under sulfur deficiency conditions—a complex allelopathic alliance including endophytic *Fusarium verticillioides*. *J. Chem. Ecol.* 33:225Y237.
- KOCH, A. M., ANTUNES, P. M., BARTO, E. K., CIPOLLINI, D., MUMMEY, D. L., and KLIRONOMOS, J. N. 2011. The effects of arbuscular mycorrhizal (AM) fungal and garlic mustard introductions on native AM fungal diversity. *Biol. Inv.* 13:1627Y1639.
- KONG, C., HU, F., XU, T., and LU, Y. 1999. Allelopathic potential and chemical constituents of volatile oil from *Ageratum conyzoides*. *J. Chem. Ecol.* 25:2347Y2356.
- KONG, C., HU, F., and XU, X. 2002. Allelopathic potential and chemical constituents of volatiles from *Ageratum conyzoides* under stress. *J. Chem. Ecol.* 28:1173Y1182.
- KONG, C. H., ZHAO, H., XU, X. H., WANG, P., and GU, Y. 2007. Activity and allelopathy of soil of flavone *O*-glycosides from rice. *J. Ag. Food Chem.* 55:6007Y6012.
- KONG, C. H., WANG, P., GU, Y., ZU, X. H., and WANG, M. L. 2008. Fate and impact on microorganisms of rice allelochemicals in paddy soil. *J. Ag. Food Chem.* 56:5043Y5049.
- KULMATISKI, A. and BEARD, K. H. 2011. Long-term plant growth legacies overwhelm short-term plant growth effects on soil microbial community structure. *Soil Biol. Biochem.* 43:823Y830.
- LANKAU, R. A. 2011a. Intraspecific variation in allelochemistry determines an invasive species' impact on soil microbial communities. *Oecologia* 165:453–463.
- LANKAU, R. A. 2011b. Resistance and recovery of soil microbial communities in the face of *Alliaria petiolata* invasions. *New Phytol.* 189:536Y548.
- LANKAU, R. A., NUZZO, V., SPYREAS, G., and DAVIS, A. S. 2009. Evolutionary limits ameliorate the negative impact of an invasive plant. *Proc. Natl. Acad. Sci. USA* 106:15362–15367.
- LANKAU, R., WHEELER, E., BENNETT, A. E., and STRAUSS, S. Y. 2011. Plant-soil feedbacks contribute to an intransitive competitive network that promotes both genetic and species diversity. *J. Ecol.* 99:176Y185.
- LARSON, M. M. and SCHWARTZ, E. L. 1980. Allelopathic inhibition of black locust, red clover, and black alder by six common herbaceous species. *Forest Sci.* 22:511Y520.
- LI, C. J., NAN, Z. B., ZHANG, C. J., ZHANG, C. Y., and ZHANG, Y. H. 2009. Effects of endophyte infected drunken horse grass on Chinese rabbit. *J. Agr. Sci. Tech.* 11:90Y96.
- LUDWIG-MULLER, J., BENNETT, R. N., GARCIA-GARRIDO, J. M., and VIERHEILIG, H. 2002. Reduced arbuscular mycorrhizal root colonization in *Tropoleum majus* and *Carica papaya* after jasmonic acid application cannot be attributed to increased glucosinolate levels. *J Plant Phys.* 159:517Y523.
- LYDON, J., TEASDALE, J. R., and CHEN, P. K. 1997. Allelopathic activity of annual wormwood (*Artemisia annua*) and the role of artemisinin. *Weed Sci.* 45:807Y811.
- MACÍAS, F. A., OLIVEROS-BASTIDAS, A., MARÍN, D., CASTELLANO, D., SIMONET, A. M., and MOLINILLO, J. M. G. 2004. Degradation studies on benzoxazinoids. Soil degradation dynamics of 2,4-dihydroxy-7-methoxy-(2H)-1,4-benzoxazin-3(4H)-one (DIM-BOA) and its degradation products, phytotoxic allelochemicals from Gramineae. *J. Agric. Food Chem.* 52:6402Y6413.
- MALINOWSKI, D. P., BELESKY, D. P., and FEDDERS, J. M. 1999. Endophyte infection may affect the competitive ability of tall fescue grown with red clover. *J. Agron. Crop. Sci.* 183:91Y101.
- MALLIK, M. A. B. and TESFAI, K. 1988. Allelopathic effect of common weeds on soybean growth and soybean-*Bradyrhizobium* symbiosis. *Plant Soil* 112:177Y182.
- MARLER, M. J., ZABINSKI, C. A., and CALLAWAY, R. M. 1999. Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. *Ecology* 80:1180Y1186.
- MEIER, C. L. and BOWMAN, W. D. 2008. Phenolic-rich leaf carbon fractions differentially influence microbial respiration and plant growth. *Oecologia* 158:95Y107.
- MIRANDA, M. I., OMACINI, M., and CHANETON, E. J. 2011. Environmental context of endophyte symbiosis: Interacting effects of water stress and insect herbivory. *Int. J. Plant Sci.* 172:499Y508.
- MUMMEY, D. L. and RILLIG, M. C. 2006. The invasive plant species *Centaurea maculosa* alters arbuscular mycorrhizal fungal communities in the field. *Plant Soil* 288:81Y90.
- NASIR, H., IQBAL, Z., HIRIDATE, S., and FUJII, Y. 2005. Allelopathic potential of *Robinia pseudo-acacia* L. *J. Chem. Ecol.* 31:2179Y2192.
- NIEMEYER, H. M. 1988. Hydroxamic acids (4-hydroxy-1,4-benzoxazin-3-ones), defence chemicals in the gramineae. *Phytochemistry* 27:3349Y3358.
- NILSSON, M.-C., HÖGBERG, P., ZACKRISSON, O., and FENGYOU, W. 1993. Allelopathic effects by *Empetrum hermaphroditum* on development and nitrogen uptake by roots and mycorrhizae of *Pinus silvestris*. *Can. J. Bot.* 71:620Y628.
- OKUMURA, M., FILONOW, A. B., and WALLER, G. R. 1999. Use of 14 C-labeled alfalfa saponins for monitoring their fate in soil. *J. Chem. Ecol.* 25:257Y–2583Y.
- OWNLEY, B. H., GWINN, K. D., and VEGA, F. E. 2010. Endophytic fungal entomopathogens with activity against plant pathogens: ecology and evolution. *BioControl* 55:113Y128.
- POLLOCK, J. L., KOGAN, L. A., THORPE, A. S., and HOLBEN, W. E. 2011. (±) Catechin, a root exudate of the invasive *Centaurea stoebe* Lam (Spotted Knapweed) exhibits bacteriostatic activity against multiple soil bacterial populations. *J. Chem. Ecol.* 37:1044Y1053.
- PRATI, D. and BOSSDORF, O. 2004. Allelopathic inhibition of germination by *Alliaria petiolata* (Brassicaceae). *Am. J. Bot.* 91:285Y288.
- PUE, K. J., BLUM, U., GERIG, T. M., and SHAFER, S. R. 1995. Mechanism by which noninhibitory concentrations of glucose increase inhibitory activity of *p*-coumaric acid on morning-glory seedling biomass accumulation. *J. Chem. Ecol.* 21:833Y847.
- REIGOSA, M. J., PEDROL, N., and GONZALEZ, L. 2006. Allelopathy: a physiological process with ecological implications. Springer. 637p.

- REINHARDT, K. O. and CALLAWAY, R. M. 2006. Soil biota and plant invasions. *New Phyt.* 170:445Y457.
- ROBERTS, K. J. and ANDERSON, R. L. 2001. Effect of garlic mustard [*Alliaria petiolata* (Bieb. Cavara & Grande)] extracts on plants and arbuscular mycorrhizal (AM) fungi. *Am. Midl. Nat.* 146:146Y152.
- ROCHA, A. C. S., GARCIA, D., UETANABARO, A. P. T., CARNEIRO, R. T. O., ARAUJO, I. S., MATTOS, C. R. R., and GOES-NETO, A. 2011. Foliar endophytic fungi from *Hevea brasiliensis* and their antagonism on *Microcyclus ulei*. *Fungal Div.* 47:75Y84.
- ROMEO, J. T. 2000. Raising the beam: moving beyond phytotoxicity. *J. Chem. Ecol.* 26:2011Y2014.
- RUDGERS, J. A. and ORR, S. 2009. Non-native grass alters growth of native tree species via leaf and soil microbes. *J. Ecol.* 97:247Y255.
- SABZALIAN, M. R. and MIRLOHI, A. 2010. *Neotyphodium* endophytes trigger salt resistance in tall and meadow fescues. *J. Plant Nutr. Soil Sci.* 173:952Y957.
- SASIKUMAR, K., VIJAYALAKSHMI, C., and PARTHIBAN, K. T. 2001. Allelopathic effects of four *Eucalyptus* species on Redgram (*Cajanus cajan* L.). *J. Trop. Agric.* 39:134Y138.
- SHREINER, R. P. and KOIDE, R. T. 1993. Mustards, mustard oils and mycorrhizas. *New Phyt.* 123:107Y113.
- SMALL, C. J., WHITE, D. C., and HARGBOL, B. 2010. Allelopathic influences of the invasive *Ailanthus altissima* on a native and a non-native herb. *J. Torrey. Bot. Soc.* 137:366Y372.
- SMITH, S. E. and READ, D. J. 2008. Mycorrhizal Symbiosis. Elsevier Science Ltd, London.
- STINSON, K. A., CAMPBELL, S. A., POWELL, J. R., WOLFE, B. E., CALLAWAY, R. M., THELEN, G. C., HALLET, S. G., PRATI, D., and KLIRONOMOS, J. N. 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *PLoS Biol.* 4:727Y731.
- TIMBAL, J., GELPE, J., and GARBAYE, J. 1990. Preliminary-study of the depressive effect of *Molinia caerulea* (L) Moench on early growth and mycorrhizal status of *Quercus rubra* seedlings. *Ann. Sci. Forest.* 47:643Y649.
- UNDERSTRUP, A. G., RAVNSKOV, S., HANSEN, H. C. B., and FOMSGAARD, I. S. 2005. Biotransformation of 2-benzoxazolinone to 2-amino-(3H)-phenoxazin-3-one and 2-acetylamino-(3H)-phenoxazin-3-one in soil. *J. Chem. Ecol.* 31:1205Y1222.
- VÁSQUEZ-DE-ALDANA, B. R., ROMO, M., GARCÍA-CIUDAD, A., PETISCO, C., and GARCÍA-CRIADO, B. 2011. Infection with fungal endophyte *Epichloë festucae* may alter the allelopathic potential of red fescue. *Ann. Appl. Biol.* 159:28Y–290Y.
- VAUGHN, S. F. and BERHOW, M. A. 1999. Allelochemicals isolated from tissues of the invasive weed garlic mustard (*Alliaria petiolata*). *J. Chem. Ecol.* 25:2495Y2504.
- VIERHEILIG, H., BENNETT, R., KIDDLE, G., KALDORF, M., and LUDWIG-MULLER 2000. Differences in glucosinolate patterns and arbuscular mycorrhizal status of glucosinolate-containing plant species. *New Phytol.* 146:343Y352.
- VOLL, E., FRANCHINI, J. C., DA CRUZ, R. T., GAZZIERO, D. L. P., BRIGHENTI, A. M., and ADEGAS, F. S. 2004. Chemical interaction of *Brachiaria plantaginea* with *Commelina bengalensis* and *Acanthospermum hispidum* in soybean cropping systems. *J. Chem. Ecol.* 30:1467Y1475.
- WALKER, A. and WELCH, S. J. 1991. Enhanced degradation of some soil-applied herbicides. *Weed Res.* 31:49Y57.
- WEIDENHAMER, J. D. and ROMEO, J. T. 2004. Allelochemicals of *Polygonella myriophylla*: chemistry and soil degradation. *J. Chem. Ecol.* 30:1067Y1082.
- WEIDENHAMER, J. D. and CALLAWAY, R. M. 2010. Direct and indirect effects on soil chemistry and ecosystem function. *J. Chem. Ecol.* 36:59Y69.
- WILLIS, R. J. 2007. The history of allelopathy. Springer, 316 p.
- WOLFE, B. E., RODGERS, V. L., STINSON, K. A., and PRINGLE, A. 2008. The invasive plant *Alliaria petiolata* (garlic mustard) inhibits ectomycorrhizal fungi in its introduced range. *J. Ecol.* 96:777Y783.
- YUE, Q., BACON, C. W., and RICHARDSON, M. D. 1998. Biotransformation of 2-benzoxazolinone and 6-methoxy-benzoxazolinone by *Fusarium moniliforme*. *Phytochemistry* 48:451Y454.
- ZABINSKI, C. A., QUINN, L., and CALLAWAY, R. M. 2002. Phosphorous uptake, not carbon transfer, explains arbuscular mycorrhizal enhancement of *Centaurea maculosa* in the presence of native grassland species. *Funct. Ecol.* 16:758Y765.
- ZHANG, Q. 1997. Effects of soil extracts from repeated plantation woodland of Chinese-fir on microbial activities and soil nitrogen mineralization dynamics. *Plant Soil* 191:205Y212.
- ZHANG, Z.-Y., L.-P. PAN, and H.-H. LI. 2010. Isolation, identification, and characterization of soil microbes which degrade phenolic compounds. *Journal of Applied Microbiology*, 108:1839-1849.
- ZHU, X., ZHANG, J., and MA, K. 2011. Soil biota reduce allelopathic effects of the invasive *Eupatorium adenophorum*. *PLoS One* 6: e25393.