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Plant allelochemical interference or soil chemical ecology?

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Abstract

While allelopathy has been defined as plant-plant chemical interference, there has been much confusion about what the concept encompasses and how important it is in nature. We distinguish between (1) direct plant-plant interference mediated by allelochemicals, and (2) the effects of secondary compounds released by plants on abiotic and biotic soil processes that affect other plants.

It very difficult to demonstrate direct effects of chemicals released by a plant on nearby plants. Although soil ecology-mediated effects of secondary plant compounds do not fit the classical concept of allelopathy, we find support in the literature for the hypothesis that the most important effects of compounds released into the soil environment by plants on other plants occur through such indirect effects. The emphasis on, and skepticism of, direct plant-plant allelopathic interference has led some researchers to demand unreasonably high standards of evidence for establishing even the existence of allelopathic interactions, standards that are not demanded for other plant-plant interactions such as resource competition. While the complete elucidation of the mechanisms by which allelochemicals function in the field is many years away, such elucidation is not necessary to establish the existence of allelopathic interactions.

We propose that most of the phenomena broadly referred to as allelopathic interference are better conceptualized and investigated in terms of soil chemical ecology. Even when direct plant-plant allelochemical interference occur, the levels of allelochemicals in the environment and their effects on plants are heavily influenced by abiotic and biotic components of the soil ecosystem. Putting allelopathy in the context of soil ecology can further research and reduce some of the less fruitful controversy surrounding the phenomenon.

Key words: allelochemical, allelopathy, chemical ecology, secondary compounds, soil ecology

Introduction

Allelopathy has been defined as all effects of plants on neighboring plants though the release of chemical compounds into the environment (Rice 1984). Such a definition has been criticized for being so broad that almost all interactions among plants can be included, and that it therefore does not have much meaning (Watkinson 1998). Allelopathy has also been defined more narrowly as “suppression of growth of one plant species by another due to the release of toxic substances" (Lambers *et al.* 1998), thus limiting the term only to "inhibitory" effects of compounds "directly" contributed by one plant to another. Many studies on allelopathy focus on the release of chemicals from the donor plant, identification of potential allelochemicals, and description of patterns of plant growth that are attributed to these allelochemicals. But allelochemical effects in the field could be due to (i) direct harmful effects of chemicals released from donor plants, (ii) degraded or transformed products of released chemicals, (iii) effect of released chemicals on physical, chemical and biological soil factors, and (iv) induction of release of biologically active chemicals by a third species (Box 1). It is not currently possible to distinguish among these four possibilities. Model (i) above (Box 1, I.) represents the original concept of allelopathy, exemplified by the work on *Juglans* litter early in the last century (Massey 1925; Davis 1928), and this model still lies behind most, but by no means all, studies on allelopathy.

We propose here that the behavior of vegetation can be better understood in terms of allelochemical interactions with soil ecological processes rather than the classical concept of direct plant-plant allelopathic interference. Our goal is to help put allelopathy in its ecological context, not to focus on the definition of the word "allelopathy".

Broadening the concept of allelochemical interference

In many natural communities it is likely that, in addition to resource competition among plants, chemicals released by plants influence community structure and vegetation dynamics. Plants cannot be completely separated from their substrate. There is a complex set of interactions between plant growth, and abiotic and biotic environmental factors (Einhellig 1999). Secondary compounds released by plants may influence resource competition, nutrient dynamics, microbial ecology, mycorrhizae and even soil abiotic factors (Wardle *et al.* 1998). Resource competition and allelopathy operate simultaneously and/or sequentially, influencing each other while influencing community structure (Darrah 1993; Inderjit & Del Moral 1997). Examples include the influence of root architecture and length on acquisition of phosphorus, root hairs and mycorrhizae, cheletion of inorganic ions, soil pH and microbial production of enzymes that influence phosphorus mineralization. Until recently, research has focused on direct plant-plant chemical interference (Box 1, I.), but now researchers have started to appreciate the ecological importance of allelochemicals on ecosystem-level processes (Wardle *et al.* 1998). We argue that the available evidence suggests that the indirect effects of allelochemicals may be more important for plant

Box 1. Classification of potential allelopathic effects, broadly defined.

I. Direct plant-plant allelopathic interference (allelopathy in the narrow sense)
Plant A produces Compound X, which interferes with Plant B

II. Indirect soil ecological interactions (indirect allelopathic effects)

A. Indirect allelopathy

1. Decomposition-mediated plant-plant allelopathy
Plant A produces Compound X which is degraded or otherwise transformed by Microorganism C into Compound Y, which interferes with Plant B

2. Induced allelopathy
Plant A produces Compound X which is released and induces Organism D to produce Compound Z which interferes with Plant B

B. Indirect toxicity
Compound X interacts with soil ecosystem and causes generation of Compound Z (which is not a breakdown product of Compound X), which interferes with Plant B

C. Indirect environmental effects
Compound X causes a change in the soil environment, which affects the nutrient status of the soil, thus reducing the growth, survival or reproductive output of Plant B, without toxic effects

communities than the direct effects of allelochemicals released by plants on other plants.

Allelochemicals may influence numerous ecosystem processes (Wardle *et al.* 1998), and even potential direct effects of allelopathic chemical on nearby plants will be modified by abiotic and biotic factors. The emphasis on the search for direct plant-plant allelopathic interactions and the difficulties in establishing such interactions has lead critics to question whether allelopathy has even been demonstrated. We think this narrow conceptual framework has retarded progress in research in allelopathy. Below we review some of the evidence for indirect effects of allelochemicals on plant growth and plant communities.

Allelochemicals and abiotic components of the soil

Chemicals released by plants can influence abiotic components of the ecosystem, such as the availability and accumulation of inorganic ions, and the activities of allelochemicals are influenced by ecological factors such as nutrient limitation, light regime and moisture deficiency (Inderjit & Del Moral 1997; Einhellig 1996). *Lupinus albus* develops clusters of rootlets called proteoid roots in response to phosphorus-poor conditions. Proteoid roots of *L. albus* excrete citrate, and the soil around proteoid roots has significantly higher levels of citrate compared to bulk soil. This lowers soil pH and mobilizes soluble phosphate and influences the solubility of Fe and Mn (Johnson *et al.* 1994; Dinkelaker *et al.* 1989, 1995).

Under iron and zinc deficient conditions, some graminaceous plants release compounds called phytosidophores, which play an important role in solubilizing metal ions, particularly iron (Römheld 1991). Phenolics, for example, form complexes with nutrient ions (Appel 1993; Inderjit 1996). By competing for anion absorption sites and binding with soluble Al, Fe and Mn, which bind to phosphate, phenolics may increase P-availability (Tan & Binger 1986; Kafkafi *et al.* 1988). In a laboratory study, phenolic acids, *p*-coumaric, ferulic, *p*-hydroxybenzoic, and protocatechuic acids influenced the accumulation of soil organic N and inorganic ions such as Al, Fe, Mn, and PO_4 (Inderjit & Mallik 1997). Protocatechuic acid has been reported to form complexes with Fe and Al, which increase their solubility (Shindo & Kuwatsuka 1977; Vance *et al.* 1986). Two anthraquinones, emodin and physcion, isolated from roots and rhizomes of *Polygonum sachalinense* and from associated soils inhibited the growth of certain plant species under controlled conditions, and allelopathy was implicated (Inoue *et al.* 1992). In laboratory studies, emodin and physcion influenced the availability of certain inorganic ions (Inderjit & Nishimura 1999). Although further studies in natural environment are needed, these studies suggest that the effect of *P. sachalinense* on other species could be directly due to two anthraquinones and/or their effect on soil inorganic ions.

Allelochemicals and soil inorganic ions

Phenolics and terpenoids may play an important role in the inhibition of nitrification (Rice 1984; White 1986, 1994) and thus influence a plant community's nutrient status. Phenolic compounds such as caffeic and ferulic acids, myricetin, tannins, and tannin derivative compounds inhibit oxidation of NH_4^+ to NO_2^- by *Nitrosomonas* (Rice 1984). Terpenoids may also play an important role in the inhibition of nitrification (White 1986, 1994). Alternatively, it has been proposed that terpenoids enhanced immobilization of ammonium-N by soil organisms rather than by inhibition of nitrification (Bremner & McCarty 1988, 1990). Rice (1984) suggested that during succession, the rate of nitrification is reduced, perhaps due to allelochemicals. Other researchers disagree, reporting an increase in nitrification during succession (Vitousek & Reiners 1975; Robertson & Vitousek 1981).

Polyphenols produced by plants have been considered to have a role in plant defense and allelopathy, but this class of chemicals has been shown to have major effects on pools and fluxes of inorganic and organic soil nutrients (Hättenschwiler & Vitousek 2000). For example, polyphenols from leaf litter of *Pinus muricata* influenced the release of dissolved organic nitrogen and mineral nitrogen in soils of northern California's pygmy forest (Northup *et al.* 1995). Soil pH is very low in these forests and polyphenols from the forest floor complex with Al, thus increasing this metal's toxicity (Northup *et al.* 1999). When added to soil, mixtures of monoterpenes, 3-carene, pinene, myrcene, phellandrene, limonene and camphene inhibit nitrification (Paavolainsen *et al.* 1998). These examples illustrate the potential effects of allelochemicals on nutrient dynamics. Any influence on nutrient dynamics may ultimately affect the growth of plants in the community, even though such a mechanism does not fit the traditional view of plant-plant allelopathy.

Phytotoxicity of phenolic acids is influenced by different factors including soil type, soil pH, mineral nutrition, and by other C-sources present in the substrate (Blum 1998). Environmental factors such as temperature and light levels may alter the allelopathic potential of residues of the weeds *Amaranthus retroflexus* and *Setaria glauca* on *Zea mays* (Bhowmik & Doll 1983). Residues of these weeds were more inhibitory when maize was grown under low temperature and low PPFD conditions. The perennial shrub *Ceratiola ericoides* produces an inactive dihydrochalcone ceratiolin (Fischer *et al.* 1994). Under certain light, heat, and pH conditions, ceratiolin undergoes transformation, producing the toxic compound hydrocinnamic acid (Tanrisever *et al.* 1987). Hydrocinnamic acid further undergoes microbial degradation to form acetophenone (Fischer *et al.* 1994). Both hydrocinnamic acid and acetophenone are reported to inhibit the germination and growth of the grass *Schizachyrium scoparium*. Thus, *C. ericoides* does not produce an active allelochemical that affects the grass, but abiotic and biotic factors transform an inactive compound (ceratiolin) into active allelochemicals (hydrocinnamic acid and acetophenone), which affect community structure. Total phenolic content in the submerged macrophyte *Myriophyllum spicatum* decreased under low light conditions, while the amount of tellimagrandin II was not influenced by the light regime (Gross 1999). Climatic factors (temperature, light, humidity), animals (herbivory), edaphic factors (mineral deficiencies in soil) and resource competition may induce qualitative and quantitative variation in flavinoids (Chaves & Escudero 1999). The amount of flavinoid synthesis in *Cistus ladanifer* is influenced by ultraviolet light and water stress and temperature (Chaves & Escudero 1999). There were high levels of apigenin and kaempferol during the dry summer and the level of apigenin-4’-(O)methylin exudates of *C. ladanifer* decreased with rainfall during months of June to September. Climatic factors may play a significant role in accumulating allelochemicals or their breakdown products to bioactive levels.

Nutrient levels and allelopathic effects

Nutrient-poor conditions may enhance the production of allelochemicals and thus influence allelochemical interference (Rice 1984; Einhellig 1996). Inhibitory effects of *Solidago canadensis* on *Acer saccharum* were reduced after addition of phosphorus (Fisher *et al.* 1978). Similarly, the total phenolic acid content of *Helianthus annuus* increased with increased nutrient stress (Hall *et al.* 1982). Growth suppression of *Schizachyrium scoparium* by hydrocinnamic acid was greater under low nitrogen and phosphorus conditions (Williamson *et al.* 1992). In many cases, addition of fertilizers is reported to eliminate allelochemical inhibition. Low nutrient conditions influence the production of allelochemicals by *Myriophyllum spicatum* through several mechanisms (Gross 1999). Nitrogen-limited non-axenic shoots of *M. spicatum* had high amounts of total phenolics and tellimagrandin II compared to milfoil grown in N-rich culture medium (Gross *et al.* 1996; Gross 1999). These and several other studies (see Inderjit & Del Moral 1997) suggest that soil nutrients have significant influence in the expression of allelochemical interference. This means that levels of nutrients play a role in expression of allelopathy, and that the levels of allelopathic compounds do not affect growth in a simple “dose-response” fashion. Habitat factors have major effects on phytotoxicity.

Effects of plant litter

Soil-plant debris bioassays are often employed to demonstrate phytotoxicity and allelopathy (Rice 1995; Blum 1999), and there are many reports of inhibitory effects of secondary compounds released by plant debris or litter. The addition of plant debris or litter to soil may influence nutrient mobilization and soil pH, which can further influence nutrient immobilization and microbial activity (Facelli & Pickett 1991; Aarino & Martikainen 1994). These changes may account for many observed effects. As Facelli & Pickett (1991) point out, “Even if phytotoxic effects where demonstrated beyond doubt in the laboratory or greenhouse, it is still possible that other factors, including other effects of litter, may override the phytotoxicity in the field.” They cite the example of desert ecosystems where, in spite of high phenolic content, litter promotes germination, and the influence of phytotoxins is diluted by improved water conditions. In their investigation of factors regulating germination of *Nicotiana attenuata*, Preston & Baldwin (1999) argued that there are simpler and more logical interpretations than allelopathy to explain germination inhibition due to litter. They proposed that *N. attenuata*'s germination niche is largely determined by stimulatory effects of smoke-driven signals on the dormant seeds and inhibitory effects of unburned litter.

In addition to adding organic molecules, plant litter may alter soil chemistry in other ways. Inderjit & Dakshini (1994) amended four different soils (sandy loam, sand, clay and silty-loam) with different amounts of leaf debris of *Pluchea lanceolata*. In addition to higher phenolic content, amended soil (sandy loam) also had significantly lower pH, and higher electrical conductivity and more inorganic ions than unamended soil. It was observed that amended soils, in general, inhibited the seedling growth of mustard and tomato. However, the observed inhibition may not be due to higher phenolic content, but other changes in soil chemistry.

In many studies, changes in soil properties after addition of plant litter or debris are not considered. Addition of *Kalmia angustifolia* leaf litter to mineral soils resulted in higher levels of Fe, Mn, Al and PO_4 as well as higher total phenolic content (Inderjit & Mallik 1996). Thus, *K. angustifolia* has potential to alter nutrient status, which might effect regeneration of black spruce seedlings, although the possibility of direct plant-plant allelopathy was not ruled out. Soils from *Picea mariana* forest with *K. angustifolia* had higher levels of Ca, higher pH and lower levels of organic matter, organic N, Mg, Fe, Mn and total phenolics in the B horizon than soils without *K. angustifolia* (Inderjit & Mallik 1999). The data suggest that higher microbial activity and altered soil chemistry are due to phenolics from *K. angustifolia*. Synergistic interactions among several ecological factors appear to explain *K. angustifolia* effects on black spruce better than allelopathy alone (Inderjit & Mallik, in press).

Secondary compounds released into the environment by a plant may not have direct effects on community structure but there may be effects through their influence on abiotic soil factors. Furthermore, abiotic aspects of the substrate may influence the type and quantity of chemicals found, influencing their inhibitory effects on nearby plants. Because chemicals leached by the plant do not directly cause growth inhibition, inhibition due to synergistic interaction of allelochemicals and soil factors is not considered as allelopathic inhibition by some researchers.

Allelochemicals and biotic components of the soil

Chemicals released by plants may influence microbial ecology through their effects on soil microbes and plant pathogens (Einhellig 1996). Many phenolic acids have potential to influence microbial population and cause a shift in the microbial community. Population densities of soil-borne microorganisms are affected by the soil enrichment with phenolic acids, ferulic, *p*-coumaric, *p*-hydroxybenzoic and vanillic acids (Blum & Shafer 1988). The effect, however, was dependent on soil, phenolic acid, and concentrations of phenolic acid and inorganic ion content of soil.

It has been proposed that microbial populations around the shrub *Adenostoma fasciculatum* produce toxins that inhibit the growth of nearby herb species (Kaminsky 1981). Connell (1990) suggested this inhibition could be an indirect interaction via shared enemies, which results in apparent competition between *A. fasciculatum* and nearby herb species, and he argued that allelopathy has not been demonstrated among plants in nature. If we define allelopathy as direct chemical plant-plant interference (Box 1, I.), it is extremely difficult to separate this from effects of allelochemicals on soil ecology. The presence of allelochemicals in a plant and its rhizosphere is not strong evidence for direct plant-plant allelopathy, because the observed growth patterns may be due to the influence of these compounds on soil ecological processes rather than direct effects on the target plants.

Allelochemicals and microorganisms

Secondary plant compounds produced by *Asparagus officinalis* appear to influence *Fusarium* spp., and *A. officinalis*'s susceptibility to *Fusarium* crown rot (Hartung & Stephens 1983). There was a positive correlation between effects of *A. officinalis* residue on the next asparagus crop and the degree of *Fusarium* infection. It was concluded that retarded growth of the following asparagus crop was due to chemicals from asparagus and from *Fusarium* infection. Compounds released by plants may influence structure and dynamics of forest ecosystems through their effects on mycorrhizae (Perry & Choquette 1987). Experiments using aqueous extracts suggest that an observed inhibition of *Pinus silvestris* growth by *Empetrum hermaphroditum* may be due to allelochemical effects on mycorrhizae (Nilsson *et al.* 1993).

There is also evidence of allelopathic suppression of mycorrhizae by actinomycetes (Friedman *et al.* 1989). Addition of a fresh shoot of the aromatic shrub *Coridothymus capitatus* into soil resulted in an increase of population of actinomycetes (Katz *et al.* 1987). Allelopathic suppression of annual species by aromatic shrubs could be due to synergistic interaction of essential oils produced by aromatic shrubs and higher densities of soil borne bacteria (Barazani & Friedman 1999).

Microbial degradation of plant phenolics in soil has been researched extensively (Blum & Dalton 1985; Blum & Shafer 1988; Inderjit *et al.* 1999). There is a debate about the allelopathic significance of organic compounds that are prone to microbial degradation. Addition of plant debris may result in enhanced microbial activity, which causes a temporary depletion of nitrogen (Harper 1977; Allison & Killham 1988). The resulting nutrient shortage, rather than effects of organic compounds, may be responsible for an observed inhibition of growth. Heterotrophic microbes often live in C-limited conditions and their populations increase significantly when additional carbon is supplied, and it has been argued that microbes compete with plants for available nutrients under such conditions (Schmidt & Ley 1999). On the other hand, microbial activity may prevent allelochemicals from building up to phytotoxic levels in natural soils (Schmidt & Ley 1999). Reversible adsorption of phenolic acids onto soil particles may protect them from microbial oxidation (Dalton 1989). This hypothesis was not supported by a recent study with ferulic acid, vanillic acid, and *p*-coumaric acid in different combinations (Blum 1998). Adsorption of ferulic and *p*-coumaric acids on soil particles did not provide protection from microbial degradation. The amount of individual phenolic acid needed for biological activity may decrease as the number of phenolic acids added to soil increases (Blum 1996). Root exudates or aerial leachates from a donor plant contain a myriad of organic compounds. It may be possible that low concentrations of individual compounds left after adsorption and microbial degradation may generate phytotoxic effects for a period of time. Many cinnamic acids (e.g. ferulic and *p*-coumaric acids) may undergo microbial degradation to produce benzoic acids (e.g. vanillic and *p*-hydroxybenzoic acids). Soil ecological processes cause quantitative and qualitative variation in chemicals present in the soil environment. Much more research is needed before we can understand the complex interaction of soil microbial ecology and allelochemical phytotoxicity.

Observed patterns of plant growth due to microbe-mediated allelochemical production or release may sometimes be attributed incorrectly to direct plant-plant allelopathy. It is very difficult to eliminate the influence of microbes on allelochemicals and to demonstrate a direct influence of chemicals leached by a donor plant on nearby individuals and populations.

Validity of protocols for the establishment of allelopathic interference

Some researchers have argued that allelopathy cannot be invoked unless the movement of chemicals from donor to target plant, their uptake and accumulation in bioactive concentration by target plant, and growth inhibition of target plant, are demonstrated (Harper 1977; Willis 1985). Willis (1985) advanced six protocols required to demonstrate allelopathy, based on "Koch's postulates" (Williamson 1990) for demonstrating that a disease is caused by an infectious agent:

1. a pattern of inhibition of one species or plant by another must be shown;
2. the putative aggressor plant must produce a toxin;
3. there must be a mode of toxin release from the plant into the environment;
4. there must be toxin transport and/or accumulation in the environment;
5. the afflicted plant must have some means of toxin uptake;
6. the observed pattern of inhibition cannot be explained solely by physical factors or other biotic factors, especially competition and herbivory.

It extremely difficult or impossible to follow these protocols in the field, and critics of such protocols have pointed out that we do not require such a high level of evidence to invoke resource competition, which is usually considered to be the alternative mechanism to allelopathy (Williamson 1990). The stringent protocols recommended by Harper (1977) and Willis (1985) are firmly based in the traditional concept of direct plant-plant allelopathy that we are arguing has been overemphasized. Physical factors or other biotic interactions may have primacy as explanations in cases where explanations are simpler than those invoking allelochemical interactions, but there are clearly cases in which an allelopathic hypothesis may be simpler than alternative explanations based on resources or other biotic factors. A classical example would be the role of the grasses such as *Aristida oligantha* and *Sorghum halepense* in retarding old-field succession in Oklahoma (Rice 1984). The observed succession sequence, in which community biomass is decreased when *Aristida* is dominant and later successional stages are delayed, suggest that resource competition was not driving this specific sequence in succession. Chemical effects of *Aristida* provide the most reasonable and parsimonious explanation for this species's domination and the retardation of "normal" succession. Rice's hypothesis that allelochemicals from *Aristida* influence vegetation dynamics though their effects on nitrification is an example of the type of mechanism that we are suggesting may be much more typical than the traditional hypothesis of direct plant-plant allelopathy. Similarly, allelopathic effects, broadly defined, are the only reasonable explanations for the many effects of the invasive species *Carduus nutans* in New Zealand pastures and *Empetrum hermaphroditum* in European boreal forests (Wardle *et al.* 1998).

We suggest that the effect of smoking on cancer would be a better medical analogy for allelopathy than that of infectious disease and Koch's postulates. Using arguments based on Koch's postulates, tobacco corporations argued for many years that, despite strong epidemiological evidence, one could not conclude that smoking contributed to lung cancer until the actual mechanism by which smoking increases the probability of cancer has been elucidated. Such an argument is based upon a misunderstanding of the scientific method. There are numerous cases in which allelopathic interactions represent the simplest and most reasonable explanation for phenomena observed in the field, even though we have a long way to go before we can elucidate the specific mechanisms involved. While the tobacco industry's resistance to the hypothesis that smoking contributes to cancer was clearly based on their economic interests, we suggest that the resistance of some plant ecologist to accepting the role of allelopathy is based on their hope that plant-plant interactions will ultimately be reducible to simple, resource-based processes. While we do not wish to challenge the importance of, and in many cases, the primacy of resource competition, evidence is accumulating that chemically-mediated processes are also important, and they can be among the driving forces in some ecosystems.

Many, but not all, of the indirect allelochemical effects that we are emphasizing will occur over a longer time scale than resource competition. The emphasis on direct plant-plant allelopathy has arisen, in part, because allelopathy has been seen as an alternative to resource competition in explaining plant-plant interactions. Both resource competition and allelopathy have been considered as alternative forms of "interference" (Harper 1977) or competition in the broad sense. We are suggesting that the attempts to directly compare resource competition and allelochemical interference have not been helpful, and that soil chemical ecology and its influence on plant growth offer a more promising context for investigating the role and mechanisms of chemically-mediated plant-plant interactions in the field than the narrower context of short-term plant interference or competition.

Conclusions

Chemicals released by plants often play an important role in influencing ecological processes in many plant communities through their effects on soil ecology, such as mycorrhizae, disease, herbivory and nutrient dynamics (Wardle *et al.* 1998). Direct effects of allelochemicals produced by plants on their neighbors may also exist, but such direct effects appear be much less important than the indirect effects mediated by soil ecology. Research on the influence of allelochemicals on different components of the soil ecosystem and their role in shaping community structure and composition is needed (e.g. Hättenschwiler & Vitousek 2000). Research in allelopathy, and criticisms of it, have been hampered by a very narrow view of allelopathic interactions, as demonstrated by protocols based on the model of infectious disease. While the ultimate goal of all scientific research is the complete elucidation of mechanisms, hypotheses concerning general classes of mechanisms can be important steps along the way. It is almost impossible to demonstrate that allelopathy is solely responsible for an observed pattern in the field, but is sometimes possible to demonstrate that allelopathy is the most likely explanation for the observed pattern. Skepticism is essential to scientific progress, but hypotheses based on allelopathy should not bear a higher burden of skepticism than other hypotheses.

We propose that progress in the study of allelopathy will be furthered if allelopathy is seen and investigated in the context of soil ecology, especially soil chemical ecology, rather than emphasizing the search for direct plant-plant chemical interactions.

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