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Role of allelopathy in plant invasion and control of invasive plants

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ABSTRACT

Allelopathy plays important role in many aspects of plants invasion (plant invasiveness, resistance to invasive plants of native community and control of invasive plants). There is urgent need to understand the integrative role of allelopathy in plant invasion, resistance of native community and management/ control of invasive plants. This review summarizes the role of allelopathy in plant invasion: (i). Facilitating the exotic plant invasion as indicated by "Novel Weapon" hypothesis, (ii). Used by native plants as weapon against invasive plants, (iii). Its potential to control exotic plant invasion by regulating the native species allelopathic effects on invasive species. It is crucial for the ecological restoration of invaded communities, to understand how the allelopathic effects of invasive and native plants counteract and which allelochemicals produced by natives are effective against invasive plants. We suggest that exotic plants invasion may be controlled by eliminating the allelopathic effects of invasive species or by enhancing the allelopathic effect of native species.

Key words: Adaptation, allelochemicals, allelopathy, control, invasive plants, native plants, resistance, restoration.

1. INTRODUCTION

Invasion ecology has grown enormously in past 50 years and become an important multi-disciplinary subfield of ecology, since the publication of Charles Elton's book *The Ecology of Invasions by Animals and Plants* in 1958 (72). It addresses all aspects of invasion, including the introduction of organisms, establishment of introduced organisms, naturalization

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and invasion in the introduced region, the interactions between introduced and resident native organisms in their new range and the potential costs and benefits of invasion with reference to human value systems (9). Allelopathy plays important roles in many aspects of plant invasion. Hence, there is urgent need to understand the integrative role of allelopathy in plant invasion (invasiveness of exotic plants, the resistance of native community to invasive plants and control/management of invasive plants using allelochemicals). These aspects are shown in Fig. 1. Exotic plant invasion may be controlled by eliminating the allelopathic effects of invasive species or enhancing the allelopathic effect of native species.

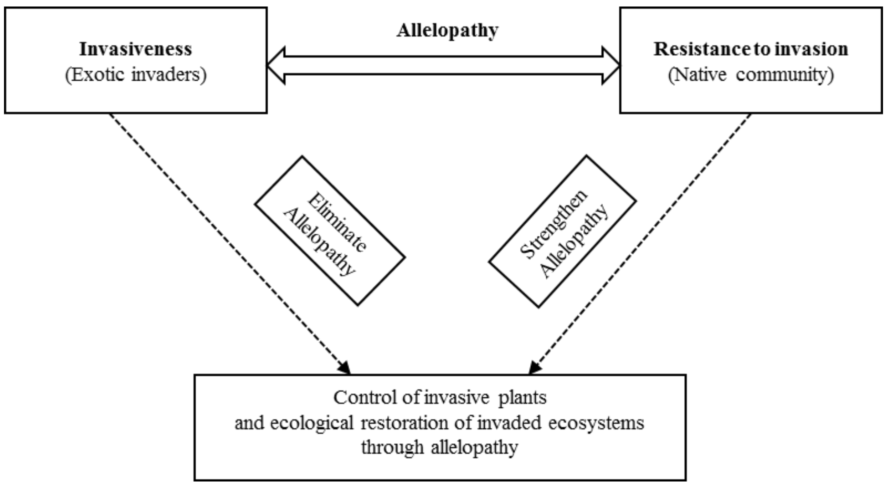

Figure 1. Role of allelopathy in invasiveness of exotic invasive plants, in resistance of native communities and in controlling the invasive plants and restoring the invaded ecosystems. The dash line indicates our efforts to control invasive plants through allelopathy.

2. ALLELOPATHY AND PLANT INVASIVENESS

Allelopathy has been considered as 'novel weapon' for the successful invasion of some exotic plants (16). Strong allelopathic effects on native plants are frequently observed, when the plants in the introduced range did not co-evolve with the invader. These plants are more susceptible to the allelopathic substances released from the exotic invaders than those from their native neighbours (4,35,73). There are many theories of invasion e.g. 'Enemies release hypothesis', the 'Niche empty hypothesis' etc. (36), allelopathy is considered as an important explanation of successful invasions through non-resource interactions among plants (12). The 'novel weapons' has been studied extensively and it contributes to the success of several destructive plant invaders, such as *centaurea diffusa* L. (13,15,29,34,65,80), *Mikania micrantha* H.B.K. (76,89,95) and *Solidago canadensis* L. (1,10,90,93). Such exotic invasive species suppresses the native neighbours and facilitate their invasion through the release of chemical compounds into the environment (4,35,73,84).

2.1 Allelopathy and competitive ability of invasive plants

Exotic invasive plants excludes/replaces the native plant species by direct interference (competition + allelopathy) (13,27,30,48,56,61,65,83). The allelopathic effects on competitive ability of several major invasive plants is summarised below:

(i). Knapweed: In growth assays the aqueous extracts of knotweed species were inhibitory to other plant species (32,43,61), which suggested that invasive knotweeds may produce allelochemicals, that acted as novel weapons and facilitated the mono-dominance in their introduced ranges. Callaway and Aschehoug (13) found that diffuse knapweed (*Centaurea diffusa* L.) had much stronger negative effects on the species from its introduced range, North America, than on the species from its native range, Europe (13). The allelochemical, (±)-catechin, was the effective component against North American species. Spotted knapweed (*Centaurea maculosa* Lam.) and *C. diffusa*, produce chemicals (particularly (±)-catechin) inhibitory to the new neighbours as suggested by "novel weapons" hypothesis (4,13,15,17,41). Although (-)-catechin was questioned as the allelochemical responsible for the successful invasion of spotted knapweed (5,6,7), but the *in situ* test of the novel weapons hypothesis supports the notion that novel biochemical constituents of some invasive species may contribute to their success (80).

(ii). *Mikania micrantha*: *Mikania micrantha* H.B.K., a perennial vine native to tropical Central and South America, one of the 10 worst weeds in the world (95). It has allelopathic effects on the neighbouring plants (44) and it contained 79 phytochemicals (e.g. phenolics, flavonoids, alkaloids, terpenes etc.), mostly terpenes and their derivatives (63). Sesquiterpenoids extracted from *M. micrantha* significantly inhibited the seedling growth of monocot ryegrass (*Lolium multiforum*) and three tree species (*Acacia mangium*, *Eucalyptus robusta*, and *Pinus massoniana*) in south China (76). The aqueous extracts from *Mikania* leaves and roots were inhibitory to seedling growth of over 20 tree species (88) and leaf extract were more harmful than root extract (89).

(iii). Canada goldenrod (*Solidago Canadensis* L.): It has been reported to exert strong allelopathic inhibition on resident native species. Leaf extracts and root/rhizome extracts of Canada goldenrod significantly inhibited the growth of test species (10). These strong allelopathic effects of Canada goldenrod may be newly evolved in the introduced range. It is reported that the amount and effects of allelochemicals (e.g. total phenolics, total flavones and total saponins) are greater in from the individuals from invaded region, China, than those from native range, USA (93).

(iv) Garlic mustard (*Alliaria petiolata*): The role of allelopathic chemicals in garlic mustard's competitive ability is inconclusive. For instance, garlic mustard exerts inhibitory effects on other species (69). Several allelochemicals such as glycosides, phenolic acids, cyanide and glucosinolate were isolated from leaf, stem and root extracts of garlic mustard (21,22,23,82). However, the extracts from garlic mustard did not affect seeds or seedlings of some recipient species (i.e. radish, winter rye, hairy vetch and lettuce) (55). The garlic mustard inhibited the growth of Chestnut oak (*Quercus prinus*) seedlings (59) and decreased the native diversity in invaded areas (79), suggesting that garlic mustard has the potential to suppress native plant spp. through allelopathy.

2.2. Allelopathic acclimation of native plants to invasive plants

The novel weapons hypothesis argues that exotics exude allelochemicals that are relatively ineffective against their well-adapted neighbours in the original range. However, these allelochemicals are highly inhibitory to the resident plants in the introduced range (36). Individuals that have co-evolved with an allelopathic invader for a while, may be less sensitive to allelopathic compounds, while newly exposed individuals (such as those in an invaded range) may be more vulnerable (13,14,86). A few studies have focused on the acclimation to the allelopathic effects of either invasive or native species though native plant species may evolve to tolerate the allelopathic effects of an exotic invader. For instance, Callaway *et al.* (17) found that some native species grown from the population that survived *Centaurea* invasion were more resistant to the direct competition by *Centaurea* and were less vulnerable to the root exudates and (±)-catechin in root exudate of *Centaurea*, indicating that native plant species may evolve to tolerate the effects of an exotic invader, in particular an invader's novel allelopathic effect. Plant species that had not experienced *Ailanthus altissima* invasion, were more susceptible to the allelochemicals released by *Ailanthus altissima* than the species that survived *Ailanthus* invasion, suggesting that the offspring of species that were previously exposed to *Ailanthus* were better adapted to *Ailanthus*-occupied habitats (50). It has also been shown that there are intraspecific differences in the vulnerability to the allelopathic influence of *Ailanthus altissima*: populations exposed to invasion were more tolerant to *Ailanthus* toxins than previously unexposed plant population (50). Evolved tolerance or adaptation may ultimately contribute to the coexistence among natives and invaders and it is helpful to elucidate the allelopathic mechanisms.

In addition, recent studies indicate that some native species can become invasive (77) and they can cause similar harmful ecological and economic impacts to native community as some non-native invasive species. More and more phenomenon of native plant invaders was reported (68,87). Our previous study showed that there were many native invaders in the Baiyun Mountain and Xiqiao Mountain in southern China (67) and their allopathic potential facilitated the invasion of these native harmful plants. Thus, more attention should be paid to native invaders in forest management.

2.3. Allelopathic effects of invasive plants

In field conditions, allelopathic effects may be either greater or less than the results from bioassay, suggesting that allelopathic potential can be influenced by biotic and abiotic conditions. A recent study (65) showed that the allelopathic potential of knotweed was greater in artificial potting substrates than in natural soils. The reason for the phenomenon may be the high cost of production of allelochemicals, which constrains the allelopathic potential of invasive species, when environmental resources are not sufficient (24,47). Thus, soil nutrients availability can influence the impact of plant invaders both directly, through resource limitation, as well as indirectly, by altering the allelopathic potential of invaders.

In addition, the interaction between soil microbes and allelochemicals may affect the allelopathic potential of invasive plants. It has been reported that allelochemicals in soils can inhibit fungal mutualists (14,18,74,79), which would enhance the negative effects. On the contrary, allelochemicals may be degraded by bacteria much more rapidly in soils, eliminating their potential effects in field condition (75). For example, garlic mustard's impact on native understory flora may interfere with plant–AMF interactions in its invaded range (18,74). High densities of garlic mustard in the field correlate with low inoculum potential of AMF and extracts of garlic mustard leaves reduces the germination of AMF spores and impair AMF colonization of cultivated tomato roots in laboratory (18,74). Others have shown that exotic plants can recruit different suites of microbial organisms in their new ranges that can be antagonistic to native plants (16). Antifungal phytochemistry of the invasive plant, *Alliaria petiolata*, a European invader of North American forests, suppresses the native plant growth by disrupting mutualistic associations between native canopy tree seedlings and belowground arbuscular mycorrhizal fungi (79). These results show an indirect mechanism by which invasive plants can impact native flora through allelopathy.

The allelochemical effect in soil may not be directly related to its actual concentration in the soil. The allelochemical or allelochemicals will not be released from single plant species, but from many different plant species in a forest. The ecosystem-scale roles of allelopathic chemicals can augment, attenuate or modify their community-scale functions (42). Therefore, allelopathy will create an additional challenge for management of invasive plants and ecological restoration of invaded ecosystems. More research is needed to examine the mechanisms underlying allelopathy of exotic invasive plants, role of allelochemicals of different functional groups and long-term effects of allelopathy in soil residues.

3. ALLELOPATHY AND INVASIVENESS OF NATIVE PLANTS

In addition to invasiveness, invasion impact of exotic invaders also depends on the invasibility of a native community (53), which is defined as the vulnerability of a community in face of exotic invasion. Invasibility can be affected by both biotic factors (species diversity, soil biota and herbivores) and abiotic factors (light, nutrient and chemical environment) (2,51,71). In lines with "Novel Weapon" hypothesis, which suggests that invasive plants may release allelochemicals that inhibit the growth of native plants, native plants may also produce allelochemicals that can effectively inhibit the growth of invasive species. It has been reported that native residents may produce allelopathic chemicals that are novel to an introduced species and this might reduce invasibility of the community (17,20,26,38,85,97). Some studies are summarized in Table 1. For instance, *Pinus ponderosa* was reported to suppress the growth of *Centaurea stoebe*, a noxious weed in western USA (60). Weidenhamer and Romeo (85) found that perennial shrubs can prevent exotic invasions in Florida. The inhibitory effect of legume species on weeds has been widely recognized in both agroecosystems and forest ecosystems (3,11,26). Cummings *et al*. (26) reviewed the allelopathic potential of 17 tree species and reported significant variations among different species, among which legume trees were most effective in inhibiting the growth of weedy C_4 grasses. It has been demonstrated that 19 plants had a allelopathic potential effect on seedlings of the invasive plant *Mikania micrantha* H.B.K. (49). Among the 19 species, *Delonix regia* (Boj.) Raf. showed the strongest phytotoxicity and the powder made from its leaves/flowers could cause 75-90% mortality of *M. micrantha* seedlings. Moreover, 4% aqueous extract of *D. regia* sprayed on leaves of *M. micrantha*

Table 1. Studies investigating allelopathy of native plant species on exotic species

No.	Donor spp. (Native species)	Recipient spp. (Exotic species)	Effects/main results	Treatments/allelochemicals	Study location	References
1	*Pinus ponderosa*	*Centaurea stoebe*, *Bromus tectorum*	Reduced the germination of *C. stoebe* and the growth of *B. tectorum*, eliminated the competitive effect of *C. stoebe* on *B. tectorum*	Pinus litter leachate	Montana, USA	60
2	*Polygonella myriophylla*	Bahiagrass (*Paspalum notatum*)	Inhibition seed germination and seedling growth	Glycosides of hydroquinone and gallic acid	Florida, USA	85
3	17 *tree species*	*Saccharum spontaneum* L.	greater inhibitory effect on performance	leaf litter	Las Pavas, Panama	26
4	*Delonix regia*	*Mikania micrantha* H.B.K.	Reduced seedling growth and led to high mortality of seedlings	Mulching powder of leaves and flowers, aqueous extract of leaves	Taiwan, China	49
5	*Vaccinium Myrtillus* L.	*Picea abies* L. Karst, *Picea mariana* (Mill.)	Reduced seed germination and root dry weight	Leaf leachates	Savoie, France	54
6	*Macaranga tanarius* (L.)	*Lactuca sativa* L. (lettuce), *Bidens pilosa* and *Leucaena Leucocephala*	Inhibited seedling growth	Leaf powder; nymphaeol-A, nymphaeol-B, nymphaeol-C, quercetin, ABA, blumenol A, blumenol B, roseoside II, tanariflavanone A, and tanariflavanone B	Taiwan, China	81
7	*Subtropical forest communities*	*Ageratum conyzoides, Bidens pilosa, Eupatorium catarium, Ipomoea triloba, Pharbitis nil, Mikania micrantha, Ipomoea cairica, Sphagneticola trilobata*	Inhibited the germination and vegetative growth of most tested invasive plants	Abscisic acid (ABA)	Guangdong, China	52
8	A native plant community	Eight invasive and eight non-invasive introduced species: *Amaranthus retroflexus,*	Neutral or even slightly positive effects	Introduced specie growing with vs. without native community; with vs. without activated carbon	Constance, Germany	64
9	*Sambucus ebulus*	*Fallopia* x *bohemica*	Decreased the number of leaves and leaf and above- and below-ground dry masses	Donor pots with *S. ebulus*, *S. ebulus* extracts; Allelochmicals: catechin, epicatechin, four compounds (dihydroxycinnamic acid family)	Chambéon, France	20
10	*Pinus densiflora*	*Lepidium sativum* L., *Lactuca sativa* L., *Medicago sativa* L., *Lolium multiflorum* Lam, *Pheleum Pratense* L., *Digitaria sanguinalis* L. *and Echinochloa crus-galli* (L.)	Inhibited root and shoot growth of *Lepidium sativum* L. and *Echinochloa crus-galli* seedlings	Aqueous methanol extracts of red pine needles; Allelochemicals: 9a,13b-epidioxyabeit-8(14)en-18-oic acid	Takamatsu, Japan	48

seedlings also led to high mortality (49). A more recent study on *M. micrantha* also showed introduced plants, the invasive and non-invasive introduced plants did not differ in their tolerance to such allelopathic effects of the native plant community (64). This indicates that tolerance to allelopathy of native plant communities may not affect the invasiveness of introduced plants (64).

These above studies indicated that particular native species can exert allelopathic inhibition on invasive species and contribute to community resistance to invasion. However, there are few studies indicating resistance to invasion through allelopathy at community level. Mallik and Pellissier (54) compared the allelopathic suppression of a native community on invasive and native species. They found that the dominant native species, *Vaccinium myrtillus* L., exerted significantly stronger suppression on invasive species, *Picea mariana* (Mill.), than co-occurring native species, *Picea abies* L. Karst. Hou *et al*. (38) reported that the allelopathic potential on invasive weed was stronger in the soil from later successional stage than in that from earlier successional stage in forest community in Southern China. Although the role of allelopathy in community resistance has received more and more recognition, only a few allelochemicals have been determined as the contributor to invasion resistance (52,81). Tseng *et al*. (81) found that allelochemicals including nymphaeol and abscisic acid has the potential to suppress weed establishment underneath the dominant native species, *Macaranga tanarius* (L.). Similarly, Liu *et al*. (52) reported that abscisic acid can suppress the growth of most tested invasive weeds. Other types of chemicals that commonly exist in natural community, such as phenolic acids, flavonoids and tannins, have also been suggested to affect the dynamic of natural community (8,31,40). However, it is not clear whether these chemicals can contribute to community resistance to exotic invasion.

4. CONTROL OF PLANTS INVASION BY NATIVE PLANTS

As the mechanical control of invasive plants require massive manpower, chemical control is costly and may lead to environmental pollutions, hence, their biological and ecological controls have received more attention (19,25,33,46,70,78,91,92). The common approaches for biological and ecological controls of invasive plants include constructing highly resistant native species and manipulating the environmental conditions to weaken the allelopathic potential of invasive species. Native species that act as antagonistic agents to control exotic invasive species are generating increasing interest (57,66). The native species that survived invasion may present the potential for adaptive coexistence with exotic invasive plants (58), which may be the ideal ecological agent to restore invaded ecosystems. The successfulness of restoration may depend on whether the component species in the restored community can suppress the exotic weeds (37,45). Thus, criteria for species selection should include plant competitiveness, similarities in plant traits and the ability to survive and establish viable populations (91).

As reviewed in section 3, more and more studies are proposed that native species have allelopathic potential to exotic invasive species (20,92,97). Many native species produce allelochemicals that may function as the novel weapon against non-native invasive species and thus has the potential to strengthen the resistance of native community to exotic invasion. Allelopathy of native species is recognized as an important trait in selection of native species to control the invasive plants. Some studies have explored the potential use of allelopathy as a tool to control exotic plant invasion. For example, Cummings *et al*. (26) studied the applicability of allelopathy of native species in restoring the forest communities. They found that leaf litter from native leguminous trees was more inhibitory to *Saccharum spontaneum* L., an invasive C4 grass that has heavily invaded the deforested areas in the Panama Canal watershed, than did litter from non-leguminous trees (26). In southern China, some species *Heteropanax fragrans* and *Hernandia sonora* have been used in controlling the invasive species *M. micrantha* due to their allopathic effects (94).

However, studies on the issue are comparatively rare and preliminary. Few specific allelochemicals have been proposed to contribute to the invasion resistance of native species or communities. Our previous study showed that ABA accumulates in forest soil with community succession and had certain inhibitory effects on native species (96). Recently, Liu *et al*. (52) explored the allelopathic effects of ABA on eight invasive plant species in southern China, they found that ABA inhibited the germination and vegetative growth of most tested invasive plants and the inhibitory effects were dose-dependent. They found that the increased accumulation of ABA in soils with forest succession proceedings, may be the reason why the late-successional forest has stronger resistance to invasive plants. It should be noted that the long-term plant-soil interaction in forests creates the soil ABA environment which is “novel” and unsuitable for introduced species. At a community level, the allelopathic potential may vary over time since the diversity, concentration and function of allelochemicals usually change with community succession (28,62,96). In addition, apart from the effects on target invasive plants, it must be considered whether allelochemicals affect the non-target organisms. Further studies are needed to isolate and identify the allelochemicals present in native species and communities which could exert allelopathic effects on invaders. Moreover, it is meaningful to test long-term allelopathic effects of native communities on invasive plants, which is helpful to control and manage the invasive plants.

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