

Allelopathy and exotic plant invasion: from genes to communities: synopsis, updates, and implications.

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Abstract

Many exotic plant species undergo astounding increases in dominance when introduced to new communities by humans. In “Allelopathy and exotic plant invasion: from genes to communities”, we used ecological, physiological, biochemical signal transduction, and genomic approaches to develop evidence for the how allelopathy may enhance the invasive ability of *Centaurea maculosa*. In this and other work we also reported much stronger allelopathic effects in invaded than in native ranges for *C. maculosa* and *C. diffusa*, suggesting a new theory for invasive success – the novel weapons hypothesis. In other words, we think that some invaders may become much more abundant abroad because they possess novel biochemical weapons that function as unusually powerful allelopathic agents against species without evolved tolerance. Other recent work suggests that some native species may resist the allelopathic effects of *C. maculosa* via exudation of high concentrations of oxalic acid, and that some allelopathically sensitive native species may be evolving tolerance to *C. maculosa*.

Media Summary

Centaurea maculosa, one of the world’s worst invasive weeds, appears to harm native species through toxins in its root exudates. These exudates appear to be more harmful to species that have never experienced them, and perhaps that have not evolved tolerance. However, some native species appear to have undergone selection for tolerance to the toxic effects of the weed, and some native species appear to possess constitutive resistance based on their own root exudates.

Introduction

Many of the world’s most ecologically devastating exotic invaders are much more successful abroad than at home. Why many exotic plant species create virtual monocultures in invaded regions, but not in their native regions remains one of the most important mysteries in ecology. Some exotic invasions have been attributed to allelopathy (Osvald 1948, Fletcher and Renney 1963, Abdul-Wahab and Rice 1967, Bell and Koepe 1972, Kanchan and Jayachandra 1979, Alsaadawi et al. 1990, El-Ghareeb 1991, Vaughn and Berhow 1999, Ridenour and Callaway 2001, Agrawal et al. 2002, Conway et al. 2002, Hierro and Callaway 2003), and T.A. Rabotnov (1982) argued that plants could evolve over time in response to the effects of allelopathic chemicals, proposing that release from evolved biochemical interactions within plant communities may explain some invasions. He proposed that the evolution of tolerance causes “allelopathically neutral” or “allelopathically homeostatic” conditions to develop in natural communities. In other words, plants and microbes may adapt to the chemicals produced by their neighbors (much like they rapidly adapt to herbicides and other chemicals) which could minimize the effect of allelopathy in natural communities. However, this raises the possibility that some plant species may possess or release biochemicals that are novel to communities that do not naturally contain these species. If species with novel biochemical effects are introduced, they may replace native plant communities because of the harmful chemicals that the naïve native inhabitants have never experienced.

Rabotnov’s ideas were inadvertently tested by Callaway and Aschehoug (2000) who compared the competitive effects of *Centaurea diffusa*, an invasive Eurasian forb, on three bunchgrass species that co-exist with *C. diffusa* in Eurasia to the effects of *C. diffusa* on three bunchgrass species from North America. *Centaurea diffusa* had much stronger negative effects on North American species than it had on Eurasian species. Correspondingly, none of the North American grass species (nor all species analyzed collectively) had a significant competitive effect on the biomass of *C. diffusa*, but the Eurasian species *K. laerssenii*, and all Eurasian species analyzed collectively, significantly reduced *C. diffusa* biomass. *Centaurea diffusa* had

no effect on the amount of ^{32}P acquired by Eurasian grass species, but significantly reduced ^{32}P uptake of all North American species. Correspondingly, North American grasses had no competitive effects on ^{32}P uptake of *C. diffusa*, but all Eurasian species demonstrated strong negative effects on the amount of ^{32}P acquired by *C. diffusa*.

With important implications for the role of allelopathy in exotic plant invasion, activated carbon had strikingly different effects on the interactions between *C. diffusa* and the grass species from the different biogeographical regions. When growing with *C. diffusa* the overall effect of carbon on North American species was positive. In contrast, the biomass of all Eurasian grass species growing with *C. diffusa* was reduced dramatically in the presence of activated carbon. Correspondingly, activated carbon put *C. diffusa* at a disadvantage against North American grasses (*Centaurea* biomass decreased) but an advantage when with Eurasian grasses (*Centaurea* biomass increased). The ameliorating effects of activated carbon in general are evidence for allelopathy, and the strong effects of the place of origin on the competitive ability of grass species against *C. diffusa* and the contrasting effects of activated carbon, suggest that *C. diffusa* produces chemicals that long-term and familiar Eurasian neighbors have adapted to, but that *C. diffusa*'s new North American neighbors have not. Vivanco et al. (2004) identified a chemical from the root exudates of *C. diffusa*, 8-hydroxyquinoline, not previously reported as a natural product. 8-Hydroxyquinoline was at least three times more concentrated in *C. diffusa*-invaded North American soils than in this weed's native Eurasian soils and had stronger phytotoxic effects on grass species from North America than on grass species from Eurasia. Furthermore, experimental communities built from North American plant species were far more susceptible to invasion by *C. diffusa* than communities built from Eurasian species, regardless of the biogeographical origin of the soil biota.

These results suggest a new hypothesis for the astounding success of some exotic species – the Novel Weapons Hypothesis (Callaway and Ridenour 2004). This proposes that some invaders become super-abundant because they possess novel biochemical weapons that function as unusually powerful allelopathic agents or as mediators of new plant-soil microbial interactions. Like the “guns, germs and steel” of European human invasions, novel weapons possessed by some plant invaders may provide an advantage based on historical coevolutionary trajectories.

Summary

In “Allelopathy and exotic plant invasion: from genes to communities”, Bais et al. (2003) provided strong evidence for the allelopathic effects of *Centaurea maculosa*, one of the world's most destructive invaders, by integrating ecological, physiological, biochemical signal transduction, and genomic approaches. This paper followed results of previous work (Bais et al. 2001; Bais et al. 2002) suggesting that the biologically active fraction of *C. maculosa* root exudates is racemic catechin. The phytotoxicity of the exudate was then thought to be entirely due to (-)-catechin, while (+)-catechin was inactive against plants. Now we know that (+)-catechin has weak allelopathic properties.

When (\pm)-catechin was added to natural field soil, at rates comparable to those documented in the field, the germination and growth of *Festuca idahoensis* and *Koeleria micrantha*, two native North American grasses were sharply reduced. (\pm)-Catechin had stronger effects on germination, which was reduced from 32-52% to 2%, than on biomass which declined from 0.60 and 1.66 g for *Festuca* and *Koeleria* in the control, respectively, to 0.38 and 0.52 g in the (\pm)-catechin treatment. More recently, field applications of (\pm)-catechin has demonstrated strong inhibition of a number of native North American species (Thelen et al. 2005, R.M. Callaway, unpublished results).

Bais et al. (2003) also planted *Arabidopsis thaliana* seedlings in soil amended with (\pm)-catechin (200 $\mu\text{g g}^{-1}$ soil DW basis), and in pots where four-month old *C. maculosa* plants had been grown previously. In both cases, germination of *A. thaliana* seedlings was strongly reduced. When *C. maculosa* rhizospheres containing (-)-catechin (239.8 \pm 28.6 $\mu\text{g g}^{-1}$ soil DW basis) was amended with activated charcoal (30 ml L⁻¹), which appears to bind allelochemical compounds including those produced by *Centaurea* species and diminish phytotoxicity (Callaway and Aschehoug 2000, Ridenour and Callaway 2001), the treatment reduced (-)-catechin's phytotoxicity by 5-fold. Considered together, these results provide evidence that the root exudate, (\pm)-catechin, may account at least in part for the negative effect of *C. maculosa* on native North American plant species.

To investigate the cellular effects of (\pm)-catechin, we added 100 $\mu\text{g ml}^{-1}$ (\pm)-catechin to the roots of *C. diffusa* and *A. thaliana*. This led to a condensation of the cellular cytoplasm that is characteristic of cell death. Cytoplasmic condensation in the meristem and elongation zone was followed by a cascade of cell death proceeding backwards up through the root stele. To more fully characterize whether this change in cell morphology represented cell death we followed the pattern of cell death in *Arabidopsis* roots over a time course of 60 min using roots loaded with the vital stain fluorescein diacetate (FDA). This dye is retained by living cells but leaks from dead cells which become non-fluorescent. With (\pm)-catechin supplementation cells from the meristematic and central elongation zones were affected first and lost viability 600 s after exposure to the allelochemical. Cells in the mature region of the root were not detectably affected during this time course. However, cells in the mature region were dead 60 min after application of (\pm)-catechin, consistent with the transport of (\pm)-catechin or a related signal back through the root. Importantly, (\pm)-catechin had no detectable effect on the viability of the main root axis or growth of root hairs of *C. maculosa* itself. Thus, it appears that *C. maculosa* has evolved mechanisms that confer (\pm)-catechin resistance.

Plants use sophisticated signal transduction cascades to sense and respond to biotic and abiotic stress. Therefore, we monitored the dynamics of various signaling events that might be associated with the initial sensing and response to (-)-catechin. Reactive oxygen species (ROS) are produced by plant and animal cells in response to a range of stimuli, and can generate responses such as modulation of gene expression (Desikan et al., 2000). We found that ROS appears to play an important role in the initial events of (-)-catechin's phytotoxicity. The fluorescent dye 6-carboxy-2',7'-dichlorodihydrofluorescein diacetate, which demonstrates increasing fluorescence with elevated ROS production, was used to show that (-)-catechin induces a rapid (within 10s) ROS generation in 4d old seedlings of *C. diffusa* and *A. thaliana*. The ROS production propagated as a wave throughout the root apex progressing back along the main axis of the root. These spatial and temporal kinetics are similar to the cell death induced by (-)-catechin but occurred at least 5-10 minutes before detectable loss of cell viability. *Centaurea maculosa* roots treated with (-)-catechin showed no increase in ROS production as monitored by DCF production (Fig. 3a-c), in keeping with the resistant nature of this plant against its own exuded chemicals. In contrast, to (-)-catechin, the (+)-catechin isomer did not induce any ROS change in any of the species tested (*A. thaliana*, *C. diffusa* and *C. maculosa*), consistent with its weak effects as a phytotoxin (Bais et al., 2002).

The rapid burst of ROS in target species in response to (-)-catechin's and the sequential cascade of ROS and Ca^{2+} leading to cell death prompted us to analyze global gene expression in *A. thaliana*. We used an *Arabidopsis* oligoarray which contains ~12,000 genes (Bais et al. 2003) and screened root transcripts for changes. After one hour of treatment with (-)-catechin (100 $\mu\text{g ml}^{-1}$), 956 genes were induced two-fold or greater. The number of induced genes increased until 12h, when extensive cell death was visible of the roots. A significant number of genes related to oxidative stress were up-regulated, including glutathione transferase (GST), monooxygenase, lipid transfer protein, heat shock protein, DNA-J protein and blue copper binding protein at 1h after (-)-catechin treatment but the same genes were down-regulated after 12h treatment (Bais et al. 2003). Metabolites synthesized by the above-mentioned enzymes are important for defense reactions against pathogens, but many of them also act as antioxidants (Lamb and Dixon 1997). Together, the genetic results suggest that the reduction of ROS formation from electron transport chains is an additional way in which plants acclimate to oxidative stress. Several signal transduction genes, such as α -cystathionase, which encodes a homologue of the calcineurin B-like calcium sensor (CBL)-interacting protein kinases, were up-regulated in affected root tissues and may be essential for establishment of oxidative stress tolerance, perhaps through Ca^{2+} mediated signaling events. We conducted a global gene expression profile 10 min after (-)-catechin treatment to identify putative transcription factors involved in stress signaling and other early event gene activation. It should be noted that 10 min is the earliest time point ever selected in global gene expression studies in plants (Albrecht et al. 2001). Unexpectedly, we found 10 genes up-regulated 10 min post (-)-catechin treatment such as genes associated with steroid sulfotransferase like protein, α -cystathionase, chlorophyll binding protein, calmodulin, ribosomal protein L9, peroxidase ATP21a and four-unknown genes which did not have any homology with known genes in any living organism. The ten genes induced after 10 min post (-)-catechin treatment were down-regulated after 1h and 12h.

Update

Since the publication of Bais et al. (2003) we have made several important discoveries. First, Perry et al. (*in press*) found that (\pm)-catechin may also play an auto-inhibitory function at the seed stage and regulate *C.*

maculosa recruitment. Also, further analysis of field soils near mature *C. maculosa* has shown that *C. maculosa* soils can contain exceptionally high (\pm)-catechin concentrations, higher than we originally thought. Soil (\pm)-catechin concentrations averaged 1.55 mg g^{-1} dry soil, and 60% of samples contained $\geq 1.0 \text{ mg } (\pm)\text{-catechin g}^{-1}$. However, even more recent and unpublished results indicate that during the winter, when *C. maculosa* is dormant, soil concentrations of (\pm)-catechin may decrease by 10-20 times (L. Perry and G. Thelen, unpublished data).

We have also investigated the effect of *C. maculosa* on natural selection in North American native species. If the root exudates of *C. maculosa* cause high mortality in native populations, allelopathy has the potential to be a powerful selective force. In a series of experiments designed to test whether native species might be selected for tolerance to *C. maculosa*'s competitive and allelopathic effects, Callaway et al. (2005) found that native North American species that experienced and survived extensive invasion had higher tolerances to the invader than individuals from communities that did not experience invasion. Some native species grown from the seed of individuals that survived *Centaurea* invasion were more resistant to the general competitive effects of *C. maculosa*, the root exudates from *C. maculosa*, and to (\pm)-catechin. Such effects may have important long-term implications for plant invasions and the organization of plant communities. Evolved tolerance may ultimately contribute to coexistence among natives and invaders. However, even though native species showed evidence of relatively rapid evolution of tolerance to novel allelochemicals, there is no quantitative evidence that *C. maculosa* invasions are showing signs of decline. Both the experienced and tolerant lines were still outcompeted by *C. maculosa*. Therefore, if evolution of tolerance is occurring, it might take some time to see this manifest in the field. There also may be costs associated with evolving resistance to novel allelopathic effects. We have seen no signs of this, but if natives resist the effects of allelochemicals by producing greater quantities of their own biochemicals, such costs may occur.

In other experiments we have found that not all North American natives are equally susceptible to the competitive effects of *C. maculosa*. *Gaillardia grandiflora* and *Lupinus argenteus* are good competitors against *C. maculosa*. Furthermore, native grasses are much more abundant near *Lupinus* in areas heavily invaded by *Centaurea* (Weir et al. *in press*). In a field experiment native *Pseudoroegneria* and *Festuca* transplanted within 10 cm of a *Lupinus* plant grew significantly larger than those planted more than 1 m from *Lupinus* (Figure 1). However, this indirect facilitative relationship only occurred in dense *Centaurea* patches; when the grasses were transplanted next to *Lupinus* in the absence of *Centaurea* the effect of *Lupinus* was competitive. These results suggest that the beneficial effects of *Lupinus* on native grass survival in *Centaurea* stands is not due to increased availability of nitrogen provided by the legume.

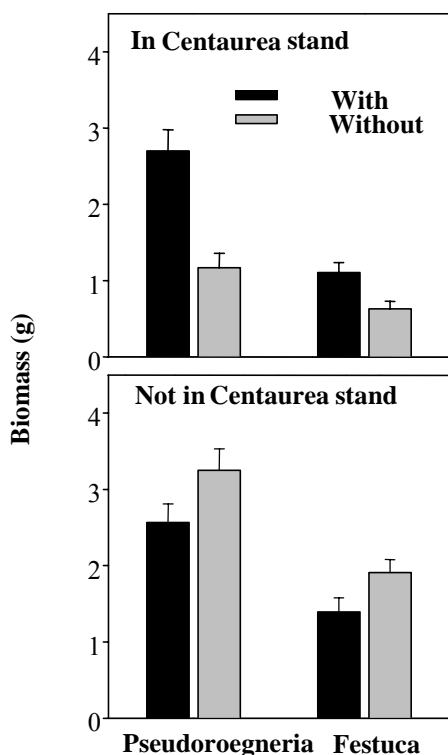


Figure 1. Aboveground biomass of *Pseudoroegneria spicata* and *Festuca idahoensis* transplanted either next to or far from *Lupinus sericeus*, and either in intermountain grassland heavily invaded by

Centaurea maculosa or in grassland with $\approx 2\%$ cover of *Centaurea*. Error bars show 1 SE. In a two way ANOVA for *Pseudoroegneria*, $F_{Lupinus}=3.56$, $df=1,59$, $P=0.064$; $F_{Centaurea}=18.97$, $df=1,59$, $P<0.001$; $F_{Lupinus \times Centaurea}=24.50$, $df=1,59$, $P<0.001$. In a two way ANOVA for *Festuca*, $F_{Lupinus}=0.24$, $df=1,59$, $P=0.877$; $F_{Centaurea}=27.43$, $df=1,59$, $P<0.001$; $F_{Lupinus \times Centaurea}=11.32$, $df=1,59$, $P=0.001$. Reprinted from Weir et al. (in press), *Plant Physiology*.

In pursuit of potential chemical explanations of the facilitative effects of *Gaillardia* and *Lupinus*, we found that the allelopathic potential of *C. maculosa* was blocked when the antioxidant ascorbic acid is added simultaneously with (\pm)-catechin. We then analyzed the root exudates of *Lupinus* and *Gaillardia* to ascertain if their root-secreted organic acids might be responsible for conferring catechin resistance. In a first experiment, control plants treated with 200 $\mu\text{g/ml}$ of (\pm)-catechin succumbed to the toxin but those grown in media containing both (\pm)-catechin and *Gaillardia* root exudates survived. Analysis using high pressure liquid chromatography and mass spectrometry showed that *Gaillardia* and *Lupinus* root exudates contained oxalic acid, suggesting the possibility of two-way crosstalk between plant roots through the exudation of biochemicals. Furthermore, when exposed to (\pm)-catechin, the roots of *Gaillardia* and *Lupinus* produced far more oxalic acid than in controls without (\pm)-catechin (Figure 2).

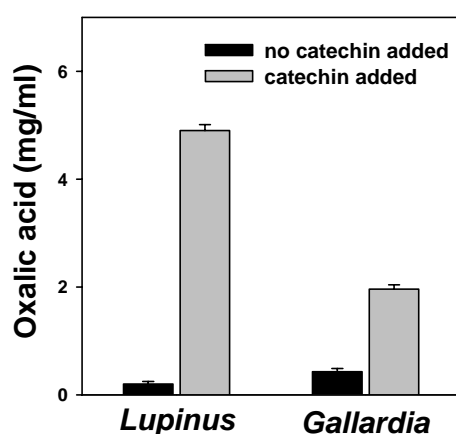


Figure 2. Oxalic acid secreted from the roots of *Lupinus argenteus* and *Gaillardia grandiflora* with and without catechin introduced into the growth medium. Error bars show 1 SE. Reprinted from Weir et al. (in press), *Plant Physiology*.

We tested the specific ability of pure oxalic acid to facilitate resistance to catechin in susceptible species. 50-100 μM oxalic acid protected *Arabidopsis* from catechin rhizotoxicity without any negative effects on biomass. Growth media supplemented with 100 μM oxalic acid was also able to protect *P. spicata* and *F. idahoensis*. In all cases, the total biomass of plants grown in media amended with both oxalic acid and catechin was not significantly different from methanol treated controls, while those treated with catechin alone showed significantly less growth. These results indicate that the root-mediated secretion of oxalic acid might be responsible for catechin resistance in *Gaillardia* and *Lupinus*. We suspect that the previously reported initial wave of ROS acts as a signal, preceding a transient Ca^{2+} flux and eventual cell death, and oxalic acid acts as a natural antioxidant. To link the field experiments to ideas for the mechanism of chemical crosstalk, we collected soil samples from the rhizospheres of *Lupinus* growing alone, *Lupinus* growing closely together with *Centaurea*, and *Centaurea* growing alone, and analyzed the soil for catechin and oxalic acid. Oxalic acid was recovered in very small amounts from the soil, possibly due to reactions with trace metals in the soil, general instability under natural conditions, or inadequate soil extraction procedures; however, significantly greater quantities of oxalic acid were detected in soil samples collected near *Lupinus* growing with *Centaurea* than with *Lupinus* growing alone. These defensive chemical responses shed light on how native communities may meet the challenges of allelopathic invaders.

Implications

Linked with previous research, our findings provide genetic, cellular, physiological, and community-scale evidence for allelopathy for an invasive weed. Allelopathy has been a highly controversial mechanism for decades, and whether or not strong allelopathic effects exist is not trivial either for community theory or from an applied perspective. Plants may be passive, only responding to fluctuations in the resources they require, or they may directly interact with other plants by transmitting, receiving, and responding to chemicals and other signals in their environment independently of resources. How plants interact with each

other is pertinent to how communities are organized. If plants react idiosyncratically to different chemicals released from particular neighbors, then the identity of neighbors may have a substantial effect on species coexistence and community composition. If such species-specific mechanisms are common then diffuse coevolution within plant communities would be much more likely (see Inoye and Stinchcombe 2001). The case we have presented for allelopathy and *C. maculosa* also challenges the conventional ecological perspective that a species' invasiveness is mainly due to enhanced resource competition after escape from natural enemies (Kennedy et al. 2002). Understanding allelopathy and evolution may provide the potential for a new approach to combating exotic plant invasion, the development of native resistance to allelopathic chemicals.

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