

Invasion of plants into native communities using the underground information superhighway

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Abstract

Many exotic plant species undergo astounding increases in dominance when introduced to new communities by humans. This is primarily attributed to escape from specialist consumers. However, strong allelopathic effects by some powerful invaders, and much stronger allelopathic effects in invaded ranges compared with native ranges suggest a new theory for invasive success – the novel weapons hypothesis. Here we discuss the evidence for allelopathic effects of *Centaurea maculosa* and *C. diffusa* and propose that some invaders transmogrify because they possess novel biochemical weapons that function as unusually powerful allelopathic agents or as mediators of new plant-soil microbial interactions. Novel biochemical weapons possessed by some plant invaders may provide an advantage based on historical coevolutionary trajectories.

Media Summary

Exotic plant invaders may succeed because they possess novel weapons; biochemicals that have powerful effects against naïve species in invaded regions that have not had an opportunity to evolve resistance.

Key Words

allelopathy, catechin, coevolution, competition, exotic plants, invasions, novel weapons, transmogrification

Introduction

Two of North America's most destructive exotic invasive plants, *Centaurea maculosa* and *C. diffusa*, produce chemicals in their root exudates with powerful toxic effects on other plants and soil microbes (Callaway & Aschehoug 2000; Bais et al. 2003; Weir et al. 2003; Vivanco et al. 2004; Callaway et al. 2004). *Centaurea maculosa* exudes large amounts of (±)-catechin from its roots, whereas *C. diffusa* roots exude 8-hydroxyquinoline. Both species can establish virtual monocultures, but only in the regions that they invade. At home (Eurasia) they are far less abundant. In a fascinating twist, both *Centaurea* species and their allelochemicals have much stronger effects on species native to invaded regions in North America than related species in their communities of origin (Callaway and Aschehoug 2000; Bais et al. 2003; Vivanco et al. 2004). These biogeographical differences in the effectiveness of root-exuded biochemicals suggest a new theory for the success of some invasive plants – the “novel weapons hypothesis” (Rabotnov 1982, Callaway and Ridenour 2004, Callaway and Hierro, *in press*).

The dramatic success, or “transmogrification”, of some plant species in places where humans have introduced them is primarily attributed to escape from specialist consumers (Williams 1954; Elton 1958; Crawley 2002; Mack *et al.* 2000; Maron and Vilà 2001). However, the biogeographic differences in allelopathic effect suggest that some invaders may succeed because they possess novel biochemical weapons that function as unusually powerful allelopathic agents, or as mediators of new plant–soil microbial interactions. These allelopathic weapons may be relatively ineffective against their natural neighbors because of adaptation by natural neighbors, but the same biochemicals may be highly inhibitory to newly encountered plants in invaded communities because of a lack of adaptation. Resistance in plants evolves rapidly in response to man-made chemical herbicides (Powles and Holtum 1994), and plants can apparently adapt rapidly to the particular chemical composition of neighboring plants (Ehlers & Thompson 2004). In other words, the novel weapons of some plant invaders may provide them with an advantage that may arise from differences in the regional coevolutionary trajectories of plant and soil microbial communities.

The allelopathic effects of *Centaurea* species

Although not a dominant, or even a common species in its native Europe, *Centaurea maculosa* is one of North America's worst invasive weeds. Probably introduced with alfalfa seed from Europe, it now occupies over 7 million acres of the US (<http://www.fs.fed.us/database/feis/plants/forb/cenmac/all.html>). *Centaurea maculosa* has been the target of an aggressive biological control effort, with 13 species of insects introduced to control the weed. So far, biocontrol has not been successful (Müller-Schärer and Schroeder 1993; Callaway et al. 1999; Ridenour and Callaway 2003; Pearson and Callaway 2003), suggesting that the lack of specialist insect herbivores may not be a major component of *C. maculosa*'s invasive success. In fact, moderate root herbivory appears to stimulate the growth and competitive ability of *C. maculosa*, possibly due to herbivory increasing the exudation of (\pm)-catechin into the rhizosphere (Callaway et al. 1999, Thelen et al. 2005).

By integrating ecological, physiological, biochemical signal transduction, and genomic approaches to the root exudates of *C. maculosa*, Harsh Bais and colleagues (2003) took a major step towards understanding allelopathy and *C. maculosa*. They found that two forms, or enantiomers, of catechin were excreted from *C. maculosa* roots. The more common enantiomer, (+)-catechin, exhibited anti-bacterial functions, whereas the less common enantiomer, (-)-catechin, has strong allelopathic effects. Recently, it has been found that (+)-catechin also exhibits phytotoxic activity, but higher concentrations of (+)-catechin are required to have the same effect as (-)-catechin on the model plant *Arabidopsis thaliana* (J. Vivanco & H. Bais, unpublished data). Bais et al. (2002) collected exudates from the roots of *C. maculosa* that had been exposed to fungal cell wall preparations and roots that had not, and found that the allelochemical activity of the former isolates were much stronger, inhibiting the germination of all species tested. When catechin was isolated from these exudates its negative effects were even stronger. *Centaurea maculosa* plants were resistant to their own exudates and purified catechin. Importantly, (\pm)-catechin was found in soil extracts in the rhizospheres of *C. maculosa* at concentrations far higher than the minimum dose required for inhibition in controlled experiments (Bais et al. 2002, 2003, Perry et al. *in review*). Bais et al. 2002 found that, depending on the distance from *C. maculosa* taproots, (\pm)-catechin concentrations ranged from 291.6 ± 17.8 to $389.8 \pm 28.6 \mu\text{g cm}^{-2}$. In a recent study with more detailed sampling conducted in April 2004 in Missoula (MT), Perry et al. (*in review*) found that the mean soil (\pm)-catechin concentration in 112 samples collected within 25 cm of 22 different *C. maculosa* individuals was 1.55 ± 1.27 (1 SD) mg g^{-1} dry soil. Catechin was not detected in six samples. Soil (\pm)-catechin concentrations in the remaining 106 samples varied between 0.18 and 7.10 mg g^{-1} . Eighty-two percent of the samples contained $\geq 0.5 \text{ mg } (\pm)\text{-catechin g}^{-1}$ and 60% contained $\geq 1.0 \text{ mg g}^{-1}$. Soil (\pm)-catechin concentrations did not change significantly with distance up to 25 cm from *C. maculosa* adults isolated from other *C. maculosa* plants.

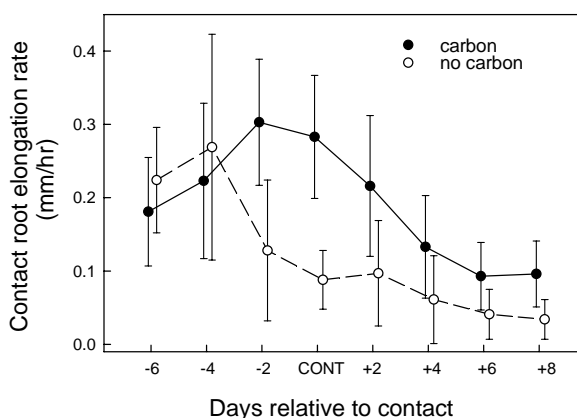


Figure 1. Elongation rates of *Festuca idahoensis* roots that made physical contact with *Centaurea maculosa* roots in root observation chambers ("contact roots"), with or without activated carbon, from six days before until eight days after contact. Elongation rates of all roots were converted to mm/hour and standardized in time by aligning their days of contact at "day 0". Error bars represent two standard errors. Carbon treatments differed significantly (Repeated measures ANOVA, $F_{\text{day} \times \text{carbon}}=7.24$; $df=7,161$; $P<0.001$). Reprinted from Ridenour and Callaway (2001).

Greenhouse experiments have demonstrated inhibitory effects of *C. maculosa* roots on the roots and overall growth of native American grass and activated carbon added as a purification agent ameliorates these inhibitory effects (Ridenour and Callaway 2001, Figure 1). Furthermore, adding low concentrations of (\pm)-

catechin to pot and Petri dish experiments suppressed the growth and germination of native species (Bais et al. 2003, Weir et al. 2003, Callaway et al. 2005a), but native species show substantial variation in susceptibility to (\pm)-catechin (Weir et al. 2003, L.G. Perry, *unpublished data*) and to the general competitive effects of *C. maculosa* itself (Callaway et al. 2004). Field injections of (\pm)-catechin in uninvaded natural intermountain grasslands substantially inhibited the growth of 7 of 8 native species (Thelen et al. 2005, Figure 2); however, despite attempts to use natural concentrations there is no certainty that applications of (\pm)-catechin accurately mimicked the way *C. maculosa* releases the chemical into the soil.

At the biological and biochemical levels, (\pm)-catechin shows cell-specific targeting against meristematic and elongation zone cells in the roots of target plants as evidenced by cytoplasmic condensation followed by a cascade of cell death proceeding backwards up through the root stele, induction of reactive oxygen species (ROS)-related signalling that leads to rhizotoxicity in susceptible plants, ROS-triggered Ca^{2+} signalling cascade leading to cellular pH decrease, and allelochemical-induced genome-wide changes in gene expression patterns.

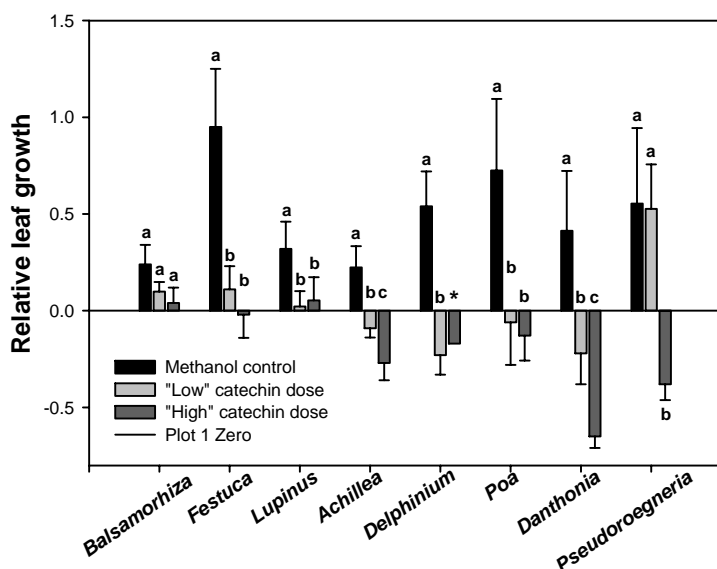


Figure 2. Relative growth as measured by leaf number and plant height of eight native species in an un-invaded prairie when exposed to three concentrations of the *C. maculosa* root exudate, (\pm)-catechin. Native species are *Balsamorhiza sagitaria*, *Festuca idahoensis*, *Lupinus sericeus*, *Achillea milleflora*, *Delphinium bicolor*, *Poa sandbergii*, *Danthonia unispicata*, *Pseudoroegneria spicata*. Doses are described in the methods and were designed to approximate *C. maculosa* without (low concentrations) and with (high concentrations) *Agapeta zoegana* in their roots. Error bars represent 1 SE and the * represents a lack of replication due to high mortality. Means with different letters within a species were significantly different in single ANOVAs (for each native species) followed by post-ANOVA Tukey tests. Reprinted from Thelen et al. (2005).

We have less detailed knowledge about allelopathy and *Centaurea diffusa*, another highly invasive species, but there is strong ecological and biochemical evidence that root exuded chemicals play an important role in *C. diffusa* invasions. Root exudates of *in vitro*-grown *C. diffusa* plants caused 80–100% mortality of a suite of species after 14 days of exposure (Vivanco et al. 2004). All tested species except *C. diffusa* showed reduced germination in response to *C. diffusa* root exudates. The only phytotoxic fraction of extracts of freeze-dried root exudate subjected to HPLC analysis was found to be 8-hydroxyquinoline. 8-Hydroxyquinoline is a common, commercially available compound well known as an analytical reagent for its metal chelating properties and as a fungistat and antiseptic. 8-Hydroxyquinoline is not structurally related to (\pm)-catechin. Like the (+) form of catechin produced by *C. maculosa*, 8-Hydroxyquinoline also displays strong antibacterial and antifungal activity against important plant pathogenic microbes and fungi (Vivanco et al. 2004).

As for *C. maculosa* and (\pm)-catechin, 8-hydroxyquinoline was abundant in soil extracts from *C. diffusa*-invaded fields in North America, and occurred at concentrations far higher than those that caused mortality

in greenhouse experiments, although the effects of the exudate might be much different in natural conditions.

Biogeographic variation in allelopathic effects

Evidence that *Centaurea* species might utilize novel allelopathic weapons preceded a detailed understanding of allelopathic effects. Callaway and Aschehoug (2000) compared the inhibitory effects of *C. diffusa* 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. Each of the three species from North America was paired with a congener (or a near-congener) from Eurasia of a similar morphology and size. *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 the ^{32}P uptake of *C. diffusa*, but all Eurasian species demonstrated strong negative effects on the amount of ^{32}P acquired by *C. diffusa*. More importantly, 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. Likewise, 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). ^{32}P uptake by Eurasian grasses growing with *C. diffusa* decreased in the presence of activated carbon. The effects of activated carbon on ^{32}P uptake by grasses corresponded with the effects of activated carbon on ^{32}P uptake by *C. diffusa*. Activated carbon enhanced uptake by *C. diffusa* in the presence of Eurasian grasses but reduced uptake in the presence of North American grasses. In a later study, Vivanco et al. (2004) found that experimental communities built from North American plant species are far more susceptible to invasion by *C. diffusa* than communities built from Eurasian species.

Not only do the effects of bulk root exudates of *C. diffusa* appear to differ between communities of origin and invaded communities, so does the specific effects of 8-hydroxyquinoline. North American plant species were much more susceptible to identical concentrations of 8-hydroxyquinoline than Eurasian species (Vivanco et al. 2004). The strong effects of the place of origin on the competitive ability of grass species against *C. diffusa*, the contrasting effects of activated carbon, and the contrasting effect of 8-hydroxyquinoline itself, 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.

Similar, but weaker, evidence exists for biogeographic differences in the allelopathic effects of *C. maculosa*. Bais et al. (2003) added (\pm)-catechin to pots in which three different North American and European grasses were grown separately, and both germination and growth responses indicated that European grasses were more resistant to ($-$)-catechin than their North American counterparts.

Little other evidence exists for novel weapons, but *Alliaria petiolata*, a devastating invader of North American temperate forests, also has stronger chemical effects on *Geum laciniatum*, a new North American neighbor, than on *Geum urbanum*, its natural European neighbor (Prati and Bosdorf 2004). In a related experiment, although not using invasive species, Mallik and Pellissier (2000) found that the Eurasian *Vaccinium myrtillus* generally had stronger biochemical effects on the North American *Picea mariana* than on the Eurasian *Picea abies*.

Implications for native communities

Evolution can occur rapidly in reaction to anthropogenic effects (Kinnison and Hendry 2001) and the introduction of exotic species to new regions is one of the most important anthropogenic effects native species experience. The extreme effects of invaders on native populations have the potential to drive genetic change and the evolution of native species. Inherent to the novel weapons hypothesis is the idea that adaptation among coexisting plants and microbes contributes to coexistence and stability, suggesting that disruption of adaptive relationships by some invaders may be the reason for community collapse. One of the implications of such adaptation is that native species in invaded systems may also adapt to the novel biochemical weapons of invaders. Callaway et al. (2005a) investigated this possibility and found that

individuals of some North American species that had survived extensive invasion by *Centaurea maculosa* had higher tolerances to the allelopathic effects of the invader than individuals from communities that had not experienced invasion. Some native species grown from the seed of individuals that survived *Centaurea* invasion were more resistant to the general competitive effects of *Centaurea*, the root exudates from *Centaurea*, and to (\pm)-catechin. For *Festuca* and *Stipa*, plants grown from seed in competition with *C. maculosa* and without activated carbon in the soil were significantly smaller than those grown with activated carbon (Figure 3).

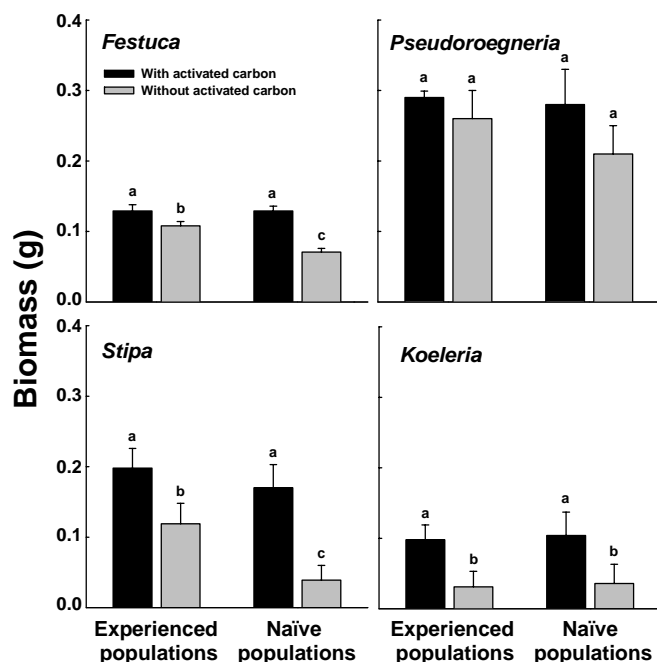


Figure 3. Total biomass of grasses grown from seeds collected from North American native grasses that had either experienced and survived invasion by *C. maculosa* or had not experienced invasion by *C. maculosa*. These plants were grown in competition with *C. maculosa* in sand or in sand modified with activated carbon to ameliorate the allelopathic effects of *C. maculosa*. Error bars represent one standard error, and different letters above the bars designate significant differences for a one-way ANOVA conducted for that particular species. In an ANOVA for all species combined, $F_{\text{naïveté}} = 7.894$, $df=1,147$; $P=0.006$; $F_{\text{activated carbon}}=33.748$, $df=1,147$; $P<0.001$; $F_{\text{naïveté} \times \text{activated carbon}} = 7.794$, $df=1,147$; $P=0.006$. Reprinted from Callaway et al. 2005a).

More importantly, *Festuca* and *Stipa* grown from the seeds of naïve maternal plants in competition with *C. maculosa* were smaller than those grown from the seed of experienced maternal plants, and activated carbon eliminated these differences, suggesting the possibility that selection for tolerance to *C. maculosa* may have occurred. Although these results may be confounded by maternal effects, they provide initial evidence that native plants species may evolve to tolerate the effects of an exotic invader, and in particular an invader's novel allelochemistry. Such effects may have long-term implications for plant invasions and the organization of plant communities. If species in invaded communities can evolve resistance, biological communities may be more coevolved and functionally organized than previously thought (Goodnight 1990; Wilson 1992; Thompson 1999). This perspective is supported by studies of co-occurring genotypes of a species that interact less strongly than genotypes of the same species that occur in different places (Martin and Harding 1981; Evans et al. 1985; Turkington and Mehrhoff 1991; Turkington and Harper 1979) and by recent work on diffuse coevolution suggesting that selection pressures due to one species can change in the presence of other species (Inouye and Stinchcombe 2001). If natives can evolve resistance to invaders, invaded communities may recover some aspects of their natural structure and function, and invaders and natives may eventually coexist.

In summary, experiments with *Centaurea* species have provided strong evidence for allelopathy, and that exceptionally strong allelopathic effects in invaded ranges may help to explain invasive success. The biogeographic differences observed for *Centaurea* species suggest that shared evolutionary trajectories (Thompson, 1997, 1999, Thorpe and Callaway, in press, Callaway et al. 2005b) in different regions may contribute to coexistence in the original communities of invaders where the species have been exposed to each other for a long time, but to competitive exclusion when these invaders arrive in new communities. We

propose that when humans introduce some plant species to new regions they may force together different biochemically driven coevolutionary trajectories from different continents and disrupt coevolved interactions.

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