Natural selection for resistance to the allelopathic effects of invasive plants

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Summary

1 Exotic plant invasions often cause high mortality in native populations and therefore have the potential to be a powerful selective force.

2 We found that surviving individuals from North American communities that have experienced extensive invasion by *Centaurea maculosa* have higher tolerances to the Eurasian invader than individuals from communities that did not experience invasion.

3 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 a chemical specific to the root exudates of *Centaurea* (±)-catechin.

4 Although these results may be confounded by maternal effects, they provide initial evidence that native plant species may evolve to tolerate the effects of an exotic invader, and in particular an invader's novel allelochemistry.

5 Such effects may have long-term implications for plant invasions and the organization of plant communities. Evolved tolerance may ultimately contribute to coexistence among natives and invaders, with our results suggesting that natural plant communities may be more coevolved and less individualistic than currently thought.

Key-words: allelopathy, catechin, *Centaurea*, evolution, invasion, natural selection, plant biochemistry, root exudates

Introduction

Ecology has been emphasized over evolution in research on the biological effects of exotic plant invasions (Rice & Emery 2003), and almost all evolutionary research on this topic has focused on the invaders themselves (Baker 1992; Ellstrand & Schierenbeck 2000; Siemann & Rogers 2001; Grosholz 2002; Lee 2002; Allendorf & Lundquist 2003; Maron *et al.* 2004; Stastny *et al.* 2005). However, evolution can occur rapidly in reaction to anthropogenic effects (Kinnison & Hendry 2001) and one of the most important anthropogenic environmental changes affecting natural ecosystems is the introduction of exotic species to new regions. Many of these non-native species become

invaders, reaching abundances that are far higher than in their native regions (D'Antonio & Vitousek 1992; Ridenour & Callaway 2001; Louda *et al.* 2003), and causing large decreases in the abundances of native species (Braithwaite *et al.* 1989; Memmott *et al.* 2000; Grigulis *et al.* 2001). The extreme effects of invaders on native populations have the potential to drive genetic change and the evolution of native species (see Mealor *et al.* 2005).

Species-specific mechanisms by which invaders might drive evolution have come to light in recent research that indicates that some invaders are allelopathic and succeed because their allelochemicals are new to the communities they invade (the 'novel weapons hypothesis'; Callaway & Aschehoug 2000; Bais *et al.* 2003; Baldwin 2003; Fitter 2003; Callaway & Ridenour 2004; Callaway *et al.* 2004; Vivanco *et al.* 2004). This hypothesis proposes that some invasive plants may perform much better in invaded regions because they

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bring unique, species-specific, biochemical impacts to naïve native plant and soil microbial communities; in other words, to communities that have never been exposed to the particular rhizosphere chemistry of the invader. Two of North America's most destructive invaders, *Centaurea maculosa* and *C. diffusa*, produce chemicals with effects that are consistent with the novel weapons hypothesis (Callaway & Aschehoug 2000; Bais *et al.* 2003; Callaway *et al.* 2004; Vivanco *et al.* 2004). Both species can establish virtual monocultures and both species have powerful antiplant and antimicrobial root exudates; *C. maculosa* exudes large amounts of (±)-catechin from its roots, whereas *C. diffusa* exudes 8-hydroxyquinoline. 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. *Alliaria peteolata*, a devastating invader of North American temperate forests, also has stronger chemical effects on *Geum laciniatum*, a new North American neighbour, than on *Geum urbanum*, its natural European neighbour (Prati & Bosdorf 2004). In a related experiment, although not using invasive species, Mallik & Pellissier (2000) found that the Eurasian *Vaccinium myrtillus* generally had stronger biochemical affects on the North American *Picea mariana* than on the Eurasian *Picea abies*.

Resistance in plants evolves rapidly in response to man-made chemical herbicides (Powles & Holtum 1994), and plants can apparently adapt rapidly to the particular chemical composition of neighbouring plants (Ehlers & Thompson 2004). Resistance may evolve as rapidly to the natural allelopathic herbicides released by invaders and this would have profound consequences for ecological and evolutionary theory and for conservation. If chemically mediated interactions are stronger in invaded plant communities than in natural communities, and if species in invaded communities can evolve resistance, biological communities may be more coevolved and functionally organized than previously thought (see Goodnight 1990; Wilson 1992; Thompson 1999). This perspective is supported by recent work on diffuse coevolution suggesting that selection pressures due to one species can change in the presence of other species (Inouye & 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.

We examined the potential for North American grasses to adapt to the allelopathic effects of *Centaurea maculosa* (spotted knapweed) by comparing the effects of the weed and one of its identified allelopathic root exudates (±)-catechin (Bais *et al.* 2003) on native grass species and their offspring that had not experienced *C. maculosa* invasion (naïve natives) with those on conspecifics and their offspring that had survived severe *C. maculosa* invasion (experienced natives).

Methods

EXPERIMENT 1

We chose paired invaded and non-invaded populations of native grasses at five different sites in the intermontane grassland of western Montana from which to sample native species for experiments. Invaded populations of native species were those remnants that survived in patches of *C. maculosa*. We estimated initial invasion dates of approximately 20–30 years ago for experienced populations, and established how naïve populations were protected from invasion through conversations with private landowners and land managers for Mt Jumbo (46°52′23″ N; 113°59′45″ W), land managers and Forest Service researchers for The National Bison Range (47°20′12″ N; 114°13′46″ W), the Clearwater Elk Refuge (47°0′34″ N; 113°23′53″ W) and the Montana State Bandy Experimental Ranch (47°03′30″ N; 113°12′42″ W), and historical data for Calf Creek Elk Refuge (46°22′52″ N; 113°56′56″ W). Native vegetation at the Mt Jumbo, Bison Range and Bandy Ranch sites had been protected by 'spot-spraying', killing colonizing *C. maculosa* with the herbicide Tordon® before populations spread. Invasion at the Calf Creek Elk Refuge had apparently been more extensive prior to eradication with Tordon® and both the weed and spraying may have affected the apparently uninvaded vegetation sampled. At the Clearwater Elk Refuge, remnants had been protected by aerial spraying of herbicide around the periphery of the refuge to prevent *C. maculosa* from advancing from the roadsides, allowing us to sample native grasslands that had not been sprayed with herbicide.

We measured and found no trace of (±)-catechin in the soils at naïve sites, whereas (±)-catechin was abundant at all invaded sites (Bais *et al.* 2003). However, we do not know how long (±)-catechin lasts in the soil (Bais *et al.* 2003) and we cannot therefore be sure whether or not *C. maculosa* has ever been present at these sites from which it is now absent. This historical uncertainty was the reason for high replication of paired sites ($n = 5$). In June 2000 at each site we excavated 20 individuals of each native grass species present and transplanted them into 2.4-L pots. Seeds were also collected from all sites in July and August 2001 (see details below for Experiment 2). *Festcua idahoensis* plants and seeds were collected at all five sites, *Pseudoroegneria spicata* and *Koeleria micrantha* plants and seeds were collected at the Mt Jumbo, Bison Range and Clearwater sites, and *Stipa occidentalis* and *Poa sandbergii* plants and seeds were collected at the Bandy Ranch site. Plants were allowed to establish in the glasshouse for 30 days, after which we excised two equally sized clones from each individual and planted them in separate 2.4-L pots with a *C. maculosa* transplant that had been grown in the glasshouse for 3 months prior to transplanting. One pot of each pair contained only silica sand averaging 0.60–0.85 mm in diameter (20/30

grit, Lane, MT, USA) whereas the other contained a mixture of activated carbon and sand at 20 mL carbon per L sand. Activated carbon has a high affinity for organic compounds, such as potentially toxic or allelopathic chemicals, and a weak affinity for inorganic electrolytes, such as those present in nutrient solution, and has previously been shown to reduce the negative effects of root exudates from *C. maculosa* and other species (Mahall & Callaway 1992; Callaway & Aschehoug 2000; Ridenour & Callaway 2001). All tillers on each individual were counted at the time of planting and again after 190 days growth with *C. maculosa*. Original tiller number was used as a covariate, and we analysed the change in the number of tillers (not transformed) in an ANOVA for each native grass species using population naïveté (*C. maculosa*-experienced vs. not experienced, fixed), sample population (for the three species with more than one population, random), and activated carbon treatment (fixed) as factors.

EXPERIMENT 2

For the second experiment we collected seed in the field from 20 naïve native individuals and 20 experienced native individuals of each of the same grass species at each of the sites used for the first experiment. Grass seeds were planted in 2.4-L pots, thinned to one individual after germination and grown for 3 weeks prior to planting *C. maculosa* seeds. Grasses were planted in either pure sand (20/30 grit) or in a mixture of activated carbon and sand at 20 mL carbon per L sand. Plants were grown together for 210 days, harvested, dried at 60 °C and weighed. The total mass of the grasses was analysed with an ANOVA using population naïveté (fixed), sample site (random), grass species (fixed) and activated carbon (fixed) as factors. In a separate ANOVA the total mass of *C. maculosa* was analysed with an ANOVA using population naïveté (fixed), grass species (fixed) and activated carbon (fixed) as factors.

EXPERIMENT 3

We tested the effect of (±)-catechin on seeds from naïve and experienced individuals of native species in a third experiment. Ten seeds from each of eight to ten naïve individuals and eight to ten experienced individuals of *Poa sandbergii*, *Koeleria cristata*, *Pseudoroegneria spicata* and *Stipa occidentalis* (we ran out of experienced *Festuca idahoensis* seeds) were germinated on filter paper in Petri dishes in either a control of 10 mL methanol diluted with 990 mL of deionized water, or 10 mL methanol mixed with 100 mg of (±)-catechin and diluted with 990 mL of deionized water. The percentage germination was analysed with an ANOVA using population naïveté, sample site (only *P. spicata*, for which we used two populations with 10 naïve and 10 experienced individuals from each), grass species and catechin as factors. Germination percentage was not normally distributed and the data were transformed by

taking the log of the percentage germination + 1. We measured seed mass for a second subsample of seeds from each individual maternal line and paired the mean mass for a parent plant with the germination for the same plant. Three species had significantly smaller seeds in experienced populations than in naïve populations, but seed mass was insignificant as a covariate and therefore not used in the final analysis.

Results

In the first experiment, with five native grass species, we found that all clones had fewer tillers after a period of growth with *C. maculosa* in sand, regardless of whether they had survived *C. maculosa* invasion (experienced natives) or were naïve. However, analysis of all native grass species combined demonstrated that *C. maculosa* suppressed naïve grass clones more than experienced clones (Fig. 1, $F_{invasion experience} = 7.089$; d.f. = 1334; $P = 0.008$). When activated carbon was added to the sand to adsorb organic exudates, the growth of experienced natives improved by 47% (ANOVA for experienced plants only, over all sites and for all species combined, $F_{carbon} = 3.22$; d.f. = 1176; $P = 0.034$) although the effect was significant for only one species (*Stipa occidentalis*, see Fig. 1) when analysed separately. In contrast, activated carbon improved the growth of the clones of all naïve native species analysed together by 105% (ANOVA for naïve plants only, $F_{carbon} = 8.22$; d.f. = 1158; $P = 0.002$), and of three species when analysed separately (*Stipa*, *Koeleria* and *Festuca*, Fig. 1). More important, the ameliorating effect of activated carbon was stronger for naïve native grasses than experienced native grasses ($F_{invasion experience} \times$ activated carbon = 3.805; d.f. = 1334; $P = 0.052$). This overall difference was primarily due to significant experience by activated carbon interactions for two species, *Festuca idahoensis* and *Koeleria cristata* (see Fig. 1). *Pseudoroegneria spicata* was the least affected by *C. maculosa* in general, and demonstrated no evidence for the development of tolerance to *C. maculosa* in this experiment.

In the second experiment we compared the effects of *C. maculosa*, which we presumed to be due to root exudates, on the progeny of experienced natives with those on the progeny of naïve natives. 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 (for *Festuca*, $F_{activated carbon} = 9.22$, d.f. = 1,52, $P < 0.001$; for *Stipa*, $F_{activated carbon} = 44.03$, d.f. = 1,46, $P < 0.001$; for *Koeleria*, $F_{activated carbon} = 10.09$, d.f. = 1,54, $P < 0.001$; Fig. 2). Activated carbon did not alleviate the effect of *C. maculosa* on *Pseudoroegneria*. Most importantly, the results for *Festuca* and *Stipa* suggested a degree of evolved tolerance to *C. maculosa*. *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
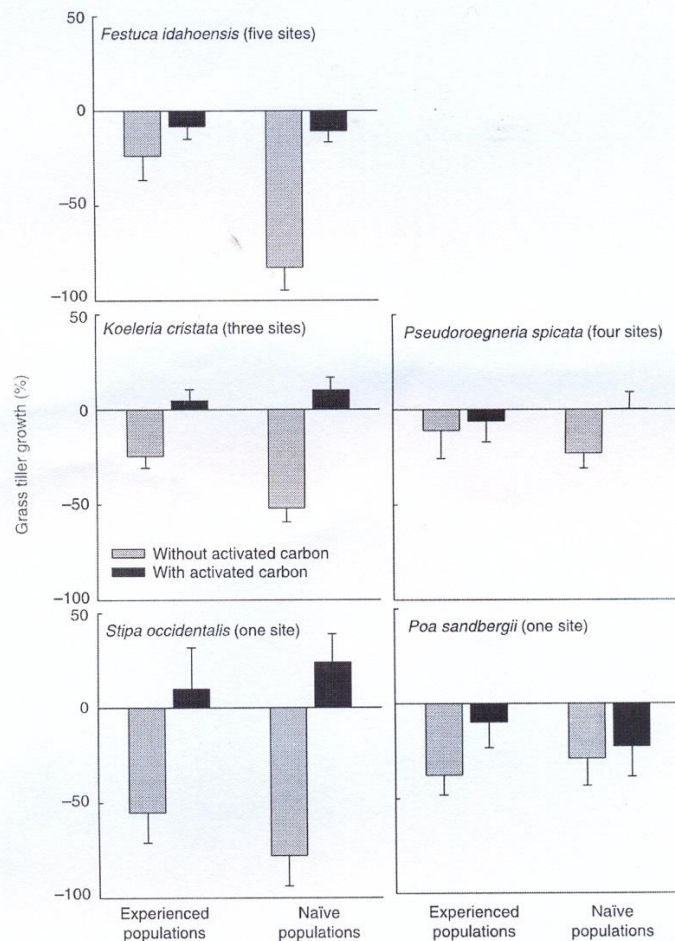
Fig. 1 Growth, measured as change in tiller number over the course of the experiment, of North American native grasses that had either experienced and survived invasion by *C. maculosa* or had not experienced invasion by *C. maculosa*. These grasses were grown in competition with *C. maculosa* in sand or in sand modified with activated carbon to ameliorate the allelopathic effects of *C. maculosa*. Error bars represent one standard error. In separate ANOVAs conducted for *Festuca*, *Koeleria* and *Stipa* with population included as a random factor: for *Festuca*, $F_{\text{naïveté}} = 3.16$, d.f. = 1,4, $P = 0.150$; $F_{\text{naïveté} \times \text{activated carbon}} = 16.40$, d.f. = 1,4, $P = 0.015$; for *Koeleria*, $F_{\text{naïveté}} = 15.67$, d.f. = 1,2, $P = 0.058$; $F_{\text{naïveté} \times \text{activated carbon}} = 106.56$, d.f. = 1,2, $P = 0.008$; for *Stipa*, $F_{\text{naïveté}} = 15.67$, d.f. = 1,2, $P = 0.058$; $F_{\text{naïveté} \times \text{activated carbon}} = 0.138$, d.f. = 1,3, $P = 0.303$. In ANOVAs conducted separately for each species, for *Psuedoroegneria* and *Poa* without population considered as a factor (non-replicated) there were no significant effects of naïveté or naïveté–carbon interactions. The effect of activated carbon was significant for *Stipa*, *Festuca* and *Koeleria* in separate ANOVAs for each species, $P < 0.01$. For all species analysed together in a single ANOVA, $F_{\text{naïveté} \times \text{activated carbon}} = 3.805$; d.f. = 1334, $P = 0.052$.

maternal plants, and activated carbon eliminated these differences (for *Festuca*, $F_{\text{naïveté} \times \text{activated carbon}} = 4.794$, d.f. = 1,52, $P = 0.034$; for *Festuca*, $F_{\text{naïveté} \times \text{activated carbon}} = 11.77$, d.f. = 1,46, $P < 0.001$). Activated carbon reduced the effect of *C. maculosa* on *Koeleria*, but there were no differences between naïve and experienced plants. Because plants grown from experienced and naïve maternal plants did not differ in size when grown with activated carbon in the soil, it appears that allelopathy may be a likely selective mechanism.

The effect of *C. maculosa* on experienced and naïve grasses was reflected in the effects of the grasses on *C. maculosa* (Fig. 3). Plants grown from the seed of experienced maternal lines reduced the biomass of *C. maculosa* by 31% relative to the invader grown without native neighbours. Plants grown from the seed of naïve maternal lines did not significantly affect the growth of *C. maculosa* competitors. Activated carbon (expected to increase the effect of the grasses on *C. maculosa* by inhibiting the invader's allelopathic advantage) increased the negative effect of grasses grown from the seeds of experienced maternal lines and naïve maternal lines by similar proportions (17% and 20%, respectively).

In the third experiment, germination of seeds from both experienced and naïve maternal lines was highly suppressed by a low concentration of (±)-catechin
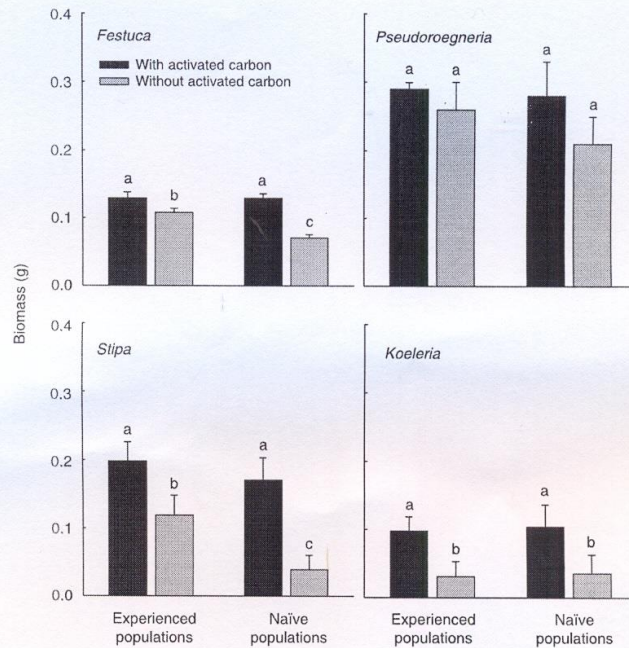
Fig. 2 Total biomass of grasses grown from seeds collected from North American native grasses that had either experienced and survived invasion by *C. maculosa* or had not experienced invasion by *C. maculosa*. These plants were grown in competition with *C. maculosa* in sand or in sand modified with 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, $F_{naïveté} = 7.894$, d.f. = 1147, $P = 0.006$; $F_{activated carbon} = 33.748$, d.f. = 1147, $P < 0.001$; $F_{naïveté \times activated carbon} = 7.794$, d.f. = 1147, $P = 0.006$. We did not use more than one site per species so site was not included in the model. ANOVA results for individual species are presented in the text of the results.
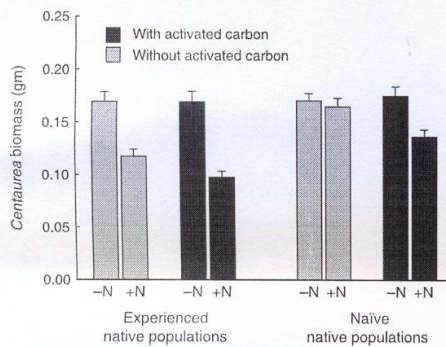
Fig. 3 Total biomass of *C. maculosa* grown in competition with North American grass species grown from seed collected from plants that had experienced and survived invasion by *C. maculosa*, or that had not experienced invasion. Means are for the effects of five native species combined. Native plants were grown in competition with *C. maculosa* in sand or in sand modified with activated carbon to ameliorate the allelopathic effects of *C. maculosa*. +N refers to *C. maculosa* grown with native neighbours, and –N refers to *C. maculosa* grown without native neighbours. Error bars represent one standard error. In a full ANOVA, $F_{naïveté} = 16.601$, d.f. = 1310, $P < 0.001$; $F_{activated carbon} = 3.790$, d.f. = 1310, $P = 0.052$; $F_{neighbour} = 55.12$, d.f. = 1310, $P < 0.001$; $F_{naïveté \times activated carbon} = 0.025$, d.f. = 1310, $P = 0.874$; $F_{naïveté \times neighbour} = 12.306$, d.f. = 1310, $P = 0.001$. In preliminary ANOVA the effect of site was weak and we did not include site in the model.

(Fig. 4). However, the effects of (±)-catechin on seed germination for naïve and experienced native grasses suggested selection for tolerance to the allelochemical. Corroborating the results of the first two experiments, 16% of *Stipa* seeds from experienced maternal lines germinated when exposed to (±)-catechin, whereas no seeds from naïve maternal lines germinated in (±)-catechin ($F_{catechin} = 11.95$, d.f. = 1,36, $P = 0.002$; $F_{naïvete} = 7.20$, d.f. = 1,36, $P = 0.011$). The results of the previous two experiments suggested that *Pseudoroegneria* would demonstrate the most tolerance to (±)-catechin, and this was supported by data from the population from the Bison Range. However, the two populations of *Pseudoroegneria* tested in this experiment were substantially different in their response to (±)-catechin. Germination of seeds from the Mt Jumbo population was almost completely suppressed by (±)-catechin; however, 6% (3 of 10 maternal lines) of seeds from experienced maternal lines germinated in comparison with none of the seed from naïve maternal lines. This small percentage of germinants from the experienced maternal lines, however, was not statistically different than the zero germination of the naïve maternal lines. Seeds from both experienced and naïve maternal lines of *Poa* (data not shown) and *Koeleria* were completely suppressed by (±)-catechin.
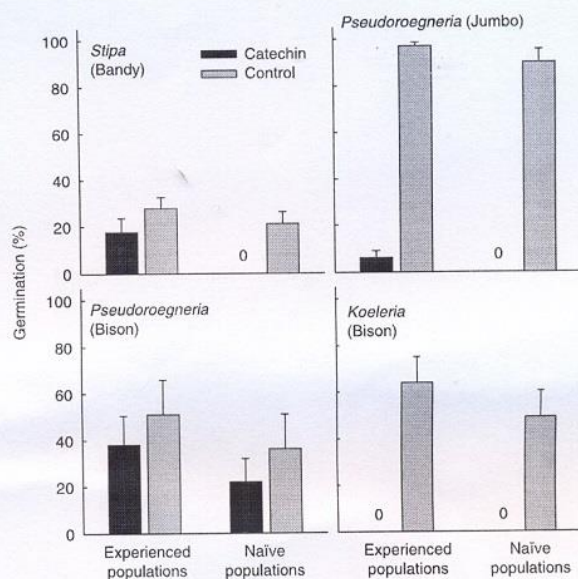
Fig. 4 Germination of seeds from populations of native species that had survived *Centaurea* invasions (experienced) and from populations of native species that had not experienced *Centaurea* invasions (naïve). Seeds of *Stipa occidentalis, Pseudoroegneria spicata* (a naïve and an experienced population was collected at each of two different sites) and *Koeleria cristata* were germinated in solutions containing (±)-catechin and control solutions. Error bars denote 1 SE. For *Stipa*, germination in catechin was significantly higher for seeds from experienced maternal plants than for seeds from naïve maternal plants (($F_{catechin}$ = 11.95, d.f. = 1,36, P = 0.002; $F_{naïveté}$ = 7.20, d.f. = 1,36, P = 0.011, post-ANOVA Tukey, P = 0.051). There was no other significant difference of the effect of catechin on experienced vs. naïve populations.

Discussion

To our knowledge, the evidence presented here is the first for selection occurring in response to the general effects of root exudates and a specific allelopathic chemical. Other researchers, however, have reported that co-occurring genotypes of a species interact less strongly than genotypes of the same species that occur in different places (Turkington & Harper 1979; Martin & Harding 1981; Evans *et al.* 1985; Turkington & Mehrhoff 1991). Ehlers & Thompson (2004) found that *Bromus erectus* showed adaptive responses to different biochemical soil modifications created by local thyme chemotypes. These studies support the notion raised here that interactions among plant species may result in selection. Our experiments demonstrate that native grasses vary substantially in their susceptibility to *C. maculosa* and (±)-catechin, and suggest that selection for resistance to the invader and tolerance to its allelochemical may be occurring for several species. Individuals, cloned and grown from seed, of native grass species that had survived *C. maculosa* invasion were affected less by general root exudates than conspecific individuals that had never experienced invasion. Also, grasses whose parents had experienced *C. maculosa* invasion suppressed *C. maculosa* growth more than grasses grown from seed of naïve parents. However, the lack of a significant naïveté by carbon interaction in this experiment suggests that factors other than tolerance to allelopathy may play

a role in the evolution of resistance. Finally, seeds collected from experienced and naïve individuals showed a similar pattern of differences in tolerance.

We cannot rule out physiological acclimatization, as opposed to genetic selection, in the first experiment with clones, and we do not know whether the grasses we collected were simply surviving remnants or if they recruited after invasion. However, these results suggest that invasion may alter the trait composition of native populations such that there are greater proportions of genotypes with traits that confer resistance to *C. maculosa*. Natural selection for resistance traits establishes the potential for evolution. As an example of potential genetic changes in natives exposed to exotic invasion, Mealor *et al.* (2005) conducted genetic (intersimple sequence repeat, ISSR) analyses of four native perennial grass species growing in and out of patches of *Acroptilon* (formerly *Centaurea*) *repens* and found that populations exposed to long-term coexistence with the invader, differed genetically from adjacent non-invaded populations. However, these genetic differences were not examined for their relationship to greater competitive ability with the invaders.

We cannot exclude the possibility that maternal effects may explain our results, but no experienced populations (the better competitors against *C. maculosa*) produced larger seeds than conspecific naïve populations, and three species had significantly smaller seeds in experienced populations than in naïve populations (R. M. Callaway, unpublished data). This is the opposite

of what would be expected if maternal effects were to explain the generally superior competitive ability of experienced native populations relative to naïve native populations. Furthermore, when grown without *C. maculosa*, seedlings from experienced or naïve seed sources did not differ in size, suggesting that maternal effects may have been minimal. Eliminating maternal effects in wind-dispersed species is difficult, because cross-pollination among lines is hard to prevent in common gardens. Nevertheless, confirming our evidence for the evolution of resistance will require eliminating the possibility of maternal effects in common garden or artificial selection experiments.

It is also possible that populations in areas not invaded by *C. maculosa* had characteristics that made them inherently resistant to the invader. However, sites were well replicated and it is unlikely that different site conditions would confer resistance to both the general competitive effects of a new neighbour and a unique chemical exuded from its roots.

Some native species showed evidence of relatively rapid evolution of tolerance to novel allelochemicals, but there is no evidence that *C. maculosa* invasions are showing signs of decline. We found some evidence for selection of tolerance in our highly controlled experiments, but it is important to note that even the experienced and tolerant lines were still outcompeted by *C. maculosa*. 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.

Our initial evidence for selection in response to the allelopathic effects of a neighbour suggests that breeding resistant natives may provide a new tool for combating the explosion of exotic invaders around the world. Our results also have important implications for understanding the organization and invasion of natural plant communities. As hypothesized by the Russian ecologist T.A. Rabotnov (1982), and supported by recent empirical results, some invasive exotic plants may be replacing native plant communities because they produce and release harmful chemicals that the naïve native inhabitants have never experienced. This process certainly does not exclude the occurrence of other important processes in exotic invasions (Hierro *et al.* 2005). Invaded ecosystems will almost certainly undergo irreversible changes; however, the evolution of resistance by natives may provide some degree of 'biotic resistance' (Shea & Chesson 2002; Von Holle 2005) and ultimately re-establish some degree of community equilibrium and species coexistence.

Acknowledgements

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