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Novel weapons and invasion: biogeographic differences in the competitive effects of *Centaurea maculosa* and its root exudate (±)-catechin

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Abstract Recent studies suggest that the invasive success of *Centaurea maculosa* may be related to its stronger allelopathic effects on native North American species than on related European species, one component of the "novel weapons" hypothesis. Other research indicates that *C. maculosa* plants from the invasive range in North America have evolved to be larger and better competitors than conspecifics from the native range in Europe, a component of the "evolution of increased competitive ability" hypothesis. These hypotheses are not mutually exclusive, but this evidence sets the stage for comparing the relative importance of evolved competitive ability to inherent competitive traits. In a competition experiment with a large number of *C. maculosa* populations, we found no difference in the competitive effects of *C. maculosa* plants from North America and Europe on other species. However, both North American and European *C. maculosa* were much better competitors against plants native to North America than congeners native to Romania, collected in areas where *C. maculosa* is also native. These results are consistent with the novel weapons hypothesis. But, in a second experiment using just one population from North America and Europe, and where North American and European species were collected from a broader range of sites, competitive interactions were weaker overall, and the competitive effects of *C. maculosa* were slightly stronger against European species than against North American species. Also consistent with the novel weapons hypothesis, (±)-catechin had stronger effects on native North American species than on native European species in two experiments. Our results suggest that the regional composition of the plant communities being invaded by *C. maculosa* may be more important for invasive success than the evolution of increased size and competitive ability.

Keywords Allelopathy · (±)-Catechin · Competition · Evolution of increased competitive ability (EICA) · Invasion · Novel weapons hypothesis

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Introduction

Successful exotic plant invasion has been linked to evolutionary changes in the invading species (Blossey and Nötzold 1995; Ellstrand and Schierenbeck 2000; Siemann and Rogers 2001, 2003a, b) and to the evolutionary naïveté of species in invaded systems (Callaway and Aschehoug 2000; Mallik and Pellissier 2000; Callaway and Ridenour 2004; Vivanco et al. 2004; Cappuccino and Arnason 2006; Callaway et al. 2008; Inderjit et al. 2008b). There is evidence for both processes, but no experiments have attempted to compare their relative importance using the same invasive species. These invasive processes are not mutually exclusive, and such a comparison does not cover the gamut of all important mechanisms for invasions (Hierro et al. 2005), but there are interesting implications for understanding plant community organization. If a plant species can rapidly evolve "invasiveness," then long-term local adaptation to a particular habitat would not appear to be crucial for community dominance. On the other hand, if a plant species can successfully invade because it possesses a trait to which native plant species are not adapted, then it would appear that evolutionary relationships among plant species may have important effects on their relative distributions and abundances.

The most common context in which invasion has been attributed to the evolution of an introduced species is the EICA or "evolution of increased competitive ability" hypothesis (Blossey and Nötzold 1995). In this case, release from natural enemies is thought to result in strong favorable selection on genotypes that allocate less to herbivore defense (see Janzen 1975), and more to growth. Greater growth could make these new genotypes more competitive than their predecessors in the native range and lead to invasive success. A number of other studies have shown that invasive genotypes are larger or more reproductive than congeners in their native range (Blossey and Nötzold 1995; Siemann and Rogers 2001, 2003a, b; Wolfe 2002; Jakobs et al. 2004), but conclusive support for the full causal process proposed for EICA is less common (Maron et al. 2004a; Bossdorf et al. 2005; Genton et al. 2005; McKenney et al. 2007; Ridenour et al. 2008). Importantly for our study, *Centaurea maculosa* Lam. (spotted knapweed, recently reported as *Centaurea stoebe* L. ssp. *micranthos* (Gugler) Hayek [USDA, NRCS 2007]) shows evidence for evolutionary changes towards increased size and competitive ability in the invaded range (Ridenour et al. in press). *Centaurea maculosa* is native to Europe, where it is relatively uncommon, and was introduced into North America in the late 1800s (Sheley et al. 1998; LeJeune and Seastedt 2001), where it is among the most destructive and successful invasive plant species in the northwestern United States (Roché and Roché 1988; Müller-Schärer and Schroeder 1993).

Invasion as a result of disrupting relationships among coadapted species within communities has most often been studied in the context of enemy release from coevolved specialist insect herbivores (Keane and Crawley 2002; Müller-Schärer et al. 2004). More recently, the possibility of disrupted coadaptation at a broader scale within communities as a driver of invasions has been considered in the context of the "novel weapons hypothesis" (Rabotnov 1982; Callaway and Ridenour 2004). This is the idea that some invaders may succeed because they possess unique allelopathic, defense, or antimicrobial biochemistry to which naïve natives have not adapted. There are a number of studies that are consistent with this hypothesis (Callaway and Aschehoug 2000; Mallik and Pellissier 2000; Bais et al. 2003; Vivanco et al. 2004; Cappuccino and Carpenter 2005; Carpenter and Cappuccino 2005; Cappuccino and Arnason 2006; Stinson et al. 2006; Callaway et al. 2008).

Centaurea maculosa appears to possess a "novel weapon." *Centaurea maculosa* exudes the compound (±)-catechin from its roots into its rhizospheres (Bais et al. 2003; Weir et al. 2003; Blair et al. 2005; Ridenour et al. 2008; N. Tharayil, unpublished data), which inhibits the growth of neighboring competing plants (Bais et al. 2003; Weir et al. 2003, 2006; Callaway et al. 2005; Perry et al. 2005a, b; Thelen et al. 2005; Thorpe 2006; Rudrappa et al. 2007; Inderjit et al. 2008a, b). A number of other authors have reported phytotoxicity of the (+)-catechin form (Buta and Lusby 1986; Iqbal et al. 2003; Furubayashi et al. 2007; Simões et al. 2008), and the (−)-catechin form has been reported to inhibit green algae (D'Abrosca et al. 2006). However, other authors have reported no phytotoxic effects of forms of catechin or phytotoxicity only at unreasonably high concentrations (Blair et al. 2005; S. Duke, personal communication; also see Furubayashi et al. 2007). There is also initial evidence that *Centaurea* is more allelopathic to North American native species than congeneric European native species in vitro (Bais et al. 2003; Inderjit et al. 2008b) and in the field (Thorpe 2006). However, this evidence is limited by the low number of species tested, the relatively high concentrations of the root exudate used, or the artificial nature of in vitro experiments.

Evidence that *C. maculosa* may have evolved greater competitive ability but also possesses a novel weapon sets the stage for the fundamental question addressed in this paper: are novel competitive or allelopathic effects of *C. maculosa* more inhibitory to North American plant species than the greater competitive ability demonstrated by North American *C. maculosa* genotypes? We tackled this question by means of a greenhouse experiment comparing the biomass of *C. maculosa* from North American and European populations, experiments with *C. maculosa* from

North American and European populations competing against congeneric North American and European competitors, and experiments applying (±)-catechin to congeneric North American and European competitors.

Methods

Comparison of North American and European populations

We used *C. maculosa* plants from nine North American and eight European populations that were selected randomly from larger pools of populations used in previous experimental comparisons (Ridenour et al. 2008). Ridenour et al. (2008) reported that plants from North American populations of *C. maculosa* were larger than plants from European populations, but we repeated the experiment with the specific populations used in our competition experiments. The phylogeny of *C. maculosa* is not fully resolved, but what is called *C. maculosa* in North America is most likely to be *C. stoebe* in Europe (http://plants.usda.gov/), which can be either diploid or tetraploid (Müller 1989). North American populations appear to be almost exclusively tetraploid (H. Müller-Schärer, personal communication). We did not measure the ploidy of our European populations, but the populations sampled were identified in Europe as *C. stoebe micranthos*, the subspecies considered to be tetraploid in Europe, and the European taxon likely to be most closely related to what is called *C. maculosa* in North America. The subspecies *C. stoebe stoebe* is likely to be the diploid form, and this was avoided in our European collections. Although we attempted to keep ploidy constant by using the *C. stoebe micranthos* taxon from Europe, it is important to note that the morphological differences between subspecies do not clearly correspond with differences in ploidy (H. Müller-Schärer, personal communication), and therefore the effects of ploidy could confound the effects of continent in our experiments. However, Ridenour et al.'s (2008) and Müller's (1989) results suggest that larger ploidy may not be the main reason that North American plants are larger. For example, Ridenour et al. (2008) found that *C. maculosa* plants from tetraploid North American populations were larger than plants from tetraploid European populations, and a recent outdoor common garden experiment comparing other populations demonstrated that tetraploid North American plants were larger than tetraploid European plants (T. Bassett and R.M. Callaway, unpublished data).

For the experiment comparing the size of North American and European populations, all plants were grown from seed in 2.4 l pots (18 cm diameter, 22 cm depth) filled with 25% field soil from Montana and 75% 20/30 grit sand. Eight individual plants were grown for each population. Greenhouse temperatures were kept between 15 and 30°C. Natural light was supplemented by metal halide bulbs, and PAR during the day remained above 1,200 μmol m^{-2} s^{-1}, well above the light saturation point of *Centaurea* leaves. Plants were watered once every two days to be sure that larger plants did not become relatively more water-limited than smaller plants, and a nutrient solution of 0.68 g/l of water-soluble fertilizer (15-2-20, The Scotts Company, Marysville, OH, USA) was applied every three weeks. In other words, we compared the characteristics of these populations under good growing conditions. We chose greenhouse rather than common garden experiments to avoid introducing novel European genotypes (via pollen and seeds) to North America. After 135 days all plants were harvested, dried at 60°C for three days, and the total mass was weighed. We used nested ANOVA in the PROC GLM module within SAS utilizing Type III sum of squares (version 9.1), where continent of population origin (Europe vs. North America) was treated as a fixed factor and population nested within continent was treated as a random factor.

Competition experiment 1

We conducted a competition experiment in the Campus greenhouse at the University of Montana, in which plants from the nine North American and eight European populations of *C. maculosa* (see the "Electronic supplementary material," or "ESM," S1) were each planted in competition with four native North American species (i.e., *Achillea millefolium*, *Linum lewisii*, *Pseudoroegneria* (Nee *Agropyron*) *spicata*, and *Stipa comata*) and four native European congeners or near-congeners (i.e., *Achillea millefolium*, *Agropyron cristatum*, *Linum austriacum*, and *Stipa capillata*). For the control pots, there was only one plant per pot. Native North American species were from western Montana and native European species were collected in areas where *C. maculosa* (*C. stoebe micranthos*) also occurred near Iasi, Romania (ESM, S2). In this experiment, all plants were grown from seeds in 525 ml pots (6.4 cm diameter, 25 cm deep) filled with the same substrate as in the first experiment. For each competitor species, one individual was grown in competition against one *C. maculosa* individual from each population from each continent, providing nine replications for each native North American species and eight for each native European species. Plants were grown alone for controls. Plants were watered and fertilized as described above, and greenhouse temperatures and lighting were as described for the previous experiment. This experiment ran from October 12, 2004 through January 22, 2005. At the end of the experiment, all plants were harvested, washed, and separated into shoots and roots. Plants were dried at 60°C for three consecutive days and then weighed. To evaluate the response of *C. maculosa* to competitors, the effects of *C. maculosa* region (North America vs. Europe, fixed factor) and competitor region (fixed factor) were analyzed with a two-way ANOVA (SPSS 13.0, SPSS Inc., Chicago, IL, USA). To evaluate the responses of each related pair of competitors, a two-way ANOVA was used to test the effects of *C. maculosa* region (fixed factor) and competitor region (fixed factor) (SPSS 13.0, SPSS Inc.).

Competition experiment 2

We conducted a second competition experiment in the Diettart greenhouse at The University of Montana. Our goals were to reduce noise due to among-population geographical genetic variability in *C. maculosa* within a continent, to increase the number of native species tested, and to broaden the regional area from which native European species were collected (in the first experiment all European competitors were from fields in Romania where *C. maculosa* occurred). In other words, do results obtained using a restricted local set of competitors correspond with results obtained from competitor species collected regionally? We did this by only using seeds from the North American *C. maculosa* population with the smallest plants (Washington, Fig. 1, electronic supplementary material, S1) and seeds from the European population with the largest plants (Romania-1, Fig. 1, ESM, S1) in our first experiment. Thus, this experiment does not test for differences between European and North American *C. maculosa* populations, but does provide a better replicated, and perhaps more conservative, test of potential biogeographical differences among European and North American competitors. We used nine native species collected as seed from western Montana, one species collected from Idaho, and 15 native species collected as seed from several different places in Europe (we could not identify all plants to species, ESM, S2). For each of these 25 species, we grew eight replicates in competition with the North American *C. maculosa* and eight with the European *C. maculosa*. Each species was also planted alone for controls ($n = 8$). The pots, substrate, growth conditions and harvesting procedure were the same as in competition experiment 1. This experiment ran from December 14, 2005 through March 14, 2006. All plants were grown from seeds, most of which germinated 3–17 days following the planting. We used a two-way ANOVA with competitor region and competition as fixed factors to test their effects on the total biomass of competitors (SPSS 13.0, SPSS Inc.).

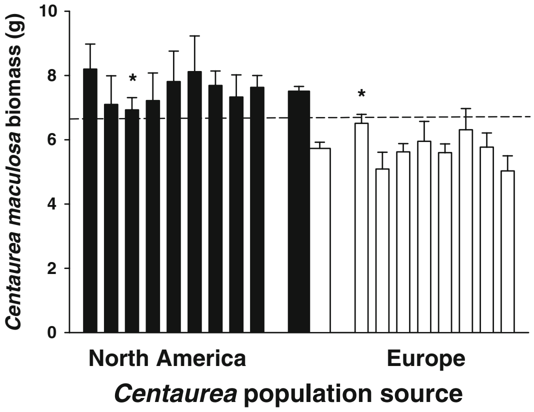

Fig. 1 Biomasses of *Centaurea maculosa* from North American and European populations. *Narrow bars* are mean + 1 SE for each population, *wide bars* (center of figure) are means + 1 SE for each region using population means. Full ANOVA is in ESM, S3. *Asterisks* denote the populations used for the second competition experiment

(±)-Catechin experiment 1

The (±) racemic form of catechin was initially reported to frequently occur at or above ≈1,000 μg g^{-1} in soils (Bais et al. 2003; Perry et al. 2005a; Thelen et al. 2005), but more detailed and extensive soil analyses have convincingly demonstrated that soil concentrations are much lower. Using a lower detection limit of 25 μg g^{-1}, Perry et al. (2007) found (±)-catechin in less than 5% of *C. maculosa* rhizospheres, but at a site sampled repeatedly they recorded a pulse, in which (±)-catechin was found in all 20 rhizospheres tested, of 650 ± 450 (SD) μg g^{-1}. More sensitive analyses have found much more frequent occurrences of very low concentrations, but a maximum concentration of 1 μg g^{-1} (Blair et al. 2006).

Applied concentrations of (±)-catechin result in far lower concentrations in solution, sand, and soil than calculated from the application rate (Inderjit et al. 2008a; J. Pollock and R.M. Callaway, unpublished data). This may be due to the interaction of the compound with components in the soils and oxidation. Therefore, calculating phytotoxic concentrations in soil, equivalent to those measured in situ and based on applied doses, is not an accurate experimental calibration approach for measured soil concentrations in the field. To calibrate our applied concentrations to soil concentrations from the literature, and in situ effective experimental concentrations actually experienced by the target plants, we first measured the fate of experimentally added (±)-catechin at 100 μg g^{-1} sand over a seven-day period. Pure (±)-catechin (Shivambu International, New Delhi, India) was dissolved in Milli-Q water (double distilled) by gently heating the solution to ≈80°C and stirring to achieve a final concentration of 300 μg ml^{-1}. (±)-Catechin was applied at 100 μg per g dry weight of the sand substrate; however, repeated measurements of pure (±)-catechin in the sand after application showed an immediate decrease to 11 ± 2 [1 SE] μg g^{-1} (measured within 1 h of application), 9 ± 4 μg g^{-1} three days after application, and 10 ± 4 μg g^{-1} seven days after application.

We applied (±)-catechin in the way described in the previous paragraph to plants in three pulses, 15–20 days apart, starting at day 40 after planting, with each pulse consisting of 100 μg g^{-1} added to the sand. Inderjit et al. (2008a) showed that repeated pulses do not increase the total amount of (±)-catechin measurable in sandy soils, but maintain low concentrations at 0–8% of the applied amounts. We ensured that the (±)-catechin solutions did not directly contact seedling shoots during application. The first pulse of (±)-catechin was applied on May 9, 2006. We used ten North American and twelve European species. Nine replicates of each species for each treatment ((±)-catechin or no (±)-catechin) were grown in 250 cm^3 rocket pots, 5 cm top diameter and 18 cm deep. We used pure 20/30 grit silica sand to eliminate possible confounding soil biota effects (see Callaway et al. 2004). All plants were grown from seeds.

Based on what we consider to be the most extensive and accurate measurements of soil concentrations (Blair et al. 2006; Perry et al. 2007), our initial application of 3 × 100 μg g^{-1} soil was high but well below the high range of episodic measurements by Perry et al. (2007). Our preliminary measurements indicated that soil concentrations of catechin rapidly stabilized at ≈10 μg g^{-1} after 100 μg g^{-1} pulses. (±)-Catechin accumulation in solutions containing *C. maculosa* seedlings in controlled environments has been reported at 83–185 μg ml^{-1} (Bais et al. 2002), 5–35 μg ml^{-1} (Weir et al. 2003, 2006), 42 ± 12 (1 SE) μg ml^{-1} (Ridenour et al. 2008), and ≤2.44 μg ml^{-1} (Blair et al. 2005), lower than the brief pulses of 300 μg ml^{-1} that occurred during application.

Pots were watered, fertilized, and grown in the same conditions described above. At the end of the experiment, all plants were harvested, washed, separated into shoots and roots, dried at 60°C for three days, and then the total biomass was weighed. This experiment ran from March 29, 2006 through July 18, 2006 at The University of Montana. We tested the effects of (±)-catechin on North American and European species with a two-way ANOVA, with (±)-catechin and region as fixed factors, and species as a random factor (SPSS 13.0, SPSS).

(±)-Catechin experiment 2

Because the phytotoxic effects of (±)-catechin are controversial and vary extensively among experiments, soils, and species (Thelen et al. 2006; Thorpe 2006; Inderjit et al. 2008a, b), we conducted a second experiment using a different batch of (±)-catechin (also from Shivambu International, New Delhi, India) in a different place, using species collected at other times and from new collection sites, and performed by different experimenters. For this experiment we used five congeneric or near-congeneric pairs of species collected as seed from natural communities in western Montana and from Europe, where *C. maculosa* also occurred. These pairs were *Festuca idahoensis–F. ovina* (France), *Pseudoroegneria spicata–Agropyron repens* (Romania), *Linum lewisii–L. austricum* (Romania), *Koeleria macrantha–K. vallesiana* (France), and *Artemisia frigida–A. absinthium* (Romania). Ten seeds of each of the ten different species were placed in each of eight sterilized Petri dishes containing 90 mm Whatman #1 filter paper for a total of 80 dishes and 800 seeds. Of the eight dishes assigned to each species, four were randomly chosen as controls and four for the (±)-catechin treatment. The control was 10 ml methanol diluted with 990 ml deionized water, and the treatment was 100 mg (±)-catechin mixed with 10 ml methanol and diluted with 990 ml deionized water to achieve an initial concentration of 100 μg ml^{-1}, within the ranges of the concentrations shown to accumulate in buffered solutions. Solutions were prepared on June 28, 2007, and immediately 4 ml of either control or treatment solution was applied to the seeds in each Petri dish. Because (±)-catechin oxidizes rapidly, it is crucial to use fresh solutions. Germination and mortality was recorded and 2 ml of freshly prepared solutions were added to each Petri dish every two days until July 14, 2007. We tested the effects of (±)-catechin on the germination and percent mortality of North American and European species ($n = 4$ for each species–treatment combination) using a two-way ANOVA with (±)-catechin and region as fixed factors and species as a random factor (SPSS 13.0, SPSS Inc.).

Results

Comparison of North American and European populations

The total biomass of *C. maculosa* plants from North American populations was on average 31% greater than that of European populations (Fig. 1; see ESM, S3 for full ANOVA). Biomass did not differ significantly among populations, where population was treated as a random effect ($F_{\text{region}} = 36.55$; $df = 1, 16$; $P < 0.001$; $F_{\text{population}} = 0.01$; $df = 1, 16$; $P = 0.914$). The mean biomass of North American populations (7.51 ± 0.15 g, 1 SE) was significantly higher than the grand mean (6.62 g), whereas the mean biomass of the European populations (5.73 ± 0.19 g) was significantly lower than the grand mean. The means of all North American populations exceeded the means of all European populations.

Competition experiment 1

There was no difference in the response of *C. maculosa* from Europe versus that from North America to competition, and the effect of competitor mass as a covariate was not significant ($P = 0.060$; Fig. 2; all competitor species

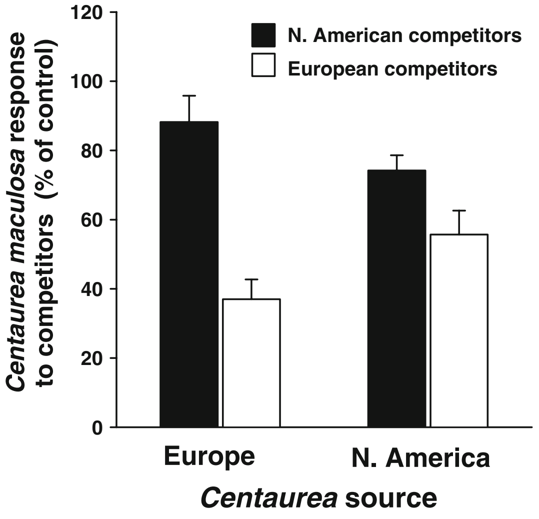

Fig. 2 Biomasses (mean + 1 SE) of European and North American *Centaurea maculosa* populations in response to competitors from either North America or Europe in the first competition experiment. See ESM, S3 for full ANOVA

combined, $F_{Centaurea\ \mathrm{region}} = 0.01$; $df = 1, 132$; $P = 0.954$; see ESM, S3 for full ANOVA). When the response of *C. maculosa* was considered for the effect of each competitor species alone, results were similar, with the exception of *Pseudoroegneria* and *Agropyron* (*Achillea*, $P_{Centaurea\ \mathrm{region}} = 0.819$; *Stipa*, $P_{Centaurea\ \mathrm{region}} = 0.906$; *Pseudoroegneria–Agropyron*, $P_{Centaurea\ \mathrm{region}} = 0.045$; *Linum*, $P_{Centaurea\ \mathrm{region}} = 0.948$). However, European competitors suppressed *C. maculosa* from both regions much more than North American competitors ($F_{\mathrm{competitor\ region}} = 23.44$, $df = 1, 16$, $P < 0.001$). European competitors performed better in competition with *C. maculosa* from North American populations than from European populations ($F_{Centaurea\ \mathrm{region} \times \mathrm{competitor\ region}} = 5.471$, $df = 1, 132$, $P = 0.021$).

North American competitors were far more inhibited by *C. maculosa* from both regions than were European competitors (Fig. 3; see ESM, S3 for full ANOVAs). The biomass of *A. millefolium* from North America was reduced by more than 75% when competing with either North American or European *C. maculosa*, whereas the biomass of *A. millefolium* from Europe was not affected by competition with *C. maculosa*. The biomass of *Stipa comata* (North America) was reduced by ≈50% by *C. maculosa* from both regions, whereas *S. capillata* (Europe) was reduced by only ≈20% by both North American and European *C. maculosa*. The *Pseudoroegneria–Agropyron* pair showed a more complex response, with the biomass of *Pseudoroegneria* reduced by ≈25% by *C. maculosa* from both regions (Fig. 3; $P_{\mathrm{competitor\ region}} = 0.030$). In contrast, *Agropyron* (Europe) tended to be larger when planted with *C. maculosa* from Europe than when alone (a nonsignificant increase of ≈25%), but *Agropyron* biomass was reduced by North American *C. maculosa*, yielding an overall significant effect of *C. maculosa* region ($P_{Centaurea\ \mathrm{region}} = 0.045$). This basic pattern was similar for *Linum*, although the strongest effect was the regional source of the *Linum* species, with the North American *L. lewisii* suppressed by *C. maculosa* more than the European *L. austriacum*. To summarize, the results of this experiment showed minor effects of the regional source of *C. maculosa* on competitive outcomes, but also that native European species were much better competitors against *C. maculosa* than native North American species.

Competition experiment 2

The results of the second competition experiment, designed to expand the number of native European and North American species tested in competition with *C. maculosa* and to test competitor species collected from a much broader geographical range, did not corroborate the results of the first experiment, whether we tested congeneric pairs alone or all species combined (Fig. 4; for individual species see ESM, S3 for full ANOVA and S4). Because we only used a single population of *C. maculosa* from each continent, we could not test the effect of continent, but in contrast to what was found in the first competition experiment, native European species (all species combined) were slightly weaker competitors against plants from the two *C. maculosa* populations we chose for this experiment. When all species were considered together, the total biomass of native European plants was reduced to 72% of the controls (see Fig. 3 for a general comparison of proportional competitive effects) when competing with *C. maculosa*, whereas the total biomass of native North American plants was reduced to only 82% of that of the controls when competing with *C. maculosa* (Fig. 4; for all species combined: $F_{\mathrm{competitor\ region}} = 80.60$, $df = 1, 521$, $P < 0.001$; $F_{\mathrm{competition}} = 13.64$, $df = 1, 521$, $P < 0.001$; $F_{\mathrm{competitor\ region} \times \mathrm{competition}} = 4.15$, $df = 1, 521$, $P = 0.042$). A significant competition by region interaction indicated that the competitive effect of *C. maculosa* was significantly stronger against European species than against North American species. The responses of individual European and North American species to *C. maculosa* were highly variable and relatively weak (ESM, S4). For example, unlike in the first experiment, *Pseudoroegneria spicata* and *Agropyron cristatum* did not respond to competition from *C. maculosa* at all ($P_{\mathrm{competition}} = 0.875$), whereas *Potentilla gracilis* and *Potentilla* sp. were very sensitive to competition ($P_{\mathrm{competition}} < 0.0001$).

There were no significant correlations between the proportional response of species to competition from *C. maculosa* and the total mass of *C. maculosa* competitors, irrespective of North American origin ($r^2 = 0.011$, $P = 0.614$), European origin ($r^2 = 0.123$, $P = 0.085$) or a

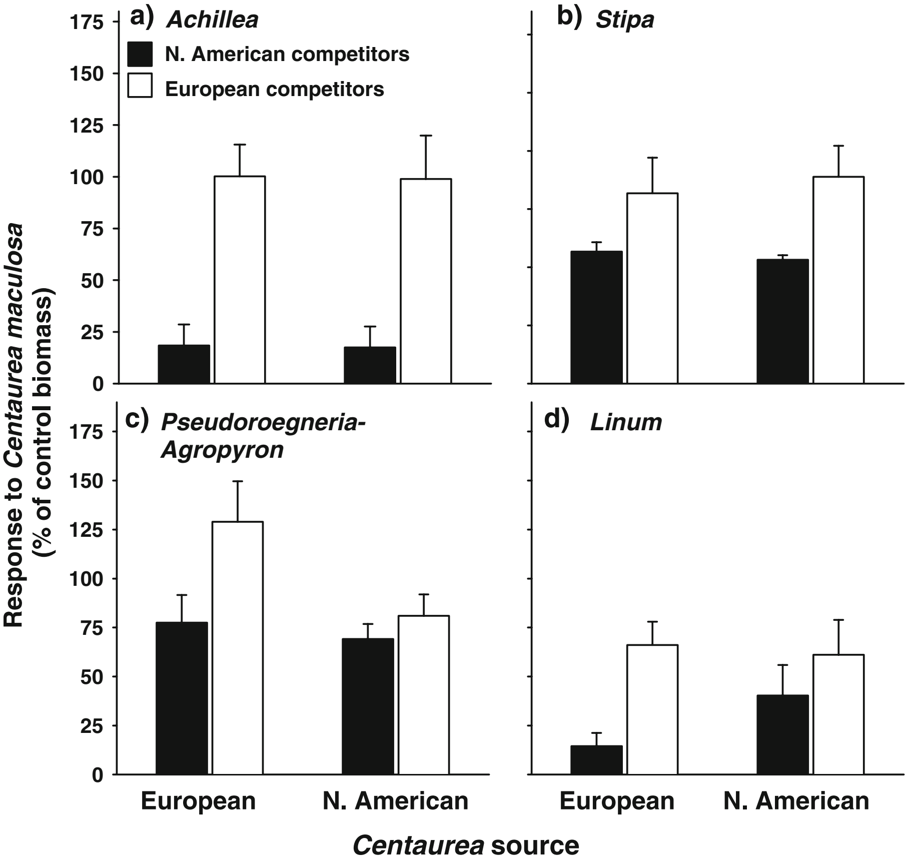

Fig. 3 Biomasses (mean + 1 SE) of four species from North America and four related species from Europe in competition with *Centaurea maculosa* from European and North American populations. See ESM, S3 for full ANOVA

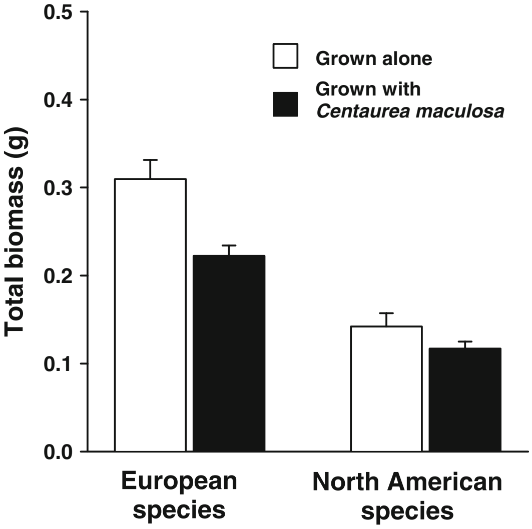

Fig. 4 Total biomasses (mean + 1 SE) of European and North American competitors when grown alone or with *Centaurea maculosa* in the second competition experiment

combination of both origins ($r^2 = 0.044$, $P = 0.142$). This, similar to the general lack of significant effects of *C. maculosa* size as a covariate in experiment 1 (see ESM, S3), suggests that the competitive effects of *C. maculosa* were not highly size-dependent in this experiment.

(±)-Catechin experiment 1

(±)-Catechin had much stronger effects on native North American species than on native European species (Fig. 5; see ESM, S3 for full ANOVA). For European species, 6.2 ± 3.2% of the individuals died in the no-(±)-catechin treatment, whereas 4.4 ± 2.4% of the individuals died in the (±)-catechin treatment ($t_{\text{catechin}} = 0.166$, $df = 1, 24$, $P = 0.600$). However, for North American species, 8.9 ± 3.2% of the individuals died in the no-(±)-catechin treatment versus 50.0 ± 7.7% of the individuals in the (±)-catechin treatment ($t_{\text{catechin}} = 19.841$, $df = 1, 20$, $P < 0.0001$). The effect of (±)-catechin on the mortality of North American species was highly variable (ESM, S5). For example, the effects of (±)-catechin on the mortality of *Artemisia frigida*, *Festuca idahoensis*, and *Poa secunda* were much weaker than on all other species.

Mortality reduced the replication of some North American species to the point that the statistical analysis of biomass should be considered with caution, because plants that died were excluded from the analysis of biomass. However, for all species considered together, and in a simple analysis with individual species means as replicates, (±)-catechin significantly inhibited the total biomass of North American natives but not European natives (Fig. 6; see ESM, S6 for individual species). In a three-way ANOVA, there was a

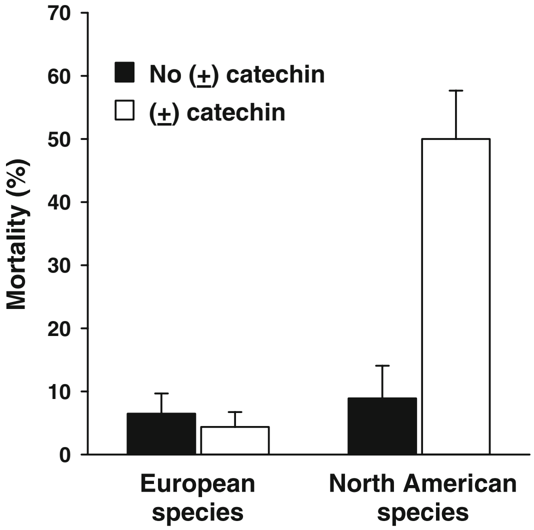

Fig. 5 Effects of (±)-catechin on the mortality of European and North American native plant species. *Bars* show means + 1 SE

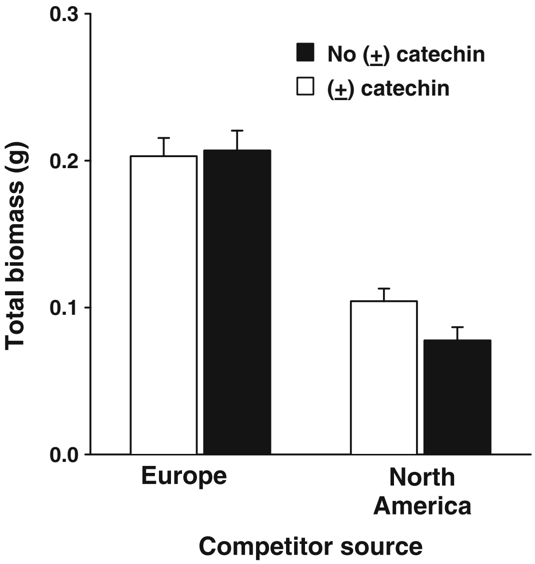

Fig. 6 Effects of (±)-catechin on the total biomasses of European and North American native plant species, combined by region. *Bars* show means + 1 SE for each treatment for each species. The ANOVA table and individual species results are shown in the ESM, S6

significant interaction between the effect of (±)-catechin and region (see legend for Fig. 6), indicating that (±)-catechin reduced the biomass of North American natives more than it reduced the biomass of European natives.

(±)-Catechin experiment 2

(±)-Catechin did not have a significant effect on the germination or subsequent mortality of European species, but decreased the germination of North American species by 46% and increased the mortality of germinants from 5% in the control to 50% in the treatment (Fig. 7; see ESM, S3 for full ANOVA). The effect of (±)-catechin was more consistent across North American species than in experiment 1, with all species showing reduced germination and increased mortality.

Discussion

Our results suggest that the larger size of *C. maculosa* plants from North American populations, as demonstrated by Ridenour et al. (2008) and here, may not be as important for competitive dominance as possessing a "novel weapon." In our first competition experiment, there were no differences in the competitive effects or responses of *C. maculosa* plants from European and North American populations. Two experiments demonstrated that a root exudate of *C. maculosa*, (±)-catechin was more effective against North American species than European species, but because of the contrasting results from the second competition experiment our conclusions remain tentative.

For the first experiment comparing size among North American and European populations, it is important to note that we measured final biomass and not growth rates. This is important, because plants may have identical growth rates but very small differences in initial seed or seedling size would produce substantial differences in final size. If growth rate is a more important determinant of competitive ability than plant size (but see Goldberg 1987), then we may have missed important relationships between growth rate and competitive ability. Relevant to this concern, we found in other experiments that the mass of individual *C. maculosa* seeds collected from North American populations was on average 42% more than that of seed from European populations (W. He and R.M. Callaway, unpublished data). However, there was no significant correlation between the mean seed size of a population and the mean biomass of plants produced from these seeds (W. He and R.M. Callaway, unpublished data).

We do not know why our two competition experiments produced such different results, but we did not find the same results for the competitive responses of regionally collected (experiment 2) European species and a restricted local collection of European species. In competition experiment 1, competition with *C. maculosa* reduced the biomass of North American species by more than 55% overall but that of related European species by less than 15%. In competition experiment 2, competition with *C. maculosa* reduced the biomass of North American species by only 18% but that of related European species by 28%. Importantly, the overall competitive effect of *C. maculosa* in experiment 1 was approximately two times stronger than the overall

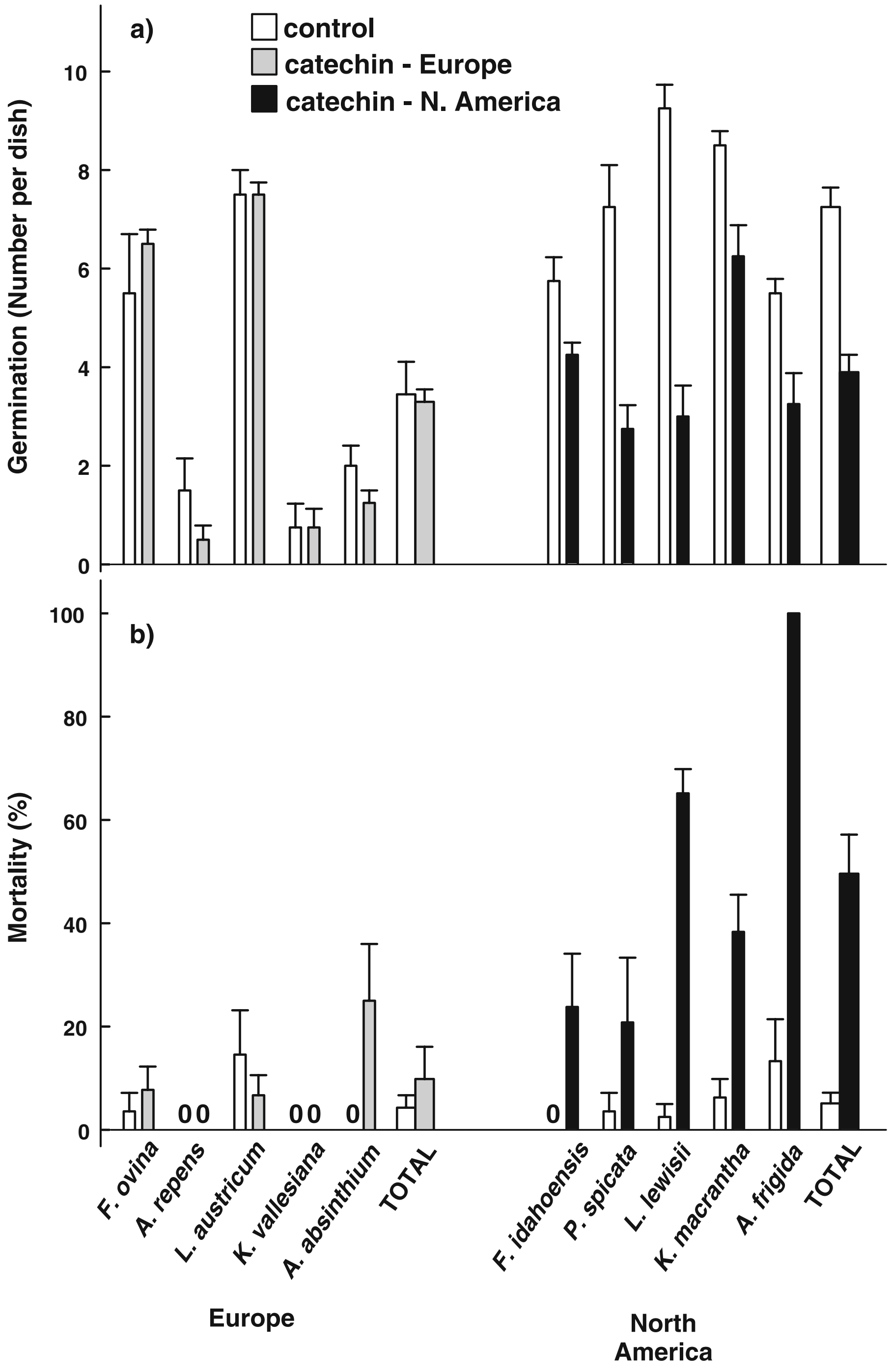

Fig. 7 The effect of (±)-catechin on **a** germination and **b** mortality of North American and European plant species. *Narrow bars* represent individual species and *thicker bars* show the totals for all species combined; means + 1 SE. The key in the figure applies to both panels, **a** and **b**. See ESM, S3 for full ANOVA

competitive effect in experiment 2, which could have been a major problem in the latter experiment. In other words, we may not have seen strong biogeographical differences in competition because the conditions in which we conducted experiment 2 did not produce strong competition for some reason . The two experiments were conducted in different greenhouses and at different times, and there were differences in the total biomass achieved by competing plants (both plants combined for total biomass) in the two experiments; 0.63 ± 0.03 in the first experiment versus 0.45 ± 0.06 in the second experiment. The outcome of a competition experiment depends in part on the total yield, and it is possible that strong competition was produced in the first experiment because of the greater biomass attained. Also, the first experiment ran for 102 days while the second one ran for 90 days. However, the average mass of *C. maculosa* plants in the pots with competitors did not differ between the experiments (0.34 ± 0.03 in experiment 1 vs. 0.31 ± 0.02 in experiment 2), suggesting that *C. maculosa* size, per se, did not determine the differences. However, the average biomass of North American plants grown *alone* in competition experiment 2 was less than half that of the European plants grown alone. In the first experiment, there was no difference in the average biomass of North American and European plants grown alone. Whatever the reason for this difference in experiment 2, perhaps the inherently smaller North American species used in this experiment competed poorly, and low inherent growth rates could have reduced the relative difference between the control and *C. maculosa* competition treatment for North American species.

The second competition experiment was designed to expand the number of European and North American natives tested. To keep the experiment manageable we used only one North American and one European population, and therefore did not consider variation among *C. maculosa* populations. If we chose *C. maculosa* populations that were relatively poor competitors and thus did not elicit strong suppression of neighbors, this could also explain the opposite biogeographic effects. In an attempt to minimize regional differences for *C. maculosa* in experiment 2, we chose the North American population that produced the smallest plants and the European populations that produced the largest plants, thinking that size would have a stronger effect on competition than it did. If indeed (±)-catechin or another allelopathic process is an important source of *C. maculosa* competitive ability, perhaps we chose populations with weaker allelopathic effects. The chance that we used populations with generally weak competitive effects is supported by examining the data from competition experiment 1. The North American population, Washington, reduced the growth of the eight competitor species by only 11%, much less than the average reduction of 35% for all populations combined.

If the allelopathic effects of (±)-catechin were an important component of *C. maculosa*'s competitive effects in our experiments, then variation in the amount of (±)-catechin released may have affected the contrasting results. Perry et al. (2007) documented sporadic or pulsed soil concentrations in *C. maculosa* rhizospheres in the field, pulsed releases appear to occur in mesocosms (M. Schultze and M. Paschke, unpublished data), and there is substantial variation among individual *C. maculosa* plants in the release of (±)-catechin into solution (J. Pollock and R.M. Callaway, unpublished data).

Alternatively, the number of native species in the first competition experiment may have not been adequate enough for a reasonable test of the novel weapons hypothesis and may therefore have exaggerated biogeographical differences. Also, the first competition experiment that showed strong support for the novel weapons hypothesis was conducted with species collected from only one site in Romania, while in the second experiment competitors were collected from many different parts of Europe (but always from communities with *C. maculosa*). Regardless, the results of the competition experiments demonstrate substantial variation in the general competitive effects of *C. maculosa*, and variation in the comparative effects of the weed on North American and European natives.

Our results for 100 μg g^{-1} of applied (±)-catechin (≈10 μg g^{-1} estimated for soil concentrations) applied three times over the course of the experiment indicated strong (±)-catechin phytotoxicity. However, (±)-catechin phytotoxicity has been shown to be variable. For example, the effects of (±)-catechin on *Festuca idahoensis* have been tested in many experiments, and the effects of (±)-catechin on just this species have varied from very strong to nonexistent in the field (Thorpe 2006; Inderjit et al. 2008b), and from very strong (Perry et al. 2005b; Callaway et al. 2005; J. Pollock, unpublished data) to weak or nonexistent in other experiments (Bais et al. 2003; Blair et al. 2005; K. Metlen et al., unpublished data). Furthermore, the general phytotoxic effects of (±)-catechin on other species have ranged from zero to significant to very strong (Thorpe 2006).

Accurate and ecologically realistic effective soil concentrations of (±)-catechin are difficult to determine, because soil concentrations are virtually always evaluated for "pure" (±)-catechin that can be detected by a specific HPLC procedure whereas phytotoxic concentrations are evaluated for the amount of (±)-catechin experimentally added to water, sand, or soil. However, pure (±)-catechin is transformed immediately into other forms upon injection into field soils (Blair et al. 2005; Inderjit et al. 2008a; J.L. Pollock et al., unpublished results), so added concentrations do not represent effective concentrations. The experimental concentrations we used (≈10 μg g^{-1}) are higher than the maximum natural soil concentrations (1 μg g^{-1}) reported by Blair et al. (2006), but more than an order of magnitude lower than the pulse reported by Perry et al. (2007). Another approach for determining reasonable experimental concentrations for (±)-catechin may be to emulate the concentration of (±)-catechin achieved by root exudation from *C. maculosa* into solution. For seedlings, this has been reported as 0 – 2.4 μg ml^{-1} (Blair et al. 2005), 5–35 μg ml^{-1} (Weir et al. 2003), 0–113 μg ml^{-1} (Ridenour et al. 2008), and 83–185 μg ml^{-1} (Bais et al. 2002). For mature plants, concentrations of 0–33 μg ml^{-1} have been measured (R.M. Callaway and J. Pollock, unpublished data). These concentrations should be considered estimates, as in all of these cases seedlings were not exposed to natural light or natural soils. Importantly, the high rates reported by Bais et al. (2002) have not been demonstrated in other experiments. Our experimental solution concentration of 300 μg ml^{-1} may have exposed plants to brief pulses of unusually high doses, but they were below the pulse recorded by Perry et al. (2007). Furthermore, because we focused on the direct effects of (±)-catechin, our experiments did not include the potential interacting effects of soil microbes, organic material in soils, or fine clay and silt mineral particles.

Our results suggest that *C. maculosa* may gain an advantage over North American organisms through its phylogenetic (e.g., Strauss et al. 2006) or biochemical (Cappuccino and Arnason 2006) novelty. However, both inherent and recently evolved aspects of *C. maculosa* may synergistically enhance competitive ability and invasion (Callaway and Maron 2006). For example, we did not find evidence that North American *C. maculosa* plants were better competitors than European plants, but another study with much higher population-level replication and using two dominant North American species (*F. idahoensis* and *P. spicata*) found stronger competitive effects of North American *C. maculosa* than European *C. maculosa* (Ridenour et al. 2008), suggesting that our results may be underestimating the importance of evolved competitive ability in the invaded range.

An unusual aspect of our results is the high mortality experienced in (±)-catechin experiment 1 by North American species. Most previous experiments (including some using much higher concentrations) with the root exudate have not resulted in mortality but in reduced growth. The mortality in our experiment occurred during or within a few weeks after a brief (several days) but hot period in the greenhouse when temperatures exceeded 35°C during the day and the experimental sand dried much faster. This occurred within the last 30 days of the experiment. (±)-Catechin affects roots more than shoots (Perry et al. 2005a), and perhaps root inhibition exacerbated the effects of high temperatures and drying soils, resulting in unusually strong effects of (±)-catechin. On the other hand, perhaps high temperatures exacerbated the effect of (±)-catechin on relatively more water-stressed roots.

Similar biogeographic differences in competitive, allelopathic, or antimicrobial effects have been shown or suggested for other species, including *Vaccinium myrtillus* (Mallik and Pellissier 2000), *Centaurea diffusa* (Callaway and Aschehoug 2000; Vivanco et al. 2004), *Lepidium draba* (McKenney et al. 2007), and *Alliaria petiolata* (Callaway et al. 2008). Biochemicals in root exudates, leaves, or litter may be relatively ineffective against their natural plant, microbial, or herbivore neighbors because these neighbors may have adapted to the biochemicals over time (Rabotnov 1982; Callaway and Ridenour 2004; Callaway et al. 2005; Cappuccino and Carpenter 2005; Cappuccino and Arnason 2006). These same biochemicals may be highly inhibitory to newly encountered species in invaded communities because the latter have not adapted. In other words, the biochemistry of some plant invaders may provide them with an advantage arising from differences in the regional coevolutionary trajectories of plant communities (Callaway and Ridenour 2004).

A number of studies suggest that invasive plants have undergone an evolved increase in size or competitive ability in their invaded habitats; some, but not all, of these studies have attributed this change to escape from natural enemies and subsequent change in allocation from defense to growth (e.g., Blossey and Nötzold 1995; Wolfe 2002; Siemann and Rogers 2001, 2003a, b; Jakobs et al. 2004; Maron et al. 2004a, b; Joshi and Vrieling 2005). As stated by Bossdorf et al. (2005), “field data suggest that increased vigor and reduced herbivory are common in introduced plant populations.” However, our study is the first to attempt a comparison of the relative importance of this evolution of increased competitive ability with other potential processes that could explain the competitive success of an invader. Our results are mixed and our conclusions are tentative because of the contrasting competition experiments, but overall they suggest that the evolution of increased competitive ability by *C. maculosa* may contribute less to the invasive success of this invader in North America than inherent biochemical traits. The stronger negative effect of (±)-catechin on native North American species than on its long-term European neighbors suggests that disproportionally strong allelopathic effects of *C. maculosa* in North America play an important role in the weed’s invasive success.

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References

Bais HP, Walker TS, Stermitz FR, Hufbauer RA, Vivanco JM (2002) Enantiomeric-dependent phytotoxic and antimicrobial activity of (±)-catechin. A rhizosecreted racemic mixture from spotted knapweed. Plant Physiol 128:1173–1179

Bais HP, Vepachedu R, Gilroy S, Callaway RM, Vivanco JM (2003) Allelopathy and exotic plant invasion: from molecules and genes to species interactions. Science 301:1377–1380

Blair AC, Hanson BD, Brunk GR, Marrs RA, Westra P, Nissen SJ, Hufbauer RA (2005) New techniques and findings in the study of a candidate allelochemical implicated in invasion success. Ecol Lett 8:1039–1047

Blair AC, Nissen SJ, Brunk GR, Hufbauer RA (2006) A lack of evidence for an ecological role of the putative allelochemical (±)-catechin in spotted knapweed invasion success. J Chem Ecol 32:2327–2331

Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. J Ecol 83:887–889

Bossdorf O, Prati D, Auge H, Schmid B (2004) Reduced competitive ability in an invasive plant. Ecol Lett 7:346–353

Bossdorf O, Auge H, Lafuma L, Rogers WE, Siemann W, Prati D (2005) Phenotypic and genetic differentiation between native and introduced plant populations. Oecologia 144:1–11

Callaway RM, Aschehoug ET (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290:521–523

Callaway RM, Maron JL (2006) What have exotic plant invasions taught us over the past 20 years? Trends Ecol Evol 21:369–374

Callaway RM, Ridenour WM (2004) Novel weapons: a biochemically based hypothesis for invasive success and the evolution of increased competitive ability. Front Ecol Environ 2:436–443

Callaway RM, Thelen GC, Rodriguez A, Holben WE (2004) Soil biota and exotic plant invasion. Nature 427:731–733

Callaway RM, Ridenour WM, Laboski T, Weir T, Vivanco JM (2005) Natural selection for resistance to the allelopathic effects of invasive plants. J Ecol 93:576–583

Callaway RM, Cipollini D, Barto K, Thelen GC, Hallett SG, Prati D, Stinson K, Klironomos J (2008) Novel weapons: invasive plant suppresses fungal mutualists in America but not in its native Europe. Ecology 89:1043–1055

Cappuccino N, Arnason JT (2006) Novel chemistry of invasive exotic plants. Biol Lett 2:189–193

Cappuccino N, Carpenter D (2005) Invasive exotic plants suffer less herbivory than non-invasive plants. Biol Lett 1:435–438

Carpenter D, Cappuccino N (2005) Herbivory, time since introduction and the invasiveness of exotic plants. J Ecol 93:315–321

D'Abrosca B, Dellagreca M, Fiorention A, Isidori M, Monaco P, Pacifico S (2006) Chemical constituents of the aquatic plant *Schoenoplectus lacustris*: evaluation of phytotoxic effects on the green alga *Selenatrum capricornutum*. J Chem Ecol 32:81–96

Ellstrand NC, Schierenbeck KA (2000) Hybridization as a stimulus for the evolution of invasiveness in plants. Proc Natl Acad Sci USA 97:7043–7050

Furubayashi A, Hiradate S, Fujii Y (2007) Role of catechol structure in the adsorption and transformation reactions of L-DOPA in soils. J Chem Ecol 33:239–250

Genton BJ, Kotanen PM, Cheptou P-O, Adolphe C, Shykoff JA (2005) Enemy release but no evolutionary loss of defence in a plant invasion: an inter-continental reciprocal transplant experiment. Oecologia 146:404–414

Goldberg DE (1987) Neighborhood competition in an old-field plant community. Ecology 68:1211–1223

Hierro JL, Maron JL, Callaway RM (2005) A biogeographic approach to plant invasions: the importance of studying exotics in their introduced and native range. J Ecol 93:5–15

Inderjit, Pollock JL, Callaway RM, Holben W (2008a) Phytotoxic effects of (±)-catechin in vitro, in soil, and in the field. PLoS ONE 3(7):e2536. doi:10.1371/journal.pone.0002536

Inderjit, Seastedt TR, Callaway RM, Pollock JL, Kaur J (2008b) Allelopathy and plant invasions: traditional, congeneric, and biogeographical approaches. Biol Invasions 10:875–890. doi:10.1007/s10530-008-9239-9

Iqbal Z, Hiradate S, Noda A, Isojima SI, Fujii Y (2003) Allelopathic activity of buckwheat: isolation and characterization of phenolics. Weed Sci 51:657–662

Jakobs G, Weber E, Edwards PJ (2004) Introduced plants of the invasive *Solidago gigantean* (Asteraceae) are larger and grow denser than conspecifics in the native range. Divers Distrib 10:11–19

Janzen DH (1975) *Pseudomyrmex nigripilosa*: a parasite of a mutualism. Science 188:936–937

Joshi J, Vrieling K (2005) The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. Ecol Lett 8:704–714

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170

Leger EA, Rice KJ (2003) Invasive Californian poppies (*Eschscholzia californica* Cham.) grow larger than native individuals under reduced competition. Ecol Lett 6:257–264

LeJeune KD, Seastedt TR (2001) *Centaurea* species: the forb that won the west. Conserv Biol 15:1568–1574

Mallik AU, Pellissier F (2000) Effects of *Vaccinium myrtillus* on spruce regeneration: testing the notion of coevolutionary significance of allelopathy. J Chem Ecol 26:2197–2209

Maron JL, Vilà M, Arnason J (2004a) Loss of enemy resistance among introduced populations of St. John's Wort, *Hypericum perforatum*. Ecology 85:3243–3253

Maron JL, Vilà M, Bommarco R, Elmendorf S, Beardsley P (2004b) Rapid evolution of an invasive plant. Ecol Monogr 74:261–280

McKenney JL, Cripps MG, Price WJ, Hinz HL, Schwarzländer M (2007) No difference in competitive ability between invasive North American and native European *Lepidium draba* populations. Plant Ecol 193:293–303

Müller H (1989) Growth pattern of diploid and tetraploid spotted knapweed, *Centaurea maculosa* Lam. (Compositae), and effects of the root-mining moth *Agapeta*. Weed Res 29:103–111

Müller-Schärer H, Schroeder D (1993) The biological control of *Centaurea* spp. in North America: do insects solve the problem? Pestic Sci 37:343–353

Müller-Schärer H, Schaffner U, Steinger T (2004) Evolution in invasive plants: implications for biological control. Trends Ecol Evol 19:417–422

Perry LG, Johnson C, Alford ER, Vivanco JM, Paschke MW (2005a) Screening of grassland plants for restoration after spotted knapweed invasion. Restor Ecol 13:725–735

Perry LG, Thelen GC, Ridenour WM, Weir TL, Callaway RM, Paschke MW, Vivanco JM (2005b) Dual role for an allelochemical: (±)-catechin from *Centaurea maculosa* root exudates regulates conspecific seedling establishment. J Ecol 93:1126–1135

Perry LG, Thelen GC, Ridenour WM, Callaway RM, Paschke MW, Vivanco JM (2007) Soil concentrations of the allelochemical (±)-catechin. J Chem Ecol 2171–2345

Prati D, Bossdorf O (2004) Allelopathic inhibition of germination by *Alliaria petiolata* (Brassicaceae). Am J Bot 91:285–288

Rabotnov TA (1982) Importance of the evolutionary approach to the study of allelopathy. Ékologia 3:5–8 (translated from Russian)

Ridenour WM, Callaway RM (2001) The relative importance of allelopathy in interference: the effects of an invader on a native bunchgrass. Oecologia 126:444–450

Ridenour WM, Vivanco JM, Feng Y, Horiuchi J, Callaway RM (2008) No evidence for tradeoffs: *Centaurea* plants from America are better competitors *and* defenders than plants from the native range. Ecol Monogr 78:369–386

Roché BF, Roché CT (1988) Distribution and amount of four knapweed (*Centaurea* L.) species in eastern Washington. Northwest Sci 62:242–253

Rudrappa T, Bonsall J, Gallagher JL, Seliskar DM, Bais HP (2007) Root-secreted allelochemical in the noxious weed *Phragmites australis* deploys a reactive oxygen species response and microtubule assembly disruption to execute rhizotoxicity. J Chem Ecol 33:1898–1918

Sheley RL, Jacob JS, Carpinelli MF (1998) Distribution, biology, and management of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). Weed Technol 12:353–362

Siemann E, Rogers WE (2001) Genetic differences in growth of an invasive tree species. Ecol Lett 4:514–518

Siemann E, Rogers WE (2003a) Increased competitive ability of an invasive tree may be limited by an invasive beetle. Ecol Appl 13:1503–1507

Siemann E, Rogers WE (2003b) Reduced resistance of invasive varieties of the alien tree *Sapium sebiferum* to a generalist herbivore. Oecologia 135:451–457

Simões K, Du J, Kretzshmar FS, Broeckling CD, Stermiz FS, Vivanco JM, Braga MR (2008) Phytotoxic catechin exuded by seeds of the tropical weed *Sesbania virgata*. J Chem Ecol 34:681–687

Strauss S, Webb CO, Salamin N (2006) Exotic taxa less related to native species are more invasive. Proc Natl Acad Sci USA 103:5841–5845

Thelen GC, Vivanco JM, Newingham B, Good W, Bais HP, Landres P, Caesar A, Callaway RM (2005) Insect herbivory stimulates allelopathic exudation by an invasive plant and suppression of natives. Ecol Lett 8:209–217

Thorpe AS (2006) Biochemical effects of *Centaurea maculosa* on soil nutrient cycles and plant communities. Ph.D. dissertation, The University of Montana, Missoula, MT

Vivanco JM, Bais HP, Stermitz F, Thelen GC, Callaway RM (2004) Biogeographical variation in community response to root allelochemistry: novel weapons and exotic invasion. Ecol Lett 7:285–292

Weir TL, Bais HP, Vivanco JM (2003) Intraspecific and interspecific interactions mediated by a phytotoxin, (±)-catechin, secreted by the roots of *Centaurea maculosa* (spotted knapweed). J Chem Ecol 29:2379–2393

Weir TL, Bais HP, Stull VJ, Callaway RM, Thelen GC, Ridenour WM, Bhamidi S, Stermitz FR, Vivanco JM (2006) Oxalate contributes to the resistance of *Gaillardia grandiflora* and *Lupinus sericeus* to a phytotoxin produced by *Centaurea maculosa*. Planta 223:785–795

Wolfe LM (2002) Why alien invaders succeed: support for the escape-from-enemy hypothesis. Am Nat 160:705–711