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Shoot herbivory on the invasive plant, *Centaurea maculosa*, does not reduce its competitive effects on conspecifics and natives

Beth A. Newingham and Ragan M. Callaway

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Herbivory can have negative, positive, or no effect on plants. However, insect biological control assumes that herbivory will negatively affect the weed and release natives from competition. *Centaurea maculosa*, an invader in North America, is tolerant to herbivory, and under some conditions, herbivory may increase its competitive effects on natives. Therefore, we investigated two hypotheses: 1) herbivory stimulates compensatory growth by *C. maculosa*, which increases its competitive effects, and 2) herbivory stimulates the allelopathic effect of *C. maculosa*. In the greenhouse, *Trichoplusia ni* shoot herbivory reduced *C. maculosa* biomass when shoot damage exceeded 40% of the total original leaf area. Conspecific neighbors had no effect on *C. maculosa* biomass, and the presence of the natives *Festuca idahoensis* and *F. scabrella* had a positive effect on *C. maculosa*. Neighbors did not alter the effects of shoot herbivory. More importantly, even intense shoot herbivory on *C. maculosa* did not benefit neighboring plants. In a field experiment, clipping 50% of *C. maculosa* aboveground biomass in the early summer and again in the late summer reduced final biomass by 40% at the end of the season; however, this clipping did not affect total biomass production or reproductive output. *Festuca idahoensis* neighbors did not increase the effects of clipping, and aboveground damage to *C. maculosa* did not release *F. idahoensis* from competition. In the greenhouse we used activated carbon to adsorb allelochemicals, which reduced the competitive effects of *C. maculosa* on *F. idahoensis* but not on *F. scabrella* or other *C. maculosa*. However, we found no increase in the allelopathic effects of *C. maculosa* after shoot herbivory. In summary, our results correspond with others indicating that exceptionally high intensities of herbivory are required to suppress *C. maculosa* growth and reproduction; however, even intense herbivory on *C. maculosa* does not insure that native bunchgrasses will benefit.

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Simultaneous herbivory and competition usually have greater negative impacts on plant performance than either process alone (Archer and Detling 1984, Cottam et al. 1986, Reichman 1988, but see Fowler and Rausher 1985, Rees and Brown 1992). The combined effects of herbivory and competition can be difficult to predict because plant responses to herbivory depend on neigh-

boring species, abiotic conditions, and the type, intensity and timing of damage. For example, root and shoot herbivores often have different effects on plants (Moran and Whitham 1990, Reichman and Smith 1991, Morón-Ríos et al. 1997, Maron 1998). Herbivory commonly has negative effects on plants (undercompensation) (Harper 1977, Crawley 1983, Belsky 1986), but herbivory can also

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have no effect (equal compensation) (Lee and Bazzaz 1980, Fowler and Rausher 1985), or positive effects (overcompensation) on plants (McNaughton 1986, Paige and Whitham 1987, Alward and Joern 1993, Lennartsson et al. 1998). Such a range in responses suggests that herbivory may not necessarily reduce the competitive ability of attacked plants.

Centaurea maculosa Lam. (spotted knapweed) is one of the most destructive and successful invasive weeds in North America (Roché and Roché 1988, Müller-Schärer and Schroeder 1993). Biological control agents were first introduced to control *Centaurea* species in 1970 based on the assumption that herbivory reduces the competitive ability of plants. Now there are at least 13 species of insects established in North America to control *C. maculosa* (Sheley et al. 1998). However, Müller-Schärer and Schroeder (1993) observed that despite extensive biological control efforts, *Centaurea* species are still expanding their ranges. The ineffectiveness of these biological controls may be because many are not yet well established, their effects will take longer to be fully realized, or that their effects on *Centaurea* are weak. The lack of success where biological controls are well established suggests the latter.

Root-boring biocontrols do not always reduce the growth of *C. maculosa* (Müller-Schärer 1991, Steinger and Müller-Schärer 1992) and in some cases caused overcompensatory root growth (Müller 1989) or flower production (Ridenour and Callaway 2003). Thelen et al. (2005) found that root herbivory increased the allelopathic output of *C. maculosa* when attacked by root boring biocontrols. Additionally, Callaway et al. (1999) found that the generalist shoot herbivore, *Trichoplusia ni*, moderately increased the competitive ability of *C. maculosa*. However, shoot herbivory did not increase allelopathic exudation (Thelen et al. 2005), and therefore, how shoot herbivory might increase *C. maculosa*'s competitive ability is unknown.

We proposed two hypotheses to explain the potential increase in competitive effects of *C. maculosa* on *F. idahoensis* after shoot herbivory. First, *C. maculosa* may compensate for shoot herbivory by increasing its growth rate, concomitantly increasing uptake of limited resources. Compensatory growth could then improve *C. maculosa*'s competitive ability by taking up nutrients that would otherwise be available to neighboring plants. Second, shoot herbivory on *C. maculosa* may stimulate the production of secondary chemicals (allelochemicals), perhaps as induced defenses, which may increase allelopathic effects on neighboring plants (Lovett and Hoult 1995, Tang et al. 1995). *Centaurea maculosa* is highly allelopathic to North American species, apparently through the exudation of large amounts of (\pm)-catechin from its roots (Ridenour and Callaway 2001, Bais et al. 2002, 2003, Weir et al. 2003). In addition, cnicin, a sesquiterpene lactone produced in *C. maculosa* shoots,

has been found to have negative effects on native species (Kelsey and Locken 1987).

We conducted experiments to test these two hypotheses as to why shoot herbivory may increase *C. maculosa*'s competitive effects. To test the compensation and allelopathy hypotheses, in the greenhouse *C. maculosa* was exposed to a gradient of *Trichoplusia ni* shoot herbivory in the presence and absence of neighbors and with or without activated carbon added to the soil to reduce allelochemical concentrations. To further test the compensatory growth hypothesis, in the field we manually defoliated *C. maculosa* in the presence and absence of neighbors in a Montana grassland.

Methods

Species information

Centaurea maculosa Lam. (spotted knapweed) (Asteraceae) is a tap-rooted, perennial forb, which typically germinates in the fall, overwinters in the rosette stage, bolts in June, and flowers in July–September. *Centaurea maculosa* is native to Eurasia and was introduced into North America in the late 1800s (Dostal 1976, Sheley et al. 1998, LeJeune and Seastedt 2001). *Centaurea maculosa* dominates over 4 million hectares in North America (Müller-Schärer and Schroeder 1993) and often invades intermountain grasslands dominated by *Festuca idahoensis* Elmer and *Festuca scabrella* Torrey ex. Hook. Both *Festuca* species are native perennial grasses, which germinate in the late winter and early spring and flower May–June.

Trichoplusia ni Hübner (Lepidoptera: Noctuidae; cabbage looper moth) is a generalist herbivore that occurs throughout North America (Shorey et al. 1962). *Trichoplusia ni* is not used as a biocontrol agent for *C. maculosa*. However, *T. ni* larvae have been observed eating *C. maculosa* leaves in the field, and other studies have demonstrated that *T. ni* does not eat *F. idahoensis* (Callaway et al. 1999). *Trichoplusia ni* was used because it was easy to manipulate, it was easy to obtain precise levels of shoot damage allowing us to obtain a gradient of shoot damage, and because it stimulated the competitive effect of *C. maculosa* in another experiment.

Greenhouse experiment

We conducted a greenhouse experiment at The University of Montana in which *C. maculosa* was planted alone, with a conspecific, or with *F. idahoensis* or *F. scabrella*. There were 60 replicates per neighbor treatment for a total of 240 pots. All seeds were planted at the same time in 4 l pots with a silica sand-field soil mixture (4:1). Twenty/thirty grade silica sand was used and field soil was collected near Missoula, Montana, where

C. maculosa was abundant. All plants were watered every other day with tap water and fertilized biweekly with ¼ strength Hoagland's solution modified by using inositol hexaphosphate. *Centaurea maculosa* and *F. idahoensis* have arbuscular mycorrhizal (AM) fungi that are important in nutrient and phosphorus uptake by plants (Koide 1991, Marschner and Dell 1994, Newsham et al. 1995). Previous studies have shown that AM fungi are important for interactions between *C. maculosa* and *F. idahoensis* (Marler et al. 1999). Inositol hexaphosphate is not directly available to plants and requires mycorrhizal fungi, soil microbes or root exudates to convert this organic form of phosphorus into inorganic phosphorus (DeLucia et al. 1997).

After 16 weeks of plant growth, we randomly chose one of the two *C. maculosa* plants in the pots with conspecifics and the single *C. maculosa* in all other treatments for shoot herbivory by *T. ni*. Cages were placed over all targets, including targets not subjected to shoot herbivory, to ensure that *T. ni* only ate the target *C. maculosa*. Immediately after the shoot herbivory treatment, we visually determined the percentage of damaged leaf area for each leaf. For each target plant, we counted the total number of leaves and expressed the percent damage of all leaves combined as a percentage of total plant leaf area. After leaving *T. ni* on plants for 3–4 days, shoot herbivory ranged in intensity from 0 (controls with no insects) to 90% of the total leaf area. Six weeks after shoot herbivory, all target plants and corresponding neighbors when present were harvested. Roots of *C. maculosa* are distinguishable from *Festuca* species because of differences in color, and therefore, can be separated. Shoots and roots of each species were dried at 60°C for 48 h and weighed. Root segments were stained with trypan blue (Phillips and Hayman 1970) and spot checked for AM fungal colonization using the magnified intersection method (McGonigle et al. 1990). All plants were colonized by AM fungi.

To investigate the role of root exudates on *C. maculosa*'s response to shoot herbivory, 20 ml of activated carbon was added per liter of sand–soil mixture to half of the pots ($n = 120$) (based on Ridenour and Callaway 2001). Activated carbon has previously been shown to reduce the negative effects of root exudates from *C. maculosa* (Ridenour and Callaway 2001) and other species (Mahall and Callaway 1992). Activated carbon has a high affinity for organic compounds, such as the suspected allelopathic chemicals, and a weak affinity for inorganic electrolytes such as the nutrients in Hoagland's solution (Cheremisinoff and Ellerbusch 1978). To remove potential contamination of activated carbon by soluble phosphates and reduce saturation of binding sites, we acid-washed the activated carbon with 2 M HCl. The activated carbon was shaken in acid in a 1:10 w/v ratio for 1 h and then filtered through Whatman no. 2 filter paper. The acid-washed

activated carbon was then washed at least once in deionized water in the same manner described above to remove any residual HCl.

In sum, there were four neighbor treatments, treatments with and without carbon, and herbivory treatments spanning a gradient of 0 to 90% damage. All data were analyzed with ANCOVA. Treatment differences in the total biomass of target *C. maculosa* were analyzed with neighbors and carbon as fixed factors. In order to include the specific level of herbivory, herbivory on *C. maculosa* was used as a covariate. Herbivory was not included as a factor to avoid auto correlation between the covariate and factor. In addition, herbivory was used as a covariate because it was assumed that the experiment started after herbivores had been applied. Leaf number immediately before herbivory was used as an additional covariate to control for initial size differences among plants since biomass before herbivory was not obtainable. The total biomass of neighboring plants was also analyzed using an ANCOVA with species and carbon as fixed factors, and herbivory and leaf number before herbivory on the target *C. maculosa* were used as covariates. In this model the interaction of leaf number and neighbor was added to examine whether neighbor effects and responses varied depending on their size. Three-way interactions were eliminated from both models because they were not significant. All data were log transformed to meet ANCOVA assumptions. All means reported in the text are mean ± 1 standard error (SE). Shoot and root biomass responded similarly to total biomass; therefore, we only present total biomass.

Field experiment

The field site was located on Mount Sentinel adjacent to The University of Montana campus (N 46°50.612', W 113°58.454'; elevation, 1374 m). The site was dominated by *C. maculosa* and *F. idahoensis*, and isolated pairs of *C. maculosa* and *F. idahoensis* were common with few or no other nearby neighbors. Environmental conditions at this site are exceptionally harsh relative to other areas where *C. maculosa* is more abundant due to shallow soils, a southern aspect, and exposure to consistent, intense winds. The extreme nature of this site provides a conservative examination of compensatory responses because compensatory responses tend to be much stronger in benign habitats and when resources are abundant (Maschinski and Whitham 1989, Whitham et al. 1991, Sadras 1996). In the spring of 2000, we chose eighty individual pairs of *C. maculosa* and *F. idahoensis*. The space between *C. maculosa* and *F. idahoensis* was on average 3.2 cm to assure shoot and root interactions. Enough space existed among the *C. maculosa* – *F. idahoensis* pairs and other large neighboring species to assure no shoot interactions and to make root

interactions unlikely. *Centaurea maculosa* target plants were approximately the same size. The mean initial number of *C. maculosa* leaves was 22.14 ± 1.58 (± 1 SE) and mean initial height was 8.71 ± 0.21 cm. The mean height of all *F. idahoensis* before clipping half of the *F. idahoensis* plants was 15.64 ± 0.40 cm.

The original 80 pairs were randomly divided into four groups of 20 and each group received one of the four following treatments: *C. maculosa* not defoliated – *F. idahoensis* present; *C. maculosa* not defoliated – *F. idahoensis* removed; *C. maculosa* defoliated – *F. idahoensis* present; *C. maculosa* defoliated – *F. idahoensis* removed. *Festuca idahoensis* was removed by clipping all aboveground biomass at the beginning of the experiment. Regrowth occurred on approximately 75% of *F. idahoensis* plants; however, regrowth was minimal and was continually removed each month. Due to experimental limitations (not disturbing the soil), it was impossible to remove *F. idahoensis* roots, and therefore, belowground competition was probably reduced but not eliminated (Cahill 2002). Although *F. idahoensis* was removed as a treatment, we did not measure the effect of defoliation on *F. idahoensis*.

We imposed a severe defoliation regime on *C. maculosa* by clipping 50% of its aboveground biomass on 1 June and again on 7 July, 2000. Previous experiments have shown that *T. ni* shoot herbivory and defoliation via clipping affect *C. maculosa* similarly (B. A. Newingham, unpubl.). All clipped biomass was saved and dried at 60°C for 48 h and weighed. This experiment was designed to run for two years; however, summer precipitation in 2000 was exceptionally low (Results), many *C. maculosa* died, and there were not enough plants to continue the experiment. Therefore, we established another 80 pairs in the spring of 2001 and repeated the experiment. We clipped the newly chosen *C. maculosa* plants on 25 June and 15 August, 2001. Survival of all *C. maculosa* plants was recorded in September of 2000 and 2001. In addition, final aboveground biomass of all surviving plants was collected and the number of flowers was counted on 13 September, 2001. Belowground biomass was not obtainable because of root breakage due to soil clumps. Final aboveground biomass was dried at 60°C for 48 h and weighed.

Survival data of *C. maculosa* for 2000 were analyzed using a binary logistic regression with clipping and neighbor as covariates. The high mortality of plants in 2000 reduced sample sizes so that statistical analyses of final biomass and flower number were not possible; therefore, final biomass and flower data are only presented for the 2001 experiment. The final biomass, flower number and total biomass production of *C. maculosa* were analyzed with a two-way ANOVA using clipping and neighbor as fixed factors. Total biomass production was calculated by adding all clipped biomass to the final biomass for each plant and analyzed in a

similar manner. The biomass and flower data of *F. idahoensis* were analyzed with a one-way ANOVA using clipping of *Centaurea* as a fixed factor. All means reported are mean ± 1 SE.

Results

Greenhouse experiment

Over the entire 0–90% damage gradient, shoot herbivory had a negative effect on the total biomass of attacked *C. maculosa* (Fig. 1, Table 1). Without shoot herbivory, the mean biomass of the target *C. maculosa* was 0.83 ± 0.05 g and when using all shoot herbivory levels combined (1–90%; mean% damage = 17.81 ± 19.91 ; $n = 229$) the mean biomass of target *C. maculosa* was reduced to 0.70 ± 0.04 g, a 16% reduction. However, the effect of shoot herbivory was strong only when the

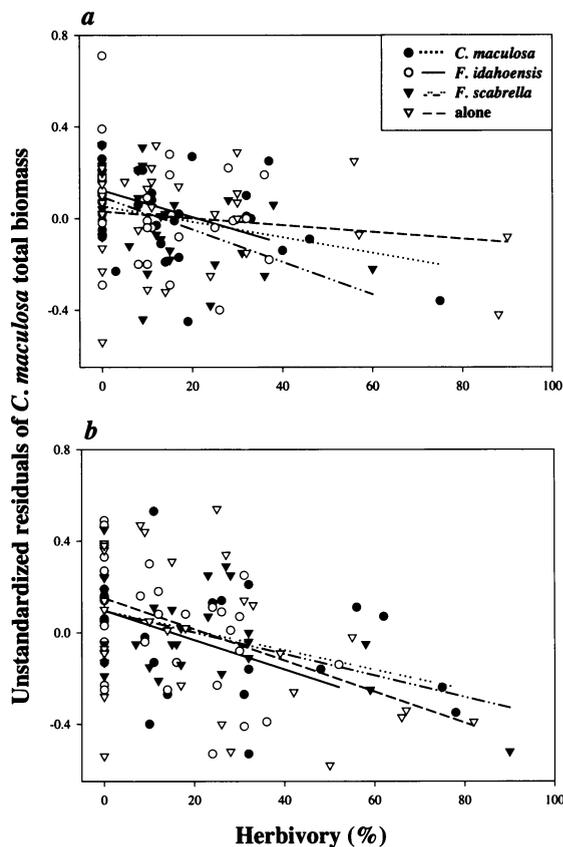


Fig. 1. Effects of herbivory on the unstandardized residuals of target *Centaurea maculosa* total biomass when grown with *Festuca idahoensis*, *Festuca scabrella* or *C. maculosa* or grown alone either (a) without activated carbon or (b) with activated carbon in pots in the greenhouse. Unstandardized residuals were obtained using a model with neighbor and carbon as fixed factors and leaf number and herbivory as covariates. Data are based on ANCOVA results from Table 1.

Table 1. ANCOVA on the effects of neighbor, activated carbon and shoot herbivory on the total biomass of *Centaurea maculosa*. The P values of significant terms ($P < 0.05$) are indicated in boldface type.

Source	df	MS	F	P
Neighbor	3	0.236	4.709	0.003
Carbon	1	0.152	3.027	0.083
Herbivory	1	1.243	24.782	<0.0005
Leaf no.	1	12.703	253.297	<0.0005
Neighbor \times carbon	3	0.116	2.311	0.077
Neighbor \times herbivory	3	0.074	0.148	0.931
Carbon \times herbivory	1	0.134	2.679	0.103
Error	215	0.050		

highest intensities of shoot herbivory were included. When analyses were conducted including only shoot herbivory intensities less than 40%, the effects of shoot herbivory were weak ($F = 3.68$, $P = 0.06$), reducing biomass by 9%. When analyses included only intensities above 40%, the effects of shoot herbivory were much stronger ($F = 9.86$, $P = 0.002$) reducing biomass by 58%. In the full analysis, neither neighbors nor activated carbon altered the growth response of the target *C. maculosa* to shoot herbivory. Leaf number of *C. maculosa* prior to clipping was significantly and positively related to the final biomass of target *C. maculosa*.

There was a positive relationship between the presence of neighbors and the total biomass of target *C. maculosa* (Fig. 2). The total biomass of *C. maculosa* alone did not significantly differ from a target *C. maculosa* when grown with a conspecific ($P = 1.00$). In contrast, the biomass of target *C. maculosa* was significantly larger when grown with *F. idahoensis* than when grown alone or when grown with a conspecific ($P = 0.03$ and $P = 0.01$, respectively). Similarly, the biomass of the target *C. maculosa* when grown with *F. scabrella* was significantly larger than when *C. maculosa* grew alone or with a conspecific but not larger than *C. maculosa* grown with

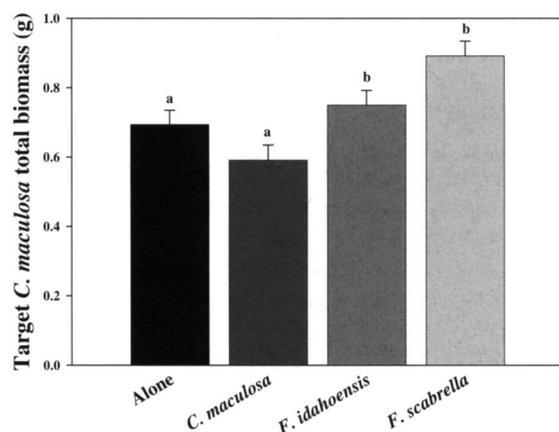


Fig. 2. Effect of neighbor treatment (alone, *Centaurea maculosa*, *Festuca idahoensis* or *Festuca scabrella*) on target *C. maculosa*. Error bars represent $+1$ SE.

F. idahoensis ($P = 0.005$, $P = 0.003$, and $P = 1.00$, respectively).

Activated carbon used to absorb allelochemicals had weak negative effects on target *C. maculosa* biomass (Fig. 1, Table 1). When combining all neighbor situations and over all herbivory intensities (0–90%), the mean total biomass of target *C. maculosa* without activated carbon was 0.76 ± 0.04 g and with activated carbon was 0.71 ± 0.05 g. In pair-wise comparisons, the only neighbor treatment that was affected by activated carbon was *C. maculosa* alone. The biomass of target *C. maculosa* when planted alone was 0.85 ± 0.06 g without activated carbon and 0.61 ± 0.09 g with activated carbon, a 29% decrease ($P = 0.03$).

Activated carbon added to the soil did not alter the effect of *C. maculosa* on neighbors in the overall analysis (Fig. 3, Table 2). However, when examining the effects of activated carbon on individual neighboring species, neighboring species responded differently to activated carbon. When examining the species by carbon

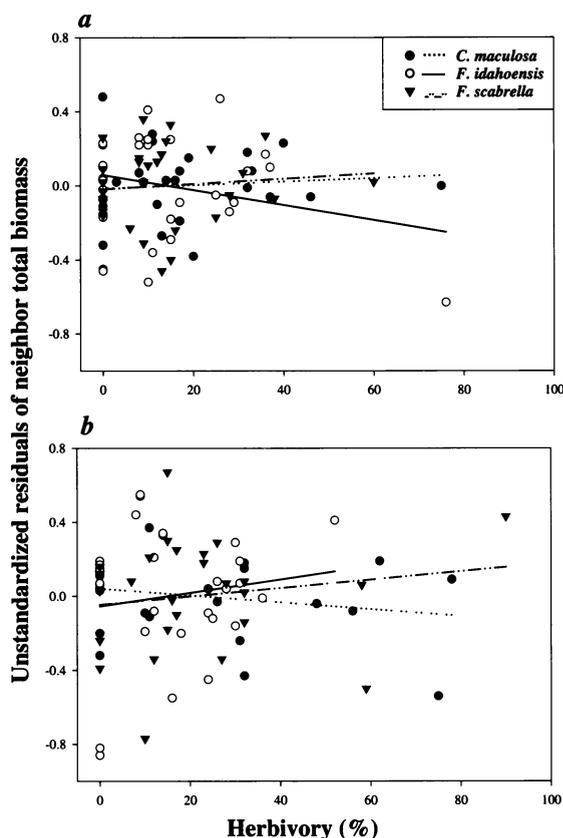


Fig. 3. Effects of target *Centaurea maculosa* herbivory on the unstandardized residuals of neighboring species total biomass either (a) without activated carbon or (b) with activated carbon in pots in the greenhouse. Unstandardized residuals were obtained using a model with neighbor and carbon as fixed factors and leaf number and herbivory as covariates. Data are based on ANCOVA results from Table 2.

Table 2. ANCOVA on the effects of species, activated carbon and shoot herbivory on the total biomass of the neighboring *Centaurea maculosa*, *Festuca idahoensis* or *Festuca scabrella*. The P values of significant terms ($P < 0.05$) are indicated in boldface type.

Source	df	MS	F	P
Species	2	1.006	13.693	<0.0005
Carbon	1	0.001	0.016	0.901
Herbivory	1	0.001	0.002	0.966
Leaf no.	1	4.943	67.284	<0.0005
Species × carbon	2	0.360	4.905	0.009
Species × herbivory	2	0.042	0.566	0.569
Carbon × herbivory	1	0.014	0.189	0.665
Species × leaf	2	1.356	18.462	<0.0005
Error	157	0.073		

interaction using pair-wise comparisons over all herbivory intensities, adding activated carbon decreased the biomass of neighboring *C. maculosa* that were not attacked by *T. ni* from 0.76 ± 0.07 g to 0.43 ± 0.05 g (43% decrease, $P = 0.03$), but increased the biomass of *F. idahoensis* from 0.11 ± 0.02 g to 0.26 ± 0.04 g (136% increase, $P = 0.08$). Activated carbon had no effect on the biomass of *F. scabrella* (without carbon = 0.05 ± 0.01 g; with carbon = 0.06 ± 0.01 g, $P = 0.77$).

Shoot herbivory on target *C. maculosa* had no effect on neighboring species (Fig. 3, Table 2). Without shoot herbivory on target *C. maculosa*, the mean biomass of unattacked *C. maculosa* neighbors was 0.63 ± 0.10 g. When the target *C. maculosa* was damaged (all herbivory levels combined) the mean biomass of neighboring, undamaged *C. maculosa* was 0.60 ± 0.52 g. The biomass of *F. idahoensis* was 0.20 ± 0.05 g without shoot herbivory on target *C. maculosa* and 0.18 ± 0.03 g when target *C. maculosa* was damaged. The biomass of *F. scabrella* was 0.05 ± 0.01 g without shoot herbivory on target *C. maculosa* and 0.06 ± 0.01 g when target *C. maculosa* was damaged. There was no significant interaction between the effect of activated carbon in the soil and the effect of shoot herbivory on *C. maculosa*, indicating that activated carbon, and by inference allelopathy, did not alter the effects of attacked *C. maculosa* on its neighbors.

Field experiment

Survival

Across all treatments, only 48% of the *C. maculosa* plants in the field experiment of 2000 (an exceptionally dry summer) survived, whereas 98% of the *C. maculosa* plants in the 2001 experiment survived (Fig. 4). In 2000, clipping *C. maculosa* decreased its survival from 64% to 30% (Wald statistic = 8.01, $P = 0.005$). *Festuca idahoensis* neighbors had no effect on the survival of *C. maculosa* in 2000 (Wald statistic = 1.15, $P = 0.28$). In 2001, experimental clipping of *C. maculosa* did not decrease its survival, with 98% of both unclipped and clipped *C. maculosa* plants surviving (Wald statistic = 0.00, $P =$

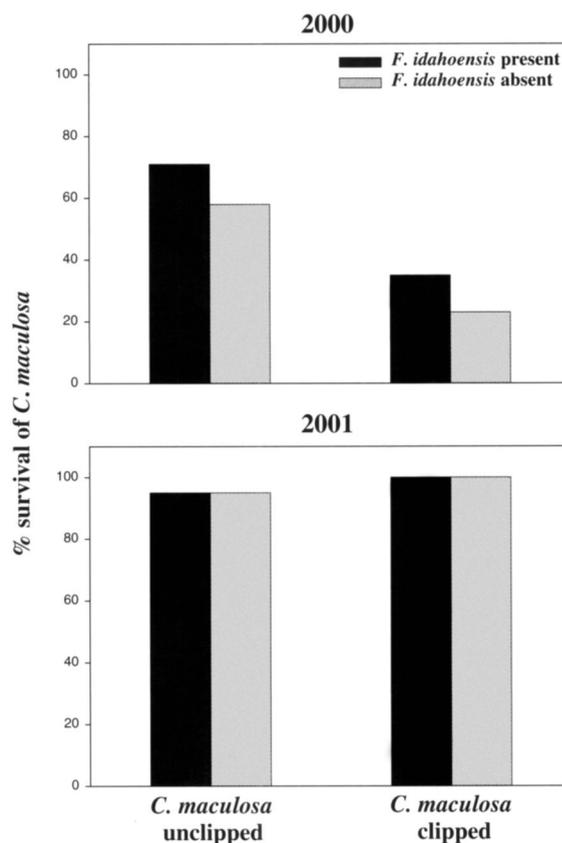


Fig. 4. Percent survival of *Centaurea maculosa* with or without *Festuca idahoensis*, with or without clipping in the field in 2000 and 2001.

1.00). In 2001, *F. idahoensis* neighbors did not affect the survival of *C. maculosa* (Wald statistic = 0.02, $P = 0.90$).

Water was not manipulated in this study; however, the timing of precipitation during the growing season is important to the growth and reproduction of *C. maculosa*, and therefore, our results. *Festuca idahoensis* flowers in May–June while *C. maculosa* flowers in July–August. Total annual precipitation was 31.45 cm and 33.73 cm for 2000 and 2001, respectively. Although total annual precipitation was similar between years, peak precipitation differed. Peak precipitation usually occurs in May–June. In 2000, May–June precipitation was only 5.10 cm, whereas in 2001 May–June precipitation was 10.95 cm. Instead, peak precipitation in 2000 occurred in September–October (11.82 cm) after a very dry summer. The very low precipitation in May–June 2000 probably accounted for the high mortality of *C. maculosa* in our experiment.

Biomass and reproduction

The shoot biomass of *C. maculosa* in the field experiment (0.52 ± 0.05 g) was equivalent to the shoot biomass

of *C. maculosa* in the greenhouse experiment (0.55 ± 0.02 g). However, the shoot biomass of *F. idahoensis* in the field (2.00 ± 0.20 g) was much larger than the shoot biomass of *F. idahoensis* in the greenhouse (0.13 ± 0.02 g), which was probably due to the field *F. idahoensis* plants being established longer. For *Centaurea*–*Festuca* pairs identified in 2001, the final biomass of *C. maculosa* was negatively affected by clipping (Fig. 5; $F = 9.03$, $P_{\text{clipping}} = 0.004$). However, the mean final biomass of *C. maculosa* was only reduced by 40% when clipped even though 50% of the existing biomass was removed at each of two different times during a single growing season, and the second clipping was conducted only one month before the harvest. Eliminating the aboveground biomass of *F. idahoensis* had no effect on the final biomass of *C. maculosa* ($F = 0.66$, $P_{\text{neighbor}} = 0.42$) and *C. maculosa* responded similarly to clipping regardless of the presence of *F. idahoensis* ($F = 0.03$, $P_{\text{clipping} \times \text{neighbor}} = 0.86$).

Although clipping reduced *C. maculosa* final biomass, total biomass production (clipped biomass + final biomass) did not differ between clipped (1.03 ± 0.13 g) and unclipped plants (0.86 ± 0.10 g; $F = 1.06$, $P_{\text{clipping}} = 0.31$). As for final biomass, total biomass production of *C. maculosa* was not affected by removing the aboveground biomass of *F. idahoensis* ($F = 1.64$, $P_{\text{neighbor}} = 0.20$), and the interaction between clipping *C. maculosa* and the presence of *F. idahoensis* did not affect *C. maculosa*'s total biomass production ($F = 0.68$, $P_{\text{clipping} \times \text{neighbor}} = 0.41$).

Neither clipping nor neighbors reduced the number of flowers produced by *C. maculosa* ($F = 0.11$, $P_{\text{clipping}} = 0.74$; $F = 0.37$, $P_{\text{neighbor}} = 0.54$), and there was no interaction between clipping and neighbor on the number of *C. maculosa* flowers ($F = 0.32$, $P_{\text{clipping} \times \text{neighbor}} = 0.58$). When *F. idahoensis* was present, *C. maculosa* flower number was 3.95 ± 1.18 when *C. maculosa* was unclipped and 4.20 ± 1.07 when *C. maculosa* was clipped. In the

absence of *F. idahoensis*, *C. maculosa* flower number was 5.20 ± 0.98 when unclipped and 4.25 ± 1.02 when clipped.

Clipping *C. maculosa* did not affect the biomass or the number of flowers of *F. idahoensis* ($F = 0.66$, $P_{\text{clipping}} = 0.42$; $F = 0.01$, $P_{\text{clipping}} = 0.93$, respectively). When *C. maculosa* was unclipped, the biomass of *F. idahoensis* was 1.65 ± 0.35 g compared to 2.12 ± 0.46 g for those with clipped *C. maculosa* neighbors. The flower number of *F. idahoensis* was 11.90 ± 3.15 when *C. maculosa* was unclipped compared to 12.30 ± 3.32 when *C. maculosa* was clipped.

Discussion

High levels of *T. ni* shoot herbivory and artificial defoliation had negative effects on the total biomass of the target *C. maculosa* suggesting undercompensation. However, low levels of *T. ni* herbivory (<40%) appeared to stimulate *C. maculosa* growth as damaged targets attained the same biomass as conspecifics that had not been attacked, i.e. equal compensation. In the field, high levels of clipping reduced the final biomass of *C. maculosa* but did not affect total *C. maculosa* biomass production or reproduction. This suggests that *C. maculosa* compensated for lost tissue but was not able to fully recover in the time allowed. Plant compensation for herbivory depends on abiotic conditions, the severity of herbivory, and the composition of the surrounding plant community (Maschinski and Whitham 1989, Whitham et al. 1991, Sadras 1996, Lennartsson et al. 1998, Freeman et al. 2003), and all of these factors may have affected our results. We caution that different herbivores may elicit different compensatory or competitive responses as well. We focused on shoot herbivory, and root herbivory may have different effects. Other studies have found that root herbivory by *A. zoegana* and *Cyphocleonus achates* Fahr. (Coleoptera: Curculionidae) has minimal negative effects on *C. maculosa* and *C. maculosa* can overcompensate for damage (Müller 1989, Müller-Schärer 1991, Steinger and Müller-Schärer 1992, Callaway et al. 1999, Ridenour and Callaway 2003).

In these previous studies, *C. maculosa* was given more time to recover from herbivory than in the experiments reported here. Also, in contrast to our study, no previous study examined herbivory along a gradient of damage intensity. Understanding the gradient of responses to herbivory may be crucial because low levels of herbivory may have weak effects or stimulatory effects on *C. maculosa* (Callaway et al. 1999), whereas high levels of herbivory may significantly reduce *C. maculosa* performance. Further experimentation is needed, as our sample sizes were low at the highest levels of herbivory, and plants in the greenhouse experiment experienced only a single bout of herbivory.

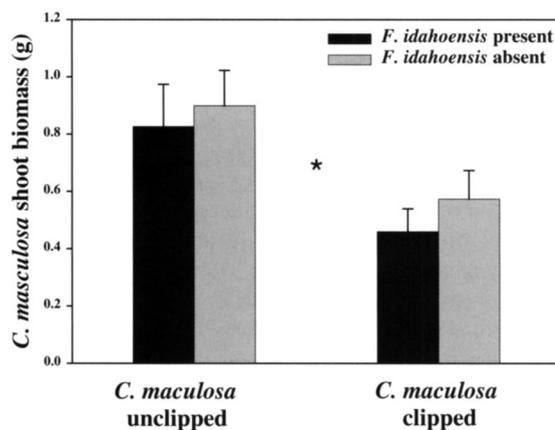


Fig. 5. Final biomass of *Centaurea maculosa* with or without *Festuca idahoensis*, with or without clipping in the field in 2001. Error bars represent +1 SE.

In the field, clipping negatively affected *C. maculosa* final biomass in 2001; however, *C. maculosa* was quite resilient to damage regardless of the harsh abiotic conditions at this site. It is remarkable that *C. maculosa* maintained over 60% of its biomass and all targets survived when 50% of *C. maculosa*'s biomass was removed twice in a single growing season and plants were given only one month to recover. More importantly, severe defoliation did not decrease final primary production or fecundity.

Contrary to plant competition theory, neighbors did not change the effect of shoot herbivory on *C. maculosa*. Most studies have shown that herbivory increases the susceptibility of a plant to competition (or vice versa) (Archer and Detling 1984, Cottam et al. 1986, Reichman 1988). However, *C. maculosa* targets subjected to shoot herbivory or defoliation grew no larger alone than with *C. maculosa*, *F. idahoensis* or *F. scabrella* neighbors. Thus, it cannot be assumed that neighboring plants will increase the negative effects of herbivory on *C. maculosa*.

Herbivory generally shifts competitive interactions in favor of undamaged plants (Crawley 1989, Louda et al. 1990, Blossey and Nötzold 1995, Tilman 1999). Even though shoot herbivory suppressed target *C. maculosa*, we found no evidence that this suppression released neighboring *C. maculosa*, *F. idahoensis* or *F. scabrella*. In contrast to Callaway et al. (1999), we found no evidence that shoot herbivory on *C. maculosa* increased its competitive ability against natives. It is possible that differential timing of defoliation on *C. maculosa* and the time given to neighboring species to respond may have produced different responses by neighboring plants. For example, clipping *C. maculosa* in the spring may have had positive effects on *F. idahoensis* since it actively grows in the spring. Regardless, our results suggest that very high levels of consistent herbivory may be required to reduce the competitive ability of *C. maculosa*.

Our greenhouse results indicated that *F. idahoensis* and *F. scabrella* might facilitate *C. maculosa*. Positive effects of *F. idahoensis* on *C. maculosa* have been described before (Marler et al. 1999, Carey et al. 2004, Callaway et al. 2004). The positive effects of these bunchgrasses could be explained in two ways. First, *F. idahoensis* and *F. scabrella* may secrete root exudates that increase nutrient availability. If root exudation increases soil nutrients, this would increase available nutrients not only to *F. idahoensis* and *F. scabrella* but also to *C. maculosa*. Second, *C. maculosa* might obtain nutrients or carbon from neighbors through AM fungi. Resource and carbon transfer between plants through mycorrhizal links has been argued for other species (Chiariello et al. 1982, Francis and Read 1984, Watkins and Fitter 1996, Simard et al. 1997) including other species of *Festuca* and *Centaurea* (Grime et al. 1987). The positive effects of *F. idahoensis* on *C. maculosa* may be explained by carbon transfer (Carey et al. 2004) or the enhanced ability of *C.*

maculosa to acquire soil phosphorus from natives through AM fungi (Zabinski et al. 2002).

Activated carbon had a negative effect on target *C. maculosa* but only when planted alone. Additionally, there was negative effect of activated carbon on the neighboring *C. maculosa*. It is unclear as to why activated carbon causes these inconsistent, negative effects on *C. maculosa*. Activated carbon has been found to have no direct effects on *C. diffusa* (Callaway and Aschehoug 2000) but can also have direct positive effects on *C. maculosa* (C. Hall and R. M. Callaway, unpubl.). Ridenour and Callaway (2001) found activated carbon to increase water retention, and also to have a direct, negative effect on *F. idahoensis*. We suspect that the variable effects of activated carbon are related to another function of *C. maculosa* root exudates; chelation, which increases the availability of phosphorus (Thorpe et al. in press). If experimental soils vary in phosphorus availability and chemistry, the effects of carbon on phosphorus acquisition could vary. As stated by Inderjit and Callaway (2003), activated carbon is useful to examine the effects of root exudates; however, further research is needed on the effects of activated carbon on soil chemical and hydrological properties.

Substantial evidence suggests shoot and root exudates of *C. maculosa* are allelopathic (Fletcher and Renney 1963, Kelsey and Locken 1987, Ridenour and Callaway 2001, Bais et al. 2002, 2003, Weir et al. 2003, Perry et al. in press, Weir et al., in press). Our results also indicated allelopathic effects of *C. maculosa* on *F. idahoensis*; however, we found no evidence that allelopathic effects increased when shoot herbivory was experimentally applied. This contrasts with the effects of root herbivory as reported by Thelen et al. (2005) who found that *C. maculosa* exudes far higher amounts of (\pm)-catechin from its roots when attacked by the root herbivores, *A. zoegana* and *C. achates*, and a parasitic fungus, *Rhizoctonia solani* Kühn. Furthermore, *C. maculosa* plants attacked by *A. zoegana* in the field exhibited greater negative effects on one native species. We may have failed to see a positive response by neighbors because 1) the amount of activated carbon was not sufficient to reduce larger amounts of allelochemicals exuded by *C. maculosa*, 2) shoot herbivory did not increase allelochemical production as much as root herbivory, and/or 3) *C. maculosa* invested more into increased plant growth than allelochemical production. Further experimentation, including analysis of soil nutrients, may reveal reasons for the unexplained patterns of activated carbon in this system.

We found that shoot herbivory did not always have strong negative effects on *C. maculosa*, and in no case did we find that shoot herbivory benefited native grasses. On the other hand, we found no evidence to support either compensatory growth or increased allelopathic effects in response to shoot herbivory as hypothesized by Callaway et al. (1999). Understanding how variable

responses to herbivory affect plant interactions is of fundamental interest to ecologists. Additionally, it is crucial for predicting the effectiveness of biocontrol herbivores against exotic, invasive weeds, which is based on the assumption that invasive plants are successful because they lack natural enemies, and that natural enemies will reduce the competitive advantage invaders have over natives (Waage and Mills 1992, Blossey and Nötzold 1995, Van Driesche and Bellows 1996, Tilman 1999, Maron and Vilà 2001, Wolfe 2002). Although this study did not focus on a current biocontrol of *C. maculosa*, understanding *C. maculosa*'s response to herbivory should be examined before further investigating the use of any other herbivores as biocontrol agents. Our results suggest that biocontrols must exert large amounts of damage if they are to negatively affect the growth and competitive ability of *C. maculosa*.

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