

Effects of *Festuca paniculata* on the compensatory growth response of *Centaurea uniflora* in the French Alps

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Abstract

The independent effects of herbivores and neighbors on plants are generally negative, and therefore the combined effects of these interactions are generally assumed to have additive or multiplicative negative effects on plant growth. However, because herbivores can stimulate the growth of plants (compensation) and neighbors can facilitate each other, the combined effects of herbivory and plant-plant interactions can be highly variable and poorly predicted by current competition and plant-herbivore theory. In some cases in North America, *Festuca* species appear to facilitate invasive *Centaurea* species and enhance their compensatory responses in controlled greenhouse conditions. We explored the interactions between herbivory and neighbor effects in the French Alps by testing the effect of the neighbor, *Festuca paniculata* L., on the compensatory growth response of defoliated *Centaurea uniflora* L. over two growing seasons. Seventy percent of aboveground *C. uniflora* biomass was clipped at each of seven times throughout two growing seasons in the presence or absence of *F. paniculata*. *Centaurea uniflora* compensated for severe damage in the first year, but was negatively affected by defoliation in the second year. Defoliating *C. uniflora* reduced final aboveground biomass by 44% and flower number by 64%, but did not affect survival. Unlike observations for other *Centaurea* and *Festuca* species, *F. paniculata* had significant competitive effects on *C. uniflora*. *Festuca paniculata* neither enhanced compensatory responses of *C. uniflora* nor increased the negative effects of defoliation. Our results show that compensatory responses can weaken over time, but that neighboring plants do not necessarily increase the negative effects of defoliation.

Introduction

Compensatory growth, or the tolerance of plants to herbivory, has been well documented in agricultural systems, but relatively few studies have examined compensation in natural systems (see reviews by Verkaar 1988; Trumble et al. 1993; Strauss and Agrawal 1999). Plants may undercompensate (Harper 1977; Crawley 1983), equally compensate (Lee and Bazzaz 1980; Fowler and Rausher 1985), or overcompensate in response to tissue damage (McNaughton 1986;

Paige and Whitham 1987; Alward and Joern 1993), and the degree of compensation is influenced by both abiotic and biotic conditions in the plant's environment. For example, the compensatory ability of *Ipomopsis arizonica* depends on the presence of neighboring plants, nutrient availability, and the timing of herbivory (Maschinski and Whitham 1989). As noted by Maschinski and Whitham (1989), plant-plant interactions can have a strong influence on compensatory growth. Competition should reduce the compensatory growth of damaged individuals because

neighbors reduce the amount of resources available for recovery (Bentley and Whittaker 1979; Whittaker 1979; Crawley 1983; Louda et al. 1990). However, plants also facilitate their neighbors via many different mechanisms (Bertness and Callaway 1994; Callaway 1995) and it is not clear what effect this has on compensatory growth.

Facilitative interactions have been reported between several *Centaurea* and *Festuca* species. For example, Grime et al. (1987) found facilitative effects of *F. ovina* on *C. nigra*, and that these effects depended upon interactions with arbuscular mycorrhizal (AM) fungi. Part of this effect was to ameliorate the effects of defoliation. Marler et al. (1999) found that *F. idahoensis* had a significant facilitative effect on *C. maculosa*, and this effect also appeared to be mediated by AM fungi. Callaway et al. (2001) found that *Nassella pulchra* had facilitative effects on *C. melitensis*, again apparently mediated by soil fungi. Further, Newingham (2002) found that the presence of *F. idahoensis* and *F. scabrella*, had a positive effect on the biomass of *C. maculosa*. Although these studies show that *Festuca* species can facilitate *Centaurea* species, this facilitation is not necessarily a two-way street. For example, *C. maculosa* is an exotic invader in North America that has strong negative effects on the native, *F. idahoensis*, which may be caused by allelopathic root exudates (Ridenour and Callaway 2001; also see Bais et al. 2003).

Insect herbivory can have relatively weak effects on *C. maculosa*, sometimes stimulating compensatory responses (Müller-Schärer 1991; Steinger and Müller-Schärer 1992; Callaway et al. 1999; Ridenour and Callaway, *in press*). Under some conditions, herbivory on *C. maculosa* may even increase its competitive effects on *F. idahoensis* (Callaway et al. 1999). The effects that neighboring plants have on *C. maculosa*'s compensatory response can vary and may be species specific. In a greenhouse experiment, neighboring *F. idahoensis* and *F. scabrella* did not affect the compensatory response of *C. maculosa* (Newingham 2002). Müller-Schärer (1991) found that European native, *F. pratensis*, was a strong competitor to *C. maculosa* in field experiments, and the presence of *F. pratensis* had negative effects on the response of *C. maculosa* to herbivory. However, he also found that "in the absence of grass competition, herbivory showed no significant impact on plant height, biomass, and fecundity".

So far, the unexpected effects of *Festuca* species on *Centaurea* species have only been demonstrated in the greenhouse or in common garden experiments outdoors. However, *Centaurea* and *Festuca* species co-occur in natural and invaded ecosystems around the world, and the natural *Centaureo-Festucetum spadiceae* association in the southwestern Alps of Europe is well described in the literature (Guinochet 1938; Braun-Blanquet 1972; Lacoste 1972). This subalpine plant community is dominated by *Centaurea uniflora* L. and *Festuca paniculata* L. (= *F. spadicea* (L.) Sch. and Thell.) and occurs in harsh abiotic conditions where low temperatures, high UV radiation, and a short growing season exist. The *Centaureo-Festucetum spadiceae* association occurs between 1700 and 2500 m but is most developed between 1900 and 2300 m.

Grazing by sheep, goats, and cattle is extensive in the subalpine and alpine meadows of the French Alps (Jouglet and Doree 1991; Braun-Blanquet 1972). There have been relatively few studies on the effects of herbivory on alpine plant community structure (Oksanen and Oksanen 1989; Blumer and Diemer 1996; Diemer 1996), and few studies have examined plant compensatory responses to herbivory in subalpine and alpine communities (see Paige and Whitham 1987).

We examined the effect of *F. paniculata* on the compensatory response of *C. uniflora* to artificial defoliation. Our experiment was designed to answer the following questions: 1) Does *F. paniculata* facilitate *C. uniflora*? 2) Does *C. uniflora* compensate for defoliation? 3) Does *F. paniculata* alter the compensatory response of *C. uniflora*?, and 4) Does the response of *C. uniflora* to *F. paniculata* and defoliation change over time?

Methods

Our field experiment was conducted near the Alpine Field Station of Lautaret in the French Alps near the Col du Lautaret, situated between Grenoble and Briançon, France (elevation, 2250 m; N 45°02'09", E 6°24'21"). The mean temperature at the Col du Lautaret in July (the warmest month) is 11 °C and average annual precipitation is 1300 mm. This site is dominated by both *C. uniflora* and *F. paniculata* and is a typical example of the *Centaureo-Festucetum spadiceae* association. The natural treeline occurs near 2350 m, but our field site was located in grass-

lands that have developed after deforestation and grazing.

In June of 1999, we selected 90 *C. uniflora* individuals of similar size surrounded predominantly by *F. paniculata* and applied one of three treatments to each individual: 1) *F. paniculata* present and not manipulated, as a control, 2) *F. paniculata* present and leaves pushed aside so that no shade was over target *C. uniflora* individuals, and 3) *F. paniculata* leaves completely clipped. For the *F. paniculata* clipped treatment, all aboveground biomass of *F. paniculata* was clipped at the beginning of the experiment and any regrowth was clipped throughout the growing season. For the *F. paniculata* pushed aside treatment, plants were left intact but the leaves were pushed aside. We conducted this treatment to mimic microclimate effects of *F. paniculata* canopies (shade and shelter from wind and snow), but without strong effects on root competition (see Cahill 2002). This treatment was intended as a microclimate control for clipping the aboveground biomass of *F. paniculata*. For half of the *C. uniflora* individuals in each of the three *F. paniculata* neighbor treatments, we repeatedly clipped 70% of *C. uniflora* leaves. We clipped approximately once per month for 2 years during the 1999 and 2000 growing seasons (June 16, July 5 and July 20, 1999, and June 3, July 1, and August 2, 2000). Prior to each clipping bout we counted the leaves and flowers of target *C. uniflora* plants. Aboveground biomass of *C. uniflora* was harvested on August 25, 2000 and harvested plants were dried at 60 °C for 48 hours and weighed.

Centaurea uniflora leaf number was analyzed using a repeated measures ANOVA with time (7 dates) as the within-subject factor and defoliation and neighbor as between-subject factors. Sphericity was violated for the leaf number analysis and the Greenhouse-Geisser correction was $\epsilon < 1$; however, the univariate and multivariate ANOVA did not produce different *P* values of significance. We only report results from the univariate ANOVA. Flower number was counted on the same dates as leaf number; however, only flower number at the end of each year was included in the analysis. A repeated measures ANOVA was used with year (two years) as the within-subject factor and defoliation and neighbor as between-subject factors. We also conducted separate ANOVAs for each year to examine treatment effects within a year. Final biomass was analyzed using a two-way ANOVA with defoliation and neighbor as factors. Data were square root transformed when

needed to meet ANOVA assumptions. Means are reported as mean \pm 1 standard error of mean.

Results

Leaf production

Leaf number was highly correlated with the biomass of *C. uniflora* ($R^2 = 0.975$); therefore, leaf number was an accurate surrogate for the effects of defoliation on the biomass of *C. uniflora* before harvesting. Overall, neighboring *F. paniculata* had a negative effect upon *C. uniflora* leaf number (Figure 1, Table 1). In pair-wise comparisons, there was no difference between unmanipulated, control *F. paniculata* and the treatment with *F. paniculata* pushed aside ($P = 1.000$), but the removal of *F. paniculata* shoots resulted in higher leaf numbers produced by *C. uniflora* than either of the former treatments ($P < 0.0005$). Although clipping *F. paniculata* increased final *C. uniflora* leaf number, the effects of clipping varied over time. In 1999, clipping *F. paniculata* shoots had no effect on *C. uniflora* leaf number ($P = 0.577$); however, by the end of 2000 clipping *F. paniculata* increased the leaf number of neighboring *C. uniflora* ($P < 0.0005$) suggesting a competitive release. When *C. uniflora* was not defoliated and *F. paniculata* was clipped, *C. uniflora* mean leaf number at the end of 1999 was 35.87 ± 4.60 and increased to 64.00 ± 10.50 at the end of 2000.

Defoliation of *C. uniflora* significantly reduced its leaf number after 2 years, demonstrating the inability of this species to equally compensate for long-term, severe defoliation; however, the effects of defoliation varied over time (Figure 1, Table 1). In the first year, defoliation did not affect *C. uniflora* leaf number ($P = 0.940$), but in the second year defoliation had a negative effect on leaf number ($P < 0.0005$). Despite the competitive effect of *F. paniculata*, neighboring *F. paniculata* did not affect the response of *C. uniflora* to defoliation.

Flower production

In the overall analysis, manipulating *F. paniculata* increased the number of flowers produced by *C. uniflora* (Figure 2, Table 2). *Centaurea uniflora* flower number did not significantly differ between the treatments where *F. paniculata* was left intact and when leaves were pushed aside ($P = 1.000$). Although

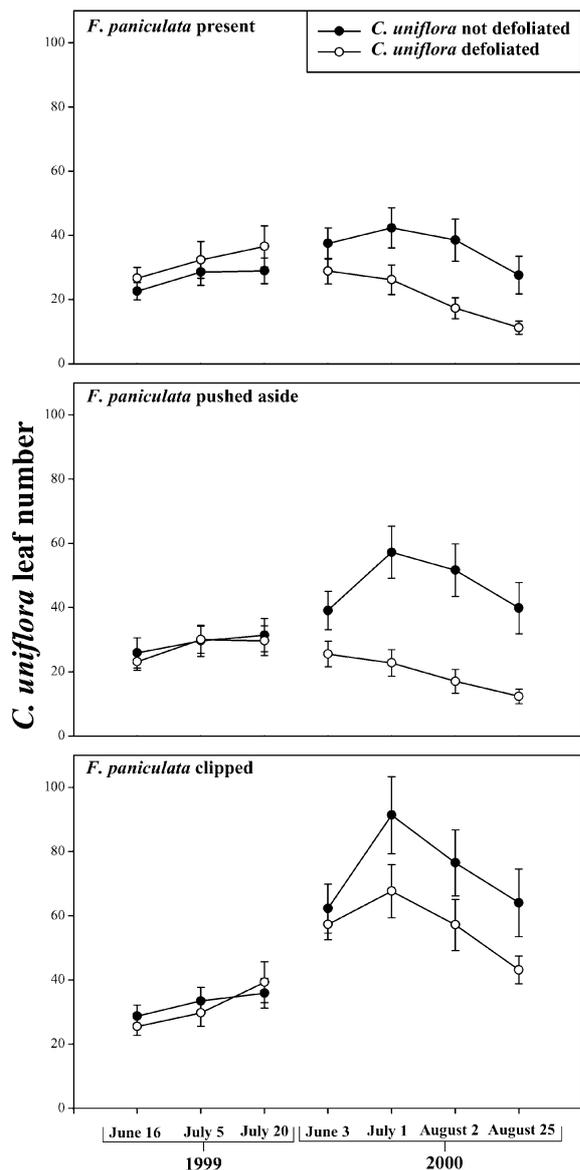


Figure 1. *Centaurea uniflora* leaf number when defoliated versus not defoliated, and when neighboring *F. paniculata* was present, pushed aside, or clipped, over 7 sampling dates in 1999 and 2000. Error bars represent \pm 1 SE.

non-significant in pair-wise comparisons, flower number tended to be greater when *F. paniculata* was clipped compared to when *F. paniculata* was present ($P = 0.078$) or when pushed aside ($P = 0.069$). Based upon repeated measures ANOVA, the effect of *F. paniculata* on the response of *C. uniflora* to defoliation did not differ between years ($P = 0.774$); however, separate two-way ANOVAs for each year

indicated that neighboring *F. paniculata* did not affect *C. uniflora* in 1999 ($P = 0.496$) but decreased flower number in 2000 ($P = 0.022$).

Across years, defoliation of *C. uniflora* significantly decreased its flower number (Figure 2, Table 2). In 1999, defoliation did not affect the number of *C. uniflora* flowers ($P = 0.293$), but by 2000 defoliation decreased flower number by 64% ($P < 0.0005$). As for leaf production, neighboring *F. paniculata* did not affect the response of *C. uniflora* flower number to defoliation.

Aboveground biomass

The presence of *F. paniculata* reduced the biomass of *C. uniflora* by 23% when the latter was not defoliated, and by 51% when *C. uniflora* was defoliated (Figure 3, $df = 2$, $F = 5.11$, $P = 0.008$). There was no difference in the biomass of *C. uniflora* between the treatments in which *F. paniculata* was not manipulated versus when *F. paniculata* leaves were pushed aside ($P = 1.000$). The biomass of *C. uniflora* was larger in treatments when *F. paniculata* was clipped ($P = 0.016$) or when leaves were pushed aside ($P = 0.021$) versus the controls, indicating both above and belowground competition. Two years of repeated defoliation of *C. uniflora* reduced its final aboveground biomass by an average of 44% across all neighbor treatments ($df = 1$, $F = 49.29$, $P < 0.0005$). The total biomass of non-defoliated plants was $1.30 \pm 0.43g$ versus $0.73 \pm 0.36g$ for defoliated plants. Although defoliation affected final biomass, both defoliated and non-defoliated plants had 100% survival. Neighboring *F. paniculata* did not affect the response of *C. uniflora* to defoliation ($df = 2$, $F = 0.32$, $P = 0.726$).

Discussion

Despite previous evidence for positive effects of *Festuca* and other bunchgrass species on *Centaurea* species (Grime et al. 1987; Marler et al. 1999; Callaway et al. 2001; Callaway et al. unpublished data), *F. paniculata* did not facilitate *C. uniflora* growth or regrowth after defoliation. In contrast, during the first year of treatments, *F. paniculata* had no effect upon *C. uniflora*, and in the second year *F. paniculata* had significant competitive effects on *C. uniflora*.

There may be several reasons we did not find a facilitative effect of *F. paniculata* on *C. uniflora*. First,

Table 1. Repeated measures ANOVA on *C. uniflora* leaf number over time when defoliated or not defoliated and when *F. paniculata* was present, pushed aside, or clipped. Significant terms ($P < 0.05$) are indicated in italics. Greenhouse-Geiger (G-G) corrected P values are listed.

Source	df	MS	<i>F</i>	<i>P</i>	<i>G-G</i>
<i>Defoliation</i>	1	129.579	9.119	<i>0.003</i>	
<i>Neighbor</i>	2	188.282	13.250	<i>< 0.0005</i>	
Defoliation x neighbor	2	9.035	0.636	0.532	
Error	83	14.209			
<i>Time</i>	6	35.097	29.695	<i>< 0.0005</i>	<i>< 0.0005</i>
<i>Time x defoliation</i>	6	22.056	18.661	<i>< 0.0005</i>	<i>< 0.0005</i>
<i>Time x neighbor</i>	12	16.613	14.056	<i>< 0.0005</i>	<i>< 0.0005</i>
Time x defoliation x neighbor	12	1.711	1.447	0.141	0.204
Error (Time)	498	1.182			

it is possible that *F. paniculata* never facilitates *C. uniflora*. The positive association between *C. uniflora* and *F. paniculata* may not be a mutualism or a commensalism in which *C. uniflora* benefits. Instead, *F. paniculata* may be the species benefiting from this association, or this association could be due simply to shared adaptations to the particular environment.

Second, if facilitation is occurring, the facilitative effects of *F. paniculata* on *C. uniflora* may be due to a different mechanism than we investigated. Our results suggest that *F. paniculata* does not play a facilitative role in *C. uniflora*'s compensatory response to defoliation. Additionally, pushing *F. paniculata* to the side revealed that any possible facilitative effect is not due to *F. paniculata* modifying the aboveground microclimate to benefit *C. uniflora*. Generally, pushing *F. paniculata* foliage to the side to reduce light competition had weaker effects on *C. uniflora* suggesting that the main effect of *F. paniculata* was via root competition rather than shade. Our results should be interpreted with caution because belowground interactions were not manipulated (see Cahill 2002). Although *F. paniculata* was continually clipped throughout both growing seasons, belowground competition may have not been eliminated. Further, the positive response of *C. uniflora* may possibly have been caused by nutrient flux from decomposing *F. paniculata* roots rather than decreased competition (see Fahey et al. 1988).

Facilitative effects of *F. paniculata* on *C. maculosa* may also depend on site microtopography. Choler et al. (2001) examined the role of facilitation and competition in subalpine and alpine communities near our experimental site, and at 2100 m they found that competition dominated plant interactions. However,

at 2600 m the general effects of neighbors were facilitative at exposed, convex sites, but at sheltered, concave sites neighbors were competitive. They attributed these differences to harsher conditions at the convex sites. Our experimental site was located between these two elevations (2250 m) and the microtopography was concave. Similar experiments in more stressful microsites or at higher elevations may have detected facilitative effects of *F. paniculata* on *C. uniflora*.

We found that *C. uniflora* recovered from repeated defoliation in the first year but could not recover in the second year. The biomass of *C. uniflora* was 44% lower at the end of the second year; however, *C. uniflora* demonstrated extraordinary compensation for damage since 70% of its leaves were removed at each of seven different times. This was especially surprising since high altitude plants usually have slower growth rates than species at lower elevations (Körner 1999). Shorter growing seasons at high elevations may also reduce the ability of plants to compensate for tissue loss. Although *C. uniflora* did not demonstrate equal compensation, its remarkable response to long-term, severe defoliation indicates that strong compensation, relative to the proportion of tissue lost, is possible even in harsh subalpine environments. In addition, it is surprising that all damaged plants survived the severe defoliation.

Most studies examining plant compensation to herbivory have been conducted in agricultural systems. It is evident from our study and others in natural systems that plant compensation in response to herbivory can be variable; however we still know little about how abiotic and biotic factors influence plant responses to herbivory. Additional studies in natural

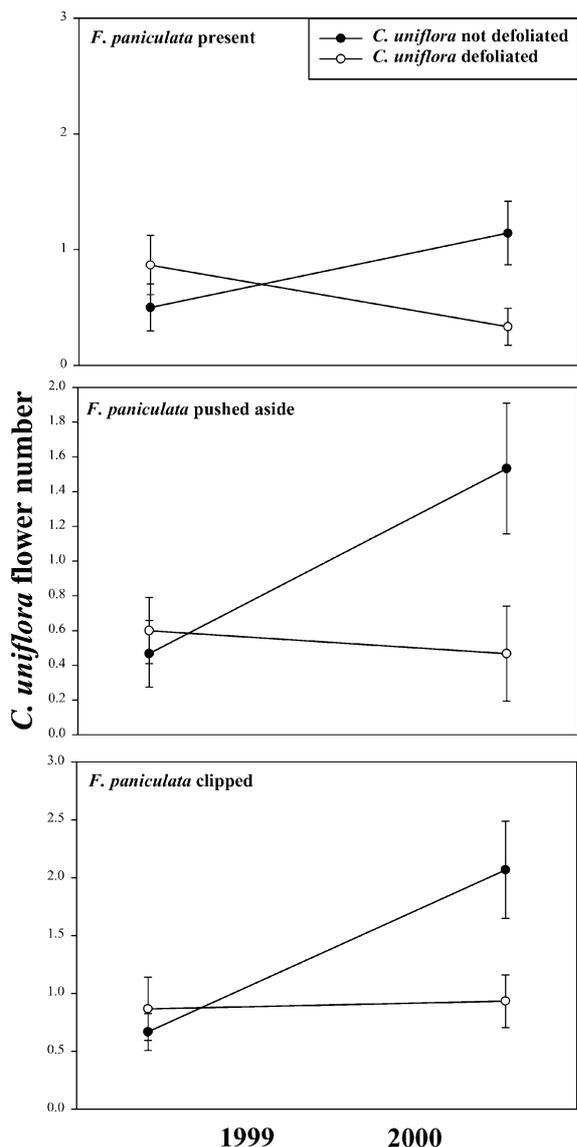


Figure 2. *Centaurea uniflora* flower number when defoliated versus not defoliated, and when neighboring *F. paniculata* was present, pushed aside, or clipped, at the end of 1999 and 2000. Error bars represent \pm 1SE.

systems will increase our knowledge of what influences compensatory growth, as well as help identify the mechanisms of compensatory growth, something we currently know little about.

Festuca paniculata had a competitive effect on *C. uniflora*, but did not affect the compensatory growth of *C. uniflora*. Clipped and unclipped plants responded similarly to competition with *F. paniculata* and indicate that competition does not always exac-

Table 2. Repeated measures ANOVA on *C. uniflora* flower number at the end of 1999 and 2000 when defoliated or not defoliated and when *F. paniculata* was present, pushed aside, or clipped. Significant terms ($P < 0.05$) are indicated in italics.

Source	df	MS	F	P
<i>Defoliation</i>	1	2.186	5.093	<i>0.027</i>
<i>Neighbor</i>	2	1.490	3.471	<i>0.036</i>
Defoliation x neighbor	2	0.034	0.079	0.924
Error	83	0.429		
<i>Year</i>	1	1.967	5.474	<i>0.022</i>
<i>Year x defoliation</i>	1	5.742	15.982	<i>< 0.0005</i>
Year x neighbor	2	0.417	1.160	0.318
Year x defoliation x neighbor	2	0.092	0.257	0.774
Error (Year)	83	0.359		

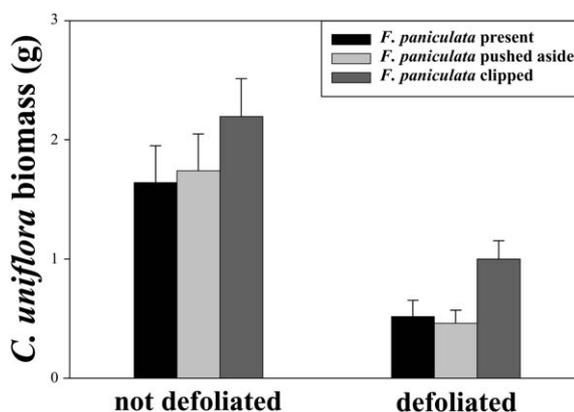


Figure 3. *Centaurea uniflora* final aboveground biomass after being defoliated versus not defoliated in 1999 and 2000 when neighboring *F. paniculata* was present, pushed aside, or clipped. Error bars represent \pm 1SE.

erbate the effects of defoliation. Previous studies have found mixed results of the combined effects of competition and herbivory. Some studies suggest that competition and herbivory are additive (Archer and Detling 1984; Fowler and Rausher 1985; Cottam et al. 1986) while others have found no interaction between competition and herbivory (Parker and Salzman 1985; Rees and Brown 1992). In a review of studies of the effects of natural enemies and competitors, Sheppard (1996) reported that the dominant factor in 10 of 12 studies in natural grasslands was competition. However, most effects of competitors and natural enemies were "multiplicative" rather than "additive".

There are two possible explanations for the change in effects of defoliation and *F. paniculata* between

years. The increased effects of defoliation in the second year may have been due to the cumulative effects of defoliation, which caused a reduction in the ability of the plant to further compensate, or environmental conditions may have been harsher in the second year reducing allocation of resources to compensatory growth. The competitive release of *C. uniflora* in the second year could have been because removing shoots in the first year did not eliminate root competition and *C. uniflora* benefited from root decomposition in the second year, or environmental conditions in the second year favored *C. uniflora* without neighbors. Our results suggest that short-term plant responses to biotic stresses may differ from long-term responses.

Our results provide evidence that competition with neighbors does not necessarily reduce the compensatory response of plants to damage as predicted by competition theory. We found no evidence that *F. paniculata* facilitated *C. uniflora* although these plants are commonly associated with one another.

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References

- Alward R.D. and Joern A. 1993. Plasticity and overcompensation in grass responses to herbivory. *Oecologia* 95: 358–364.
- Archer S. and Detling J.K. 1984. The effects of defoliation and competition on regrowth of tillers of two North American mixed-grass prairie graminoids. *Oikos* 43: 351–357.
- Bais H.P., Vepachedu R., Gilroy S., Callaway R.M. and Vivanco J.M. 2003. Allelopathy and exotic plant invasion: from molecules and genes to species interactions. *Science* 301: 1377–1380.
- Bentley S. and Whittaker J.B. 1979. Effects of grazing by a chrysomelid beetle, *Gastrophysa viridula*, on competition between *Rumex obtusifolius* and *Rumex crispus*. *Journal of Ecology* 67: 79–90.
- Bertness M.D. and Callaway R.M. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9: 191–193.
- Blumer P. and Diemer M. 1996. The occurrence and consequences of grasshopper herbivory in an alpine grassland, Swiss Central Alps. *Arctic and Alpine Research* 28: 435–440.
- Braun-Blanquet J. 1972. L'alliance du Festucion spadicaceae des Alpes sud-occidentales. *Bulletin de societe botanique de France* 119: 591–602.
- Cahill J.F. 2002. What evidence is necessary in studies which separate root and shoot competition along productivity gradients? *Journal of Ecology* 90: 201–205.
- Callaway R.M. 1995. Positive interactions among plants. *Botanical Review* 61: 306–349.
- Callaway R.M., DeLuca T.H. and Belliveau W.M. 1999. Biological control herbivores may increase competitive ability of the noxious weed *Centaurea maculosa*. *Ecology* 80: 1196–1201.
- Callaway R.M., Newingham B.A., Zabinski C.A. and Mahall B.E. 2001. Compensatory growth and competitive ability of an invasive weed are enhanced by soil fungi and native neighbors. *Ecology Letters* 4: 429–433.
- Callaway R.M., Brooker R.W., Chole P., Kikvidze Z., Lortie C.J., Michalet R., Paolini L., Pugnaire F.I., Newingham B., Aschehoug E.T., Armas C., Kikodze D. and Cook B.J. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844–848.
- Choler P., Michalet R. and Callaway R.M. 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology* 82: 3295–3308.
- Cottam D.A., Whittaker J.B. and Malloch A.J.C. 1986. The effects of chrysomelid beetle grazing and plant competition on the growth of *Rumex obtusifolius*. *Oecologia* 70: 452–456.
- Crawley M.J. 1983. *Herbivory: the dynamics of animal-plant interactions*. Blackwell Scientific Publications, UK.
- Diemer M. 1996. The incidence of herbivory in high-elevation populations of *Ranunculus glacialis*: a re-evaluation of stress-tolerance in alpine environments. *Oikos* 75: 486–492.
- Fahey T.J., Hughes J.W., Pu M. and Arthur M.A. 1988. Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. *Forest Science* 34: 744–768.
- Fowler N.L. and Rausher M.D. 1985. Joint effects of competitors and herbivores on growth and reproduction in *Aristolochia reticulata*. *Ecology* 66: 1580–1587.
- Grime J.P., Mackey J.M.L., Hillier S.H. and Read D.J. 1987. Floristic diversity in a model system using experimental microcosms. *Nature* 328: 420–422.
- Guinochet M. 1938. *Etudes sur la végétation de l'étage alpin dans le bassin supérieur de la Tinée (Alpes-Maritimes)*. Thèse. a la faculté des sciences de Grenoble, France.
- Harper J.L. 1977. *Population biology of plants*. Academic Press, New York, USA.
- Jouglet J.P. and Doree A. 1991. Les pelouses à fétuque paniculée: Un enjeu pour les Alpes du sud. *Congrès International des Terres de Parcours*, France, pp. 479–482.
- Körner C. 1999. *Alpine plant life: functional plant ecology of high mountain ecosystems*. Springer.
- Lacoste A. 1972. *La végétation de l'étage subalpin du supérieur de la Tinée (Alpes-Maritimes)*. Thèse. Paris-Sud Centre D'Orsay, France.
- Lee T.D. and Bazzaz F.A. 1980. Effects of defoliation and competition on growth and reproduction in the annual plant *Abutilon theophrasti*. *Journal of Ecology* 68: 813–821.
- Louda S.M., Keeler K.H. and Holt R.D. 1990. Herbivore influences on plant performance and competitive interactions. In: *Grace*

- J.B. and Tilma D. (eds), Perspectives on Plant Competition. Academic Press, pp. 414-444.
- Marler M., Zabinski C.A. and Callaway R.M. 1999. Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. *Ecology* 80: 1180-1186.
- Maschinski J. and Whitham T.G. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *American Naturalist* 134: 1-19.
- McNaughton S.J. 1986. On plants and herbivores. *American Naturalist* 128: 765-770.
- Müller-Schärer H. 1991. The impact of root herbivory as a function of plant density and competition: survival, growth, and fecundity of *Centaurea maculosa* in field plots. *Journal of Ecology* 28: 759-776.
- Newingham B.A. 2002. Insect herbivory and defoliation on *Centaurea* species: the roles of neighbors, allelopathy, and arbuscular mycorrhizal fungi. Ph.D. Dissertation, University of Montana, Montana, USA.
- Oksanen L. and Oksanen T. 1989. Natural grazing as a factor shaping out barren landscapes. *Journal of Arid Environments* 17: 219-233.
- Paige K.N. and Whitham T.G. 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. *American Naturalist* 129: 407-416.
- Parker M.A. and Salzman A.G. 1985. Herbivore exclusion and competitor removal: effects of juvenile survivorship and growth in the shrub *Gutierrezia microcephala*. *Journal of Ecology* 73: 903-913.
- Rees M. and Brown V.K. 1992. Interactions between invertebrate herbivores and plant competition. *Journal of Ecology* 80: 353-360.
- Ridenour W.M. and Callaway R.M. in press. Root herbivores, pathogenic fungi, and competition between *Centaurea maculosa* and *Festuca idahoensis*. *Plant Ecology*.
- Ridenour W.M. and Callaway R.M. 2001. The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. *Oecologia* 126: 444-450.
- Sheppard A.W. 1996. The interaction between natural enemies and interspecific plant competition in the control of pasture weeds. Pages 47-53. In: Moran V.C. and Hoffman J.H. (eds), Proceedings of the IX International Symposium on Biological Control of Weeds. University of Cape Town, Stellenbosch, South Africa.
- Steinger T. and Müller-Schärer H. 1992. Physiological and growth responses of *Centaurea maculosa* (Asteraceae) to root herbivory under varying levels of interspecific plant competition and soil nitrogen availability. *Oecologia* 91: 141-149.
- Strauss S.Y. and Agrawal A.A. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution* 14: 179-185.
- Trumble J.T., Kolodny-Hirsch D.M. and Ting I.P. 1993. Plant compensation for arthropod herbivory. *Annual Review of Entomology* 38: 93-119.
- Verkaar H.J. 1988. Are defoliators beneficial for their host plants in terrestrial ecosystems - a review? *Acta Botanica Neerlandica*. 37: 137-152.
- Whittaker J.B. 1979. Invertebrate grazing, competition and plant dynamics.. In: Anderson R.M., Turner B.D. and Taylor L.R. (eds), Population dynamics. Symposium of the British Ecological Society, No. 20. Blackwell Scientific Publications, UK.