2002

Insect herbivory and defoliation on Centaurea species: The roles of neighbors allelopathy and arbuscular mycorrhizal fungi

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Insect herbivory and defoliation on *Centaurea* species: the roles of neighbors, allelopathy, and arbuscular mycorrhizal fungi

by

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B.S. University of Nebraska-Lincoln 1994

Presented in partial fulfillment of the requirements

for the degree of

Doctor of Philosophy

The University of Montana

May 2002

Approved by:

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ABSTRACT

Newingham, Beth A. Ph.D. May 2002. Division of Biological Sciences, OBE

Insect herbivory and defoliation on *Centaurea* species: the roles of neighbors, allelopathy, and arbuscular mycorrhizal fungi

Director: Dr. Ragan M. Callaway

Herbivory is assumed to have negative effects on plants, but many species compensate for herbivory by accelerating growth and reproduction after damage. Little is known about how biotic interactions influence variation in plant responses to herbivory. The assumption that herbivory significantly reduces plant performance and competitive effects on native neighbors is central to biocontrol theory. In this context, numerous biocontrols have been introduced to control invasive plants, including *Centaurea* species. I examined how herbivory altered the interactions between *Centaurea* and *Festuca* species in three different systems. First, I investigated how *Festuca* species influenced the compensatory response of *Centaurea maculosa* to herbivory and whether herbivory altered the allelopathic effects of *C. maculosa* on *Festuca*. *Centaurea maculosa* compensated for herbivory (up to 40% leaf damage) and *Festuca* neighbors did not increase the negative effects of herbivory. *Centaurea maculosa* was allelopathic to *F. idahoensis*; however, herbivory on *C. maculosa* did not increase these allelopathic effects. In a second study I determined whether a North American genotype (the tetraploid *C. stoebe* ssp. *micranthos*) differed ecologically from a western European genotype (the diploid *C. stoebe* ssp. *stoebe*). Both subspecies responded similarly to defoliation, the presence of *F. ovina*, and arbuscular mycorrhizal (AM) fungi. Defoliation negatively affected *C. stoebe*, but *F. ovina* positively affected *C. stoebe*. AM fungi positively affected *C. stoebe*, but did not increase compensatory growth. In a third study I examined interactions between *C. uniflora* and *F. paniculata* in subalpine communities of the French Alps. *Centaurea uniflora* fully compensated for defoliation in the first year, but biomass was negatively affected after repeated defoliation for two growing seasons. *Festuca paniculata* neighbors had competitive effects on *C. uniflora*, but did not affect its compensatory response. My results suggest that herbivory has weak or no effect on *Centaurea* and competitors do not exacerbate the effects of herbivory. In addition, herbivory on *Centaurea* does not decrease its competitive effects on neighbors nor does herbivory increase allelopathic effects. In this study, AM fungi did not enhance *Centaurea* compensatory growth. My results suggest that biocontrols may be less effective at reducing the competitive ability of *Centaurea* than previously thought.

ACKNOWLEDGEMENTS

I am especially grateful to my advisor, Ray Callaway, for providing me with the opportunity to increase my worldliness as a scientist and as a person. I also thank my committee members, Anna Sala, Cathy Zabinski, Diana Six and Doug Emlen, for help and advice throughout this process. Jon Graham, who should have been on my committee, was a tremendous help with statistics. I would like to thank Tony Joern and Svata Louda for inspiring me to become an ecologist.

The National Science Foundation, Mellon Foundation, and the Mount Sentinel Weed Management Committee helped fund this research. In addition, I thank Jody Anderson and the Missoula Chapter BO of the Philanthropic Educational Organization for giving me a scholarship and providing me with food during stressful times like comprehensive exams!

Christian Richey was my 'right hand man' who provided me with technical and emotional support throughout this crazy adventure. Eileen Carey, October Seastone-Moynahan, Brad Cook, Kurt Reinhart, Jose Hierro, Derek MacKenzie, Dean Pearson, Andrea Thorpe and Jason Sexton provided a great backboard to bounce ideas off and helped with editing. Willow Foster, Erik Aschehoug, Jonathan Rothman, Adam Collins, Nate Olson and Giles Thelen kept it real in the lab. Richard Michalet and Emmanuel Corcket assisted me in getting on my feet in France. Gregoire Boquien was essential in helping me learn French and conduct research in that crazy country. Pierre Liancourt and Mathieu Tilquin provided me with a unique French experience filled with bad accents and rolled cigarettes.

Hugh Powell and John Lloyd were my two best fellow graduate students and friends that helped make graduate school a blast. I would also like to thank my 'non-school' friends and fellow residents of 648 E. Sussex - Chase, Amber, Emmanuel, Kari, MJ, Bevin, Chris, and Keith. And last, but not least, special thanks go out to the Beastie Boys, Johnny Cash, the Rolling Stones, and the band members of Love Magma for helping me remember that life isn't just about science – it's also about rock n' roll. ☆

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INTRODUCTION

Aboveground and belowground biotic interactions are important in structuring plant communities. Neighboring plants, herbivores and soil microorganisms can influence plant performance resulting in changes at the population, community and ecosystem level. None of these biotic factors act independently, nor even in simple pair-wise interactions; therefore, to gain more realistic insight into direct and indirect biotic effects in plant communities, it is crucial to examine them in concert. In my research I have examined how herbivores, microbes, and the presence of specific neighbors modify plant competitive interactions. My ultimate goal is to understand how complex interactions influence plant communities.

Herbivory generally has negative effects on plants. However, plants often compensate for herbivory by increasing growth or reproduction. Plants can undercompensate (Harper 1977, Crawley 1983), equally compensate (Lee and Bazzaz 1980, Fowler and Rausher 1985), or overcompensate (McNaughton 1986, Paige and Whitham 1987, Alward and Joern 1993) for herbivory. This spectrum of responses to herbivory may dramatically alter plant interactions within the community.

Herbivory and competition with neighboring plants occur simultaneously and competition can exacerbate the negative effects of herbivory (Archer and Detling 1984, Cottam et al. 1986, Reichman 1988). However, cases when herbivory and competition do not interact synergistically (Fowler and Rausher 1985, Parker and Salzman 1985, Rees and Brown 1992), suggest that: 1) herbivory does not have a negative effect on the target plant (i.e., compensation), or 2) neighboring plants are not necessarily competitors. Thus, it is important to understand how plants respond to herbivory, how neighboring plants affect this response, and how herbivory alters the interactions between plants.

It is generally assumed that neighboring plants are competitors, and plant competition is clearly one of the most dominant forces influencing plant communities (Connell 1983, Aarssen and Epp 1990, Goldberg and Barton 1992). However, plants can also have neutral or positive effects on each other. Plants can facilitate one another by ameliorating environmental conditions such as light, water, temperature, and damage by herbivores, and plants can positively affect one another via shared pollinators or microbial symbionts such as mycorrhizal fungi (Callaway 1995, Callaway 1997). Such a broad range of potential interactions among plants again suggests the importance of considering plant interactions in the context of other biotic interactions.

Within the last ten years plant community ecology has been revolutionized by a new understanding of the role of soil microbes in plant communities. Soil microbes can alter competitive outcomes (Goodwin 1992, Newman et al. 1992, Hartnett et al. 1993, Moora and Zobel 1996), reverse the outcome of herbivory (Callaway et al. 2001), and drive diversity changes in communities (van der Heiden et al. 1998, Smith et al. 1999). Furthermore, plants and soil microbes can participate in negative or positive feedback loops with strong implications for community composition, diversity, and dynamics (Bever et al. 1997, Watkinson 1998, Klironomos 2002). As for herbivory and plant-plant interactions, it is clear that a realistic understanding of microbial effects must come within the context of other biotic interactions.

My dissertation examines the role of herbivory in the interactions between *Centaurea* and *Festuca* species. Numerous species of insects have been introduced as biological controls to reduce the spread of invasive *Centaurea* species in North America; however, *Centaurea* species continue to expand their ranges (Müller-Schärer and Schroeder 1993). Biological control theory assumes that herbivory has negative effects upon *Centaurea* and that herbivore damage on *Centaurea* will decrease its competitive ability, releasing native neighbors from competition. However, this outcome has not been tested rigorously in the context of multiple interactions.

In contrast to biological control theory, previous research suggests that herbivory may not have strong negative effects on the invasive weed, *C. maculosa* Lam., and in some cases, may *increase* its competitive ability (Callaway et al. 1999). I examined the effects of herbivory on *Centaurea* in three different systems with the following objectives: 1) to determine the effects of herbivory on *Centaurea*, 2) to examine whether neighboring plants exacerbate the effects of herbivory on *Centaurea*, 3) to assess whether herbivory on *Centaurea* has positive indirect effects on neighbors, and 4) to identify the mechanism for *C. maculosa's* increased competitive ability after herbivory.

Centaurea may increase its competitive ability by increasing its allelopathic effects on neighbors. Allelopathy is the production of secondary chemicals by a plant that has negative effects upon neighboring plants (Rice 1984). Evidence suggests that *C. maculosa* is allelopathic to *F. idahoensis* (Ridenour and Callaway 2001). Plants also produce secondary chemicals for protection from herbivores (Zangerl et al. 1997, Underwood 1998); therefore, it is possible that anti-herbivore secondary chemicals may have a dual function as allelopathic chemicals (Lovett and Hoult 1995, Tang et al. 1995, Siemens et al. 2002). Thus, herbivory could increase the negative effects of allelopathy and increase *Centaurea's* competitive ability.

Arbuscular mycorrhizal (AM) fungi are important in plant growth (Koide 1991, Newman et al. 1992, Marschner and Dell 1994) and can form mycorrhizal links between plants (Newman et al. 1992). AM fungi are important in the interactions between *C. maculosa* and *F. idahoensis*. Marler et al. (1999) suggests that *C. maculosa* may parasitize *F. idahoensis* through AM fungi. Since AM fungi are important for resource and water uptake, it is possible they play an important role in plant compensatory response to herbivory (Callaway et al. 2001). If herbivory increases nutrient uptake through AM fungi and plants are linked via mycorrhizal hyphae, herbivory may increase the amount of carbon or nutrients transferred from the undamaged plant to the damaged plant. Therefore, herbivory could increase *C. maculosa's* competitive ability through AM fungi.

In Chapter 1, I examine the compensatory response of the North American invader, *C. maculosa*, over a range of *Trichoplusia ni* Hübner herbivory either alone or in the presence of a neighboring *C. maculosa*, or the North American natives, *F. idahoensis* and *F. scabrella*. Additionally, I determine whether herbivory on *C. maculosa* has positive effects on neighboring plants. In this experiment I also investigate whether herbivory increases the allelopathic effects of *C. maculosa* thereby increasing its competitive ability.

Chapter 2 examines the interactions between herbivory and neighboring *F. ovina* on two *Centaurea* genotypes, *C. stoebe* ssp. *micranthos* and *C. stoebe* ssp. *stoebe*. *Centaurea stoebe* ssp. *micranthos* (=*C. maculosa*) is the invasive genotype in North America and *C. stoebe* ssp. *stoebe* occurs in western Europe. In this experiment I also assess whether AM fungi assist *C. stoebe* subspecies in their compensatory response and if this increases its competitive effects on *F. ovina*.

Chapter 3 looks at how herbivory and neighboring *F. paniculata* interact to affect *C. uniflora*. *Centaurea uniflora* and *F. paniculata* are commonly associated with one another in subalpine and alpine communities of the French Alps. This experiment is designed to also determine if the interactions between *C. uniflora* and *F. paniculata* are similar to those found between *C. maculosa* and North American *Festuca* species.

The results of my dissertation are important not only for understanding how simultaneous biotic factors in the community interact to determine plant-plant interactions, but also to determine whether insect herbivory by biological control agents will reduce the competitive ability of *Centaurea*. If herbivory is not effective at reducing its competitive ability, we may need to re-assess the use and introduction of numerous non-native insect species to control *Centaurea* species.

In summary, my findings indicate that herbivory can negatively affect *Centaurea* species, but only at high levels or under unusually stressful conditions. In contrast to theoretical predictions, neighboring native plants were not good competitors to *Centaurea* and did not exacerbate the effects of herbivory on *Centaurea* in any of my experiments. Consistent with this lack of competitive interaction, neighboring plants never responded positively to damage upon *Centaurea*. However, in contrast to Callaway et al. (1999) (also see Siemens et al. 2002) no experiment demonstrated that *Centaurea* increased its competitive ability after herbivory. *Centaurea maculosa* was allelopathic to *F. idahoensis*; however, herbivory did not increase allelopathic effects suggesting allelopathy does not play a role in enhancing the competitive ability of damaged *C. maculosa*. AM fungi were important in plant growth, but did not affect the compensatory response of *Centaurea* subspecies.

My dissertation research suggests that herbivory by biological control agents may be less effective than hoped to reduce the competitive ability of *Centaurea* species. *Centaurea* species are often resilient to damage and neighbors are unlikely to benefit from damage on *Centaurea*. This has important implications on the assumption that biological control agents will benefit native plants. Complex interactions in this system make it difficult to predict whether herbivory is an effective method of control for *Centaurea*.

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CHAPTER 1

Effects of herbivory on *Centaurea maculosa*: roles of compensatory growth and allelopathy

ABSTRACT

Herbivory can have negative, positive or no effect on the final biomass or reproduction of plants. However, the use of insects as biological controls is based on the fundamental assumption that herbivory will negatively affect target weeds and release natives from competition. Previous studies in North America and Europe found that *Centaurea maculosa*, one of western North America's worst invasive, exotic plants, is remarkably tolerant to herbivory, and under some conditions, herbivory may *increase* its competitive effects on native plant species. I conducted experiments to investigate the following mechanisms hypothesized increase the competitive ability of *C. maculosa* when subjected to herbivory: 1) herbivory stimulates compensatory growth by *C. maculosa* which increases its competitive effects, and 2) herbivory stimulates secondary chemical production by *C. maculosa*, perhaps as induced defenses, which increases allelopathic effects on neighboring plants. I conducted a greenhouse and field experiment to test the compensatory growth hypothesis. In the greenhouse experiment, herbivory by *Trichoplusia ni* had a negative effect on the final biomass of *C. maculosa*, but the effects of herbivory were absent below 40% leaf damage. Contrary to plant competition theory, which holds that neighbors should have negative effects on plants, the presence of a conspecific had no effect upon the biomass of *C. maculosa*; in contrast, the biomass of *C. maculosa* was larger when grown with *Festuca idahoensis* and *F. scabrella*. The presence of another *C. maculosa*, *Festuca idahoensis* or *F. scabrella* did not increase negative effects of herbivory on *C. maculosa*. Furthermore, herbivory on *C. maculosa* did not have positive effects on neighboring plants. Similar results were found with defoliation of *C. maculosa* in the field. Fifty percent defoliation of *C. maculosa* had a negative effect on the shoot biomass of *C. maculosa*; however, defoliation did not affect the number of *C. maculosa* flowers produced per plant. *Festuca idahoensis* neighbors did not increase the negative effects of herbivory on *C. maculosa*, and there was no positive effect on *F. idahoensis* when *C. maculosa* was damaged. In the greenhouse experiment, activated carbon added to absorb allelopathic chemicals reduced the competitive effects of *C. maculosa* on *F. idahoensis*, but not on *F. scabrella* or on conspecifics. However, there was no evidence that *C. maculosa* was more allelopathic after herbivory. In sum, the total range of herbivory applied in these experiments reduced the final biomass of *C. maculosa*, but not its reproduction. More importantly, the negative effects of herbivory on *C. maculosa* biomass did not alter the effects of this invader on native bunchgrasses.

KEYWORDS: allelopathy, *Centaurea maculosa*, compensatory growth, competition, herbivory

INTRODUCTION

Herbivory and competition are two of the most important forces structuring plant communities. 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 neighboring species, abiotic conditions, and intensity of the damage. Herbivory can have negative effects on plants (undercompensation) (Harper 1977, Crawley 1983), no effects (equal compensation) (Lee and Bazzaz 1980, Fowler and Rausher 1985), or positive effects (overcompensation) (McNaughton 1986, Paige and Whitham 1987, Alward and Joern 1993). Such a range in responses suggests that herbivory may not necessarily reduce the competitive ability of a plant. However, no studies have investigated the effects of compensatory growth on competitive ability.

Understanding how variable responses to herbivory affect plant interactions is of fundamental interest to ecologists, and is crucial for predicting the effectiveness of biological control herbivores against exotic, invasive weeds. Over 949 exotic species have been introduced around the globe as biological controls to reduce the spread of invasive plants (Julien and Griffiths 1998). The introduction of exotic insects is based on the assumption that invasive plants are successful because they lack natural enemies and that the introduction of 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). Based on a relatively simplistic interpretation of plant competition theory, herbivore damage is expected to decrease the competitive ability of weeds and release undamaged neighbors from competition. However, the indirect effects of biological controls on native plants have rarely been tested.

Centaurea species from Europe and Asia are some of the most damaging and invasive weeds in North America (Maddox and Mayfield 1985, Maddox et al. 1985, Roché and Roché 1988, Müller-Schärer and Schroeder 1993). *Centaurea maculosa* Lam. (spotted knapweed) is one of North America's worst weeds and was introduced from Eurasia in the late 1800's. *Centaurea maculosa* invasion often results in the development of dense, almost monospecific stands of *C. maculosa* and the competitive exclusion of virtually all native species (Ridenour and Callaway 2001).

Biological control agents were first introduced to control *Centaurea* species in 1970, and now there are at least 13 species of insects established in North America for this purpose (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.

The lack of success of biological control agents to control *C. maculosa* populations is consistent with a recent experiment which showed that, in contrast to the general expectations that herbivory will reduce the competitive ability of a plant, herbivory by biocontrols may slightly *increase* the competitive ability of *C. maculosa* (Callaway et al. 1999). In their experiment, the reproductive output and root biomass of native *Festuca* *idahoensis* were slightly but significantly lower when neighboring *C. maculosa* were attacked by *Agapeta zoegana* L. (Lepidoptera: Cochylidae), a common specialist biocontrol, and *Trichoplusia ni* Hübner (Lepidoptera: Noctuidae), a non-biocontrol generalist herbivore. Other studies have shown that herbivory by biocontrol herbivores does not reduce the growth of *C. maculosa* (Müller-Schärer 1991, Steinger and Müller-Schärer 1992) and in some cases causes overcompensatory root growth (Müller 1989) or flower production (Ridenour and Callaway, *in press*).

I propose two hypotheses to explain the potential increase in competitive effects of *C. maculosa* on *F. idahoensis*. First, *C. maculosa* may compensate for herbivory by increasing its growth rate, concomitantly increasing uptake of limited resources. Compensatory growth to herbivory would then improve the competitive ability of *C. maculosa*. Second, herbivory on *C. maculosa* may stimulate the production of secondary chemicals, perhaps as induced defenses, which may increase allelopathic effects on neighboring plants (Lovett and Hoult 1995, Tang et al. 1995). Plant secondary metabolites can provide protection against herbivores (Zangerl et al. 1997, Underwood 1998) and may alter plant-plant interactions (Gant and Clebsch 1975, Petranka and McPherson 1979, Mahall and Callaway 1992). Siemens et al. (2002) found that the induced chemical defenses of *Brassica rapa* also acted as allelopathic agents against competitors. Herbivory-stimulated growth and allelopathy may explain why *C. maculosa* can increase its competitive effect on neighbors after being damaged. I tested whether *C. maculosa* increased its competitive ability through compensatory growth or allelopathy in a greenhouse and field experiment. In the greenhouse, *C. maculosa* was exposed to *Trichoplusia ni* herbivory in the presence and absence of neighbors and with or without activated carbon added to the soil to reduce concentrations of allelochemicals. In a field experiment, I defoliated *C. maculosa* in the presence and absence of a neighbor.

METHODS

Greenhouse experiment

A greenhouse experiment was conducted at The University of Montana in which *C. maculosa* was planted alone, with a conspecific, and with each of two dominant native grasses in the intermountain prairie of Montana, *F. idahoensis* Elmer or *F. scabrella* Torrey ex. Hook. There were 60 replicates per neighbor treatment for a total of 240 pots. All plants were grown from seed 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).

To investigate the role of root exudates on *C. maculosa's* response to herbivory, 20 ml of activated carbon was added per liter of sand-soil mixture to half of the pots (120 total). 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, I 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 hour and then filtered through Whatman #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. I measured the pH of the activated carbon and the sand-soil-activated carbon mixture to determine if acid-washing altered soil properties relative to the sand-soil mixture without activated carbon.

After 16 weeks of growth, I randomly chose one of the two *C. maculosa* plants in the pots with conspecifics and the single *C. maculosa* in all other treatments, for herbivory by *T. ni*. After leaving *T. ni* on plants for 3-4 days, herbivory ranged in intensity from 0 (controls with no insects) to 90% of the total leaf area. *Trichoplusia ni* Hübner (cabbage looper moth) is native to Europe, but abundant in North America. *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 is easy to manipulate and measure precise levels of leaf damage. Cages were placed over all targets to ensure that *T. ni* only ate the target *C. maculosa*. Immediately after the herbivory treatment, I visually determined the percentage of damaged leaf area for each leaf. For each target plant, I counted the total number of leaves and expressed the percent damage of all leaves combined as a percentage of total plant leaf area. Six weeks after herbivory, all target plants and corresponding neighbors when present were harvested, dried at 60°C for 48 hours, and shoots and roots of both species were weighed.

In sum, there were 4 neighboring treatments, the presence or absence of carbon and a gradient of herbivory from 0 to 90%. All data were analyzed with ANCOVA. Treatment differences in 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. Herbivory was used as a covariate because it was assumed that the experiment started after herbivores had been applied. This allowed me to examine the plant's response to herbivory after damage. 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, leaf number was used as a surrogate for biomass. 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 either model because they were not significant. All data were log transformed to meet ANCOVA assumptions. Comparison of means was performed using the Bonferroni correction method. All means reported are mean ± 1 standard error.

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, 1374m). This site was dominated by both *C. maculosa* and *F. idahoensis*. In the spring of 2000, I chose eighty individual pairs of *C. maculosa* and *F. idahoensis*. Environmental conditions at this site are exceptionally harsh, relative to other areas where *C. maculosa* is more abundant, and there are fairly isolated pairs of *C. maculosa* and *F. idahoensis* with few or no other nearby neighbors. *Centaurea maculosa* target plants were approximately the same size and age. The initial mean number of *C. maculosa* leaves was 22.14±1.58 (± 1 standard error) and mean height was 8.71±0.21cm. The mean height of all *F. idahoensis* before clipping was 15.64±0.40 cm. Twenty pairs, chosen at random from the original 80 pairs, received one of the four following treatments: *C. maculosa* not defoliated-*F. idahoensis* present; *C. maculosa* not defoliated-*F. idahoensis* absent; *C. maculosa* defoliated-*F. idahoensis* present; *C. maculosa* defoliated-*F. idahoensis* absent. *Festuca idahoensis* was removed by clipping all aboveground biomass at the beginning of the experiment and each month if regrowth occurred. I imposed severe defoliation upon *C. maculosa* by clipping 50% of its aboveground biomass with scissors on June 1 and July 7, 2000. Although *F. idahoensis* was removed in some neighbor treatments, *F. idahoensis* was not defoliated as a "herbivory' treatment. This experiment was designed to run for two years; however, summer precipitation in 2000 was exceptionally low (see discussion) and there was high mortality of *C. maculosa*. Therefore, I established another 80 pairs in the spring of 2001 and repeated the same experiment. Clipping in 2001 occurred on June 25 and August 15, 2001. Survival of all *C. maculosa* plants was recorded at the end of 2000 and 2001 (alive or dead). In addition, aboveground biomass of all plants was collected and the number of flowers was counted on September 13, 2001.

Survival data of *C. maculosa* for 2000 were analyzed using a binary logistic regression with defoliation and neighbor as covariates. The high mortality of plants in 2000 reduced sample sizes so that statistical analyses of biomass and flower number were not possible; therefore, biomass and flower data were only analyzed for pairs identified in 2001. The biomass and flower data of *C. maculosa* were analyzed with a two-way ANOVA using defoliation and neighbor as fixed factors. The biomass and flower data of *F. idahoensis* were analyzed with a one-way ANOVA using defoliation as a fixed factor. All means reported are mean ± 1 standard error.

RESULTS

Greenhouse experiment

Herbivory had a negative effect upon the total biomass of the target *C. maculosa* when considering the entire 0-90% herbivory intensity gradient (Fig. 1, Table 1). Without herbivory, the mean biomass of the target *C. maculosa* was 0.83±0.053g and when using all herbivory levels combined (1-90%, mean % damage = 17.81±19.91) the mean biomass of target *C. maculosa* was reduced to 0.70±0.04g, a 16% reduction. However, the effect of herbivory was only evident when the highest intensities of herbivory were included. When analyses were conducted with all intensities >40% excluded, the effects of herbivory were weak on the biomass of target *C. maculosa* (P=0.069). In the full analysis, neither neighbors nor activated carbon altered the growth response of the target *C. maculosa* to herbivory. Leaf number before clipping was significantly related to the final biomass of target *C. maculosa*.

Activated carbon used to absorb allelochemicals did not significantly affect the total biomass of the target *C. maculosa* (Fig. 1, Table 1). When combining all neighbor situations, the mean total biomass of the target *C. maculosa* without activated carbon was 0.76±0.04g and with activated carbon was 0.71±0.05g. Neighboring plants did not affect the response of the target *C. maculosa* to activated carbon. Acid-washing the activated carbon altered the pH of the activated carbon or sand-soil-activated carbon mixture relative to the sand-soil mixture without activated carbon (P=0.001). The pH of soil without activated carbon was 7.49±0.12 and with activated carbon was 7.98±0.03.

The presence of neighbors significantly affected the total biomass of the target *C. maculosa* (Fig. 2), but effects were not competitive. The total biomass of *C. maculosa* alone was 0.69±0.04g. When grown with a conspecific, *C. maculosa* biomass decreased to 0.59±0.04g; however, this was not significant (*P*=1.000). The biomass of *C. maculosa* was significantly larger when grown with *F. idahoensis* (0.75±0.04g) than when grown alone or with a conspecific (*P*=0.025 and *P*=0.014, respectively). Target *C. maculosa* biomass was 0.89±0.04g when grown with *F. scabrella,* which was significantly larger than when grown alone or with a conspecific, but not when grown with *F. idahoensis* (*P*=0.005, *P*=0.003, and *P*=1.000, respectively).

The neighbors of target *C. maculosa* also differed in their total biomass (Fig. 3, Table 2). The mean total biomass of the undamaged *C. maculosa* was 0.85±0.04g, which was significantly larger than *F. idahoensis* and *F. scabrella* (*P*<0.0005 and *P*<0.0005, respectively). The biomass of *F. idahoensis* (0.11±0.03g) and *F. scabrella* (0.11±0.06g) were not significantly different from each other (*P*=0.065). Leaf number of the neighbor before herbivory on target *C. maculosa* significantly explained the total biomass of the neighboring plant and the relationship between leaf number and biomass differed for each species.

Over all treatments, activated carbon did not affect neighboring species (Fig. 3, Table 2). However, species responded differently to activated carbon. Adding activated carbon increased the biomass of *F. idahoensis* from 0.08±0.03g to 0.14±0.04g, slightly increased the biomass of *F. scabrella* from 0.10±0.06g to 0.12±0.06g, and decreased *C. maculosa* biomass from 0.96±0.04g to 0.74±0.06g. This suggests that activated carbon has a strong positive effect upon *F. idahoensis* but not on *F. scabrella* or *C. maculosa.*

Herbivory on the target *C. maculosa* did not have positive effects on neighboring species and all species responded similarly to herbivory on the target *C. maculosa* (Fig. 3,

Table 2). There was no interaction between activated carbon in the soil and herbivory on the target *C. maculosa* suggesting activated carbon did alter the neighbors' response when *C. maculosa* was damaged.

Field experiment

Survival

Across all treatments, only 48% of the *C. maculosa* plants identified in 2000 (the exceptionally dry summer) survived while 98% of the *C. maculosa* plants identified in 2001 survived (Table 3). In 2000, defoliating *C. maculosa* significantly decreased its survival (Wald statistic=8.013, *P*=0.005). Sixty-four percent of the non-defoliated *C. maculosa* plants survived while only 30% of defoliated *C. maculosa* plants survived. The presence of *F. idahoensis* tended to increase the survival of *C. maculosa* in 2000, but this was not significant (Wald statistic=1.145, *P*=0.284).

Biomass and reproduction

For pairs identified in 2001, the final shoot biomass of *C. maculosa* was negatively affected by defoliation (Fig. 4, $P_{\mathrm{defoliation}}$=0.004). The mean aboveground biomass of *C. maculosa* was reduced by 40% when clipped, even though 50% of the biomass was removed at two different times and the final harvest was only six weeks after the last clipping. Eliminating the aboveground biomass of *F. idahoensis* had no effect upon the shoot biomass of *C. maculosa* (Fig. 3, P_{neighbor}=0.420). *Centaurea maculosa* responded similarly to defoliation regardless of the presence of *F. idahoensis* (Fig. 3, $P_{\mathrm{defoliation\ x\ neighbor}}$=0.860). Neither defoliation nor neighbor affected the number of *C. maculosa* flowers ($P_{\mathrm{defoliation}}$=0.744, P_{neighbor}=0.544), and there was no interaction between defoliation and neighbor upon the number of *C. maculosa* flowers ($P_{\mathrm{defoliation\ x\ neighbor}}$=0.575). However, the trend was towards overcompensation in the presence of *F. idahoensis* and undercompensation in its absence. When *F. idahoensis* was present, *C. maculosa* flower number was 3.95±1.18 when *C. maculosa* was not defoliated and 4.20±1.07 when *C. maculosa* was defoliated. In the absence of *F. idahoensis*, *C. maculosa* flower number was 5.20±0.98 when not defoliated and 4.25±1.02 when defoliated. Defoliation of *C. maculosa* did not affect the final shoot biomass or the number of flowers of *F. idahoensis* ($P_{\mathrm{defoliation}}$=0.422, $P_{\mathrm{defoliation}}$=0.931, respectively); however defoliating *C. maculosa* tended to release *F. idahoensis* from competition. When *C. maculosa* was not defoliated, the shoot biomass of *F. idahoensis* was 1.65±0.35g compared to 2.12±0.46g for those with defoliated *C. maculosa* neighbors, and the flower number of *F. idahoensis* was 11.90±3.15 compared to 12.30±3.32.

DISCUSSION

I first hypothesized that *C. maculosa* might increase its competitive ability through compensatory growth. However, in both experiments, high levels of *T. ni* herbivory and artificial defoliation had negative effects upon the biomass of the target *C. maculosa*. *Centaurea maculosa* appeared to grow at faster rates after herbivory and was able to attain its original biomass at low levels of herbivory in the greenhouse experiment. High levels of defoliation had a negative effect upon the biomass of *C. maculosa* in the field, but did not affect *C. maculosa* reproduction. Other studies have found that artificial defoliation, leaf herbivory (*T. ni*) and root herbivory (*Agapeta zoegana* and *Cyphocleonus achates* Fahr. (Coleoptera: Curculionidae)) have minimal negative effects upon *C. maculosa* and *C. melitensis* biomass and sometimes cause overcompensation (Müller 1989, Müller-Schärer 1991, Steinger and Müller-Schärer 1992, Callaway et al. 1999, Callaway et al. 2001). However, in these experiments, *C. maculosa* was given more time to recover from herbivory than in my experiment. Also in contrast to my study, none of the previous studies examined herbivory along a gradient of damage intensity. Understanding the gradient of responses may be crucial because low levels of herbivory may not have strong negative effects on *C. maculosa*, but high levels of herbivory may significantly reduce *C. maculosa* biomass. It is difficult to predict the generality of the greenhouse results since sample sizes were low at the highest levels of herbivory and plants only experienced a single bout of herbivory.

Defoliation had a negative effect upon the final shoot biomass of *C. maculosa* in the field in 2001; however, *C. maculosa* appears to be resilient to damage. It is remarkable that *C. maculosa* maintained 40% of its shoot biomass and survival was

100% in 2001 when 50% of the shoot biomass of *C. maculosa* was removed twice in a growing season and plants had only one month to recover. More importantly, severe defoliation did not decrease fecundity. Long-term damage may cause a reduction in reproduction in successive years; however, within this study period, defoliated plants were just as fecund as undamaged plants.

Water was not manipulated in this study; however, my field experiment suggested the timing of precipitation throughout the year was important to the survival of *C. maculosa*. Annual precipitation was 31.45cm and 33.73cm for 2000 and 2001, respectively. However, peak precipitation in 2000 occurred in September (6.38cm) after a very dry summer, whereas in 2001 precipitation patterns were more typical of the region with the peak in June (9.93cm). In Missoula, MT, peak precipitation usually occurs in May and June and changes in the timing of precipitation have the potential to affect the phenologies of *C. maculosa* and *F. idahoensis*. *Festuca idahoensis* flowers in May-June while *C. maculosa* flowers in July-August. Low precipitation in June of 2000 likely contributed to the reduced survival of *C. maculosa*. The mean number of *F. idahoensis* flowers in 2000 and 2001 were 0.263±0.129 and 16.921±2.025, respectively. The drastic increase in *F. idahoensis* flowers in 2001 suggests that late precipitation in 2000 had a strong positive effect upon reproduction. This may have been due to the high mortality of *C. maculosa* in 2000 or the late precipitation in 2000 directly benefited *F. idahoensis*.

According to theory of plant competition, neighboring plants should have negative effects upon the biomass of the target plant. However, in the experiments reported here neighboring plants positively affected target *C. maculosa* biomass. In the field, the presence of *F. idahoensis* was correlated with a slight increase in the survival of *C. maculosa*. In the greenhouse, *C. maculosa* grown with *F. idahoensis* and *F. scabrella* neighbors were significantly larger than controls and when grown with conspecifics. The fact that conspecifics had stronger competitive effects than natives on target *C. maculosa* may have been simply because natives were much smaller than *C. maculosa* plants. The positive effects of *Festuca* corroborate with the results of Marler et al. (1999) who showed *F. idahoensis* can have a positive effect on *C. maculosa* through mycorrhizal fungi.

Herbivory had negative effects upon *C. maculosa*, but neighbors did not exacerbate this effect. Most previous studies have shown that herbivory makes an individual more susceptible to competition (or vice versa), with generally additive negative effects on the target plant (Archer and Detling 1984, Cottam et al. 1986, Reichman 1988). However, *C. maculosa* subjected to herbivory or defoliation grew no larger alone than with *C. maculosa*, *F. idahoensis* or *F. scabrella* neighbors. Although target *C. maculosa* plants with neighbors may have fewer resources immediately available to them, it is possible that *C. maculosa* obtains resources from neighbors or benefits from soil microbial changes caused by neighbors. Resource and carbon transfer between plants through mycorrhizal links has been documented in several cases (Chiariello et al. 1982, Francis and Read 1984, Grime et al. 1987, Watkins et al. 1996, Simard et al. 1997). Marler et al. (1999) hypothesized that *C. maculosa* might obtain nutrients or carbon from neighbors through arbuscular mycorrhizal (AM) fungi, and similar processes appear to occur for *C. melitensis* (Callaway et al. 2001, *in press*).

However, the question of carbon transfer from native plants to *C. maculosa* is still unresolved (Carey and Callaway *in review*, Zabinski et al. *in review*).

Herbivory is assumed to shift competitive interactions in favor of undamaged plants (Crawley 1989, Louda et al. 1990, Blossey and Nötzold 1995, Tilman 1999). Herbivory negatively affected target *C. maculosa*, but herbivory on the target *C. maculosa* did not have positive effects on neighboring *C. maculosa*, *F. idahoensis* or *F. scabrella*. However, in contrast to Callaway et al. (1999), I found no evidence that herbivory on *C. maculosa* increased its competitive ability. Biological control theory and practice assumes that herbivory will reduce the competitive ability of the weed releasing natives from competition; however, the results from this study suggest that herbivory may not be effective at reducing the competitive ability of *C. maculosa*.

Fletcher and Renney (1963) found that *C. maculosa* and *C. repens* exudates have phytotoxic effects on the germination and growth of barley and lettuce, and Kelsey and Locken (1987) isolated the compound cnicin from *C. maculosa* which had negative effects on the germination and growth of native North American plant species. In my experiment, *C. maculosa* had a strong allelopathic effect upon *F. idahoensis*. Other studies have shown that *C. maculosa* inhibits the growth of *F. idahoensis* through allelopathy (Ridenour and Callaway 2001) and that the closely related *C. diffusa* is also allelopathic (Callaway and Aschehoug 2000). Activated carbon did not alter the effects of herbivory on *C. maculosa*, suggesting that reducing its allelochemical effect on neighbors does not affect its growth response to herbivory. In addition, as levels of herbivory increased on *C. maculosa*, neighboring plants did not benefit from activated carbon. Therefore, there was no evidence that *C. maculosa* increased its competitive ability via increased allelochemical exudation. However, I may have failed to see a positive response by neighbors if the amount of activated carbon used was not sufficient to reduce large amounts of allelochemicals exuded by *C. maculosa*.

It is important to examine plant responses to herbivory under various competitive situations. This is especially important in the context of biological control of weeds where it is assumed that herbivory will decrease the competitive ability of the weed releasing natives from competition. In contrast, my results suggest that herbivory does not always have strong negative effects on *C. maculosa* and that herbivory does not decrease its competitive ability. In addition, compensatory growth and allelopathy do not appear to be mechanisms for any potential increase in *Centaurea's* competitive ability. Most importantly, in this experiment, there was no evidence that herbivory on the noxious invader, *C. maculosa*, benefits either neighboring conspecifics or native grasses.

ACKNOWLEDGEMENTS

I thank Kim Oldehoft, Claire Savon, Kevin Simonin, and Zachary Franz for providing assistance with the greenhouse experiment. Christian Richey and Adam Collins were a great help in the field. I thank Elizabeth Crone, Jon Graham and Brian Steele for statistical advice, and Eileen Carey, October Seastone-Moynahan and Catherine Zabinski for endless support and advice. Dean Pearson thankfully noted the different precipitation patterns between years. I also thank Kathy Poole at the New York State Agricultural Experiment Station for providing me with *T. ni*. This work was supported in part by NSF DEB 9726829 to R.M. Callaway and C.A. Zabinski, a NSF supplement to R.M. Callaway and C.A. Zabinski, and a grant from the Andrew W. Mellon Foundation to R.M. Callaway.

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Table 1 ANCOVA on the effects of neighbor, carbon and herbivory on the total biomass of *C. 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 #	1	12.703	253.297	< **0.0005**
Neighbor x Carbon	3	0.116	2.311	0.077
Neighbor x Herbivory	3	0.074	0.148	0.931
Carbon x Herbivory	1	0.134	2.679	0.103
Error	215	0.050		

Table 2 ANCOVA on the effects of species, carbon and herbivory on the total biomass of the neighboring *C. maculosa, F. idahoensis*, or *F. 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 #	1	4.943	67.284	< **0.0005**
Species x Carbon	2	0.360	4.905	**0.009**
Species x Herbivory	2	0.042	0.566	0.569
Carbon x Herbivory	1	0.014	0.189	0.665
Species x Leaf	2	1.356	18.462	< **0.0005**
Error	157	0.073		

Table 3 Survival of *C. maculosa* during 2000 and 2001 with or without defoliation and with or without *F. idahoensis*.

	2000			2001		
Treatment	Alive	Dead	Survival	Alive	Dead	Survival
C. maculosa not defoliated *F. idahoensis* present	12	5	71%	19	1	95%
C. maculosa not defoliated *F. idahoensis* absent	11	8	58%	20	0	100%
C. maculosa defoliated *F. idahoensis* present	7	13	35%	19	1	95%
C. maculosa defoliated *F. idahoensis* absent	3	10	23%	20	0	100%
Total	33	36	48%	78	2	98%

Fig. 1 Effects of herbivory on the unstandardized residuals of target *C. maculosa* total biomass when grown with *F. idahoensis*, *F. 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 as a covariate. Herbivory as a covariate was removed from this model. Data are based on ANCOVA results from Table 1.

Fig. 2 Effect of neighboring species on target *C. maculosa*. Adjusted means and standard errors shown are from untransformed data. Error bars represent + 1 SEM.

Fig. 3 Effects of target *C. 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 as a covariate. Herbivory as a covariate was removed from this model. Data are based on ANCOVA results from Table 2.

Fig. 4 Total biomass of *C. maculosa* with or without *F. idahoensis*, with or without defoliation in the field in 2001. Error bars represent + 1 SEM.

Fig. 1

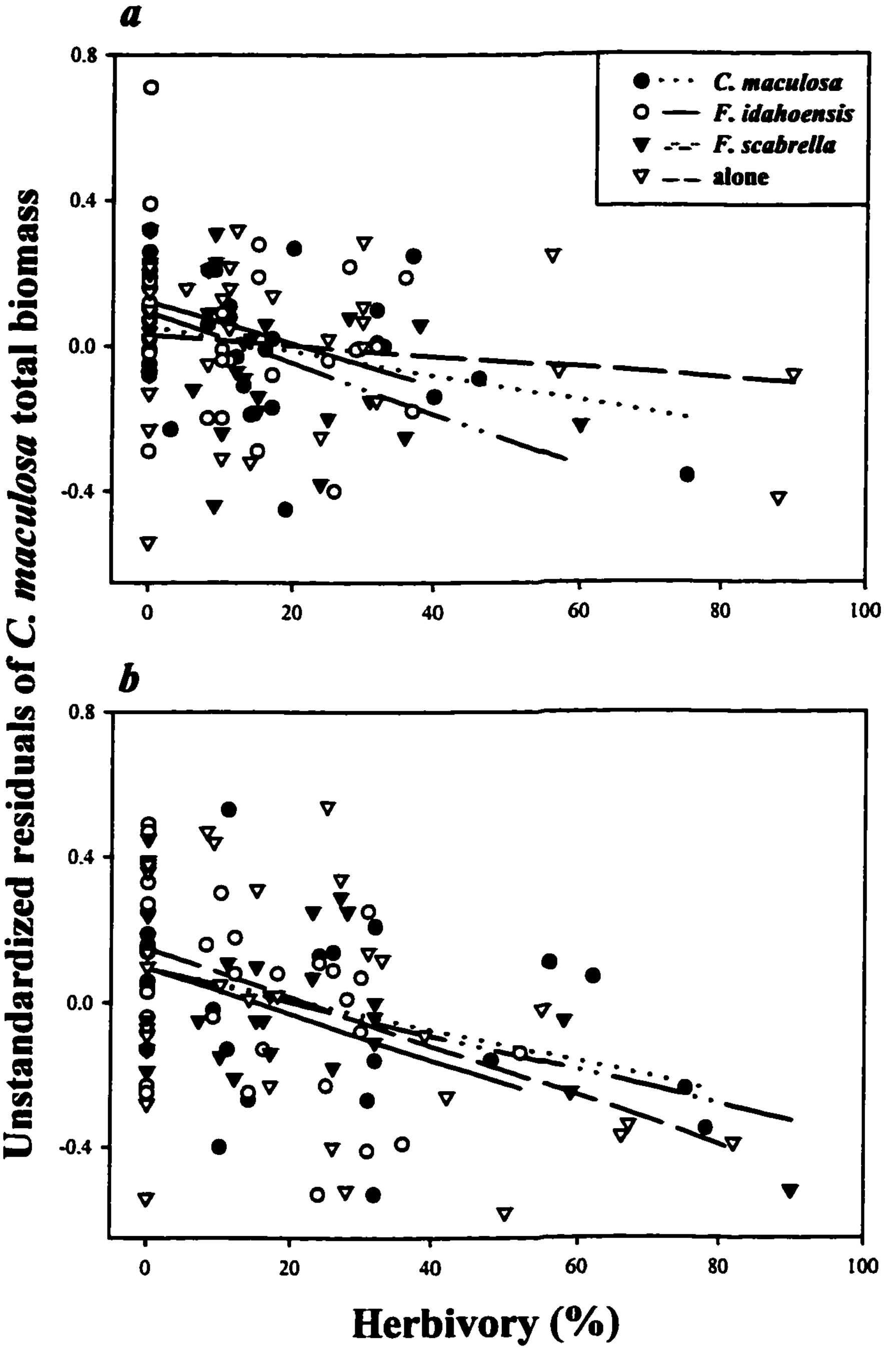

a
b
● · · · C. maculosa
○ —— F. idahoensis
▼ -·-·- F. scabrella
▽ — — alone
Unstandardized residuals of C. maculosa total biomass
0.8
0.4
0.0
-0.4
0
20
40
60
80
100
Herbivory (%)

Fig. 2

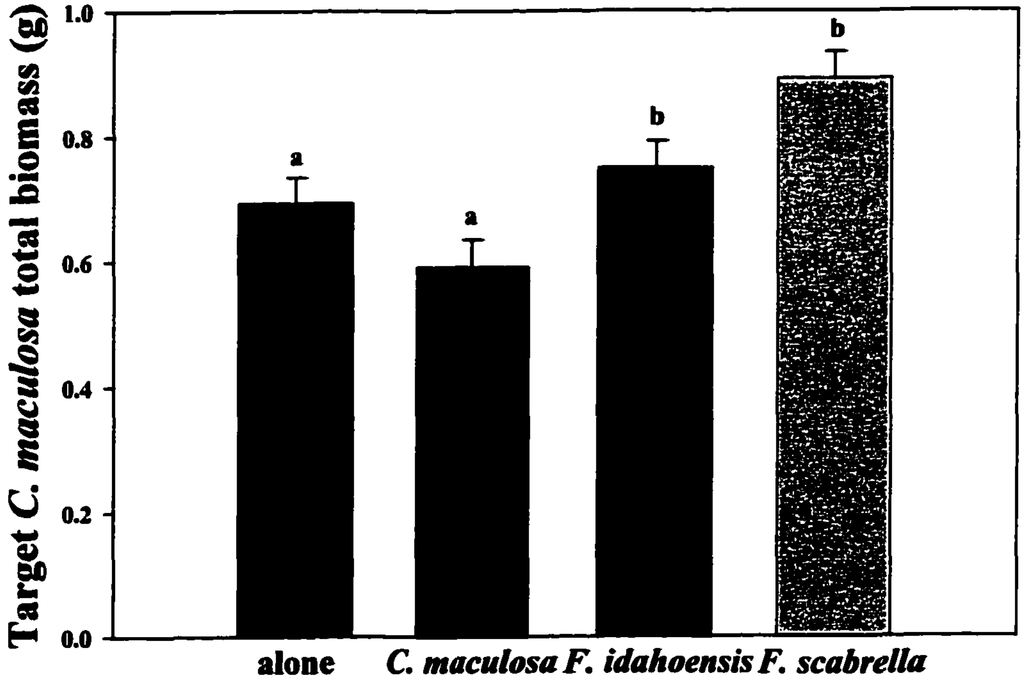

Target *C. maculosa* total biomass (g)
1.0
0.8
0.6
0.4
0.2
0.0
a
a
b
b
alone
C. maculosa
F. idahoensis
F. scabrella

Fig. 3

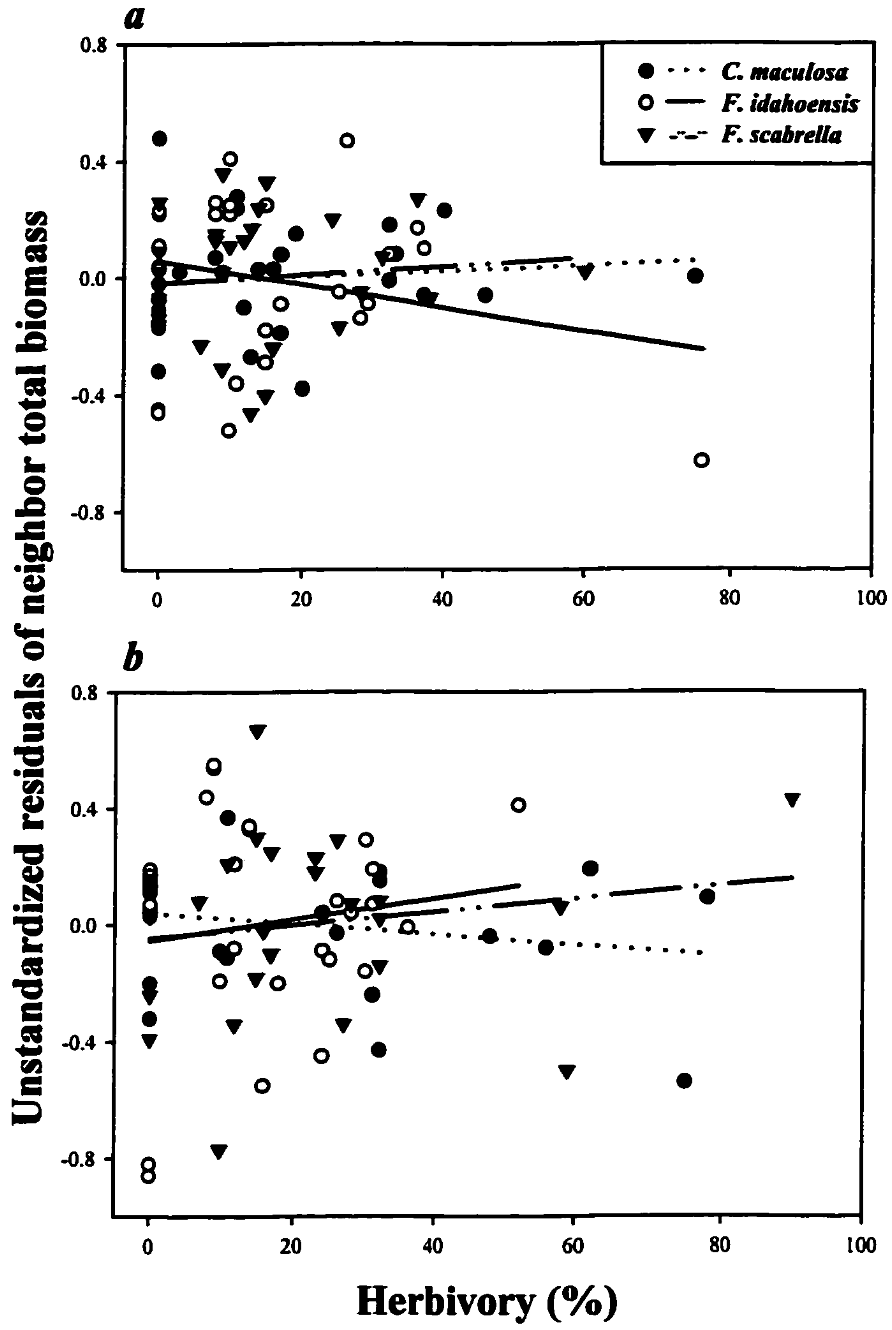
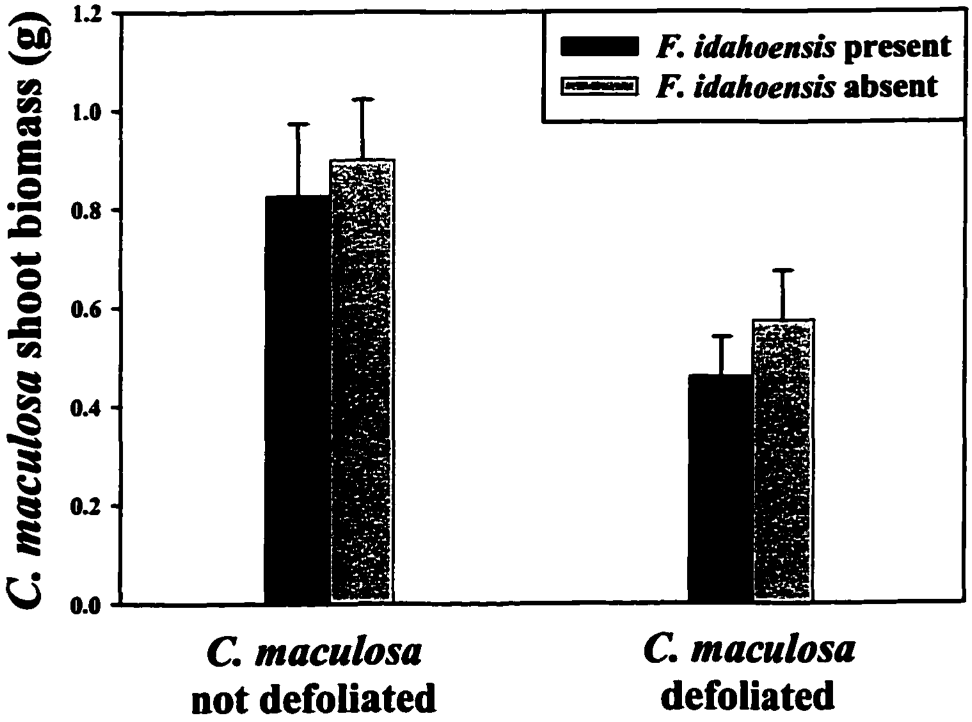

a
● C. maculosa
○ F. idahoensis
▼ F. scabrella
0.8
0.4
0.0
-0.4
-0.8
0
20
40
60
80
100
b
Unstandardized residuals of neighbor total biomass
Herbivory (%)

Fig. 4


C. maculosa shoot biomass (g)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
F. idahoensis present
F. idahoensis absent
C. maculosa not defoliated
C. maculosa defoliated

CHAPTER 2

North American and European genotypes of *Centaurea stoebe* respond similarly to neighbors, defoliation, and arbuscular mycorrhizal fungi

ABSTRACT

Invasive species may be superior competitors in their recipient communities due to unusual competitive ability, mutualistic interactions, or lack of herbivore pressure. However, the relative importance of these processes is poorly understood. Comparing ecological traits of invasive species to those of closely related, non-invading taxa may provide insight to why invasive species are so successful. *Centaurea stoebe (C. maculosa)* is an exotic, invasive plant in North America that is native to Europe and Asia. However, there are two genotypes of *C. stoebe* in Europe: tetraploid *C. stoebe* ssp. *micranthos* and diploid *C. stoebe* ssp. *stoebe*. *Centaurea stoebe* ssp. *micranthos* is the only one of these taxa identified in North America to date. To determine whether the American genotype possesses ecological characteristics that may confer it advantages over the European genotype, I investigated the effects of the European neighbor *Festuca ovina*, defoliation, and European arbuscular mycorrhizal (AM) fungi on the growth responses of *C. stoebe* ssp. *micranthos* and *C. stoebe* ssp. *stoebe*. Both *C. stoebe* subspecies were grown with *F. ovina*, defoliated or not defoliated, and AM fungi colonization were reduced using the fungicide, benomyl. Over all treatments combined, there were no differences in the total biomass between the genotypes of *C. stoebe*, but positive effects of *F. ovina* (*P*=0.023), negative effects of defoliation (*P*=0.003), and negative effects of fungicide (*P*<0.001) on *C. stoebe* subspecies biomass. Severe defoliation of *C. stoebe* did not have positive effects on *F. ovina*. However, the response of *F. ovina* depended upon which subspecies of *C. stoebe* was defoliated and whether or not fungicide was applied. Defoliation of *C. stoebe* ssp. *micranthos* without fungicide had positive effects upon *F. ovina* biomass, but defoliation with fungicide reduced *F. ovina* biomass. In contrast, for *C. stoebe* ssp. *stoebe* fungicide did not change the interactions between defoliated *C. stoebe* ssp. *stoebe* and *F. ovina* suggesting that *F. ovina* may interact slightly different with *C. stoebe* ssp. *micranthos* than with *C. stoebe* ssp. *stoebe*. The lack of strong differences between the invader, *C. stoebe* ssp. *micranthos*, and the genotype found only in Eurasia to date, *C. stoebe* ssp. *stoebe*, suggest that the invasive success of the former cannot be attributed to particular ecological traits. In addition, these results suggest that polyploidy does not affect the response of *C. stoebe* ssp. *micranthos* to the presence of *F. ovina*, defoliation, and AM fungi.

KEYWORDS: AM fungi, *Centaurea maculosa*, *Centaurea stoebe*, compensatory growth, *Festuca ovina*, herbivory

INTRODUCTION

Why some species successfully invade new regions is a central question in ecology (Vitousek et al. 1996, Davis et al. 2000, Mack et al. 2000). In addition to possessing key population-level characteristics (Mack 1985, Sakai et al. 2001), a successful invader must be able to competitively exclude local residents or at least prevent them from retaking colonized habitat. Successful invaders may gain competitive advantages by rapid growth and resource uptake (Baker 1974, Roy 1990), mutualistic interactions (Richardson et al. 2000), and the absence of consumers (Crawley 1989, Blossey and Nötzold 1995, Williamson 1996); however, we still lack a fundamental understanding of why some species are successful at invasion while other related and ecologically similar species are not. One promising approach for understanding the ecology of invasive success is the quantitative comparison of ecological traits of successful invaders to those of closely related taxa (Radford 2000, Lambrinos 2001, Sultan 2001). For example, closely related taxa may differ in ploidy levels which may result in different physiological, ecological, and genetic traits among related species (Lumaret 1988, Thompson and Lumaret 1992). In some cases, it has been suggested that traits derived from polyploidy may be responsible for the invasive success of plants (Roy 1990, Soltis and Soltis 2000). There have been few explicit ecological comparisons of successful genotypes of invaders to closely related genotypes that are not currently invasive.

There are over 500 species in the genus *Centaurea* in Eurasia and northern and eastern Africa, and more than a dozen of these have become highly successful invaders in North America, South America, Australia, and southern Africa (Bremer 1994). One of the most widespread invasive *Centaurea* species, *C. maculosa* Lam. (Asteraceae, spotted knapweed), has extensively invaded native grasslands in western North America since the late 1800's. *Centaurea maculosa* is a superior competitor, often excluding virtually all native species and creating dense monocultures (Ridenour and Callaway 2001). However, the taxonomy of the genus *Centaurea* is exceptionally complex (Garcia-Jacas et al. 2000). Earlier literature indicates that the North American invader is the tetraploid, *C. biebersteinii* DC. (2n=36) (Dostal 1976, Müller 1989, Stinson et al. 1994, Garcia-Jacas 1998). The most recent genetic and morphological research indicates that the North American invader is *C. stoebe* L. ssp. *micranthos* (Gugler) Hayek, a perennial, polycarpic, tetraploid plant (2n=36) (Ochsmann 2001). This taxon is very difficult to distinguish from what has been called *C. maculosa* and is often confused with a closely related, almost morphologically identical conspecific, *C. stoebe* L. ssp. *stoebe*. *Centaurea stoebe* ssp. *stoebe* is biennial, monocarpic, and diploid (2n=18) (Dostal 1976, Ochsmann 2001). There is no current evidence that *C. stoebe* ssp. *stoebe* has been introduced and become invasive in North America. For taxonomic accuracy, from here on I use the names *C. stoebe* ssp. *stoebe* for the non-invader and *C. stoebe* ssp. *micranthos* for the invader in North America. However, virtually all published papers refer to the latter as *Centaurea maculosa*. Comparisons of the ecology of these two genotypes have the potential to shed light on the basis for the success of one of the most devastating invasive plants in North America and on general principles of invasion in plant communities.

A crucial ecological aspect of the success of *C. stoebe* ssp. *micranthos* is its strong competitive effect on North American species. The competitive superiority of *C.*

stoebe ssp. *micranthos*, and the closely related *C. diffusa*, over natives has been attributed to a number of different mechanisms including allelopathy (Muir and Majak 1983; Callaway and Aschehoug 2000; Ridenour and Callaway 2001), competition for resources (Jacobs and Sheley 1999, Callaway and Aschehoug 2000, LeJeune and Seastedt 2001), lack of herbivores, and mechanisms meditated by arbuscular mycorrhizal (AM) fungi (Marler et al. 1999).

Understanding the effects of herbivory on *C. stoebe* subspecies is also fundamental to understanding the success of *C. stoebe* ssp. *micranthos*. Numerous insects have been introduced as biological control agents to reduce the spread of *C. stoebe* ssp. *micranthos* (Müller-Schärer and Schroeder 1993, Story and Piper 2001) and sheep are often used in efforts to control it (Olson and Wallander 1997, Olson and Wallander 2001). However, previous research suggests that herbivory and defoliation are not highly effective at controlling *C. stoebe* subspecies. *Agapeta zoegana* L. (Lepidoptera: Cochylidae) and *Cyphocleonus achates* Fahr. (Coleoptera: Curculionidae), both root feeders, have weak effects on *C. stoebe* ssp. *stoebe* in native systems (Müller 1989, Müller-Schärer 1991, Steinger and Müller-Schärer 1992) and on *C. stoebe* ssp. *micranthos* in invaded systems (Callaway et al. 1999), and some experiments suggest that both *C. stoebe* subspecies have the potential to compensate for biomass lost to herbivory in a matter of weeks. The shoot herbivore, *Trichoplusia ni* Hübner (Lepidoptera: Noctuidae), also has been shown to have weak effects on *C. stoebe* ssp. *micranthos*, failing to decrease its biomass (Callaway et al. 1999, Newingham and Callaway, *in prep*). In addition, sheep grazing often fails to have significant negative impacts on *C. stoebe* ssp. *micranthos* (Olson and Wallander 1997). Thirteen species of insects have been introduced to control *C. stoebe* ssp. *micranthos*; however, *C. stoebe* ssp. *micranthos* continues to spread in North American grasslands (Müller-Schärer and Schroeder 1993). Due to the taxonomic confusion, these biological control agents appear to have been collected from *C. stoebe* ssp. *stoebe, C. vallesiaca* Jordan and *C. stoebe* ssp. *serbica* (Prodan) Ochsmann instead of *C. stoebe* ssp. *micranthos* (Smith 2001) which may affect their ability to significantly impact *C. stoebe* ssp. *micranthos* populations.

Biological control theory assumes that herbivory has negative effects upon weeds that will release neighboring natives from competition (Blossey and Nötzold 1995, Van Driesche and Bellows 1996, Tilman 1999). This assumption is based on previous evidence that herbivory and competition are additive in their negative effects (Archer and Detling 1984, Reichman 1988). However, herbivory is not always negative, neighboring plants are not always competitors, and herbivory and competition are not always additive. Plants often compensate for herbivory (Fowler and Rausher 1985, McNaughton 1986, Paige and Whitham 1987, Alward and Joern 1993) and neighbors can act as facilitators rather than competitors (Callaway 1995, Callaway 1997). Variable responses to herbivory and interactions with neighbors may complicate predictions of how herbivory by biological controls will affect the interactions between invasive plants and natives.

AM fungi can enhance plant growth by increasing nutrient and water uptake (Koide 1991, Newman et al. 1992, Marschner and Dell 1994) and can form fungal links whereby nutrients and carbon are transferred from one plant to another (Chiariello et al. 1982, Francis and Read 1984, Grime et al. 1987, Simard et al. 1997). In addition, AM fungi may be important in plant compensatory responses to herbivory (Callaway et al. 2001). AM fungi are a crucial component of the ecology of *C. stoebe* ssp. *micranthos*.

Marler et al. (1999) found that AM fungi did not have an effect on *C. stoebe* ssp. *micranthos* when grown alone, but when *Festuca idahoensis* was grown with *C. stoebe* ssp. *micranthos*, AM fungi were highly beneficial to *C. stoebe* ssp. *micranthos*. They hypothesized that either AM fungi played a role in the transfer of fixed carbon or nutrients from *F. idahoensis* to *C. stoebe* ssp. *micranthos* (see Grime et al. 1987) or that *F. idahoensis* altered the soil fungal community in a way that favored *C. stoebe* ssp. *micranthos*. AM fungi have also been shown to have strong, but inconsistent, effects on other *Centaurea* species (Callaway et al. 2001, Callaway et al. *in press*).

Here I report on a greenhouse experiment in which I measured the effects of defoliation, AM fungi, and neighbors on the growth of *C. stoebe* ssp. *stoebe* from eastern France and *C. stoebe* ssp. *micranthos* from western Montana. This experiment was designed to ask the following questions: 1) Does the compensatory growth response of *C. stoebe* ssp. *micranthos* differ from that of *C. stoebe* ssp. *stoebe*? 2) How do AM fungi affect the compensatory response of *C. stoebe* subspecies? 3) Does the presence of *F. ovina* alter the compensatory response of *C. stoebe* subspecies? 4) What are the indirect effects on *F. ovina* when the two *C. stoebe* subspecies are damaged?

METHODS

An experiment was conducted in an outdoor garden at Joseph Fourier University in Grenoble, France. I chose to conduct the experiment within the native range and biological communities of both *C. stoebe* subspecies for two reasons. First, I could not predict how *C. stoebe* ssp. *stoebe* might respond to North American conditions, and more importantly, to eliminate any risks of introducing *C. stoebe* ssp. *stoebe* in North America. All plants were planted in 4L pots that were placed outside, but not submerged in the ground. Pots consisted of a 1:8 soil:sand mixture that was evenly mixed throughout the pot. Soil was collected at Saillans du Gua in the Vercors Massif (N 45° 2', E 5° 40'), and the sand was collected at Saint-Lattier in the Bas-Dauphiné area (N 45° 09', E 5° 19'), both near Grenoble, France. *Centaurea stoebe* ssp. *stoebe* is present at both of these sites. *Centaurea stoebe* ssp. *micranthos* seeds were collected near Missoula, MT, and *C. stoebe* ssp. *stoebe* seeds were collected in the Rhine valley north of Mulhouse, France.

Centaurea stoebe individuals were planted either with or without single *F. ovina* neighbors. *Festuca ovina* commonly occurs with *C. stoebe* ssp. *stoebe* in western European grasslands. *Festuca ovina* transplants were collected from Saint-Lattier, France, where sand was collected, and were transplanted into pots on April 26, 1999. At the time of transplant, *F. ovina* mean leaf number was 8.39±3.35 cm and the mean height was 8.52±1.97cm (± 1 standard error). *Centaurea* seeds were germinated on petri dishes on May 3, 1999, and seedlings were transplanted into pots on May 5, 1999. Plants grew for the first 7 weeks in soil inoculum to ensure AM fungi were present to allow establishment of plants. Then half of the pots were treated with the fungicide, benomyl (Benlate, Dupont). Benzimidazole fungicides have been shown to consistently reduce

AM fungi in other experiments with *Centaurea* species (Marler et al. 1999, Callaway et al. 2001). Benomyl was added at a rate of 50 mg kg^{-1} soil every two weeks and non-benomyl pots were given an equivalent amount of water. Plants were fertilized once on May 11, 1999 with Compo Floranid (N-P-K=20-5-8). This low phosphorus fertilizer was chosen to increase colonization of AM fungi.

After allowing the plants to grow for 2 months, I clipped all *C. stoebe* leaves except one that was ≈3 cm long. The biomass of all clipped leaves was recorded. Clipping the plants allowed me to inflict a specified amount of damage to the plant and avoid the variability encountered when using insects. Plants were grown for another 4 weeks and then harvested. Aboveground and belowground biomass was dried at 60°C for 48 hours and weighed. Root segments of all plants were washed, cleared with 2.5% KOH for 48 hours, acidified in 5% HCl for 12 hours, and stained with trypan blue for 12 hours (Phillips and Hayman 1970). AM fungal colonization was assessed using the magnified intersection method developed by McGonigle et al. (1990).

There were 15 replicates for each treatment combination of subspecies, neighbor, defoliation and fungicide. Sample sizes were reduced due to slug herbivory on seedlings. The effects of subspecies, neighbor, defoliation and fungicide on *C. stoebe* biomass were analyzed using a four-way ANOVA. The effects of subspecies, defoliation and fungicide on *F. ovina* biomass were analyzed using a three-way ANOVA. Data were log transformed to obtain homogeneity of variance and normality. *Centaurea stoebe* biomass at the time of harvest was used and previously clipped biomass was not included. Adding the clipped biomass did not change the results. Reported means are mean ± 1 standard error.

RESULTS

The American genotype, *C. stoebe* ssp. *micranthos* did not grow larger (Figure 1 & 2, Table 1), nor was it more competitive than the French genotype, *C. stoebe* ssp. *stoebe*, and there were no differences in biomass between the subspecies for any treatment. Overall, the presence of *F. ovina* had positive effects on the biomass of *C. stoebe* subspecies, but these effects did not differ between *C. stoebe* ssp. *micranthos* and *C. stoebe* ssp. *stoebe*. Defoliation reduced the biomass of both *C. stoebe* subspecies by 50% across all treatments, but the effects of defoliation did not differ between *C. stoebe* ssp. *micranthos* and *C. stoebe* ssp. *stoebe*. Fungicide had strong negative effects on both subspecies, reducing biomass across all treatments by 82%. However, as for the other primary effects, the biomass of *C. stoebe* ssp. *micranthos* and *C. stoebe* ssp. *stoebe* did not differ among fungicide treatments.

Not only were there no differences in the effect of *F. ovina* on the two *C. stoebe* subspecies, but also there was no difference in the overall competitive effect of the *C. stoebe* subspecies on *F. ovina* (Figure 3, Table 2). There was also no overall effect of subspecies on the response of *F. ovina* to defoliation on *C. stoebe* or fungicide. Defoliating *C. stoebe* did not affect total biomass of *F. ovina*, suggesting that damage to *C. stoebe* did not reduce its competitive effects on *F. ovina*. The only ecological difference that I detected between the subspecies was that the combined effects of defoliation and fungicide depended upon the subspecies of *C. stoebe* grown with *F. ovina*. Defoliating *C. stoebe* ssp. *micranthos* without fungicide increased the biomass of *F. ovina*, whereas defoliating *C. stoebe* ssp. *micranthos* with fungicide decreased *F.*

ovina biomass. In contrast, defoliating *C. stoebe* ssp. *stoebe* had no significant effect on the biomass of *F. ovina* with or without fungicide.

The presence of *Festuca ovina* had a significant positive effect on the total biomass of *C. stoebe* ssp. *micranthos* and *C. stoebe* ssp. *stoebe* (Fig. 1 & 2, Table 1). In addition, over all treatments fungicide had a negative effect on the total biomass of both *C. stoebe* subspecies. The biomass of *C. stoebe* was 5.6 times larger without fungicide application. However, the response of *C. stoebe* to the presence of *F. ovina* depended on the use of fungicide. The biomass of both *C. stoebe* subspecies when grown with *F. ovina* was 3.5 times larger when with fungicide and 1.6 times larger without fungicide compared to *C. stoebe* was grown alone in each respective fungicide treatment. Both subspecies of *C. stoebe* were largest when grown with *F. ovina* and without fungicide.

Defoliation reduced the biomass of both *C. stoebe* subspecies across all treatments combined by 50% (Fig. 1 & 2, Table 1). However, the strength of this negative effect was not consistent across all treatments. In pair-wise comparisons, defoliation had a significant negative effect on *C. stoebe* ssp. *micranthos* only when grown with *F. ovina* with fungicide (P=0.05). Over all treatments, defoliation tended to have a stronger negative effect on *C. stoebe* without fungicide. However, there was no significant interaction between defoliation and neighbors or defoliation and fungicide.

Over all treatments, fungicide significantly decreased the total biomass of *F. ovina* (Figure 3, Table 2). However, fungicide reduced the total biomass of *F. ovina* but only when *C. stoebe* was defoliated. For both subspecies combined, defoliating *C. stoebe* without fungicide increased the biomass of *F. ovina* by 18%. Defoliating *C. stoebe* in addition to adding fungicide decreased the biomass of *F. ovina* by 33% suggesting that defoliation and fungicide were additive in their negative effects. For all neighbor and defoliation treatments combined, fungicide reduced percent AM fungal colonization from 55.0±5.3% to 18.3±3.8% for *C. stoebe* ssp. *micranthos*, 53.8±5.1% to 22.3±4.6% for *C. stoebe* ssp. *stoebe*, and 41.9±4.4% to 11.1±3.1% for *F. ovina*.

Shoot and root biomass were also analyzed separately for *C. stoebe* in response to all treatments, and overall, these results did not differ from those for total biomass. For shoot biomass, neighbor, defoliation, and fungicide were all significant ($P_{\mathrm{neighbor}} < 0.0005$, $P_{\mathrm{defoliation}} = 0.004$, $P_{\mathrm{fungicide}} < 0.0005$), with a marginally significant interaction between neighbor and fungicide ($P_{\mathrm{neighbor\ x\ fungicide}} = 0.057$). Neighbor, defoliation and fungicide were also significant for root biomass ($P_{\mathrm{neighbor}} < 0.0005$, $P_{\mathrm{defoliation}} = 0.002$, $P_{\mathrm{fungicide}} < 0.0005$), with a significant interaction between neighbor and fungicide ($P_{\mathrm{neighbor\ x\ fungicide}} = 0.037$). Neighbor, defoliation and fungicide were not significant for the root:shoot biomass of *C. stoebe* ($P_{\mathrm{neighbor}} < 0.519$, $P_{\mathrm{defoliation}} = 0.495$, $P_{\mathrm{fungicide}} < 0.116$), indicating that none of the factors affected biomass allocation.

DISCUSSION

I predicted that the tetraploid American genotype, *C. stoebe* ssp. *micranthos*, would possess ecological characteristics different from the diploid French genotype, *C. stoebe* ssp. *stoebe*, explaining the invasive success of *C. stoebe* ssp. *micranthos* in North America. Although I have no direct comparison of the invasive capabilities of the two *C. stoebe* subspecies, in the particular conditions of this experiment *C. stoebe* ssp. *micranthos* did not differ for any of the ecological factors tested from its closely related counterpart, *C. stoebe* ssp. *stoebe.* Both subspecies were almost identical in total biomass combined across all treatments and responded similarly to the presence of *F. ovina* defoliation, and fungicide. Other responses may occur in different abiotic conditions, different neighbors and herbivores, or different microbial communities, but my results suggest that the success of *C. stoebe* ssp. *micranthos* in North America is not due to unique characteristics relative to its non-invasive conspecific subspecies.

As noted, a potentially important difference between these two genotypes is that *C. stoebe* ssp. *micranthos* is tetraploid while *C. stoebe* ssp. *stoebe* is diploid. Polyploids can be better competitors, more resistant to herbivores and pathogens, and able to colonize broader ecological habitats than their diploid ancestors (Levin 1983, Schoen et al. 1992, Otto and Whitton 2000, but see Thompson et al. 1997). Furthermore, exotic invaders have been hypothesized to gain an advantage through polyploidy (Rodriguez 1996, Soltis and Soltis 2000). However, it appears that polyploidy does not confer any advantage to *C. stoebe* ssp. *micranthos* in its response to the presence of *F. ovina* defoliation, or AM fungi. However, polyploidy may increase the invasive success of *C.*

stoebe ssp. *micranthos* via other physiological and ecological characteristics not tested here.

In contrast to my results, but also in contrast to the general ecological assumption that polyploids tend to be vegetative- and reproductively superior, Müller (1989) found that the diploid, *C. stoebe* ssp. *stoebe* had a larger dry weight, basal diameter, seeds/flower head and flower heads/plant than the tetraploid, *C. stoebe* ssp. *micranthos*. Müller (1989) also found significant differences between the two *C. stoebe* subspecies when subjected to root herbivory by the root-boring biocontrol insect, *Agapeta zoegana*. Root herbivory increased the rooting intensity of the diploid *C. stoebe* ssp. *stoebe* causing overcompensation, but this did not occur in the tetraploid, *C. stoebe* ssp. *micranthos*. I did not find any differences in the effect of above-ground defoliation on the root, shoot or total biomass of the diploid and tetraploid *C. stoebe* subspecies, which suggests that shoot damage can rapidly be compensated for (but see below), but may not induce the same kind of over compensatory response as root damage.

AM fungi appear to have important effects on interactions between several *Centaurea* species and native neighbors (Marler et al. 1999, Callaway et al. 2001). In my experiment there was weak evidence that AM fungi have different effects on interactions between *C. stoebe* subspecies and *F. ovina* after defoliation on *C. stoebe*. Defoliating *C. stoebe* ssp. *micranthos* without fungicide increased the biomass of *F. ovina*, whereas defoliating *C. stoebe* ssp. *micranthos* with fungicide decreased *F. ovina* biomass. Defoliating *C. stoebe* ssp. *stoebe* had no significant effect on the biomass of *F. ovina* with or without fungicide. It is difficult to interpret the ecological significance of the different effects of *C. stoebe* on *F. ovina* since this interaction was weak. Other experiments are necessary to clarify differences between subspecies.

Across all treatments combined, neither *C. stoebe* subspecies compensated fully in biomass during the relatively short, four-week period following defoliation. However, this low compensation was only significant for *C. stoebe* ssp. *micranthos* grown with *F. ovina* with fungicide. Many other studies have demonstrated that *C. stoebe* ssp. *micranthos* is highly tolerant of herbivory and defoliation, and under some conditions, may even overcompensate (i.e. grow larger or reproduce more after herbivory). In field experiments in Switzerland, Müller-Schärer (1991) found that low levels of *Agapeta zoegana* root herbivory *increased* (overcompensation) survival, shoot number, and fecundity of *C. stoebe* ssp. *stoebe*, but the effects of herbivory were highly complex and were negative under other conditions. Callaway *et al.* (1999) reported that *C. stoebe* ssp. *micranthos* plants experiencing leaf herbivory from *T. ni* and *A. zoegana* were stronger competitors against *F. idahoensis*. Kennett et al. (1992) found that defoliating 75% of potted *C. stoebe* ssp. *micranthos* leaves 4 times in ≈6 months had no effect on the final biomass of the defoliated plants. In other experiments, the root-feeding weevil, *Cyphocleonus achates* reduced the seed output of *C. stoebe* ssp. *stoebe*. However, when *C. stoebe* ssp. *stoebe* was grown without neighbors, the presence of *C. achates* and *A. zoegana* increased seed output (Müller and Schroeder 1989). In this experiment, both *C. stoebe* subspecies only grew for four weeks after defoliation, which may have limited its ability to compensate for defoliation.

Understanding the conditions in which herbivory harms invasive plants is crucial to the success of biological control. For example, Machinski and Whitham (1989) found that *Ipomopsis arizonica* overcompensated when resources were abundant, but could not compensate when resources were low. Furthermore, artificial defoliation does not always elicit the same results as true herbivory (Hartley and Lawton 1987, Baldwin 1990, Agrawal et al. 2001). Artificially defoliating *C. stoebe* may not provide the chemical cues needed to cause strong compensatory growth, but other experiments have demonstrated compensatory responses by *C. melitensis* and *C. solstitialis* in response to clipping (Callaway et al. 2001, Callaway et al. *in press*). Another possible reason for the lack of compensation in this experiment might be the particular soil properties (microbes or nutrients) of European soil supporting natural populations of *C. stoebe* ssp. *stoebe* versus soil from other origins used in experiments by Marler et al. (1999), Callaway et al. (2001), and Callaway et al. (*in press*). Soil microbes play a crucial role in the competitive ability of *Centaurea* species (Marler et al. 1999, Callaway et al. 2001, Callaway et al. *in press*) and microbial communities from different habitats may have different ecological effects.

Most literature suggests that plant competition reduces plant compensatory responses to herbivory (Mueggler 1972, Bentley and Whittaker 1979, Crawley 1989). For example, Maschinski and Whitham (1989) found that the compensatory response of *I. arizonica* was dependent upon plant competition and the timing of herbivory. Steinger and Müller-Schärer (1992) found that *C. stoebe* ssp. *stoebe* compensated less when grown with the European native, *F. pratensis*. However, Newingham and Callaway (*in prep*) found that the presence of conspecifics, *F. idahoensis*, or *F. scabrella* did not increase the negative effects of *Trichoplusia ni* herbivory on *C. s. micranthos*. This suggests that North American native plants and conspecifics may have minimal effects on the response of *C. stoebe* ssp. *micranthos* to herbivory, whereas European natives may have negative effects on the growth response of *C. stoebe* ssp. *stoebe* (see Callaway and Aschehoug 2000).

Across all treatments, the biomass of the two *C. stoebe* subspecies was 1.7 times larger in the presence of *Festuca ovina*. However, *F. ovina* did not promote a compensatory growth response by *C. stoebe* as has been found in experiments with *C. melitensis* and *Nassella pulchra* (Callaway et al. 2001). Why *C. stoebe* benefits from the presence of *F. ovina* is unclear, but the role of AM fungi may be important. Grime et al (1987) found that *C. nigra* increased almost 10 times in biomass when grown with *F. ovina* when AM fungi were present in the soil. In these same experiments, *C. nigra* received far more of a ^{14}C label applied to *F. ovina* when AM fungi were present. Marler et al. (1999) found that *F. idahoensis* had a positive effect on *C. stoebe* ssp. *micranthos* in the presence of AM fungi, but the evidence for carbon transfer has been contradictory (Carey et al. *in review*; Zabinski et al. *in review*). It is possible that the positive effect of *F. ovina* on *C. stoebe* may have been mediated through AM fungi. However, in this experiment fungicide slightly increased the positive effect of *F. ovina* rather than decreasing it.

Even in the absence of *F. ovina*, AM fungi had a very strong positive effect on the biomass of both *C. stoebe* subspecies. This is in contrast to findings by Marler et al. (1999) who did not see direct effects of AM fungi on either *C. maculosa* or *F. idahoensis*, but did find that AM fungi increased indirect negative effects of *C. maculosa* on *F. idahoensis*. The positive effects of AM fungi on plants can depend on both the species of

AM fungi and the plant species (van der Heijden et al. 1998*a*, *b*), and fungal communities are likely to differ between American and French soils.

Although defoliation had a negative effect on *C. stoebe*, defoliation did not positively affect *F. ovina*. This contrasts with competition theory of plants (Crawley 1989, Herms and Matson 1992) and the fundamental assumption of controlling invasive weeds with insects and grazers, both of which predict that damage to a plant will reduce its competitive ability (Blossey and Nötzold 1995, Tilman 1999). The opposing responses of *F. ovina* with or without fungicide suggest that it is difficult to predict how defoliation will change competitive interactions between plants. These results support a number of others demonstrating that artificial and herbivore damage to invasive *Centaurea* species does not decrease its competitive aggressiveness (Callaway et al. 1999, Callaway et al. 2001, Newingham and Callaway, *in prep*).

Closely related species of plants provide an opportunity to investigate whether certain genotypes possess characteristics that increase invasive success (Lambrinos 2001, Sultan 2001). In this study, *C. stoebe* subspecies did not respond differently to defoliation in the presence or absence of neighboring plants or fungicide; however, fungicide had weak effects on the way that the subspecies interacted with *F. ovina*. Therefore, it is still unclear why *C. stoebe* ssp. *micranthos* is such a successful invader in North America. These results and those of Müller (1989) suggest that generalizations about closely related plants with different ploidy levels may be difficult, and that tetraploidy does not necessarily provide the invasive *C. stoebe* ssp. *micranthos* any clear advantage over its diploid congener, *C. stoebe* ssp. *stoebe*.

ACKNOWLEDGEMENTS

I am indebted to Gregoire Boquien for his hard work on this project. Philippe Choler, Pierre Liancourt, Emmanuel Corcket, and Mathieu Tilquin were extremely helpful and supportive throughout this project. Christian Richey prepared the roots for mycorrhizal analysis. Le jardin botanique de la ville de Lyon, Parc de la Tête D'Or provided me with the *C. stoebe* ssp. *stoebe* seeds. This study was funded by a grant and International Supplement to R. Callaway and C. Zabinski from the National Science Foundation, DEB-9726829, and a grant to R. Callaway from the Andrew W. Mellon Foundation.

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Table 1 ANOVA on the effects of subspecies, neighbor, defoliation and fungicide on the total biomass of *C. stoebe* subspecies. The *P* values of significant terms (P<0.05) are indicated in boldface type.

Source	df	MS	*F*	*P*
Subspecies = S	1	4.76E-07	2.05E-06	0.999
Neighbor = N	1	5.122	22.029	< **0.0005**
Defoliation = D	1	2.133	9.173	**0.003**
Fungicide = F	1	23.219	99.861	< **0.0005**
S x N	1	0.450	1.937	0.166
S x D	1	0.117	0.505	0.478
N x D	1	0.143	0.614	0.434
S x N x D	1	0.065	0.278	0.599
S x F	1	0.131	0.562	0.455
N x F	1	0.937	4.028	**0.047**
S x N x F	1	0.089	0.382	0.537
D x F	1	0.001	0.002	0.963
S x D x F	1	0.119	0.513	0.475
N x D x F	1	0.067	0.288	0.592
S x N x D x F	1	0.062	0.269	0.605
Error	136	0.232		

Table 2 ANOVA on the effects of subspecies, defoliation and fungicide on the total biomass of *F. ovina*. The *P* values of significant terms ($P<0.05$) are indicated in boldface type.

Source	df	MS	*F*	*P*
Subspecies = S	1	0.022	0.065	0.800
Defoliation = D	1	0.032	0.096	0.758
Fungicide = F	1	1.501	4.453	**0.039**
S x D	1	0.229	0.679	0.413
F x D	1	2.040	6.052	**0.016**
F x S	1	0.091	0.270	0.605
S x D x F	1	1.431	4.245	**0.043**
Error	67	0.337		

Fig. 1 Total biomass of *C. stoebe* ssp. *micranthos* alone or with *F. ovina*, with or without fungicide, and with or without defoliation. Error bars represent + 1 SE. Asterisks represent *P*<0.05 in pair wise comparisons.

Fig. 2 Total biomass of *C. stoebe* ssp. *stoebe* alone or with *F. ovina*, with or without fungicide, and with or without defoliation. Error bars represent + 1 SE.

Fig. 3 Total biomass of *F. ovina* with *C. stoebe* ssp. *micranthos* or *C. stoebe* ssp. *stoebe*, with or without fungicide, and with or without defoliation. Error bars represent + 1 SE.

Fig. 1

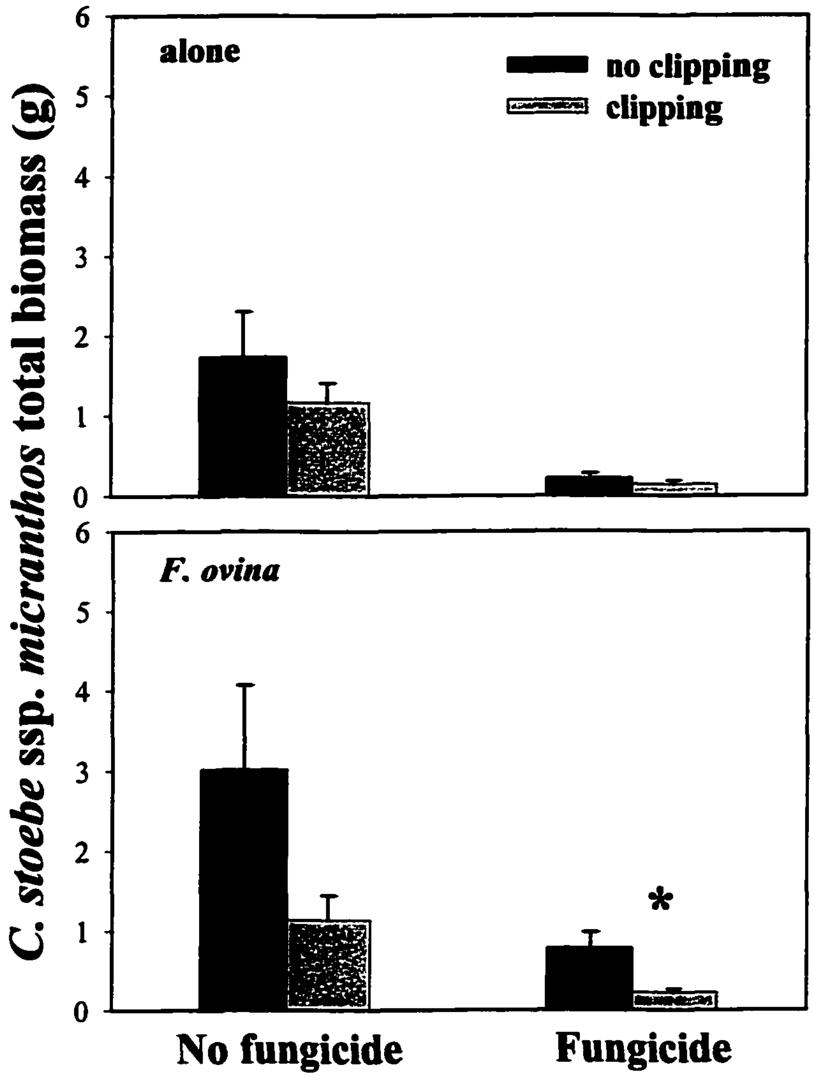

C. stoebe ssp. micranthos total biomass (g)
alone
no clipping
clipping
F. ovina
*
0
1
2
3
4
5
6
No fungicide
Fungicide

Fig. 2

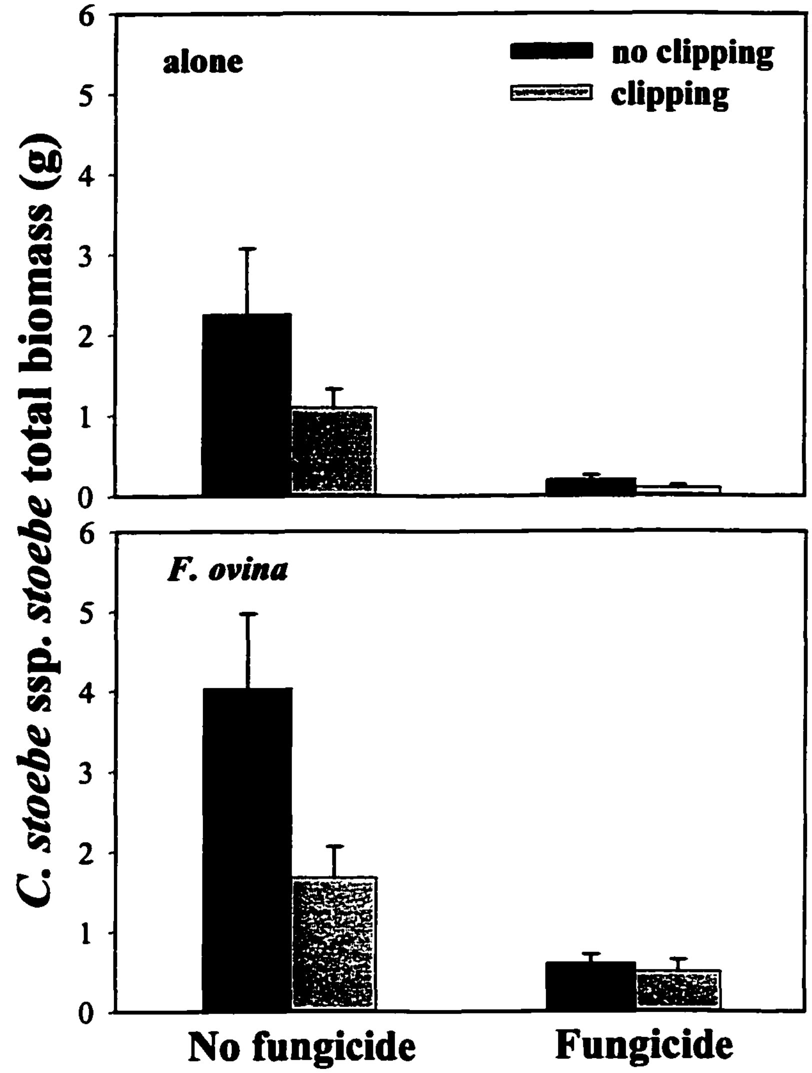
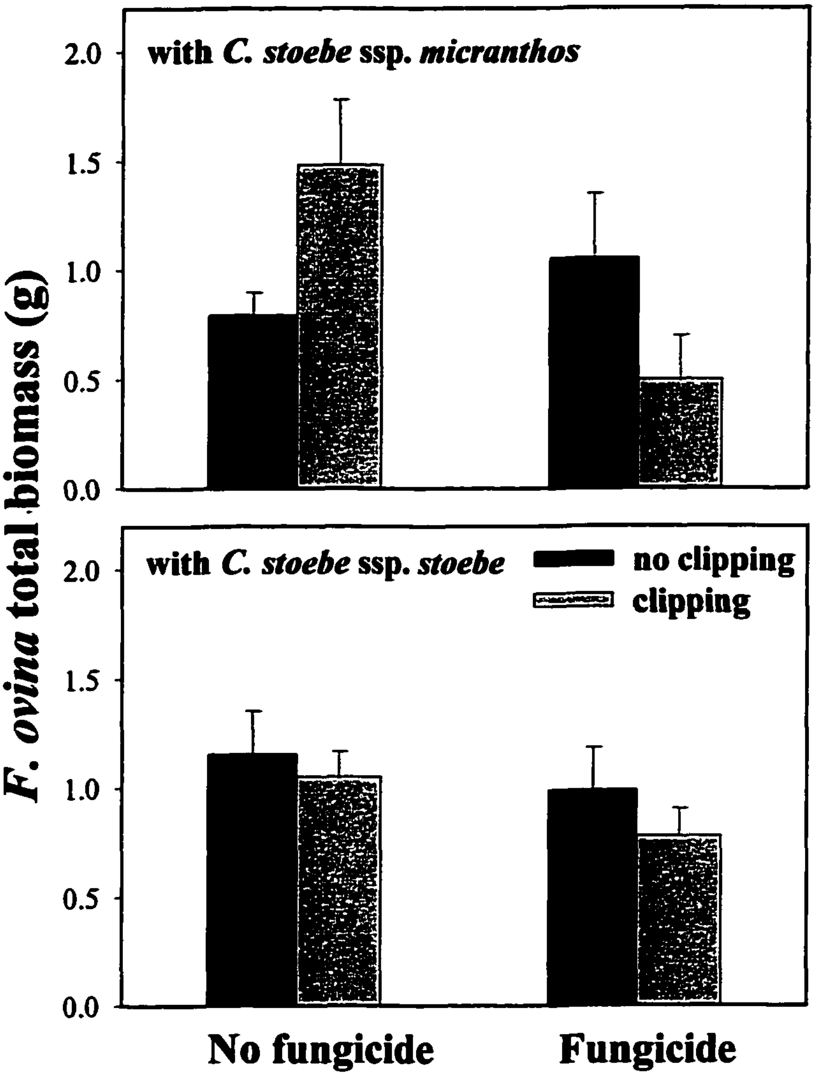

C. stoebe ssp. stoebe total biomass (g)
alone
no clipping
clipping
F. ovina
0
1
2
3
4
5
6
No fungicide
Fungicide

Fig. 3


with *C. stoebe* ssp. *micranthos*
with *C. stoebe* ssp. *stoebe*
no clipping
clipping
F. ovina total biomass (g)
2.0
1.5
1.0
0.5
0.0
No fungicide
Fungicide

CHAPTER 3

The effects of *Festuca paniculata* on the compensatory growth response of *Centaurea uniflora* to defoliation

ABSTRACT

Biotic and abiotic conditions affect compensatory growth by plants, and plant competition theory assumes that neighboring plants will augment the negative effects of herbivory. In contrast to competition theory, *Festuca* species appear to enhance the compensatory response of *Centaurea* species in highly controlled conditions. Therefore I tested the effect of *Festuca paniculata* L. on the compensatory growth response of *Centaurea uniflora* L. in the field over two growing seasons in subalpine vegetation in the French Alps. These species compose the well-known European plant association, "*Centaureo-Festucetum spadiceae*". Over 50% 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* equally compensated for 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%. Although *C. uniflora* did not fully recover from defoliation, *C. uniflora* had a strong compensatory response considering the large amount of leaf tissue that was removed. In general, *Festuca paniculata* had significant competitive effects on *C. uniflora*, but *F. paniculata* neither enhanced compensatory responses of *C. uniflora* nor increased the negative effects of defoliation as predicted by competition theory.

KEYWORDS: *Centaurea uniflora*, compensatory growth, defoliation, *Festuca paniculata*, subalpine

INTRODUCTION

Compensatory growth, or the tolerance of plants to herbivory, has been well documented in agricultural systems, but 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 experienced by the plant. For example, the compensatory ability of *Ipomopsis arizonica* depended on the presence of neighboring plants, nutrient availability, and the timing of herbivory (Maschinksi and Whitham 1987).

Plant-plant interactions can have a strong influence on compensatory growth. Competition theory of plants predicts that neighbors should reduce compensatory growth because neighbors reduce the amount of resources available to a plant recovering from damage (Bentley and Whittaker 1979, Whittaker 1979, Crawley 1983, Louda et al. 1990). However, plants may facilitate their neighbors (Bertness and Callaway 1994, Callaway 1995) and may not always decrease plant compensatory responses. Newingham and Callaway (*in prep*) found that the presence of *Festuca idahoensis* Elmer and *F. scabrella* Torrey ex. Hook, had no effect on the compensatory response of *Centaurea maculosa* Lam. Other species of *Festuca* appear to enhance the compensatory response of *Centaurea* species to defoliation or herbivory (Grime 1987, Callaway et al. 2001).

The *Centaureo-Festucetum spadiceae* group is a well-known plant association in the European literature and occurs in the southwestern Alps (Braun-Blanquet 1972, Guinochet 1938, Lacoste 1972). This subalpine/alpine 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 can be found between 1700 and 2500 m but is most developed between 1900 and 2300 m. This plant association is widespread, but no one has investigated interactions between *C. uniflora* and *F. paniculata*.

Since facilitation is common in harsher climates, facilitation may occur between *F. paniculata* and *C. uniflora* and therefore explain this common association. Not only are *Centaurea* and *Festuca* species co-members of defined plant communities, but also several studies have demonstrated facilitative interactions between *Centaurea* and *Festuca* species. Grime et al. (1987) found that the facilitative effect of *F. ovina* depended upon the identity of neighboring plant species and that it had a strong facilitative effect upon *Centaurea nigra* through interactions with arbuscular mycorrhizal (AM) fungi. Part of this effect was to ameliorate the effects of defoliation. Other research suggests that interactions between *C. maculosa* and *F. idahoensis* depend on indirect effects of AM fungi. Marler et al. (1999) found that *F. idahoensis* had a significant facilitative effect on *C. maculosa* via AM fungi. In a field experiment, Callaway et al. (*unpublished data*) found that *F. idahoensis* and *Koeleria cristata* had facilitative effects upon *C. maculosa* in the presence of AM fungi, whereas other species had competitive effects upon *C. maculosa*.

Studies also show that the invasive plant, *C. maculosa*, has strong competitive effects on the North American native, *F. idahoensis*. First, Ridenour and Callaway

(2001) found that *C. maculosa* had strong allelopathic effects on *F. idahoensis*. Second, insect herbivory can have relatively weak effects on the invasive non-native, *C. maculosa* (Müller-Schärer 1991, Steinger and Müller-Schärer 1992, Callaway et al. 1999), and under some conditions, herbivory on *C. maculosa* increases its competitive effects on *F. idahoensis* (Callaway et al. 1999). The numerous studies reporting that *Festuca* facilitates *Centaurea* and *Centaurea* has strong competitive effects on *Festuca* suggest that there may be important species-specific interactions between *Centaurea* and *Festuca*.

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); therefore, defoliation may play an important role in structuring subalpine and alpine plant communities. However, 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). Furthermore, few studies have examined plant compensatory responses to herbivory in subalpine/alpine communities (but see Paige and Whitham 1987). Considered with the unusual interactions that have been reported for *Centaurea* and *Festuca* species, the *Centaureo-Festucetum spadiceae* association provides a exceptional setting in which to examine the role of plant-plant interactions on plant compensatory growth responses to herbivory. I examined the role of *F. paniculata* in the compensatory response of *C. uniflora* to artificial defoliation. My experiment was designed to answer the following questions: 1) does *F. paniculata* facilitate *C. uniflora*, 2) does *C. uniflora* compensate for defoliation, 3) when repeatedly defoliated, does the compensatory response of *C. uniflora* decrease over time, and 4) does *F. paniculata* alter the compensatory response of *C. uniflora*?

METHODS

The 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, 2250m; N 45°02'09", E 6°24'21"). Mean temperature at the Col du Lautaret in July (the warmest month) is 11°C and average annual precipitation is 1300 mm. This site was dominated by both *C. uniflora* and *F. paniculata* and therefore was characterized as the *Centaureo-Festucetum spadiceae* association. The natural treeline occurs near 2350 m, but this field site was located in grasslands that have developed after deforestation and grazing.

In June of 1999, I selected ninety *C. uniflora* individuals of similar size surrounded predominantly by *F. paniculata*. There were three different treatments of the neighboring *F. paniculata*: *F. paniculata* present and not manipulated, *F. paniculata* present and leaves pushed aside so that no shade was over target *C. uniflora* individuals, and *F. paniculata* leaves completely clipped. All aboveground biomass of *Festuca paniculata* was continually clipped throughout the growing season to remove any regrowth. I left one-third of *F. paniculata* plants intact but with the leaves pushed aside to mimic microclimate alteration (increased light and exposure to wind and snow) that occurred when *F. paniculata* was clipped. This allowed me to compare root effects alone to shoot and root effects combined (Cahill 2002). For half of the *C. uniflora* individuals in each neighbor treatment, I clipped 70% of *C. uniflora* leaves. Clipping occurred approximately monthly (June to August) during the 1999 and 2000 growing seasons. Leaves and flowers were counted and *C. uniflora* leaves were clipped on the following dates: June 16, July 5 and July 20, 1999, and June 3, July 1, and August 2, 2000.

Aboveground biomass of *C. uniflora* was harvested on August 25, 2000. 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 using defoliation and neighbor as between-subject factors. Sphericity was violated for the leaf number analysis and the Greenhouse-Geisser correction was $\varepsilon<1$; however, the univariate and multivariate ANOVA did not produce different *P* values of significance. I 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 (2 years) as the within-subject factor and defoliation and neighbor as between-subject factors. 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. Post hoc comparison of means was performed using the Bonferroni correction method. Means are reported as mean ± 1 standard error of mean.

RESULTS

Leaf production

Leaf number was highly correlated with the biomass of *Centaurea uniflora* (R^2=0.975); therefore leaf number was an accurate surrogate for the effects of herbivory on the biomass of *C. uniflora*. Neighboring *F. paniculata* had a significant negative effect upon *C. uniflora* leaf number (Fig. 1, Table 1). There was no difference between *F. paniculata* present and *F. paniculata* pushed aside; but the removal of *F. paniculata* shoots resulted in higher leaf numbers produced by *C. uniflora* than when *F. paniculata* was present or pushed aside. Clipping *F. paniculata* increased *C. uniflora* leaf number, but 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 2000 clipping *F. paniculata* significantly increased the leaf number of neighboring *C. uniflora* (P<0.0005) suggesting 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 *Centaurea uniflora* significantly reduced leaf number after 2 years, demonstrating a lack of equal compensation to severe defoliation, but the effects of defoliation varied over time (Fig. 1, Table 1). In the first year, defoliation did not affect *C. uniflora* leaf number, but in the second year defoliation had a negative effect on leaf number. Neighboring *F. paniculata* did not the response of *C. uniflora* to defoliation.

Flower production

The number of flowers produced by *C. uniflora* was also affected by neighboring *F. paniculata* (Fig. 2, Table 2). *Centaurea uniflora* flower number was not significantly different in pair-wise comparisons of the two treatments where *F. paniculata* was left intact versus its leaves pushed aside. Although 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). The response of *C. uniflora* to neighboring *F. paniculata* did not change over time; however, separate one-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 (Fig. 2, Table 2). In 1999, defoliation did not affect the number of *C. uniflora* flowers, but by 2000 defoliation decreased flower number by 64%. As for leaf production, neighboring *F. paniculata* did not affect the response of *C. uniflora* flower number to defoliation.

Aboveground biomass

Festuca paniculata reduced the biomass of *C. uniflora* (Fig. 3, df=2, *F*=5.11, *P*=0.008). There was no difference in biomass of *C. uniflora* between the treatments in which *F. paniculata* was not manipulated versus when *F. paniculata* leaves were pushed aside. The biomass of *C. uniflora* was greater when *F. paniculata* was clipped than when *F. paniculata* was not manipulate (*P*=0.016) or when leaves were pushed aside (*P*=0.021). Two years of repeated defoliation of *Centaurea uniflora* reduced its final aboveground biomass 44% (df=1, *F*=49.29, *P*<0.0005). The total biomass of non-defoliated plants was 1.30±0.43g versus 0.73±0.36 g for defoliated plants. 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. In the first year of treatments, *F. paniculata* had no effect upon *C. uniflora*, and in the second year *F. paniculata* had competitive effects on *C. uniflora*. Generally, pushing *F. paniculata* foliage to the side did not alter its effects on *C. uniflora* suggesting that the main effect of *F. paniculata* was via root competition rather than shade. However, my results should be interpreted with caution, in particular because belowground interactions were not manipulated. Although *F. paniculata* was continually clipped throughout both growing seasons, belowground competition may have remained important. Furthermore, the positive response of *C. uniflora* may have been caused by nutrient flux from decomposing *F. paniculata* roots rather than decreased competition (see Fahey et al. 1988).

A second caveat involved the conditions at my study site. Choler et al. (2001) examined the role of facilitation and competition in subalpine and alpine communities near my 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. My 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*.

I 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). Additionally, the shorter growing seasons at high elevations may 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 compensation is possible even in harsh subalpine environments.

Festuca paniculata had a competitive effect on *C. uniflora*; however, it 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 exacerbate 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).

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 were harsher in the second year. 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.

Festuca paniculata did not facilitate the compensatory growth response of *C. uniflora*; however, the presence of *F. paniculata* did not reduce *C. uniflora* compensatory growth. These results provide evidence suggesting that competition with neighbors does not always reduce the compensatory response of plants to damage as predicted by competition theory of plants. I found no evidence that *F. paniculata* facilitated *C. uniflora* although these plants are commonly associated with one another.

ACKNOWLEDGEMENTS

I thank Rolland Douzet and Serge Aubert for logistical support and advice at the Lautaret field station. I also thank Jon Graham for statistical advice. This study was funded by a grant and International Supplement (for B. Newingham) to R. Callaway and C. Zabinski from the National Science Foundation, DEB-9726829, and a grant to R. Callaway from the Andrew W. Mellon Foundation.

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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 bold. Greenhouse-Geiger (G-G) corrected *P* values are listed.

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

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 bold.

Source	df	MS	*F*	*P*
Defoliation	1	2.186	5.093	**0.027**
Neighbor	2	1.490	3.471	**0.036**
Defoliation x neighbor	2	0.034	0.079	0.924
Error	83	0.429		
Year	1	1.967	5.474	**0.022**
Year x defoliation	1	5.742	15.982	**< 0.0005**
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		

Fig. 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 +1SE.

Fig. 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 +1SE.

Fig. 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 +1SE.

Fig. 1

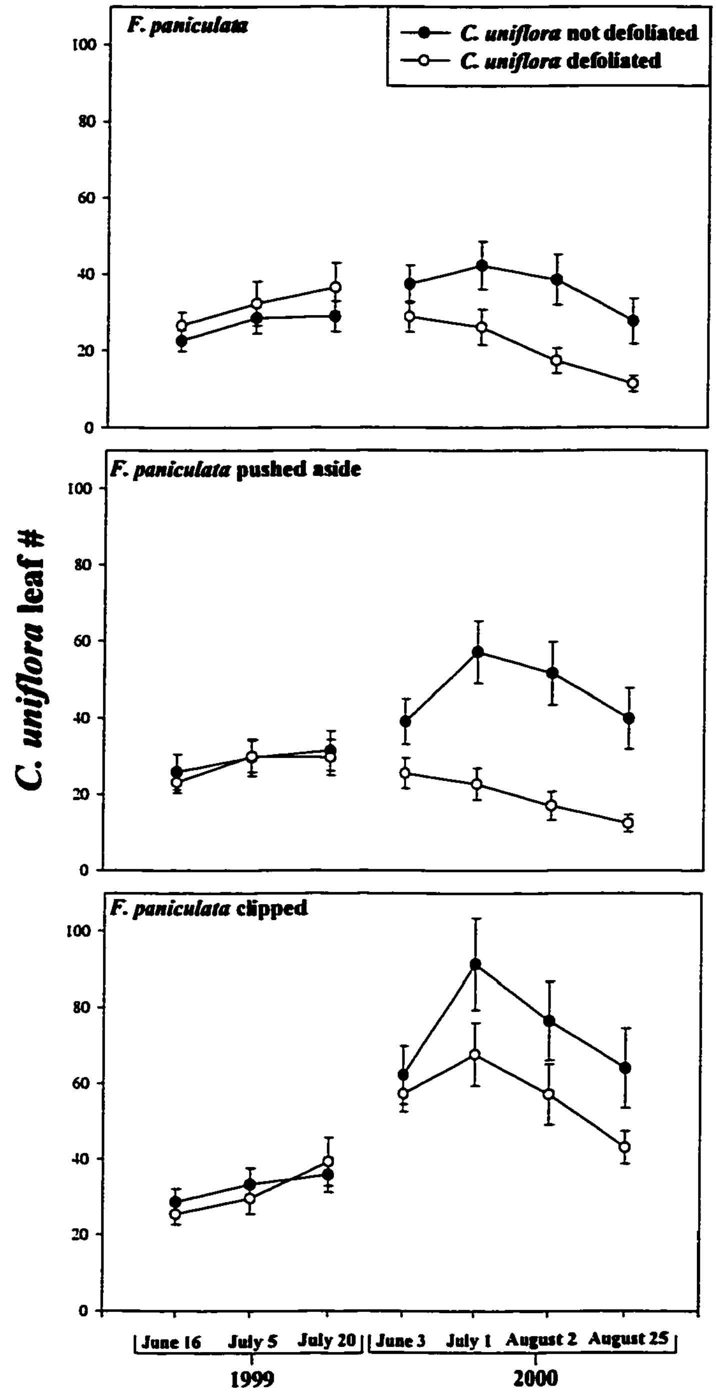

C. uniflora leaf #
F. paniculata
F. paniculata pushed aside
F. paniculata clipped
C. uniflora not defoliated
C. uniflora defoliated
0
20
40
60
80
100
June 16
July 5
July 20
June 3
July 1
August 2
August 25
1999
2000

Fig. 2

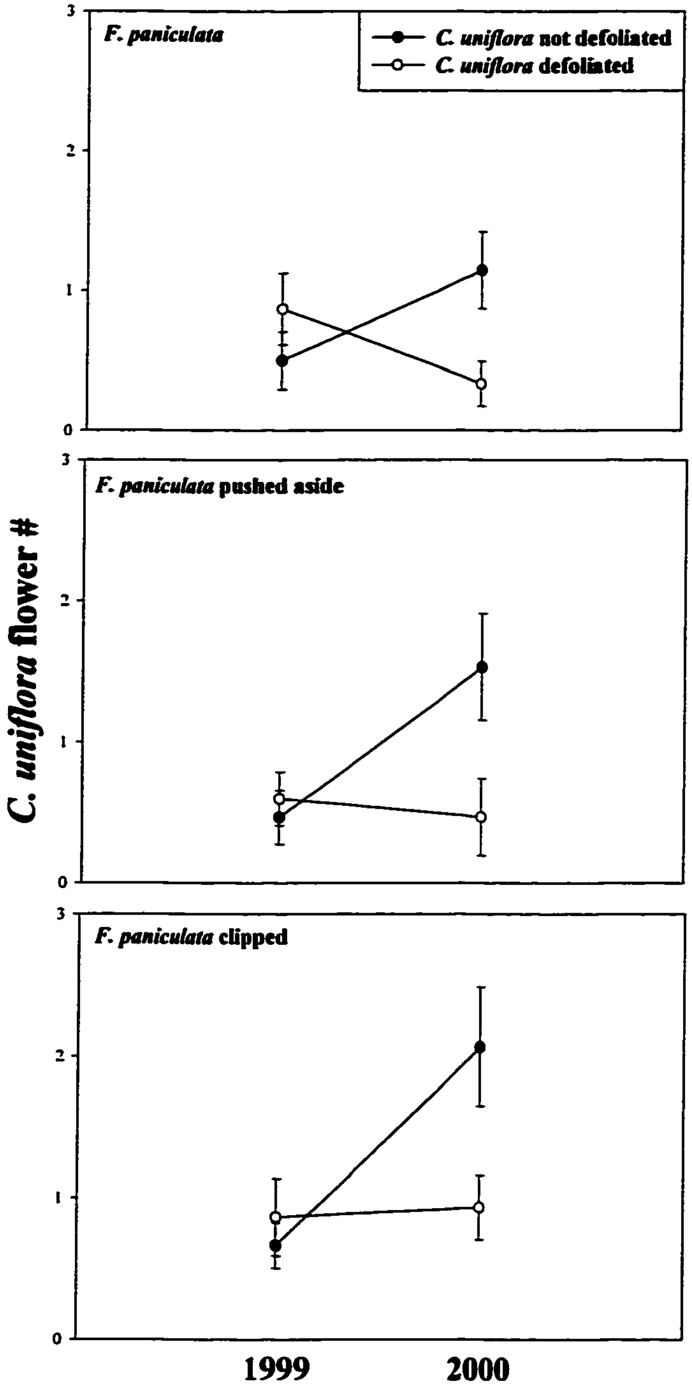
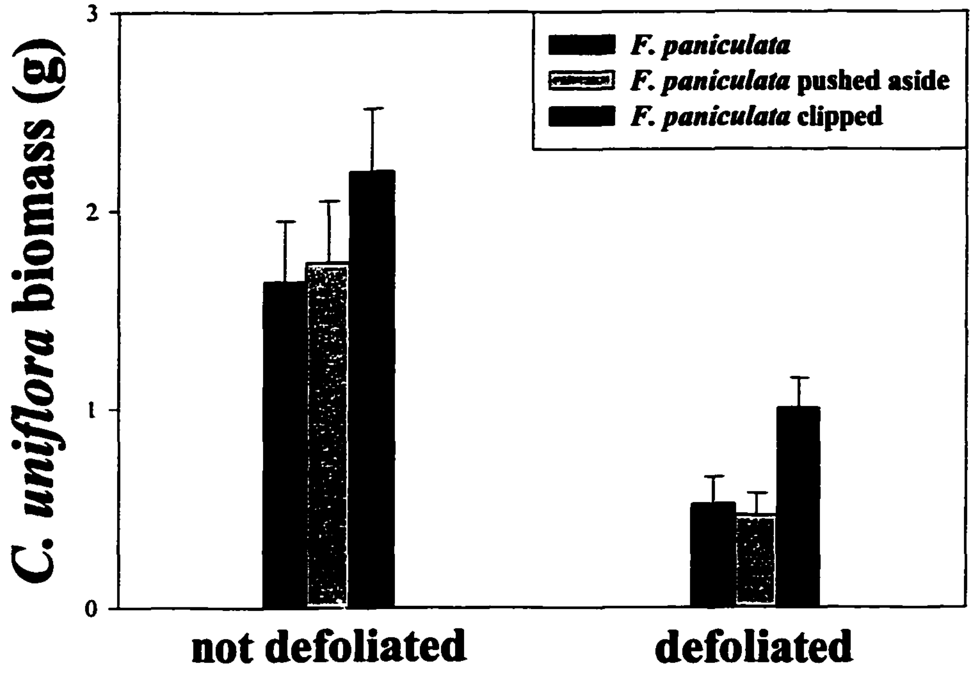

F. paniculata
C. uniflora not defoliated
C. uniflora defoliated
F. paniculata pushed aside
F. paniculata clipped
C. uniflora flower #
0
1
2
3
1999
2000

Fig. 3



C. *uniflora* biomass (g)
3
2
1
0
F. paniculata
F. paniculata pushed aside
F. paniculata clipped
not defoliated
defoliated