

Influence of Herbivory and Competition on Invasive Weed Fitness: Observed Effects of *Cyphocleonus achates* (Coleoptera: Curculionidae) and Grass-Seeding Treatments on Spotted Knapweed Performance

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Environ. Entomol. 35(6): 1590–1596 (2006)

ABSTRACT The root-feeding weevil *Cyphocleonus achates* (Fahraeus) is a promising biological control agent for managing the exotic, invasive weed spotted knapweed. The objective of this study was to compare the relative and potentially interactive effects of competition and specialized herbivory on spotted knapweed fitness. Competition was assessed through three grass seeding treatments: a nonseeded control and seeding to long-lived wheatgrasses originating either from North America, *Pseudoroegneria spicata* (Pursh) A. Löve ssp. *spicata*, or Europe, *Thinopyrum intermedium* (Host) Barkworth and D.R. Dewey. Comparisons were made of above-ground biomass, stem length, number of flowers, and life stage densities for spotted knapweed plants either infested or free of *C. achates* and growing under one of the grass seeding treatments. Infested adult spotted knapweed plants had lower shoot weight, stem length, and flowers/plant. The density of adult spotted knapweed plants was lower in grass-seeded plots than in nonseeded control plots. Results indicate *C. achates* herbivory is correlated with a reduction in measures of fitness and reproductive potential in field populations of spotted knapweed in North America. Furthermore, these results suggest that this agent might play a significant role in reducing spotted knapweed populations when competitive grasses are also present.

KEY WORDS integrated weed management, biological control, *Centaurea stoebe*, *Pseudoroegneria spicata*, *Thinopyrum intermedium*

The knapweed root weevil, *Cyphocleonus achates* (Fahraeus) (Coleoptera: Curculionidae), is considered an effective control agent against introduced spotted knapweed, *Centaurea stoebe* L. ssp. *micranthos* (Gugler) Hayek (= *Centaurea maculosa* Lamarck; = *Centaurea biebersteinii* de Candolle) (Story et al. 2006) in North America (Duncan et al. 2002, Story 2004). The native range of *C. achates* extends through northern, eastern, and southeastern Europe, Asia Minor, and Syria (Volvnik 1989, Stinson et al. 1994). First introduced to North America in British Columbia, Canada, in 1987 (Stinson et al. 1994) and in the United States in 1988 (Story et al. 1997), *C. achates* is now established in much of the western United States (Story 2004).

The biology of *C. achates*, briefly summarized here, has been fully described in Stinson et al. (1994) and Story et al. (1996). Females of this univoltine species lay in excess of 100 eggs, which are individually oviposited in notches chewed into the *C. stoebe* root crown. *C. achates* larvae hatch in 10–12 d and then mine into the vascular tissue of the *C. stoebe* root,

which also provides the overwintering site for this species. Feeding activities by the third and final fourth instar typically result in gall-like enlargements on the root, creating a chamber where a 2-wk pupation period subsequently occurs in late spring to early summer. The adult weevils have a relatively long lifespan, 8–15 wk, beginning when they emerge from the host gall in June to mid-September to feed on knapweed leaves, mate, and oviposit.

The effect of feeding on *C. stoebe* by adult weevils is believed to be minimal, with the larvae considered the most significant destructive stage (Story 2004). Field observations of reductions in *C. stoebe* density and biomass have been correlated with *C. achates* herbivory (Story et al. 1996, 2006, Jacobs 2004).

Blossey and Hunt-Joshi (2003) suggested that the effect of nitrogen and carbon loss in plants subjected to below-ground herbivory might extend beyond the individual plant under attack and influence population dynamics, including successional trajectories, of the wider vegetation community. Limitations on soil-available nitrogen and within-plant reallocation of nitrogen resources resulting from a compensatory response to root herbivory were cited as key factors in the effect of *C. achates* on two target weeds: *Centaurea diffusa* Lam. (Lejeune et al. 2005) and *C. stoebe* (Steinger and Müller-Schärer 1992). The objective of this study was to compare the relative and potentially

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interactive effect of competition between native and exotic grass and specialized herbivory by *C. achates* on *C. stoebe* fitness and to determine whether an additional stress factor, in this case interspecific competition from other plant species, increases the successful biological control of the target weed (Hinz and Schroeder 2003).

Materials and Methods

Study Site. The study was conducted on the Calf Creek Game Range, which is situated within a *Festuca scabrella* Torr./*Pseudoroegneria spicata* (Pursh.) Löve habitat type (Mueggler and Stewart 1980) in southwestern Montana (46°17' N, 114°1' W) at an elevation of 1,341 m. Site soils are classified as moderate depth Stecun stony loamy coarse sand (mixed typic Cryorthents). The site has a southwest aspect with an average slope <5%. Site 30-yr average January and July temperatures were -4 and 19°C, respectively, with a 30-yr average annual precipitation of 315 mm. The existing plant community on the site was dominated by *C. stoebe* before application of the experimental grass seeding treatments. A census conducted in July 1997 found an average density of 21 ± 20 (SD; $n = 18$) adult (=reproductively mature, flowering) *C. stoebe* and 218 ± 86 ($n = 18$) rosettes/m². Before seeding treatments were applied, *Bromus tectorum* L. and *Poa bulbosa* L. were the predominant grasses (cover = 21.4%, SD = 21.9), with remnant *F. scabrella* and various forb species sparsely represented. The predominant graminoid species on the study site were known to be sensitive to disturbance linked to cattle and horse grazing; Johnston and MacDonald (1967) have suggested that maintenance of this habitat type in climax condition may be impossible if subjected to grazing pressure.

Grass-Seeding Treatments. Three grass-seeding treatments were applied: no seeding and seeding to either *P. spicata* ssp. *spicata* (bluebunch wheatgrass) or *Thinopyrum intermedium* (Host) Barkworth and D.R. Dewey (intermediate wheatgrass). *P. spicata* is a long-lived, cool season perennial bunchgrass native to North America and common to the northern Great Plains and Intermountain region. *T. intermedium*, native to Europe and Asia, is a long-lived perennial with short rhizomes, deep feeding roots. These species were chosen to (1) determine the feasibility of establishing perennial, grazing tolerant grasses on a *Centaurea*-infested rangeland and (2) explore the relative competitive ability of native and exotic grasses against invasive forb species such as spotted knapweed.

Grass seed used in these seeding treatments was purchased from Granite Seed (Lehi, UT) in 1995. The *P. spicata* cultivar seeded was Goldar, which originated in Washington. The *T. intermedium* cultivar was Oahe, which originated from Russia. Each of the grass species was seeded in randomly ordered 2.5 by 14-m plots within four replicate treatment blocks; each block contained a nonseeded control plot. The plots were seeded with a tractor-pulled rangeland drill at a

rate of 18 kg/ha pure live seed during the first week of November 1995. In 2003, *P. spicata* and *T. intermedium* densities were found to be 51 ± 53 (SE; $n = 12$) and 136 ± 112 tillers/m² ($n = 12$), respectively, where seeded.

Herbivore Treatments. *Cyphocleonus achates* adults released on the study site in August 1995 were obtained from a colony reared at the Montana State University Western Agricultural Research Station in Corvallis, MT (Story et al. 1996), located ≈10 km northwest of the study site. Thirty-six adult weevils were released in each of the grass-seeding treatment plots, for a total of 432 adult weevils introduced to the study site. Although lots of 36 adult weevils were released on each of the 12 grass seeding treatment plots, it is more appropriate to consider this aspect of the experiment as a full-site scale treatment than on a per-treatment plot basis, because the weevils were not caged or otherwise confined at release points. The ubiquitous knapweed seedhead flies *Urophora affinis* and *U. quadrifasciata* and the root-boring moth *Agapeta zoegana* were likely present at the study site, although their impact was not specifically measured. Results from Corn et al. (2006) indicate that levels of attack by knapweed biocontrol agents other than *C. achates* should be fairly consistent across uncaged plots within the same study site.

Insect and Plant Sampling. The study site was sampled August–September 2003, ≈8 yr after the insect and grass seeding treatments had been applied. Three 1.0-m² frames were placed at random on the ground within each of the 12 grass-seeding treatment plots, and all seeded grass and *F. scabrella* tillers were counted. All seedling, rosette, and adult *C. stoebe* plants within each frame were also enumerated. All *C. stoebe* adult plants and rosettes were excavated to expose the taproots. These taproots were dissected, and the presence or absence of larvae or larval root galls was used to categorize plants as attacked or free of attack by *C. achates*. This method was adopted based on the determination of Clark et al. (2001a) that larval sampling through root dissection was by far the most accurate method for determining levels of knapweed infestation by *C. achates*. Larvae and galls were found only in adult plants. In total, 928 adult plants were collected, and each was bagged separately and transported to the laboratory where they were oven-dried. Once dried, the roots were removed from each plant, and individual shoot weight, stem length, and flower head number were recorded. Per-plant above-ground biomass, stem length, and flower numbers were used as a relative measure of the impact of *C. achates* on the fitness of individual adult *C. stoebe* plants. Rosettes and seedlings were also clipped and bagged by plot and transported to the laboratory where they were oven-dried and weighed.

Analysis. The data from the three samples taken within each grass seeding treatment plot were averaged before analysis to reduce reported SE/SD and to improve *F* and *P* values. Data for above-ground biomass, stem length, and number of flowers for adult plants were analyzed using a randomized split plot

Table 1. ANOVA determining the effects of interspecific competition and specialized herbivory on mean per plant above-ground biomass, stem length, and no. of flowers produced by adult *C. stoebe* plants

Source	n	df	Biomass/plant (g)		Stem length/plant (cm)		Flowers/plant (n)	
			F	P	F	P	F	P
Grass ^a	8	2	0.91	0.4530	1.53	0.2903	0.60	0.5686
Herbivory ^b	12	1	8.00	0.0198 ^d	69.69	<0.0001 ^d	47.88	<0.0001 ^d
Grass × herbivory ^c	4	2	1.90	0.2028	0.14	0.8723	0.43	0.6665

^a Grass-seeding treatments: *P. spicata* or *T. intermedium* seeded at 18 kg/ha or nonseeded control.
^b Herbivory treatment: *C. achates* applied at 36 adult weevils per grass-seeding treatment plot.
^c Interaction of grass-seeding treatment and herbivory by *C. achates*.
^d $P < 0.05$ indicates that significant treatment effects were detected by ANOVA.

model with grass seeding treatments as main plots and *C. achates* attack class (infested versus uninfested) as subplots. Differences in proportion of adult plants attacked, calculated as the number of adult plants in the sample plot that were attacked by *C. achates* divided by the total number of adult plants in the sample plot, along with density and biomass of adult plants, rosette density and biomass, seedling density per square meter, and age group ratios within each grass seeding treatment, were tested using a two-way parametric analysis of variance (ANOVA) with replication and grass seeding treatment in the model. Means were compared using Fisher protected least significant difference (LSD) test at the 0.05 level of confidence (Peterson 1985).

Stepwise multivariate regression analysis was used to determine the relationship between the proportion of mature *C. stoebe* plants attacked by *C. achates* and the densities of *C. stoebe* adult plants, rosettes, the two seeded grass species, and the resident grass species *F. scabrella*. Only the density of adult *C. stoebe* plants met the significance level for entry into the model.

Results

Grass-Seeding and Herbivory Treatment Effects. Grass-seeding treatments did not affect the per plant above-ground biomass, stem length, and number of flowers of adult *C. stoebe* plants (Tables 1 and 2). Mean values of the same indicators of plant fitness were significantly lower in plants presenting *C. achates* larvae or root galls compared with adult *C. stoebe* plants uninfested by *C. achates* (Tables 1 and 3). The presence of *C. achates* larvae or root galls was correlated with a decrease of ≈19% in mean above-ground biomass for adult *C. stoebe* plants. Mean stem length in individual adult *C. stoebe* plants was similarly reduced

by ≈25% when a weevil larva or gall was present in the root. The number of flowers/stem for weevil-infested plants was also lower by 30% than in uninfested adult *C. stoebe* plants.

Level of *C. achates* Attack on *C. stoebe*. Species and seeding rates selected for the grass seeding treatments used in this study did not affect the proportion of adult *C. stoebe* plants infested by *C. achates*, as measured by the presence of a larvae or root gall (Tables 4 and 5). Evaluations of the same growth parameters of *C. stoebe* plants conducted under different seeding densities of the same grass species may result in a different outcome. The proportion of adult *C. stoebe* plants containing larvae or root galls averaged 0.62 over the three grass seeding treatments, although the number of available hosts fluctuated significantly: 13–39 adults/m² among the two grass treatments and the nonseeded control (Table 5). Although the the lowest density of *C. stoebe* rosettes and adult plants were found on the *T. intermedium* treatment plots, the proportion of adult plants attacked by *C. achates* on those plots was equivalent to the proportion attacked on the *P. spicata* and nonseeded control treatment plots (Table 5).

Fewer rosettes were available to develop into mature plants when *C. stoebe* populations were subjected to attack by *C. achates* combined with interference competition from *T. intermedium* (Table 5). The density of adult *C. stoebe* plants was lower in the *P. spicata* plots compared with the nonseeded control plots, but corresponding total biomass for adult *C. stoebe* plants on a per unit area basis from these respective treatments was not different (Table 5).

Influence of Grass-Seeding Treatments on *C. stoebe* Population Characteristics. Age class distributions within the *C. stoebe* populations associated with specific grass-seeding treatments were variable, although *C. stoebe* seedling densities were unaffected by treatment type (Tables 4 and 5). Seedling stage plants constituted a lower, although not significant, proportion of the *C. stoebe* population in nonseeded control (0.28) compared with grass-seeded treatment plots (*P. spicata*: 0.41; *T. intermedium*: 0.51; $F = 0.66$, $df = 5$; $P = 0.3956$), although respective counts were similar (Table 5). The number of rosettes and their total biomass reported from the *P. spicata* and *T. intermedium* treatments were similar but lower than in the nonseeded control plots (Table 5). Both the density

Table 2. Mean per plant above-ground biomass, stem length, and no. flowers ± SEM for adult *C. stoebe* plants growing under three separate grass-seeding treatment regimens

Grass-seeding treatment	Biomass/plant (g)	Stem length/plant (cm)	Flowers/plant (n)
Nonseeded control	1.68 ± 0.10	11.14 ± 0.70	6.61 ± 0.63
<i>P. spicata</i>	2.35 ± 0.21	12.95 ± 0.78	8.73 ± 0.72
<i>T. intermedium</i>	2.15 ± 0.40	10.97 ± 1.13	7.27 ± 1.40

Table 3. Mean per plant above-ground biomass, stem length, and no. flowers $\pm$ SEM for adult *C. stoebe* plants with a *C. achates* larvae or root gall absent or present

<i>C. achates</i> root gall	Biomass/plant (g)			Stem length/plant (cm)			Flowers/plant (n)		
	Mean $\pm$ SEM	<i>t</i>	<i>P</i>	Mean $\pm$ SEM	<i>t</i>	<i>P</i>	Mean $\pm$ SEM	<i>t</i>	<i>P</i>
Absent	2.27 $\pm$ 0.22	1.37	0.1845	133.30 ^a $\pm$ 0.50	4.03	0.0006 ^b	8.59 $\pm$ 0.60	1.93	0.0676
Present	1.85 $\pm$ 0.22			100.40 ^a $\pm$ 5.00			6.59 $\pm$ 0.83		

^a Denotes mean values that were significantly different.

^b $P < 0.05$ indicates that a *t*-test detected significant differences in means between plants containing or free of *C. achates* galls.

and total biomass of adult *C. stoebe* plants were lowest in the *T. intermedium* plots (Table 5).

Discussion

Our results contradict findings from an earlier field study that clearly implicated intraspecific and interspecific competition as playing a greater role in *C. stoebe* stem length reduction than herbivory. Müller (1992) found that *C. stoebe* stem length was reduced in high-density *C. stoebe* treatments, equivalent to our nonseeded treatment that had the highest adult *C. biebersteinii* density and in treatments featuring interspecific competition with grasses, analogous to our grass treatments, and additionally concluded that effects of intraspecific and interspecific competition were not intensified by herbivory.

In our study, the observed reduction in specific correlates of *C. stoebe* fitness in plants infested by *C. achates* were consistent, regardless of plant community composition. Although an interactive effect of grass competition and herbivory in the *C. stoebe* adult age class was anticipated, our results indicate otherwise. Steinger and Müller-Schärer (1992) found that, in the absence of grass competition, *C. stoebe* shoot biomass for plants attacked by *C. achates* was significantly lower than shoot biomass in herbivore-free plants. However, in the presence of grass competition, overall shoot biomass was significantly reduced both in herbivore-free and herbivore-affected *C. stoebe*, and no significant interaction of grass competition and herbivory on shoot biomass was detected (Steinger and Müller-Schärer 1992). Our results indicate that the effect of *C. achates* attack on *C. stoebe* performance was similar, regardless of whether plant-to-plant interactions were predominantly intra- or interspecific.

Table 4. ANOVA determining the effect of grass-seeding treatment on *C. stoebe* proportion of adults infested by *C. achates*, adult density and above-ground biomass, rosette density and above-ground biomass, and seedling density on a per unit area (1 m²) basis

Plant stage	Parameter	<i>n</i>	<i>F</i>	<i>df</i>	<i>P</i>
Adult	Proportion infested/m ²	4	2.56	2	0.1570
	Density/m ²	4	24.62	2	0.0013 ^a
	Biomass/m ²	4	6.15	2	0.0353 ^a
Rosette	Density/m ²	4	30.82	2	0.0007 ^a
	Biomass/m ²	4	26.17	2	0.0011 ^a
Seedling	Density/m ²	4	0.01	2	0.9925

^a $P < 0.05$ indicates that significant treatment effects were detected by ANOVA.

Steinger and Müller-Schärer (1992) determined that potted *C. stoebe* plants responded to *C. achates* root herbivory by increasing biomass allocation to the roots at the expense of shoot growth. They reported reductions in flower head development because compensatory root growth reduced the production of fructans, sugars typically associated with flower stalk growth (Steinger and Müller-Schärer 1992). Our field observations of reduced shoot biomass, length, and flower head numbers in plants affected by *C. achates* herbivory concur with their results.

The "resource concentration" hypothesis, which predicts that the highest levels of herbivory will occur in resource-rich areas of large, dense, or pure stands of the host plant (Root 1973), suggests that we should have observed a significantly higher proportion of attack on our nonseeded treatment plots where *C. stoebe* was most abundant. Our analysis indicates a negative relationship between the density of mature *C. stoebe* plants and the proportion of mature plants attacked by *C. achates* (Fig. 1), a result more consistent with a "resource dilution" effect characterized by a strong negative linear relationship between herbivore load and host resources (Otway et al. 2005).

Although the *T. intermedium* plots had the lowest density of *C. stoebe* rosettes and mature plants, the proportion of adult plants attacked by *C. achates* in those plots equaled the proportion attacked in the other two seeding treatments. The intensity of *C. achates* attack in the *T. intermedium* plots suggests that host apparency (Feeny 1976, Rhoades and Cates 1976), a common strategy for perennial plant species such as *C. stoebe* with complex phytochemically based defenses (Kelsey and Locken 1987, Thelen et al. 2005), may have played a major role in the high proportion of attack on the locally scarce target hosts. Finally, these results suggest that host finding was not impeded by "associational resistance" (Tahvanainen and Root 1972), because we found no significant difference in the proportion of *C. stoebe* attacked on grass-seeded versus nonseeded treatments.

Clark et al. (2001b) determined that the probability of *C. achates* establishment increased with the size and spatial continuity of a knapweed infestation but not with host density. For some weed biological control agents, attack rate or larval load can become increasingly more independent of available host resources as the herbivore population moves beyond the early colonization phase (Sheppard et al. 2001). Our results suggest that *C. achates* has no difficulty with local

Table 5. Mean per unit area (=1 m²) *C. stoebe* proportion of adult plants infested by *C. achates*, adult plant density and above-ground biomass, rosette density and above-ground biomass, and seedling density ± SEM according to grass-seeding treatment

Grass-seeding treatment	Adults			Rosettes		Seedlings
	Proportion infested/m ²	Density (n)/m ²	Biomass (g)/m	Density (n)/m ²	Biomass (g)/m ²	Density (n)/m ²
Nonseeded control	0.58 ± 0.01a	39.00 ± 2.56a	60.06 ± 4.75a	27.33 ± 1.73a	10.56 ± 0.98a	26.43 ± 5.87a
<i>P. spicata</i>	0.60 ± 0.06a	25.25 ± 4.67b	54.45 ± 14.48a	9.84 ± 1.73b	4.21 ± 0.75b	25.00 ± 15.79a
<i>T. intermedium</i>	0.68 ± 0.01a	13.42 ± 0.84c	28.66 ± 8.85b	10.92 ± 1.83b	3.88 ± 0.65b	24.43 ± 7.33a

Values are means ± SEM.
Letters following means indicate significant differences within columns determined by Fisher's protected LSD text.

dispersal or in detecting and infesting its host, even when the plants are relatively sparse. Harris (2003) stated that these weevils have difficulty ovipositing into *C. stoebe* growing in dense grass; we did not find this to be the case in our study.

Stinson et al. (1994) reported a significantly lower number of final-instar larvae in the roots of mature *C. stoebe* plants field-collected in Durnstein, Austria, in 1984 and 1985. Steinger and Müller-Schärer (1992) reported that *C. achates* failed to infest potted *C. stoebe* at a rate of 27% when the weed was grown alone compared with 52% when *C. stoebe* was grown in pots along with *Festuca pratensis* Huds. In contrast, we found no clear correlation between any of the grass competition treatments at our field site and the rate of *C. achates* attack on *C. stoebe*.

We found that the density and total biomass of mature *C. stoebe* plants were lowest in the *T. intermedium* plots. Our 2003 census indicated that *T. intermedium* generated more tillers than *P. spicata* on a per area basis, suggesting that the observed reductions in mature *C. stoebe* biomass resulted from interference competition. *T. intermedium* is described as a sod-forming grass that grows to an average height of 1.4 m, whereas *P. spicata* attains a mature height of <1.0 m (USDA-NRCS 2006); of the two seeded grass species

used in this study, *T. intermedium* is a potentially superior competitor with mature *C. stoebe* for both light and space than *P. spicata*. Eurasian grass species have been found to be more competitive with *Centaurea* spp. compared with North American grass species (Callaway and Aschehoug 2000, Vivanco et al. 2004). In our study, we found that fewer rosettes were available to develop into mature plants; however, survival of adult plants was greater than where *T. intermedium* was present but less than where neither grass species was present. It seems that once established, both grass species were able to hold their niche in competition with *C. stoebe* when *C. achates* was present over the 8 yr since establishment. This result may have been predicted by the inhibition model of succession proposed by Connell and Slayter (1977).

We found the number of flowers produced by *C. stoebe* plants infested by *C. achates* to be lower than in uninfested plants, suggesting that *C. achates* presence is most likely correlated with a decline in seed output. Using life history study and sensitivity analysis (Sagar and Mortimer 1976), Jacobs and Sheley (1998) identified seed output as a critical phase in the life history of *C. stoebe* in terms of population sustainability. *C. achates* may also affect the survival of adult *C. stoebe* plants, an important life history transition in

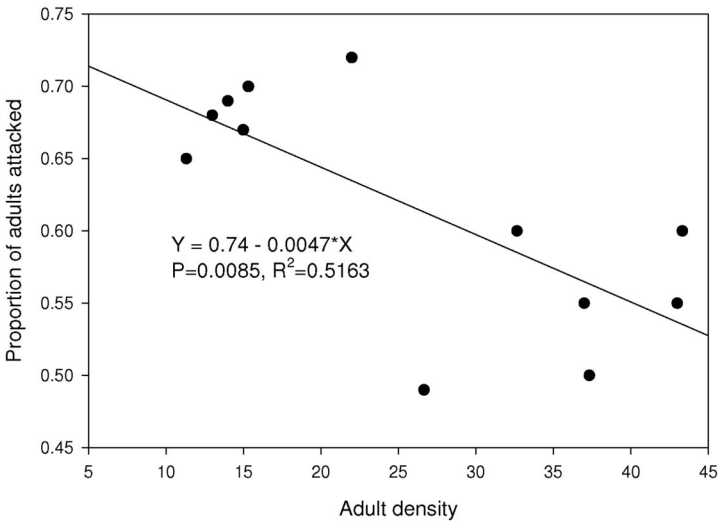


Fig. 1. Relationship between the proportion of adult *C. stoebe* plants attacked by *C. achates* and adult *C. stoebe* density per square meter.

population regulation of this weed, when competition with grasses is a factor (Jacobs and Sheley 1998). Further field studies on the effect of *C. achates* on the survival of adult *C. stoebe* plants are clearly warranted.

Sensitivity analysis of *C. stoebe* life history data (Jacobs and Sheley 1998) resulted in low values for seedling survivorship and the transition from seedling to rosette, indicating that these transitions are not important in maintaining *C. stoebe* populations.

Müller (1992) suggests that competition with grass for light may significantly reduce the competitive ability of *C. stoebe* rosettes. Rosette survivorship and the transition from the rosette to the reproductively mature life history stage were identified as important transitions in *C. stoebe* life history for maintaining populations (Jacobs and Sheley 1998). Our results suggest that where the two perennial, seeded grasses established, they occupied niches opened by dying adult *C. stoebe* plants and suppressed *C. stoebe* rosettes through competition. Where perennial grasses were not seeded, rosettes were able to replace dying adult *C. stoebe* plants. Because *C. achates* larvae did not directly affect *C. stoebe* rosettes (we found no larval galls in the roots of rosettes examined from our experimental populations), we believe the effect of *C. achates* on *C. stoebe* population regulation is through reduced performance and life span of reproductively mature *C. stoebe*.

Age group ratios may predict future population growth; an expanding population usually contains a large proportion of young individuals, a stationary population may have an even distribution, and a declining population may have a large proportion of old individuals (Odum 1971). When considering rosettes and adult plants, the mean proportion of *C. stoebe* rosettes in *P. spicata* treatment plots was 0.29, lower than in the *T. intermedium* treatments (0.44), but the same as found in the nonseeded control plots (0.42, $F = 2.78$, $df = 5$, $P = 0.0753$). The averages over 3 yr of the proportion of rosettes to adult plants in August 1994–1996 reported by Jacobs and Sheley (1998) were 0.66 and 0.63 for two sites in western Montana. From this we speculate that under specialized herbivory by *C. achates*, the populations of *C. stoebe* in the control and *T. intermedium* treatments may be stable, although at different levels, and the population of *C. stoebe* may be declining in the *P. spicata* treatment.

Because the weevils in this study were free-ranging, we cannot prove cause and effect of *C. achates* herbivory on *C. stoebe* performance. It could be argued that *C. achates* selected for smaller *C. stoebe* plants, although the literature suggests otherwise (Stinson et al. 1994). Our results show that *C. stoebe* plants attacked by *C. achates* were smaller, with lower reproductive potential, than plants free from attack. Although we were not able to detect a formal interaction effect of grass treatment and *C. achates* attack, we conclude that the effects of herbivory and competition seem to have had additive effects on spotted knapweed. Finally, we found no evidence that the combined effects of herbivory and grass seeding were antagonistic.

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Received for publication 31 December 2005; accepted 6 August 2006.