Biological Control 51 (2009) 140–146

Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Plant community changes after the reduction of an invasive rangeland weed, diffuse knapweed, *Centaurea diffusa*

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ARTICLE INFO

Article history:
Received 13 February 2009
Accepted 24 June 2009
Available online 8 July 2009

Keywords:
Centaurea diffusa
Larinus minutus
Weed biocontrol
Invasive species treadmill
Ecological restoration
Bromus spp.
Diversity

ABSTRACT

The expected outcome of weed control in natural systems is that the decline of a dominant weed will result in an increase in diversity of the plant community but this has seldom been tested. Here we evaluate the response of the plant community following the decline of diffuse knapweed (*Centaurea diffusa*) in six different pastures at White Lake, BC, Canada over five years. This period followed the establishment, spread and high levels of attack by the introduced European weevil, *Larinus minutus*, as part of a biological control program. Knapweed declined immediately before and during the study period, but, contrary to expectations, the species richness and diversity of the rangeland plant community did not increase. The absolute cover of native and introduced forbs and grasses increased following knapweed decline, but only the introduced grasses showed a consistent increase in cover relative to the other life-forms. However, unlike in other studies, the native plants dominated the study site. We conclude that the changes in plant communities following successful biological control are variable among programs and that the impact of replacement species must be evaluated in assessing the success of ecological restoration programs that use biological control to manage an undesirable weed.

1. Introduction

Control of invasive weeds is often proposed as a key element of ecosystem restoration (Harms and Hiebert, 2006) because it is assumed that the removal of the target weed will be associated with an increase in the abundances of species previously suppressed by the weed and an increase in diversity of the plant community. Thus, reducing plant dominance in a community should promote diversity (Lesica and Hanna, 2004); an increase in native species diversity is often considered to be a measure of success in restoration ecology (Ruiz-Jaen and Aide, 2005). Biological control can be a cost-effective method of achieving long-term weed control in natural ecosystems and there are a number of cases where this has been successful in reducing weed population density (Myers and Bazely, 2003; Myers, 2008).

Ding et al. (2006) pointed out that, for most weed biological control programs, the majority of pre-release funding goes to host-specificity testing and far less is available for assessing the impact of the agent on the weed's performance. In the post-release period, priorities are either the assessment of non-target impacts (e.g. Louda et al., 2003; Paynter et al., 2004) and/or documentation of the response of the weed (e.g. Grevstad, 2006; Hoffmann and Moran, 1991; Supkoff et al., 1988). However, few studies quantify the effects of weed reduction on plant community composition or ecosystem processes despite the fact that the restoration of natural communities and/or natural ecosystem processes is often the stated goal of restoration projects, and thus the primary motivation for biological control projects (Denslow and D'Antonio, 2005). For example, less than 1% of weed biological control programs in Australia assessed the effect that the reduction of the weed through successful biological control had on the wider plant community (Thomas and Reid, 2007). Given the long history of interest in the invasion of exotic plants into plant communities (Darwin, 1859; Elton, 1958; Stohlgren et al., 2008), the lack of interest in what happens when a former community dominant declines, is notable.

Evaluations that have been done tend to show that plant community responses are highly site specific (Denslow and D'Antonio, 2005). For example, successful biological control of purple loosestrife (*Lythrum salicaria* L.) by *Galerucella* spp. (Blossey et al., 2001) resulted in one of two outcomes: either monotypic stands of purple loosestrife were replaced by a diverse wetland plant community or other invasive species such as common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) or reed canary grass (*Phalaris arundinacea* L.) expanded as purple loosestrife declined. This suggests that, in some sites, additional restoration techniques may be needed, as well as biological control, to achieve goals of community restoration and ecosystem processes.

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doi:10.1016/j.biocontrol.2009.06.015

Diffuse knapweed (*Centaurea diffusa* Lam., Asteraceae) and spotted knapweed (*Centaurea stoebe* L. subsp. *micranthos*) are Eurasian weeds that are prevalent in dry rangelands in many areas of western North America. They share many common attributes and biological control agents, but occur in slightly different habitats (Bourchier et al., 2002). Diffuse knapweed has colonized up to 1.4 million hectares of rangelands in western North America, from Washington to Michigan and British Columbia to New Mexico (Seastedt et al., 2005). It is unpalatable to livestock and is able to outcompete a range of native plant species (LeJeune and Seastedt, 2001; Seastedt et al., 2005).

A biological control program for diffuse knapweed was initiated in 1970. Over the next 20 years, 12 insect species were introduced for the control of this species and nine of these are now common throughout knapweed infested areas of British Columbia (Myers, 2007). The most common insect species in British Columbia include the two species of gallflies *Urophora affinis* Frauenfeld and *U. quadrifasciata* (Meigen) (Diptera: Tephritidae), the root boring beetles *Sphenoptera jugoslavica* Obenberger (Coleoptera: Buprestidae) and *Cyphocleonus achates* (Fåhraeus) (Coleoptera: Curculionidae), the root boring moth *Agapeta zoegana* (L.) (Lepidoptera: Cochylidae) and the weevil *Larinus minutus* Gyllenhal (Coleoptera: Curculionidae).

Larinus minutus was the most recent of these agents to be introduced and established. Following its establishment, diffuse knapweed has declined in British Columbia (Myers, 2007; Myers et al., 2009) and Colorado (Seastedt et al., 2003, 2005, 2007). Larvae develop in the flower-heads and prevent reproduction of the plant while the adults feed on the stems and leaves. Under some conditions the adult weevils can kill the host outright (Myers, 2007).

Here, we report changes that were measured in plant community composition following the decline of diffuse knapweed through biological control in six different pastures at White Lake, British Columbia, Canada. Prior to the initiation of this study in 2001, knapweed had already declined from peaks in abundance following the establishment of *L. minutus* in the late 1990s (Myers, 2007; Myers et al., 2009). We test whether the expected outcome of weed biological control in natural systems occurs, i.e. that native communities will recover, by monitoring the vegetation in a series of permanent quadrats.

2. Materials and methods

2.1. Study site

White Lake Basin (Okanagan Falls) (49°19.18N, 119°37.82W) belongs to the National Research Council's Dominion Radio Astrophysical Observatory and is managed by The Nature Trust of British Columbia in cooperation with a local rancher. The management goals for this area include restoration of native vegetation and sustainable grazing intensities. The vegetation type here is sagebrush (*Artemisia tridentata* Nutt. and *Artemisia tripartita* Rydb.) shrub-steppe. The elevation of the basin is 550 m and the average annual total precipitation for this region (1971–2000) is 333 mm. The average precipitation for the growing season (1st May–30th August) is approximately 135 mm based on data from the Penticton A weather station (WMO ID 71889) (Environment Canada, 2002) which classifies the habitat as semi-desert. Spring rainfall (March–May) showed little variation over the period 2001–05 but summer rainfall (May–August) was highly variable with below average rainfall occurring during the summers of 2002 and 2003 and above average rainfall in 2004. Total annual precipitation for 2001–2005 was 320, 197, 281, 427 and 303 mm respectively while growing season precipitation was 154, 82, 49, 183 and 128 mm for the same years.

The knapweed invasion in this area was associated with disturbance of the land that occurred with the installation of a radio telescope at the White Lake Observatory in the 1960s. The research quadrats were distributed over a distance of several kilometers through the White Lake basin, to the south and west of the Observatory. Both *Urophora* spp. were present in the area, *S. jugoslavica* was introduced in 1976 and *L. minutus* was introduced in this vicinity in 1991, 1995 and 2000. *Cyphocleonus achates* and *A. zoegana* were present in low numbers (Myers, 2007).

2.2. Monitoring methods

In the spring of 2001, 422 permanent quadrats (20×50 cm; 0.1 m^2) were established. The quadrats were spaced approximately 10 m apart along haphazardly placed transects. There were three to nine transects and 50–90 quadrats per pasture for six pastures of 100–200 ha (Table 1).

Surveys were conducted in late May to early June of 2001, 2002, 2003 and 2005. In 2004 complete sampling was not done due to personnel constraints, and only quadrats that had previously contained knapweed were sampled. As this is a non-random subset, only the complete data set was used for most analyses.

Cover of all plant species was visually estimated to the nearest 1% in each quadrat and total cover of each quadrat was calculated as the sum of percent cover of every plant species in the quadrat. Absolute cover was recorded but the totals do not reach 100% because there are substantial amounts of bare ground in these pastures. Relative cover (absolute cover of a plant species divided by total cover of all plant species) was calculated because substantial variation in rainfall influenced total plant cover between years with bare ground diminishing during wet years.

2.3. Statistical analyses

All statistical analyses, described below, were conducted using R (R Core Development Team, 2008). Both absolute and relative plant cover data were used to investigate how species diversity and the abundance of plant life-forms changed in these pasture communities during the period of knapweed decline.

2.3.1. Knapweed cover

Absolute knapweed cover in the pastures was determined by taking the average of all quadrats in each transect and then taking the average of the transects to give a figure for each pasture. Standard errors were calculated for each pasture from the averages of the transects.

2.3.2. Species richness

The number of introduced and native species found in each year in each of the six pastures was counted. χ^2 tests were conducted to determine whether there was a change in total, native or introduced species richness over time or across the different pastures.

2.3.3. Diversity indices

Shannon's *H* diversity index ($H = -\sum_{i=1}^{S} p_i * \ln p_i$, Spellerberg and Fedor, 2003; Begon et al., 1996) was calculated for all pastures

Table 1
The number of monitoring transects and quadrats in each pasture studied in the White Lake Basin, British Columbia, Canada.

Pasture	No. transects	No. plots
Park Rill North	9	90
Park Rill South	8	80
Set Aside	5	50
White Ranch South	3	67
White South	6	60
White North	8	75

and all years using the absolute cover data.; p is the proportion of species i (No. of species i absolute percent cover/total absolute percent cover of all species) in each quadrat, then summed for each pasture. Absolute cover data only were used because the diversity index converts data to proportions. The diversity index was calculated on individual quadrats in each pasture. Thus, a single number was obtained for each pasture in each year. An analysis of variance (ANOVA) was used to determine if the change in diversity with year was significant. Because the same quadrats in the pastures were measured in each year, data were not independent. Therefore, pasture was used as a random effect to account for the repeated measures nature of the design. Shannon's H Index was calculated because it is sensitive to rare species, as opposed to Simpson's D which emphasizes common species.

2.3.4. Plant community response

Plant species were separated into four different life-form categories based on Klinkenberg (2008). The categories were native forb, introduced forb, native grass and introduced grass. *Juncus balticus* Willd. (Baltic rush, Juncaceae), *Equisetum laevigatum* A. Braun (smooth horsetail, Equisetaceae) and *Selaginella densa* Rydberg (lesser spikemoss, Selaginellaceae) were all classified as forbs for the purposes of this analysis, however, excluding them from this category does not qualitatively change the results. Knapweed was excluded from the introduced forbs category.

The absolute and relative plant cover for each quadrat in each transect was averaged to give the mean value for each transect. The transects for each pasture were averaged to give the mean absolute and mean relative cover of each species in each pasture. The absolute and relative cover of each species for each life-form were summed to give the absolute and relative cover for each life-form in each pasture.

All the data were analyzed in two ways. Firstly, a multivariate analysis of variance (MANOVA) was conducted to determine whether relative or absolute cover of the life-forms and *C. diffusa* changed significantly during the period studied. *Centaurea diffusa* was included in the model to account for co-variance associated with it. Because the same quadrats were measured each year in the pastures, pasture was included as the first term in the model to remove the variation attributable to pasture prior to testing for Year. Secondly a paired Student's t-test was used to determine if significant differences occurred between 2001 and 2005 for each life-form category. For both analyses each pasture was treated as a replicate.

2.3.5. Response of Bromus spp.

The cover of knapweed was compared to the cover of *Bromus* spp. (Poaceae, the cheatgrasses). Here, only the quadrats that had knapweed in them at some point between 2001 and 2003 were used, thus the 2004 data were included. It must be noted that these quadrats were not evenly distributed across the pastures, with 32 occurring in White North, 19 in Park Rill North and 11, nine and eight in Set Aside, White South and Park Rill South respectively. The one quadrat with knapweed in the White Ranch South pasture was not monitored.

3. Results

3.1. Knapweed

The cover of knapweed in the six pastures at White Lake declined during the period of the study 2001–05 (Fig. 1).

3.2. Species richness

In total, 122 plant species were found during the survey, of which 91 were native and 31 introduced. There was no change in total, native or introduced plant species richness over time (Table 2) and an almost significant ($p = 0.07$; Table 3) difference in the total species richness occurred across the pastures. Neither native nor introduced species richness differed between pastures.

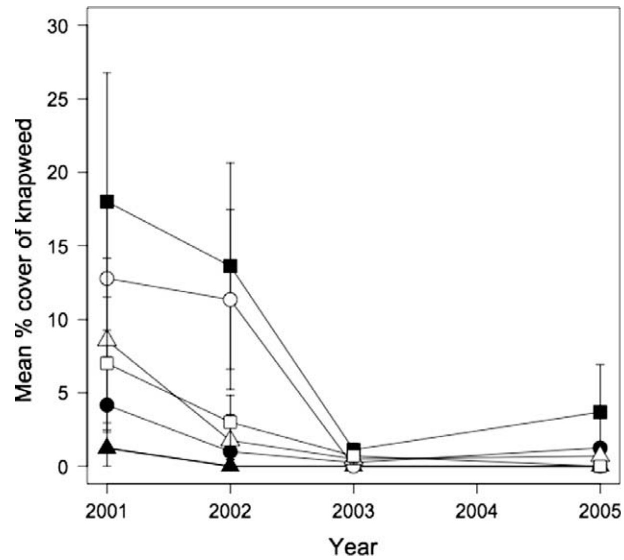

Fig. 1. Average percentage absolute cover of knapweed (*Centaurea diffusa)* in all six pastures (mean ± SEM of the transects) at White Lake, British Columbia, Canada between 2001 and 2005. Transects were not monitored in 2004. Different symbols represent different pastures; open circles, Park Rill North; open triangles, Park Rill South, open squares, Set Aside; closed circles, White South; closed squares, White North; and closed triangles, White Ranch South.

3.3. Shannon's H diversity index

The six pastures at White Lake showed no change in the average diversity as measured by the Shannon's H index ($F_{3,15} = 0.411$, $p = 0.747$) between 2001 and 2005.

3.4. Plant community response

The absolute cover of all plant life-forms varied over time (Fig. 2, Tables 4 and 5). Native and introduced grasses and native forbs significantly increased in all pastures between 2001 and 2005 (Fig. 2). Native forbs increased between 2001 and 2003 and then remained constant while the increases in the grasses occurred predominately after 2003 (Fig. 2). Introduced forbs (knapweed excluded) did not change in absolute cover over time (Fig. 2, Tables 4 and 5).

Relative cover showed similar trends (Fig. 3, Tables 4 and 5). Again the responses in relative cover of the native and introduced grasses and native forbs varied significantly among years, but each life-form responded in a different manner. The relative cover of na-

Table 2
Total, native and introduced numbers of species in the various pastures at White Lake. H_o = no differences in species richness across the pastures.

Pasture	Total	Native	Introduced
Park Rill North	78	56	22
Park Rill South	82	59	23
Set Aside	67	47	20
White North	51	36	15
White Ranch South	82	60	22
White South	78	57	21
χ^2	10.027	8.257	2.024
p	0.0745	0.1426	0.8458

Table 3
Total, native and introduced numbers of species over time at White Lake. H_o = no differences in species richness over time.

Year	Total	Native	Introduced
2001	100	73	27
2002	94	72	22
2003	102	76	26
2005	101	73	28
χ^2	0.39	0.122	0.806
p	0.9422	0.989	0.8481

tive grasses declined between 2001 and 2003 and showed a slight recovery in 2005 (Fig. 3), with an overall lack of change in relative cover over the study years (Fig. 3). The introduced grasses changed little between 2001 and 2003 but increased between 2003 and 2005 (Fig. 3, Table 4). This resulted in an overall increase in the relative cover of introduced grasses by 2005 (Fig. 3). The native forbs initially increased from 2001 to 2003 but then declined between 2003 and 2005 (Fig. 3, Table 4) resulting in no overall change in relative cover (Table 5). The relative cover of the other introduced forbs (Fig. 3, Tables 4 and 5) did not change significantly during the study.

3.5. Response of *Bromus* spp. to knapweed decline

After the knapweed decline that occurred between 2001 and 2003, cover of *Bromus* spp. increased, but not until 2005 following a wet spring in 2004 (Fig. 4).

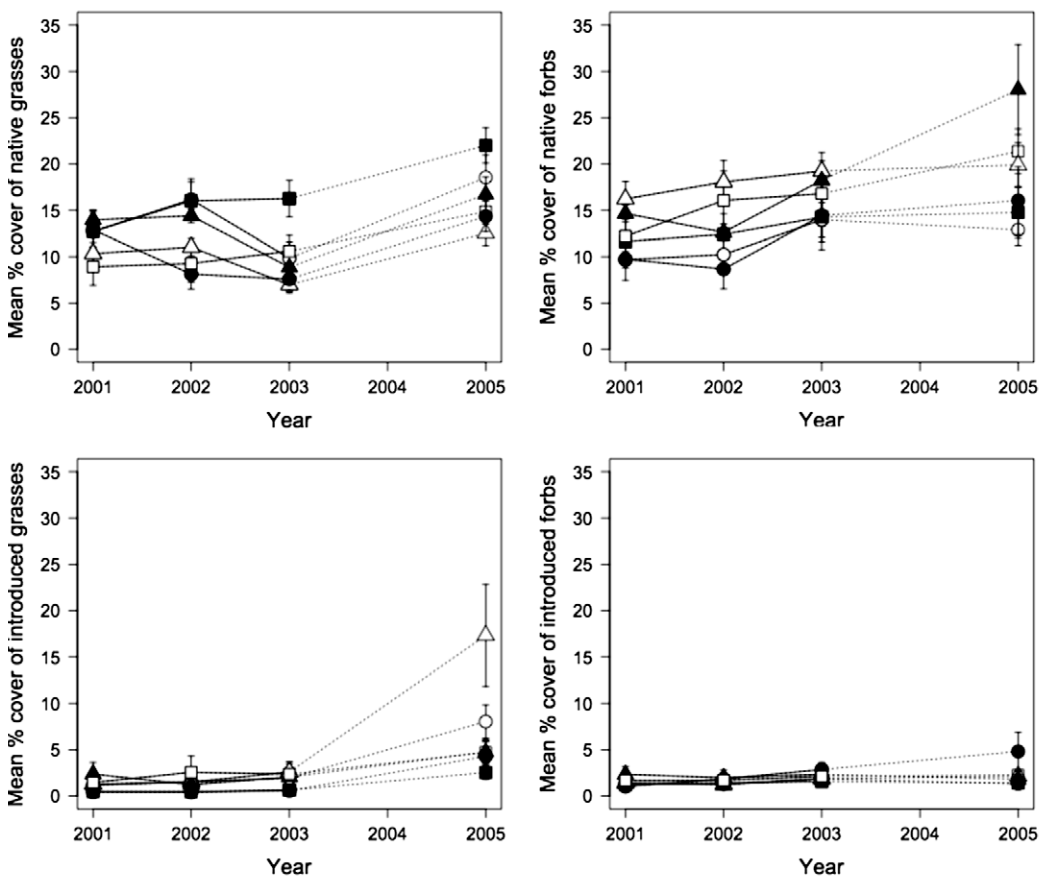

Fig. 2. Change in absolute percentage cover of the native and introduced grasses and forbs in all six pastures (mean ± SEM of the transects) at White Lake, British Columbia, Canada between 2001 and 2005. Introduced forb does not include *Centaurea diffusa*. Transects were not monitored in 2004. Different symbols represent different pastures; open circles, Park Rill North; open triangles, Park Rill South; open squares, Set Aside; closed circles, White South; closed squares, White North; and closed triangles, White Ranch South.

Table 4
Changes in the absolute and relative abundances of the life-forms and *Centaurea diffusa* over the four-year period (MANOVA).

	Native grasses	Introduced grasses	Native forbs	Introduced forbs	*C. diffusa*
Absolute cover					
Pasture	$F_{5,15}$ = 6.44 p = 0.0022	$F_{5,15}$ = 1.59 p = 0.2218	$F_{5,15}$ = 6.51 p = 0.0021	$F_{5,15}$ = 2.02 p = 0.0.1341	$F_{5,15}$ = 3.91 p = 0.0181
Year	$F_{3,15}$ = 10.93 p = 0.0005	$F_{3,15}$ = 6.88 p = 0.0039	$F_{3,15}$ = 9.35 p = 0.0010	$F_{3,15}$ = 2.08 p = 0.1458	$F_{3,15}$ = 7.67 p = 0.0024
Relative cover					
Pasture	$F_{5,15}$ = 8.33 p = 0.0006	$F_{5,15}$ = 2.15 p = 0.1158	$F_{5,15}$ = 4.87 p = 0.0078	$F_{5,15}$ = 4.48 p = 0.0107	$F_{5,15}$ = 3.55 p = 0.0256
Year	$F_{3,15}$ = 4.94 p = 0.0139	$F_{3,15}$ = 6.98 p = 0.0037	$F_{3,15}$ = 5.74 p = 0.008	$F_{3,15}$ = 1.49 p = 0.2577	$F_{3,15}$ = 8.88 p = 0.0013

Table 5
Comparisons (paired Student's *t*-test) of the absolute and relative abundances (percentages) of the life-forms between 2001 and 2005. Introduced forb and introduced grass data were log-transformed prior to both analyses.

	2001 mean ± SEM	2005 mean ± SEM	*t*-value, *p* value
Absolute cover			
Native grasses	11.92 ± 0.77	16.49 ± 1.38	$t = -3.76$, df = 5, $p = 0.013$
Introduced grasses	1.20 ± 0.29	6.94 ± 2.20	$t = -5.95$, df = 5, $p = 0.002$
Native forbs	12.35 ± 1.08	18.83 ± 2.25	$t = -3.85$, df = 5, $p = 0.012$
Introduced forbs	1.50 ± 0.19	2.29 ± 0.53	$t = -1.38$, df = 5, $p = 0.226$
Relative cover			
Native grasses	43.14 ± 2.94	37.73 ± 4.23	$t = 1.56$, df = 5, $p = 0.179$
Introduced grasses	4.20 ± 0.88	15.03 ± 4.10	$t = -4.42$, df = 5, $p = 0.007$
Native forbs	44.20 ± 2.55	41.74 ± 3.54	$t = 0.69$, df = 5, $p = 0.523$
Introduced forbs	5.34 ± 0.50	5.27 ± 1.41	$t = 0.48$, df = 5, $p = 0.652$

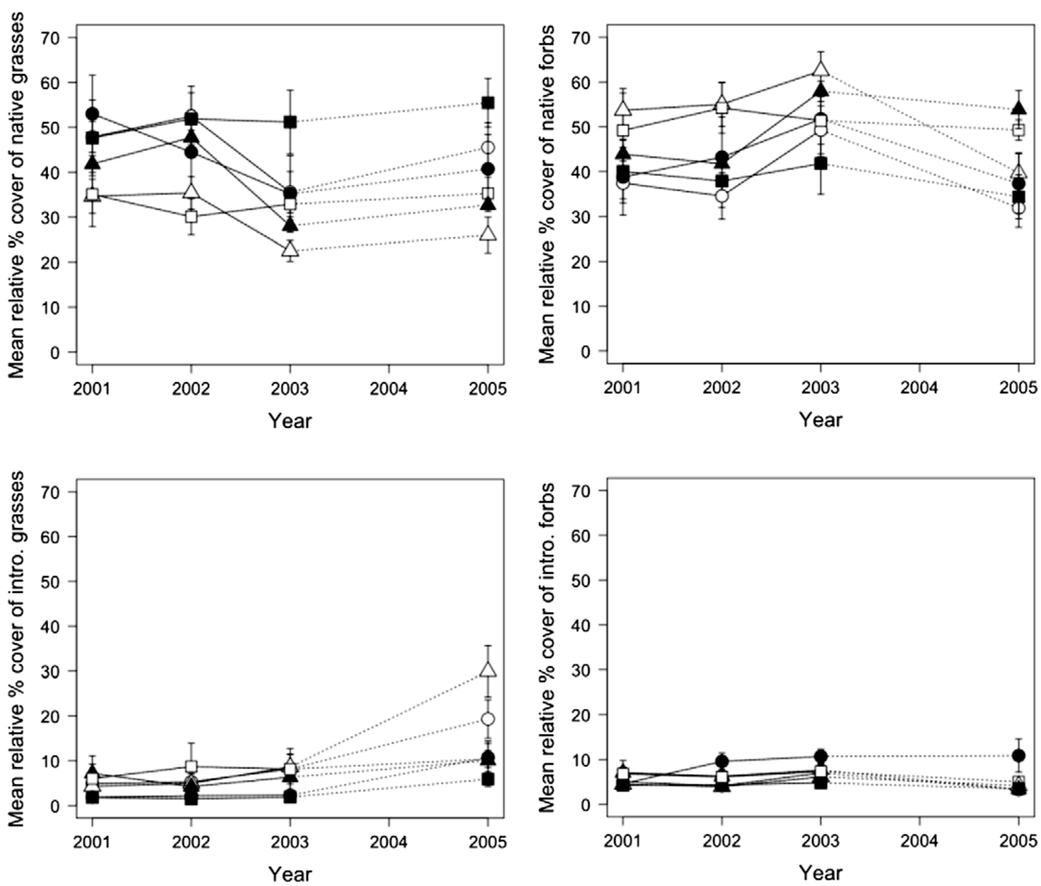

Fig. 3. Change in relative percentage cover of the native and introduced grasses and forbs in all six pastures (mean ± SEM of the transects) at White Lake, British Columbia, Canada between 2001 and 2005. Introduced forb does not include *Centaurea diffusa*. Transects were not monitored in 2004. Different symbols represent different pastures; open circles, Park Rill North; open triangles, Park Rill South; open squares, Set Aside; closed circles, White South; closed squares, White North; and closed triangles, White Ranch South.

4. Discussion

At the White Lake Ranch in British Columbia in 2001, 73 native species and 27 introduced ones were identified in the quadrats. On average the native grasses and forbs had greater percent cover, in both relative and absolute terms, than their introduced counterparts. Therefore, although introduced species make up approximately a third of the plant diversity in this area, they are less dominant as ground cover. Diffuse knapweed has been a major rangeland weed in the dry interior of British Columbia but has declined substantially in recent years following the introduction of *L. minutus* (Myers, 2007; Myers et al., 2009). Over the course of this study it represented a small but declining component of the community of introduced forbs in the area.

One might predict an increase in diversity following the decline of the invasive weed. Species richness and diversity (as measured by Shannon's *H* index) however did not increase over the course of the study. The relative and absolute cover of the introduced grasses increased following the decline of the knapweed especially after 2003 (Figs. 3 and 4, Table 4). While absolute cover of the native grasses and native forbs increased between 2001 and 2005, relative cover did not change overall (Table 5). This suggests that the native plants potentially responded to the decline in knapweed and increase in rainfall but, not as much as the introduced grasses. Thus, native grasses and forbs were apparently not able to take full advantage of the decline in knapweed. The more common native grasses are perennial bunch grasses and these may respond more slowly to increased rainfall and reduced densities of knapweed

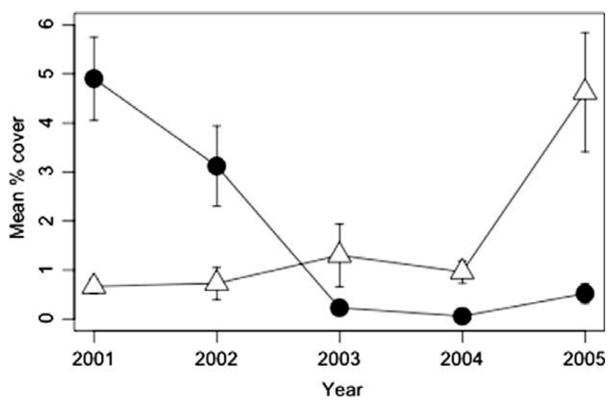

Fig. 4. The mean absolute cover of knapweed (*Centaurea diffusa*; closed circles) and *Bromus* spp. (open triangles) in quadrats that contained knapweed at some point between 2001 and 2003.

than the introduced annual grasses, *Bromus* species (primarily *Bromus tectorum* L. (cheatgrass) and *B. hordeaceus* L. (soft brome)). In this area disturbed sites are commonly invaded by *Bromus* spp. (Nicholson et al., 1991).

Two other published studies report the change in the plant community following knapweed decline. These also found that the decline in knapweed was associated with an increase of introduced grasses. When spotted knapweed (*Centaurea stoebe* subsp. *micranthos*) declined in Montana, USA, due to biological control by *C. achates*, two annual invasive weeds, *B. tectorum* and *Descurainia sophia* (L.) Webb ex Prantl (Brassicaceae), became the dominant plants (Story et al., 2006). Story et al. (2006) found that by 2004 *B. tectorum* comprised 50–89% of the vegetation at their two sites. In Colorado, USA, a decline in diffuse knapweed was more than compensated for by increases of introduced grasses, and non-native plant species continued to dominate at this site (Bush et al., 2007). They found that the introduced grasses increased their relative cover from approximately 14–40% between 1997 and 2005. In comparison the introduced grasses increased at White Lake from 4% to 15% cover, less than that found in the studies in Montana and Colorado but a larger percentage increase.

The higher density of *B. tectorum* in Montana following spotted knapweed decline might have been due to the initial level of introduced grass in the area. However, Story et al. (2006) reported that, spotted knapweed initially formed a near monoculture, and therefore little grass would be expected to occur. Spotted knapweed densities of 14 and 40 plants per m^2 at the two sites studied by Story et al. (2006) were similar to the pre-*L. minutus* densities of approximately 17 flowering and rosette diffuse knapweed plants per m^2 in the White Lake area between 1989 and 1994 (Myers, unpublished). The higher densities of *B. tectorum* in Montana and Colorado are likely to be associated with differences in succession resulting from various site-specific factors, such as native species seed bank, grazing regime, amount of open soil and various rainfall parameters.

White Lake is now managed primarily for its conservation value, however, grazing still occurs. *Bromus tectorum* is negative for both conservation and grazing. It is a highly invasive species and is competitively superior in disturbed environments. Colonization by *B. tectorum* also increases fire frequency in some areas because it accumulates fine fuels early in the season (Rowe and Brown, 2008). In terms of grazing, it is an inferior forage crop because of its early maturation (Currie et al., 1987). Mature seeds have long stiff awns that may puncture the mouth tissue of livestock and thus can be problematic in late summer.

Attempts at area-wide control of a species are normally justified on the assumption that the community that replaces the dominating species will somehow be better than the invader-dominated community (Denslow and D'Antonio, 2005). The perceptions of 'better' depend on the goals of the agencies or individuals undertaking the control. Increase in native vegetation is almost universally considered to be beneficial while increases in other exotic plant species may be considered desirable if their traits are more beneficial for human activities than the weed (e.g. more palatable to stock or less prickly). Without considering the overall changes to the plant community the success of this program would not be fully evaluated. If the reduction in one weed led to an increase in another equally destructive weed, it could be argued that the ecological restoration goal of the biological control program had not been achieved even though biological control had successfully reduced the population density of the target weed (Carson et al., 2008). Of the three areas (White Lake, Colorado and Montana) in which biological control has been successful in reducing the densities of the knapweed, ecological restoration goals have been more successful at White Lake, BC than in Colorado or Montana. In all three sites introduced grasses increased dramatically, however, thus far this increase was substantially less at White Lake. Here native species are the dominant members of the plant community. Identifying the factors that have led to these variable outcomes may help to enable managers of rangelands to promote the desired outcomes from the biological control program through additional restoration techniques.

Acknowledgments

The authors are grateful to The Nature Trust of British Columbia and The National Research Council's Dominion Radio Astrophysical Observatory for access to their property at White Lake Basin. We thank T. Duralia, S. Arnesen, C. Klym and M. Justice for help in the field. Funding was provided by Environment Canada and Natural Science and Engineering Research Council of Canada. We would also like to thank M. Vellend, M. Tseng, M. Franklin, A. Brown and J. Clarke for helpful comments on a draft of this paper, and D. Srivastava and R. FitzJohn for assistance with statistics and R.

References

Begon, M., Harper, J.L., Townsend, C.R., 1996. Ecology: Individuals, Populations and Communities, third ed. Blackwell Science, Oxford.

Blossey, B., Skinner, L.C., Taylor, J., 2001. Impact and management of purple loosestrife (*Lythrum salicaria*) in North America. Biodiversity and Conservation 10, 1787–1807.

Bourchier, R.S., Mortensen, K., Crowe, M., 2002. *Centaurea diffusa* Lamarck, diffuse knapweed, and *Centaurea maculosa* Lamarck, spotted knapweed (Asteraceae). In: Mason, P.G., Huber, J.T. (Eds.), Biological Control Programmes in Canada, 1981–2000. CABI, Wallingford, UK, pp. 302–313.

Bush, R.T., Seastedt, T.R., Buckner, D., 2007. Plant community response to the decline of diffuse knapweed in a Colorado grassland. Ecological Restoration 25, 169–174.

Carson, W.P., Hovick, S.M., Baumert, A.J., Bunker, D.E., Pendergast, T.H., 2008. Evaluating the post-release efficacy of invasive plant biocontrol by insects: a comprehensive approach. Arthropod–Plant Interactions 2, 77–86.

Currie, P.O., Volesky, J.D., Hilken, T.O., White, R.S., 1987. Selective control of annual bromes in perennial grass stands. Journal of Range Management 40, 547–550.

Darwin, C., 1859. On the Origin of Species. Murray, London.

Denslow, J.S., D'Antonio, C.M., 2005. After biocontrol: assessing indirect effects of insect releases. Biological Control 35, 307–318.

Ding, J., Blossey, B., Du, Y., Zheng, F., 2006. Impact of *Galerucella birmanica* (Coleoptera: Chrysomelidae) on growth and seed production of *Trapa natans*. Biological Control 37, 338–345.

Elton, C., 1958. The Ecology of Invasion by Animals and Plants. Meuthuen, London.

Environment Canada, 2002. National Climate Data and Information Archive. http://climate.weatheroffice.ec.gc.ca. (accessed 8.01.08).

Grevstad, F.S., 2006. Ten-year impacts of the biological control agents *Galerucella pusilla* and *G. Calmariensis* (Coleoptera: Chrysomelidae) on purple loosestrife (*Lythrum salicaria*) in Central New York State. Biological Control 39, 1–8.

Harms, R.S., Hiebert, R.D., 2006. Vegetation response following invasive tamarisk (*Tamarix* spp.) removal and implications for riparian restoration. Restoration Ecology 14, 461–472.

Hoffmann, J.H., Moran, V.C., 1991. Biocontrol of a perennial legume, *Sesbania punicea*, using a florivorous weevil, *Trichapion lativentre*: weed population dynamics with a scarcity of seeds. Oecologia 88, 574–576.

Klinkenberg, B. (Ed.), 2008. E-Flora BC: Electronic Atlas of the Plants of British Columbia [eflora.bc.ca]. Lab for Advanced Spatial Analysis, Department of Geography, University of British Columbia, Vancouver (accessed 2.02.09).

LeJeune, K.D., Seastedt, T.R., 2001. *Centaurea* species: the forb that won the West. Conservation Biology 15, 1568–1574.

Lesica, P., Hanna, D., 2004. Indirect effects of biological control on plant diversity vary across sites in Montana grasslands. Conservation Biology 18, 444–454.

Louda, S.M., Pemberton, R.W., Johnson, M.T., Follett, P.A., 2003. Nontarget effects – the Achilles' Heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. Annual Review of Entomology 48, 365–396.

Myers, J.H., 2007. How many and what kind of agents for the biological control of weeds: a case study with diffuse knapweed. In: Vincent, C., Goettel, M.S., Lazarovits, G. (Eds.), Biological Control: A Global Perspective. CAB International.

Myers, J.H., 2008. One agent is usually sufficient for successful biological control of weeds. In: Julien, M.H., Sforza, R., Bon, M.C., Evans, H.C., Hatcher, P.E., Hinz, H.L., Rector, B.G. (Eds.), Proceedings of the XII International Symposium on Biological Control of Weeds. CAB International, Wallingford, UK, pp. 601–606.

Myers, J.H., Bazely, D.R., 2003. Ecology and Control of Introduced Plants. Cambridge University Press, Cambridge, UK.

Myers, J.H., Jackson, C., Quinn, H., White, S., Cory, J.S., 2009. Successful biological control of diffuse knapweed, *Centaurea diffusa*: the role of *Larinus minutus*. Biological Control 50, 66–72.

Nicholson, A., Hamilton, E, Harper, W.L., Wilkeem, B.M., 1991. Bunchgrass zone. In: Meidinger, D., Pojar, J. (Eds.), Ecosystems of British Columbia. British Columbia Ministry of Forests, Special Report Series No. 6. URL: http://www.for.gov.bc.ca/hfd/pubs/Docs/Srs/Srs06.htm (accessed 17.04.08).

Paynter, Q.E., Fowler, S.V., Gourlay, A.H., Haines, M.L., Harman, H.M., Hona, S.R., Peterson, P.G., Smith, L.A., Wilson-Davey, J.R.A., Winks, C.J., Withers, T.M., 2004. Safety in New Zealand weed biocontrol: a nationwide survey for impacts on non-target plants. New Zealand Plant Protection 57, 102–107.

Rowe, H.I., Brown, C.S., 2008. Native plant growth and seedling establishment in soils influenced by *Bromus tectorum*. Rangeland Ecology and Management 61, 630–639.

Ruiz-Jaen, M.C., Aide, T.M., 2005. Restoration success: how is it being measured? Restoration Ecology 13, 569–577.

R Core Development Team, 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, URL: www.R-project.org.

Seastedt, T.R., Suding, K.N., LeJeune, K.D., 2005. Understanding invasions: the rise and fall of diffuse knapweed (*Centaurea diffusa*) in North America. In: Inderjit (Ed.), Invasive Plants: Ecological and Agricultural Aspects. Birkhäuser Verlag, Switzerland, pp. 129–139.

Seastedt, T.R., Gregory, N., Buckner, D., 2003. Effect of biocontrol insects on diffuse knapweed (*Centaurea diffusa*) in a Colorado grassland. Weed Science 51, 237–245.

Seastedt, T.R., Knochel, D.G., Garmoe, M., Shosky, S.A., 2007. Interactions and effects of multiple biological control insects on diffuse and spotted knapweed in the Front Range of Colorado. Biological Control 42, 345–354.

Spellerberg, I.F., Fedor, P.J., 2003. A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon–Wiener' Index. Global Ecology & Biogeography 12, 177–179.

Stohlgren, T.J., Barnett, D.T., Jarnevich, C.S., Flather, C., Kartesz, J., 2008. The myth of plant species saturation. Ecology Letters 11, 313–322.

Supkoff, D.M., Joley, D.B., Marois, J.J., 1988. Effect of introduced biological control organisms on the density of *Chondrilla juncea* in California. Journal of Applied Ecology 25, 1089–1095.

Story, J.M., Callan, N.W., Corn, J.G., White, L.J., 2006. Decline of spotted knapweed density at two sites in western Montana with large populations of the introduced root weevil, *Cyphocleonus achates* (Fahraeus). Biological Control 38, 227–232.

Thomas, M.B., Reid, A.M., 2007. Are exotic natural enemies an effective way of controlling invasive plants? Trends in Ecology and Evolution 22, 447–453.