GRASSLAND COMMUNITY RESEARCH

Plant Community Response to the Decline of Diffuse Knapweed in a Colorado Grassland

R. T. Bush, T. R. Seastedt and D. Buckner

ABSTRACT

Long-term reductions in invasive plant species are few, and studies documenting the response of plant communities to such reductions are equally rare. We quantified plant species richness and cover during a nine-year period at a grassland site in central Colorado where the introduction of biological control insects reduced the invasive non-native forb diffuse knapweed (*Centaurea diffusa*). This reduction opened up 25 percent of the relative plant cover for other plant species. Based upon repeated inventories of plant species from four transects at the site we found no changes in native or non-native plant species richness. Although we documented a modest increase from 2.4 percent to 8.6 percent in the relative cover of native forbs as knapweed declined, we observed no significant shifts in the relative cover of total native and total non-native vegetation. Two introduced grasses, field brome (*Bromus arvensis [= B. japonicus]*) and intermediate wheatgrass (*Thinopyrum intermedium*) showed significant increases. Native warm- and cool-season grasses at the site were unable to exploit the vacuum left by the decline of the knapweed. We found little evidence of native grassland restoration following the reduction of a non-indigenous, invasive plant. Our findings support the conclusion that the reduction of a regionally abundant, non-native plant species alone is not sufficient to promote restoration of the formerly dominant native plant species, and that further management activities are necessary.

Keywords: Colorado, diffuse knapweed (*Centaurea diffusa*), field brome (*Bromus arvensis*), grassland restoration, intermediate wheatgrass (*Thinopyrum intermedium*), invasive plants, mixed-grass prairie, plant species richness

Our understanding of the ecology of plant invasions has increased dramatically in the last decade (e.g. DiTomaso 2000, Myers and Bazely 2003, Mitchell et al. 2006), but very little is known about what happens when a dominant invasive species is extirpated from a community (Zavaleta et al. 2001, D’Antonio and Meyerson 2002). Current views predict that removal may be insufficient to result in meaningful restoration (Hobbs and Humphries 1995, Smith et al. 2006). Few control efforts have been successful at permanently removing the invaders. Herbicides, while effective mortality agents, often have non-target effects and can alter the plant community so that it does not exhibit a natural progression of restoration or recovery. Further, herbicide effects are usually ephemeral; unless herbicides applications are repeated, the target species either reinvades or emerges from a surviving seed-bank. In contrast, the use of biological control agents to reduce invasive plant species, while not without its own risks, has the potential to reduce the target species for extended periods (perhaps permanently) while minimizing some of these negative side-effects of herbicide use on plant communities. In this study we evaluated plant community response to the decline of an invasive plant as the result of the introduction of biological control agents. Diffuse knapweed (*Centaurea diffusa*) is a biennial member of the Asteraceae from Eurasia that has colonized over a million hectares of rangeland in western North America (DiTomaso 2000). Recently, this plant has decreased in abundance due to biological control insects released over the last thirty years (Seastedt et al. 2003, 2005, Myers 2004, Smith 2004, Story and Coombs 2004). This study evaluates the plant community response to the decline of this dominant species over a nine-year interval, 1997–2005. Through annual and semi-annual inventories, we assessed a) changes in species richness of native and non-native species over time; b) the ability of native forbs to recover and spread into the space vacated by the non-native forb; and c) the ability of native grasses to reassert their historical role as the dominant species at this site.

The Advent of Diffuse Knapweed

Research was conducted on grassland owned by Boulder County near Superior, Colorado. Prior to European settlement, the site was mixed-grass prairie dominated by a mixture of...
both warm- and cool-season plants (Bennett 1997). Average precipitation (1971–2000) for this area is about 51 cm (NOAA 2006). Half of our study area had apparently been plowed and used in small grain production sometime in the early part of the twentieth century, and was then converted to improved pasture of primarily intermediate wheatgrass (*Thinopyrum intermedium*) over 50 years ago. The second half of the site was rangeland that had been heavily grazed by cattle for more than a century until it was purchased by Boulder County in 1997. Grazing ceased between 1997 and 2003. The site was lightly grazed in late spring and early summer of the final two years of our study.

Knapweed invaded this area sometime during the 1980s, and federal and county land managers deemed it sufficiently problematic by 1996 to merit aerial herbicide spraying (Woodall et al. 2000, Luken and Seastedt 2004). The U.S. Department of Energy and Boulder County hired commercial applicators to apply herbicides from helicopters and trucks to grasslands surrounding the research site between 1997 and 2002. Our site was set aside to investigate other forms of knapweed control.

**Research Methods**

Seastedt and personnel of the Colorado Department of Agriculture released a small number of biological control agents, including the seed-head weevil (*Larinus minutus*) and the root weevil (*Cyphocleonus achates*), to feed upon diffuse knapweed at the site in 1997. For each point we recorded plant presence or absence, species identification, and observations of bare soil, standing dead plant matter produced the previous year, litter, or rock (fragments > 1 cm maximum diameter).

We established four permanent 50-meter transects on the insect release site in 1997. We sampled vegetation along each transect every summer from 1997 to 2005, except for 1998, which was not surveyed due to funding limitations. The exact dates of data collection varied among years, and starting in 2001 transects were monitored both in June and again in late August or early September of each year.

Vegetation cover was obtained with a point-intercept procedure. A tripod-mounted optical device with fine crosshairs (reticle) in the eyepiece that defines a 0.07 mm point was used to precisely target vegetation and non-vegetation cover. All species found intercepting this point were identified using a focusing objective lens. We were able to systematically collect data from 200 such projected points along each transect. As per convention with this method (originally beginning with Winkworth and Goodall, 1962) data were taken as interceptions of the projected point with live vegetation, standing dead, litter, or bare soil. We projected points 50 cm to either side of each transect in order to avoid any interference in vegetation growth or composition due to trampling or to the transect tape. We placed the tripod at 50 cm intervals along a 50 m transect, beginning at the 50 cm mark. Hence, with a point projected 50 cm to both sides at each of these 100 tripod placements, a total of 200 points were collected per transect.

For each point we recorded plant presence or absence, species identification, and observations of bare soil, standing dead plant matter produced the previous year, litter, or rock (fragments > 1 cm maximum diameter). We evaluated in terms of both absolute (number of hits of that plant or group of plants per 200 observations) and relative (number of hits of that plant or group divided by total plant hits) plant abundance. We grouped plant species by provenance (native or introduced) and life form: annual/biennial forbs, perennial forbs, annual grasses, perennial cool-season (C3) grasses, warm-season (C4) grasses, and succulent species. There are no introduced warm-season grasses in the area. We measured plant species richness as the number of species found within the area one meter to either side of the 50 m transect. All species observed within this 100 m² area were listed, not just those censused by the point-intercept procedure.

Our analyses involved preparing simple descriptive statistics and evaluating directional trends using linear and stepwise multiple regression. All procedures were conducted using SAS (SAS 1999). Time (year since the start of the study) and annual precipitation were used as independent variables to test for directional patterns as influenced by precipitation. For those years with multiple surveys, we performed analyses on the means of the two surveys so that uneven sampling intensity was not a factor influencing results. As a final analysis, relative cover of the abundant common life forms found at the site (introduced annuals or biennial dicots, introduced annual grasses, introduced perennial grasses, native perennial cool-season grasses, and native perennial warm-season grasses) were compared between the 1997–2001 and the 2002–2005 intervals. Relative covers of these groups were averaged for each transect for each of the two intervals, and a paired t-test was performed to see if the average relative cover differed significantly between these intervals.

**Results**

Absolute plant cover showed a relationship to precipitation, but exhibited substantial variability due to the timing of precipitation and other factors (Figure 1). This region in Colorado experiences a strong, continental climate, with large interannual fluctuations in precipitation. During this study, precipitation ranged from 69 percent to 134 percent of the 1971–2000 average. The study period included the end (as of 1999) of a run...
of years (beginning in 1989) during which precipitation was much above average for nine of the eleven years. The study years 2000 and 2002 were particularly dry (NOAA 2006).

The linear relationship between absolute cover and annual precipitation was not significant (t = 1.10, p = 0.32) but the unusually dry years of 2000 (79 percent of average precipitation) and 2002 (69 percent of average precipitation) did show relatively low plant cover values. A comparison of vegetation cover and the four-month total for spring precipitation (March–June) did produce a significant linear relationship (t = 2.83, p = 0.025). Importantly, rainfall did not exhibit any directional trends during this interval (Figure 1). Hence, while individual species and functional groups show interannual variation in response to precipitation patterns and amounts, we do not believe that this climate pattern would produce consistently increasing or decreasing trends in the abundance of these species.

Absolute diffuse knapweed cover declined over time, and also showed a negative response to precipitation, whereas relative cover of this plant was negatively related only to time (Table 1). By 2005, the relative cover of diffuse knapweed was 4.6 percent, down from 27.8 percent in 1997, and no knapweed intercepted the transects in 2006 (D. Buckner, unpublished data).

Species richness of natives, non-natives, and total species did not change during this study. The average number of species found per transect was 23.3, of which 15.8 were native species and 7.5 were non-native. While no directional trends in richness were noted, one native forb species, dotted blazing star or gayfeather (Liatis punctata), appeared on the site in 2005 for the first time during the study.

The native forbs, including the North American relatives to diffuse knapweed, increased from about 2.4 percent relative cover in 1997 to 8.3 percent in 2005 (Table 1). While exhibiting large interannual variability, the relative abundance of this group was highest in 2005 (Figure 2). Within this group, tarragon (Artemisia dracunculus [= Oligosporus dracunculus]), white heath aster (Symphyotrichum ericoides [= Virgulus ericoides]), trailing fleabane (Erigeron flagellaris), and false goldenaster (Heterotheca villosa) comprised the majority of cover in 2005.

No other group of native flora exhibited a positive directional response during the study interval. The cool-season native grasses, dominated by western wheatgrass (Pascopyrum smithii) and two bluegrass species, Kentucky bluegrass (Poa pratensis) and Canada bluegrass (P. compressa), exhibited a negative absolute cover response to the dry years (Table 1), but showed no directional trend. However, a comparison of relative cover during the early (1997–2001) and later (2002–2005) years shows a significant decline for this group (Figure 3). The warm-season grasses, dominated by blue grama (Bouteloua gracilis), buffalograss (Buchloe dactyloides), and three-awn (Aristida purpurea), showed no directional changes with respect to time or precipitation (Table 1, Figure 3).

The decline in diffuse knapweed was more than compensated for by increases in the relative cover of introduced annual and perennial grasses, and non-native plant species continued to dominate the relative cover at this site. The native perennial grasses, the assumed historical dominant vegetation at this site, did not show an immediate benefit from the demise of the non-native dominant, and the native cool-season species showed a decline in relative abundance (Figure 3). The introduced annual grasses, consisting of two brome species, cheatgrass (Bromus tectorum) and particularly field brome (B. arvensis), increased from 11.5 percent relative cover in 1997 to 21.1 percent relative cover in 2005. This group also significantly increased relative and absolute cover in wet years (Table 1). Similarly, the introduced cool-season intermediate wheatgrass (Thinopyrum intermedium) exhibited a significant increase from 5.2 percent of relative cover in 1997 to 15.7 percent in 2005 (Table 1). Overall, the introduced perennial grasses matched the abundance of the introduced annual grasses and dominated the post-knapweed community (Figure 3).

### Table 1. Directional changes in abundance of life history groups and diffuse knapweed, 1997–2005. The strength of the independent variables (time or annual precipitation) is indicated by the regression coefficient (r²), or multiple regression coefficient (R²) if two variables used; ns indicates p > 0.05.

<table>
<thead>
<tr>
<th>Group/Species</th>
<th>Abundance</th>
<th>Slope of Regression</th>
<th>r² or R²</th>
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<tr>
<td></td>
<td></td>
<td>Time</td>
<td>Precipitation</td>
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<tr>
<td><strong>Forbs</strong></td>
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<td>ns</td>
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<tr>
<td></td>
<td>absolute</td>
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<tr>
<td>Diffuse knapweed</td>
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<td>-4.2</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>absolute</td>
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<td>0.30*</td>
</tr>
<tr>
<td>Native perennials</td>
<td>relative</td>
<td>0.51</td>
<td>ns</td>
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<tr>
<td></td>
<td>absolute</td>
<td>0.30</td>
<td>ns</td>
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<tr>
<td><strong>Grasses</strong></td>
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<tr>
<td></td>
<td>absolute</td>
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<td>0.52</td>
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<td></td>
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* p = 0.053
Implications

While our study lacked an ungrazed control, results observed here have been repeated throughout the Front Range of Colorado (Seastedt, unpublished results) and elsewhere in western North America (Myers 2004, Smith 2004, Story and Coombs 2004). Clearly, the species that benefit from the demise of knapweed at our site would come from the local species pool, and these species may not be common across the large regions now recovering from the diffuse knapweed invasion. Thus, the species-level results reported here may have limited generality. Examining the life forms or life history traits of the species that replaced knapweed may provide more regional-scale generalizations. Are there any clear patterns regarding what species or groups of species benefit when a dominant, tap-rooted member of the Asteraceae is extirpated?

Under the conditions of our study, we found little evidence of native grassland restoration following the reduction of a non-indigenous, invasive plant. While this confirms current thoughts about weed replacement, the fact that this is shown for species with large regional abundances is of concern if the replacement patterns observed here occur throughout that regional distribution. Although native perennial forbs increased in cover (three- to four-fold, from the perspective of this group), species richness was unchanged. Two introduced grasses, one annual and one perennial, were largely responsible for accruing the relative cover formerly represented by knapweed.

The dominant annual grass, field brome, is a winter annual like its close relative, cheatgrass, which has affected large areas further west in North America, especially the Great Basin. Story et al. (2006) reported that when biological control agents produced a significant decline in the abundance of spotted knapweed (Centaurea stoebe [= C. maculosa]), a sibling species of diffuse knapweed that also...
is regionally abundant, cheatgrass significantly increased in response to the decline in spotted knapweed. Thus, the non-native, annual grasses appear to exploit the decline in both species of knapweed.

These cool-season annual grasses should, in theory, not do particularly well in our climate. These species show the ability to exploit wet years (Table 1), and tend to germinate in the fall preceding the year of flowering. From other studies, we recognize these species as among those that exploit human disturbances and high soil nutrient conditions as well (Knapp 1996, Lejeune et al. 2006). During a wet-summer scenario (that is, the climate of the Great Plains), these opportunists are believed to indicate past disturbance and the lack of competing perennial vegetation. Their continuation as a dominant group at our site will likely be determined by future grazing management activities.

The introduced perennial, intermediate wheatgrass, was believed to have been planted at the site when it was converted back to grassland from a small grain field some 60 or more years ago. This domesticated forage species is a strong competitor at most locations where it occurs, and this was true under the conditions presented by the decline of knapweed in our study area. Its success is related to its growth characteristics, which in turn are due to a combination of species and community characteristics (e.g., Daehler 2003, Mitchell et al. 2006).

Historically, warm-season and cool-season grasses co-dominated grasslands along the Colorado Front Range. This contention is supported by soil carbon isotope findings (Sinton et al. 2000) and reports of a historical fire return interval of 7–12 years for this area (Veblen et al. 2000). Efforts that focus on retaining or restoring the historical configuration of these grasslands should identify those mechanisms that favor native C3 and C4 species. Not only have portions of the present study area been replanted and heavily grazed, but also the entire area has been fire-suppressed since the time of European settlement. More recently, increased nitrogen deposition in our region (Baron 2006) is believed to amplify the effects of fire suppression and may also be altering the competitive interactions among plant species (Stevens et al. 2004). Beneficiaries of the demise of knapweed, particularly in the absence of grazing as was the case for much of the study period here, might be expected to include those opportunistic species that do well in the absence of fire, and those species that benefit from relatively high nitrogen conditions. Many cool-season species, which include all of the non-native species in our area, fit these characteristics.

Conclusion

Opportunistic species are able to rapidly establish in the niche spaces created by declines in other species. Post-invasion community dynamics may be best viewed within a successional framework or from the more synthesized viewpoint of vegetation change as a whole (D’Antonio and Meyerson 2002; Davis et al. 2005). Because large-scale successful reductions of aggressive invasive species are still a rarity, there is little precedent for the study of shifts in community composition after the removal of a regionally dominant invasive. However, emerging success using biological control agents to reduce regional dominants, such as leafy spurge (Euphorbia esula) (Hansen et al. 2004) and toadflax (Linaria dalmatica) (Hansen 2004, Nowierski 2004), in addition to the two knapweed species discussed above, suggest that extensive, formerly grass-dominated areas are experiencing changes such as those observed here. Our finding that non-native grasses will replace the non-native forb may be of value to grazing interests, but benefits to conservation and restoration appear minimal.

Evidence from the present study suggests that the elimination of a regionally abundant, aggressive invader alone does not (in the first several years) benefit original native dominant species or native species in general, save for a narrow spectrum of native opportunistic species. If restoration of original ecosystem composition and resistance to invasion is sought, the use of a more proactive approach that includes the addition of selected species during the removal of the target species is necessary. Management procedures to encourage original native dominant C3 and C4 grass species are needed as well.

Acknowledgements

We thank the Boulder County Commissioners and the current and former weed manager of Boulder County for providing the study area and for funding a portion of this effort. Additional support was provided by a USDA National Research Institute Competitive Grant, 01–35320–10628.

References


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