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The relationships among plant cover, density, seed rain, and dispersal of *Bromus tectorum* in high-elevation populations

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THE RELATIONSHIPS AMONG PLANT COVER, DENSITY, SEED RAIN, AND DISPERSAL OF *BROMUS TECTORUM* IN HIGH-ELEVATION POPULATIONS

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ABSTRACT.—The invasive species *Bromus tectorum* L. is recognized as one of the most ecologically and economically devastating weeds in the western United States. Although *B. tectorum* has been studied extensively, few studies have examined its dispersal and spread. We collected data from sites with *B. tectorum* in and around Rocky Mountain National Park to quantify the relationships between plant cover/density and seed rain and dispersal distance. Results suggest that there is a positive relationship between density within a patch and local seed rain and that *B. tectorum* exhibits relatively limited short-distance dispersal (where seeds fell in close proximity to plants and no seeds were found to have dispersed more than 0.1 m from the edge of a patch). These data can inform modelers and managers who are attempting to better understand population dynamics and options for controlling this species.

RESUMEN.—La especie invasora *Bromus tectorum* L. se considera una de las hierbas más devastadoras ecológica y económicamente del oeste de Estados Unidos. Aunque se ha estudiado extensamente, se han hecho pocos estudios sobre su dispersión y distribución. Colectamos datos de sitios donde crecía *B. tectorum* en Rocky Mountain National Park y sus alrededores para cuantificar la relación entre la cobertura y la densidad de plantas, la lluvia de semillas y la distancia de dispersión. Los resultados sugieren que hay una relación positiva entre la densidad dentro de una parcela y la lluvia local de semillas, y que *B. tectorum* exhibe una distancia de dispersión relativamente corta (las semillas caen cerca de las plantas y no encontramos ninguna semilla que se hubiera dispersado a más de 0.1 m del borde de la parcela). Estos datos pueden informar a los modeladores y administradores en su esfuerzo por comprender la dinámica poblacional y las opciones de control para esta especie.

Identifying mechanisms that regulate the spread of invasive species are crucial to both our understanding of species distributions and our ability to control invasions (Hastings et al. 2005). One of the most problematic weeds in North America is the annual grass *Bromus tectorum* L. (cheatgrass, downy brome). While this is a well-studied species (e.g., Hulbert 1955, Mack and Pyke 1983, Rice et al. 1992, Novak and Mack 1993, Beckstead et al. 1996, Meyer et al. 1997, 2004, 2007, Kao et al. 2008), little work has been done to quantify propagule dispersal and to determine the relationship between cheatgrass density and seed rain.

To assess these relationships, we collected data on cheatgrass density and cover, seed rain, and local dispersal. All sampling took place at the upper elevational limit of cheatgrass in the Rocky Mountains of northern Colorado, because this is an area where cheatgrass is actively invading (Kao et al. 2008). Although it has been suggested that the success of cheatgrass depends on local adaptation (Rice and Mack 1991, Meyer et al. 2004), Kao et al. (2008) did not find consistent differences between high- and low-elevation sites. Hence, propagule pressure is likely to play a larger role in the ongoing range expansion than adaptive evolution and is, therefore, the focus of this preliminary analysis.

To establish a method of quantifying the number of individual plants in an area, we determined the relationship between plant density and cover at 6 sites in 2006 (Table 1). Within each site, three 1 × 0.5-m plots (sectioned off into eight 0.25 × 0.25-m quadrats) were located based on a random angle and distance (up to 200 m) from a central point in the cheatgrass patch, with a minimum distance of 5 m between plots. Within each plot, we visually estimated the percent cover (to the nearest 5%) and counted the number of cheatgrass individuals in up to 3 randomly chosen 0.25 × 0.25-m quadrats from the sectioned-off plot (Table 1). Only the plots and quadrats that contained cheatgrass were used for the statistical analysis (for example, due to the small size of site 5, only data from 3

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TABLE 1. Colorado field sites used for density-cover estimates for *Bromus tectorum* in 2006. Sites are listed by latitude and longitude with information on elevation, number of quadrats measured, mean percent cover, mean number of individuals, and *P* value (for the relationship between percent cover and number of individuals across quadrats in each site for the cover-density analysis).

Site	Latitude	Longitude	Quadrats	Elevation (m)	Mean % cover	Mean number of individuals	*P*
1	40.26664°	–103.79773°	9	1321	34.67	79.89	<0.001
2	40.28598°	–103.69603°	7	1321	16.43	73.43	0.004
3	40.43366°	–105.17077°	9	1569	27.22	152.22	<0.001
4	40.24879°	–105.20487°	6	1696	58.33	191.67	<0.001
5	40.45247°	–105.44818°	3	2083	48.33	61.67	0.096
6	39.94975°	–105.51029°	9	2667	6.33	5.33	0.821

quadrats were included; see Table 1 for number of quadrats at each site). Linear regression (SYSTAT 10.2) with site included as a fixed effect was used to analyze the relationship between density and percent cover across 43 quadrats. We modeled a site × cover interaction to independently estimate the effect of percent cover on plant density at each of our sites.

In July 2007, to assess the relationship between plant cover and seed rain, we set up three 10-m transects on each of 10 relatively discrete cheatgrass patches on one hillside site in Rocky Mountain National Park (RMNP; 40.37253°, –105.58369°). Each of the 3 transects were 6 m apart and parallel to each other. The transects were positioned near the edge of the patch such that cheatgrass was dense in the first 5 m and tapered off in the remaining 5 m. At every meter along each transect, we estimated the percent cover of cheatgrass within each 0.25 × 0.25-m quadrat. We also collected all of the loose aboveground soil and litter within each quadrat to obtain an estimate of the seed rain within that quadrat. We took this material to the laboratory, where we sifted it and counted the cheatgrass seeds. At 5 of the cheatgrass patches, we also measured percent cover in the entire 1-m^2 area surrounding the initial 0.25 × 0.25-m quadrat to quantify the effect of scale on the plant cover–seed rain relationship.

For our investigation of dispersal distance, on 11 July 2007, we deployed seed traps that consisted of inverted petri plates with a nail through the middle to secure the plate in the ground. Tangle-Trap™ Insect Trap Coating (Pressurized) (The Tanglefoot Company, Grand Rapids, MI) was used to adhere a piece of filter paper to the bottom of the plate, and after the plate was placed in the ground, the filter paper was covered in Tangle-Trap (Werner 1975). We set up seed traps along 2 perpendicular transects at one discrete patch in RMNP (adjacent to the previous site used to assess the relationship between plant cover and seed rain). Transects ran from 2 m into the middle of the patch to 16 m outside the patch. We then placed traps every 0.1 m from the start of each transect to 2 m outside of the patch. Traps beyond 2 m outside the patch were placed at the following distances along the transects, with increasing number of traps to maintain equal sampling effort with distance from patch: 2.5 m (1 trap), 3 m (1), 3.5 m (1), 4 m (2), 8 m (8), and 16 m (32) (Nathan and Muller-Landau 2000). We visually inspected the site each week to ensure that there were no cheatgrass individuals outside the patch within 20 m of the transects. We counted the seeds caught on the filter paper during 2 separate time periods, 18 July and 25 July, after which we replaced the filter paper and reapplied Tangle-Trap.

These preliminary data collections provide interesting insight into cheatgrass patch characteristics. In 2006, plant cover predicted plant density relatively well across all 6 sites when site was included as a fixed effect ($r^2 = 0.77$, $F_{6,36} = 19.56$, $P < 0.001$). Specifically, plant cover predicted density at 4 of the 6 sites, with a similar though nonsignificant ($P > 0.05$) trend at the fifth site (Table 1; Fig. 1).

There was also a positive relationship between plant cover and seed density in the 0.25 m × 0.25-m quadrats along all 10-m transects from the 10 patches studied in 2007 ($r^2 = 0.53$, $F_{1,326} = 362.82$, $P < 0.001$). To ensure that the spatial scale of the sampled quadrats adequately captured the relationship between plant cover and seed density, we sampled a larger area for a subset of patches (i.e., 5 of the 10). We found that at the 1-m^2 scale, plant cover and seed density was consistently positively correlated ($r^2 = 0.46$, $F_{1,163} = 140.35$, $P < 0.001$). Thus, either of the 2 scales at which the measurements were taken in this study was sufficient to describe the plant cover–seed rain relationship.

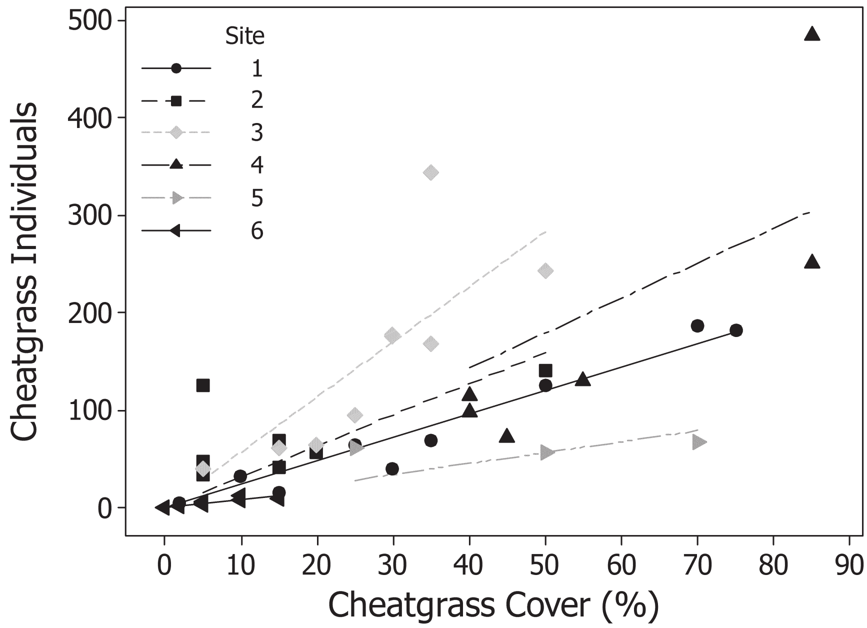

Fig. 1. The number of *Bromus tectorum* individuals by percent cheatgrass cover in each 0.25 × 0.25-m quadrat, separated by site number according to Table 1. All sites except for 5 and 6 showed a significant relationship between cover and number of individuals (see Table 1 for *P* values).

Extending our analysis to include the effect of plant cover and distance from the patch on seed rain, we used model selection (AIC) on a multiple linear regression analysis in SYSTAT 10.2 (www.systat.com). The data presented in Figure 2 show the proportion of seeds collected by patch as a function of quadrat (i.e., distance from location of the innermost point of the transect within the patch [0 m] to the outermost point [10 m]) and the observed percent plant cover. As previously mentioned, plant cover predicts seed density reasonably well ($r^2 = 0.53$, $F_{1,326} = 362.82$, $P < 0.001$, AIC = 1138.36); however, the location of the quadrat (i.e., distance from the beginning of the transect toward the outside of the patch) alone has less explanatory power ($r^2 = 0.18$, $F_{1,326} = 72.86$, $P < 0.001$, AIC = 1216.65). Overall, we found that cover and distance combined do a better job of predicting seed density than either does alone ($r^2 = 0.55$, $F_{2,325} = 202.3$, $P < 0.001$, AIC = 1132.26).

Using 2 different methods (seed traps and collections of loose soil), we found that *B. tectorum* has very limited short-distance dispersal, because no seeds were found in quadrats and traps where plants were absent within 1 m in any direction of the point of collection. Specifically, in terms of the seed trap study, we collected the majority of seeds in traps located within the patch, and we found that no seeds dispersed more than 0.1 m from the edge of the patch. Due to the nature of the variation in the seed trap data (Fig. 3) and the distinction between the inside and outside of the patch (resulting from inspection and the physical removal of all plants beyond the discrete boundary), we used a bilinear regression with a breakpoint at the edge of the patch and found that there is indeed a significant relationship between the number of seeds collected and the location of the seed trap ($r^2 = 0.42$, $F_{1,328} = 44.94$, $P < 0.001$). Mack (1981) noted that due to the morphology of the seed, *B. tectorum* is especially prone to dispersal by animals and inadvertent dispersal by humans, but there is little research that explicitly explores dispersal distance. Given the patchy nature of many populations and the invasion success of this species, it seems likely that long-distance dispersal plays an important role in *Bromus tectorum* invasion dynamics (Mack 1981). Although our dispersal data does not include distances from the patch beyond 16 m, we suggest that it is likely that cheatgrass seed dispersal may be characterized as leptokurtic (most

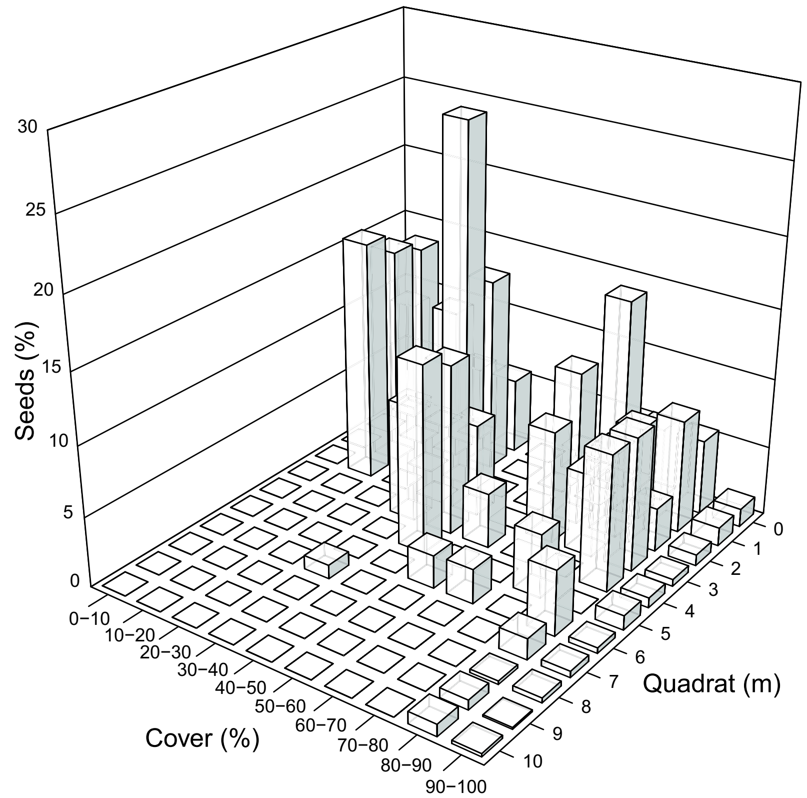

Fig. 2. The percentage of the number of *Bromus tectorum* seeds collected by patch as a function of quadrat (i.e., distance from location of the innermost point of the transect within the patch [0 m] to the outermost point [10 m]) and the observed percent cheatgrass cover.

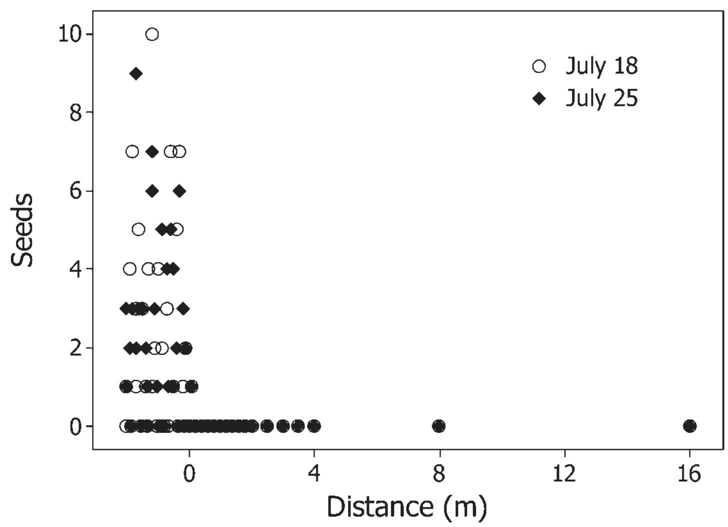

Fig. 3. Number of seeds collected in seed traps by distance from edge of *Bromus tectorum* patch on 2 collection dates in 2007.

seeds falling near the parental plant) with some long-distance dispersal events.

While knowledge of the number of individuals in a population is important in demographic studies, it is nearly impossible to actually measure number of individuals in grass populations. Plant cover is often used as a proxy for number of individuals (Rich et al. 2005), yet the exact relationship between cover and number of individuals is different for each species and can be highly variable, both spatially and temporally. We quantified this relationship for *B. tectorum* across multiple study sites and found that, except for cases where the size of the site was small (e.g., site 5) or the number of plants was few (e.g., site 6), cheatgrass density can be reasonably estimated from plant cover. Although the results are based on a comparatively small data set, sufficient evidence for a linear relationship existed in at least 4 of the 6 sites. These results may suggest a general trend, but further consideration should be applied in a site-specific manner in order to reduce sample error (Greig-Smith 1983).

In addition to being used as a relatively good proxy for the number of cheatgrass individuals, plant cover is also correlated with seed density. Given that most seeds fall under or near the adult plants, our study suggests that the abundance of adults can influence the overall reproductive performance and seed rain in a patch; however, it should be noted that there is high interannual variability in abundance and fecundity of annual plants like *B. tectorum*. As a starting point, in order to slow range expansion, we suggest that land managers prioritize their focus toward eradication of more abundant and aggressive patches in a given year.

As this study is one of the first of its kind for cheatgrass, the primary exploratory goal of our data collection and analyses was to gain a preliminary understanding of cheatgrass patch characteristics. Since it is not easy to quantify larger scale dynamitcs of cheatgrass empirically, to better understand and predict continued growth and spread and provide useful management options, future work should incorporate models that track changes in population density and distribution through time. Future work should incorporate models that track changes in cheatgrass population density and distribution through time. Our field data provide a starting point for recognizing the relevant parameters in modeling population growth and spread; however, further exploration of the role of dispersal modes (local versus long-distance dispersal) is needed. Our field data does not address long-distance dispersal, but models that do include animal and human behavior in seed dispersal (e.g., Westcott et al. 2005, Russo et al. 2006) would help evaluate the relative roles of local- and long-distance dispersal on population spread. For example, if incorporating long-distance dispersal into models does not significantly increase rates of population spread, management should focus on controlling local populations. Alternatively, if long-distance dispersal appears to be important, management efforts should focus on preventing cheatgrass spread through educational programs and by controlling small isolated populations as they appear.

Clearly, more work is needed to fully understand the factors that contribute to rapid growth and spread of this invasive species. Despite this study's limited scope, our results suggest significant relationships between abundance and dispersal that will be useful in modeling and managing the spread of cheatgrass. Even though the predictive capacity of our data can be used only narrowly for landscape-scale inferences and other locations beyond our study sites, our goal was not to exhaustively monitor seed dispersal across various habitats but rather to encourage future work of this kind.

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