Alien Smooth Brome (*Bromus inermis* Leyss.) in a Tallgrass Prairie Remnant: Seed Bank, Seedling Establishment, and Growth Dynamics

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ABSTRACT: The natural diversity of tallgrass prairie remnants in the northern Great Plains of North America is being threatened by alien smooth brome (*Bromus inermis* Leyss.). We report the results of two studies designed to increase our knowledge of the invasion dynamics of this species. Smooth brome seedling establishment in unbroken native tallgrass vegetation did not occur even when conditions for establishment were optimal. The soil at a lowland smooth brome site had finer texture, greater percent water, lower pH, and lower potassium than did the soil at an upland site. Tiller, stem base, and root biomass were greater in smooth brome individuals transplanted into the lowland site than in individuals transplanted into the upland site. Although the total length of rhizomes of individuals was not different between the two sites, rhizome length per tiller was greater at the upland site. This result indicates that the rate of horizontal spread of smooth brome may be greater at upland sites than at lowland sites.

Index terms: alien plant species, Bromus inermis, *invasion dynamics, smooth brome, tallgrass prairie remnants.*

INTRODUCTION

Currently, there is considerable interest in the causes and consequences of alien species invasion into native ecosystems (Mooney and Drake 1986, Drake et al. 1989, D'Antonio and Vitousek 1992). Temperate grassland systems, in particular, appear to be vulnerable to invasion (Mack 1989); in North America, arid grasslands in the Intermountain West and California's Central Valley have been substantially invaded by annual grasses and bunchgrasses of African, European, and South American origin (D'Antonio and Vitousek 1992). Grasslands in central North America are thought to be less vulnerable because native grasses in this region tend to be rhizomatous and sprawling, rather than cespitose (Mack 1989). However, invasion is occurring in these grasslands, especially in the north, where many prairie remnants are being threatened by alien smooth brome (*Bromus inermis* Leyss.) (Becker 1989, Boettcher and Bragg 1989, Wilson 1989, Christiansen 1990, Blankespoor and Larson 1994, Grilz and Romo 1995).

Smooth brome, a cool-season, rhizomatous species introduced from Eurasia in the 1880s (Kennedy 1899), is used as a forage grass and to stabilize roadside banks and ditches. Presently, it is distributed across much of North America, often occurring in nearly monocultural stands in seeded pastures, roadside ditches, railroad right-of-ways, and along fencelines (Elliott 1949).

The pattern of invasion into tallgrass prairie remnants typically involves an advancing smooth brome front at the outside boundary of the remnant and the establishment of expanding islands in the interior (Grilz and Romo 1995, pers. obs.). The width of the advancing front typically varies from one location to another (Christiansen 1990), suggesting that there are site-related differences in invasion dynamics. Rates of invasion by horizontal spreading could be influenced by differences in soil moisture, texture, and chemistry, or in plant community composition.

Little is known about the role seedling establishment plays in the invasion dynamics of smooth brome. Likely, wind-blown soil and soil disturbances by animals and humans provide suitable germination sites for smooth brome seed. Potentially, seedling establishment could also occur in undisturbed prairie, where it could be facilitated by the litter-removing effect of burning, especially if burning was followed by an influx of wind-blown silt and clay.

Here we report on two studies designed to increase our understanding of smooth brome establishment and growth in tallgrass prairie remnants. Information of this sort is required before effective control strategies can be designed and implemented. The two studies and their objectives were as follows:

> *Seed bank and seedling establishment*—The objective of this study was to characterize the smooth brome seed bank at a tallgrass prairie remnant and then to examine how readily smooth brome seedlings become established in unbroken prairie under a variety of germination environments.
>
> *Growth of smooth brome individuals*—The objective of this study was to compare growth characteristics of smooth brome individuals at an upland site and a lowland site. Smooth brome invades both upland and lowland sites in prairie remnants.

METHODS

Seed Bank and Seedling Establishment

We conducted this experiment at Makoce Washte Prairie, a 16-ha tallgrass prairie remnant owned by The Nature Conservancy and located in Minnehaha County, in eastern South Dakota. This remnant, bounded on three sides (north, east, south) by fencerows and on the fourth side (west) by a roadside ditch, shows the typical pattern of smooth brome invasion. Portions of the remnant not invaded by smooth brome are dominated by big bluestem (*Andropogon gerardii* Vit.). Grass species that occur less frequently include Kentucky bluegrass (*Poa pratensis* L.), little bluestem (*Schizachryium scoparium* Michx.), and switchgrass (*Panicum virgatum* L.). Forb species that occur commonly include Missouri goldenrod (*Solidago missouriensis* Nutt.), white sage (*Artemisia ludoviciana* Nutt.), and stiff-leaved sunflower (*Helianthus rigidus* [Cass.] Desf.). Smooth brome rings the remnant in a strip that varies in width from less than 2 m to more than 30 m. Smooth brome appears to grow most vigorously where there are substantial deposits of soil blown in from surrounding agricultural fields, as is the case at the fencerows. Each year smooth brome individuals growing at the fencerows produce large numbers of flowering culms.

We assessed the smooth brome seed bank in litter along nine 50-m transects that began at and were perpendicular to the remnant boundary. Transects originated at the remnant boundary and extended inward from all four sides, two each from the east, south, and west, and three from the north. Transect locations were determined arbitrarily and each transect crossed the smooth brome invasion front at some point. On April 7, 1993, litter material was scraped from a total of fifty-four 0.1-m^2 plots located at 10-m intervals along the transects, beginning at the remnant boundary. Twenty-three of the plots were located in the smooth brome strip and 31 were in "true" prairie ahead of the invasion front. Samples were taken to the laboratory, air dried, and then tested for smooth brome seed germination in germination trays placed in a greenhouse under natural photoperiod. Litter samples were evenly scattered over Perlite and then covered by a thin layer of sterile soil. Germination was monitored daily for three weeks. Smooth brome seedlings were identified by comparing them to seedlings known to be smooth brome and by examining the florets from which seedlings had emerged.

To examine seedling establishment potential in unbroken prairie vegetation, under conditions of burning and no burning and in the presence of added surficial soil, we arbitrarily marked 30 point locations 1–3 m ahead of invading smooth brome fronts where smooth brome apparently was absent. On April 24, 1993, four 0.1-m^2 plots were situated at each of these point locations, oriented in northeast, southeast, southwest, and northwest directions from the point. Each plot was separated from adjacent plots by a distance of 10 cm. Fifteen of the four-plot complexes were located in portions of the prairie that had been burned in May 1992, and 15 were located in portions of the prairie that had not been burned since 1988. The vegetation of each plot was clipped to about 10 cm, and the four plots of each complex were treated as follows: (1) the southeast plot received 150 g of heat-treated, dry silt and clay collected from the soil surface at the prairie perimeter and scattered evenly over the plot; (2) the northeast plot received 1 g of smooth brome seed and then 150 g of heat-treated, dry silt and soil, both scattered evenly over the plot; (3) the southwest plot received 1 g of smooth brome seed; (4) the northwest plot received no smooth brome seed and no soil and acted as a control. Prior to the experiment, smooth brome seed was field-collected in January and tested for viability using the germination test described previously. Five 1-g samples produced an average of 177 ± 4 (SE) seedlings during the 3-week germination period. During the growing season, each plot was monitored monthly for smooth brome germination and then, on October 20, 1993, examined for the purpose of counting smooth brome seedlings.

Growth of Smooth Brome Individuals

We used transplanted smooth brome individuals to examine differences in vegetative growth at an upland site and a lowland site at Makoce Washte Prairie. Both sites were located in flat portions of the smooth brome strip and supported mostly smooth brome vegetation. On April 14, 1993, each of two 5-m x 7-m sites was treated with glyphosate, which killed all potentially competing vegetation. On April 29, 1993, 35 individual smooth brome plants, grown in 1-gallon pots in a greenhouse from field-collected seed, were transplanted to each site. Average tiller numbers for transplanted individuals were 2.46 ± 0.14 (SE) and 2.51 ± 0.10 for the upland and lowland sites, respectively. Individuals were randomly assigned to points in a 5 x 7 grid at the interior of each site. Spacing between individual plants was about 40 cm, leaving a buffer strip of approximately 2 m at the border of each site. At 2-week intervals, during the months of May, June, and July, numbers of tillers and flowering culms were counted for each plant at each site. At the end of the growing season, on October 20, 1993, each of the plants was dug out of the soil and transported to the laboratory. Soil was carefully washed away from the roots and rhizomes and dry weights of aboveground biomass, roots, stem bases, and rhizomes were determined. In addition, the number of tillers was counted and the total length of rhizomes was determined. Soil cores, 1.6 cm in diameter and 30 cm deep, were taken from the centers and corners of each site three times during the growing season and were used to characterize bulk density and to make gravimetric determinations of percent soil moisture. Eighteen additional 30-cm soil cores were taken from scattered locations across each site. Eleven of these cores were used to make hydrometric (American Society for Testing and Materials 1981) determinations of soil texture, and the other seven were sent to the South Dakota State University Soil Testing Laboratory, where pH, soluble salts, percent organic matter, nitrate nitrogen, available phosphorus, and potassium were determined.

Statistical Analysis

We used the Mann-Whitney *U*-test to test for significant differences in mean numbers of germinating seeds in litter samples taken from the smooth brome strip and from the true prairie ahead of the invasion front. We used the repeated measures ANOVA to test for season-long differences in tiller numbers between the upland and lowland sites and used the unpaired, two-tailed Student's *t*-test to test for significant differences between end-of-season means in plant and soil characteristics between the two sites. When assumptions of the *t*-test were not met, we used the Mann-Whitney *U*-test. Percentage data were subjected to arcsine transformation before analysis. Means were considered to be different if $P < 0.05$.

RESULTS AND DISCUSSION

Seed Bank and Seedling Establishment

A total of 147 smooth brome seeds germinated from the fifty-four 0.1-m^2 plots. An average of 132 ± 43 (SE) viable seeds/m^2 of smooth brome occurred at the remnant boundary, 10 ± 6 seeds/m^2 occurred at 10 m into the remnant, and only 2 ± 2 seeds/m^2 occurred at 50 m into the remnant (Figure 1). The litter of the 23 plots in the smooth brome strip had significantly more smooth brome seeds than did the litter of the 31 plots in true prairie ahead of invasion front (smooth brome strip, $\bar{X} = 57 \pm 21$; prairie, $\bar{X} = 6 \pm 2$; $P = 0.0028$). In the prairie portions of the transects, most of the smooth brome seeds occurred in plots close to the invasion front (Table 1). Nine of the 31 true prairie sampling plots had viable smooth brome seeds, averaging 19 ± 5 seeds/m^2.

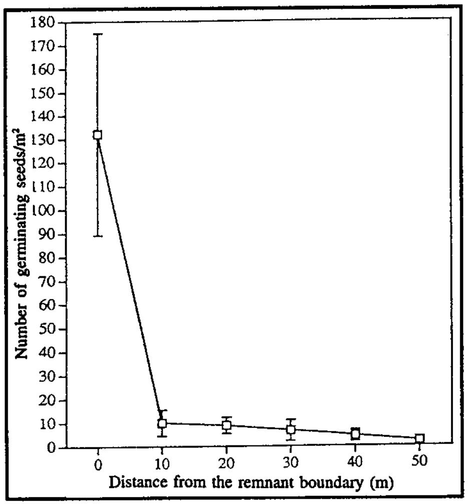

Figure 1. Smooth brome seed bank at Makoce Washte Prairie in relation to distance from the remnant boundary. Data points are of means with standard error bars.

Because most of the smooth brome flowering culms at Makoce Washte Prairie are produced at the remnant boundary, the seed bank profile (Figure 1) demonstrates that smooth brome seed undergoes little horizontal displacement. Even so, seed dispersion dynamics do result in the location of at least some smooth brome seeds ahead of the invasion front, where they could, potentially, germinate and become established as seedlings.

In the seedling establishment experiment, some seed germination was observed but no smooth brome tillers were established from seed. At the end of the growing season, a few of the plots had small numbers of smooth brome tillers, but an examination of underground plant parts revealed that these tillers had grown from previously existing rhizomes. The treatment in which smooth brome seed was added to burned plots and then covered with a layer of soil provided optimal conditions for germination, especially since the growing season was one of the wettest on record (mean May–July precipitation for 1964–1992 at Sioux Falls, South Dakota, 16 km distant from the remnant, was 231 mm; May–July 1993 precipitation was 573 mm; source: U.S. Weather Bureau, Sioux Falls, South Dakota). Although some seeds germinated, apparently the roots of the small brome seedlings were not able to penetrate the thatch or were not able to compete effectively with established plants. A number of workers have previously demonstrated that seedling establishment in unbroken swards of grass vegetation is difficult (Snaydon and Howe 1986, Fowler 1988, McConnaughay and Bazazz 1991, Potvin 1993). Seedling establishment in small gaps produced by animal disturbances is more likely (Laycock 1958, Platt 1975, Foster and Stubbendieck 1980, Huntly and Inouye

Table 1. Number of smooth brome seeds (individuals/m^2) germinating from litter sampled at varying distances ahead of the smooth brome invasion front. N = sample size; $\bar{X}$ = mean; SE = standard error. For smooth brome strip, mean smooth brome seed density = 57 + 21 individuals/m^2.

Distance from Invasion Front (m)[a]	Number of Individuals N	$\bar{X}$	SE
0–10	9	13	5
11–20	9	4	3
21–30	5	0	—
31–40	5	2	2
41–50	3	0	—

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[a] Distance values are given as ranges because locations of sampling plots relative to the the invasion front varied from transect to transect.

1988, Gibson 1989, Hobbs 1991, Benedix and Seastedt 1993). The question of whether or not smooth brome seedlings become established in small disturbance gaps at Makoce Washte Prairie remains to be addressed. Also unknown is whether smooth brome seedling establishment occurs in undisturbed prairie during the fall.

Growth of Smooth Brome Individuals

Twenty-two of 35 individuals transplanted into the lowland site survived to the end of the growing season,while 30 of 35 individuals survived at the upland site. Lower survival in the lowland plants probably was the result of heavy rains early in the growing season, which produced standing water and water-logged soil.

Tillers were produced from transplanted plants throughout the growing season at both lowland and upland sites (Figure 2). Typically, smooth brome shows two episodes of tiller growth, a smaller one in the spring and a larger one after anthesis (Lamp 1952). Apparently, the unusual absence of an extended hot and dry period during the middle of the growing season enabled smooth brome individuals to produce at least some tillers all season long. This response undoubtedly enhances the competitive ability of smooth brome. Season-long tiller numbers were greater at the lowland site than at the upland site (repeated measures ANOVA, $F_{1,50} = 9.61$, $P = 0.0032$). Most of this difference occurred at the end of the growing season (Figure 2; repeated measures ANOVA interaction between site and time during growing season, $F_{6,300} = 13.64$, $P = 0.0001$).

At the end of the growing season, mean total length of rhizomes, weight of all rhizomes, rhizome weight/length, and tiller weight/number of tillers in smooth brome individuals did not differ between the lowland and upland sites (Table 2). The last two variables are measures of individual rhizome thickness and individual tiller size, respectively. However, mean total number of tillers, weight of all tillers, and weight of all roots and stem bases were significantly greater at the lowland site, while mean rhizome length/tiller was significantly greater at the upland site.

Individual smooth brome plants grew more vigorously at the lowland site, as evidenced by the larger number and greater weight of tillers and the greater weight of roots and stem bases (Table 2). However, even though total rhizome length and weight did not differ at the two sites, rhizome length/tiller was greater at the upland site. This is potentially important because tillers regularly are produced along and from the end of rhizomes, and an increase in this ratio may indicate a more rapid rate of horizontal vegetative expansion. Currently, there is much interest in plant species that are able to adapt foraging strategies to the quality and distribution of resources in their environment (Sutherland and Stillman 1988, Campbell et al. 1991). It is possible that smooth brome is another species capable of using different foraging strategies.

Mean soil bulk density, soluble salts, percent organic matter, nitrate nitrogen, and phosphorus did not differ between the lowland and upland sites (Table 3). However, soil texture was significantly finer, percent soil moisture greater, pH higher, and potassium lower at the lowland site. The differences in pH and potassium probably are unimportant, because the difference in pH was small and the concentrations of potassium probably were not limiting. The differences in soil texture and soil moisture are of greater interest. Fine-textured soils are able to store more water, and this water may support plant growth during later times of low rainfall (Barnes and

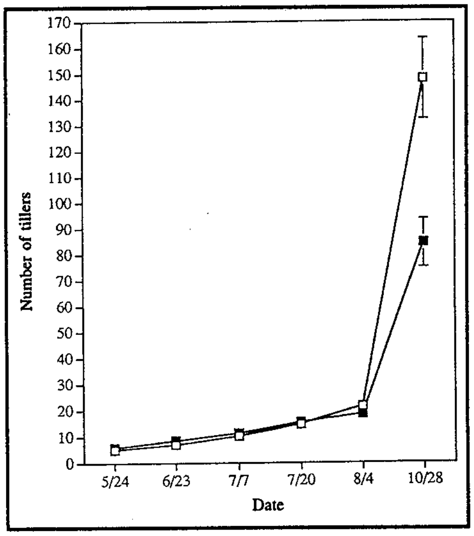

Figure 2. Production of tillers by individual smooth brome plants during the 1993 growing season. Open squares = lowland site, closed squares = upland site. Data points are of means with standard error bars.

Table 2. Characteristics of individual smooth brome plants growing at a lowland site and an upland site. N = 22 for plants growing in the lowland site and N = 30 for plants growing in the upland site.

	Lowland	*Upland*		
Plant Characteristic	$\bar{X}$ ± SE	$\bar{X}$ ± SE	*t*	*P*
No. of tillers	147.9 ± 15.5	84.3 ± 9.3	–3.71	0.0005
Weight of all tillers (g)	10.91 ± 1.23	6.30 ± 0.83	–3.22	0.0022
Tiller weight/ tiller no. (mg/ind.)	73.5 ± 3.6	72.8 ± 4.6	–0.11	0.9134
Wt. of all roots and stem bases (g)	8.36 ± 1.25	3.56 ± 0.44	–4.07	0.0002
Length of all rhizomes (cm)	165.3 ± 21.0	189.1 ± 18.2	0.85	0.3972
Weight of all rhizomes (g)	1.04 ± 0.21	1.18 ± 0.19	0.48	0.6323
Rhizome weight/ rhiz. length (mg/cm)	5.57 ± 0.67	5.68 ± 0.51	0.13	0.8980
Total rhizome length/ tiller no. (cm/ind.)	1.16 ± 0.14	2.52 ± 0.24	4.41	0.0001

Table 3. Soil characteristics at lowland and upland smooth brome transplantation sites.

Soil Characteristic	Lowland $\bar{X} \pm$ SE	Upland $\bar{X} \pm$ SE	N	*t*	*P*
Texture (% silt and clay)	80.0 ± 2.3	67.1 ± 2.5	11	3.77	0.0012
Moisture (% water)	43.7 ± 2.6	31.2 ± 1.4	15	4.28	0.0002
Bulk density (g cm^{-3})	0.58 ± 0.05	0.58 ± 0.09	15	–0.02	0.9134
pH	6.6 ± 0.6	6.2 ± 0.0	7	–5.85	0.0001
Soluble salts (mmhos cm^{-1})	1.04 ± 0.06	0.90 ± 0.07	7	–1.55	0.1473
Organic matter (%)	5.6 ± 0.2	5.5 ± 0.3	7	–0.21	0.8405
Nitrate nitrogen (ppm)	2.39 ± 0.53	1.89 ± 0.46	7	–0.71	0.4914
Phosphorus (ppm)	17.0 ± 1.4	15.1 ± 1.0	7	–1.12	0.2834
Potassium (ppm)	299 ± 18	399 ± 23	7	3.50	0.0044

Harrison 1982). Greater soil moisture may explain, at least in part, the greater vigor of plants at the lowland site (Knapp et al. 1993). Soil moisture and texture, acting separately or interacting in some way, may also have influenced rates of horizontal expansion at the two sites. For example, at the upland site, lower soil moisture may have stimulated rhizome elongation, and coarser soil may have enhanced the ability of rhizomes to penetrate the soil.

CONCLUSIONS

The results of these studies lead to the following conclusions about smooth brome seedling establishment and vegetative growth at Makoce Washte Prairie, Minnehaha County, South Dakota. First, this prairie remnant has a smooth brome seed bank, part of which exists ahead of the invasion front as well. Second, seedling establishment in unbroken true prairie portions of this remnant is probably a rare occurrence. Third, smooth brome individuals grow better (i.e., produce more above- and below-ground biomass) at lowland sites than at upland sites. These differences in growth might be related to differences in soil moisture, soil texture, or both. Fourth, rates of horizontal spread possibly are greater at upland sites than at lowland sites.

It is important to note that these conclusions are preliminary and not necessarily generalizable to tallgrass prairie remnants at other locations. Controlled and replicated studies at several locations are required to confirm these conclusions. Should they be confirmed by other studies, these conclusions will be helpful in designing and implementing effective strategies for controlling smooth brome. For example, knowledge that smooth brome vegetative growth is limited by available soil moisture might lead a manager to schedule burns for dry years.

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