Vegetation Biomass Dynamics and Patterns of Sexual Reproduction in a Northern Mixed-Grass Prairie

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ABSTRACT.—The sustainability of natural grasslands is in large part dependent upon the successful ingress and propagation of alien plant species. We attempted to characterize the propagation potential of the dominant plant species of a southeastern Montana mixed-grass prairie community including two introduced grasses, *Bromus japonicus* and *B. tectorum.* Aboveground standing crops and densities of seeds were estimated on 10 dates between September 1991 and August 1993 and seedling densities were estimated on 21 dates between September 1991 and July 1993. Total aboveground standing crop ranged from about 110 to 340 g m^{-2} and was dominated by three grasses: *Bouteloua gracilis,* a warm-season, perennial; *Pascopyrum smithii,* a cool-season, perennial; and *B. japonicus,* a cool-season, annual grass. Seed production was dominated by *B. japonicus* ($\sim$10,400 seeds m^{-2}). *Bouteloua gracilis* and *P. smithii* seed production was negligible with maximum densities of about 120 and 25 seeds m^{-2}, respectively. Density of seedlings was greatest for *B. japonicus* ($\sim$2100 seedlings m^{-2}), *Festuca octoflora* ($\sim$1100 seedlings m^{-2}), and *Plantago patagonica* ($\sim$350 seedlings m^{-2}). Maximum number of *B. gracilis* seedlings was 25 m^{-2}. No *P. smithii* seedlings were observed during the study. Temporal differences in seedling densities were closely tied to late summer-early fall precipitation patterns. Although community-level seed production and seedling establishment processes were dominated by *B. japonicus,* the overwhelming presence of herbage produced by the two vegetative propagating species, *B. gracilis* and *P. smithii,* casts doubt on a trend in ecological succession toward an annual grass-dominated community.

INTRODUCTION

The indigenous flora of the Great Plains region of North America evolved under widely fluctuating climatic conditions and chronic herbivory (Coupland, 1958; Dix, 1962; Wells, 1970; Milchunas *et al.,* 1988; Lauenroth *et al.,* 1994). Currently, florae in this region are evolving with the additional influence of recently ($<$100 years) introduced alien species. One of the most ubiquitous introduced species is *Bromus japonicus,*[2] a cool-season, annual grass, that has successfully invaded large portions of grazed as well as ungrazed North American Great Plains, mixed-grass prairie (*e.g., see* Whisenant, 1990; Haferkamp *et al.,* 1993; Heitschmidt *et al.,* 1987, 1995).

We know from general observation that *Bromus japonicus* can modify the physiognomy of mixed-grass prairie communities. We know also that the invasion of *Bromus tectorum,* another introduced cool-season, annual grass, has resulted in a successional conversion of many western North America sagebrush-perennial bunchgrass-dominated communities to *B. tectorum*-dominated communities (Mack, 1981; Mack and Pyke, 1984). However, we are uncertain as to the potential of *B. japonicus* to be a keystone species in altering the rate,

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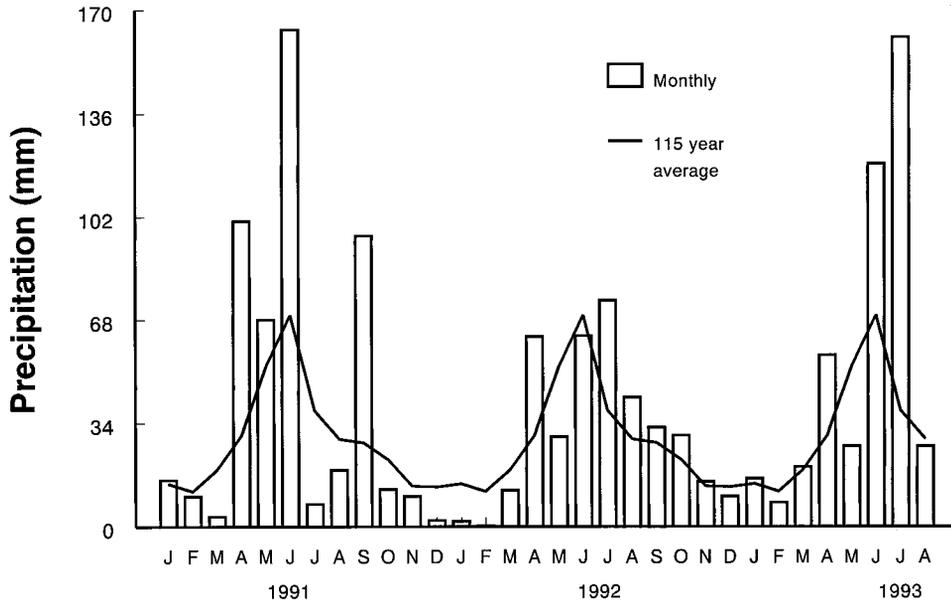
[2] See Table 1 for plant nomenclature authorities.

FIG. 1.—Monthly precipitation (mm) received between January 1991 and August 1993 at Frank Wiley Airfield, located 11 km NNW of study area and average monthly precipitation (mm) for the period 1878–1992 (NOAA, 1994)

direction and extent of ecological succession in the North American mixed-grass prairie region. Such knowledge is critical if we intend to manage these grasslands for long-term sustainability. Thus, our objective in this study was to characterize potential plant propagation processes by quantifying vegetation growth dynamics and sexual reproduction patterns of a northern mixed grass prairie community containing an abundance of *B. japonicus.*

STUDY SITE

The study site was the Fort Keogh Livestock and Range Research Laboratory located near Miles City, Montana (105°50′W, 46°20′N). Regional topography ranges from rolling hills to broken badlands with small intersecting streams flowing intermittently into large permanent rivers located in broad, nearly level valleys. Indigenous vegetation on the 22,500-ha station is a *Bouteloua-Stipa-Agropyron* mixed-grass dominant (Küchler, 1964). Long-term annual precipitation averages 338 mm with about 60% received from April through August (Fig. 1). Daily temperatures occasionally exceed 37 C during summer whereas winter temperatures occasionally dip below −40 C. The average frost-free period is 150 d.

The 3-ha study area was located within a 30-ha livestock grazing exclosure established in 1985. The indigenous plant community was dominated by *Bouteloua gracilis,* a warm-season, perennial grass, and *Pascopyrum smithii,* a cool-season, perennial grass. Other important species were *Bromus japonicus,* a cool-season, annual grass; *Poa secunda,* a cool-season, perennial grass; *Sporobolus cryptandrus,* a warm-season, perennial grass; *Festuca octoflora,* a cool-season, annual grass; *Plantago patagonica,* a cool-season, annual forb; and *Opuntia polyacantha,* a warm-season, succulent. Soils were fine, montmorillonitic Borollic Cambor-

thids of the Kobar series. A-horizon soil texture graded from silty loam to silty clay loam. Slope was <3%.

Methods

Three 0.025 ha (10 by 25 m) sample sites were selected for study from within the 3 ha study area. Site selection was based on a visual assessment of the communities' emulation of a ''typical'' Northern Great Plains indigenous plant community. Each site consisted of 20 proximate, 10-m long transects alternating between a width of 1 m (sample area) and 1.5 m (sample collection access area). Each 1-m wide sample belt was subdivided into ten 1-m^2 plots that were then subdivided into sixteen 625 cm^2 (25 by 25 cm) sample plots. Thirteen of these plots were randomly selected for sampling on each sample date using a centrally placed 100 cm^2 circular ring quadrat. We harvested herbage and seed standing crops on 10 dates between September 1991 and August 1993 and counted seedlings on 21 dates.

Aboveground standing crops were estimated by species by clipping at soil surface and weighing after drying at 60 C for 48 h. Seedling densities were estimated by counting before harvest. Number of seeds was estimated by species in the laboratory after drying. Because we could not discriminate between *Bromus japonicus* and *B. tectorum* seedlings, and because our standing crop data showed *B. japonicus* was the overwhelming dominant *Bromus* species, we considered all *Bromus* seedlings as *B. japonicus*.

Results

Aboveground standing crops.—Seven species of perennial grasses, 1 species of sedge, 4 species of annual grasses, 14 species of forbs, and 3 species of shrubs and succulents contributed to standing crop estimates (Table 1). Total standing crop ranged from about 110 g m^{-2} in late winter to about 380 g m^{-2} in midsummer. Perennial grasses dominated standing crop (Fig. 2) with the two dominant species being *Bouteloua gracilis* and *Pascopyrum smithii* with a combined standing crop of about 210 g m^{-2} in late spring, 1992 and also in midsummer, 1993. The contribution of *B. gracilis* and *P. smithii* to total standing crop ranged from 48% in the spring of 1992 to 79% in late fall, 1992, whereas their contribution to perennial grass standing crop ranged between 84 and 95% in the same interval.

Standing crop of annual grasses ranged from a high of about 41 g m^{-2} in late spring 1992 to 3 g m^{-2} in August 1993 (Fig. 2) and was dominated by *Bromus japonicus* (Table 1). Except during summer 1993 when *B. japonicus* standing crop was near zero, its contribution to total standing crop was relatively constant across dates ranging from 8 to 14%. Standing crop of other annual grasses never exceeded 4 g m^{-2} on any sample date whereas standing crop of forbs never exceeded 8 g m^{-2} except during summer, 1993. Shrub/succulent standing crop was dominated by *Opuntia polyacantha* (Table 1) with only a scattering of *Ceratoides lanata* and *Coryphantha missouriensis*.

Seed production.—Four species of annual grasses, 7 species of perennial grasses, 6 species of forbs and *Opuntia polyacantha* yielded harvestable seed (Table 1). Temporal patterns of seed production, retention and dissemination were similar among species groups (Fig. 3), although absolute seed densities differed. Seed densities peaked in late spring and were dominated by the annual grasses (12,435 m^{-2}) with the dominant species being *Bromus japonicus* (10,430 m^{-2}). Except during summer 1993 when both aboveground standing crop and seed density of *B. japonicus* were low, its contribution to total seed production ranged from 18% (670 m^{-2}) in early winter 1992, to 68% (4530 m^{-2}) in midsummer 1992. Thus, its relative contribution to total seed production was much greater than its 8 to 13% contribution to standing crop. The only other annual grass displaying prolific seed production

TABLE 1.—Range in aboveground standing crop (g m^{-2}), seed density (no. m^{-2}), and seedling density (no. m^{-2}) estimates by plant species. Date is the month/year of maximum value. Standing crops and seed densities were estimated on 10 dates between September 1991 and August 1993 whereas seedling densities were estimated on 21 dates

Species	Standing crop (g m^{-2})		Seed density (no. m^{-2})		Seedling density (no. m^{-2})	
Perennial grasses & sedges						
Bouteloua gracilis (H.B.K.) Lag. ex Griffiths	50–1132;	7/92	0–720;	9/91	0–25;	9/91
Buchloë dactyloides (Nutt.) Engelm	<1–20;	8/93	0–50;	9/91	0	
Carex filifolia Nutt.	0–2;	8/93	0		0	
Hesperostipa comata (Trin. & Rupr.) Barkworth	0–17;	7/92	0–110;	7/92	0–8;	8/92
Pascopyrum smithii (Rydb.) Love	20–94;	8/93	0–25;	9/92	0	
Poa secunda Presl.	<1–10;	6/92	3–3900;	6/92	0–60;	4/93
Schedonnardus paniculatus (Nutt.) Trel.	0–3;	9/92	0–345;	8/93	0–3;	(7 dates)
Sporobolus cryptandrus (Torr.)	0–7;	6/92	0–2340;	1/92	0–3;	7/93
Annual grasses						
Bromus japonicus Thunb.	2–40;	6/92	80–10,430;	6/92	0–2080;	9/91
Bromus tectorum L.	0–<1;	9/92	0–35;	6/92	[3]	
Festuca octoflora Walt.	0–4;	4/92	0–1865;	6/92	0–1090;	3/92
Hordeum pusillum Nutt.	0–<1;	6/92	0–105;	6/92	0–20;	12/91
Forbs						
Androsace occidentalis Pursh	0–<1;	4/92	0		0–205;	2/92
Astragalus sp. L.	0		0		0–3;	7/93
Camelina microcarpa Andre. ex DC.	0		0		0–3;	12/91
Draba reptans (Lam.) Fern.	0–<1;	4/92	0–160;	6/92	0–85;	12/91
Euphorbia glyptosperma Engelm.	0–<1;	9/91	0		0–8;	5/93
Hedeoma hispidum Pursh.	0–<1;	6/92	0–250;	6/92	0–115;	7/93
Helianthus annuus L.	0–2;	12/92	0		0	
Lactuca serriola L.	0–<1;	6/92	0		0–15;	5/92
Linum rigidum Pursh.	0–2;	10/91	0–11;	9/91	0–15;	7/93
Lomatium orientale Coult. & Rose.	0–<1;	12/92	0		0	

TABLE 1.—Continued

| Species	Standing crop (g m^{-2})		Seed density (no. m^{-2})		Seedling density (no. m^{-2})	
Picradeniopsis oppositifolia (Nutt.) Rydb.	0–2;	2/92	0–20;	2/92	0	
Plantago patagonica Jacq.	0–2;	6/92	0–880;	6/92	0–355;	9/91
Polygala alba Nutt.	0–<1;	1/92	0		0	
Salsola iberica Senn. & Pau	0<1;	7/92	0		0–3;	7/92
Sphaeralcea coccinea (Pursh) Rydb.	0–<1;	12/92	0		0	
Taraxacum officinale Weber	0		0		0–8;	7/93
Tragopogon dubius Scop.	0–4;	8/93	0–320;	8/93	0–20;	7/93
Shrubs and succulents						
Ceratoides lanata (Pursh) Howell	0–26;	8/93	0		0	
Coryphantha missouriensis (Sweet) Britt. & Rose.	0–1;	7/92	0		0	
Opuntia polyacantha Haw.	0–75;	7/92	0–295;	7/92	0	

[3] Included in *B. japonicus* estimate. See Methods
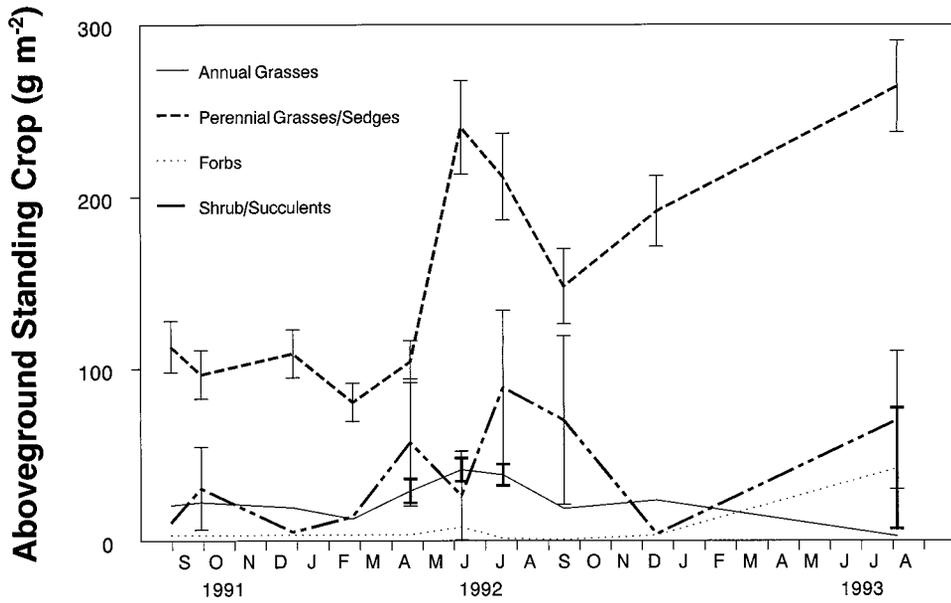
FIG. 2.—Means and standard errors (for means >25) for aboveground standing crops (g m^{-2}) of annual grasses, perennial grasses and sedges, forbs, and shrubs and succulents on 10 dates between September 1991 and August 1993

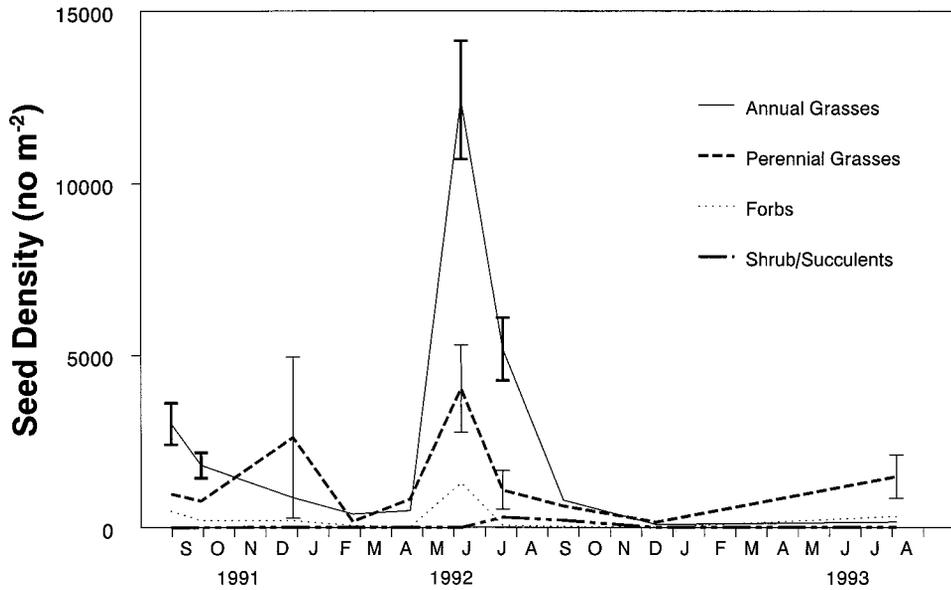FIG. 3.—Means and standard errors (for means >1000) for seed densities (no m^{-2}) of annual grasses, perennial grasses, forbs, and shrubs/succulents on 10 dates between September 1991 and August 1993
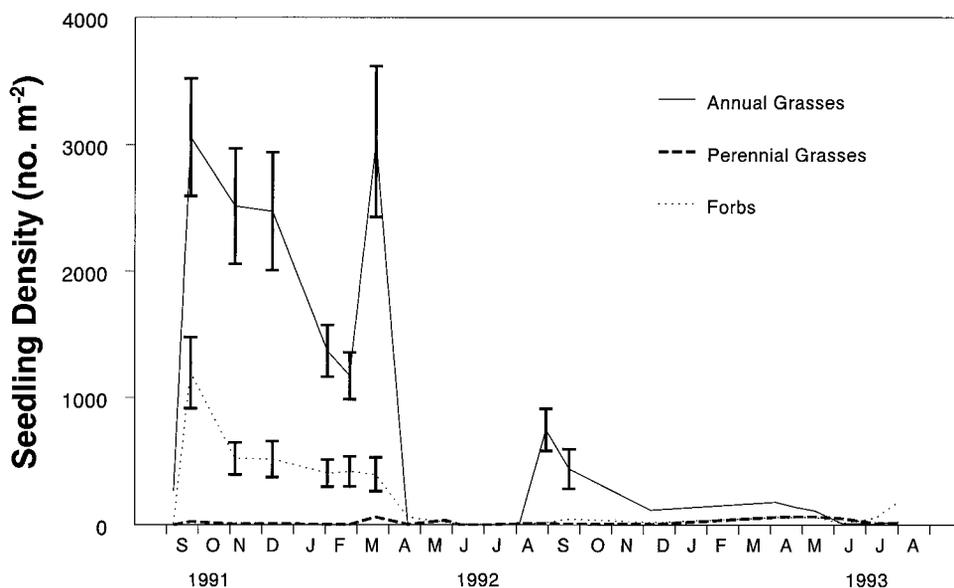
FIG. 4.—Means and standard errors (for means >300) for seedling densities (no m^{-2}) of annual grasses, perennial grasses, and forbs on 21 dates between September 1991 and August 1993

capacity was *Festuca octoflora* with a peak density of 1865 seeds m^{-2} in late spring 1992 (Table 1).

Peak seed density for the perennial grasses was 4020 seeds m^{-2} (Fig. 3). Major contributors were *Poa secunda* (3900 seeds m^{-2}) and *Sporobolus cryptandrus* (2340 seeds m^{-2}) (Table 1). On a relative basis, the two dominant standing crop species, *Bouteloua gracilis* and *Pascopyrum smithii,* contributed considerably less to seed than herbage production as their seed densities never exceeded 120 and 25 seeds m^{-2}, respectively.

Maximum aerial seed density of forbs was 1290 seeds m^{-2} (Fig 3). Dominant species were *Plantago patagonica* (880 seeds m^{-2}), *Hedeoma hispidum* (250 seeds m^{-2}) and *Draba reptans* (160 seeds m^{-2}) (Table 1). Seed densities of several species of forbs were presumably underestimated since their periods of seed rain were very short (*i.e.,* <30 d). *Opuntia polyacantha* was the only shrub/succulent species for which seed densities were estimated with a peak of 295 seeds m^{-2} in July 1992.

Seedling densities.—Five species of perennial grasses, four species of annual grasses and 12 species of forbs contributed to seedling populations (Table 1). Annual grasses were the dominate species (Fig. 4) with *Bromus japonicus* seedling density peaking at 2080 seedlings m^{-2} in late September 1991. *Festuca octoflora* was a subdominant species with seedling density peaking at 1090 seedlings m^{-2} in spring 1992. Dominant forb species were *Plantago patagonica, Hedeoma hispidum, Draba reptans* and *Androsace occidentalis.* Seedling densities of perennial grasses were substantially less than for the annual grasses and forbs. The dominant perennial grass seedlings were *Poa secunda* with 60 seedlings m^{-2} in April 1993. Seedling densities of biennial and perennial forbs were negligible during the study with a cumulative density for *Taraxacum officinale, Tragopogon dubius,* and *Astragalus* sp. of <30 seedlings m^{-2}.

Temporal patterns of seedling emergence were dominated by annual plants (Fig. 4).

Patterns of emergence for annual grasses and forbs were similar between September 1991 and July 1992 although *Bromus japonicus* seedlings emerged about 1 wk earlier than other annual grasses and forbs in 1991. A flush in rates of germination and seedling establishment occurred in late September 1991 following above-normal rainfall (Fig. 1). Seedling densities in late September were 3100 annual grass seedlings m^{-2} and 1200 annual forb seedlings m^{-2}.

Annual plant seedling densities declined greatly between late September 1991 and late February 1992 (Fig. 4). This decline was presumably the result of two factors: (1) cold winter temperatures; and (2) herbivory by larvae of *Grammia blakei,* a moth in the Arctiidae family (identified by D.C. Ferguson, Research Entomologist, United States Department of Agriculture–Agricultural Research Service, Beltsville, Maryland). An apparent second wave of annual grass seedlings was observed between late February and late March 1992. However, close examination revealed only a minor portion of this pulse was from newly emergent seedlings; rather most of the pulse was attributable to regrowth of previously defoliated annual grass plants, particularly *Bromus japonicus* plants. Surprisingly, only a few other annual grasses regrew and no regrowth of annual forb seedlings was observed. The rapid decline in seedling densities from March to April 1992 was caused by maturation of annual seedlings and their concomitant removal from the seedling classification. Seedling densities of perennial grasses during the fall and winter of 1991–1992 did not exceed 30 seedlings m^{-2}. Small populations of *Poa secunda* (51 m^{-2}) and *Bouteloua gracilis* (10 m^{-2}) seedlings were observed in March 1992.

From midspring to midsummer 1992, rates of emergence of both annual and perennial species was quite limited (Fig. 4). Similarly, seedling densities were sharply less in the fall and winter of 1992–1993 than 1991–1992 following a peak annual-grass seedling density in late August of about 750 *Bromus japonicus* seedlings m^{-2}. Although August precipitation was slightly above normal (Fig. 1), intensity of rainfall was low with no single rain >17 mm and no 7 d accumulation >31 mm. Seedling densities in September 1992 were 20, <2, and 3% of densities in September 1991 for *B. japonicus,* other annual-grasses and annual forbs, respectively.

Bromus japonicus seedling densities declined 80% between late summer 1992 and early spring 1993 (Fig. 4). The 1992–1993 population entering anthesis was only about 8% of the 1991–1992 population for *B. japonicus,* 2% for other annual grasses and 13% for annual forbs.

DISCUSSION

The results of this study show that plant species dominance varies in accordance with the variable of assessment. For example, aboveground standing crop was dominated by two perennial grasses, *Bouteloua gracilis* and *Pascopyrum smithii,* whereas seed production and seedling emergence were dominated by the annual grass, *Bromus japonicus.* Other important, subdominant species were: (1) aboveground biomass—*B. japonicus* and *Opuntia polyacantha,* a perennial succulent; (2) seed production—*Poa secunda* and *Sporobolus cryptandrus,* perennial grasses, *Festuca octoflora,* an annual grass and *Plantago patagonica,* an annual forb; and (3) seedling emergence—*Festuca octoflora, Pascopyrum patagonica,* and two annual forbs, *Androsace occidentalis* and *Hedeoma hispida.*

Study data also show that genet production of perennial grasses is meager in comparison with the annual species in this northern mixed-grass prairie community. Still, despite low densities, seedlings of all perennial grass species, except *Buchloë dactyloides* and *Pascopyrum smithii,* were observed. These findings are in general agreement with those of Weaver and Mueller (1942) who reported *B. dactyloides* seedling densities of only 2 m^{-2} in the central

Great Plains with no *P. smithii* seedlings observed. The limited seed production of both *Bouteloua gracilis* and *P. smithii,* the dominant producers of aboveground biomass in this community, is typical for these species regardless of location (Blake, 1935; Branson, 1941; Riegel, 1941; Brown, 1943). However, *B. gracilis* seed production (720 filled caryopses m^{-2}) may have been further suppressed in this study as a result of the high clay content of the study site soils (>20%) as Coffin and Lauenroth (1992) have shown seed production of *B. gracilis* tends to decrease as clay content of surface soils increases. Also, *B. gracilis* seedling morphology has been shown to restrict recruitment (Hyder *et al.,* 1971), especially in low soil temperature and/or low soil water potential environments (Briske and Wilson, 1977, 1978 ; Wilson and Briske, 1979). In the shortgrass prairie region of NE Colorado, it has been shown that *B. gracilis* rarely, if ever, reproduces from seed (McGinnies *et al.,* 1988). Thus, it can be reasoned that *B. gracilis* population dynamics are primarily a function of tiller natality and mortality rates (Hyder *et al.,* 1975). Similarly, asexual regeneration via rhizomes is the primary mode of reproduction for *P. smithii* (Albertson and Weaver, 1944) as seed production is characteristically low and seedling survival rates below average (Mueller and Weaver, 1942). However, Albertson and Weaver (1944) did observe some *P. smithii* seedlings originating from seed located 5 cm beneath Great Plains' wind-blown soil. Interestingly, we found both *B. dactyloides* and *P. smithii* seedlings emerging from incubated seed bank samples collected in these same study sites (pers. obs.) providing evidence of the ability of these species to sexually regenerate.

Field observations of perennial grass seedlings revealed that *Bouteloua gracilis, Hesperostipa comata* and *Schedonnardus paniculatus* seedlings were located generally in gaps in the vegetation characterized by bare mineral soil. This is consistent with previous observations by Blake (1935), Weaver and Mueller (1942), Albertson and Weaver (1944) and Costello (1944). More recently, Aguilera and Lauenroth (1993) have provided experimental evidence that successful sexual regeneration of *B. gracilis* is strongly dependent on the presence of both above- and belowground gaps in vegetation. However, as reported by Fowler (1986), this type of microsite is not the optimum for all perennial grasses and support for this observation was gleaned from our observations that most *Poa secunda* seedlings were located within the canopy area of established perennial grasses.

The time of introduction of *Bromus japonicus* into northern mixed-grass prairie is unclear. Newspaper reports from the Miles City region suggest the presence of annual brome plants (*Bromus* spp.) was first noted along railroads in the late 1930s. However, it seems reasonable to assume that actual introduction was near the end of the 19th century, the same time as the introduction of *Bromus tectorum* into the Great Basin region of the U.S. (Mack, 1981). But regardless of time of introduction, neither *B. japonicus* nor *B. tectorum* appears to have been prevalent in northern mixed-grass prairies before the 1960s (Black *et al.,* 1937; Ellison, 1960; Reed and Peterson, 1961). Evidence from our study and those of Haferkamp *et al.* (1994) and Haferkamp *et al.* (1995), show that seedling emergence of *B. japonicus* can be environmentally constrained, yet the precipitation threshold in late summer-early fall required to induce *Bromus* seedling emergence, is apparently less than that for most indigenous annual grasses and forbs. Thus, we hypothesize that availability of suitable microsites permitting sexual regeneration of perennial grasses in northern mixed-grass prairie has been reduced since the arrival of *B. japonicus*. But we further hypothesize that because *Bouteloua gracilis* and *Pascopyrum smithii,* the dominant producers of aboveground biomass in this study, propagate vegetatively and undoubtedly have long lifespans, these species effectively buffer the impacts of *B. japonicus* on these mixed-grass ecosystems. This is in contrast to the overwhelming successful invasion of *B. tectorum* into Intermountain West of North America. Mack (1981) speculated ''that both long association with herding ungulates

and the prominence of the rhizomatous life form among the Great Plains grasses has played a part in their resistence to alien invasion.'' We believe the results of this study support Mack's hypothesis, and as such, we do not anticipate an ecological shift of northern mixed-grass prairies towards an annual grass dominance.

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