

SEMIARID OLD-FIELD RESTORATION: IS NEIGHBOR CONTROL NEEDED?

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Abstract. Restoration practice suggests that neighbor control is essential in semiarid grasslands, but ecological theory predicts that neighbor effects are relatively small in young fields. We investigated the effectiveness of neighbor control (mowing and herbicide) for establishing native grasses in a recently abandoned field in southwestern Saskatchewan, Canada. We also examined its interactions with common restoration techniques, such as mulching (straw and sawdust) and contrasting sowing methods (drilling, and broadcasting cleaned seeds, cleaning remainders, and native hay). The experiment was repeated over three years to examine the effect of weather. Neighbor control had no effect on establishment and rarely any effect on first-year survival. This contrasted with significant effects of neighbor control on community and ecosystem-level variables (species richness, water, N). The lack of neighbor effects is concordant with theory which predicts low competition intensity from ruderal annuals. Establishment in seeded plots varied two-fold among years in drilled plots and 50-fold in broadcast plots, and it was lowest during a cool, dry summer. Thus, variables beyond human control are a major factor determining restoration success. Overall, broadcasting was as effective as drilling. The highest long-term establishment of native species was produced by broadcasting cleaning remainders. Almost no seedlings emerged from plots supplied with native hay. Straw mulch increased soil moisture and available N, and sawdust decreased N, but neither had any long-term effect on native grasses. Our results suggest that restorations of semiarid old fields should focus less on neighbor control and more on strategies for exploiting suitable years for germination, either by monitoring soil moisture or through repeated seeding.

Key words: *Agropyron cristatum*; *Bouteloua gracilis*; *broadcasting*; *competition*; *drilling*; *grasslands*; *semiarid*; *herbicide*; *mulch*; *prairie restoration*; *precipitation*; *Saskatchewan, Canada*; *species richness*; *temporal variability*.

INTRODUCTION

An axiom of grassland restoration is that neighboring vegetation must be controlled to allow the establishment of native grasses. This assertion appears to be well supported in the case of introduced perennial neighbors (Jordan 1988, Roundy and Call 1988, Wilson and Gerry 1995, Bakker et al. 1997, 2003), which have been called the greatest challenge to restoration success (Duebber et al. 1981). The case for annual neighbors dominating early successional old fields, however, may be different. Basic ecological theory (Grime 1979) predicts that the intensity of competition increases with field age. Competitive effects on grass seedlings are

modest in young fields (Wilson 1999). Annual companion crops typically have little effect on the performance of agricultural perennials such as alfalfa (Waddington and Malik 1987), and early successional annuals disappeared from a tallgrass prairie restoration after three years (Baer et al. 2003). Neighbor control by hand weeding or dicot-specific herbicides significantly improved perennial grass establishment in two restorations (Cox and McCarty 1958, Bovey et al. 1986). In a two-year experiment, however, the benefit of controlling annual neighbors disappeared by the second growing season (King et al. 1989). In another study, neighbor control improved the establishment of one native grass (*Andropogon gerardii*) but not another (*Calamovilfa longifolia*, Masters et al. 1990). Thus, theory and measurements of competition intensity suggest that neighbor control in annual neighborhoods will have little positive effect, but restoration studies provide mixed results. Here we report the results of a four-year experiment designed to test the influence of neighbor control on native grass establishment and survivorship in a semiarid old field. We also examined how the effectiveness of neighbor control varied with other common restoration techniques, such as seeding method, native hay addition, and mulching.

Manuscript received 11 September 2002; revised 13 June 2003; accepted 18 June 2003; final version received 18 July 2003.
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There is considerable discussion about the best method of sowing seeds in semiarid restorations. Management guidelines favor drilling over broadcasting (Hyder et al. 1975), but reviews show that each method is superior in certain cases (Duebber et al. 1981, Wilson 2002), with the advantage over the long term varying among years (Newman and Redente 2001, Bakker et al. 2003). Survivorship, however, in one semi-arid restoration was consistently higher in broadcast than drilled plots (Bakker et al. 2003), probably because seedlings in drilled plots were crowded into lines and suffered more intense intraspecific competition. Broadcasting also allows the emergence of plant-induced heterogeneity within the community (Coffin et al. 1996). Our second objective was to compare the effects of drilling and broadcasting on establishment and survivorship of native grass seedlings.

Any seed mix is unlikely to represent the full diversity and composition of the natural seed rain, and will also lack other parts of the community such as insects, fungi, and monerans. This problem could be overcome by adding native hay instead of cleaned seeds (Bakker and Berendse 1999). Native hay has received little attention relative to using cleaned seeds (Wilson 2002), so our third goal was to examine the effectiveness of native hay addition.

Another widespread practice that has produced mixed results is the use of mulch. Mulch may promote restoration by increasing soil moisture and seedling establishment (Jacoby 1969). Mulch may also serve as a carbon source for bacteria, allowing them to immobilize nutrients such as nitrogen, and more quickly return disturbed, nutrient-rich soil to predisturbance conditions with lower nutrient availability (Wilson and Gerry 1995, Morghan and Seastedt 1999, Török et al. 2000, Baer et al. 2003). Our fourth objective was to test the ability of mulch to promote restoration.

Lastly, the great among-year variability of rainfall in semiarid ecosystems (Knapp and Smith 2001) suggests that restoration success will vary among years. For example the establishment of native seedlings from seed sown at the same density for three years in southern Saskatchewan varied four-fold among years (Bakker et al. 2003). The establishment of the dominant grass *Bouteloua gracilis* is especially sensitive to drought because of its dependence on adventitious roots (Wilson and Briske 1979a, b). As a result some years will be more suitable for restoration than others, echoing Westoby et al.'s (1989) call for grassland managers to exploit temporal windows of opportunity. Variable rainfall creates other restoration problems: precipitation in our region occurs primarily as storms (James et al. 2003), resulting in runoff and erosion, and the sensitivity of grassland productivity to precipitation (Sala et al. 1988) results in variable and unreliable production of seeds among years. The last of our goals was to examine among-year variation in establishment and survival, and to explore whether the efficacy of

other practices, such as neighbor control, seeding method, and mulch, also varied among years.

In summary, we examined the influence of neighbor control, seeding method, and mulch on the establishment and survival of native grass seedlings in each of three years in an early successional semiarid old field.

METHODS

We worked in Grasslands National Park (49°11' N, 107°43' W), about 140 km south of Swift Current, Saskatchewan, Canada. The natural vegetation of the region is mixed-grass prairie dominated by blue grama (*Bouteloua gracilis*), needle-and-thread grass (*Stipa comata*), and spikemoss (*Selaginella densa*; Christian and Wilson 1999). Long-term (30-year) weather data from the nearest meteorological station (Val Marie, 10 km southeast; Environment Canada, unpublished data) showed that annual precipitation was 313 mm, with almost half falling during May–July. Mean monthly temperatures range from –13°C in January to 19°C in July. During our study, temperature during the peak of seedling establishment (May–July) was significantly ($P < 0.05$, t tests) higher in 1994 (15.8°C) and 1997 (16.0°C) than the 30-year mean (15.0°C). Total precipitation during May–July was significantly different from the 30-year mean (149 mm) in 1995, 1996, and 1997 (212, 128, and 78 mm, respectively).

Our field (78 ha, Appendix A) was dominated by the annuals *Kochia scoparia*, *Erigeron canadensis*, and *Lactuca scariola* at the start of the study. The field faces north with a 5° slope and has chernozemic loam to clay loam soils (Agriculture Canada 1992). Aerial photographs show that it was under cultivation in 1955 and in 1982 (M. Hansen, personal communication), and it was presumably cultivated during that period. Cultivation stopped about 1984 (K. Foster, personal communication).

Experimental design

We established 240 plots (each 3 × 10 m, separated by 1-m corridors) and one-third of them were randomly assigned to each of three seeding years (1994, 1995, 1996) to examine the effect of seeding year on restoration success. Plots were sampled for dependent variables during the year they were seeded and annually thereafter until 1997.

The experiment was a complete factorial design with seeding method (none, broadcast, drilled, native hay), and neighbor control (applied or not) as main factors, for a total of eight treatment combinations in each of three years. Each treatment combination was randomly assigned to each of ten replicate plots in 1995 and 1996. In 1994 there were five replicates of each treatment, and another five replicates of each treatment were assigned to an additional treatment (mulch).

Seeding times (late May), rates, and mixes (Table 1) were identical for broadcast and drilled plots. The seed mix was dominated by *Bouteloua gracilis*, reflecting

TABLE 1. Seeding rates of native grasses seeded in three years.

Species	1994		1995		1996	
	kg/ha	seeds/m ²	kg/ha	seeds/m ²	kg/ha	seeds/m ²
<i>Bouteloua gracilis</i>	23.4	3670	23.4	3670	23.4	3670
<i>Stipa comata</i>	5.3	130	8.4	210	5.9	150
<i>Koeleria cristata</i>	4.4	1910	0		0	
<i>Agropyron dasystachyum</i>	0		7.6	250	4.5	150
<i>Agropyron smithii</i>	0		7.7	190	6.2	150
Total	33.1	5710	47.1	4320	40.0	4120

Note: Values reported are kilograms of pure live seed per hectare (kg/ha) and pure live seeds per square meter (seeds/m²).

its relative abundance in native vegetation (Christian and Wilson 1999). Other species varied in abundance among years according to the availability of seed, so the total number of seeds varied among years (Table 1). The only species that germinated in any numbers, however, was *B. gracilis* (see *Results*), which was sown at identical rates among years. Seed was obtained from the closest commercial source (Enviroscapes, Lethbridge, Alberta, Canada) and had been collected the year before. Plots broadcast with seed were lightly tilled immediately before broadcasting to improve contact between seed and soil. Seed was drilled 1 cm deep in rows 30 cm apart.

Native hay was collected from undisturbed prairie a few km from the site using a rear-bagging lawn mower and applied at 200 g/m², an amount similar to the average standing crop of native grassland. Hay gathered in August 1994 was immediately scattered on plots designated to be seeded in 1995, and hay gathered in August 1995 was immediately scattered on plots designated to be seeded in 1996. This allowed seed stratification in situ and snow melt to bring the hay into contact with the soil, ensuring that seeds in hay would be in place for germination in the appropriate year. Native hay was unavailable in 1994, the first year of the experiment, so cleaning remainders were scattered at 180 g/m², the highest rate possible with the amount of remainders available. Cleaning remainders comprised material remaining after native hay was processed to collect seed of *Stipa comata*, and were expected to be rich in seeds of other prairie species.

Plots receiving neighbor control were treated each year, starting in the year they were seeded. In 1994, plots were mowed in June and again in July. Biomass was removed from the plots. In subsequent years plots were sprayed with herbicide. We switched from mowing to herbicide because preliminary analyses showed that mowing had no effect on unwanted species or on native seedling establishment (Christian 1996) and we wanted to know whether herbicide was effective. We sprayed Killlex (95 g/L 2,4-D, 50 g/L mecoprop (d-isomer), 9 g/L dicamba), a dicot-specific herbicide, at 27 L/ha in July 1995, and 12 L/ha in June 1996 and 1997. Almost all unwanted species at the start of the study were dicots. We used high rates in 1995 to ensure

control, and lower rates in later years after we observed effective control in 1995. Thus, control methods varied among years, allowing us to compare treated and control plots in each year, but not allowing direct comparisons of control methods.

Mulch was an additional factor applied as a main effect in the 1994 seeding year, and as a split-plot factor in the 1996 seeding year. In May 1994, a 1:16 mix of flax and wheat straw was shredded and spread at 200 g/m². In May 1995, an additional 400 g/m² of shredded wheat straw was applied to 2 × 2-m subplots within the plots mulched in 1994. Mulch type varied according to availability. Following the second mulch application, all subsequent measurements of dependent variables were taken from within the subplots. In May 1996, sawdust (from white spruce, *Picea glauca*) was applied at 1000 g/m² to 3 × 5-m subplots in plots broadcast with seed and treated with herbicide starting in 1996. Sawdust was spread prior to tilling and broadcasting. The quantity and C:N ratio of mulch were increased over time because initial results showed little effect.

In each of the three years in which seeds were sown, we counted seedlings in late June to determine establishment and in August of the same year to determine survivorship. Seedlings were counted within transects (3 m long) running across plots. Transect numbers and widths varied with seedling density, between three 20 cm wide transects in cases where seedlings were sparse, and five 5 cm wide transects where seedlings were abundant. In all cases density was expressed on a square-meter basis. Long-term seedling changes in plots seeded in 1994 and 1995 were followed by annual sampling in June and August until 1997.

Species composition was assessed annually in August in three quadrats (0.5 × 1 m) along the diagonal of each plot. The proportion of each quadrat occupied by each species was determined using Daubenmire's (1959) scale, with the use of an additional class (0–1%).

Standing crop was sampled annually in August in three quadrats (0.1 × 1 m) arrayed along the diagonal of each plot. Samples from each plot were pooled and frozen until drying and weighing. Root mass was sampled annually in two soil cores (2 cm diameter, 10 cm

deep) per quadrat. Root samples from each plot were pooled and frozen until washing, drying, and weighing. We washed roots by hand using a sieve and running water. All roots were collected, and leaves and stems were discarded.

Soil moisture and available N (sum of ammonium and nitrate) were sampled annually in May and August. Five soil cores (2 cm diameter, 10 cm deep) were taken from each plot, one near each corner and one from the center, and pooled. Gravimetric soil moisture was calculated by weighing a subsample, drying it to constant mass, and reweighing it. Soil moisture was calculated as a percentage of wet mass. Available N was extracted using a 0.02 M KCl solution. The KCl solution was then decanted and frozen until analysis with an ion-selective electrode (Orion, Boston, Massachusetts, USA).

Proportional data were square-root or arcsine square-root transformed prior to analysis, and other data were log transformed. For each year we performed a two-way ANOVA with seeding method and herbicide as main effects. For analysis of establishment and survivorship, we included only two seeding methods (broadcast and drilling) in ANOVAs because the other two methods (unseeded controls and native hay) produced almost no seedlings. Including the latter methods would violate the assumptions of ANOVA because almost all the values were 0, which precludes the estimate of variance needed for the analysis.

Plots seeded in 1994 had a third treatment, straw mulch, included as a main effect in the analysis. Sawdust mulch was applied in 1996 to subplots in plots that were broadcast seeded and treated with herbicide; the effect of sawdust was tested by comparing mulched and unmulched subplots in the same plots using one-way ANOVA. Statistical analyses were conducted using JMP (version 3.0.2, SAS Institute, Cary, North Carolina, USA) and NCSS (version 6.0.22, NCSS, Kaysville, Utah, USA) software.

Results for establishment are from June of the seeding year, and results for survivorship are from August of the same year. Results for other variables (species covers and richness, standing crop, soil moisture, available nitrogen) are reported from the end of the second growing season after seeding, as this was the longest time span common to all three seeding years.

RESULTS

Establishment and survival

Seedlings of all species sown were found, but we considered all species together because almost all were *Bouteloua gracilis* (e.g., 99% in 1994). The seeding rate for all species combined varied among years, but because almost all established individuals were *B. gracilis*, which was sown at the same rate each year (Table 1), among-year comparisons are possible. In general, seedlings of native species were found only

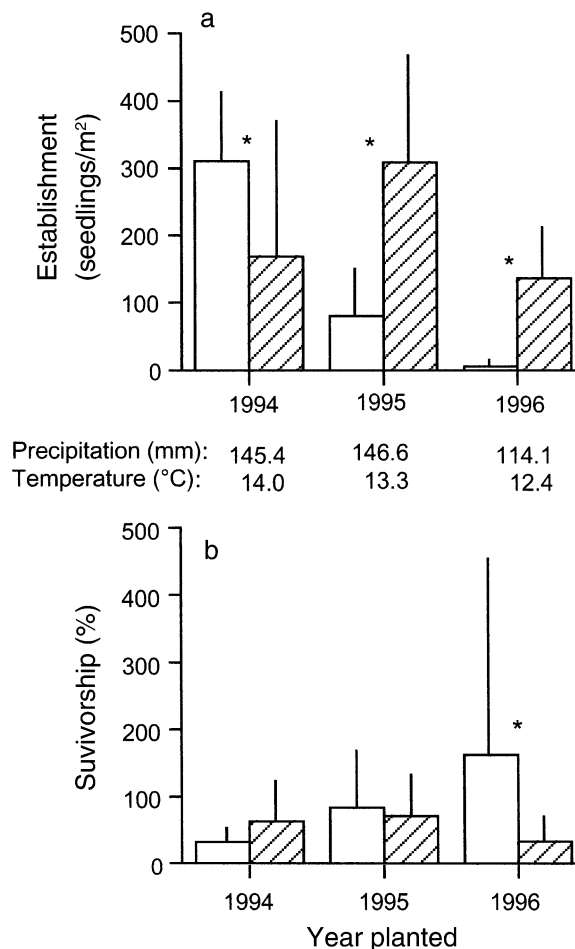


FIG. 1. Mean (+1 SD) (a) establishment and (b) survivorship of seedlings of native grasses broadcast (open bars) or drilled (hatched bars) in each of three years. Data shown are averaged over other treatments. Survivorship values >100% indicate new establishment. Asterisks indicate significant differences ($P < 0.05$) between broadcast and drilled treatments. Precipitation data are totals for May and June each year. Temperature data are means for the same period.

in plots supplied with seeds by broadcasting or drilling. The maximum density of native seedlings in plots not supplied with seeds was <1 seedling/m².

Establishment did not vary significantly ($P < 0.05$) with neighbor control, either as a main effect or as an interaction with another factor, in any year (Appendix B). Establishment was significantly higher in broadcast than drilled plots sown in 1994, but significantly higher in drilled than broadcast plots in 1995 and 1996 (Fig. 1a, Appendix B). Differences between broadcasting and drilling in their effects on establishment persisted for at least three years: plots sown in 1994 continued to have a higher mean density of native seedlings in the broadcast treatment, whereas plots sown in 1995 continued to have higher densities in the drilled treatment (Fig. 2).

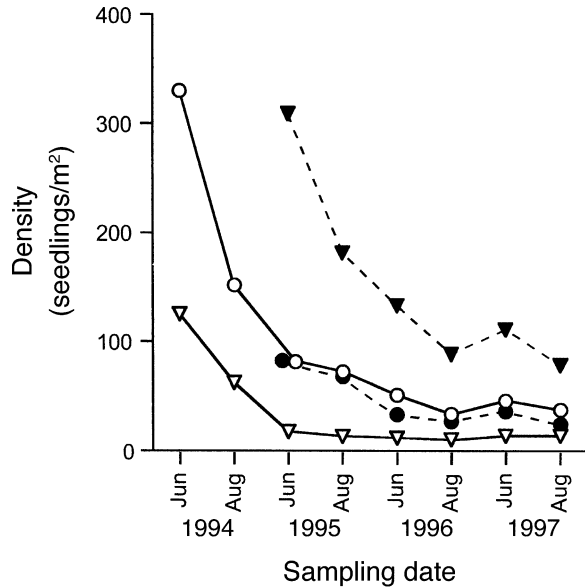


FIG. 2. Density of native grass seedlings in plots seeded in 1994 (open symbols) or 1995 (closed symbols), either by broadcasting (circles) or drilling (triangles). Differences between broadcasting and drilling were significant ($P < 0.05$) on every sampling date.

Establishment did not vary significantly with mulch in any year (Appendix B). Establishment varied greatly among years, 50-fold in broadcast plots and two-fold in drilled plots (Fig. 1a). Establishment was lowest in 1996, the coolest and driest of the three years (Fig. 1a).

Survivorship was not affected by neighbor control in plots sown in 1994 or 1995, but neighbor control significantly improved survivorship in 1996 plots (Appendix B). A significant interaction between seeding method and neighbor control occurred because neighbor control significantly increased survivorship in broadcast plots (no control, 0.14%; control, 2.22%) but not in drilled plots (no control, 0.37%; control, 0.31%).

Survivorship did not vary significantly between seeding treatments in 1994 or 1995, but was significantly higher in broadcast than drilled plots in 1996 (Fig. 1b, Appendix B). Mulch had no main effect on survivorship in any year, but in 1994 plots there was a significant interaction between mulch and seed method because mulch increased survivorship in broadcast plots (no mulch, 32.3%; mulch, 69.5%) but decreased survivorship in drilled plots (no mulch, 62.9%; mulch, 37.9%).

Cleaning remainders produced the highest densities of native grasses. The addition of remainders in 1994 produced higher densities four years after seeding (68 seedlings/m² averaged over other treatments) than either broadcasting (33 seedlings/m²) or drilling (15 seedlings/m²). In contrast, the maximum density of native seedlings in plots supplied with native hay in 1995 and 1996 was <1 seedling/m².

Species composition

The total cover of nonnative species at the end of the second growing season (the longest period with data available for all three planting years) was reduced by neighbor control every year, but significantly so only in plots seeded in 1994 and 1995 (Fig. 3a, Appendix C). The cover of nonnative species did not vary significantly with any other factor in any year (Appendix C).

The total cover of native species at the end of the second growing season was not affected significantly by neighbor control for any planting year (Appendix C). Native species cover was significantly increased by seed addition in plots sown in 1994 and 1995 (Appendix C, data not shown). In 1994 plots, broadcast plots had significantly higher cover of native species than did unseeded plots, and drilled plots were intermediate. In 1995 plots, however, native cover was significantly higher in drilled plots, and did not vary between unseeded and broadcast plots. Native cover was not affected significantly by mulch (Appendix C).

Annual monitoring of untreated plots established in 1994 revealed that the total cover of annuals dropped

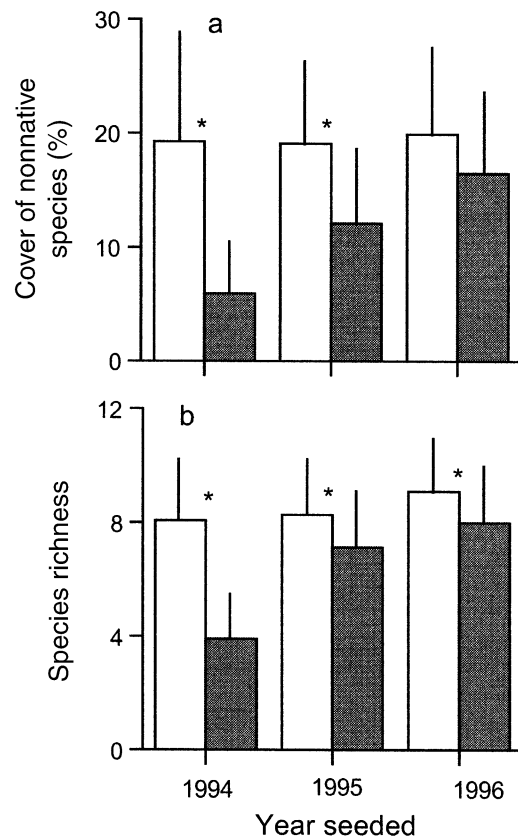


FIG. 3. Mean (+1 SD) cover of (a) nonnative species and (b) species richness in untreated plots (open bars) and plots in which neighbors were controlled for two growing seasons (shaded bars). Asterisks indicate significant differences ($P < 0.05$) between treatments.

sharply after the first year of the experiment as species such as *Kochia scoparia* and *Erigeron canadensis* declined. Perennials, mostly alien species such *Taraxacum officinale*, increased steadily. The nonnative perennial grass *Agropyron cristatum* accounted for almost 25% of the total cover by 1997.

Species richness at the end of the second growing season was decreased significantly by neighbor control each year (Fig. 3b, Appendix C). Richness was increased, however, by seed addition each year (Appendix C, *data not shown*). Richness did not vary with any other factor or interaction.

Standing crop and roots

Standing crop at the end of the second growing season was reduced by neighbor control only in plots sown in 1994 (Appendix D). Examination of each year's data, however, revealed that the effect of neighbor control on standing crop changed from significantly negative to significantly positive over the period 1994–1997 (F values for the effect of neighbor control for each year: 118.08, 34.14, 0.77, 4.25 [df for each year were 1 and 48]; *data not shown*). The same pattern was found for plots sown in 1995, the other planting year for which at least three years of data were available. Standing crop was not affected by mulch in any year (Appendix D).

Seeding method did not affect standing crop for plots seeded in 1995, but had significant and opposite effects on plots seeded in 1994 and 1996. In 1994 plots, standing crop was significantly lower in broadcast (44.1 g/m²; Appendix D) than drilled plots (87.2 g/m²), and control plots were intermediate between these two treatments (72.4 g/m²). In 1996 plots, standing crop was significantly higher in broadcast (99.9 g/m²) than either drilled (93.8 g/m²) or control plots (90.0 g/m²).

Root mass in plots seeded in 1994 (at the end of the second growing season) was significantly decreased by neighbor control (no control, 668.9 g/m²; control, 540.1 g/m²) and mulch (unmulched, 668.6 g/m²; mulched, 540.4 g/m²; Appendix D), but was unaffected by seeding. Root mass in plots seeded in 1995 did not vary with any factor. Plots started in 1996 had root mass significantly increased by seeding (unseeded, 682.0 g/m²; broadcast, 989.2 g/m²; drilled, 706.7 g/m²; Appendix D).

Soil resources

Soil moisture at the end of the second growing season in plots sown in 1994 was increased significantly by both neighbor control and straw mulch (Appendix E). A significant interaction occurred between these factors because neighbor control significantly increased soil moisture in mulched plots (no control, 13.0%; control, 16.5%), but not in plots without mulch (no control, 12.9%; control, 13.8%). In other words, neither neighbor control or mulch alone influenced soil moisture, but both working together increased moisture signifi-

cantly. Soil moisture in 1994 plots was unaffected by seeding (Appendix E).

Soil moisture in plots sown in 1995 and 1996 was unaffected by neighbor control and mulch, but varied significantly among seeding methods (Appendix E). Pairwise comparisons showed that, for plots sown in 1995, soil moisture was significantly lower in both broadcast (5.8%) and drilled (5.9%) plots than in control plots (6.5%). In plots sown in 1996, soil moisture was significantly lower in broadcast (5.2%) than control plots (6.2%), and drilled plots were intermediate between these two treatments (5.8%).

Available N at the end of the second growing season was significantly increased by neighbor control for plots sown in 1994 (no control, 0.63 mg N/kg soil; control, 2.47 mg N/kg soil) and 1995 (no control, 1.24 mg N/kg soil; control, 2.43 mg N/kg soil; Appendix E), but not for plots sown in 1996.

Straw mulch slightly but significantly increased available N (Appendix E; unmulched, 1.17 mg N/kg soil; mulched, 1.38 mg N/kg soil, averaged across other treatments in plots sown in 1994). In contrast, sawdust mulch significantly decreased N (unmulched, 2.85 mg N/kg soil; mulched, 1.53 mg N/kg soil; Appendix E).

Available N varied among seeding treatments only for 1996 plots. Pairwise comparisons showed that N was significantly higher in broadcast plots (2.45 mg N/kg soil) than in drilled (1.12 mg N/kg soil) or control plots (0.94 mg N/kg soil; Appendix E).

DISCUSSION

Neighbor control had no effect on establishment in any of the three years examined. Further, there were no significant interactions between neighbor control and other experimental factors (Appendix B). The similarity of results among years and the absence of interactions suggest that the absence of control effects can be expected to vary little with environment. Similarly, neighbor control had no effect on survivorship, except for a very small improvement in one seeding treatment in one year.

A lack of response to neighbor control was not caused by failure to suppress neighbors: the cover of nonnative species was decreased by neighbor control in every year (Fig. 3). Standing crop and root mass were significantly reduced by neighbor control in 1994 plots, soil moisture and available nitrogen were significantly increased by neighbor control in 1994 plots, and available nitrogen was also increased by neighbor control in 1995 plots. Species richness was significantly reduced by neighbor control in every year (Fig. 3), reflecting the loss of weedy species from the vegetation.

The reason for the difference between establishment and vegetation responses to neighbor control probably lies in timing. Both mowing in 1994 and spraying herbicide in 1995 and 1996 affected established annuals. These individuals may already have exerted some com-

petitive suppression on the sown native grasses, so treating them after establishment had little benefit. Pre-emergence control, which suppresses weed seedling establishment, is widely used in agriculture (Vleeshouwers and Kropff 2000), and might be effective in restoration. On the other hand, our results are consistent with increasing competition intensity with field age (Wilson 1999). Other prairie restoration experiments in early successional fields have also found mixed results from neighbor control on establishment success (Cox and McCarty 1958, McGinnies 1968, Masters et al. 1990).

Control methods varied among years as we attempted to find effective controls. This does not influence our interpretation of the results, however, because neighbor control did not affect establishment in any year.

In contrast to neighbors having small effects in early-successional annual neighborhoods, established stands of introduced perennial grasses are among the greatest obstacles to prairie restoration (Jordan 1988, Roundy and Call 1988, Wilson 2002), and neighbor control consistently improved establishment and survivorship in a simultaneous study about 10 km away in which native grass seeds were sown into stands of the perennial introduced grass *Agropyron cristatum* (Bakker et al. 2003).

The results for mulch were similar to those for neighbor control in that mulch had no significant effect on establishment or survivorship, in spite of several significant effects on ecosystem-level variables. Straw mulch applied in 1994 increased soil moisture in plots in which neighbors were controlled, and also increased available N. This may reflect higher rates of mineralization caused by increased soil moisture. In contrast, sawdust mulch applied in 1996 decreased available N. Differences between years in available N in control plots presumably reflect among-year variation in climate. Sawdust mulch had no significant effect in the nearby *A. cristatum* stand (Bakker et al. 2003), but did significantly reduce N availability in other restorations (Wilson and Gerry 1995, Morghan and Seastedt 1999, Baer et al. 2003).

Variation in establishment among years was far greater than variation between neighbor control treatments (Table 1), reflecting the sensitivity of *B. gracilis* to moisture (Wilson and Briske 1979b). Establishment in drilled plots varied two-fold among years, whereas establishment in broadcast plots varied 50-fold. The difference between drilled and broadcast plots in the magnitude of variation among years presumably reflects the ability of drilling to buffer seeds from short-term variation in temperature and moisture. Regardless of seeding method, the results suggest that restoration resources would be more wisely allocated to repeated seeding among years, as opposed to controlling annuals.

Drilling was significantly better than broadcasting for establishment in two years, but broadcasting was

significantly better in one year, and for survivorship in another year (Fig. 1). High survivorship in broadcast plots in 1996 was actually net recruitment (survivorship >100%) between June and August. Each method produced the highest cover of native grasses and standing crop in different years, and both increased species richness. Overall, therefore, neither method was distinctly advantageous, echoing results from the nearby *A. cristatum* stand (Bakker et al. 2003). Differences among years in the success of drilling and broadcasting persisted through the course of the experiment (Fig. 2), echoing results from Colorado, where initial differences among establishment techniques persisted for 20 years (Newman and Redente 2001). Thus, the choice to drill rather than broadcast seed is likely to create long-lived rows of grasses which impose unnatural spatial structure on the community (Looman and Heinrichs 1973). This can be avoided by broadcasting seed.

Seed-cleaning remainders scattered in plots produced the highest density of native seedlings, as occurred elsewhere (Bakker et al. 2003). Remainders are normally discarded, but they are clearly a valuable restoration resource. Their success also reinforces the notion that broadcasting can produce successful establishment. The lack of seedlings produced by spreading native hay suggests that this method might be best reserved for years of unusually high seed production.

The effects of herbicide on standing crop reversed over the course of the experiment: herbicide significantly decreased standing crop in 1995, had no effect in 1996, and significantly increased it in 1997, for plots sown in both 1994 and 1995. Dicot-selective herbicide killed dicots and reduced standing crop in 1995, but the results suggest that the effect of killing dicots in 1997 was to release perennial graminoids from competition. Similarly, the suppression of nonnative species decreased continuously over the course of the experiment (Fig. 3a). Lastly, root mass decreased in 1994 plots in response to tilling in preparation for broadcasting, but increased in 1996 plots in response to seed addition (see *Results: Standing crop and roots*). All of these results reflect the successional changes from annual dicots to perennial grasses.

Succession in our old field was accompanied by an increase in the cover of the introduced perennial grass *Agropyron cristatum* to 25%, suggesting that this old field is susceptible to invasion by nonnative species. In contrast, fields abandoned during the 1930s–1950s returned to dominance by native prairie (Judd 1940, Coffin et al. 1996, Christian and Wilson 1999). The difference in the successional end points may have two causes: *A. cristatum* has been widely planted since the 1930s, so dispersal from planted stands into unplanted abandoned fields has increased over time, and the seed bank of native species probably had been extirpated by the time our field was abandoned (Bekker et al. 1997, Wilson 2002).

We used relatively high seeding rates (about 4000 seeds/m²) to allow investigation of other factors (neighbor control, seeding method, mulch). Although this is much higher than recommended restoration rates (e.g., 30 seeds/m²; Duebber et al. 1981) and other experimental rates (e.g., 1450 seeds/m²; Betz 1986), our rates are similar to the range of seed density in prairie soils (1000–3000 seeds/m²; Iverson and Wali 1982, Grilz et al. 1994). We used high rates in order to enhance our ability to detect experimental effects such as neighbor control. Optimum seeding densities are well studied for agricultural crops, but not for perennial grasses (Pyke and Archer 1991).

In summary, neighbor control had no effect on native grass establishment. Given the enormous variability of establishment among years, our results suggest that restorations of semiarid old fields should focus less on neighbor control and more on strategies for exploiting suitable years for germination, either by monitoring soil moisture or through repeated seeding.

ACKNOWLEDGMENTS

We thank E. Bakker, M. Bast, J. Buraczewski, C. Elchuk, C. Elkin, A. Jensen, M. Kalcounis, M. Köchy, J. Morissette, K. Muir, D. Peltzer, M. Schellenberg, and T. Willow for help in the lab and field, M. Hansen and reviewers for comments on the paper, and J. Masyk, K. Foster, and especially P. Fargey of Grasslands National Park for logistical support. Funded by Grasslands National Park, the Canada-Saskatchewan Green Plan Agreement in Agriculture, and the Natural Sciences and Engineering Research Council.

LITERATURE CITED

- Agriculture Canada. 1992. Soil landscapes of Canada: Saskatchewan. Centre for Land and Biological Resources Research, Research Branch, Agriculture Canada, Contribution 87–45, Publication **5243/B**, Ottawa, Ontario, Canada.
- Baer, S. G., J. M. Blair, S. L. Collins, and A. K. Knapp. 2003. Soil resources regulate productivity and diversity in newly established tallgrass prairie. *Ecology* **84**:724–735.
- Bakker, J. D., J. Christian, S. D. Wilson, and J. Waddington. 1997. Seeding blue grama in old crested wheatgrass fields in southwestern Saskatchewan. *Journal of Range Management* **50**:156–159.
- Bakker, J. D., S. D. Wilson, J. M. Christian, X. Li, L. G. Ambrose, and J. Waddington. 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. *Ecological Applications* **13**:137–153.
- Bakker, J. P., and F. Berendse. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology and Evolution* **14**:63–68.
- Bekker, R. M., G. L. Verweij, R. E. N. Smith, R. Reine, J. P. Bakker, and S. Schneider. 1997. Soil seed banks in European grasslands: does land use affect regeneration perspectives? *Journal of Applied Ecology* **34**:1293–1310.
- Betz, R. F. 1986. One decade of research in prairie restoration at the Fermi National Accelerator Laboratory (Fermilab), Batavia, Illinois. Pages 179–185 in G. K. Clambey and R. H. Pemble, editors. Proceedings of the Ninth North American Prairie Conference, Tri-College University Center for Environmental Studies, Fargo, North Dakota, USA.
- Bovey, B. W., R. E. Meyer, M. G. Merkle, and E. C. Bashaw. 1986. Effect of herbicides and handweeding on establishment of kleingrass and buffelgrass. *Journal of Range Management* **39**:547–551.
- Christian, J. M. 1996. Revegetation of abandoned cropland in southwestern Saskatchewan using native species, alien species and natural succession. Thesis. University of Regina, Regina, Saskatchewan, Canada.
- Christian, J. M., and S. D. Wilson. 1999. Long-term ecosystem impacts of an introduced grass in the northern Great Plains. *Ecology* **80**:2397–2407.
- Coffin, D. P., W. K. Lauenroth, and I. C. Burke. 1996. Recovery of vegetation in a semiarid grassland 53 years after disturbance. *Ecological Applications* **6**:538–555.
- Cox, M. L., and M. K. McCarty. 1958. Some factors affecting establishment of desirable forage plants in weedy bluegrass pastures of eastern Nebraska. *Journal of Range Management* **11**:159–164.
- Daubenmire, R. 1959. Canopy-coverage method of vegetational analysis. *Northwest Science* **33**:43–64.
- Duebber, H. F., E. T. Jacobson, K. F. Higgins, and E. B. Podoll. 1981. Establishment of seeded grasslands for wildlife habitat in the prairie pothole region. US Department of the Interior, Fish and Wildlife Service Scientific Report on Wildlife No. **234**, Washington, D.C., USA.
- Grilz, P. L., J. T. Romo, and J. A. Young. 1994. Comparative germination of smooth brome and plains rough fescue. *Prairie Naturalist* **26**:157–170.
- Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley, Chichester, UK.
- Hyder, D. N., R. E. Bement, E. E. Remmenga, and D. F. Hervey. 1975. Ecological responses of native plants and guidelines for management of shortgrass range. US Department of Agriculture Technical Bulletin No. **1503**, Washington, D.C., USA.
- Iverson, L. R., and M. K. Wali. 1982. Buried, viable seeds and their relation to revegetation after surface mining. *Journal of Range Management* **35**:648–652.
- Jacoby, Jr., P. W. 1969. Revegetation treatments for stand establishment on coal spoil banks. *Journal of Range Management* **22**:94–97.
- James, S. E., M. Pärtel, S. D. Wilson, and D. A. Peltzer. 2003. Temporal heterogeneity of soil moisture in grassland and forest. *Journal of Ecology* **91**:234–239.
- Jordan, W. R., III. 1988. Ecological restoration. Pages 311–316 in E. O. Wilson and F. M. Peter, editors. Biodiversity. National Academy Press, Washington, D.C., USA.
- Judd, B. I. 1940. Natural succession of vegetation on abandoned farmlands in Teton County, Montana. *Journal of the American Society of Agronomy* **32**:330–336.
- King, M. A., S. S. Waller, L. E. Moser, and J. L. Stubbendieck. 1989. Seedbed effects on grass establishment on abandoned Nebraska Sandhills cropland. *Journal of Range Management* **42**:183–187.
- Knapp, A. K., and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary productivity. *Science* **291**:481–484.
- Looman, J., and D. H. Heinrichs. 1973. Stability of crested wheatgrass pastures under long-term pasture use. *Canadian Journal of Plant Science* **53**:501–506.
- Masters, R. A., K. P. Vogel, P. E. Reece, and D. Bauer. 1990. Sand bluestem and prairie sandreed establishment. *Journal of Range Management* **43**:540–544.
- McGinnies, W. 1968. Effect of post-emergence weed control on grass establishment in north-central Colorado. *Journal of Range Management* **21**:126–128.
- Morghan, K. J. R., and T. R. Seastedt. 1999. Effects of soil nitrogen reduction on nonnative plants in restored grasslands. *Restoration Ecology* **7**:51–55.
- Newman, G. J., and E. F. Redente. 2001. Long-term plant community development as influenced by revegetation techniques. *Journal of Range Management* **54**:717–724.
- Pyke, D. A., and S. Archer. 1991. Plant-plant interactions affecting plant establishment and persistence on revege-

- tated rangeland. *Journal of Range Management* **44**:550–557.
- Roundy, B. A., and C. A. Call. 1988. Revegetation of arid and semiarid rangelands. Pages 607–635 in P. T. Tueller, editor. *Vegetation science applications for rangeland analysis and management*. Kluwer, Dordrecht, The Netherlands.
- Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. *Ecology* **69**:40–45.
- Török, K., T. Szili-Kovács, M. Halassy, T. Tóth, Z. Hayek, M. W. Paschke, and L. J. Wardell. 2000. Immobilization of soil nitrogen as a possible method for the restoration of sandy grassland. *Applied Vegetation Science* **3**:7–14.
- Vleeshouwers, L. M., and M. J. Kropff. 2000. Modeling field emergence patterns in arable weeds. *New Phytologist* **148**:445–457.
- Waddington, J., and N. Malik. 1987. Effects of establishment method and a rapeseed companion crop on alfalfa seed yield. *Canadian Journal of Plant Science* **67**:263–266.
- Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* **42**:266–273.
- Wilson, A. M., and D. D. Briske. 1979a. Drought and temperature effects on the establishment of blue grama seedlings. Pages 359–361 in *Proceedings of the First International Rangeland Congress (Denver, Colorado, 1978)*. Society for Range Management, Denver, Colorado, USA.
- Wilson, A. M., and D. D. Briske. 1979b. Seminal and adventitious root growth of blue grama seedlings in the central Plains. *Journal of Range Management* **32**:209–213.
- Wilson, S. D. 1999. Plant interactions during secondary succession. Pages 629–650 in L. R. Walker, editor. *Ecosystems of disturbed ground*. Elsevier, Amsterdam, The Netherlands.
- Wilson, S. D. 2002. Prairies. Pages 443–465 in A. J. Davy and M. R. Perrow, editors. *Handbook of ecological restoration*. Cambridge University Press, Cambridge, UK.
- Wilson, S. D., and A. K. Gerry. 1995. Strategies for mixed-grass prairie restoration: herbicide, tilling and nitrogen manipulation. *Restoration Ecology* **3/4**:290–298.

APPENDIX A

A digital photograph of one of 240 study plots (3 × 10 m) in an old field in southwest Saskatchewan, Canada, is available in ESA's Electronic Data Archive: *Ecological Archives* A014-005-A1.

APPENDIX B

A table showing effects of neighbor control, seeding method, and mulch on seedling establishment and survivorship in three seeding years is available in ESA's Electronic Data Archive: *Ecological Archives* A014-005-A2.

APPENDIX C

A table showing effects of neighbor control, seeding method, and mulch on the total cover of nonnative species, the total cover of native species, and species richness in three seeding years is available in ESA's Electronic Data Archive: *Ecological Archives* A014-005-A3.

APPENDIX D

A table showing effects of neighbor control, seeding method, and mulch on standing crop and root mass in three seeding years is available in ESA's Electronic Data Archive: *Ecological Archives* A014-005-A4.

APPENDIX E

A table showing effects of neighbor control, seeding method, and mulch on soil moisture and available N in three seeding years is available in ESA's Electronic Data Archive: *Ecological Archives* A014-005-A5.