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CONTINGENCY OF GRASSLAND RESTORATION ON YEAR, SITE, AND COMPETITION FROM INTRODUCED GRASSES

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Abstract. Semiarid ecosystems such as grasslands are characterized by high temporal variability in abiotic factors, which has led to suggestions that management actions may be more effective in some years than others. Here we examine this hypothesis in the context of grassland restoration, which faces two major obstacles: the contingency of native grass establishment on unpredictable precipitation, and competition from introduced species. We established replicated restoration experiments over three years at two sites in the northern Great Plains in order to examine the extent to which the success of several restoration strategies varied between sites and among years. We worked in 50-yr-old stands of crested wheatgrass (*Agropyron cristatum*), an introduced perennial grass that has been planted on $>10 \times 10^6$ ha in western North America.

Establishment of native grasses was highly contingent on local conditions, varying fourfold among years and threefold between sites. Survivorship also varied greatly and increased significantly with summer precipitation. No consistent differences were found between drilling and broadcasting in their effects on establishment, but survivorship was nearly threefold higher in broadcast plots. Plots without seed added, or with native hay added, had almost no seedlings of native grasses. In contrast, broadcasting the residue remaining after cleaning seeds from native hay produced the highest seedling densities of any treatment.

Competition from *A. cristatum* was significantly and consistently reduced through annual application of a generalist herbicide (glyphosate), which increased native grass establishment and survivorship and the richness and total cover of native species. Herbicide decreased standing crop and increased soil moisture and available nitrogen. *A. cristatum* was controlled without suppressing native vegetation, both by spraying in early spring, which selectively killed the cool-season *A. cristatum*, and by application with a wick, which selectively killed the taller *A. cristatum*. *A. cristatum* persisted over four years, however, in spite of annual herbicide application. *A. cristatum* cover in control plots increased significantly with summer precipitation.

In summary, broadcasting and drilling differed little in their effects on establishment, but broadcasting increased survivorship and will allow the emergence of plant-induced heterogeneity. Competition from introduced species can be reduced but not eliminated by continuing herbicide application. Lastly, the positive relationships between precipitation and both *A. cristatum* and native seedling survivorship suggest that management should focus on controlling *A. cristatum* during dry years and on introducing native species during wet years.

Key words: Agropyron cristatum; Bouteloua gracilis; *broadcasting; competition; grass seed; herbicide in grassland restoration; mulch; prairie restoration; precipitation; seed drilling; site effects; species richness; temporal variability.*

INTRODUCTION

Semiarid ecosystems such as grasslands are characterized by relatively high among-year variation in rainfall (Knapp and Smith 2001). Because precipitation influences species composition (Weaver 1950), productivity (Sala et al. 1988), and establishment (Lauenroth et al. 1994), grassland management may need to be timed to exploit windows of opportunity: some management actions may be most successful in dry years and others in wet years (Westoby et al. 1989). We examined this hypothesis in the context of grassland restoration in the northern Great Plains where $>10 \times 10^6$ ha have been planted with introduced perennial grasses (Pyke 1990, Lesica and DeLuca 1996). Prairie restoration can conserve biodiversity, improve soil nutrient status, and enhance belowground storage of CO_2 (Wilson 2002).

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Among the greatest challenges to prairie restoration are the variability of precipitation and the presence of introduced perennial grasses. These obstacles have been addressed using a variety of seeding methods, such as drilling or broadcasting, and management approaches, such as herbicide application. A recent review, however, found little agreement among experimental studies about the usefulness of contrasting strategies, largely due to differences among study sites in weather, vegetation, and soil moisture (Wilson 2002). Our overall goal was to use experiments repeated in space and time to determine which aspects of restoration are contingent on among-site or among-year variability. This allowed us to examine whether any restoration practices give consistent results despite the great climatic variability of the Great Plains. Restoration problems of particular current interest include seeding methods, the control of non-native species, and the use of mulch.

The relative effectiveness of seeding methods, primarily drilling and broadcasting, may be contingent on weather and soil conditions. Drilling has been favored for restoration because ''. . . broadcasting of seed is generally a waste of time on semiarid rangeland. . . '' (Hyder et al. 1975). Drilled seeds are more buffered from drying than are those broadcast on the soil surface. In our region germination was significantly higher for grass seeds buried 1 cm deep than for those scattered on the soil surface (Ambrose and Wilson 2003) suggesting that drilling should be more effective. Drilling produced much higher establishment than broadcasting at one site in Saskatchewan, but the opposite result occurred at another site 200 km away where broadcasting was more effective (Bakker et al. 1997), suggesting that the relative efficiency of the methods depends on local conditions. Broadcasting has been successful for native restorations in Kansas (Kindscher and Tieszen 1998) and Wisconsin (Howe 1999), and naturally dispersed native seeds can colonize dry western prairies (Coffin and Lauenroth 1994). Reviews find few consistent differences between drilling and broadcasting (Duebbert et al. 1981, Wilson 2002), suggesting that differences in their success are contingent on local weather and soils. Broadcasting is more likely than drilling to produce natural plant-induced patterns of spatial heterogeneity (Allen 1988, Coffin et al. 1996, Kleb and Wilson 1997). Thus one of our goals was to determine whether drilling or broadcasting was consistently more successful in establishing native grasses.

Both drilling and broadcasting use particular seed mixes, which may differ from the seed rain in natural prairie. This could be overcome by scattering locally collected native hay on restorations (Bakker et al. 1997). Native hay might also contain other important ecosystem components such as insects and microbes. We therefore examined the effectiveness of scattered native hay as a seed source.

One of the species most commonly used for restoration is the C_3 tussock grass *Agropyron cristatum*, native to Russia but planted on 6–10 $\times$ 10^6 ha of the Great Plains (Lesica and DeLuca 1996) and on $\sim$7.5 $\times$ 10^6 ha of the US intermontane west during 1985–1987 (Pyke 1990). Compared with similarly aged fields dominated by native prairie species, *A. cristatum* stands are characterized by low plant diversity and soils that are low in moisture, carbon, and nitrogen (Christian and Wilson 1999). Introduced grasses have also altered diversity and ecosystem function in Hawaii (D'Antonio and Vitousek 1992) and the intermontane west (Mack and Pyke 1984). Returning *A. cristatum* stands to native vegetation could increase diversity and belowground carbon storage, and extend the grazing season by providing a mix of cool- and warm-season grasses.

Introduced grasses such as *A. cristatum* preempt native grass establishment and have been cited as the greatest obstacle to restoration (Duebbert et al. 1981, Jordan 1988, Roundy and Call 1988, Wilson and Gerry 1995). Tilling, burning, grazing, and herbicide application all reduce the cover of alien perennials, but regrowth from meristems and seed banks is prompt (Grilz and Romo 1995, Masters et al. 1996, Wilson 2002). For example, early spring herbicide application in our study area decreased *A. cristatum* cover by only 50% by the end of the growing season (Bakker et al. 1997) and four years of herbicide application had no significant effect on the size of the seed bank of *A. cristatum* (Ambrose and Wilson 2003). Thus another of our goals was to determine whether the application of herbicide to *A. cristatum* in restorations provided consistent control.

Mulch has the potential to increase soil moisture (Ringe and Graves 1987) and reduce nutrient levels by immobilizing nutrients. Decreased nutrient availability can favor native species over introduced species in competition (Wedin and Tilman 1993), but mulch did not promote native plant establishment in Saskatchewan (Wilson and Gerry 1995) or Colorado (Morghan and Seastedt 1999). Because reports of the effects of mulch are contradictory, we included mulch as a factor in our design.

Our first goal was to compare the drilling and broadcasting of seed, and the scattering of native hay, on the establishment and survival of native grasses in fields dominated by an introduced species. A second goal was to examine the impact of controlling non-native species and applying mulch on restoration success. Our third goal was to examine the contingency of restoration strategies in a semiarid environment by repeating the experiments at two sites in each of three years.

METHODS

Study sites

We worked in a valley and on a tableland in order to examine the effect of site on restoration success. The

TABLE 1. Seeding rates of native grasses planted as pure live seed at two sites (valley and tableland) in three years.

					Both sites			
	Valley 1994		Tableland 1994		1995		1996	
Species	kg/ha	seeds/m^2	kg/ha	seeds/m^2	kg/ha	seeds/m^2	kg/ha	seeds/m^2
Bouteloua gracilis	19.5	3600	23.4	3670	23.4	3670	23.4	3670
Stipa comata	4.4	110	5.3	130	8.4	210	5.9	150
Koeleria cristata	0		4.4	1910	0		0	
Agropyron dasystachyum	0		0		7.6	250	4.5	150
Agropyron smithii	0		0		7.7	190	6.2	150

two sites were not replicated examples of valley and tableland habitats but they allowed us to explore the extent to which restoration success depended on location, in the same way that repeating the experiment over three years allowed assessment of contingency over time. The valley site (50°39′ N, 107°59′ W) is on the floodplain of the South Saskatchewan River, in Saskatchewan Landing Provincial Park, ~70 km north of Swift Current, Saskatchewan (Canada). The site was cultivated before being sown with *Agropyron cristatum* in 1948. The tableland site (49°22′ N, 107°53′ W) is above the Frenchman River in Grasslands National Park, ~130 km south of Swift Current, and was cultivated until *Agropyron cristatum* was sown in 1951. Both sites have brown Chernozemic clay loam soils (Anonymous 1992). 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]). Previous work at these sites has described first-year seeding success (Bakker et al. 1997), ecosystem-level impacts of *A. cristatum* (Christian and Wilson 1999), and seed banks (Ambrose and Wilson 2003).

Long-term weather data from the nearest meteorological stations (valley: Pennant, 40 km southwest; tableland: Val Marie, 15 km northwest; Environment Canada, *unpublished data*) showed that precipitation was similar between sites (valley: 356 mm; tableland: 313 mm) with almost half of annual precipitation falling during May–July. Mean monthly temperatures at both sites range from −13°C in January to 19°C in July. During the study (1994–1997) data were not available from Pennant so we used data from Stewart Valley, 35 km southeast of the valley site. Data during 1984–1993 for Stewart Valley and Pennant were closely correlated (precipitation: $r^2 = 0.85$; temperature: $r^2 = 0.97$).

During our study, the mean May–July temperature for the valley site was significantly ($P < 0.05$, t test) different from the 30-yr mean (15.4°C) only in 1996 (14.6°C). Total precipitation during May–July was significantly different from the 30-yr mean (162 mm) each year (185, 202, 221, 139 mm in 1994–1997, respectively). For the tableland, temperature was significantly higher than the 30-yr mean (15.0°C) in 1994 (15.8°C), and 1997 (16.0°C). Total precipitation was significantly different from the 30-yr mean (149 mm) in 1995, 1996, and 1997 (212, 128, and 78 mm, respectively).

Experimental design

We established 120 plots (each 3 × 10 m, separated by 1 m corridors) in the valley and 240 plots on the tableland. One-third of the plots 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.

At each site the experiment had a complete factorial design with seeding method (none, broadcast, drilled, native hay) and herbicide (applied or not) as main factors, for a total of eight treatment combinations in each of three years. In the valley, each treatment combination was randomly assigned to each of 5 replicate plots each year. On the tableland, each treatment combination was randomly assigned to each of 10 replicate plots in 1995 and 1996. In 1994 on the tableland, there were 5 replicates of each treatment, and another 5 replicates of each treatment combination 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* because it is the dominant native grass in the area (Christian and Wilson 1999), seed was available, and it would potentially provide ranchers with a warm-season grass complementary to the cool-season *Agropyron cristatum*. Other species varied in abundance according to the availability of seed (Table 1). Forbs were not added because seed was unavailable and because they are a small component of the natural vegetation (Christian and Wilson 1999).

We drilled seed 1 cm deep in rows 30 cm apart. Plots broadcast with seed were lightly tilled immediately before broadcasting. We tilled evenly across each plot using a walk-behind (1994) or tractor-mounted tiller (1995–1996). Tilling was shallow (5 cm), just enough to allow broadcasted seed to contact soil instead of litter. Seed was broadcast by hand evenly across each plot.

We collected native hay from undisturbed prairie within a few kilometers of each site using a rear-bagging lawn mower and applied it at 200 g/m^2, an amount similar to average standing crop. 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 allowed snow melt to bring the hay into contact with the soil, ensuring that seeds in the hay would be in place for germination in the appropriate year. Native hay was unavailable in 1994, the first year of the experiment, so we scattered seed cleanings at 180 g/m^2 in July 1994. Cleanings comprised material remaining after native hay was commercially processed to remove awns from seeds of *Stipa comata* in order to produce seed that would pass through a seed drill. Cleanings were expected to be rich in seeds because the hay was collected from an area with high seed production and because awn removal is difficult and inefficient. Seeds in the cleanings could not germinate until fall 1994 at the earliest, and therefore establishment and survivorship in this treatment could not be compared with the broadcast and drilled treatments.

Plots receiving herbicide were treated each year starting in the year they were seeded. In 1994 we sprayed herbicide (glyphosate, *N* [(phosphonomethyl)-glycine]) in early May (1.1 kg active ingredient/ha). At this time the C_3 *A. cristatum* had begun to grow but C_4 native plants were still dormant, allowing the herbicide to selectively kill *A. cristatum*. Initial results indicated that this method decreased *A. cristatum* cover by only ~50% (Bakker et al. 1997), so in subsequent years we applied herbicide later in the growing season using a tractor-mounted wick applicator. The wick traveled ~10 cm above the ground and applied herbicide (1:2 mix of glyphosate and water) to the relatively tall *A. cristatum* but not to the shorter native species. Herbicide was sprayed in May 1994 and applied by wick in May, June, and September 1995, May and June 1996, and May 1997. The number of applications varied among years according to the perceived amount of regrowth following the previous application.

Mulch was an additional factor on the tableland, where it was applied as a complete additional main effect in the 1994 seeding year, and as a split-plot factor in the 1996 seeding year. In May 1994 we spread 200 g/m^2 of shredded flax and wheat straw (1:16 mix). In May 1995 we spread an additional 400 g/m^2 of shredded wheat straw over 2 × 2 m subplots within the plots mulched in 1994. Following the second mulch application all subsequent measurements of dependent variables were taken from within the subplots. In May 1996 we applied 1 kg/m^2 of sawdust 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. We increased the quantity and C:N ratio (higher for sawdust than hay) of mulch 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 (percentage change in density between June and August). 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. Long-term dynamics of seedlings in tableland plots seeded in 1994 were followed by sampling in June and August each year until 1997.

We measured species composition annually in August in three quadrats (0.5 × 1 m) along the diagonal of each plot. We determined the proportion of each quadrat occupied by each species using Daubenmire's (1959) scale, with the use of an additional class (0–1%). The total cover of lichens was also noted. We calculated species richness and the total cover of native species (including lichens) for each quadrat, and means were determined for each plot.

We measured standing crop 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 sampled soil moisture and available N (sum of ammonium and nitrate) annually in May and August. In each plot five soil cores (2 cm diameter, 10 cm depth, one from each corner and one from the center) were taken 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. We extracted available N using a 0.02 mol/L KCl solution. The KCl solution was then decanted and frozen until analysis with an ion-selective electrode (Orion, Boston, Massachusetts).

Proportional data were square-root or arcsine square-root transformed prior to analysis and other data were log-transformed to reduce heteroscedasticity and improve normality. For each site in each year we performed a two-way ANOVA with seeding method and herbicide as main effects. Site was not included as a factor in ANOVA because the habitats were not replicated. For analysis of establishment and survivorship we included only two seeding methods (broadcast and drilling) in ANOVAs because plots that were unseeded controls or received native hay produced almost no seedlings, and plots receiving cleanings were sown later.

Plots on the tableland seeded in 1994 had a third treatment, straw mulch, included as a main effect. Sawdust mulch was applied in 1996 to subplots in plots

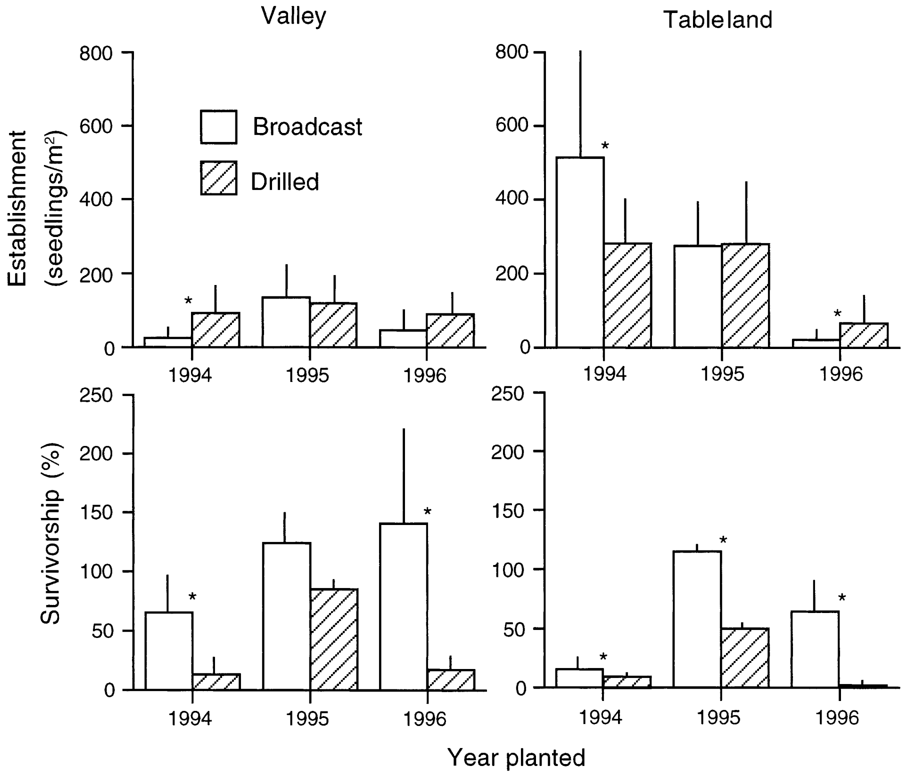

FIG. 1. Mean (+1 SD) establishment (top) and survivorship (bottom) of seedlings of native grasses broadcast (open bars) or drilled (hatched bars) in a valley (left) or on a tableland (right) in each of three years. Data shown are averaged over herbicide (Fig. 2) and mulch treatments. Survivorship values >100% indicate new establishment. Asterisks indicate significant differences ($P < 0.05$) between broadcast and drilled treatments (Table 2).

that were broadcast-seeded and treated with herbicide; we tested the effect of sawdust 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; Kaysville, Utah, USA) software.

Results for establishment are from June of the seeding year, and results for survivorship are from August of the seeding 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.

Relationships between selected response variables (establishment, survivorship, *A. cristatum* cover, species richness) and weather (precipitation and temperature during the growing season) were examined using simple and multiple regression.

RESULTS

Establishment and survivorship: overview

Seedlings of every sown species were found but we considered all species together because almost all seedlings were *Bouteloua gracilis* (e.g., 99% in 1994). In general, seedlings of native species were found only in plots supplied with seeds: the maximum density of native seedlings in plots not supplied with seeds was <1 seedling/m^2.

Establishment (seedling density 1 mo after sowing) varied greatly between sites and among years. Establishment varied nearly threefold between sites (valley: 85 seedlings/m^2, tableland: 239 seedlings/m^2, averaged across years and treatments) and fourfold among years (1994: 228 seedlings/m^2, 1996: 56 seedlings/m^2, averaged across sites and treatments). Further, the rank order of years in terms of suitability for germination differed between sites (Fig. 1: valley 1995 > 1996 > 1994; tableland 1994 > 1995 > 1996). Thus establishment was highly contingent upon location and year.

Survivorship (from June to August of the first year) varied greatly among years. Average survivorship varied threefold between years in the valley (1994: 34.1%, 1995: 103.7%, 1996: 64.0%) and eightfold between years on the tableland (1994: 10.3%, 1995: 79.0%, 1996: 22.7%). Values >100% reflect a net gain in seedlings between June and August. Survivorship at both sites was highest in 1995 and lowest in 1994.

Mulch had no effect on establishment or survivorship in any site or year (Table 2).

Establishment and survivorship: seeding method

The relative efficacy of broadcasting and drilling varied among years. Establishment in the valley was sig-

TABLE 2. Effects of herbicide (H), seeding method (S), and mulch (M) on seedling establishment (density in June of the seeding year) and survivorship (percentage change from June to August of the seeding year) in three seeding years in each of two sites (valley and tableland).

Source of variation	df	Establishment			Survivorship		
		SS	*F*	*P*	SS	*F*	*P*
Valley							
Valley plots seeded in 1994							
Herbicide	1	2.780	29.23	0.000	2.366	23.06	0.000
Seeding method	1	0.859	9.03	0.008	1.005	9.79	0.006
H × S	1	0.421	4.43	0.051	0.003	0.03	0.865
Error	16	1.521			1.641		
Total	19	5.581			5.015		
Valley plots seeded in 1995							
Herbicide	1	0.089	1.59	0.225	0.819	11.01	0.004
Seeding method	1	0.009	0.16	0.694	0.184	2.47	0.136
H × S	1	0.197	3.52	0.079	0.631	8.47	0.010
Error	16	0.896			1.191		
Total	19	1.191			2.824		
Valley plots seeded in 1996							
Herbicide	1	0.106	0.38	0.548	0.142	0.29	0.598
Seeding method	1	0.944	3.35	0.086	2.983	6.17	0.024
H × S	1	0.000	0.00	0.969	0.314	0.65	0.432
Error	16	4.502			7.728		
Total	19	5.553			11.167		
Tableland							
Tableland plots seeded in 1994							
Herbicide	1	0.051	1.18	0.285	0.539	35.33	0.000
Seeding method	1	0.526	12.22	0.001	0.087	5.70	0.023
Mulch	1	0.005	0.12	0.731	0.004	0.27	0.607
H × S	1	0.000	0.00	1.000	0.049	3.18	0.084
H × M	1	0.017	0.39	0.537	0.010	0.67	0.419
S × M	1	0.005	0.12	0.731	0.007	0.44	0.512
H × S × M	1	0.091	2.12	0.155	0.009	0.56	0.460
Error	32	1.377			0.488		
Total	39	2.072			1.193		
Tableland plots seeded in 1995							
Herbicide	1	0.640	22.54	0.000	0.121	4.18	0.048
Seeding method	1	0.006	0.22	0.642	1.329	46.11	0.000
H × S	1	0.072	2.54	0.120	0.032	1.11	0.299
Error	36	1.022			1.038		
Total	39	1.741			2.520		
Tableland plots seeded in 1996							
Mulch	1	0.143	0.71	0.411	0.080	0.29	0.597
Error	18	3.634			4.911		
Total	19	3.777			4.992		
Herbicide	1	2.981	14.72	0.000	0.030	0.20	0.657
Seeding method	1	1.875	9.26	0.004	4.223	28.94	0.000
H × S	1	1.190	5.88	0.020	0.003	0.02	0.888
Error	36	7.291			5.254		
Total	39	13.337			9.509		

Notes: All statistics are from ANOVAs within each combination of site (valley, tableland) and seeding year (1994, 1995, 1996). Significant *F* values are underlined. Herbicide (applied or not) and seeding method (broadcast or drilled) were main factors in all sites and years. Mulch (applied or not) was a main factor in tableland plots seeded in 1994. Mulch effects in tableland plots that received herbicide and were broadcast seeded in 1996 were examined with one-way ANOVA. Two other seeding methods (none and native hay) had low seedling densities and were omitted from the analysis. Seedling densities were log-transformed, and survivorship percentages were square-root transformed prior to analysis of survivorship.

nificantly ($P < 0.05$) higher in drilled than broadcast plots sown in 1994, but there was no significant difference between broadcasting and drilling in other years (Fig. 1, Table 2). On the tableland broadcasting produced significantly higher establishment than drilling in 1994 but there was no significant difference between broadcasting and drilling in 1995, and broadcasting produced significantly fewer seedlings than drilling in 1996 (Fig. 1, Table 2).

In addition to differences between broadcast and drilling among years, there was a difference between sites: in 1994, broadcasting produced significantly lower es-

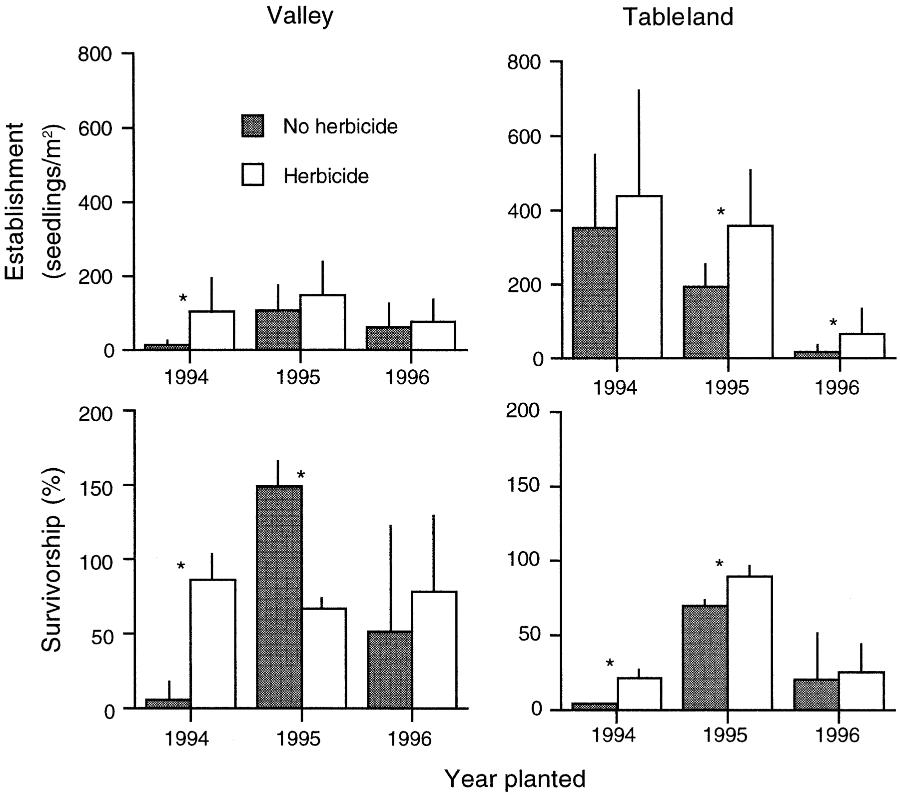

FIG. 2. Mean (+1 SD) establishment (top) and survivorship (bottom) of seedlings of native grasses in control plots (solid bars) or plots treated with herbicide (open bars) in a valley (left) or on a tableland (right) in three years. Data shown are averaged over seed (Fig. 1) and mulch treatments. Survivorship values >100% indicate new establishment. Asterisks indicate significant differences ($P < 0.05$) between herbicide treatments. ANOVA results are presented in Table 2.

tablishment than drilling in the valley but significantly higher establishment on the tableland (Fig. 1).

Survivorship was significantly higher in broadcast than drilled plots in two of three years in the valley and in all years on the tableland (Fig. 1, Table 2). Averaged across sites, years, and other treatments, mean survivorship was 86.6% in broadcast plots and 29.8% in drilled plots.

Establishment and survivorship: herbicide

In contrast to the results comparing broadcasting and drilling, which were contingent on years and sites, herbicide generally had consistently positive effects on establishment (Fig. 2), although the increase was significant in the valley only in plots seeded in 1994 and on the tableland in plots seeded in 1995 and 1996 (Table 2).

Herbicide significantly increased survivorship in one year in the valley (1994) and two years on the tableland (1994 and 1995; Fig. 2, Table 2). Similar but nonsignificant results were obtained from both sites in plots seeded in 1996. In contrast, continuing establishment in July and August resulted in significantly higher survivorship (~150%) in plots without herbicide in one case (valley plots seeded in 1995, Fig. 2). Averaged across sites, years, and other treatments, mean survivorship was 61.5% in plots receiving herbicide and 51.0% in control plots.

Significant statistical interactions between herbicide and seeding method occurred in two cases (Table 2): establishment on the tableland in 1996 (because herbicide had little effect in broadcast plots but increased establishment fivefold in drilled plots; *data not shown*), and survivorship in the valley in 1995 (because recruitment over the summer in plots without herbicide was much higher in drilled than broadcast plots). In spite of these exceptions, the effects of seeding method and herbicide were generally direct and without interactions.

Establishment and survivorship: weather

Establishment in plots that were broadcast and treated with herbicide increased significantly with June precipitation and decreased significantly with June temperature (multiple regression; establishment = 11.24(June precipitation) − 291.61(June temperature) + 3945.38, where precipitation is in millimeters and temperature in degrees Celsius, as they are throughout this paper; $r^2 = 0.88$). Establishment in plots that were

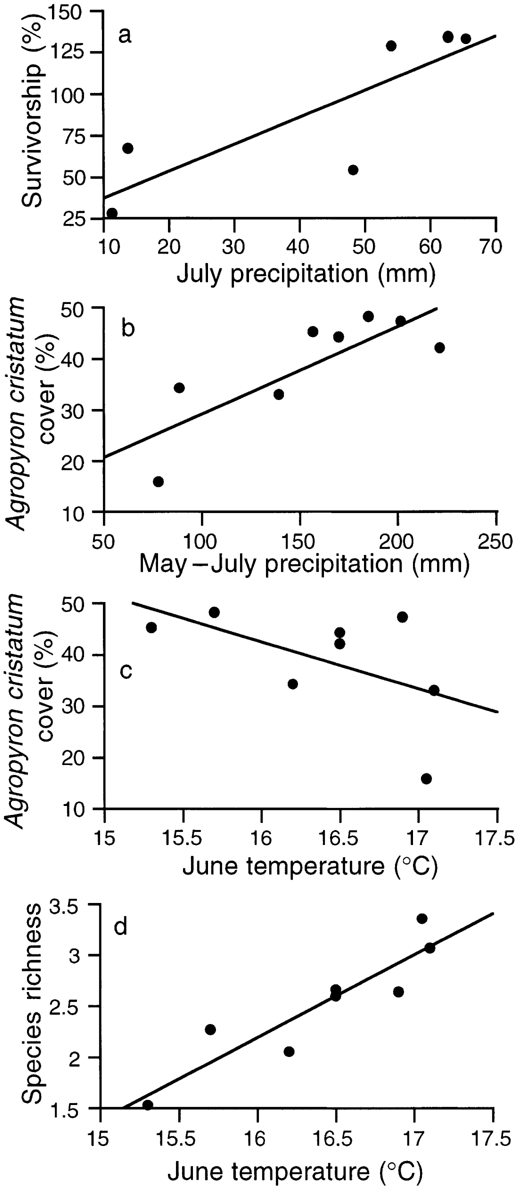

FIG. 3. Relationships between (a) survivorship of native seedlings and July precipitation in plots broadcast with seed and treated with herbicide; (b) cover of the introduced grass *Agropyron cristatum* and total precipitation during May–July in untreated plots; (c) cover of *Agropyron cristatum* and mean June temperature in untreated plots; and (d) species richness and June temperature in untreated plots. In all cases, each symbol represents one site (valley or tableland) in one year (1994–1997).

drilled and treated with herbicide did not vary significantly with any aspect of weather examined.

Survivorship in plots that were broadcast and treated with herbicide increased significantly with July precipitation (Fig. 3; survivorship = 1.64(July precipitation) + 21.05; $r^2 = 0.69$). Prediction was improved by including the negative effect of June precipitation in a multiple regression (survivorship = −1.14(June precipitation) + 1.82(July precipitation) + 113.16; $r^2 = 0.87$). Survivorship in plots that were drilled and treated with herbicide increased significantly with total precipitation in June and July ($r^2 = 0.79$).

Seed cleanings and hay

Seed cleanings were very successful. In the valley, native seedling density after 4 yr was significantly higher in plots receiving seed cleanings (14 seedlings/m^2) than in those broadcast (<1 seedling/m^2) or drilled (1 seedling/m^2, $F_{2,12} = 21.40$, $P < 0.001$, data for plots established in 1994 and treated with herbicide). On the tableland, native seedling density after 4 yr was significantly higher in plots that received cleanings (41 seedlings/m^2) or were broadcast with seed (31 seedlings/m^2) than those which were drilled (11 seedlings/m^2; $F_{2,27} = 9.05$, $P < 0.001$). Because of the species composition of the added seeds, the dominants of plots supplied with cleanings (*Koeleria cristata*, *Stipa comata*) were different from that in broadcast or drilled plots (*Bouteloua gracilis*).

In contrast to the success of cleanings, scattering native hay produced almost no seedlings at either site in any year (range: 0–2 seedlings/m^2 in sprayed plots).

Species composition and richness

Agropyron cristatum accounted for 79% of vascular plant cover in control plots in the valley and 95% on the tableland, averaged across all years.

The cover of *A. cristatum* was significantly reduced by two seasons of herbicide application in the valley for plots sown in 1994 and 1995, and on the tableland in all years (Fig. 4, Table 3). The effect of seeding on *A. cristatum* cover was nonsignificant in two cases, significantly positive in two others, and significantly negative in two others (Fig. 5, Table 3).

The cover of *A. cristatum* in control plots increased significantly with early summer precipitation (sum of precipitation during May–July, Fig. 3b; cover = 0.172(precipitation) + 12.14; $r^2 = 0.74$) and decreased with increasing June temperature (Fig. 3c; cover = −9.131(temperature) + 188.643; $r^2 = 0.30$). Prediction was improved by including both precipitation and temperature in a multiple regression (cover = 0.158(precipitation) −6.449(temperature) + 119.046; $r^2 = 0.91$).

In the valley, the total cover of native plants and species richness were both increased by two seasons of herbicide application but significantly so only in two years (Fig. 4, Table 3). On the tableland, native plant cover and species richness were significantly increased by herbicide in all years (Fig. 4, Table 3). Species richness in control plots increased significantly with June temperature (Fig. 3d; richness = 0.811(temperature) − 10.782; $r^2 = 0.90$).

The cover of native species in the valley was unaffected by seeding, but on the tableland native species cover was significantly decreased in broadcast plots in

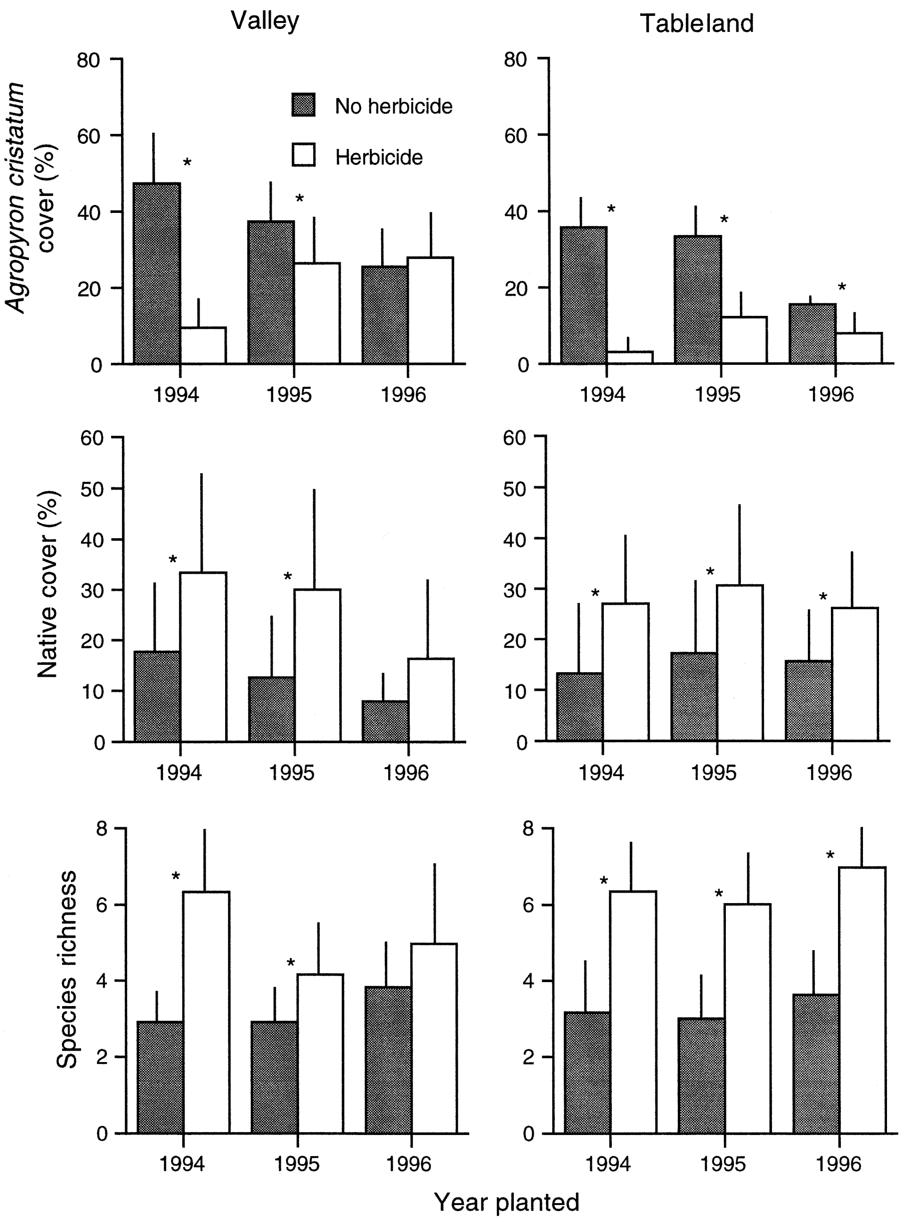

FIG. 4. Mean (+1 SD) cover of the introduced grass *Agropyron cristatum* (top), total cover of native species (middle), and species richness (bottom) in control plots (solid bars) or plots treated with herbicide (open bars) in a valley (left) and on a tableland (right) in three years. Data are averaged across seed (Fig. 5) and mulch treatments and are from the end of the second growing season for each year. Asterisks indicate significant differences ($P < 0.05$) between herbicide treatments. ANOVA results are presented in Table 3.

two years (Fig. 5, Table 3). Species richness, in contrast, was significantly increased by seeding in most cases (Fig. 5, Table 3).

Neither straw or sawdust mulch had any effect on the cover of *Agropyron cristatum* (Table 3). Straw mulch applied on the tableland in 1994 (Table 3) significantly reduced the cover of native species (control: 28.3%; mulched: 12.0%) and species richness (control: 5.07 species; mulched: 4.43 species).

Biomass, soil moisture and available N

Standing crop was significantly reduced by two seasons of herbicide application in every case (Fig. 6, Table 4). Standing crop did not vary with any aspect of weather examined. Root mass was unaffected by herbicide (data not shown). Neither standing crop (Table 4) nor root mass were significantly affected by mulch.

TABLE 3. Effects of herbicide (H), seeding method (S), and mulch (M) on cover of the introduced grass *Agropyron cristatum*, cover of native species, and species richness in three seeding years in each of two sites (valley and tableland). All measurements were made in August of the year after seeding.

Source of variation	df	*A. cristatum*			Native cover			Richness		
		ss†	*F*	*P*	ss†	*F*	*P*	ss†	*F*	*P*
Valley										
Valley plots seeded in 1994										
Herbicide	1	16.119	91.63	0.000	3.058	7.16	0.013	8.726	52.55	0.000
Seeding method	2	0.138	0.39	0.681	1.062	1.24	0.307	0.181	0.55	0.584
H × S	2	0.112	0.32	0.729	0.424	0.50	0.613	0.014	0.04	0.961
Error	24	4.222			10.255			3.985		
Total	29	20.591			14.799			12.907		
Valley plots seeded in 1995										
Herbicide	1	1.207	7.63	0.011	3.956	8.20	0.009	1.750	12.93	0.001
Seeding method	2	0.646	2.04	0.152	1.863	1.93	0.167	2.055	7.59	0.003
H × S	2	0.168	0.53	0.595	0.822	0.85	0.440	0.242	0.89	0.424
Error	24	3.797			11.581			3.248		
Total	29	5.817			18.222			7.295		
Valley plots seeded in 1996										
Herbicide	1	0.039	0.45	0.509	0.792	2.65	0.117	0.680	3.63	0.069
Seeding method	2	2.471	14.18	0.000	0.200	0.33	0.722	4.217	11.27	0.000
H × S	2	0.288	1.65	0.213	0.899	1.50	0.243	0.290	0.77	0.474
Error	24	2.091			7.189			4.490		
Total	29	4.888			9.081			9.676		
Tableland										
Tableland plots seeded in 1994										
Herbicide	1	34.630	604.88	0.000	6.491	36.65	0.000	17.069	112.04	0.000
Seeding method	2	0.529	4.62	0.015	0.005	0.01	0.990	3.428	11.25	0.000
Mulch	1	0.018	0.31	0.580	7.794	44.01	0.000	1.270	8.33	0.006
H × S	2	0.174	1.52	0.229	0.018	0.05	0.951	0.406	1.33	0.274
H × M	1	0.073	1.27	0.265	0.900	5.08	0.029	0.897	5.89	0.019
S × M	2	0.126	1.10	0.341	1.346	3.80	0.029	0.097	0.32	0.728
H × S × M	2	0.604	5.28	0.008	0.344	0.97	0.386	0.566	1.86	0.167
Error	48	2.748			8.501			7.313		
Total	59	38.903			25.401			31.045		
Tableland plots seeded in 1995										
Herbicide	1	10.542	143.69	0.000	4.780	25.71	0.000	16.434	86.61	0.000
Seeding method	2	0.429	2.93	0.062	8.423	22.65	0.000	2.236	5.89	0.005
H × S	2	0.233	1.59	0.213	0.697	1.87	0.164	1.000	2.64	0.081
Error	54	3.962			10.039			10.247		
Total	59	15.166			23.938			29.917		
Tableland plots seeded in 1996										
Mulch	1	0.120	1.89	0.186	0.200	4.26	0.054	0.016	0.22	0.645
Error	18	1.146			0.847			1.316		
Total	19	1.266			1.047			1.332		
Herbicide	1	2.784	58.91	0.000	3.070	43.96	0.000	13.620	138.69	0.000
Seeding method	2	0.304	3.22	0.048	7.542	54.00	0.000	0.835	4.25	0.019
H × S	2	0.508	5.38	0.007	0.171	1.22	0.303	1.236	6.30	0.003
Error	54	2.552			3.771			5.303		
Total	59	6.149			14.553			20.994		

Notes: All statistics are from ANOVAs within each combination of site (valley, tableland) and seeding year (1994, 1995, 1996). Significant *F* values are underlined. Herbicide (applied or not) and seeding method (unseeded, broadcast, drilled) were main factors in all sites and years. Mulch (applied or not) was a main factor in tableland plots seeded in 1994. Mulch effects in tableland plots that received herbicide and were broadcast seeded in 1996 were examined with one-way ANOVA. Cover data were arcsine square-root transformed, and species richness data were log-transformed prior to analysis.

† All sums of squares (ss) have been multiplied by 10 for presentation.

Soil moisture was increased by two seasons of herbicide application in the valley but significantly so only for plots sown in 1995 (Fig. 6, Table 4). Herbicide significantly increased soil moisture on tableland plots sown in 1994 but had no effect in other years (Fig. 6, Table 4). Straw mulch applied in 1994 produced a small but significant increase in soil moisture after two growing seasons (control: 9.6%; mulch: 10.9%; Table 4).

Soil available nitrogen was significantly increased by two seasons of herbicide application in valley plots sown in 1994 and in tableland plots sown in 1994 and 1995 but was unaffected in plots sown in other years (Fig. 6, Table 4). Straw mulch applied in spring 1994

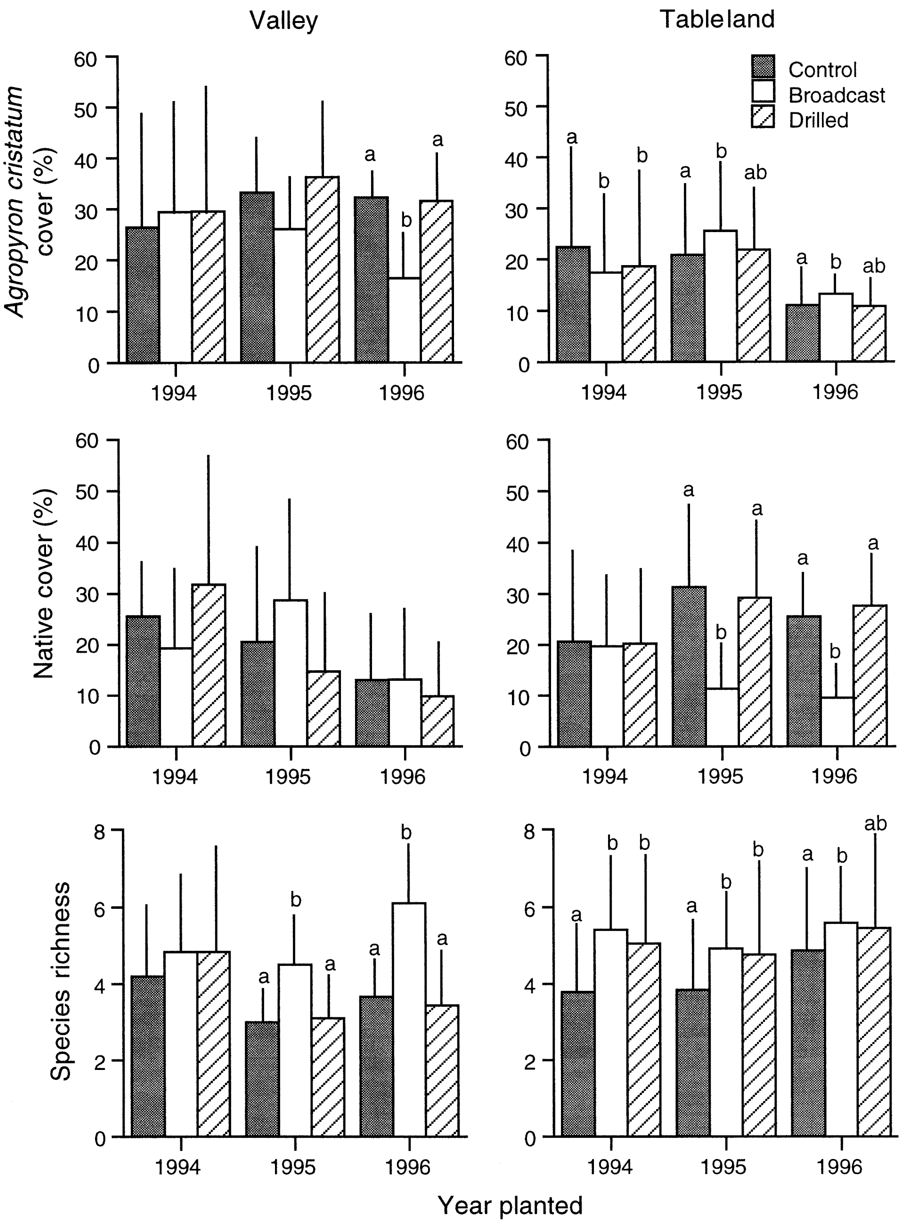

FIG. 5. Mean (+1 SD) cover of the introduced grass *Agropyron cristatum* (top), total cover of native species (middle), and species richness (bottom) in unseeded plots (solid bars), plots broadcast with native seed (open bars), or plots drilled with native seed (hatched bars) in a valley (left) and on a tableland (right) in three years. Data are averaged across herbicide (Fig. 4) and mulch treatments and are from the end of the second growing season for each year. Lowercase letters indicate significant differences ($P < 0.05$) among seeding treatments. ANOVA results are presented in Table 3.

significantly increased soil available nitrogen after two growing seasons (control: 0.79 mg N/kg soil; mulch: 1.20 mg N/kg soil; Table 4).

Long-term trends in seedling density and Agropyron cristatum

We examined four years of data in the case where they were available (tableland plots planted in 1994). Seedling density stopped decreasing in the last two years of the experiment in both broadcast and drilled plots (Fig. 7) suggesting that density had stabilized. *A. cristatum* cover was reduced by herbicide application in each year, but its cover in herbicide-treated plots varied among years and showed no sign of decreasing over time (Fig. 7).

DISCUSSION

Our results show that some aspects of semiarid grassland restoration, such as establishment and the relative benefits of broadcasting and drilling, are contingent on

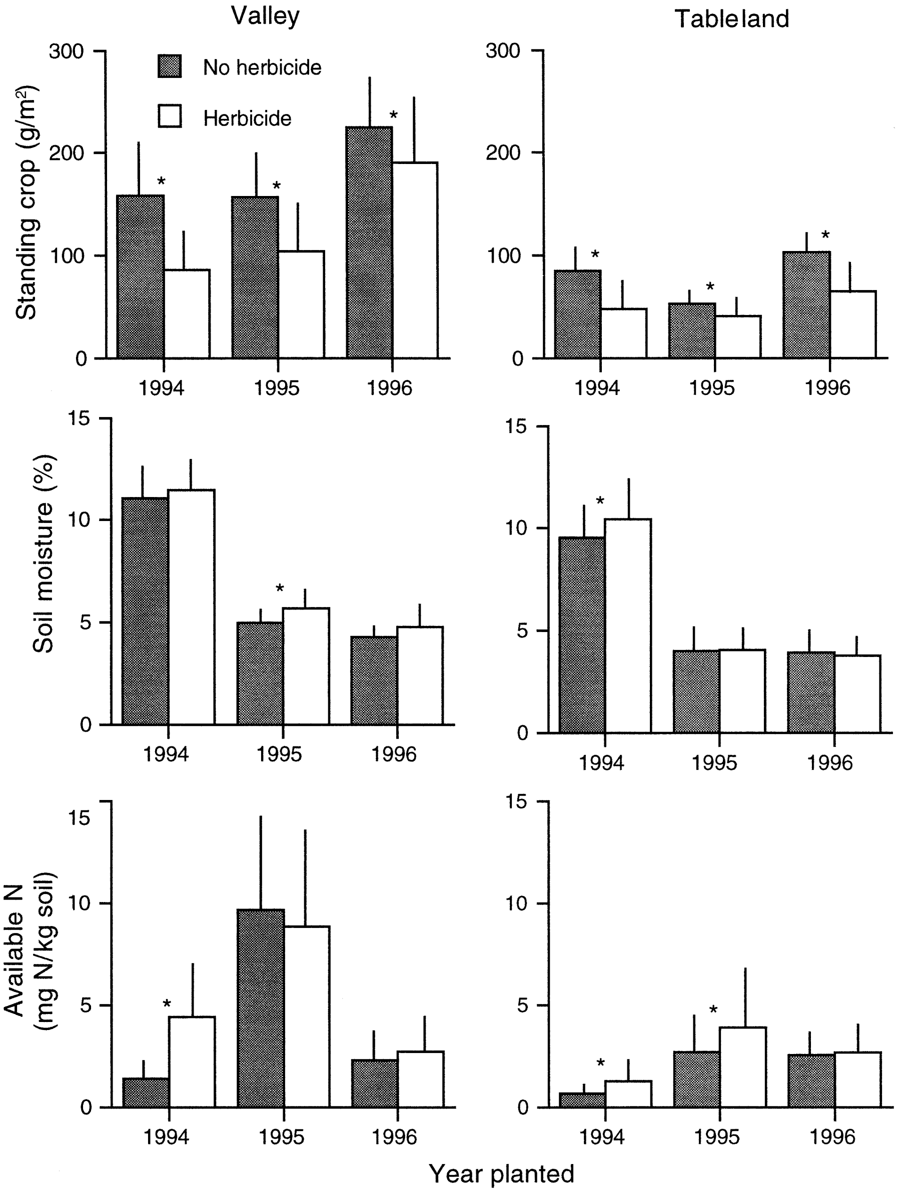

FIG. 6. Mean (+1 SD) standing crop (top), soil moisture (middle), and soil available N (bottom) in control plots (solid bars) or plots treated with herbicide (open bars) in a valley (left) and on a tableland (right) in three years. Data are averaged across seed and mulch treatments and are from the end of the second growing season for each year. Asterisks indicate significant differences ($P < 0.05$) between herbicide treatments. ANOVA results are presented in Table 4.

weather and location, whereas others, such as reducing competition from *A. cristatum*, are consistent regardless of environmental variation.

Our design allowed us to examine six combinations of years and sites (three years × two sites, Fig. 1). Establishment was by far the response that varied most among years and sites and appeared to be most contingent on local conditions. This suggests that the factors that influence establishment vary over relatively small temporal and spatial scales. Precipitation in this region typically falls from small thunderstorms (Ambrose and Wilson 2003). Small-scale variation in precipitation and soil water-holding capacity (Epstein et al. 1997) may be most important in determining establishment (Lauenroth et al. 1994), and they are beyond the control of restoration managers. Among-year variation in establishment might be addressed by spreading seeding over a number of years or by attempting restorations in years when autumn rain or deep snow are likely to provide water. The seasonality of precipitation also needs consideration. Multiple regression showed that June rainfall increased establishment but decreased survivorship. This probably resulted because high seedling densities produced by high June precip-

TABLE 4. Effects of herbicide (H), seeding method (S), and mulch (M) on standing crop, soil moisture, and available nitrogen in three seeding years in each of two sites (valley and tableland). All measurements were made in August of the year after seeding.

Source of variation	df	Standing crop			Soil moisture			Available N		
		ss†	*F*	*P*	ss†	*F*	*P*	ss†	*F*	*P*
Valley										
Valley plots seeded in 1994										
Herbicide	1	0.591	18.14	0.000	0.025	0.41	0.528	0.762	21.20	0.000
Seeding method	2	0.119	1.82	0.184	0.056	0.46	0.637	0.030	0.41	0.668
H × S	2	0.044	0.68	0.516	0.210	1.72	0.201	0.001	0.02	0.980
Error	24	0.750			1.406			0.827		
Total	29	1.518			1.709			1.622		
Valley plots seeded in 1995										
Herbicide	1	0.295	11.83	0.002	0.175	6.34	0.019	0.018	0.58	0.454
Seeding method	2	0.058	1.17	0.327	0.051	0.92	0.412	0.203	3.35	0.052
H × S	2	0.055	1.11	0.346	0.031	0.55	0.584	0.138	2.27	0.125
Error	24	0.599			0.661			0.729		
Total	29	1.007			0.917			1.088		
Valley plots seeded in 1996										
Herbicide	1	0.058	5.31	0.030	0.095	2.93	0.100	0.014	0.30	0.588
Seeding method	2	0.061	2.76	0.083	0.027	0.42	0.662	0.107	1.16	0.330
H × S	2	0.172	7.82	0.002	0.048	0.74	0.488	0.006	0.06	0.939
Error	24	0.264			0.780			1.103		
Total	29	0.555			0.951			1.230		
Tableland										
Tableland plots seeded in 1994										
Herbicide	1	1.217	48.18	0.000	0.287	4.23	0.046	0.174	9.17	0.004
Seeding method	2	0.295	5.84	0.005	0.375	2.76	0.075	0.058	1.53	0.228
Mulch	1	0.000	0.00	0.955	0.494	7.28	0.010	0.097	5.11	0.029
H × S	2	0.198	3.92	0.026	0.047	0.34	0.714	0.004	0.11	0.896
H × M	1	0.015	0.60	0.442	0.045	0.67	0.418	0.000	0.01	0.921
S × M	2	0.087	1.72	0.190	0.070	0.52	0.598	0.088	2.31	0.112
H × S × M	2	0.058	1.15	0.325	0.135	0.99	0.380	0.009	0.23	0.796
Error	48	1.213			2.854			0.797		
Total	59	3.083			4.470			1.279		
Tableland plots seeded in 1995										
Herbicide	1	0.293	11.62	0.001	0.005	0.06	0.809	0.233	4.93	0.031
Seeding method	2	0.096	1.90	0.159	0.080	0.52	0.596	0.059	0.62	0.539
H × S	2	0.029	0.58	0.563	0.001	0.01	0.993	0.111	1.17	0.318
Error	54	1.360			4.143			2.555		
Total	59	1.777			4.229			2.958		
Tableland plots seeded in 1996										
Mulch	1	0.000	0.01	0.931	0.022	0.25	0.623	0.000	0.02	0.889
Error	18	0.753			1.590			0.372		
Total	19	0.754			1.611			0.373		
Herbicide	1	0.840	38.29	0.000	0.017	0.30	0.586	0.002	0.11	0.741
Seeding method	2	0.066	1.51	0.230	0.041	0.35	0.706	0.115	2.80	0.070
H × S	2	0.107	2.45	0.096	0.177	1.51	0.230	0.033	0.80	0.455
Error	54	1.185			3.173			1.089		
Total	59	2.199			3.408			1.234		

Notes: All statistics are from ANOVAs within each combination of site (valley, tableland) and seeding year (1994, 1995, 1996). Significant *F* values are underlined. Herbicide (applied or not) and seeding method (unseeded, broadcast, drilled) were main factors in all sites and years. Mulch (applied or not) was a main factor in tableland plots seeded in 1994. Mulch effects in tableland plots that received herbicide and were broadcast seeded in 1996 were examined with one-way ANOVA. The native hay seeding method was omitted from the analyses. Standing crop and available nitrogen data were log-transformed, and soil moisture data were arcsine square-root transformed prior to analysis.

† All sums of squares (ss) have been multiplied by 10 for presentation.

itation increased competition-induced mortality over the course of the summer, or because the cover of *Agropyron cristatum* increased significantly with June precipitation (Fig. 3a), which also might have increased competition. In any case, seeding may be most effective if its timing is chosen based on weather-related opportunities (Westoby et al. 1989).

The relative efficacy of broadcasting and drilling was contingent on year and site. In three cases there were no significant differences between drilling and broad-

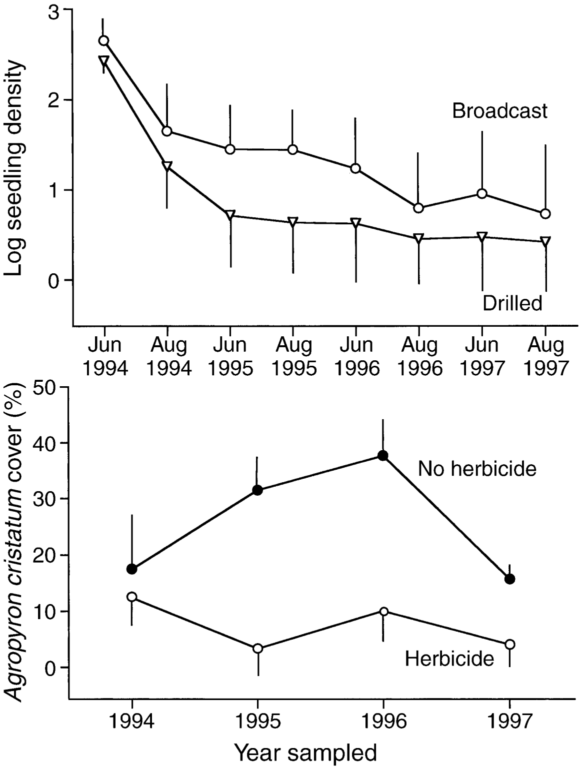

FIG. 7. (Top) Mean (and 1 SD) density of native grass seedlings (seedling density measured as seedlings/m^2) in tableland plots either broadcast (circles) or drilled (triangles) in 1994. Data are averaged across herbicide and mulch treatments. Seedlings were counted in June and August each year. (Bottom) cover of the introduced grass *Agropyron cristatum* in tableland plots that were broadcast-seeded in 1994 and either treated repeatedly with herbicide (open circles) or not treated with herbicide (solid circles). Data are averaged across mulch treatments.

casting on establishment (Fig. 1). Broadcasting produced higher establishment on the tableland in 1994 and drilling produced higher establishment in two cases, the valley in 1994 and on the tableland in 1996. This unpredictable variability in establishment reflects a survey of the prairie restoration literature: drilling was more effective in some cases, and broadcasting in others, with no differences in others (Wilson 2002).

In contrast, survivorship in broadcast plots was greater than in drilled plots in every case (Fig. 1) as well as over the long term (Fig. 7). This was presumably because of relatively intense competition among seedlings in drilled rows and because of reduced competition from *Selaginella densa*, the second most common species in *Agropyron cristatum* fields (Christian and Wilson 1999), in plots tilled before broadcasting. Because drilling results in lines that persist for decades (Bleak et al. 1965, Looman and Heinrichs 1973), it produces patterns of heterogeneity different from those in native prairie (Hook et al. 1991, Kleb and Wilson 1997) and should be avoided if the goal is to produce communities with both the appearance and function of native prairie (Allen 1988).

Drilling and broadcasting had no effect on the total cover of native species in the valley, but broadcasting in the tableland decreased native cover in two years (Fig. 5). This probably occurred because cryptogams such as *Selaginella densa* contributed $<1\%$ of native cover in the relatively mesic valley, but 60–70% on the xeric tableland, and cryptogams are sensitive to even small amounts of tilling (Wilson and Tilman 2002). Broadcast plots were lightly tilled to ensure that seed contacted soil. Given the ubiquity of cryptogams in once-tilled *A. cristatum* stands (Christian and Wilson 1999), they are expected to recover over the long term. Seed addition generally increased species richness, especially in broadcast plots (Fig. 5). This was probably attributable to the addition of the sown species (Table 1) as well as to opportunistic invasion of bare soil by native composites such as *Antennaria neglecta* and *Ratibida columnifera*.

Seed addition was essential for establishing native grasses: almost no native grasses were found in unseeded plots. Another study in our 1994 tableland plots found a single seedling of the native grass *Bouteloua gracilis* in 1997, even though water was added to simulate the wettest of the previous 30 yr (Ambrose and Wilson 2003). Very low rates of dispersal of native seed from surrounding native prairie is typical of semiarid grasslands (Coffin et al. 1996, Wilson 2002).

Native hay produced almost no seedlings, suggesting that selective seed collection by combining or picking in years and locations with high seed production is required to obtain sufficient quantities of seed. Our most successful establishment resulted from scattering seed cleanings, which produced seedling densities that exceeded those of our relatively high seeding rates. Cleanings were produced when awns of *Stipa comata* were removed from native hay in order to allow seeds to pass through a seed drill. This native hay was presumably collected from an area with high seed production. In contrast, spreading native hay collected at the study site each year regardless of seed production produced almost no establishment. Seed production in our region varies greatly among years (Clark 1997). C_3 species such as *Koeleria cristata* and *Stipa comata* dominated plots on which cleanings were scattered in contrast to the lack of C_3 species in plots drilled or broadcast, suggesting that C_3 species can establish if sown in sufficiently high density. Our results suggest that cleanings are a valuable resource for hand-broadcasting on restorations.

We used relatively high seeding rates for broadcasting and drilling (~4000 seeds/m^2) in order to explore the effects of other restoration practices on establishment and survivorship. This exceeds recommended rates (e.g., 30 seeds/m^2 [Duebbert et al. 1981]) and high experimental rates (e.g., 1450 seeds/m^2 [Betz 1986]), but is close to the range for seed density in native prairie (1000–3000 seeds/m² [Iverson and Wali 1982, Grilz et al. 1994]). Excessively high seeding rates may waste seed but might also contribute to the control of unwanted introduced species (Wilson 2002). Optimum seeding rates have not been determined for native species as they have been for introduced species (Pyke and Archer 1991).

Our seed mix was dominated by *Bouteloua gracilis* and it is likely that different mixes would produce different results. We used *B. gracilis* because it is a C_4 grass that increases in abundance with hot, dry conditions (Weaver 1950) and was likely to be relatively successful in dry years. Mixes dominated by other native grasses, mostly C_3 in this region, might not be as successful. In spite of their inclusion in the seed mix (Table 1), almost no C_3 grasses emerged. We did not include forbs because of their rarity in our vegetation (Christian and Wilson 1999) but a complete restoration should include them.

Mulch had no significant effects on establishment or survivorship, or the cover of *A. cristatum* (Tables 2 and 3). Straw mulch applied to tableland plots in 1994 significantly reduced both species richness and the total cover of native species (Table 3). This probably resulted from straw covering the major cryptogam, *Selaginella densa*: the total cover of native vascular plants was unaffected by mulch (control: 8.4%; mulched: 10.5%). Soil resources, however, were slightly higher in mulched plots. Increased N availability in mulched plots (Table 4) ran counter to expectations (Wilson and Gerry 1995, Morghan and Seastedt 1999) and might be attributable to mulch increasing soil moisture. These small improvements need to be weighed against the cost of applying mulch and the risk of introducing weed seeds. The small but significant positive effects of mulch on soil moisture and available N may have resulted from reduced evaporation and increased mineralization. Mulch effects have also been found to be small in other northern grasslands (Wilson and Gerry 1995, Peltzer et al. 1998).

In contrast to the contingent and unpredictable effects of seeding method on establishment, applying herbicide to *A. cristatum* stands consistently increased native grass establishment, survivorship (Fig. 2), the cover of native species, and species richness (Fig. 4). Herbicide significantly reduced standing crop in every case (Fig. 6), which should reduce resource demand and competition. Every herbicide-related significant difference in soil resource availability (water and nitrogen) in our study was an increase in plots treated with herbicide (Fig. 6). Competition in grasslands is primarily for soil resources (Wilson 1998) and in addition to its effects on establishment and survivorship (Fig. 2), *A. cristatum* also decreases the growth of native grass seedlings (Bakker and Wilson 2001).

Differences in stature between the tall *A. cristatum* and shorter native species allowed the application of herbicide with a wick in 1995 and 1996 to suppress *A. cristatum* and promote the cover of native species (Fig. 4). Similarly, differences in seasonal growth of the C_3 *A. cristatum* and the mostly C_4 native species allowed the application of herbicide with a sprayer in 1994 to have the same effect. In general, careful wicking and spraying selectively suppresses *A. cristatum* and promote natives.

The only apparently negative effect of herbicide on native species was on survivorship in the valley in 1995 (Fig. 2). In fact, however, survivorship was high (~75%) in plots with herbicide, but establishment continued in July and August in plots without herbicide, resulting in high (~150%) ‘‘survivorship.’’ There is no obvious reason why neighbors promoted establishment in one year in one location, but this result serves to underscore the variability of native species responses.

Herbicide did not eliminate *A. cristatum*. After two growing seasons of repeated application, there was still considerable cover of *A. cristatum* in every case (Fig. 4). Four years of data from plots established in 1994 showed that the cover of *A. cristatum* in plots receiving herbicide had stabilized at 5–10% despite annual herbicide application (Fig. 7). Examination of these plots in 1997 showed that the seed bank of *A. cristatum* was unaffected by herbicide application, with an average of ~1000 seeds/m² (Ambrose and Wilson 2003). This may be caused by decreased intraspecific competition resulting in higher seed production in sprayed plots (S. D. Wilson and M. Pärtel, *unpublished data*), as well as rapid regrowth from the few meristems that escape herbicide application. Intensive strategies may be required to eliminate *A. cristatum*, such as cultivation prior to restoration (Howe and Brown 1999, Kindscher and Tieszen 1998).

Soil disturbance caused by seed drilling and tilling prior to broadcasting had inconsistent effects on *A. cristatum* (Fig. 5), possibly because response of the grass is closely linked to weather, which varied among years (Fig. 3). The relationship between *A. cristatum* cover and weather suggests that management should focus on controlling *A. cristatum* in dry years, since cover in untreated control plots increased significantly with spring precipitation and decreased significantly with increasing June temperature. Similarly, the aboveground net production of *A. cristatum* nearby increased significantly with May precipitation (Curtin et al. 2000). The extirpation of 17-yr-old stands of *A. cristatum* in Utah was attributed to drought (Bleak et al. 1965). A combination of treatments, including competition from native grasses, herbicide, and other factors such as intense grazing, all applied in hot dry years, might move populations of *A. cristatum* in restorations closer to extirpation. In contrast to its negative effects on *A. cristatum*, increasing June temperature increased the richness of plots receiving no herbicide (Fig. 3). This result suggests that restoration programs can take advantage of among-year weather variation to decrease *A. cristatum* and increase natives simultaneously (Westoby et al. 1989). Given the great variation in grassland precipitation (Knapp and Smith 2001), few years are close to average, and most can be characterized as wet or dry. Wet years are ideal for establishing native grasses and dry years are more suitable for *A. cristatum* control.

In summary, unpredictable rainfall and large differences among years and sites suggest that restorations in semiarid grasslands may require opportunistic exploitation of wet years for seedling establishment and dry years for the control of non-native species. Broadcasting is recommended over drilling because there were no consistent differences between these methods in their effects on establishment, because broadcasting promoted survivorship, and because broadcasting allows the formation of plant-induced heterogeneity. Although *A. cristatum* was not extirpated, consistent herbicide application over the long term cut its cover in half and doubled species richness. Other management, such as grazing, may have similar effects.

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