



Effects of prairie restoration on weed invasions

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Abstract

Restoration of late-successional plant communities may reduce weed invasion in non-cropland. In studies of natural succession and invasion, however, the presence of late-successional vegetation is often confounded with lower weed propagule pressure and greater time since disturbance. This paper reports a study in which propagule pressure and time since disturbance were controlled by adding weed species to experimental plots dominated by early and late-successional perennial grass species. Seeds of 12 weed species were added to randomized, 6-year-old plots of restored prairie and non-restored, old-field vegetation. Restoration reduced added weed biomass by 92% in year one and 72% in year two, and reduced biomass of four individual weed species, each by more than 82%. Likely mechanisms through which restoration may have reduced invasion include competition and establishment limitation. To examine these mechanisms, subplots were treated with N addition and burning, to reduce competition and remove litter, respectively. Several patterns suggest that competition may have mediated reductions in weed invasion: restoration increased biomass of resident vegetation, decreased light levels, and decreased weed size. Furthermore, adding N reduced effects of restoration on resident and added weeds. The importance of establishment limitation in reducing invasion is suggested by increased litter mass and decreased weed density with restoration. Burning removed litter, and reduced effects of restoration on added weeds. These results suggest that tallgrass prairie restoration can reduce weed invasion, and that this reduction may involve multiple mechanisms, including competition and establishment limitation.

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1. Introduction

Restoration of late-successional plant communities may be a useful weed control strategy in areas not actively managed for agricultural production, such as field margins, roadsides and old fields. Because the competitive ability of dominant species often increases with successional stage (Tilman, 1988; Bazzaz, 1996), while levels of available resources decline (Vitousek

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and Walker, 1987), late-successional plant communities may be more difficult to invade than early-successional plant communities (Rejmanek, 1989; Lepart and Debussche, 1991). Early-successional, agricultural weeds may be particularly susceptible to control through restoration of late-successional vegetation. Such weeds are often categorized as “r-selected” or “ruderal” species, and are characterized by rapid growth, short life span, and abundant seed production (Baker, 1965; MacArthur and Wilson, 1967; Grime, 1977), a life-history strategy that relies on high resource availability (Grime, 1977; Chapin, 1980). Conversely, given the necessity of evolutionary tradeoffs among adaptive traits (Huston and Smith, 1987; Tilman, 1990), early-successional weeds are likely to be poorly adapted to resource-poor, competitive, late-successional environments. It is important to note, moreover, that early-successional species are not limited to annual or herbaceous species. For example, the invasiveness of species within the genus *Pinus* can be successfully predicted by short juvenile periods, frequent reproduction, and small seed size, all characteristics of early-successional trees (Rejmanek and Richardson, 1996).

Evidence suggesting that late-successional vegetation may control weeds comes from declines in invasive species richness and abundance with successional stage (Ramakrishnan and Vitousek, 1989; Rejmanek, 1989; Blumenthal et al., 2003). In such studies, effects of successional stage on invasive species are often confounded with those of propagule pressure (Roy, 1990; Williamson, 1996). Experiments in which propagule pressure is controlled through seed addition (reviewed by Turnbull et al., 2000) provide stronger evidence that late-successional vegetation reduces invasion. Even where propagule pressure is controlled, however, studies of natural succession confound the presence of late-successional vegetation with greater time elapsed since disturbance. If time since disturbance alone accounts for observed effects of natural succession on invasion, then restoration would not be expected to slow invasion. To assess the effect of restoration on invasion two questions must be answered. Does restored late-successional vegetation reduce invasion relative to early-successional vegetation given equal time since disturbance? Furthermore, where the process of restoration requires disturbance, does restored vegetation reduce invasion relative to undisturbed perennial vegetation?

In this experiment, these questions were addressed by adding seed of early-successional weeds to randomized plots of three plant communities: tallgrass prairie restored with disturbance, tallgrass prairie restored without disturbance, and undisturbed resident perennial vegetation. Our three objectives were: (1) to test whether tallgrass prairie restoration can be used as a method of weed control; (2) to assess effects of tallgrass prairie vegetation on weed invasion in the absence of confounding effects of propagule pressure and disturbance; and (3) to examine potential roles of resource competition and establishment limitation in mediating effects of prairie restoration on weed invasion.

2. Methods

This study was located in an old field within the Cedar Creek Natural History Area (CCNHA) in Bethel, MN, an area characterized by very low soil nitrogen (Tilman, 1984). The field was last cultivated in 1965, and contained an excessively-drained fine sand soil (Grigal et al., 1974). The vegetation in the field was dominated by a cool-season grass, *Poa pratensis* L. Both *P. pratensis* and the most common restored prairie grass species in this experiment, *Schizachyrium scoparium* (Michx.) Nash, are common at CCNHA, *P. pratensis* being most abundant in mid-successional fields, and *S. scoparium* in later-successional fields (Tilman, 1988). *P. pratensis* has been shown to be a good competitor for N relative to other perennial cool-season grass species at CCNHA (Tilman and Wedin, 1991; Wedin and Tilman, 1993). The old-field vegetation, by providing a relatively competitive environment, therefore provided a conservative standard against which to evaluate the weed control value of restored prairie.

Weed invasion was compared among three prairie restoration treatments: no restoration (control), prairie seed addition only (sown), and prairie seed addition plus site preparation (intensively restored). Prairie restoration treatments were arranged in a randomized complete block design, with one replication in each of five blocks. The limited number of whole plots, a necessity imposed by a previous experiment, meant that this experiment had relatively little power to test for effects of restoration. Four subplots within each

whole plot, across all five blocks, received the following treatments: control (untreated), burning, N addition, and burning plus N addition. Subplot treatments were completely randomized within whole plots. Seed of 12 locally abundant weed species was added to all subplots.

Whole plot prairie restoration treatments were applied to 6 m × 6 m plots in 1993 (Svenson, 1995). Intensive restoration plots were treated with glyphosate, burned, rototilled to a depth of 5–8 cm, raked, and packed in May 1993. Sown plots received no site preparation. Both sown and intensively restored plots were seeded with 5 prairie grasses and 13 prairie forbs in June 1993. Control plots received no treatment in 1993. In the fall of 1995 all plots were burned. No other management was applied between 1995 and the initiation of subplot treatments in 1998.

Four, 1 m × 2 m subplots were established within each whole plot in the fall of 1998, leaving at least 1 m between subplots. Burning and N addition treatments were randomly assigned to subplots. Burning was conducted to remove litter, which might be expected to reduce seedling establishment. If litter mediates effects of restoration on invasion by reducing establishment, those effects should be reduced by burning. Burning treatments were applied in October 1998. Nitrogen was applied to reduce competition for N. If N competition mediates effects of restoration on invasion, those effects should be reduced by N addition. To ensure that N was the primary limiting nutrient, all plots were treated with P, K and micronutrients. Nitrogen addition plots also received 10 g m⁻² N in May 1999, July 1999, May 2000 and August 2000. In May 1999, N plots were treated with 50 g m⁻² 20-20-20 fertilizer. Non-N subplots received 16.3 g m⁻² potash (0-0-62), 21.5 g m⁻² treble super phosphate (0-46-0), and 2.02 g m⁻² Peters soluble trace element mix (Peters fertilizer products, Fogelsville, PA). For both N and non-N subplots, fertilizer was mixed with 6 l of water and applied by hand with a watering can. At subsequent dates, N was applied as 25 g m⁻² of 40-0-0 slow-release urea pellets (Meister fertilizer; Chisso Corp., Tokyo, Japan), scattered by hand.

Weed species were chosen on the basis of presence on the Minnesota noxious weed list (Durgan, 1998), local abundance, and seed availability. Annual species included were *Chenopodium album* L., *Digitaria ischaemum* (Schreb.) Schreb. ex Muhl., *Polygonum*

convolvulus L., and *Setaria glauca* (L.) Beauv. Biennial/perennial species were *Asclepias syriaca* L., *Berteroa incana* (L.) DC., *Cirsium arvense* (L.) Scop., *Crepis tectorum* L., *Silene latifolia* Poir. spp. *alba* (P. Mill.) Greuter & Burdet, *Sonchus arvensis* L., *Tragopogon dubius* Scop., and *Verbascum thapsus* L., *Berteroa incana* and *C. tectorum* are sometimes winter annuals but functioned as biennials in this experiment. Of these species, all except *D. ischaemum*, *S. glauca*, *T. dubius*, and *V. thapsus* are listed as primary or secondary noxious weeds in Minnesota. Only *A. syriaca* is native to the USA. All weed seed was collected from within 15 km of the study site during the fall of 1998, and stored at 5 °C until seeding. Seeding rates were determined by available quantity, with a maximum seeding rate of 3 g m⁻², similar to rates used in other studies at CCNHA in which seed was added to established perennial plant communities (Tilman, 1997). Seed quantities used were 3 g m⁻² for *A. syriaca*, *B. incana*, *C. album*, *S. glauca*, and *S. latifolia*, 2.5 g m⁻² for *C. arvense* and *D. ischaemum*, 2 g m⁻² for *P. convolvulus*, *S. arvensis*, *T. dubius*, and *V. thapsus*, and 1 g m⁻² for *C. tectorum*. Seed of all weed species was mixed with 200 cc of sand and hand broadcast within subplots in November 1998.

In September 1999, two 15 cm × 2 cm diameter soil cores were taken from each subplot, pooled within subplots, and extracted with 2 M KCl (Carlson et al., 1990). Three grams of soil were added to 30 ml of KCl, shaken for 1 h, and centrifuged at 12,500 × 9.80665 ms⁻² for 10 min. The supernatant was stored for several days at 8 °C before analysis for NO₃ and NH₄ in a flow injection analyzer (Zellweger Analytics Inc., Milwaukee, WI, USA). Due to concern that 1999 methods may not have been sufficiently sensitive to discern differences among treatments, given the very low levels of N present at the site, different methods were used in July 2000: five 20 cm × 2 cm diameter soil cores were pooled from each subplot and extracted with 0.01 M KCl. Concentrations of available N were measured using methods A303-S170 for NO₃ (Alpkem Corporation, 1986) and A303-S020 for NH₄ (Alpkem Corporation, 1989) on a continuous flow RFA 300 Alpkem autoanalyzer (Alpkem Corporation, Clackamas, OR, USA). Remaining soil was weighed, dried at 105 °C, and re-weighed to determine soil water content.

Light measurements were taken on clear or partly cloudy days within 2 h of solar noon. Photosynthetic

photon flux density was measured over a period of 5 s with a LI-COR Quantum line sensor for soil surface measurements, and a LI-COR Quantum point sensor for above canopy measurements (LI-COR Inc., Lincoln, NE, USA). Two or three (depending on the date) soil-surface measurements were made in each subplot. Percent light penetration was calculated as the ratio of soil-surface to above-canopy light intensity.

In each year of the study a separate 1 m × 1 m area within each subplot was harvested to determine weed density and mass. Harvest was timed to allow for maximum growth prior to harvest while avoiding senescence or seed loss. In 1999, few weed species set seed, and all species were harvested in late August and early September. In 2000, several species set seed earlier in the season. *Berteroa incana*, *C. tectorum* and *S. latifolia* were therefore harvested in July, *S. glauca* in August, and all other species in September. All added weed species were clipped within 1 cm of the soil surface, counted, dried at 60 °C and weighed. In 1999, resident vegetation was clipped, separated into prairie forbs, prairie grasses, *P. pratensis*, and other resident species, dried and weighed. In 2000, resident vegetation was separated by species, dried and weighed, allowing calculation of species richness and resident weed biomass. Litter was collected by hand following the September 2000 clipping, dried, and weighed.

Data were analyzed using JMP IN statistical software (version 3.2.6; Sall and Lehman, 1996). All analyses involved a split-plot ANOVA with the response being a function of block (random), restoration treatment (whole plot factor), burning (subplot factor), and N addition (subplot factor). Normality and homoscedasticity assumptions were evaluated for all response variables. Power transformations were used to correct heteroscedasticity and non-normality when necessary, and appropriate transformations were determined using empirical methods described by Kuehl (1994).

3. Results

3.1. Added weeds

Because little seed was produced by any of the weed species, annual weeds were more abundant in

1999, the year following seed addition, than in 2000. Conversely, biomass of biennial/perennial weed species, except for *A. syriaca*, was higher in 2000, following a second year of growth. Discussion was therefore limited to 1999 data for annuals and *A. syriaca*, and 2000 data for perennials and *C. tectorum*. However, statistical analyses were presented for both years for all commonly observed species (Table 1). Commonly observed species include those observed in more than 1/3 of the subplots in a given year. No data was presented for three perennial weed species that were only rarely observed: *C. arvensis*, *S. arvensis*, and *V. thapsus*. Total weed biomass includes biomass of both annual and perennial weeds in each year.

Restoration reduced total biomass of added weed species in both years (Fig. 1, Table 2), and reduced biomass of four of the nine commonly observed weed species (Table 1). No weed species increased in biomass in response to restoration. Relative to controls, intensive restoration and sowing, respectively, reduced total weed biomass by 93% and 90% in 1999 and 76% and 68% in 2000 (Fig. 1, Table 2). Restoration also reduced biomass of individual weed species (Table 1). Compared to controls, intensive restoration and sowing reduced biomass of *C. album* (from 0.35 to 0.053 and 0.075 g m⁻², respectively), *D. ischaemum* (2.4–0.73 and 0.15 g m⁻²), and *S. glauca* (8.5–0.22 and 0.26 g m⁻²), while intensive restoration reduced biomass of *B. incana* (14–0.89 g m⁻²).

Burning and N addition ameliorated the effect of intensive restoration on total weed biomass in 1999 (Fig. 1, Table 2). N addition increased total weed biomass across restoration treatments in 2000. Among individual species, burning increased biomass of *B. incana* and *C. tectorum* across restoration treatments, and reduced the negative effect of restoration on biomass of *C. album* and *D. ischaemum* (Table 1). Effects of N addition on individual species varied widely, and in no case did N ameliorate effects of restoration on individual species biomass (Table 1).

Restoration reduced the density of four weed species: *B. incana* ($P = 0.003$), *C. album* ($P = 0.002$), *D. ischaemum* ($P = 0.0008$), and *S. glauca* ($P = 0.034$) (data not shown). Restoration reduced density of *C. album* only in unburned plots ($P = 0.002$). Restoration reduced the biomass per individual of *C. album* ($P < 0.0001$), *D. ischaemum* ($P < 0.0001$), *S. glauca* ($P = 0.0003$) (data not shown).

Table 1

Transformation used and ANOVA results for weed species biomass as a function of restoration, N-addition and burning

Species	Transformation	Restoration		N-addition		Burning		R × N P-value	R × B P-value	B × N P-value	R × N × B P-value
		Tukey	P-value	Trend	P-value	Trend	P-value				
Annual species 1999											
<i>C. album</i>	log(M)	C ^a S ^b IR ^b	0.0006	+	0.0029	+	<0.0001	NS	0.0039	0.047	NS
<i>S. glauca</i>	log(M)	C ^a S ^b IR ^b	0.0004		NS		NS	NS	NS	NS	NS
<i>D. ischaemum</i>	log(M + 0.0022)	C ^a S ^b IR ^b	<0.0001	–	0.0002	+	<0.0001	NS	0.041	NS	0.042
<i>P. convolvulus</i>	log(M + 0.0039)		NS		NS	–	0.0004	NS	NS	NS	NS
Biennial/perennial species 1999											
<i>A. syriaca</i>	log(M + 0.0009)		NS	–	0.0049		NS	0.0256	NS	NS	NS
<i>C. tectorum</i>	M ^{0.2}		NS		NS	+	0.0006	NS	NS	NS	NS
<i>S. latifolia</i>	log(M)		NS	+	0.0002		NS	NS	0.0015	NS	0.021
<i>B. incana</i>	log(M)	C ^a S ^a IR ^b	0.0007	+	<0.0001	+	<0.0001	NS	NS	NS	0.013
Annual species 2000											
<i>S. glauca</i>	log(M + 0.001)	C ^a S ^{ab} IR ^b	0.021	–	0.041	–	0.034	0.02	NS	NS	NS
<i>D. ischaemum</i>	log(M + 0.001)	C ^a S ^b IR ^b	0.0035	–	<0.0001		NS	<0.0001	NS	NS	NS
<i>P. convolvulus</i>	log(M + 0.001)		NS		NS		NS	NS	NS	NS	NS
Biennial/perennial species 2000											
<i>S. latifolia</i>	log(M + 0.01)		NS	+	<0.0001		NS	NS	NS	NS	NS
<i>B. incana</i>	M ^{0.10}	C ^a S ^a IR ^b	0.0006	+	<0.0001	+	0.0044	NS	NS	NS	NS
<i>C. tectorum</i>	log(M + 0.001)		NS	–	<0.0001	+	0.0062	NS	NS	NS	NS
<i>T. dubius</i>	M ^{0.5}		NS	–	0.018		NS	NS	NS	NS	NS

“M” denotes species biomass. For each main effect the first column denotes the direction of the effect. Pairwise comparisons were conducted among control (C), sown (S), and intensively restored (IR) treatments, using Tukey’s HSD test ($P < 0.05$). Restoration treatments (listed in order of decreasing means) followed by different letters are significantly different from one another. Restoration (R) was tested against Block × R. Burning, N-addition and interactions were tested against residual error. Degrees of freedom were 2 (R), 4 (Block), 8 (Block × R), 1 (Nitrogen[N]), 1 (Burn[B]), 2 (R × N), 1 (B × N), 2 (R × B), 2 (R × B × N) and 35 (Error).

3.2. Resident vegetation

Restoration increased total aboveground biomass of species other than added weeds (Fig. 2). Averaged over years, total biomass was 170 g m⁻² in control plots, 286 g m⁻² in sown plots, and 302 g m⁻² in intensively restored plots. Nitrogen addition increased total biomass in 1999; this positive effect of N addition was stronger in non-restored and in burned plots (Table 2).

Species richness of resident vegetation, measured only in 2000, increased with intensive restoration but not sowing (Table 2). Average richness was 6.7, 7.2, and 10.3 species m⁻² in control, sown, and intensively restored plots, respectively. In all treatments, however, the majority of plant biomass was comprised of one or more dominant grass species. *Andropogon gerardii* Vitm., *S. scoparium* and *Sorghastrum nutans* (L.) Nash, dominated restored plots, while *P. pratensis* dominated control plots. Averaged among years these

species comprised 75%, 96%, and 91% of the total plant biomass in control, sown and intensively restored plots.

As would be expected, the combined biomass of restored prairie species increased with restoration (Table 2). The three dominant C₄ grass species, *A. gerardii*, *S. scoparium*, and *S. nutans*, made up the majority of restored prairie biomass. The following species were also present: *Asclepias tuberosa* L., *Elymus canadensis* L., *Helianthus pauciflorus* Nutt., *Rudbeckia hirta* L., *Solidago rigida* L., *Solidago speciosa* Nutt., *Dalea candida* Michx. ex Willd., *Dalea purpurea* Vent., *Lespedeza capitata* Michx., *Monarda fistulosa* L., *Penstemon gracilis* Nutt., and *Penstemon grandiflorus* Nutt. Six and seven years after prairie restoration, respectively, prairie species made up 82% and 79% of biomass in intensively restored plots, 75% and 67% of biomass in sown plots, and only 17% and 27% of aboveground biomass in control plots (data not shown). Nitrogen addition decreased restored prairie

Table 2

Transformation used and ANOVA results for measurements of vegetation and resource availability as functions of restoration, N-addition and burning

Variable	Transformation	Restoration		N-addition		Burning		R × N	R × B	B × N	R × N × B
		Trend	P-value	Trend	P-value	Trend	P-value	P-value	P-value	P-value	P-value
Added weeds											
Total biomass 1999	log(biomass)	C ^a S ^b IR ^b	<0.0001	+	0.0036	+	<0.0001	0.006	0.0054	0.016	0.0029
Total biomass 2000	log(biomass)	C ^a S ^b IR ^b	0.0008	+	<0.0001		NS	NS	NS	NS	NS
Resident vegetation											
Total biomass 1999	log(biomass)	IR ^a S ^a C ^b	<0.0001	+	<0.0001	+	<0.0001	0.0088	NS	0.0047	NS
Total biomass 2000	log(biomass)	IR ^a S ^a C ^b	0.0003		NS		NS	NS	NS	NS	NS
Prairie 1999	(biomass) ^{0.5}	IR ^a S ^a C ^b	<0.0001	–	0.024	+	0.007	0.01	NS	NS	NS
Prairie 2000	(biomass) ^{0.5}	IR ^a S ^a C ^b	<0.0001	–	0.0018		NS	NS	NS	NS	NS
Non-prairie 1999	log(biomass)	C ^a S ^b IR ^c	<0.0001	+	<0.0001	–	<0.0001	NS	NS	0.0003	NS
Non-prairie 2000	log(biomass)	C ^a S ^{ab} IR ^b	0.0043	+	<0.0001		NS	NS	NS	0.0072	NS
Resident Weeds 2000	log(biomass)	C ^a S ^{ab} IR ^b	0.024	+	0.041		NS	0.046	NS	NS	NS
Species richness	None	IR ^a S ^b C ^b	0.0015	–	<0.0001		NS	NS	NS	NS	NS
Litter	log(litter)	IR ^a S ^a C ^b	<0.0001		NS	–	0.021	NS	NS	NS	NS
Light (% penetration)											
June 1999	None	C ^a S ^b IR ^b	<0.0001	–	<0.0001	+	<0.0001	NS	NS	0.02	NS
August 1999	log(light)	C ^a S ^b IR ^c	<0.0001	–	0.059	+	0.04	NS	NS	NS	NS
June 2000	None	C ^a S ^b IR ^c	<0.0001	–	0.034		NS	NS	NS	0.034	NS
September 2000	None	C ^a S ^b IR ^b	<0.0001		NS		NS	NS	NS	0.0004	NS
Soil NO ₃ (g/μg)											
September 1999	(NO ₃ + NO ₂) ^{-0.5}		NS	+	0.045		NS	NS	NS	NS	NS
July 2000	(NO ₃ + NO ₂) ^{-0.5}		NS	+	<0.0001		NS	NS	NS	NS	NS
Soil NH ₄ (g/μg)											
September 1999	(NH ₄) ^{-0.5}		NS	+	<0.0001	–	0.045	NS	NS	NS	NS
July 2000	(NH ₄) ^{-0.5}		NS	+	<0.0001		NS	NS	NS	NS	NS
Soil water content											
September 1999	None	IR ^a S ^a C ^b	0.0008	–	<0.0001		NS	NS	NS	NS	NS
July 2000	None		NS	+	0.031		NS	0.026	NS	NS	NS

For each main effect the first column denotes the direction of the effect. Restoration (R) was tested against Block × R. Burning, N-addition and interactions were tested against residual error. Degrees of freedom were 2 (R), 4 (Block), 8 (Block × R), 1 (Nitrogen[N]), 1 (Burn[B]), 2 (R × N), 1 (B × N), 2 (R × B), 2 (R × B × N) and 35 (Error). Pairwise comparisons were conducted among control (C), sown (S), and intensively restored (IR) treatments, using Tukey's HSD test ($P < 0.05$). Restoration treatments are listed in order of decreasing means, and those followed by different letters are significantly different from one another.

species biomass in control plots in 1999 and across restoration treatments in 2000. Burning increased prairie species biomass in 1999, but did not significantly affect prairie species biomass in 2000.

Non-prairie resident species included native and exotic species that were present prior to prairie and weed seed addition. Biomass of non-prairie species was dominated by *P. pratensis*, but also included *Achillea millefolium* L., *Ambrosia artemisiifolia* L., *Ambrosia psilostachya* DC., *Artemisia ludoviciana* Nutt., *Bromus inermis* Leyss., *Conyza canadensis* (L.) Cronq., *Cyperus* sp., *Elymus repens* (L.) Gould, *Euphorbia maculata* (L.) Small, *Panicum oligo-*

santhes J.A. Schultes, *Potentilla argentea* L., and *Rumex acetosella* L. Restoration reduced biomass of non-prairie species in both 1999 and 2000 (Table 2). Nitrogen addition increased biomass of non-prairie species in both years. In the absence of N addition, burning reduced biomass of non-prairie species in both 1999 and 2000.

Non-prairie species were classified as resident weeds if they were either exotic to the USA (according to Gleason and Cronquist, 1991) or included in weed keys (USDA, 1971; Stubbendieck et al., 1994). Resident weed biomass was comprised of 2% annual species (*A. artemisiifolia*, *C. canadensis*, *E. maculata*)

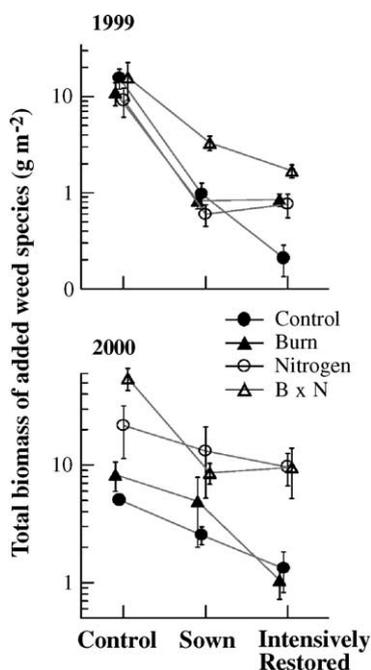


Fig. 1. Total biomass (\pm S.E.) of added weed species as a function of restoration, burning and N addition. Note logarithmic scales and differences in scales of y-axis. ANOVA results in Table 2.

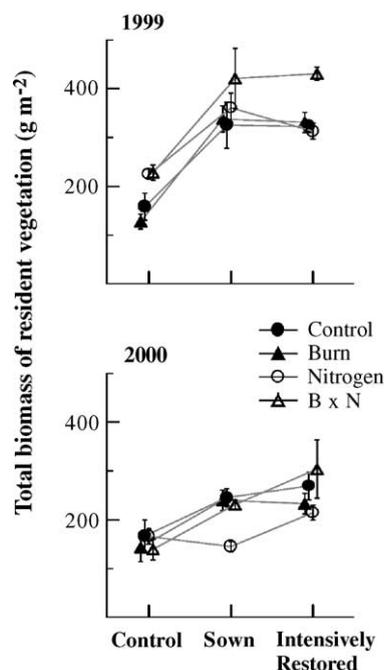


Fig. 2. Total biomass of resident vegetation (\pm S.E.), including all species except for added weed species, as a function of restoration, burning and N addition. ANOVA results in Table 2.

and 98% perennial species (*A. millefolium*, *A. artemisiifolia*, *A. psilostachya*, *A. ludoviciana*, *E. repens*, *P. argentea*, and *R. acetosella*). Patchy distributions of individual resident weed species precluded species-specific analyses. We have previously reported that total biomass of resident weed species decreased with intensive restoration but not sowing (Blumenthal et al., 2003). Nitrogen addition increased resident weed biomass and ameliorated the negative effect of restoration on resident weed biomass (Table 2). Nitrogen increased resident weed biomass by 460% in intensively restored plots (from 0.63 to 2.9 g m⁻²), 46% in sown plots (from 3.0 to 4.4 g m⁻²) and 34% (from 9.8 to 13 g m⁻²) in control plots.

Burning completely eliminated litter from burned plots in October 1998. Less than 2 years after burning, litter mass in burned plots had recovered to 71% of that in unburned plots. Restoration increased litter accumulation across burning treatments, from 47 g m⁻² in control plots to 147 g m⁻² in sown plots and 178 g m⁻² in intensively restored plots.

3.3. Available resources

Restoration consistently reduced light penetration (Table 2), from an average of 48% in control plots to 29% in sown plots and 22% in intensively restored plots. Restoration had no effect on available NH₄ and NO₃, and increased soil water content across treatments 1999 and in plots without N addition in 2000 (data not shown). Nitrogen addition reduced light penetration at three of four sampling dates, and increased NO₃ and NH₄ in both years (data not shown). Burning increased light penetration and decreased NH₄ in 1999, the year following the burning treatment (data not shown).

4. Discussion

In this experiment, restoration of relatively late-successional prairie species reduced invasion by early-successional weeds (Fig. 1). Two factors that commonly confound the relationship between succes-

sional stage and invasion, time since disturbance and propagule pressure (Rejmanek, 1989), were unlikely to have caused the reduction in invasion with successional stage in this experiment. Were invasion caused by disturbance, it would have been greater in the more recently disturbed, intensively restored plots than in the other two treatments, the opposite of the observed pattern. Furthermore, propagule pressure was controlled by adding weed species to all treatments. Although two added weed species were also present at the site prior to seed addition, one, *B. incana*, was rarely observed outside seed addition subplots, suggesting that the pre-existing seedbank was negligible relative to added seed. Differences in pre-existing seedbanks among restoration treatments could have contributed to observed decreases in numbers and total biomass of *S. glauca*. A conservative approach to the response of *S. glauca* would be to consider only average plant size, which also decreased with restoration.

The degree to which prairie restoration reduced weed growth in this experiment, the apparent consistency of the response among weed species, and the difficulty of attributing weed responses to propagule pressure or disturbance, suggest that prairie restoration can be an effective means of controlling early-successional weeds. Furthermore, the reductions in invasion observed in sown plots suggest that simply adding seed of prairie species to resident vegetation may sometimes be sufficient to control weeds. It should be noted, however, that the infertile study site may have contributed to the success of sowing alone in this study.

Understanding why prairie restoration reduced weed invasion in this experiment would help to predict the invasibility of other restored prairies and other late-successional plant communities by early-successional weeds. Our data suggest that both resource competition and establishment limitation may have played a role in inhibiting invasion of restored prairie.

Competition is hypothesized to decrease invasion (Cavers and Harper, 1967; Crawley, 1989), while high resource availability is thought to increase invasion (Davis et al., 2000). In this experiment, restoration greatly increased biomass of resident vegetation (Fig. 2), decreased light availability, and decreased per-plant size of three weed species. These results are

consistent with the hypothesis that competition from prairie species and consequent reductions in resource availability may have reduced weed invasion. Although differences in N availability were not observed with restoration (Table 2), N addition increased biomass of added weeds (Fig. 1, 1999 only) and resident weeds more in restored than in control plots, suggesting that prairie may have reduced weed invasion by reducing N availability.

In as much as restored and non-restored plant communities differ in their ability to compete with weeds, this effect could be caused by differences in species phenology, richness or identity (Crawley, 1989; Levine and D'Antonio, 2000; Naeem et al., 2000). In this experiment two C₄ weed species and two C₃ weed species had lower biomass in the predominantly C₄ restored plots than the predominantly C₃ non-restored plots. Therefore, differences in phenology associated with photosynthetic pathway cannot alone account for the observed reductions in weed biomass. Because restored plots contained more species than non-restored plots in this experiment, species richness could underlie the effect of restoration on weed invasion. However, given that all plots were dominated by very few species, and average richness differed by less than 4 species per plot, species identity rather than number is likely to have been the primary influence on weed environments (e.g., Crawley et al., 1999).

The idea that establishment limitation can reduce community invasibility is suggested by observed correlations between bare ground and invasibility (Harper, 1965; Crawley, 1987). Restored prairie may reduce bare ground, and therefore weed establishment, through the deposition of litter. The large increases in litter mass and decreases in weed numbers with prairie restoration are consistent with this hypothesis. The effects of burning are also consistent with this hypothesis: burning removed litter, increased light penetration, and ameliorated the effect of restoration on biomass of *C. album* and *D. ischaemum* (Table 1), and total biomass of added weed species in 1999 (Fig. 1).

While prairie restoration may hold promise as a method of weed control, important limitations to this approach can be anticipated. First, the competitive ability of native species depends on the environment in which that competition occurs (Wedin and Tilman,

1993; Bobbink et al., 1998). Where the environment has been substantially altered, native late-successional species are less likely to be competitively superior to weeds. Understanding how the influence of prairie restoration on weeds varies with soil, climate and disturbance regime will be necessary to predict large-scale effects of prairie restoration on weeds. Second, the observation that all communities are invulnerable (Crawley, 1987; Roy, 1990) suggests that there will be important invaders, particularly those of relatively undisturbed ecosystems, that are not excluded, or are even facilitated, by restoration. To gauge the utility of prairie restoration for weed control, we will need to discover which and how many weeds are inhibited by prairie restoration. If the pattern seen in this experiment holds for other early-successional weeds, such as those important to cropping systems, prairie restoration may be particularly useful in intensively managed agricultural landscapes.

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