Assessing grassland restoration success: relative roles of seed additions and native ungulate activities

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Summary

1. Grassland restorations often lack rare forb and grass species that are found in intact grasslands. The possible reasons for low diversity include seed limitation, microsite limitation and a combination of both. Native ungulates may create microsites for seedling establishment in tallgrass prairie restorations by grazing dominant species or through trampling activities, but this has never been tested in developing prairies.

2. We experimentally tested for seed and microsite limitation in the largest tallgrass prairie restoration in the USA by adding rare forb and grass seeds in two trials inside and outside native ungulate exclosures. We measured seedling emergence because this stage is crucial in recruiting species into a community. We also measured light, water and standing crop biomass to test whether resource availability could help to explain seedling emergence rates.

3. Ungulates increased light availability for each sampling time and also increased above-ground net primary productivity (ANPP) during summer.

4. Seedling emergence of rare prairie forbs and grasses was consistently greater when we added seeds.

5. Seedling emergence was conditionally greater with a combination of seed additions and grazing, but grazing alone was unable to increase emergence.

6. When ungulates increased seedling enhancement, the mechanism was partially associated with increased water and light availability.

7. Exotic and cosmopolitan weed seedling emergence was not affected by grazing.

8. Synthesis and applications. These results suggest that tallgrass prairie restorations are primarily seed limited and that grazing alone may not be able to increase seedling emergence of rare species without the addition of seeds. Therefore, adding seeds to grassland restorations may increase seedling emergence of rare species, and mimicking effects of grazing may increase emergence when seeds are added.

Key-words: Bos bison, Cervus elaphus, diversity, grazing, Iowa, net primary productivity, seedling emergence, tallgrass prairie

Introduction

Ecosystem restoration is becoming a more common way to increase native species habitat. Typically, restorations are attempted by adding seeds from nearby remnants to a previously converted ecosystem (Sluis 2002; Polley, Derner & Wilsey 2005). Seedlings of multiple species are expected to emerge, survive and establish reproducing populations, and then populations are expected to assemble into a community similar to the original system. The seedling emergence stage is important in this process because it funnels individuals into the system. Contrary to expectations, restored ecosystems often have lower plant species richness and diversity than their unaltered counterparts (Galatowitsch & van der Valk 1996; Martin, Moloney & Wilsey 2005; Polley, Derner & Wilsey 2005) and species richness has been observed to decline over time instead of increase as expected (Sluis 2002).

Typically, low species diversity is attributed to either (i) seed limitation or (ii) seedling microsite limitation.
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(Eriksson & Ehrlen 1992; Zobel et al. 2000; Foster et al. 2004; Henry et al. 2004). The seed limitation hypothesis suggests that plant community richness and diversity are limited by the species pool (Gough, Grace & Taylor 1994). Seed additions have increased species richness and diversity of some native plant communities and agriculturally improved grasslands (Pywell et al. 2002; Smith et al. 2002; but see Wilsey & Polley 2003). If restorations are seed limited, then adding seeds of a large number of species should increase diversity and recruitment of rare species even in systems with high dominance. Alternatively, the microsite hypothesis suggests that one or a few strongly dominant species suppress seedlings (Hartnett, Hickman & Walter 1996; Collins et al. 2000). In this scenario, seeds or propagules are not limiting but seedlings fail to establish reproducing populations. Dominant grass patches are usually larger in restorations than in intact grassland (Derner et al. 2004). Dominance by C₄ grasses, which can occur as soon as 3 years after establishment, can be especially high in the nutrient-rich environments that characterize most restorations (Baer et al. 2002; Baer et al. 2004; Camill et al. 2004). Large grass canopies and abundant litter can reduce light and water availability, which are crucial to seedling survival (Fahnestock & Knapp 1993; Haugland & Froud-Williams 1999; Xiong & Nilsson 1999). Common management practices, such as frequent spring burning and grazing exclusion, could exacerbate this problem (Collins et al. 1998; Howe 2000). Thus, anything that reduces grass dominance should alleviate competition with rare species and should increase seedling establishment and diversity (Foster & Gross 1997).

According to the intermediate disturbance and grazing optimization hypotheses, intermediate levels of grazing should produce the highest levels of species diversity, but also the highest levels of net primary productivity (NPP) in an ecosystem (Grime 1973; Connell 1978). The question of whether native ungulate grazing can increase seedling emergence and diversity is becoming more relevant because grazers such as bison Bos bison L. and wapiti Cervus elaphus L. are increasingly being reintroduced (Knapp et al. 1999; Larkin et al. 2004). Management strategies, such as mowing, aimed at decreasing the biomass of dominant species have shown increased seedling survival in some experimental and pasture plantings (Burke & Grime 1996; Hutchings & Booth 1996; Lawson, Ford & Mitchley 2004). Moderate grazing by native ungulates, a common grassland disturbance, could have positive impacts on plant species diversity in intact grasslands by reducing dominant grasses and increasing light availability (Hartnett, Hickman & Walter 1996; Collins et al. 1998; Knapp et al. 1999). Moderate grazing would therefore be expected to produce non-linear effects on diversity in restorations, with higher levels of diversity at intermediate grazing intensities (Smith et al. 2000). However, this may be restricted to intact systems, where there is a propagule source available for recruitment into the community (Hartnett, Hickman & Walter 1996; Collins et al. 1998). Furthermore, because intermediate levels of grazing can also produce the highest levels of NPP (McNaughton 1979; Dyer, Turner & Seastedt 1993), grazing may lead to increased resource uptake by plants. Productivity is already high in grassland restorations, often higher than in comparable remnants (Baer et al. 2002; Camill et al. 2004; Martin, Moloney & Wilsey 2005). If intermediate grazing increases production of dominant species above and beyond what is already high, then intermediate grazing in restorations, unlike in intact grasslands, may actually lessen positive effects on seedling emergence and diversity. Thus increased productivity in restorations because of moderate grazing might nullify potentially positive effects of grazing on microsite availability.

Finally, seed limitation and low seedling emergence because of grass dominance may interact to limit diversity in grassland restorations. A combination of adding seeds and increasing microsite availability may be necessary to favour seedling emergence (Burke & Grime 1996; Turnbull, Crawley & Rees 2000; Foster & Dickson 2004).

Our objectives were to determine: (i) if native ungulates increase availability of resources crucial to seedling emergence and (ii) whether seed additions, native ungulate grazing or a combination of both enhance native prairie seedling emergence while having little or no effect on non-native and cosmopolitan weeds in tallgrass prairie restorations. Our focus was on seedling emergence, a key stage in the establishment of grassland plants. Whether seedlings can establish viable populations is a longer term question that will not be considered here.

Materials and methods

STUDY SITE

The objective of the Neal Smith National Wildlife Refuge (NS) prairie project is to restore a large tallgrass prairie ecosystem using locally collected seeds combined with prescribed fire and grazing by native ungulates. The restoration is located on the Walnut Creek watershed in Jasper County, Iowa, USA (41°33′N, 93°17′W). The refuge currently spans 2104 ha, approximately 1200 ha of which have been seeded with tallgrass prairie species, beginning in 1992 and continuing to the present day. Grazing ungulates (B. bison and C. elaphus) were introduced to a 303-ha enclosure in 1996 and 1998, respectively, which is where our study took place. Approximately 35 B. bison and 15 C. elaphus occupied the area during our study. Land use prior to prairie seeding included corn Zea mays L. and soybean Glycine max (L.) Merr rotations and a few scattered pastures. There were 20 different plantings in this area (mean of approximately 14 ha each) and each planting was seeded with separate bulk seed mixes collected from local prairie remnants. Management practices after planting included
Native ungulates and seed additions in restorations

yearly spring burning during the early years followed by 2-year burn rotations, which is a common practice for beginning restorations (Packard & Mutel 1997; Copeland, Sluis & Howe 2002). Mowing was done when necessary to control weedy and invasive species (P. Drobeny, personal communication). Our plots were not burned or mowed in 2003 or 2004, the years of sampling.

Historically, precipitation at the site has a unimodal distribution and peaks in May and/or June, with an average of approximately 880 mm year$^{-1}$. Weather in 2003 was much warmer and drier than during 2004. Between May and August, the peak growing months, temperatures and monthly precipitation averaged 21.7 °C and 13.3 mm in 2003 and 19.7 °C and 143.8 mm in 2004.

To standardize our sampling, we randomly selected eight plantings within the enclosure that were seeded between 1994 and 1996 on formerly cropped areas. Four plantings north of a dirt road included 6.7 kg ha$^{-1}$ of Elymus canadensis L. in the seed mixture as a putative cover crop, whereas four plantings south of the road did not (for effects of the cover crop see Martin, Moloney & Wilsey 2005).

EXPERIMENTAL DESIGN

A randomized complete block split-plot design with unequal replication was used, with grazing or exclosures applied to main plots and seed addition treatments (described below) applied to subplots. Two 6 × 8-m grazed plots were established 5 m away on either side of a permanent 6 × 8-m permanent enclosure in June 2003 in each of the eight plantings (blocks). Two grazed plots were sampled per planting because of increased heterogeneity with grazing (Knapp et al. 1999). By request of the refuge staff, exclosures were kept out of view of visitors where possible and this precluded completely random locations.

MAIN PLOT SAMPLING DESIGN

Biomass and above-ground net primary productivity (ANPP) (general indicators of resource uptake and competition intensity) were estimated to compare grazed and exclosed plots (Baer et al. 2004). Above-ground biomass was clipped to 2 cm in a 40 × 100-cm quadrat randomly placed in each exclosure (ng) and grazed plot (gr), and surface litter was collected in June and August 2003 and in March, June and August 2004. Biomass was sorted into live and dead components, and live material was sorted by species, dried for 48 h at 65 °C, and weighed. Subsequently, estimates were made for the following biomass components: proportion of exotic biomass (exotic/total), proportion of total grass biomass (grass/total) and C$_4$ grass biomass (C$_4$/total), and combined litter and standing dead biomass. Each of these different components of biomass could suppress seedling emergence and species richness in grassland restorations (Howe 2000; Camill et al. 2004). Plant species were designated as native or exotic based on Eilers & Roosa (1994).

We estimated grazing intensity (GI) and used polynomial regressions to determine if GI was quadratically related to response variables (McNaughton 1979, 1985). Simply comparing grazed and ungrazed plots can be misleading in cases where grazing is non-linearly related to response variables (Grime 1973; Connell 1978; McNaughton 1979). Above-ground NPP and GI were estimated for grazed plots ($n = 16$) using the moveable exclosure approach (McNaughton 1985; McNaughton, Milchunas & Frank 1996) during three periods: June–August 2003 and March–June and June–August 2004. One 3 × 4-m temporary exclosure was established at each site in March 2004 and was moved in June 2004 to measure consumption and GI (McNaughton 1985). Above-ground NPP (g m$^{-2}$ day$^{-1}$) was calculated as a positive biomass increment + consumption for each time period. Grazing intensity was calculated as GI = C/NPP (McNaughton 1985; Wilsey et al. 2002), with GI set to 0 if consumption estimates were negative.

Environmental variables were measured to determine whether grazing was creating microsites favourable for seedling emergence. Soil moisture and percentage light at the soil surface were measured monthly from July to September 2003 and from May to October 2004 (soil moisture was not measured in July–August 2003 because of equipment failure) in each plot using a Moisture Point® MP-917 Time Domain Reflectometry system (30 cm rods; Environmental Sensors, Victoria, Canada) and a 1-m Decagon® AccuPar Ceptometer (Decagon Devices Inc., Pullman, WA). Sampling points were randomly located, and two measures of incident light were taken during each sampling time.

Species diversity was calculated from biomass to determine if grazing exclusion affected diversity. Diversity was calculated at the quadrat scale for each grazed and exclosed plot. Diversity was quantified with Simpson’s diversity ($1/D$), where $D = 1/\Sigma p_i^2$ and $p_i$ = relative biomass of each species $i$, and was then decomposed into species richness ($S$) and evenness ($1/D/S$) to determine if each component of diversity differed (Buzas & Hayek 1996; Smith & Wilson 1996; Martin, Moloney & Wilsey 2005).

SUBPLOT SEED ADDITIONS

Two seed additions of rare native prairie forbs and grasses were made to separate, randomly located 1-m$^2$
subplots within each plot using two different methods. These were compared to one control subplot (no seed addition) within each main plot. Therefore, three subplots were located in each main plot (exclosure or grazed plot), with a total of nine subplots in each block. The first seed addition treatment consisted of adding seeds of 10 species collected by hand from local remnants in June 2003. The second treatment consisted of adding seeds of 25 species from a local seed company (Allendan Seed Co., Winterset, IA, USA) in April 2004 in a second set of subplots. More species were used in the second trial than the first because seeds were more readily available from the seed company, and we wanted to mimic the high number of species found at the neighbourhood scale in remnants (Martin, Moloney & Wilsey 2005). Seeds were added with equal relative abundances at a rate of 19 700 seeds m\(^{-2}\) for both trials (1970 and 788 per species for addition experiments 1 and 2, respectively). Seed numbers were based on number of seeds in a typical seed rain rate found by Rabinowitz & Rapp (1980) in a Missouri tallgrass prairie. Seed viability was not tested with seeds collected from remnants, but all but one species readily germinated in greenhouse pots grown for seedling reference samples. Mean seed viability for seeds obtained from the seed company was 81\% (range 49–96\%). Seeds were hand-scattered in each 1-m\(^2\) subplot and existing vegetation and litter were shaken to aid seeds in reaching the soil surface. Species added in the first experiment were *Bouteloua curtipendula* (Michx.) Torrey, *Sporobolus asper* (Michx.) Kunth, *Solidago speciosa* Nutt., *Pycnanthemum virginianum* (L.) Dur. & Jackson, *Dalea purpurea* Vent., *Chamaecrista fasciculata* (Michx.) Greene, *Amorpha canescens* Pursh, *Lespedeza capitata* Michx., *Monarda fistulosa* L. and *Eryngium yuccifolium* (Michx.) (Eilers & Roosa 1994). Species added in the second experiment included all those added in the first experiment, plus *Potentilla arguta* Pursh, *Silphium laciniatum* L., *Echinacea pallida* Nutt., *Ratibida pinnata* (Vent.) Barnh., *Artemisia ludoviciana* Nutt., *Liatrix pycnostachya* (Michx.), *Verbena stricta* Vent., *Helianthus rigidus* (Cass.) Desf., *Gentiana andrewsii* Griseb., *Tradescantia bracteata* Small, *Viola pedatifida* G. Don, *Anemone cylindrica* Gray, *Phlox pilosa* L., *Schizachyrium scoparium* (Michx.) Nash and *Solidago rigidia* L. (Eilers & Roosa 1994).

All forb seedlings, including species added from the mix as well as volunteers, were identified to species and counted in a randomly placed 20 \times 50\-cm quadrat within each subplot, to estimate seedling emergence. Volunteers were included because some added species were already in the seed bank and therefore could not be distinguished from experimentally sown seedlings. Exotic and cosmopolitan weed seedlings were counted to test concerns about disturbance from native ungulates increasing weeds in grasslands (Smith & Knapp 1999). Grass seedlings were only counted if the species was added. Seedlings were counted if they were up to 7.5 cm tall or up to any height if they were annuals, and were counted once per month during the growing season, beginning the month after seeds were added.

### Statistical Analyses

Randomized block split-plot *ANOVAs* were used, with planting as a random block term. All grazing effects were tested with the main plot error term (planting \(\times\) grazed), and seed and seed–grazed interactions were tested with the subplot error term. Repeated-measures *ANOVA* was used to compare grazed \((n = 16)\) and exclosed plots \((n = 8)\) for existing vegetation and resource variables, with time 0 data (measurements taken before enclosures were constructed) as a covariate (except for NPP, for which time 0 data could not be calculated). We dropped the covariate from each model if it was not significant \((P > 0.05)\). Variables were logarithmically transformed (biomass, standing dead and litter), square-root transformed (proportion of exotic biomass) or arcsin square-root transformed (proportion of C\(_4\) and grass) to improve normality when necessary. All analyses were done with *PROC MIXED* in SAS (Littell, Stroup & Freund 2002).

The first and second seed additions were analysed separately because they had different numbers of species, addition dates and weather conditions. A seedling enhancement effect, ln\[(added seedlings + 1)/(control seedlings + 1)\], was calculated to quantify the number of seedlings that did not emerge from the existing seed bank but emerged from added seeds. This derived variable eliminated non-normality in data as a result of having many zeroes in control subplots. To test if seed additions increased seedling numbers above those of controls, seedling enhancement effects were tested against 0 with a \(t\)-test. Grazing effects on seedling enhancement over time were analysed with repeated-measures *ANOVA* of corresponding data. Exotic seedling and seedling diversity variables were analysed with repeated-measures (means for 2003 and 2004) *ANOVA* for the first seed addition, and with regular *ANOVA* for the second addition. Data were averaged across months because raw data had too many zeroes to analyse each sampling time. Seedling Simpson’s diversity \((1/D)\), species richness \((S)\) and evenness \((1/D/S)\) were calculated in each subplot to determine if seed additions or grazing improved seedling diversity.

We used polynomial regression to test for quadratic and linear relationships between mean GI (grazed plots only) and response variables. Mean GI was calculated by averaging GI across time because of non-normally distributed data. We used path analysis to test for direct and indirect associations of grazing on seedling enhancement. A direct pathway was tested of GI on biomass, biomass on light and water availability, and light and water on seedling enhancement. An indirect path was tested of GI on NPP, and NPP on seedling enhancement. This indirect pathway could be significant if increased NPP had additional effects on seedlings.
because of non-light and water effects, such as increased nutrient uptake of vegetation.

Results

GRAZING EFFECTS ON VEGETATION

Only two response variables differed significantly between grazed and exclosed plots and another was marginally significant (Tables 1 and 2). Above-ground NPP m$^{-2}$ was 1.2, 1.1 and 8.0 times as large in grazed plots depending on time period, and the difference was only significant for June–August 2004 (Table 1 and Fig. 1a). Light availability at the soil surface was 1.7 times as great in grazed plots, and this was fairly consistent across time periods (Table 1 and Fig. 1b). Combined standing dead and litter biomass m$^{-2}$ was marginally significantly lower in grazed plots (Tables 1 and 2).

No response variables were quadratically related to mean GI (grazing intensity) ($F_{1,15}$ between 0.03 and 3.07, $P$ between 0.10 and 0.88). Mean GI was highest in June–August 2004, when 68% of NPP was consumed (range 0–100%, SE 6), followed by 49% during June–August 2003 (range 0–100%, SE 8). It was much lower during spring 2004 (mean 14%, range 0–37%, SE 3). Biomass m$^{-2}$ was negatively related to mean GI

![Fig. 1. Grazing (n=16) or exclosure from grazing (n=8) differences for (a) ANPP ($P<0.01$) and (b) percentage light availability at soil surface ($P<0.01$). Vertical bars are ±1 SE.](image)
Table 2. Mean (SE) of response variables measured to test effects of native ungulate grazing in a tallgrass prairie restoration

<table>
<thead>
<tr>
<th>Grazed (n = 16)</th>
<th>Exclosed (n = 8)</th>
</tr>
</thead>
<tbody>
<tr>
<td>August 2003</td>
<td>June 2004</td>
</tr>
<tr>
<td>Biomass (m⁻²) 5.87 (0.14)</td>
<td>5.82 (0.14)</td>
</tr>
<tr>
<td>Litter and standing dead (m⁻²) 6.28 (0.14)</td>
<td>6.09 (0.14)</td>
</tr>
<tr>
<td>Proportion exotic biomass (0.4 m⁻²) 0.17 (0.06)</td>
<td>0.33 (0.06)</td>
</tr>
<tr>
<td>Proportion exotic S (0.4 m⁻²) 0.35 (0.03)</td>
<td>0.37 (0.03)</td>
</tr>
<tr>
<td>Proportion grass (0.4 m⁻²) 1.13 (0.06)</td>
<td>1.01 (0.06)</td>
</tr>
<tr>
<td>Proportion C₄ grass (0.4 m⁻²) 0.95 (0.08)</td>
<td>0.83 (0.08)</td>
</tr>
<tr>
<td>Alpha S (0.4 m⁻²) 10.53 (0.82)</td>
<td>12.63 (0.82)</td>
</tr>
<tr>
<td>Alpha E (0.4 m⁻²) 0.25 (0.02)</td>
<td>0.24 (0.02)</td>
</tr>
<tr>
<td>Alpha 1/D (0.4 m⁻²) 2.55 (0.33)</td>
<td>2.89 (0.33)</td>
</tr>
</tbody>
</table>

Table 2. Mean (SE) of response variables measured to test effects of native ungulate grazing in a tallgrass prairie restoration

Percentage water

<table>
<thead>
<tr>
<th>Grazed (n = 16)</th>
<th>Exclosed (n = 8)</th>
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</thead>
<tbody>
<tr>
<td>38.92 (1.04)</td>
<td>38.24 (1.04)</td>
</tr>
</tbody>
</table>

Figure 2. Relationships between (a) biomass and (b) evenness as expected. Species evenness at the 0.4 m scale was significantly related to mean GI (r = 0.54, slope = 0.89, Fig. 2b).

Mean change in evenness (1/D/S) Mean change in biomass (ln g m⁻²)

(a) Grazing intensity

(b) Grazing intensity

(c) Grazing intensity

(d) Grazing intensity

(e) Grazing intensity

(f) Grazing intensity

(g) Grazing intensity

(h) Grazing intensity

(i) Grazing intensity

(j) Grazing intensity

(k) Grazing intensity

(l) Grazing intensity

(m) Grazing intensity

(n) Grazing intensity

(o) Grazing intensity

(p) Grazing intensity

(q) Grazing intensity

(r) Grazing intensity

(s) Grazing intensity

(t) Grazing intensity

(u) Grazing intensity

(v) Grazing intensity

(w) Grazing intensity

(x) Grazing intensity

(y) Grazing intensity

(z) Grazing intensity

[Table 2 continued]
Table 3. Mean numbers of seedlings m$^{-2}$ counted in the first and second seed addition experiments. Species listed comprised approximately 90% of those counted. Added species are denoted with an asterisk (*) and exotic species are in bold (Eilers & Roosa 1994)

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common name</th>
<th>2003</th>
<th>2004</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Grazed, no seed (n = 16)</td>
<td>Grazed, seed (n = 16)</td>
<td>Exclosed, no seed (n = 8)</td>
</tr>
<tr>
<td><strong>Seed addition 1</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ambrosia artemesiifolia</td>
<td>Common ragweed</td>
<td>24.1 (20.1)</td>
<td>11.6 (5.2)</td>
</tr>
<tr>
<td>Aster pilosus</td>
<td>Hairy aster</td>
<td>5.3 (2.9)</td>
<td>6.3 (3.7)</td>
</tr>
<tr>
<td>Chamaecrista fasciculata*</td>
<td>Partridge pea</td>
<td>4.4 (1.6)</td>
<td>5.3 (1.7)</td>
</tr>
<tr>
<td>Conyza canadensis</td>
<td>Horseweed</td>
<td>3.4 (1.8)</td>
<td>3.4 (1.3)</td>
</tr>
<tr>
<td>Daucus carota</td>
<td>Queen Anne's lace</td>
<td>25.9 (15.0)</td>
<td>18.8 (6.5)</td>
</tr>
<tr>
<td>Lespedeza capitata*</td>
<td>Round-headed bush clover</td>
<td>0.0 (0.0)</td>
<td>6.6 (2.5)</td>
</tr>
<tr>
<td>Monarda fistulosa*</td>
<td>Wild bergamot</td>
<td>2.5 (1.8)</td>
<td>6.6 (2.2)</td>
</tr>
<tr>
<td>Taraxacum officinale</td>
<td>Dandelion</td>
<td>30.6 (11.3)</td>
<td>30.6 (7.3)</td>
</tr>
<tr>
<td>Other</td>
<td></td>
<td>15.3 (7.7)</td>
<td>15.5 (19.0)</td>
</tr>
<tr>
<td><strong>Total number of seedlings</strong></td>
<td></td>
<td>111.6 (35.6)</td>
<td>104.1 (14.8)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Seed addition 2</strong></th>
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<tr>
<td>Aster pilosus</td>
<td>Hairy aster</td>
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<td></td>
</tr>
<tr>
<td>Chamaecrista fasciculata*</td>
<td>Partridge pea</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conyza canadensis</td>
<td>Horseweed</td>
<td>6.4 (5.1)</td>
<td>3.6 (3.8)</td>
</tr>
<tr>
<td>Dalea purpurea*</td>
<td>Purple prairie clover</td>
<td>0.0 (0.0)</td>
<td>18.4 (4.2)</td>
</tr>
<tr>
<td>D. c. carota</td>
<td>Queen Anne's lace</td>
<td>17.6 (10.1)</td>
<td>39.9 (14.6)</td>
</tr>
<tr>
<td>Lespedeza capitata*</td>
<td>Round-headed bush clover</td>
<td>0.0 (0.0)</td>
<td>96.9 (9.6)</td>
</tr>
<tr>
<td>Monarda fistulosa*</td>
<td>Wild bergamot</td>
<td>2.1 (1.1)</td>
<td>9.6 (2.5)</td>
</tr>
<tr>
<td>Taraxacum officinale</td>
<td>Dandelion</td>
<td>87.3 (26.5)</td>
<td>100.6 (25.4)</td>
</tr>
<tr>
<td>Other</td>
<td></td>
<td>10.1 (2.6)</td>
<td>59.3 (9.7)</td>
</tr>
<tr>
<td><strong>Total numbers of seedlings</strong></td>
<td></td>
<td>139.3 (34.5)</td>
<td>135.1 (35.0)</td>
</tr>
</tbody>
</table>
relationship with GI in either experiment (first experiment, linear effects $F_{1,13} = 0.01, P = 0.93$, quadratic effects $F_{1,13} = 1.68, P = 0.22$; second experiment, linear effects $F_{1,13} = 0.63, P = 0.44$, quadratic effects $F_{1,13} = 2.14, P = 0.17$).

Path analysis from both experiments indicated that biomass m$^{-2}$ was negatively related to light and soil water availability, and that water was positively related to seedling enhancement more regularly and strongly than light (Fig. 4 and Table 5). The indirect pathway indicated that GI was positively related to NPP in the first (significant for 2004 only) and second experiments, but NPP never significantly explained seedling enhancement beyond effects of light and water (Fig. 4 and Table 5).

Exotic species seedling emergence

Exotic and cosmopolitan weed seedling emergence were not clearly affected by treatments in either experiment (Table 4). Exotics such as *Taraxacum officinale*...
Table 5. Path analysis results to determine direct effects of grazing intensity on biomass, biomass on light and water, and indirect effects of grazing intensity on NPP and NPP on seedling enhancement for the first and second seed addition experiment. Ten (first) or 25 (second) rare prairie species were added to plots. Numbers represent standardized regression coefficients. Significance is indicated by *P between 0·02 and 0·05 and **P ≤ 0·01

<table>
<thead>
<tr>
<th>Variable</th>
<th>First experiment</th>
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<th>Second experiment</th>
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<tbody>
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<td></td>
<td>Second half 2003</td>
<td>First half 2004</td>
<td>Second half 2004</td>
<td>First half 2004</td>
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<td>Direct effects</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GI → biomass</td>
<td>0·00</td>
<td>0·05</td>
<td>−0·27</td>
<td>0·05</td>
</tr>
<tr>
<td>Biomass → light</td>
<td>−0·73**</td>
<td>0·04</td>
<td>−0·65**</td>
<td>0·04</td>
</tr>
<tr>
<td>Biomass → water</td>
<td>−0·61**</td>
<td>−0·24</td>
<td>−0·65**</td>
<td>−0·24</td>
</tr>
<tr>
<td>Light → enhancement</td>
<td>0·30</td>
<td>0·15</td>
<td>−0·16</td>
<td>0·16</td>
</tr>
<tr>
<td>Water → enhancement</td>
<td>−0·23</td>
<td>0·51**</td>
<td>0·43**</td>
<td>0·56**</td>
</tr>
<tr>
<td>Indirect effects</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GI → NPP</td>
<td>0·09</td>
<td>0·75**</td>
<td>0·55*</td>
<td>0·75**</td>
</tr>
<tr>
<td>NPP → enhancement</td>
<td>0·11</td>
<td>−0·19</td>
<td>−0·16</td>
<td>−0·06</td>
</tr>
<tr>
<td>Unobserved</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>o1 → biomass</td>
<td>1·00**</td>
<td>1·00**</td>
<td>0·96**</td>
<td>1·00**</td>
</tr>
<tr>
<td>o2 → light</td>
<td>0·68**</td>
<td>1·00**</td>
<td>0·76**</td>
<td>1·00**</td>
</tr>
<tr>
<td>o3 → enhancement</td>
<td>0·95**</td>
<td>0·82**</td>
<td>0·91**</td>
<td>0·81**</td>
</tr>
<tr>
<td>o4 → water</td>
<td>0·79**</td>
<td>0·97**</td>
<td>0·76**</td>
<td>0·97**</td>
</tr>
<tr>
<td>o5 → NPP</td>
<td>1·00**</td>
<td>0·66**</td>
<td>0·83**</td>
<td>0·66**</td>
</tr>
</tbody>
</table>
Seedling enhancement was limited by seed availability in these tallgrass prairie restorations, which suggests that restorations are similar to many old fields in their lack of propagule availability (Tilman 1997; Zobel et al. 2000; Pywell et al. 2002). Many tallgrass prairie restorations are initiated by harvesting seeds from remnants in the autumn (Polley, Derner & Wilsey 2005), when C₄ grass seed is most abundant relative to other species. Evidence from this study suggests that seedling emergence of rare forbs is very low nearly 10 years after initial seeding, and that adding seeds of rare forb and grass species that are typically lacking in restorations can increase seedling emergence, the first step in recruiting species into the community.

Our finding that seed additions and grazing combined could increase seedling emergence suggests that grazing mammals might increase seedling recruitment in some situations. Turnbull, Crawley & Rees (2000) found that, overall, a combination of adding seeds and inducing disturbance to reduce dominant vegetation was most important for recruitment. Rhinanthus minor, a parasitic plant, also increased seedling recruitment of added species by reducing competitive effects of dominant vegetation (Pywell et al. 2004). However, the effect of grazing on seedling emergence with seed additions in the restoration was conditional. This conditionality may have been the result of very different weather between years, but our design could not determine this definitively. Although grazing combined with seed additions conditionally improved seedling emergence, we did not find that emergence was quadratically related to grazing intensity, as predicted by the intermediate disturbance hypothesis. Knapp et al. (1999) proposed that target grazing intensity in intact tallgrass prairies should be about 25% of annual above-ground primary production, based on historic grazing intensities. We observed grazing intensities in the restoration that were sometimes double that estimate. In our study, it appears that grazing had an increasingly beneficial (i.e. linear) effect on seedling emergence when seeds were added.

Increases in exotic or cosmopolitan weed species may negatively impact diversity and are a primary concern in grazed grasslands (Smith & Knapp 1999; Hulme & Brenner 2006). Grazing, which is utilized in management of both intact grasslands and restorations (Collins et al. 1998; Knapp et al. 1999), could increase weeds by the same mechanisms that increase native plant recruitment (Smith & Knapp 1999). In contrast, high dominance may enhance seedling emergence in some grasslands (Wilsey & Polley 2002; Smith et al. 2004). We found no relationships with grazing on exotics, suggesting that grazing may not be important to exotic recruitment in these restored grassland communities.

Discussion

Previously, we found that conventional prairie restoration at the study site was able to restore common native species but not species diversity of nearby prairie remnants (Martin, Moloney & Wilsey 2005). Here we tested hypotheses regarding why diversity was lower. Our results suggest that seedling emergence in low diversity restorations is seed limited but that native ungulates can sometimes increase emergence as well. Seedling enhancement increased with water and light availability, which suggests that, when grazing is enhancing emergence, the mechanism may be associated with grazers having a direct effect on water and light. A combination of seed additions and grazing led to the highest amount of seedling emergence, but this result was conditional, i.e. it was found only in the second trial and year. However, grazing alone did not increase seedling emergence in either trial.

Biomass and NPP, general indicators of resource uptake in grasslands, are usually affected by grazing (Semmartin & Oesterheld 1996). We found that total biomass declined with grazing intensity, and water and light availability were higher when biomass was lower, which suggests that grazing decreased biomass enough to increase resource availability. However, ANPP was also higher with grazing, suggesting that defoliated plants were readily recovering from defoliation and utilizing available resources (Knapp et al. 1999; Wilsey et al. 2002). Nevertheless, increased levels of ANPP did not appear to have effects above and beyond those correlated with water and light availability in reducing seedling enhancement.
associated with a decrease in dominance from ungulate activities (Hartnett, Hickman & Walter 1996). However, grazers may not be able to recruit new species and enhance richness if rare plant species are not available either in the seed bank or as vegetative propagules, which appears to be the case in this restoration. Seed additions, on the other hand, tended to increase richness but had a smaller negative effect on evenness.

It is important to point out that we only tested for seed limitation with the emerging seedling community. Although seedling emergence is a crucial step towards recruitment into a community, seedlings must establish viable populations before they will influence diversity in the longer term. Wilsey & Polley (2003) found that, even when seedling emergence was high, plant diversity was unchanged because of low seedling survival in a Texas grassland. It is too early to estimate establishment success, and longer term monitoring is needed to test the hypothesis that seed additions and grazing will increase diversity of vegetation in the long term.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Seedling numbers of rare species increased greatly when seeds were added, suggesting that these restorations were severely seed limited. Grazers increased water and light availability by decreasing above-ground biomass, and water increased seedling enhancement more regularly and strongly than did light. Grazing increased ANPP, but ANPP did not explain seedling emergence above and beyond water and light effects. Under certain conditions, seedling emergence was positively influenced by grazing when seeds were added. However, grazing by itself did not increase seedling emergence, probably because seeds of rare species were not available to emerge. These results suggest that it may be advantageous to mimic positive effects of native ungulates in restorations when seeds or propagules of rare species are available to emerge. If propagule availability is low, positive effects of grazing alone will not increase seedling emergence. Improving seedling emergence in restorations may therefore require adding seeds even after dominant plants are established, while simultaneously mimicking grazing effects to increase light and water availability. In contrast to management strategies in intact grasslands (Collins et al. 1998), utilizing grazing without propagules may not improve seedling emergence in restorations. However, longer term monitoring is necessary to determine if seed additions and grazing promote long-term plant diversity.

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References


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