

RESEARCH ARTICLE

Testing Disturbance, Seeding Time, and Soil Amendments for Establishing Native Warm-Season Grasses in Non-Native Cool-Season Pasture

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Abstract

Incorporating native C4 grasses into pastures dominated by C3 grasses can augment tallgrass prairie restoration efforts while improving pasture production. We examined grazing and burning disturbances to promote the establishment of native C4 grasses sown in fall and spring into existing C3 pastures. A second objective was to test the role of resource availability on C4 grass establishment by manipulating inorganic nitrogen (N) availability within each seeding time and management treatment combination. We drill seeded three C4 native prairie grasses (*Andropogon gerardii* Vitman [big bluestem], *Panicum virgatum* L. [switchgrass], and *Sorghastrum nutans* (L.) Nash [Indiangrass]) into an existing C3 grass pasture and applied combinations of disturbance (grazed or burned) and soil amendments (carbon [+C], ambient [N0], nitrogen [+N]) treatments. We monitored native grass recruitment within these treatments over a 3-year period (2005 through 2007). Whereas

native grasses established under rotational grazing, higher recruitment was observed with annual burning. There were periods of N immobilization with C addition, but we observed no benefit to native grass recruitment. Native grasses did not establish under N addition, irrespective of disturbance and seeding, and were not affected by seeding time. Regression tree analyses showed that the best predictor of native grass density in 2006 and 2007 was belowground net primary production in 2006, which was greater under burned plots in 2006 but did not differ between C addition and ambient soil N treatments. This research demonstrates that burning facilitates and nutrient enrichment inhibits native warm-season grass reintroduction and establishment into non-native cool-season grass dominated pastures.

Key words: ANCOVA, carbon addition, grazed pasture, linear mixed-effects models, regression tree, tallgrass prairie.

Introduction

Conservation and restoration efforts can be limited by the amount and condition of available land. Furthermore, protected and refuge areas are threatened by increasing anthropogenic pressures (DeFries et al. 2007). These areas often occur in patchy distributions across the landscape (Rosenzweig 2003) and there is increasing need to restore habitat connectivity (Western 2001). In the United States, 52% of the land area is used for agricultural purposes (USDA-ERS 2002). Thus, bringing restoration projects to agricultural lands could connect plant communities across the landscape, aiding in the recovery and preservation of native species.

Coexistence of native tallgrass warm-season (C4) grasses in established exotic cool-season (C3) grasslands has been promoted both as a realistic restoration goal (Bakker et al. 2003) and an agronomically useful plant community for grass-based production agriculture (Jackson 1999). Native C4 grasses once dominated tallgrass prairies of North America, but they have almost vanished from the landscape (Samson & Knopf 1994) as a consequence of changes in land management (e.g. fire suppression) and conversion of prairie to crop and grazing systems, resulting in profound ecological consequences (Rhemtulla et al. 2007). Reintroducing native grasses to pasture lands could greatly expand restoration efforts in the temperate grasslands of the United States. Furthermore, coexisting C3 and C4 grasses can improve the distribution and quantity of forage production (Albertson & Weaver 1944; Lorenz & Rogler 1972; Springer et al. 2007). In an agricultural setting, however, studies investigating combined use of C3 and C4 grasses have typically either involved extensive pasture renovation and/or C3 and C4 grasses in spatially separate areas (Jung et al. 1985; Moore et al. 2004). Pasture renovation can incur high costs from taking land out of production for months, as well as create massive disruption to a system—increasing

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the potential for soil erosion and soil carbon loss. Introducing C4 species to an intact C3-dominated plant community may be a sound alternative to potentially costly and disturbance promoting pasture renovations (Conant et al. 2007).

Some level of disturbance is necessary to introduce C4 grasses into established C3 grass systems (Lawson et al. 2004; Pywell et al. 2007). Burning is an effective management tool to enhance C4 grass growth (Copeland et al. 2002; Towne & Kemp 2003), but it has not yet been established whether grazing could substitute for burning as a restoration approach, particularly in production-oriented agricultural systems or in areas where burning is less feasible. Furthermore, there is limited information on how grazing affects C4 grasses sown into C3 pastures. Grazing and burning both remove vegetation and alter aboveground competitive interactions, but may have different effects on native grass establishment in pastures stemming from the differing ways that these disturbances remove biomass and affect ecosystem processes (Collins et al. 1998). Unlike burning, grazing usually occurs in repeated pulses of defoliation within a year—the amount, intensity, and frequency of which are determined by the management regime. Grazing involves not only defoliation but also trampling and nutrient redistribution (Bardgett & Wardle 2003), whereas burning defoliates plants and affects net primary production, species dominance, soil moisture, nitrogen availability, and hydrology of grasslands (Knapp et al. 1988). In addition, because of selective grazing the vegetation structure of grazed grasslands can be more spatially variable than after burning, which can uniformly and completely remove vegetation (Fuhlendorf & Engle 2004).

Belowground resource availability may also affect the restoration of C4 grasses into C3 pastures. Differences in nitrogen (N) availability have been shown to alter competitive interactions in N-limited ecosystems. If more resource-efficient C4 grasses become established in existing C3 pastures they should dominate over time if the resource for which competition is strongest becomes limiting (Tilman 1985). Carbon (C) addition—in the form of sugar, sawdust, or wood chips—can promote microbial immobilization of soil N in grasslands and reduce the available N (Wilson & Gerry 1995; Morghan & Seastedt 1999; Blumenthal et al. 2003). The photosynthetic pathway of C4 grasses makes them more nutrient use efficient than C3 species, which should lead to greater dominance under N-limited conditions relative to C3 grass species.

The overall goal of this study was to determine whether agronomic and restoration goals can be compatible in a production-oriented grassland ecosystem. Specifically, the first objective of this study was to test whether grazing or burning in combination with seed addition was a more effective management approach to promote the establishment of native C4 grasses into existing C3 temperate pastures. We also included fall and spring seeding time treatments to increase inference across restoration approaches. The second objective was to test the effects of resource availability on C4 grass establishment by manipulating inorganic N availability levels within each seeding time and management treatment combination. To

address these objectives, we drill seeded three C4 native prairie grasses (*Andropogon gerardii* Vitman [big bluestem], *Panicum virgatum* L. [switchgrass], and *Sorghastrum nutans* (L.) Nash [Indiangrass]) into an existing C3 pasture at two seeding times (fall 2003 or spring 2004). We then applied disturbance (grazed or burned) and soil amendment (nitrogen, carbon, or ambient) treatments according to a split–split plot design. From 2005 through 2007 we measured native grass establishment and environmental variables that we hypothesized would be important correlates with native grass recruitment including soil texture, nitrogen mineralization, total above- and below-ground productivity, and plant cover.

Methods

Study Site

This study was conducted in southwestern Wisconsin, U.S.A. The climate is temperate-continental with cold winters and warm summers. Average temperatures range from -7°C in January to 20°C in July. Temperatures during the study period (2004 through 2007) were close to these averages. Average annual precipitation is approximately 850 mm, with about two-thirds of the annual precipitation falling during the growing season, roughly April to October. Yearly total precipitation for 2004, 2005, 2006, and through 2007 were 872, 646, 1141, and 1396 mm, respectively. The soil of the experiment area was classified as Fayette silt loam (fine-silty, mixed, superactive, mesic Typic Hapludalfs) with 12–20% southeast facing slopes. In 2000, the study site had a soil pH of 6.2, an organic matter content of 3.8%, phosphorous (P) concentrations of 14 ppm, and potassium concentrations of 68 ppm. The farm produced beef cattle (*Bos taurus*) using a management-intensive rotational grazing system (i.e. short duration [<12 hours to 3 days] grazing with high stocking densities and 2- to 5-week rest periods [Paine et al. 1999]). The plots in the 1.5-ha experiment area all had the same management history, rotational grazing for more than 15 years. The pasture was dominated by non-native C3 grasses—*Schedonorus pratensis* Huds. P. Beauv. (meadow fescue), *Schedonorus phoenix* (Scrop.) Holub (tall fescue), and *Poa pratensis* L. (Kentucky bluegrass)—but had a relatively high species richness with approximately 25 species of grasses, forbs, and legumes (Woodis & Jackson 2009). There were no fertilizer inputs since 2001. Prior to this, N and P fertilizers were applied as needed based on soil test results.

Experimental Design and Restoration Approach

The native grass seed was collected from Wisconsin prairie sites in October 2003 and was not de-awned prior to sowing. Before disturbance or soil amendments' treatments were applied, we seeded three native C4 species (*Andropogon gerardii* Vitman [big bluestem], *Panicum virgatum* L. [switchgrass], and *Sorghastrum nutans* (L.) Nash [Indiangrass]) at a rate of approximately 1.0 g pure live seed/m² into an existing 1.5-ha cool-season pasture in fall (November 2003) and

spring (May 2004). The seed mix (based on weight) consisted of 70% big bluestem, 15% Indiangrass, and 15% switchgrass. Based on published data of native grass seed number per unit weight (Diboll 1997), we estimate that we added approximately 400 pure live seeds/m² into the pasture. No-till drills were used for fall (Truax “Flex-II,” Truax Company, Inc., Minneapolis, MN, U.S.A.) and spring (Tye “Pasture Pleaser,” The Tye Company, Lockney, TX, U.S.A.) seeding. Seeds were drilled to depth of 3–6 mm. Seeding of native grasses into the experimental plots only occurred once (fall 2003 and spring 2004).

Following seeding, disturbance and soil amendment treatments were applied from 2004 through 2007 in a hierarchical design (split–split) using three 0.5-ha pastures as experimental blocks (Fig. 1). The whole-plot factor disturbance (i.e. grazed or burned) was randomly applied to one-half of each 0.5-ha block. There was no untreated control as C4 grasses do not recruit in these grasslands unless there is some level of disturbance (Lawson et al. 2004; Martin & Wilsey 2006; Pywell et al. 2007). Each disturbance level was split and randomly assigned to fall (2003) or spring (2004) seeding of native grasses. Each seeding time was split in three subplots randomly assigned to one of the three soil amendment levels: ambient (N0), N fertilization (+N), or C application in the form of sawdust (+C). Grazing treatments followed the rotational grazing system and were initiated in early June of 2004. The burn treatment occurred every April from 2005 through 2007 and removed all of the aboveground vegetation. These plots were not defoliated for the remainder of the year. The +C plots received sawdust in two applications (June and August) at a total rate of 1.2 kg sawdust m⁻² yr⁻¹ (approximately 600 g C m⁻² yr⁻¹) in 2004 and 2005. The sawdust came from several Wisconsin sawmills, was finely textured and dry, and had a C:N ratio of 174. The +N plots received a total of 135 kg N ha⁻¹ yr⁻¹ applied in June and August in 2004, 2005, and 2007. In 2004 and 2005, N was applied in the form of ammonium nitrate (NH₄NO₃) and in 2007 urea ([NH₂)₂CO) was used. The ambient treatment did not receive soil amendments.

This experimental design resulted in three replicates (one per block) for each treatment combination with a total of 36 experimental units (each 5 × 70 m) with $n = 3$ for disturbance levels, $n = 6$ for seeding time, and $n = 12$ for the amendment treatment levels. In 2007, half of the area in each burned plot was removed from the experiment to be used for other purposes, which reduced the sample size for seeding time to $n = 3$ and amendments to $n = 6$ for that year.

Data Collection

Percent cover of all pasture plant species cover was measured twice annually (spring and fall) from 2004 through 2006 using the line-point method, where the first interception of a sharpened rod with any part of herbaceous vegetation was recorded for 10 hits along a 10 × 50-cm quadrat (Heady et al. 1959). Native grasses were not detected using the line-point method until 2005, at which point a detailed approach to quantify native grass density was initiated. Native grass density

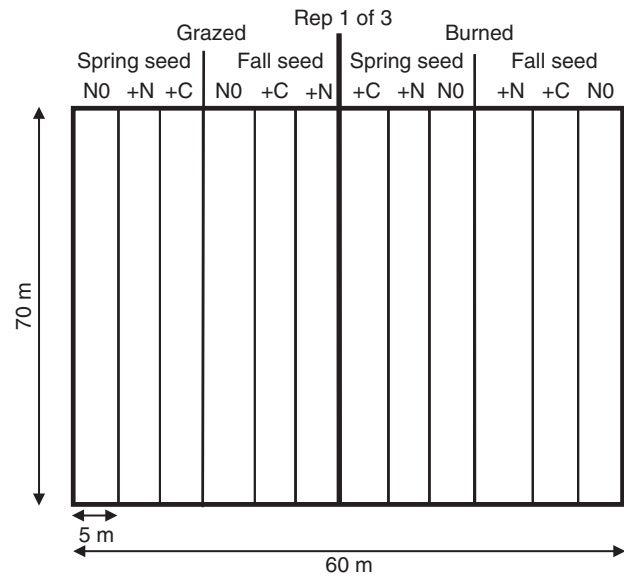


Figure 1. One of three blocks representing the split–split plot field experiment design. The whole factor treatment was disturbance—plots were either spring burned (2005–2007) or grazed (2004–2007) under a monthly rotational grazing system. Under each of those treatments, plots were further split into season of seeding of three native species (fall 2003 or spring 2004). Within each seeding time, plots received one of three soil amendments: ambient (N0) plots were not amended; +C plots received 1.2 kg sawdust·m⁻²·yr⁻¹ (2004 and 2005); and +N plots received 135 kg N·ha⁻¹·yr⁻¹ (2004, 2005, and 2007).

was measured in late August/early September from 2005 through 2007 by counting the number of native grass tillers in a 1-m² quadrat placed every 10 m along the experimental unit. Totals from these plots were averaged to calculate density as native grass tillers/m². This was repeated five times at 10-m intervals for a total of 50 hits per experimental unit.

Annual aboveground net primary production (ANPP) was calculated as the sum of monthly differences in biomass between the inside and outside of grazing-exclusion cages during the growing season of 2004 and then from allometric relationships between biomass and leaf area index in 2005 and 2006 (Doll et al. 2009). Belowground net primary production (BNPP) was determined in 2005 and 2006 using root in-growth cores (Bledsoe et al. 1999); detailed methods described in Doll et al. (2009).

Soil samples were collected in the spring (2004 through 2006), summer (2005 and 2006), and fall (2004 through 2006) for gravimetric water content (GWC), net nitrogen mineralization, soil texture, and percent C and N. Soil cores (2.5 cm diameter × 10 cm deep) were taken at 12 locations stratified randomly along each experimental unit. For each experimental unit, cores were composited and sieved (2 mm) then subdivided for subsequent analyses. Approximately, 15 g of soil was weighed, dried at 105°C to constant mass, and reweighed to calculate GWC. We used 2 M KCl extractions with an aerobic incubation period of 7 days (28°C) to measure potential net

N mineralization (or immobilization) by calculating the difference between final and initial inorganic N levels (Robertson et al. 1999). In 2004 and 2005, flow injection analysis (Lachat QuikChem, Lachat Instruments, Loveland, CO, U.S.A.) was used to determine soil NH_4^+ and NO_3^- . For samples collected in 2006, we used an adapted microplate spectrophotometer method (Rhine et al. 1998) to determine soil NH_4^+ and NO_3^- . Soil texture was determined from fall 2005 soils using the hydrometer method (Elliot et al. 1999). Soil percent N and C were determined using an automated elemental analyzer (Flash EA 1112, CE Elantech, Lakewood, NJ, U.S.A.) after soils were dried at 60°C and pulverized.

Statistical Analyses

A two-phase approach was used to determine treatment effects on native grass establishment. First, we assessed whether native grasses recruited above a threshold of one tiller/m² by 2007. If this criterion was met, we tested whether the rate of recruitment was affected by treatment level. We used a linear mixed-effects model to evaluate native grass recruitment in each treatment combination over time, measured by native grass tillers/m². The approach was analogous to an analysis of covariance (ANCOVA) with disturbance, soil amendment, and seeding time as fixed effects and year as a covariate. The random effects were specified as block, disturbance nested within block, seeding time nested within disturbance, and amendments nested within seeding time. This random effects structure accounted for the restrictions on randomization imposed by the hierarchical experimental design. Native grass tiller density was transformed ($\log[\sqrt{y} + 1]$) to meet the assumptions of normality, and regressed against year with treatment combinations as grouping factors. We used Akaike Information Criterion (AIC) to select the simplest model, and the restricted maximum likelihood algorithm (REML) to fit the data to the model by estimating random and fixed effects,

and the variance–covariance structure among factors. Model selection procedures followed Crawley (2002), where terms were dropped and the subsequent model compared to the more complex model with likelihood ratio tests. If models were significantly different ($p < 0.05$), the model with the lower AIC was chosen, otherwise we continued model selection with the more parsimonious model. Model simplification for the fixed effects structure started with a fully parameterized model with each level of disturbance, seeding time, and soil amendment fit with a separate slope and intercept. This model was tested against reduced models where the slope parameters for factor levels were removed. If separate slopes were needed for treatment levels, it would signify that native grasses were recruiting at different rates per treatment level. To test for nonlinear components in the model, the square power of the covariate year was used and tested against a linear model. The variance–covariance structure was determined by fitting saturated models with the autoregressive function (AR1) that fit a parameter describing residuals whose correlation structure declines exponentially with time. We also tested for heteroskedasticity by fitting separate error terms for each treatment level combination. After the random effects and error matrices were in place, we visually assessed residual versus fitted plots for randomness and quantile–quantile plots for departures from normality, but found none.

For the second phase of analysis, we used regression trees to determine which environmental variables (Table 1) explained the most deviance in native grass tiller density in 2006 and 2007 (transformed as mentioned above). Regression trees are a useful nonparametric method for exploring patterns in data (De'ath & Fabricius 2000; Crawley 2002). They explain the variation of a single response variable (in this case, native grass density) by repeatedly splitting the data into more homogenous groups using combinations of predictor variables, which can be numeric and/or categorical. The split that maximizes the

Table 1. Variables used in regression trees as potential predictors of 2006 and 2007 native grass tiller density.

Variable	Time Points
Soil GWC (w/w)	June 2004, November 2004, May 2005, July 2005, October 2005, May 2006, July 2006
Net nitrogen mineralization ($\mu\text{g N gds}^{-1}\text{day}^{-1}$)	June 2004, November 2004, May 2005, July 2005, October 2005, May 2006, July 2006, October 2006
NH_4^+ pools (ppm)	June 2004, November 2004, May 2005, July 2005, October 2005, May 2006, July 2006, October 2006
NO_3^- pools (ppm)	June 2004, November 2004, May 2005, July 2005, October 2005, May 2006, July 2006, October 2006
Soil silt (%)	October 2005
Soil sand (%)	October 2005
Soil clay (%)	October 2005
ANPP ($\text{g m}^{-2}\text{ yr}^{-1}$)	2004, 2005, 2006
BNPP ($\text{g m}^{-2}\text{ yr}^{-1}$)	2005, 2006
Soil carbon:nitrogen	June 2004, November 2004, May 2005, July 2005, October 2005, May 2006, July 2006
Soil nitrogen (%)	June 2004, November 2004, May 2005, July 2005, October 2005, May 2006, July 2006
Soil carbon (%)	June 2004, Nov 2004, May 2005, July 2005, October 2005, May 2006, July 2006
Species cover* (%)	June 2004, September 2004, May 2005, September 2005; May 2006, September 2006
Bare ground cover (%)	June 2004, September 2004

* Species with >10% average cover ($n = 38$). gds = g dry soil.

homogeneity of the two resulting groups is chosen from all possible splits of all the predictor variables (De'ath & Fabricius 2000). If a split is based on a numeric variable, it is defined by values less than, and greater than a cut-off value; if it is based on a categorical variable, a certain level or combination of levels defines a group. This process is repeated on each subset of data, and continues until no further reduction in deviance is obtained or there are too few data points to justify further subdivision (Crawley 2002). Trees can be "pruned" to a certain number of nodes based on the objectives of a given analysis. The environmental predictor variables used in the regression trees are listed in Table 1. Because ancillary data were not collected in 2007, the same environmental variables were used for both the 2006 and 2007 regression trees. Trees were pruned by calculating the deviance explained by each predictor variable. If a split did not contribute to 10% or more of the deviance explained in the tree it was removed. S-Plus 8.0 (Insightful Corporation, Seattle, WA, U.S.A.) was used for all data analyses.

Results

Native grasses did not recruit above the threshold level (1 tiller/m²) in any +N plots, so those plots were not used in ANCOVA or regression tree analyses. Native grass averages for all other treatment levels were greater than or equal to 1 tiller/m². Model selection for native grass recruitment resulted in different slopes for both disturbance and soil amendment levels, but not for seeding time (Table 2). The direction and magnitude of factor level slopes differed from that of the grand slope (Table 2, column 3); there was a greater slope for burned and N0 plots compared to grazed and +C plots (Table 2), that is, native grasses recruited faster under burning than grazing and under ambient than +C plots (Fig. 2).

After pruning the regression trees to include only those factors that accounted for at least 10% of the deviance, BNPP in 2006 was the only factor remaining in each tree and therefore best predicted both 2006 and 2007 native grass tiller densities. The regression trees explained 72.5 and 77.9% of the deviance in 2006 and 2007 tiller density, respectively. The regression trees split the plots into two levels of native tiller grass density (low or high): plots with BNPP levels of

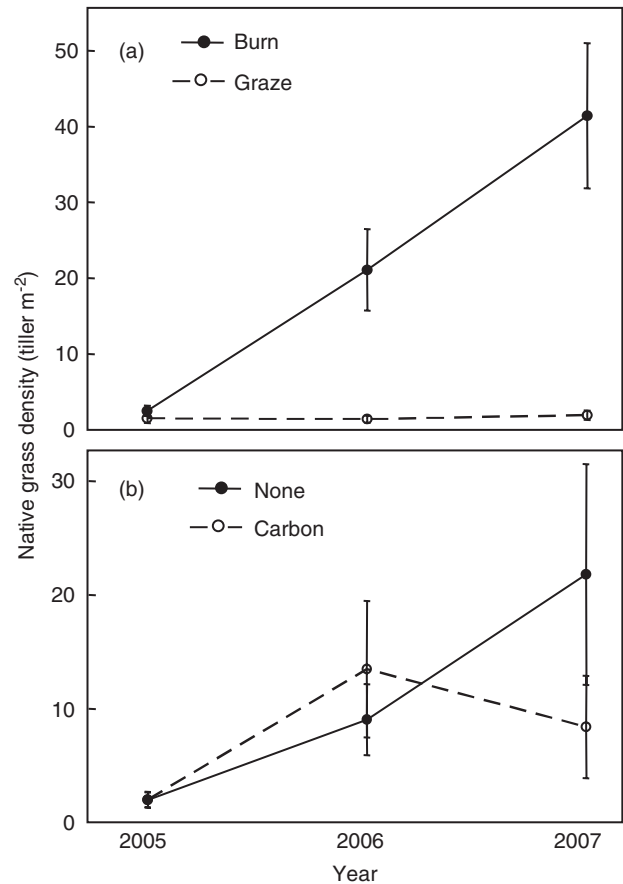


Figure 2. Native grass density (tiller/m²) from 2005 through 2007 (mean \pm 1 SE, $n = 12$ for 2005 and 2006; for 2007 $n = 12$ for graze, 6 for burn, and 9 for soil amendment plots) under (a) disturbance (burn and graze) and (b) soil amendment (ambient and carbon) treatments. No native grasses established under the +N treatment.

>314.5 g/m² in 2006 and 355.2 g/m² in 2007 had greater native tiller densities than plots with BNPP levels below those values. Native grass density (tillers/m²) was transformed ($\log[\sqrt{y} + 1]$) as such, in those units, low and high plots averaged 0.53 and 1.54, respectively; for 2007, low and high plots averaged 0.60 and 1.92, respectively. Carbon addition

Table 2. ANCOVA output from the mixed-effects model with native grass density (tiller/m², transformed as $\log[\sqrt{y} + 1]$) regressed on treatment combinations (disturbance, soil amendment, seeding time) with year as a continuous covariate.

Parameter	Interpretation	Estimate	df	t Value	p Value
Intercept	Grand intercept	0.399	50	1.985	0.052
Year	Grand slope	0.419	50	5.342	<0.001
Disturbance	Intercept adjustment for grazed plots	0.169	2	0.841	0.489
Seeding time	Intercept adjustment for spring seeded plots	0.367	5	2.730	0.041
Soil amendment	Intercept adjustment for ambient plots	-0.232	50	-1.343	0.185
Year \times disturbance	Slope adjustment for grazed plots	-0.508*	50	-6.991	<0.001
Year \times soil amendment	Slope adjustment for ambient plots	0.180*	50	2.346	0.023

df, degrees of freedom.

* This value indicates the direction and magnitude of difference from the grand slope.

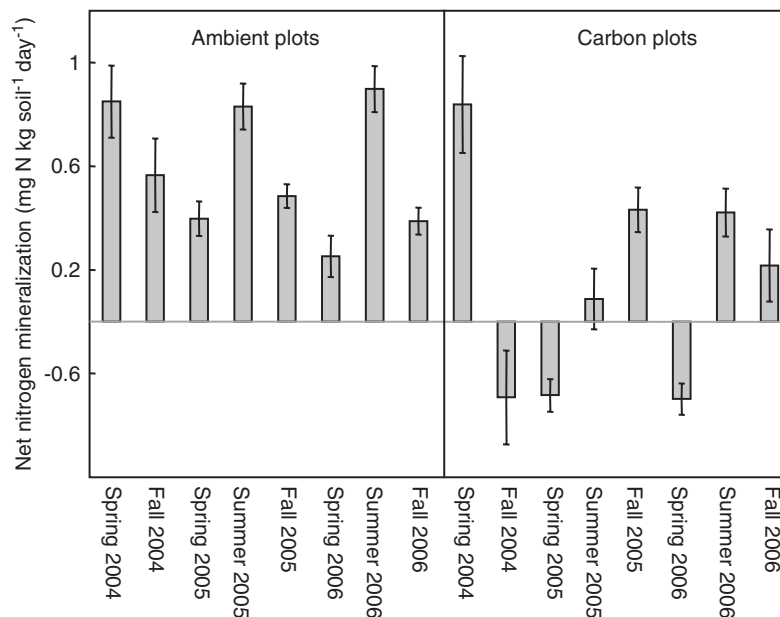


Figure 3. Net nitrogen mineralization (mean \pm 1 SE, $n = 12$ [$n = 11$ for spring 2005 ambient; $n = 24$ for fall 2005, spring 2006, and summer 2006]) from 2004 through 2006 for ambient and carbon amendment plots.

appeared to have the intended effect as there were periods of N immobilization (Fig. 3). Aboveground NPP was not lowered by C addition from 2004 through 2006; in 2006, burned plots had greater BNPP than grazed plots (Doll et al. 2009).

Discussion

Compared to burning, grazing did not increase native grass recruitment as measured by native grass tiller density. Our results are consistent with many who have documented increased C4 grass abundance with prescribed fire (Howe 1995; Cuomo et al. 1998; Prober et al. 2005) and suggest that burning favored the native seeded species within this highly competitive matrix of C3 grasses. In contrast, grazing resulted in low levels of native grass recruitment, suggesting that it may have limited use as a restoration tool in an existing cool-season pasture. The lower recruitment of native C4 grasses in grazed plots may have resulted from the management regime rather than an effect of grazing, per se. For example, less intense and/or less frequent defoliation than our grazing treatment (i.e. >10 cm clipping height and/or >40 days recovery period) may have better promoted the persistence of the C4 grasses (Mousel et al. 2005). However, C4 grasses have the ability to be highly productive in a cool-temperate environment under frequent defoliation, and certain C3 and C4 grasses appear to be suitable for use in mixtures (Belesky & Fedders 1995). In addition, other studies have found that reducing the existing biomass in grasslands by grazing or clipping can enhance the survival of sown species (Hutchings & Booth 1996; Lawson et al. 2004). Our results are not consistent with these studies, and suggest that perhaps the high intensity of our grazing treatment negatively affected native grasses directly (sensu

Jackson et al. 2010) rather than having the intended effect of decreasing competition from other species in the system.

Native grasses also may have recruited more in burned compared to grazed plots because plants in burned plots were allowed to mature into their reproductive phase. The grazed plots in our study were defoliated regularly throughout the growing season so seeds were never allowed to develop and fall into the grazed plots. It is possible that greater recruitment under burning occurred in part due to this additional seed input, but others have found that recruitment by seed of warm-season grasses in established native prairie is small relative to vegetative spread (Benson & Hartnett 2006).

The best predictor of 2006 and 2007 native grass tiller density was 2006 BNPP, which was greater in burned plots (Doll et al. 2009). Our methods do not allow us to attribute the increase in BNPP to either C3 or C4 grasses. This suggests that increased root production in response to burning may promote native grasses within a competitive C3 pasture. Others have found that grass root production in native prairie can increase in response to burning (Johnson & Matchett 2001). On the other hand, the effect of grazing on grassland root mass has been mixed (Milchunas & Lauenroth 1993; Bardgett & Wardle 2003).

Native grasses recruited best under ambient soil conditions compared to both C and N additions. The C addition treatment resulted in periods of immobilization, but this did not confer a competitive advantage to the C4 species as we had expected. Responses of native species to C addition, however, have been equivocal across a range of grassland types (Corbin & D'Antonio 2004; Bleier & Jackson 2007). Responses of non-native species have been more consistent than native species, with many studies reporting lower productivity or cover of

non-native species with C addition (Blumenthal et al. 2003; Baer et al. 2004; Prober et al. 2005). In our study system, C addition did not lower total productivity of the grassland (C3 and C4 species combined) (Doll et al. 2009). The amount of C added in this study was close to the middle of the range added in similar studies, so the lack of strong plant responses likely was not the result of inadequate C addition. As the sawdust was surface applied, perhaps already established root systems in the pasture were at depths below the area of reduced net N mineralization.

Although native grasses did not respond positively to lowered potential net N supply rate in the +C plots, they failed to establish in +N plots, which is consistent with the results of other grassland ecosystems where N addition has been shown to reduce species richness (Foster & Gross 1998). Our previous work has shown greater or equal total aboveground productivity (existing pasture species and introduced native species) at times under N addition compared to ambient and C addition plots. Greater total pasture productivity with N addition may have limited the introduced native grasses' ability to establish via competitive exclusion.

We found no effect of seeding time on recruitment rates. Fall seeding is desirable from an agricultural management perspective as it offers more flexibility in timing than spring seeding, which is dependent on thawing and drying of soils before seeding equipment can be used in the field. However, when sown in the fall, seeds have a longer time in the field before germination and are therefore more vulnerable to destruction and predation, which can be high in agricultural fields and prairies (O'Rourke et al. 2006). Our results suggest that seeding time is not as important a factor as disturbance or N availability for C4 grass recruitment.

Conclusion

We found that greater establishment of native grasses may occur with a spring burning regimen compared to a rotational grazing system in cool-season grass dominated pastures, suggesting that grazing may have limited application as a restoration tool in established cool-season temperate pastures. Further research is needed to identify the extent to which these results can be generalized across tallgrass prairie. Our findings indicate that C addition may not be as effective as commonly thought for restorations, particularly in systems dominated by C3 grasses. At best, C addition may provide a window of opportunity rather than a long-term treatment (Prober et al. 2005), but it requires time, labor, and financial inputs that may render it infeasible for large areas of land. Our data suggest that surface applied C addition may actually hinder native grass recruitment in C3-grass dominated systems. Further, whereas N fertilization is a common practice to promote productivity in temperate pastures, our results show that this management would need to be suspended during C4 grass establishment.

This research provides information for land managers who want to incorporate native grasses into cool-season grasslands without complete renovation. More broadly, this research should inform efforts that attempt to integrate agricultural and

restoration goals in the landscape and restoration theory that seeks to augment grassland plant diversity via seed addition to existing grasslands.

Implications for Practice

- Burning in combination with seed addition can promote C4 grass establishment in C3 grass dominated pasture systems.
- Nitrogen fertilization inhibits C4 grass establishment into existing C3 pastures.
- Surface applied C can lead to N immobilization, but this alteration to resource availability may not enhance native C4 grass recruitment in an established C3 grass dominated system.

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