

RESEARCH ARTICLE

# Can Carbon and Phosphorous Amendments Increase Native Forbs in a Restoration Process? A Case Study in the Northern Tall-grass Prairie (U.S.A.)

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## Abstract

In the northern Great Plains (United States), sites with less than 20% of native species are difficult to restore. We have experimented with a restoration method that shows some promise. It consists of systematically installing simulated small-scale patches (8.0 m<sup>2</sup> in size) over 25% of an old field and then seeding these patches with native species. The working hypothesis is that these patches will generate a constant source of propagules which in time will lead to increases in native species diversity within the surrounding grass matrix. The objective of this paper was to determine whether soil amendments should be used to facilitate the establishment and persistence of native species (primarily forbs) within these patches. We seeded the patches with a mixture of native grass and forb species and applied four soil treatments: P fertilization, C additions, C + P, and a control (no amendments). Results for the first 5 years

were as follows: (1) seeded forb richness was mostly unaffected by soil amendments; (2) seeded and nonseeded forb biomass and density were substantially reduced by C additions, whereas they were unaffected or increased under P additions; (3) both seeded and non-native grass biomass substantially increased with C additions; and (4) there was an inverse relationship between native seeded forbs and non-native grass biomass. Our conclusions are that: (1) P amendments are a potential tool for enhancing native seeded forb biomass in simulated small-scale disturbance patches; and (2) C additions, although enhancing seeded grass biomass do not reduce the biomass of non-native grasses.

**Key words:** C amendments, forb biomass, grass biomass, P amendments, prairie restoration, precision prairie reconstruction.

## Introduction

A notable problem in prairie restorations is a decline in seeded forb species richness over time, and one of the main causes is the presence of large stands of non-native perennial grasses (Wilson 2002). Non-native grass species such as *Bromus inermis* Leyss and *Poa pratensis* L. cover millions of hectares of pastures and old fields that were formally species-rich prairie landscapes, and attempts at restoration have not always been satisfactory (Wilson & Gerry 1995; Blankespoor & May 1996; Lesica & DeLuca 1996; Duckwitz 2005; Murphy & Grant 2005). *B. inermis* is especially problematic in the northern Great Plains (United States), where it can comprise more than 80% of the biomass and form stable monocultures (Larson & Newton 2001). Prescribed burning, mowing, and herbicide application can reduce the abundance of *B. inermis*, but without sustained efforts this grass species is remarkably

persistent (Willson & Stubbendieck 2000). Fire as well as other control methods (like herbicide applications) depend heavily for their success on the presence of a minimum of 20% of native species (Dill et al. 1986; Willson & Stubbendieck 2000). In sites dominated by *B. inermis*, with less than 20% of native species, Willson and Stubbendieck (2000) suggest that alternative methods for prairie restoration should be attempted.

Our research team is experimenting with a restoration method, designated precision prairie reconstruction (PPR), that has shown some promise (Grygiel et al. 2009). The method consists of systematically installing and seeding 25% of an old field with simulated small-scale-disturbance patches. The working hypothesis is that by installing and seeding specific patterns and quantities of these small-scale disturbances with native species, a self-sustaining community will be established that will generate a constant source of propagules which, over time and when conditions are favorable, will colonize the surrounding vegetation matrix, thus increasing native species diversity. In the first 5 years, the PPR method using strategically placed, broadcast-seeded, simulated small-scale disturbances (8.06 m<sup>2</sup>) covering 25% of the area was as effective as the standard method of roto-tilling and broadcast seeding the entire area for increasing total species richness,

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native seeded forb richness, native seeded forb density, and native seeded grass frequency in the matrix of an old field dominated by *B. inermis* and *P. pratensis* (Grygiel et al. 2009). A key question regarding this method is whether soil amendments should be used in these simulated patches to facilitate the establishment and persistence of native species (primarily native forbs) communities.

Ecological invasions, or the dominance of non-native species, are often associated with persistent changes to underlying ecological processes, including nutrient cycling (Vinton & Goergen 2006). Restoration of these communities, thus, is dependent on manipulation of these processes to favor the target species composition and impart resistance to further invasion (Prober et al. 2005). There is a growing interest by restoration ecologists in the use of carbon (C) amendments (sugar and/or sawdust) as a tool to reduce plant-available nitrogen (N) and alter competitive interactions among species. The hypothesis is that C addition changes N availability and thereby competitive dynamics between native and non-native species (Averett et al. 2004). The proposed mechanism is that C additions result in higher microbial biomass N, and lower rates of net N mineralization, which should favor slow growing late succession native species over early succession native species (Baer et al. 2004), and fast growing non-native and invasive species (Corbin & D'Antonio 2004), because the former have higher N-use efficiency (NUE) than the latter (Levang-Brilz & Biondini 2002, 2007). Experimental results, however, have varied. In some studies, C additions have led to increases of native species and decreases in non-native and weedy species (Alpert & Maron 2000; Blumenthal et al. 2003; Averett et al. 2004; Prober et al. 2005; Eschen et al. 2006, 2007). In others, however, no significant responses to C additions were found (Morghan & Seastedt 1999; Corbin & D'Antonio 2004; Wilson et al. 2004; Kardol et al. 2008, Mangold & Sheley 2008).

Another tool used for altering species composition in restored grasslands is phosphorous (P) additions (Biondini 2007), with native forbs as the main species of interest. In an extensive analysis of 55 species common to the Great Plains grasslands (United States), Johnson and Biondini (2001) and Levang-Brilz and Biondini (2002) found that native forbs have (1) higher uptake rates of P per unit of root surface area than native or non-native grasses; (2) lower P-use efficiency; and (3) higher levels of root plasticity that allow them to exploit areas of higher soil nutrient concentration, a trait that is particularly useful for low mobility nutrients, like P. These physiological and morphological characteristics, plus results from greenhouse and field competition experiments (Levang-Brilz & Biondini 2002; Biondini 2007) suggest that P additions could provide native forbs with a competitive advantage. There are caveats, however, that need to be carefully considered. Thorpe et al. (2006) has shown that P additions could favor exotic forbs over native forbs due to their greater ability to acquire P. In a large-scale analysis of P effects in temperate ecosystems, Wassen et al. (2005) showed that P additions can promote exotic forbs, whereas P limitations tend to promote endangered forb species.

The objectives of this study were to investigate the effects of C and P soil amendments on a seeded native species mixture seeded in small-scale disturbance patches (8.0 m<sup>2</sup>) located within a *B. inermis* and *P. pratensis* dominated matrix. Specific objectives were to measure soil amendment effects on (1) seeded and nonseeded forb richness and density; and (2) total biomass, seeded grass, non-native grass, seeded forb and native nonseeded forb biomass. The working hypothesis was (1) C additions should favor the establishment of native C<sub>4</sub> grasses and reduce the invasion by non-native *B. inermis* and *P. pratensis*; and (2) P additions should increase the establishment and persistence of seeded and nonseeded native forbs. This paper presents results from the first 5 years of the study.

## Methods

### Location and Site Characteristics

The study was conducted in an old field on The Nature Conservancy's (TNC) Bluestem Prairie Scientific and Natural Area near Glyndon, MN, U.S.A. (Clay County Twp 139N Rng 46W Sec 10–12; ECS Province: Prairie Grasslands; ECS Subsection: Red River Prairie, Latitude 46°49'49.096"N, Longitude 96°27'21.017"W). The soils at the study site are classified as Aquic Haploborolls, Sandy Mixed (66—Flaming fine sand) and Udorthentic Haploborolls, Sandy Mixed (245B—Lohnes coarse sandy loam).

The 30-year mean growing season precipitation is 383 mm (annual precipitation 538 mm), with the highest levels occurring as rain in May (66 mm), June (89 mm), July (73 mm), and August (64 mm). Growing season precipitation was 358 mm in 2001, 422 mm in 2002, 312 mm in 2003, 429 mm in 2004, 527 mm in 2005, and 317 mm in 2006. The 30-year mean temperature is 5°C and mean monthly temperatures range from –14°C in January to 21°C in July and August.

The site was purchased by TNC 16 years prior to our study and was managed with a 5-year prescribed burn cycle. The site had not been burned for 3 years prior to the installation of our study and burning was suspended post-installation of the research plots. Although we do recognize the importance of fire for the maintenance of grasslands (native or restored), data from the Sheyenne grasslands (which are near our site and in the same eco-region) indicate an average fire return interval of 6–8 years (Higgins 1984). Wright and Bailey (1982) calculated an average fire return interval of 8–9 years for the entire northern tall-grass prairie eco-region, which is significantly higher than the 3–5 years they estimated for the southern tall-grass prairie from which the bulk of the data and research on fire and fire response has come (Hartnett et al. 1996). This 6–8 year fire return interval is the burning schedule adopted by TNC. Our experiment is a long term one and thus includes the normal prescribed burn cycle. The data we have presented fall between two burn events. We continue to sample the experiment and in 5 more years we will analyze data that include an entire burn cycle.

Native vegetation on the surrounding area is northern tall-grass prairie (Barker & Whitman 1988), but at the time

of the study the site was dominated by *Bromus inermis*, *Poa pratensis*, and a few native and exotic forbs (*Lithospermum incisum*, *Melilotus officinalis*, *Physalis longifolia*, *Rosa arkansana*, and *Symphotrichum falcatum*). Existing vegetation was verified by a baseline study conducted prior to installing the experimental study plots.

### Experimental Design

The experiment was organized as a completely randomized block design, with 10 blocks and 4 treatments per block. We used this experimental design to isolate the potential effects of field spatial variability from the treatment and year effects. The blocks were 20 × 20 m, whereas the treatment plots within each block were 2.84 × 2.84 m with 4.77 m as a buffer zone between both the treatment plots and the edge of the block. All four treatments were seeded with a combination of native grasses and forbs (Table 1) acquired from Prairie Restoration, Inc. (Hawley, MN, U.S.A.). Each treatment plot was roto-tilled and broadcast seeded in the fall of 2000 at a rate of 25 kg/ha. Fall planting was used because our prior experience in a similar site has shown that it is, in general, more effective to seed in the fall than the conventionally used spring/summer planting (Biondini 2007). Fall planting solves the stratification and/or scarification requirement of many of

the seeded native forbs through the freezing and thawing of the soil (Levang-Brilz & Biondini 2002). It also provides a favorable moisture environment for seed germination resulting from snow melt and April rains (Biondini 2007). There is a drawback that we recognize, however, which involves some C<sub>4</sub> grasses, particularly *Bouteloua gracilis* (Willd. Ex Kunth) Lag. ex Griffith, and *Bouteloua curtipendula* (Mich.) Torr., which clearly do better in spring/summer planting. For that reason these species were not included in the mixture (they are marginal species in this eco-region).

The treatment consisted of (1) no amendments control (Ct); (2) P amendment (22 gP/m<sup>2</sup>) using Sierra slow release fertilizer prills (Pursell Technologies, Inc., Sylacauga, AL, U.S.A.); (3) C amendment using granular sugar (S) (0.5 kg C m<sup>-2</sup>); and (4) a P + C amendment (PS) at the same rates as the P and S treatments. The amendments were applied in the spring of 2001. We used the same sugar application rate for which Eschen et al. (2006) found a 60% reduction in biomass production. The level of C application used in this experiment is within the range used in other experiments (Morghan & Seastedt 1999; Alpert & Maron 2000; Torok et al. 2000; Averett et al. 2004; Corbin & D'Antonio 2004; Prober et al. 2005; Bleir & Jackson 2007; Mangold & Sheley 2008). The P amendment was equivalent to the high-level application used by Biondini (2007) on a restoration experiment in a

**Table 1.** List of seeded species and nonseeded species that were found during sampling.

Seeded Grasses	Seeded Forbs	Nonseeded Forbs
<i>Andropogon gerardii</i> , Vitman	<i>Achillea millefolium</i> , L.	<i>Ambrosia psilostachya</i> DC
<i>Schizachyrium scoparium</i> (Michx.) Nash	<i>Allium stellatum</i> , Fraser ex Ker Gawl.	<i>Artemisia frigida</i> Willd
<i>Sorghastrum nutans</i> (L.) Nash	<i>Amorpha canescens</i> , Pursh	<i>Asclepias verticillata</i> L.
	<i>Anemone cylindrica</i> , A. Gray	<i>Asclepias viridiflora</i> Raf
<hr/>		
<i>Nonseeded Grasses and Sedges</i>		
<i>Bouteloua curtipendula</i> (Michx.) Torr	<i>Dalea candida</i> , Michx.	<i>Chenopodium album</i> L.
<i>Bouteloua gracilis</i> (Willd. ex Kunth) Lag. ex Griffiths	<i>Dalea purpurea</i> (Vent.) Rydb.	<i>Cirsium undulatum</i> (Nutt.) Spreng
<b><i>Bromus inermis</i>, <i>Leys</i></b>	<i>Echinacea angustifolia</i> , DC.	<i>Conyza canadensis</i> (L.) Cronquist
<i>Carex brevior</i> (Dewey) Mack	<i>Galium boreale</i> L.	<i>Geum triflorum</i> Pursh
<i>Dichanthelium oligosanthos</i> (Schult.) Gould	<i>Helianthus rigidus</i> (Rydb.) Heiser	<i>Hedeoma hispida</i> Pursh
<b><i>Elymus repens</i> (L.) Gould</b>	<i>Monarda fistulosa</i> L.	<i>Helianthus maximiliani</i> Schrad
<i>Elymus trachycaulus</i> (Link) Gould ex Shinnars	<i>Oligoneuron rigidum</i> L.	<i>Heterotheca villosa</i> (Pursh) Shinnars var. minor (Hook.) Semple
<i>Eragrostis spectabilis</i> (Pursh) Steud	<i>Penstemon grandiflorus</i> , Nutt.	<i>Liatris aspera</i> Michx
<i>Koeleria macrantha</i> (Ledeb.) Schult	<i>Potentilla arguta</i> , Pursh	<i>Lithospermum incisum</i> Lehm
<i>Panicum virgatum</i> L.	<i>Ratibida columnifera</i> (Nutt.) Woot. & Standl.	<b><i>Medicago lupulina</i> L.</b>
<b><i>Poa compressa</i> L.</b>	<i>Solidago nemoralis</i> , Aiton	<b><i>Melilotus officinalis</i> (L.) Lam</b>
<b><i>Poa pratensis</i> L.</b>	<i>Solidago speciosa</i> , Nutt.	<i>Penstemon gracilis</i> Nutt
<i>Sporobolus cryptandrus</i> (Torr.) A. Gray	<i>Verbena stricta</i> , Vent.	<i>Rosa arkansana</i> Porter
	<i>Zizia aurea</i> (L.) W.D.J. Koch	<i>Solidago missouriensis</i> Nutt
		<i>Symphotrichum falcatum</i> (Lindl.) G.L. Nesom var. <i>falcatum</i>
		<i>Symphotrichum sericeum</i> (Vent.) G.L. Nesom
		<i>Tradescantia occidentalis</i> (Britton) Smyth
		<b><i>Tragopogon dubius</i> Scop</b>

Species nomenclature follows: USDA, NRCS (2010). Species in bold are non-native to the site.

similar vegetation type, except that in this experiment the P was applied all at one time rather than yearly over a 5-year period. We used a single C and P treatment amount because the main objective of the experiment was to determine how these amendments affect (1) establishment and post-first-year growth; and (2) to test whether a single treatment has a lasting effect. From a practical perspective, the single application is necessary because the rationale for this experiment was to determine if C and P additions could improve on the success of the PPR restoration method developed by Grygiel et al. (2009). The PPR method involves a single installation process, thus the need for testing a single application amendment.

### Sampling Methods

On the basis of our prior experience (Biondini 2007), the plots were not sampled during the first growing season to allow for a good establishment of the seeded species, and to prevent the accidental uprooting of young plants during sampling. Sampling began in 2002. Forbs were sampled every year (2002–2006) in August for density by species using four 0.25 m<sup>2</sup> plots randomly located within each plot. Grasses were sampled at the same time for presence or absence using a 0.1 m<sup>2</sup> plot nested inside the 0.25 m<sup>2</sup> plot used for forbs. We used forb density as a valuable indicator for establishment and persistence. We did not measure grass density as it is very difficult to do because the complex tillering of grasses can result in a wide range of variability in the number of culms for each root system (Bonham, 1989). A wide variety of studies have shown that even large bunchgrasses break into smaller individual groups, thus making the determination of individual plants difficult (Bonham 1989). We instead measured grass frequency which we used to estimate grass richness.

In 2006, we also measured aboveground biomass by clipping the 0.25 m<sup>2</sup> plots. The clipped biomass was separated by species, oven-dried at 60°C for 12 hours, and weighed.

### Statistical Analysis

Species richness was estimated as the average number of species per sampling unit (0.25 m<sup>2</sup> quadrat). Overall differences among treatments in species richness and forb density (total and by individual species) were analyzed with a randomized block analysis of variance (RAOV) with a repeated observation model (years being the repeated observation factor) (Winer 1962). This analysis model allowed us to (1) block out any field spatial variability from the treatment and time effects; and (2) test for treatment, year, and treatment × year interactions.

In the first analysis iteration, we used growing season precipitation as a covariate, but it had no impact on the results. To check further for any significant precipitation effects, we ran regressions between precipitation and richness or density stratified by treatment. The results were not significant. Finally, we ran a regression between year and precipitation to determine if there was a trend; there was none. Growing season precipitation thus was dropped as a covariate from further analysis.

Biomass differences (total and by individual species) were analyzed using an RAOV (Zar 1999). All mean differences were tested using a Tukey honestly significance difference (HSD) test (Zar 1999). Biomass relationships among various groups of species were analyzed using linear regression.

## Results

### Species Richness

Total species richness declined with time ( $p < 0.001$ ,  $F_{[4,144]} = 99.75$ ) from an average of 20 ( $\pm 2$ ) species in 2002 to 10 ( $\pm 1$ ) in 2006. The decline was mostly due to forb richness, which declined from 14 ( $\pm 1$ ) in 2002 to 6 ( $\pm 1$ ) in 2006 ( $p < 0.001$ ,  $F_{[4,144]} = 90.96$ ). Total grass richness declined slightly from 5 ( $\pm 0.5$ ) in 2002 to 3 ( $\pm 0.5$ ) in 2006 ( $p < 0.01$ ,  $F_{[4,144]} = 15.98$ ). There was a significant year effect ( $p < 0.00001$ ,  $F_{[4,144]} = 23.56$ ) on seeded native forb richness, which declined from an average of 5 ( $\pm 1$ ) species in 2002 to an average of 3 ( $\pm 1$ ) species in

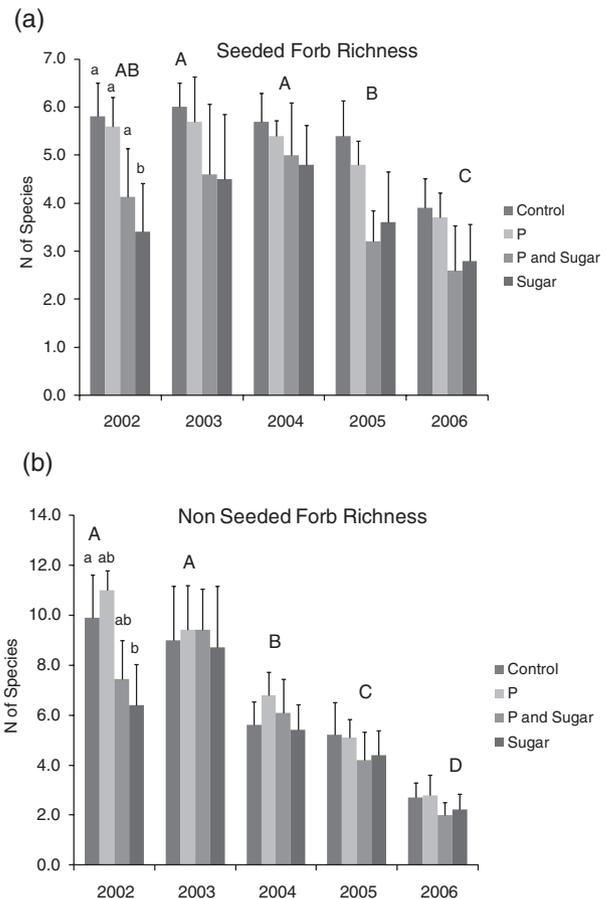


Figure 1. Forb species richness (average number of species taxa per sampling plot averaged by treatment). (a) Seeded forbs; (b) Nonseeded forbs. Capital letters represent overall differences among years, whereas lower-case letters represent differences among treatments within a year. Treatments or years with no common letters are statically different at  $p < 0.05$ . Vertical bars represent 95% confidence intervals.

2006 (Fig. 1a), but there was no year  $\times$  treatment interaction ( $p = 0.33$ ,  $F_{[12,144]} = 1.15$ ). Nonseeded forbs experienced a much steeper decline than seeded ones ( $p < 0.00001$ ,  $F_{[4,144]} = 85.68$ ) going from 8 ( $\pm 1.3$ ) species in 2002 to 2.4 ( $\pm 0.6$ ) species in 2006 (Fig. 1b) with a significant year  $\times$  treatment interaction ( $p = 0.02$ ,  $F_{[12,144]} = 2.12$ ). The effects of the treatments were discernible in 2002 ( $p < 0.001$ , Tukey HSD test) when seeded native forbs averaged 5.5 ( $\pm 0.65$ ) species in the Ct and P treatments versus 3.8 ( $\pm 1$ ) species in the PS and S treatments (Fig. 1a). For nonseeded forbs the corresponding values were 10.4 ( $\pm 1.5$ ) and 7.7 ( $\pm 1.6$ ) species, respectively ( $p < 0.05$ , Tukey HSD test).

### Forb Density

The general pattern for both seeded and nonseeded forb density was similar. Their overall density declined from 2002 to 2006, with the decline being more pronounced for the nonseeded species than for the seeded species (Table 2). Treatment, year, and treatment  $\times$  year interaction were significant ( $p < 0.01$ ) for both seeded and nonseeded forb density ( $F_{[3,36]} = 64.38$ ,  $F_{[4,144]} = 65.34$ , and  $F_{[12,144]} = 11.43$  for seeded forbs;  $F_{[3,36]} = 42.07$ ,  $F_{[4,144]} = 99.09$ , and  $F_{[12,144]} = 24.05$  for

nonseeded forbs). In both cases, the densities were substantially higher ( $p < 0.05$ ) in the Ct and P treatments than in the PS and S treatments (Table 2). A similar pattern was followed by some of the main seeded native forb species (average density of 1 plant/m<sup>2</sup> or higher): *Achillea millefolium*, *Echinacea angustifolia*, *Penstemon grandiflorus*, *Ratibida columnifera*, and *Oligoneuron rigidum* (Table 2). These species were the only ones that showed a significant treatment, year, or treatment  $\times$  year interaction.

### Biomass

As was shown with density, seeded, nonseeded, and total forb biomass was substantially higher ( $p < 0.01$ ,  $F_{[3,36]} = 7.3$ , 6.28, and 14.31, respectively) in the Ct and P treatments than in the PS and S treatments (a range of 2–3 times higher) (Table 3). The same pattern was followed by individual species that showed statistically significant responses: *A. millefolium*, *Artemisia frigida*, and *Chrysopsis villosa* (Table 3).

Seeded, nonseeded, and total grass biomass showed the exact opposite pattern to forb biomass, higher ( $p < 0.01$ ,  $F_{[3,36]} = 13.17$ , 21.25, and 55.93, respectively) in the PS and S treatments than in the Ct and P treatments (a range of 6–8

**Table 2.** Total seeded, nonseeded, and major species forb densities (plants/m<sup>2</sup>).

Seeded density ( $p < 0.0001$ , $F_{[12,144]} = 11.43$ )					Nonseeded density ( $p < 0.0001$ , $F_{[12,144]} = 24.05$ )			
Year	Ct	P	PS	S	Ct	P	PS	S
2002	128 <sup>a</sup>	137 <sup>a</sup>	27 <sup>b</sup>	27 <sup>b</sup>	186 <sup>a</sup>	233 <sup>a</sup>	34 <sup>b</sup>	30 <sup>b</sup>
2003	63 <sup>a</sup>	93 <sup>a</sup>	12 <sup>b</sup>	16 <sup>b</sup>	158 <sup>a</sup>	148 <sup>a</sup>	50 <sup>b</sup>	70 <sup>b</sup>
2004	119 <sup>a</sup>	97 <sup>a</sup>	29 <sup>b</sup>	35 <sup>b</sup>	38 <sup>a</sup>	57 <sup>a</sup>	43 <sup>a</sup>	39 <sup>b</sup>
2005	100 <sup>a</sup>	95 <sup>a</sup>	13 <sup>b</sup>	18 <sup>b</sup>	55 <sup>a</sup>	60 <sup>a</sup>	23 <sup>a</sup>	28 <sup>b</sup>
2006	30 <sup>a</sup>	30 <sup>a</sup>	7 <sup>b</sup>	9 <sup>b</sup>	32 <sup>a</sup>	33 <sup>a</sup>	17 <sup>a</sup>	13 <sup>b</sup>
<i>Achillea millefolium</i> ( $p < 0.0001$ , $F_{[12,144]} = 10.27$ )					<i>Echinacea angustifolia</i> ( $p < 0.01$ , $F_{[12,144]} = 4.28$ )			
Year	Ct	P	PS	S	Ct	P	PS	S
2002	18 <sup>a</sup>	34 <sup>a</sup>	1 <sup>b</sup>	1 <sup>b</sup>	3 <sup>a</sup>	2 <sup>a</sup>	2 <sup>a</sup>	1 <sup>a</sup>
2003	36 <sup>a</sup>	51 <sup>a</sup>	2 <sup>b</sup>	2 <sup>b</sup>	4 <sup>a</sup>	2 <sup>a</sup>	1 <sup>a</sup>	1 <sup>a</sup>
2004	30 <sup>a</sup>	31 <sup>a</sup>	3 <sup>b</sup>	2 <sup>b</sup>	3 <sup>a</sup>	1 <sup>a</sup>	1 <sup>a</sup>	1 <sup>a</sup>
2005	58 <sup>a</sup>	55 <sup>a</sup>	5 <sup>b</sup>	5 <sup>b</sup>	6 <sup>a</sup>	5 <sup>a</sup>	1 <sup>b</sup>	2 <sup>a</sup>
2006	11 <sup>a</sup>	15 <sup>a</sup>	2 <sup>b</sup>	1 <sup>b</sup>	1 <sup>a</sup>	1 <sup>a</sup>	1 <sup>a</sup>	1 <sup>a</sup>
<i>Penstemon grandiflorus</i> ( $p < 0.0001$ , $F_{[12,144]} = 29.58$ )					<i>Ratibida columnifera</i> ( $p < 0.01$ , $F_{[12,144]} = 5.88$ )			
Year	Ct	P	PS	S	Ct	P	PS	S
2002	96 <sup>a</sup>	86 <sup>a</sup>	18 <sup>b</sup>	17 <sup>b</sup>	4 <sup>b</sup>	6 <sup>b</sup>	18 <sup>a</sup>	1 <sup>b</sup>
2003	94 <sup>a</sup>	84 <sup>a</sup>	14 <sup>b</sup>	30 <sup>b</sup>	14 <sup>a</sup>	28 <sup>a</sup>	14 <sup>b</sup>	4 <sup>b</sup>
2004	68 <sup>a</sup>	46 <sup>a</sup>	19 <sup>b</sup>	23 <sup>b</sup>	14 <sup>a</sup>	15 <sup>a</sup>	19 <sup>a</sup>	6 <sup>b</sup>
2005	12 <sup>a</sup>	16 <sup>a</sup>	5 <sup>b</sup>	0 <sup>b</sup>	25 <sup>a</sup>	27 <sup>a</sup>	5 <sup>b</sup>	6 <sup>b</sup>
2006	1 <sup>a</sup>	0 <sup>a</sup>	0 <sup>a</sup>	1 <sup>a</sup>	10 <sup>a</sup>	10 <sup>a</sup>	0 <sup>b</sup>	3 <sup>b</sup>
<i>Oligoneuron rigidum</i> ( $p < 0.01$ , $F_{[12,144]} = 3.96$ )								
Year	Ct	P	PS	S				
2002	4 <sup>a</sup>	5 <sup>a</sup>	1 <sup>b</sup>	1 <sup>b</sup>				
2003	4 <sup>a</sup>	6 <sup>a</sup>	1 <sup>b</sup>	1 <sup>b</sup>				
2004	2 <sup>a</sup>	1 <sup>b</sup>	1 <sup>b</sup>	0 <sup>b</sup>				
2005	8 <sup>a</sup>	6 <sup>a</sup>	1 <sup>b</sup>	1 <sup>b</sup>				
2006	4 <sup>a</sup>	2 <sup>a</sup>	1 <sup>a</sup>	1 <sup>a</sup>				

Different letters within a year signify that the densities are statistically different at  $p < 0.05$  (treatment–year interactions). Ct = control; P = Phosphorous treatment; PS = P plus sugar treatment; and S = sugar treatment. For details, see “Methods” section.

**Table 3.** Total, seeded, nonseeded, and major species biomass ( $\text{g}/\text{m}^2$ ).

	Grasses			
	Ct	P	PS	S
Total ( $p < 0.01$ , $F_{[3,36]} = 55.93$ )	28.2 <sup>b</sup>	23.9 <sup>b</sup>	208.0 <sup>a</sup>	172.3 <sup>a</sup>
Seeded ( $p < 0.01$ , $F_{[3,36]} = 13.17$ )	3.9 <sup>b</sup>	4.1 <sup>b</sup>	93.6 <sup>a</sup>	91.9 <sup>a</sup>
Nonseeded ( $p < 0.01$ , $F_{[3,36]} = 21.25$ )	25.1 <sup>b</sup>	21.0 <sup>b</sup>	114.4 <sup>a</sup>	80.4 <sup>a</sup>
<i>Andropogon gerardii</i> ( $p < 0.001$ , $F_{[3,36]} = 19.13$ )	1.9 <sup>b</sup>	1.7 <sup>b</sup>	69.6 <sup>a</sup>	80.9 <sup>a</sup>
<i>Schizachyrium scoparium</i> ( $p < 0.05$ , $F_{[3,36]} = 4.03$ )	1.2 <sup>b</sup>	1.1 <sup>b</sup>	24.1 <sup>a</sup>	10.9 <sup>ab</sup>
<i>Bouteloua curtipendula</i> ( $p < 0.01$ , $F_{[3,36]} = 5.38$ )	0.1 <sup>b</sup>	0.1 <sup>b</sup>	3.6 <sup>ab</sup>	6.3 <sup>a</sup>
<i>Bromus inermis</i> (nonseeded, $p < 0.001$ , $F_{[3,36]} = 18.95$ )	11.3 <sup>c</sup>	9.7 <sup>c</sup>	76.1 <sup>a</sup>	46.9 <sup>b</sup>
<i>Poa pratensis</i> (nonseeded, $p < 0.05$ , $F_{[3,36]} = 3.81$ )	8.5 <sup>ab</sup>	6.9 <sup>b</sup>	28.6 <sup>a</sup>	20.6 <sup>ab</sup>
<i>Koeleria macrantha</i> ( $p < 0.05$ , $F_{[3,36]} = 3.31$ )	4.7 <sup>a</sup>	4.0 <sup>a</sup>	0.0 <sup>b</sup>	0.4 <sup>b</sup>

	Forbs			
	Ct	P	PS	S
Total ( $p < 0.01$ , $F_{[3,36]} = 14.31$ )	167.8 <sup>a</sup>	170.6 <sup>a</sup>	55.6 <sup>b</sup>	94.3 <sup>b</sup>
Seeded ( $p < 0.01$ , $F_{[3,36]} = 7.3$ )	46.6 <sup>a</sup>	48.7 <sup>a</sup>	10.0 <sup>b</sup>	11.7 <sup>b</sup>
Nonseeded ( $p < 0.01$ , $F_{[3,36]} = 6.28$ )	121.2 <sup>a</sup>	121.9 <sup>a</sup>	47.6 <sup>b</sup>	83.8 <sup>ab</sup>
<i>Achillea millefolium</i> ( $p < 0.0001$ , $F_{[3,36]} = 10.54$ )	22.0 <sup>a</sup>	22.5 <sup>a</sup>	1.4 <sup>b</sup>	2.8 <sup>b</sup>
<i>Artemisia frigida</i> ( $p < 0.01$ , $F_{[3,36]} = 5.03$ )	4.8 <sup>a</sup>	9.4 <sup>a</sup>	0.6 <sup>b</sup>	0.5 <sup>b</sup>
<i>Chrysopsis villosa</i> ( $p < 0.0001$ , $F_{[3,36]} = 10.57$ )	67.9 <sup>a</sup>	51.0 <sup>a</sup>	4.9 <sup>b</sup>	5.9 <sup>b</sup>

Different letters within a row signify that biomass is statistically different at  $p < 0.05$ . Ct = control; P = Phosphorous treatment; PS = P plus sugar treatment; and S = sugar treatment. For details, see "Methods" section.

times higher) (Table 3). Two of the seeded native grasses (*Andropogon gerardii* and *Schizachyrium scoparium*), the native *B. curtipendula*, and the original non-native dominant grasses of the matrix vegetation (*B. inermis*, and *P. pratensis*) followed the same pattern (Table 3). The only exception was the native grass *Koeleria macrantha*, which responded like the forbs, higher ( $p < 0.05$ ,  $F_{[3,39]} = 3.31$ ) in the Ct and P treatments and lower in the PS and S treatments (Table 3). We found two interesting (if weak) biomass relationships: (1) non-native grass biomass was inversely related to seeded forb biomass ( $R^2 = 0.14$ ,  $p < 0.02$ ) (Fig. 2a); and (2) non-native grass biomass was positively related to native grass biomass ( $R^2 = 0.22$ ,  $p < 0.002$ ) (Fig. 2b).

## Discussion

There was a decline in seeded and nonseeded forb richness and density throughout the study period. The decline cannot be attributed to rainfall, because: (1) as discussed in the statistical section growing season precipitation was not a statistically significant variable; and (2) growing season precipitation for the entire period was within the range of the long term average. This decline is not unusual; in fact, one of the main problems in grassland restoration is that they often revert to species-poor sites dominated by a few grasses (Kindscher & Tieszen 1998; Allison 2002; Sluis 2002; Grygiel et al. 2009). It is also consistent with survival rates of native forb seedlings in soil disturbance gaps in old fields in the tall-grass prairie ecosystem (Goldberg 1987). A similar pattern was found by Biondini (2007) in restored grasslands within the northern tall-grass prairie ecosystem, where the decline in forb richness

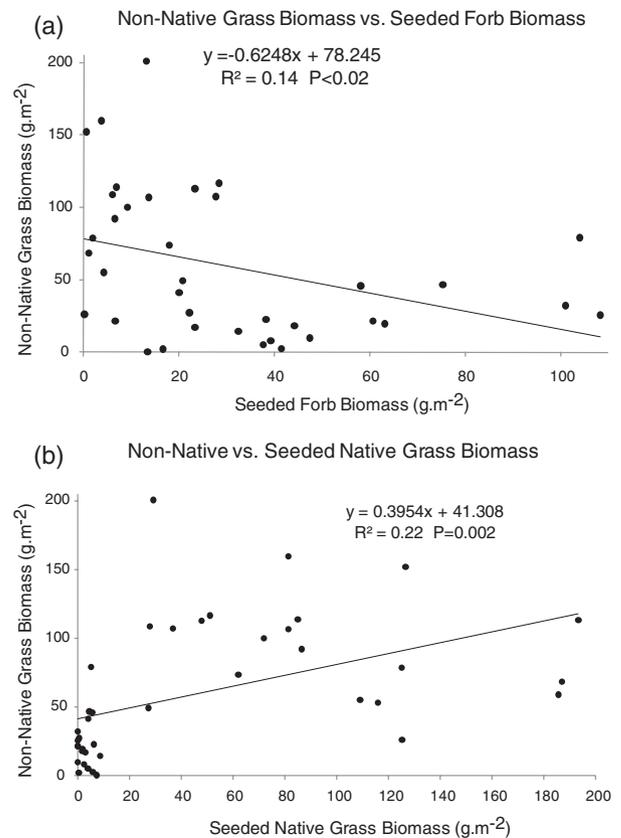


Figure 2. (a) Relationship between seeded forb biomass and nonseeded grass biomass in 2006 ( $\text{g}/\text{m}^2$ ). (b) Relationship between seeded and nonseeded grass biomass in 2006 ( $\text{g}/\text{m}^2$ ).

and density lasted 3 years. It is important to note that the richness reported in this study is average number of species per sampling unit (0.25 m<sup>2</sup> quadrat). The total forb richness by 2006 (average of approximately six species per 0.25 m<sup>2</sup> quadrat) compared favorably with an average of three species per 0.25 m<sup>2</sup> quadrat (those located only inside the small-scale disturbances) found by Grygiel et al. (2009) in the PPR experiment. The differences were larger in terms of forb density. In the PPR experiment, the average density of *Achillea millefolium*, *Echinacea angustifolia*, *Penstemon grandiflorus*, and *Oligoneuron rigidum* within the small-scale disturbances were 14, 0.4, 1.5, 3.5 plants/m<sup>2</sup>, respectively, which is substantially lower than the ones we found in this study under the P treatment. This suggests that the addition of P amendments to the PPR patches could significantly improve forb richness in the PPR method.

Treatment effects for seeded and nonseeded forbs were similar for richness and density: higher in the Ct and P treatments and lower in the S and S + P treatments. The main difference was that the treatment effect in richness was found only in the second year of planting (we did not sample in the first year after planting), whereas the density effect was present throughout the length of the experiment. A similar pattern was observed for biomass. In this case, total forb biomass as well as the biomass of some individual seeded and native species was higher in the Ct and P treatment than in the S and S + P treatments.

To explain the response of forbs to P fertilization, we propose the following conjectures: (1) P fertilization decreases the need of mycorrhizal association to access P; (2) forbs are less efficient than the grasses, therefore they need more P; and (3) the high root plasticity of forbs suggests that they have a facultative association with mycorrhizae. The evidence for these conjectures is as follows. Seven of the forb species found in the experiment were studied by Wilson and Hartnett (1998) for mycorrhizal association. Five of these species: *A. millefolium*, *Geum triflorum*, *Liatris aspera*, *O. rigidum*, and *Symphitrichum sericeum* are nonmycorrhizal. Two of these species are mycorrhizal: *E. angustifolia* and *Helianthus maximiliani* (though *E. angustifolia* has a low colonization rate (RC) of 24.8%). For the nonmycorrhizal forbs, the average mycorrhizal responsiveness (MR) and RC are 61.4% and 40%, respectively. The equivalent number for the two mycorrhizal forbs is 91% and 36%, respectively. That is lower than the MR and RC for the native warm season grasses found in the study (*Andropogon gerardii*, *Bouteloua curtipendula*, *Bouteloua gracilis*, *Panicum virgatum*, *Schizachyrium scoparium*, and *Sporobolus cryptandrus*) which averaged an MR = 92% and RC = 47%. The non-native cool season grasses in the study (*Bromus inermis* and *Poa pratensis*), however, were strongly non-mycorrhizal (MR = -23%). Our group also conducted an extensive mycorrhizal analysis in a nearby restoration experiment, this time investigating mycorrhizal total hyphal length in the soil itself (Bingham & Biondini 2009). In this study, we found that mycorrhizal length in the soil was only correlated with the presence of late successional C<sub>4</sub> grasses (*A. gerardii*, *P. virgatum*, *S. scoparium*, and *Sorghastrum*

*nutans*) which are obligatory mycorrhizal and characterized by high root to shoot ratios, and root surface area per unit of root biomass.

Data from Johnson and Biondini (2001) and Levang-Brilz and Biondini (2002) showed that on average, the forbs found in our study have P-use efficiency of 131 g/gP (which is lower than the 174 and 213 g/gP for C<sub>3</sub> and C<sub>4</sub> grasses, respectively). Johnson and Biondini (2001) and Levang-Brilz and Biondini (2002) also showed that although forbs have lower P-use efficiency they have on average: (1) higher P uptake rates per unit of root surface area (0.18 gP m<sup>-2</sup> d<sup>-1</sup>) in comparison with C<sub>3</sub> grasses (0.15 gP m<sup>-2</sup> d<sup>-1</sup>), and C<sub>4</sub> grasses (0.07 gP m<sup>-2</sup> d<sup>-1</sup>); and (2) higher root plasticity than the major native and non-native grasses of this study ( $\tau = 0.69$  vs.  $\tau = 0.2$ ,  $p < 0.05$ , where  $\tau = 0$  is no plasticity). These results suggest that under P fertilization, the higher P uptake rate and root plasticity of forbs may compensate for the lack of mycorrhizae without the additional energy drain required to maintain the mycorrhizal association.

The literature on the effect of C additions on forbs is contradictory. Eschen et al. (2006) showed increases in forb cover and decreases in grass cover as a result of C additions, whereas Averett et al. (2004) showed reductions in both forb and grass cover, stem density, and biomass from C additions. Our results were more in accordance with those from Eschen et al. (2006) showing a significant decline in forb density and biomass as a result of C addition. Furthermore, the inverse relationship (though weak) between seeded forb biomass and non-native grass biomass (mostly *B. inermis* and *P. pratensis*) indicates that there may be some competition between the two life forms. To further investigate whether this negative relationship is more than a regression artifact, we partitioned the biomass of seeded forb biomass in two categories: low (<30 g/m<sup>2</sup>) and high (>30 g/m<sup>2</sup>). The results still show a negative association, nonseeded grass biomass averaged 77 g/m<sup>2</sup> under low seeded forb biomass versus 26 g/m<sup>2</sup> under high seeded forb biomass ( $p < 0.001$ , *T* test with unequal variance and 33 df).

The differential response of grasses and forbs to C additions could be partially explained by their NUE, because C amendments tend to reduce (sometimes significantly) N availability (Averett et al. 2004). The main C<sub>4</sub> grasses (*A. gerardii*, *B. curtipendula*, and *S. scoparium*) and C<sub>3</sub> grasses (*B. inermis*, *Koeleria macrantha*, and *P. pratensis*) have average NUE of 65 g/gN while the NUE of the main forbs was much lower, 46 g/gN (Levang-Brilz & Biondini 2002; Biondini 2007). Furthermore, the dominant grasses in the study allocated more biomass to roots than the forbs in question: average root to shoot ratio of 1.25 vs. 0.9 (Levang-Brilz & Biondini 2002; Biondini 2007). Higher NUE and R:S should provide grasses with a better ability than forbs to overcome potential N limitation caused by C additions.

Reed et al. (2007) have shown that P fertilization cannot be analyzed independently from N effects, because soil N fixation rates tend to increase with P fertilization. These results highlight potential difficulties for fertilization studies of nutrient limitation in recovering prairie ecosystems and

imply opportunities for prairie restoration (Reed et al. 2007). In nutrient-poor environments, the authors suggest that the absolute availability of soil P more strongly controls rates of N fixation than the N-to-P ratio of the soil. The P + C treatment behaved very similarly to the C only treatment suggesting a limited P effect (the P only treatment behaved very similarly, but consistently, with the control). Part of the problem could have been that we (1) applied P only once; and (2) used a slow release fertilizer that may have diluted the P effect over a 4–6 month period.

Recent studies have suggested a connection between P cycling and increased P availability with invasive plant competitiveness and the loss of rare plant species. Thorpe et al. (2006) showed that P fertilization can facilitate invasive species like *Centaurea maculosa* (spotted knapweed) in native and restored grasslands, whereas Wassen et al. (2005) in an extensive analysis of the available data showed that in temperate regions increased levels of available soil P can be highly detrimental to endangered or subdominant (mostly forbs) species. P fertilization in restoration management, thus, should be considered within an ecosystem perspective.

Total grass biomass and the biomass of some native (*A. gerardii*, and *S. scoparium*) and non-native species (*B. inermis* and *P. pratensis*) was higher in the C amendment treatments. The grass species results partially aligned themselves with studies that have shown increases in native grasses (in particular C<sub>4</sub> grasses) as a result of C applications (Alpert & Maron 2000; Blumenthal et al. 2003; Averett et al. 2004; Prober et al. 2005; Eschen et al. 2006, 2007; Bleir & Jackson 2007). There were, however, two main differences: (1) total grass biomass actually increased as a result of C amendments (average of 180 g/m<sup>2</sup> in the S and PS treatment vs. 50 g/m<sup>2</sup> in the Ct and P treatments), whereas in most of the above-mentioned studies grass biomass substantially declined as a result of C amendments; (2) these studies also showed reductions in non-native grass species (in particular *B. inermis*, Bleir & Jackson 2007) with carbon amendments, which was not the case in our experiment. In fact, seeded and nonseeded grass biomass were positively, if weakly, related indicating that favorable growth conditions for one group may also benefit the other. The relationship is weak, possibly due to other factors. To ascertain whether this positive relationship is more than a regression artifact, we partitioned the seeded grass biomass into low (<10 g/m<sup>2</sup>) versus high (>10 g/m<sup>2</sup>). The results still show a positive association, non-native grass biomass averaged 23 g/m<sup>2</sup> under low seeded grass biomass versus 97 g/m<sup>2</sup> under high seeded grass biomass ( $p < 0.0001$ ,  $T$  test with unequal variance and 27 df).

### Implications for Practice

- Seeded forb richness was mostly unaffected by C or P amendments.
- Seeded and nonseeded forb biomass and density were substantially reduced by C additions (with and without P), whereas they were unaffected or increased by P additions.

- Both native and non-native grass biomass was substantially increased as a result of C additions (with and without P)
- We found an inverse relationship between seeded forb biomass and non-native grass biomass, but a positive relationship between native and non-native grass biomass.
- P amendments could be a potential tool for enhancing native seeded forb biomass and reducing non-native grass biomass in soil disturbance patches located within a matrix dominated by *Bromus inermis* and *Poa pratensis*. The caveat is that it could potentially facilitate the invasion of exotic forbs.
- C additions, although enhancing native grass biomass, do not appear to be useful in reducing the biomass of non-native grasses.

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