POTENTIAL C SEQUESTRATION INCREASES WITH C4 GRASS ABUNDANCE IN RESTORED PRAIRIE OF SOUTHERN WISCONSIN

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DEDICATION

To my Grandfather, who as an agronomist, farmer and teacher, planted the first seeds of love and appreciation for nature in my very young heart.

To my Mom, whose example of resilience and hard work inspired me to progress and re-create my profession.

To my Husband, who showed me a world within that did not exist until he arrived.

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ABSTRACT

The tallgrass prairie ecosystem is one of the most endangered ecosystems in North America. Interest in restoring prairie is growing because of the potential for increasing soil organic carbon (SOC) sequestration when degraded soils and ecosystems are restored. Also, finding long-term C storage in terrestrial ecosystems is being promoted as a key part to climate stabilization as greenhouse gases (GHG) continue to accumulate in the atmosphere. Re-introducing warm-season grasses (C4) to cool-season (C3) pastures has the potential not only to increase forage production, but also improve wildlife habitat, soil organic matter, and resilience to drought. While much is known about C4 prairie grasses and C3 pastures, there is a paucity of information about mixed C4-C3 grasslands in the upper Midwest. We conducted a mensurative experiment in two restored prairies in southern Wisconsin to assess their carbon sequestration potential under a gradient of C4-C3 grass ratios. We identified areas of naturally occurring C4-C3 gradients in two restorations (10 and 17-year-old) that have been recolonized by C3 grasses and quantified above- and below-ground net primary productivity and soil respiration for two years. Across both sites and years, we found a weak but positive relationship between NEP and C4 grass cover. However, this relationship was driven by the abundance of a particular species, *Andropogon gerardii*. Also, the relationships between the major components of the C cycle (ANPP, BNPP, and Rs) and C4 grass cover and A. gerardii cover were modified primarily by site, indicating that aboveground dynamics were driving C balance at the high-productivity site and belowground processes controlled the site with lower productivity. These results have important implications for land managers and policymakers seeking to promote C sequestration.

INTRODUCTION

The grasslands of the world occupy about 40% of the total land area (White et al., 2000) and provide important ecosystem services that have been categorized by the Millennium Ecosystem Assessment into four main areas (Farber et al., 2006): 1) supporting services such as conversion of solar energy into biomass that supports all the other trophic levels, 2) regulating services such as carbon storage, prevention of soil erosion and maintenance of water quality, 3) provisioning services such as production of food, forage, fiber and fuel, and 4) cultural services such as ecotourism, bird watching, and education. Among all of these services, temperate grasslands are known for a high stock of carbon mainly allocated belowground in roots, which lead to formation of the characteristic dark soil of the North American prairie (Jones and Donnelly, 2004). However, of all the grasslands, the temperate grasslands are the least protected (Henwood, 1998 as cited by Gibson, 2009) and the tallgrass prairie ecosystem is one of the most endangered ecosystems in North America (Samson and Knopf, 1994). Only 9.4% of the original tallgrass prairie remains with most being highly fragmented increasing the edge-to-area of the remaining prairies, which compromises their capacity to protect the soil from erosion, maintain watershed functions for drinking and irrigation water, and provide wildlife habitat, bioenergy crops, and carbon sequestration (Burke et al., 1995; Knops and Tilman, 2000; Tilman 2006; Gibson 2009).

The tallgrass prairie, which is dominated by warm-season (C4 photosynthesis) grasses such as *Andropogon gerardii* Vitman (big bluestem), *Panicum virgatum* L. (switchgrass), and *Sorghastrum nutans* (L.) Nash (indiangrass) has been transformed mainly into grassland/agricultural mosaics if not totally converted to annual crops (Rhemtulla et al.,

2007). Interest in restoring the native prairie has increased at the same time that the potential for increasing soil organic carbon (SOC) sequestration when degraded soils and ecosystems are restored have been touted (Lal, 2003). Finding long-term C storage in terrestrial ecosystems is being promoted as a key part to climate stabilization as greenhouse gases (GHG) continue to accumulate in the atmosphere (Bruce et al., 1999; Smith, 2004). Much emphasis has been placed on the adoption of best management practices and restoration to perennial vegetation in agricultural systems (Smith et al., 2008; Johnson et al., 2005) because soil carbon increases the most after a carbon enhancing land-management change is adopted (Smith, 2004; McLauchlan et al., 2006; Matamala et al., 2008). Indeed, studies have reported that the restoration of tallgrass prairie has the potential to accumulate soil organic carbon (SOC) on the order of 40 to 60 g C m^{-2} yr^{-1} (Baer et al., 1992; McLauchlan et al., 2006; Mahaney et al., 2008). A successful example of unification of food production and conservation is the conservation reserve program (CRP), whose primary goal is to protect erodible land with the establishment of perennial grasslands, but it also has been adopted because of the reported potential to increase SOC levels decreasing atmospheric CO_2 (Gebhart et al., 1994; Reeder et al., 1998; Follett et al., 2001; Baer et al., 2002; Post et al., 2004).

Working grasslands, such as sown pastures, tend to be dominated by European species that are highly productive in the spring and fall since they are mostly cool-season (C3 photosynthesis) grasses (Paine et al., 1999). These pastures sustain the profitable dairy (Taylor and Foltz, 2006) and beef industry (CIAS, 2008) in Wisconsin. Combining the challenges of food production and the need for environmental conservation on such working

lands have the potential to positively impact a large part of the landscape since in the U.S. alone, over 50% of US is cropped or grazed (Robertson and Swinton, 2005). The reintroduction of C4 prairie grasses into working lands offers a compromise between the complete restoration and the complete eradication of the native prairie (Woodis, 2008; Nelson and Burns, 2006) and simultaneously promotes the multifunctional use of the rural landscape (Buttel, 2003; Western, 2001; Hilderbrand et al., 2005).

While much is known about C4 prairies and C3 dominated pastures ecosystems, there is a lack of information about mixed C3-C4 grasslands in the upper Midwest. Most of the recent studies evaluating the effects of photosynthetic pathway on ecosystem services focus on the effects of totally converting agricultural lands to prairie or to CRP (Camill et al., 2004; McLauchlan et al., 2006). Only a few studies have recognized the need to understand how ecosystems are affected by the reintroduction of C4 native grasses into C3 grassland (sensu Hooper et al., 2005); but even then, the comparisons are made between C4 dominated and C3 dominated communities (Mahaney et al., 2008), not mixed C3-C4 grasslands per se. Little is known about how the C3 dominated grasslands may change as C4 prairie grasses are reintroduced to working lands—this information will assist land managers in decision-making on issues such as: How much prairie grass is needed to boost productivity? Is the ecosystem storing carbon? How does the seasonality of production change with various rations of C3 and C4 grasses?

To address these questions, we compared how net ecosystem production (NEP) and the major components of this metric, net primary production (NPP) and soil respiration (Rs), were influenced by the relative abundance of C3 and C4 grasses in restored tallgrass prairie

of southern Wisconsin over two years. We expected that NEP would increase as C4 grass abundance increased because C3 and C4 grasses differ in important functional traits such as quantity and quality of below- and above-ground biomass that can directly and indirectly alter soil processes (Dijkstar et al., 2006). We also expected that the major components of the C cycle, ANPP, BNPP, and Rs would be influenced by the increase in C4 grasses in opposite directions (i.e., net primary production would increase, while soil respiration would decrease) because C4 grasses typically produce more below- than above-ground biomass and are more productive overall than C3 grasses (Wedin and Tilman, 1990; Baer et al., 2002; Camill et al., 2004) and that 2) and C4 grasses tissues are more resistant to decay (Luo et al., 1996; Craine et al., 1998).

METHODS

Study site

This study was conducted at two Wisconsin prairie restoration sites, Bison Ridge Ranch (BR Ranch) in Marquette County (89° 27' W, 43° 44' N) and the Wisconsin Integrated Cropping Systems Trial (WICST) at the University of Wisconsin–Madison's Arlington Agricultural Research Station in Columbia County (89° 19' W, 43° 18' N). At both locations the climate is temperate-continental with cold winters and warm summers. Annual total precipitation during the study period (2007 and 2008) was 727 and 738 mm, respectively (AWON-WI). Historical average annual precipitation is 803 mm and the average mean temperatures in July and January are 21 ºC and -11 ºC, respectively (NOAA).

The soils of BR Ranch were classified as Gotham loamy fine sand and Metea fine sandy loam on 2 to 6 % slope (NRCS). Both series consist of very deep, well-drained soils

with rapid permeability. The 4-ha pasture at BR Ranch was seeded with a diverse prairie mix in 1990 and subsequently harvested for hay annually at summer's end. The hay harvest during our study occurred on August 31, 2007 and September 1, 2008. The grass community is comprised of *Elymus repens* (L.) Gould (quackgrass), *Andropogon gerardii* Vitman (big bluestem), *Bouteloua curtipendula* (Michx.) Torr. (side oats grama), *Bromus tectorum* L. (downy brome), *Digitaria cognata* (Schult.) Pilg. (fall witchgrass), *Panicum virgatum* L.(switchgrass), *Poa pratensis* L. (Kentucky bluegrass), *Schizachyrium scoparium* (Michx.) Nash (little bluestem) and *Sorghastrum nutans* (L.) Nash (indiangrass) (Table 1).

Soils at WICST were classified as Plano silt loam on 0 to 2% slopes (NRCS). Annual total precipitation in 2007 and 2008 was 892 and 938 mm, respectively (AWON-WI). Historical average annual precipitation in Arlington, Wisconsin is 833 mm and average temperatures in July and January are 21 ºC and -9 ºC, respectively (NOAA). At WICST, our experiment was conducted on six plots, each 0.33 ha in size. In 1999 these plots were seeded with one of two mixtures (high and low diversity seed mixes); prior to that it was plowed and planted with soybeans in 1998. The low diversity prairie seed mix contained six species and the high diversity seed mix contained 25 species comprised of forbs, legumes and grasses (Simonsen, 2004).

TABLE 1 - List of species found at BR Ranch and WICST in 2007 and 2008.

FUNCTIONAL GRASS GROUP	SCIENTIFIC NAME †	COMMON NAME	BR RANCH	WICST
PERENNIAL C4 GRASSES	*Andropogon gerardii* Vitman	Big bluestem	☑	☑
	Bouteloua curtipendula (Michx.) Torr.	Side oats grama	☑	☐
	Digitaria cognata (Schult.) Pilg.	Fall witchgrass	☑	☐
	Panicum virgatum L.	Switchgrass	☑	☐
	Schizachyrium scoparium (Michx.) Nash	Little bluestem	☑	☐
	Sorghastrum nutans (L.) Nash	Indiangrass	☑	☑
ANNUAL C3 GRASS	*Bromus tectorum* L.	Downy bromegrass	☑	☐
PERENNIAL C3 GRASSES	*Bromus inermis* Leyss.	Smooth bromegrass	☑	☑
	Dactylis glomerata L.	Orchardgrass	☑	☑
	Elymus canadensis L.	Canada wildrye	☐	☑
	Elymus repens (L.) Gould	Quackgrass	☑	☑
	Phleum pretense L.	Timothy	☐	☑
	Poa pratensis L.	Kentucky bluegrass	☑	☑

†Nomenclature followed USDA Plants Profile at http://plants.usda.gov/index.html

The prairie plots in WICST were burned approximately every three years since the spring of 2003, including a burn in 2007 but not 2008. Today the grass community is mainly comprised of *Elymus repens* (L.) Gould (quackgrass), *Andropogon gerardii* Vitman (big bluestem), *Bromus inermis* Leyss. (smooth brome), *Dactylis glomerata* L.(orchardgrass), *Elymus canadensis* L. (Canada wildrye), *Phleum pratens* L. (timothy), *Poa pratensis* L. (Kentucky bluegrass), and *Sorghastrum nutans* (L.) Nash. (indiangrass) (Table1).

At each site, we chose thirty ~100-m^2 plots (15 in 2007 and 15 in 2008) for their respective C3:C4 grass ratio. At each plot, a centralized 1-m^2 quadrat was permanently marked to monitor soils, environmental conditions, nutrient content, and respiration over time (Figure 1). Plant species cover was estimated with the line-point method performed on permanently marked soil monitoring stations, root ingrowth core areas, and transient biomass harvest areas that were located within each 100-m^2 experimental unit (Figure 1). The quadrat area to be sampled was divided by 5 horizontal and vertical lines forming 25 intersections where the first intercept of a sharpened rod with any part of herbaceous vegetation at each intersection was recorded (Heady, 1959). During the months when two distinctly vertical layers of different vegetation could be observed, we recorded the first hit with the taller herbaceous vegetation and the second hit with the herbaceous vegetation in the layer below the first one totaling for 50 hits per quadrat.

For each sampling event, total species cover was calculated as total species hits divided by the total possible hits for each quadrat. Plants were identified to the species level and grouped into functional groups. The classification of plants into groups can be based on different traits such as taxonomy (graminoids or forbs), ability to host bacteria nitrogen fixing (leguminous or not), the dominant photosynthetic pathway (C4, C3 or CAM), and the origin (native to the area or introduced). We mirrored the classification method used in previous prairies studies (Kindscher and Wells, 1995; Tilman et al., 1997). All the species found in our plots, and the group to which they were assigned can be found in Table 1.

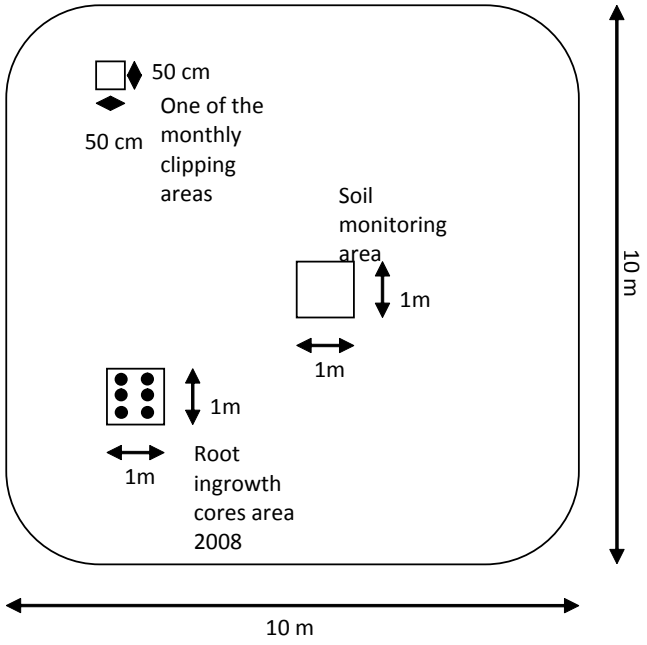

FIGURE 1. Layout of one of 60 experimental units (15 at each site for 2 years). A ~10x10-m area was delineated for it C4:C3 cover ratio. Within each area were located 1 permanent and 2 transient quadrats .

Plant cover data per species and functional groups were taken three times during the season and aggregated to calculate an annual average of cover for each experimental unit. The sampling events were mid-season (July), peak of standing biomass (end of August, beginning September) and fall (end of October, beginning November). The mid-season, peak of standing biomass, and fall cover were calculated by averaging the total cover estimated in each individual sampling event from the permanent and transient sample stations noted above. We also calculated the average and maximum number of species for each experimental unit for each year.

The annual average of C4 grass cover ranged from 0 to 74% in the first year and from 8 to 52% for the second year at BR Ranch. At WICST, the annual average C4 grass cover varied from 0 to 86 % in 2007 and 0 to 76% in 2008. The average number of species for

each experimental unit was similar for both sites, averaging 6.18 ± (0.14)[†] species per square meter. Therefore, most plots had not only similar functional richness but also similar species richness. The two main dominant C4 grass species were the same for both sites, e.g. *Andropogon gerardii* Vitman and *Sorghastrum nutans* (L.) Nash*;* however, there were differences in the plant communities worth noting. For instance, BR Ranch had other species of C4 grasses present such as *Panicum virgatum* L., *Schizachyrium scoparium* (Michx.) Nash and *Bouteloua curtipendula* (Michx.) Torr. The dominant C3 grass species in both sites were also quite similar. Yet, only BR Ranch had the winter annual *Bromus tectorum* L. and only WICST had *Elymus canadensis* L. and *Phleum pratense* L. present (Table 1).

Net ecosystem production

Annually, SOC storage or loss is the net balance between inputs and outputs of C (Six et al., 2002). Carbon sequestration is calculated as the difference between C inputs as NPP and C outputs as heterotrophic respiration (Rh), harvest, and fire. Net primary production is the sum of aboveground net primary production (ANPP) and belowground net primary production (BNPP). Soil respiration (Rs) is a combination of autotrophic (i.e., root respiration, Ra) and heterotrophic respiration (i.e., microbial respiration, Rh). Because separating these forms of respiration is quite difficult (Kuzyakov and Larionova, 2006), we used literature estimates of Ra and calculated Rh from Rs measurements. We estimated potential carbon sequestration in grams of carbon per unit area by measuring the major fluxes of C such as ANPP, BNPP, and Rs of each experimental unit (Chapin et al., 2002). Because

[†] mean ± (s.e.)

our intention was to compare the potential in C sequestration of different areas along the C3:C4 gradient for each year, we did not estimate C loss from burning, which occurred intermittently (i.e., every 3 years or so).

Net primary production

Within each delineated 100-m^2 experimental unit, we clipped available biomass within a single 50 × 50-cm randomly placed quadrat to ~3 cm residual stubble height (Figure 1). Biomass was bagged, dried to constant weight at 60°C, and weighed. Prior to each clipping event, we estimated leaf area index (LAI) on the 50 × 50-cm quadrat ,which was calculated from intercepted photosynthetically active radiation readings (Accupar LP-80, Decagon, Inc., Pullman, WA) made above and below the leaf canopy at four points along each quadrat. Clipping dates at BR Ranch were: May 9, Jun 27, July 11, August 14, and August 31 in 2007; June 10, June 24, July 3, August 26 and November 14 in 2008. The clipping dates at WICST were: June 21, July 25, September 5 and October 24 in 2007; May 22, June 23, July 24, August 29, September 25, and October 30 in 2008. Biomass was never clipped after the August 31 harvest at BR Ranch in 2007.

Because the focus of our study was to capture differences along the C3:C4 grass gradient, we estimated ANPP not by simply harvesting the biomass at peak standing biomass, as is normally done to estimate ANPP in prairie, but by summing the biomass increments between clipping events throughout the season to account for the simultaneous and overlapping production and mortality of both plant functional groups (Vogt et al., 1986). In each experimental unit, annual ANPP was calculated as the sum of monthly aboveground production values for a growing season (approximately May through October). The

aboveground biomass monthly production was calculated as the difference in biomass measured at one month from biomass at an earlier month. Since we did not measure the biomass production after the harvest in August 2007 at the BR Ranch, we estimated the fall biomass with an allometric equation. The allometric equation (r^2 =0.69) was developed from the relationship between LAI and biomass weight measurements taken from both sites and both years. In the same way, we estimated the amount of biomass left on the pasture after harvesting events.

Belowground NPP was estimated using root ingrowth cores in each experimental unit (4 subsamples per experimental unit in 2007 and six subsamples per experimental unit in 2008). Soil cores were removed prior to the growing season (~ end of May, beginning of June) with a hammer-core and sieved to remove rocks, roots, and debris (Fahey et al., 1999). Cores were made of 2-mm plastic mesh (5 cm diameter × 15 cm long) and were filled with the sieved soil: sand (1:1). These mesh cylinders were inserted back into the original holes and two cores were harvested at each of the following time periods: in 2007, peak of standing biomass and fall and in 2008, mid-season, peak of standing biomass and fall. The root biomass of each core was bagged, refrigerated until washing, dried to constant weight at 60°C, and weighed. We did not attempt to separate live to dead roots assuming that only a very small fraction was dead (Fahey and Hughes, 1994). For each experimental unit, we averaged the two root biomass weights to estimate root biomass per unit area for each harvest. We calculated the belowground biomass production as the difference in root biomass harvested at one time from the root biomass of an earlier harvest. The root net production was calculated as the sum of positive production values. Since the root ingrowth

cores do not account for the amount of roots that are produced and die during the period when the cores are deployed (i.e., fine root turnover (FRT)), we corrected the net root production using the FRT rates using equation 2 from the literature (Gill and Jackson, 2000; Fahey et al.,1999).

$$FRT = 0.2884\, e^{(0.046 * (\text{Mean Annual Temperature}))} \quad (2)$$

The rate obtained by this equation is within the range that had been published for temperate grasslands, 30% to 65% (Jackson et al., 1997). We also estimated the belowground root stock of C4 and C3 grasses at the end of April, August, and November of 2008 using soil coring (Fahey et al., 1999). Soil cores were 5 cm in diameter and taken to a 60-cm depth immediately above six C4, and six C3 individual grasses totaling 12 randomly chosen plants in each site. The 60-cm soil cores were divided into four 15-cm sections, sieved in 2-mm mesh, washed out of debris, rocks and soil, dried to constant weight at 60°C, and weighed. No attempt was made to separate living from dead roots. For each functional group of grasses, the six root weight values per segment were averaged to access the vertical distribution of root stock biomass. We used the percent average of biomass found in the first 15 cm of the soil profile to later extrapolate BNPP to 60-cm depth.

Above- and below-ground production was calculated by multiplying shoot and root biomass estimates by a constant C concentration of the prairie plant tissues as 50% (studies in restored and remnant prairies found 40 to 50% C in shoot and root tissues, i.e. Brye et al., 2002 and Matamala et al., 2008).

Soil Respiration

Soil respiration was measured once monthly between 0900 to 1500 hours with a soil respiration chamber linked to an infrared gas analyzer (LiCor 6400-09, Li-Cor Biosciences, Lincoln, NE) (Norman et al., 1992). The efflux chamber was used in conjunction with polyvinyl chloride (PVC) thin-walled collars that were inserted 2 cm into the soil surface at least 30 min prior to conducting measurements. There were three collars per 1-m² quadrat, which were repositioned in a random manner within each experimental unit every month. At BR Ranch, soil respiration measurements were taken on May 9, Jun 12 & 20, July 12, August 14, September 19 & 26, and October 24 in 2007 and May 16, June 24, July 16, August 25, September 23 and October 12 in 2008. In the WICST, sampling dates were June 18, July 25, September 5 and October 5 of 2007 and May 13, June 17, July 15, August 21, September 25 and October 11 of 2008. We estimated the soil CO_2 efflux ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) in each experimental unit by averaging the three measurements taken in each of the three collars. Because shoots were clipped prior to measuring soil CO_2 fluxes, the efflux of soil CO_2 measured excludes shoot respiration. Annual soil CO_2 efflux, the mass of C per unit area respired annually was estimated for each experimental unit by summation of daily interpolations of the monthly measurements (Brye et al., 2002; Chou et al., 2008). In the winter, when soil temperature at the upper 4 cm was consistently below 0ºC for at least a week, we assumed that soil respiration was zero (Brye et al., 2002). The weather data from Hancock and Arlington weather stations showed that the upper 4 cm of soil layer reaches consistently zero 0ºC between the day of the year 10 to 71 and 14 to 77 in BR Ranch and Arlington area respectively (AWON-WI).

Soil temperature was measured at the same time as soil respiration with a 15-cm probe attached to the LiCor 6400. Soil moisture measurements were taken at the same time when possible. In 2007, soil cores 5 cm in diameter and 10 cm long were extracted from three random locations near each permanent quadrat for each experimental unit in order to estimate gravimetric water content (GWC). These cores were aggregated and sieved through 2-mm mesh to remove vegetative and mineral materials. Approximately 15 g of soil was weighed, dried at 105°C to constant weight, and reweighed to calculate GWC (Jarrell et al., 1999). Soil moisture content in 2007 was measured on Jun 12 & 20, August 14 and September 19 at the BR Ranch and July 25 at WICST. In 2008, soil moisture was measured using a time domain reflectometer (TDR) (Jarrell et al., 1999, FIELDSCOUT - TDR 300 soil moisture meter–Spectrum Technologies, Inc., IL) The TDR was inserted in three random locations in the permanent 1-m² quadrat to a 12-cm depth to determine the average volumetric moisture content of the soil layer. The dates of soil moisture content measurements in 2008 were: June 24, July 28, August 25, September 23, and October 12 at the BR Ranch and June 17, July 15, August 21 and October 11 at the WICST. Soil temperature and moisture had no relationship to soil CO_2 daily efflux.

In the fall of 2007 and spring of 2009, we used the hammer-type core sampler when the soil was not too wet or dry to minimize compaction and extracted one soil core (5 × 15-cm) per experimental unit. To determine soil texture we used the hydrometer (Bouyucous) procedure and bulk density was calculated as oven-dried mass of dry soil per unit volume of soil. We discounted the weight and volume of pebbles that were > 2mm. Volume was calculated using volumetric displacement in water (Elliot et al., 1999).

Soils were sent to The University of Wisconsin Soil & Plant Analysis Lab to determine soil total carbon (TC) and total nitrogen (TN), potassium (K), phosphorus (P), and organic matter (OM). Percent of TC and TN were determined by dry combustion using a Leco CNS-2000 analyzer (Organic Carbon Dry Combustion method, Leco CN-2000, FP 2000, or CNS-2000). Plant available K and P were estimated using the Bray P method. Soil organic matter was estimated by the loss of weight in a sample heated at a temperature high enough to burn organic matter but not so high as to decompose carbonates (Weight Loss-on-Ignition - LOI 360o). Soil pH was measured in water using a 1:1 soil: solution ratio and in a buffer solution with a 1:1:1 of soil: water: buffer ratio.

Data analysis and calculations

First, we used linear regression to address potential relationships between NEP and vegetation cover by functional group, by plant species cover, and then by plant species richness. Cook's distance test, which measures the influence of individual observations on the regression coefficients, was assessed to identify potential outliers. Furthermore, the fit of a quadratic function was compared to a linear fit using the generalized least squares algorithm in S-plus (S-Plus 8.0, Insightful Corporation Seattle, WA). Models were compared with likelihood ratio tests. When significant differences were determined ($p < 0.05$) the model with the lowest AIC values were chosen, otherwise the simpler model was determined to be the better fit.

We built regression trees (S-Plus 8.0, Insightful Corporation Seattle, WA) to explore how groupings of potential predictor variables (Table 2) related to soil and cover characteristics might explain variability in NEP. Because site differences were obvious,

regression trees were also constructed for each site using the same set of potential predictors of NEP described in Table 2 plus ANPP, BNPP, Rs.

TABLE 2. List of potential predictors variables of NEP.

TYPE	VARIABLE
CATEGORICAL	Site and year
NUMERICAL	Soil pH, O.M %, and bulk density
	Soil P (ppm),soil K (ppm), soil TC, TN, C:N
	June, July, peak of the season and fall C3 and C4 grass cover (%)
	Average of C3 and C4 grass cover (%)
	Average and maximum species richness and of individual species cover (%) from table 1, and forb cover

Regression trees are nonparametric models used to explore dependencies among continuous and/or categorical variables. The predictor variable that explains the greatest amount of the deviance in the response variable is chosen. They are constructed by splitting a dataset into smaller and smaller groups, where each split depends on a single variable (Gotelli and Ellison, 2004). The splitting process continues until there is only one explanatory variable at the end of a "branch" and no further improvement in the fit of the model is obtained relative to the number of split ends, also called nodes (Gotelli and Ellison, 2004). The means of the groupings from the same split were further compared using the Welch Modified Two-Sample t-Test (S-Plus 8.0, Insightful Corporation Seattle, WA) If groupings were not significant, the tree was pruned meaning the data was not longer divided.

RESULTS

Net ecosystem production and C4 grass cover (%) were better described by a quadratic than a linear function ($p < 0.01$, Figure 2A). Net ecosystem production was not related to C3 grass cover, species richness, or cover of any of the individual species with the exception of *Andropogon gerardii*. A quadratic fit best represented the relationship between NEP and *Andropogon gerardii* cover ($p = 0.0001$, Figure 2B).

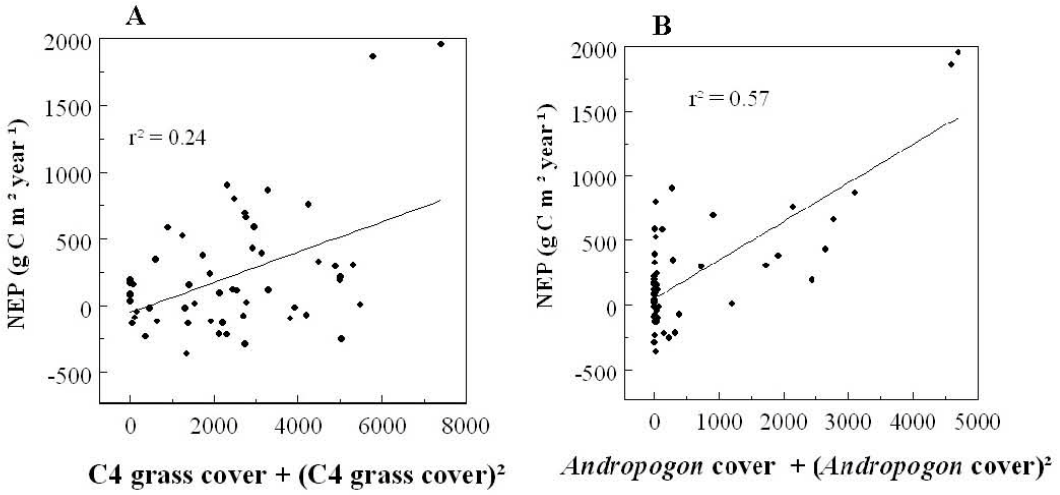

FIGURE 2. Linear relationships between NEP and A) the quadratic term for C4 grass cover and B) the quadratic term for *Andropogon* cover. The r^2 value was determined with ordinary least squares regression.

Total NPP was not significantly correlated to C4 grass cover (Figure 3A). While ANPP increased significantly with increasing C4 grass cover (Figure 3B), no relationship was found between C4 grass cover and BNPP (Figure 3C). Warm-season grass cover explained 17% of the annual variability in soil CO_2 efflux (Figure 3D).

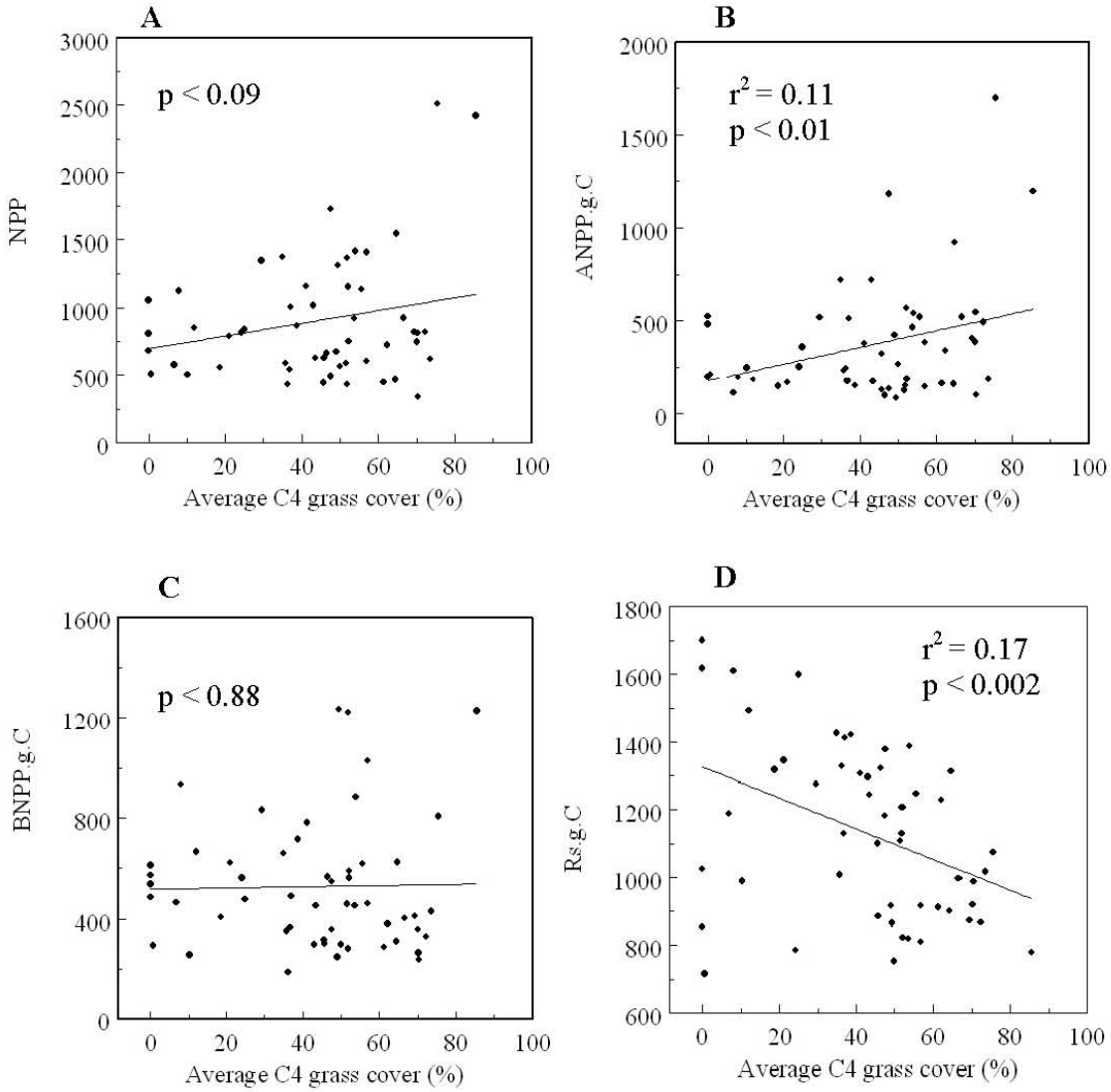

FIGURE 3. Linear relationship between A) NPP and C4 grass cover (%), B) ANPP and C4 grass cover (%), C) BNPP and C4 grass cover (%), and D) Rs and C4 grass cover (%). All C cycle components are in grams of carbon per unit area per year (g C m^{-2} y^{-1}). The r^2 value was determined with ordinary least squares regression.

While we did not find a correlation between BNPP and plant cover, we did find significant differences in root stock biomass found immediately below C4 and C3 grasses at both sites (Figure 4).

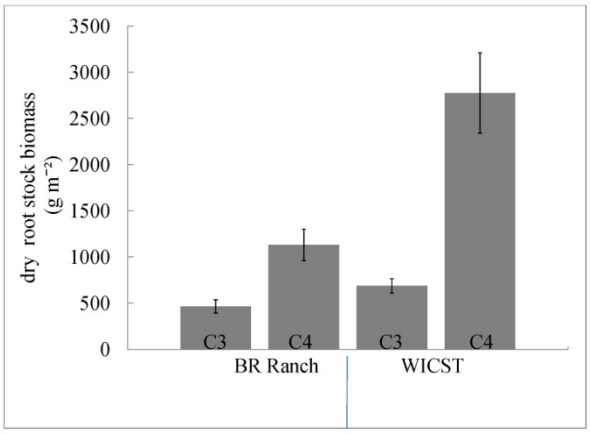

FIGURE 4. Average of root stock biomass (0-15 cm).

According to the regression tree results, the best predictor for NEP was *Andropogon gerardii* cover. If *Andropogon* cover was lower than 42%, soil K was the next variable used to split the data (Figure 5). In plots with soil K lower than 90.5, the next predictor chosen by the model did not split the data in significantly different groups at the 5% level so the tree was pruned to four terminal nodes. In the experimental units with soil K higher than 90.5, the best predictor was C4 grass cover in July. Plots with a higher C4 grass cover than 32% were grouped into a terminal node that in average had a higher NEP than the group with lower C4 grass cover. It is important to note that the soil K splits effectively separated the dataset by site. Soils were very different at each site for all variables (Table 4), so we explored the linear relationship between NEP and the C cycle components to C4 grass cover (%) and *Andropogon gerardii* cover (%) for each site separately (Table 5).

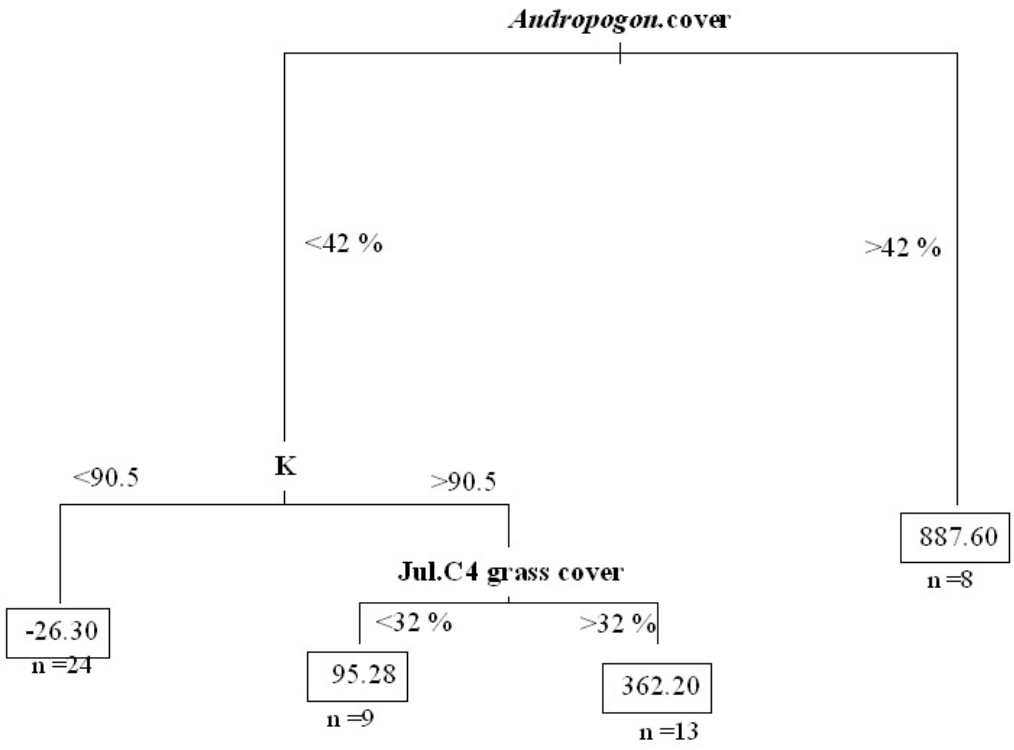

FIGURE 5. Regression tree predicting response variable (NEP) to the explanatory variables listed in table 3. The value in each terminal node is the NEP average for the respective group and n is the number of experimental units grouped under that node. The first and best predictor of NEP is *Andropogon* cover. After that the data was separated into experimental units with higher and lower K than 90.5 ppm. Units with higher K than 90.5 ppm were further separated into units with higher and lower than 32% of C4 grass cover in July.

TABLE 4. Climate and soil characteristics at Bison Ridge Ranch, Marquette County, WI and Wisconsin Integrated Cropping Systems Trial, Columbia County, WI.

CHARACTERISTIC	BR RANCH mean ± s.e.	WICST mean ± s.e.
SOIL PHYSICAL PROPERTIES		
Sand (%) †	89 ± 0.72	31.7 ± 2.21
Silt (%) †	5 ± 0.49	37.5 ± 2.34
Clay (%) †	5.7 ± 0.38	30.7 ± 0.67
Bulk density (g cm^{-3}) †	1.43 ± 0.01	1.17 ± 0.02
SOIL CHEMICAL PROPERTIES ‡		
Total soil C (%)	0.78 ± 0.02	2.65 ± 0.03
Total soil N (%)	0.06 ± 0.002	0.22 ± 0.005
C:N	12.45 ± 0.23	12.20 ± 0.24
pH	6.59 ± 0.07	6.74 ± 0.04
K(ppm)	64.1 ± 2.84	150.06 ± 7.90
P(ppm)	76.73 ± 6.35	53.16 ± 2.21
Organic matter (%)	1.31 ± 0.04	4.49 ± 0.08
CLIMATE		
Annual mean maximum temperature (ºC)	11.77	12.33
Annual mean minimum temperature (ºC)	0.88	2.38
Annual mean temperature (ºC)	6.33	7.38
Annual precipitation (mm)	803.25	833.12

† Averaged values from 2007 (n=15) on 0-15 cm soil depth
‡ Averaged values from both years (n=30) on 0-15 cm soil depth

TABLE 5. Kind and magnitude of the linear relationships between NEP and the C cycle components and C4 grass cover (%) and *Andropogon gerardii* cover (%) for each site.

EXPLANATORY VARIABLE	RESPONSE VARIABLE	BR RANCH	WICST
AVERAGE C4 GRASS COVER	NEP	none	POSITIVE $r^2 = 0.35$ $p < 0.001$
	ANPP	none	POSITIVE $r^2 = 0.25$ $p < 0.008$
	BNPP	none	none
	Rs	NEGATIVE $r^2 = 0.33$ $p < 0.002$	NEGATIVE $r^2 = 0.11$ $p < 0.09$
ANDROPOGON COVER	NEP	none	POSITIVE $r^2 = 0.53$ $p < 0.000$
	ANPP	none	POSITIVE $r^2 = 0.28$ $p < 0.004$
	BNPP	none	POSITIVE $r^2 = 0.24$ $p < 0.01$
	Rs	none	NEGATIVE $r^2 = 0.14$ $p < 0.05$

When NEP data were analyzed separately by sites with the regression tree, we found that at WICST, the best predictor of NEP was ANPP—calculated as peak standing biomass—and that at BR Ranch, the best predictor of NEP was BNPP. At WICST, 73% of the deviance was reduced by the split of the database by ANPP estimated as peak standing biomass and at BR Ranch, 76% of the deviance was reduced when the database was split by BNPP (trees not shown). Clearly, the aboveground parameters were most important at the more productive site which was reflected in NEP, ANPP, and BNPP estimates (Table 6).

TABLE 6. Table summarizing the values of C3 and C4 grass cover (%), C cycle components and net ecosystem production (NEP) per experimental unit (EU) per year (Y). The C cycle components are the aboveground production estimated as the biomass harvested at the peak of the season period (peak biomass), and as net primary production (ANPP), the belowground net primary production (BNPP), and the soil respiration (Rs).

EU	*Site*	*Y*	*S*[†]	*% C3 grass cover*	*% C4 grass cover*	*peak biomass*[#] *(g m*$^{-2}$ *y*$^{-1}$*)*	*ANPP mean (g dry biomass m*$^{-2}$ *y*$^{-1}$*)*	*BNPP mean (g dry biomass m*$^{-2}$ *y*$^{-1}$*)*	*Rs (g C m*$^{-2}$ *y*$^{-1}$*)*	*NEP 40% Ra*[§] *(g C m*$^{-2}$ *y*$^{-1}$*)*
1	BR Ranch	07	7	**64**	**3**	310.80	316.67	619.78	901.30	-72.55
2	BR Ranch	07	7	**46**	**23**	235.84	254.45	634.90	1,100.28	-215.49
3	BR Ranch	07	5	**7**	**79**	210.22	220.91	929.67	1,188.70	-137.93
4	BR Ranch	07	8	**74**	**10**	343.98	373.89	861.65	1,016.92	7.62
5	BR Ranch	07	8	**48**	**10**	245.40	264.95	718.04	1,182.00	-217.71
6	BR Ranch	07	7	**61**	**13**	299.84	324.56	574.43	911.03	-97.12
7	BR Ranch	07	6	**21**	**51**	318.64	331.67	1,247.12	1,345.48	-17.89
8	BR Ranch	07	8	**43**	**28**	331.40	344.43	907.00	1,244.02	-120.70
9	BR Ranch	07	5	**37**	**26**	330.64	351.36	733.16	1,129.21	-135.27
10	BR Ranch	07	7	**62**	**6**	652.84	683.48	763.39	1,228.43	-13.63
11	BR Ranch	07	7	**70**	**2**	184.30	200.72	476.17	986.93	-253.71
12	BR Ranch	07	5	**0**	**98**	379.08	395.50	1,224.45	1,023.85	195.67
13	BR Ranch	07	7	**70**	**20**	1,073.64	1,092.25	529.08	986.92	218.51
14	BR Ranch	07	6	**19**	**64**	266.39	292.96	816.30	1,317.35	-235.78
15	BR Ranch	07	6	**57**	**2**	258.88	287.19	922.12	809.43	118.99
AVG	**BR Ranch**	**07**	-	-	-	**363±58**	**382 ± 58**	**797 ± 59**	**1091±41**	**-65±39**
16	WICST	07	6	**0**	**98**	392.24	392.24	975.02	854.83	170.73
17	WICST	07	5	**52**	**43**	1,135.12	1,135.12	1,179.10	822.97	663.33
18	WICST	07	7	**86**	**12**	2,386.44	2,386.44	2,456.46	779.98	1,953.46
19	WICST	07	5	**72**	**24**	985.32	985.32	658.93	867.39	301.69
20	WICST	07	7	**54**	**44**	932.24	932.24	907.98	818.75	428.86
21	WICST	07	5	**50**	**48**	531.52	531.52	597.11	752.60	112.75
22	WICST	07	4	**24**	**72**	506.92	506.92	1,126.19	786.09	344.90
23	WICST	07	6	**1**	**93**	423.40	423.40	589.70	715.86	77.04
24	WICST	07	6	**57**	**42**	703.92	771.09	2,055.86	915.25	864.33
25	WICST	07	5	**69**	**27**	815.40	815.40	824.61	871.76	296.95
26	WICST	07	5	**46**	**50**	647.12	647.12	604.67	884.15	95.40
27	WICST	07	5	**70**	**28**	773.60	773.60	718.04	919.02	194.41
28	WICST	07	5	**10**	**84**	494.12	494.12	513.36	989.03	-89.68
29	WICST	07	4	**49**	**47**	849.96	849.96	498.24	915.39	124.87
30	WICST	07	5	**67**	**31**	863.76	1,040.61	809.12	996.92	326.71
AVG	**WICST**	**07**	-	-	-	**829±125**	**846±125**	**968±147**	**391±128**	**391±128**

EU	*Site*	*Y*	*S*†	*% C3 grass cover*	*% C4 grass cover*	*peak biomass*‡ *(g m⁻² y⁻¹)*	*ANPP mean (g dry biomass m⁻² y⁻¹)*	*BNPP mean (g dry biomass m⁻² y⁻¹)*	*Rs (g C m⁻² y⁻¹)*	*NEP 40% Ra*§ *(g C m⁻² y⁻¹)*
91	BR Ranch	08	7	**46**	**30**	170.16	191.29	1,132.92	1,322.54	-131.42
93	BR Ranch	08	7	**52**	**5**	251.00	251.00	919.70	1,108.85	-79.96
94	BR Ranch	08	7	**52**	**24**	349.80	371.69	1,124.45	1,206.95	23.90
95	BR Ranch	08	7	**36**	**31**	449.52	470.67	703.98	1,007.03	-16.89
96	BR Ranch	08	6	**12**	**75**	348.84	370.52	1,331.17	1,493.08	-45.00
97	BR Ranch	08	6	**8**	**81**	375.44	389.49	1,863.73	1,609.57	160.87
98	BR Ranch	08	5	**52**	**17**	302.40	302.40	564.61	1,207.15	-290.79
101	BR Ranch	08	6	**49**	**8**	167.88	167.88	2,468.32	864.54	799.38
102	BR Ranch	08	7	**39**	**33**	250.60	300.44	1,431.85	1,421.32	13.35
103	BR Ranch	08	8	**52**	**28**	255.92	299.06	2,440.96	1,130.68	691.61
104	BR Ranch	08	8	**41**	**44**	740.00	757.69	1,563.59	1,305.75	377.19
105	BR Ranch	08	6	**36**	**53**	433.88	491.09	374.21	1,329.35	-364.96
AVG	**BR Ranch**	**08**	-	-	-	**341±45**	**364±46**	**1327±195**	**1251±60**	**95±104**
106	WICST	08	5	**56**	**32**	926.80	1,040.00	1,240.12	1,247.56	391.52
108	WICST	08	6	**0**	**94**	749.24	962.74	1,145.24	1,700.07	33.95
109	WICST	08	6	**0**	**92**	1,044.80	1,044.80	1,075.55	1,618.43	89.12
111	WICST	08	6	**43**	**43**	1,320.00	1,440.00	596.81	1,295.57	241.06
112	WICST	08	6	**65**	**28**	1,838.60	1,838.60	1,249.92	1,313.58	756.11
114	WICST	08	6	**76**	**17**	3,400.00	3,400.00	1,614.46	1,072.97	1,863.45
115	WICST	08	7	**37**	**49**	1,000.00	1,026.20	982.58	1,412.32	157.00
116	WICST	08	6	**25**	**57**	720.00	720.00	957.26	1,599.76	-121.22
117	WICST	08	8	**48**	**38**	2,240.00	2,360.00	1,096.86	1,378.92	901.08
118	WICST	08	7	**54**	**32**	1,080.00	1,080.00	1,763.28	1,387.55	589.11
119	WICST	08	7	**29**	**63**	794.70	1,038.90	1,664.57	1,276.40	585.89
120	WICST	08	5	**35**	**51**	1,440.00	1,440.00	1,318.70	1,426.30	523.57
AVG	**WICST**	**08**	-	-	-	**1380±226**	**1449 ± 220**	**1225 ± 96**	**1394±51**	**501±152**

† S = species richness, maximum number of species found in each experimental unit.
‡ Peak biomass harvest dates = August 30 and 31, 2007 and August 25, 26 in 2008.
§ Autotrophic respiration is assumed to be 40% of soil respiration (valued reported by Kucera & Kirkham 2001)

DISCUSSION

Net ecosystem production increased as C4 grass abundance increased, but the results indicated that species composition was more important than functional groupings for C dynamics. The relationships between the estimated major components of the C cycle (ANPP, BNPP, and Rs) to functional group and plant species cover followed the predicted directions but were modified primarily by site productivity. One of the caveats of a mensurative experiment such as this is that it is set in a natural setting where consistently representing all possible variations of species composition may be impossible. While, field experiments may improve ecosystem representativeness, it also may increase the chances of randomly picking combinations of species that are dominated by one or more highly productive species that drive the system. We found a clear dominance of *Andropogon gerardii*, which was highly productive in all the experimental units at the higher end of the C4 grass cover gradient in our study. In addition, all the plots that on average were covered with more than 55% of *A. gerardii* yielded two to three times the average of all the other plots. Simultaneously, of all the species from either functional group, only one of the C4 grasses (*A. gerardii)* was correlated positively to NEP, ANPP, and BNPP. Hence, our study indicates that increasing *A. gerardii* cover can positively affect NEP and that the composition drives changes in C dynamics more that the functional groupings. Similarly, comparing soils under three C4 grasses to soils from adjacent C3 dominated fields, Mahaney et al. (2008) found that the identity of the C4 species influenced the magnitude of the effects on soil carbon and nitrogen cycling, particularly *A. gerardii* cover. Other studies that had manipulated the functional diversity and species richness in Minnesota found that only C4 grasses and legumes significantly affected productivity and they suggest that the increase in productivity with

diversity was partially caused by high yielding C4 species in high-diversity plots (Tillman and Downing, 1994). Inferences beyond those 2 sites should be carefully drawn (Hurlbert, 1984) and a more complete representation of the C3:C4 grass gradient with replicated plots can help to clarify if the observed quadratic fit suggesting that there might be a threshold of C4 grass cover above which the ecosystem responds in a non-linear fashion is general. Also, a manipulative experiment could help determine if our results were driven by coincidentally selecting very productive sites in the high end of the gradient or if compositional identity of the C4 group really drives the system.

We predicted that net primary productivity should increase with higher abundance of C4 grass cover and that soil respiration would decrease. Our study supports the prediction that soil respiration decreases with increasing C4 abundance and that ANPP increases as documented in several prairie studies (Seastedt et al., 1994; Tilman et al., 1997; Mahaney et al., 2008). However, despite differences in root stock biomass found under C4 and C3 grasses, we did not find a correlation between BNPP and plant cover. This result runs counter to our prediction and it is inconsistent with other studies that report positive changes in BNPP when community composition shifts to C4 dominance in restored prairies (Baer et al., 2002; Camill et al., 2004; Mahaney et al., 2008) and CRP lands (Kucharik et al., 2001). This result may not be surprising considering that aboveground functional cover may not translate directly into belowground functional cover. One possible explanation is that spatial variability under bunch and sod forming grasses is high enough that estimates of aboveground cover do not match well belowground composition. Another point to consider is that most of the studies mentioned above compared cool-season pastures or agricultural

lands that were restored into grasslands highly dominated by C4 grasses (60-80%). An efficient and productive technique to separate roots by functional groups is necessary to access the belowground responses along a C3:C4 grass gradient. Because BNPP provides most of the carbon to the soil in grassland systems (Jobbagy and Jackson, 2000; Gill et al., 2002), we need a more precise estimate of BNPP along the C3:C4 gradient to evaluate the potential carbon sequestration in either working lands that intend to reintroduce warm-season grasses to pastures or in restored prairies recolonized by introduced C3 grasses.

Our result indicating that the effect of C4 grass annual cover on NEP, ANPP and BNPP was inconsistent across sites suggests that changes in C dynamics may depend not only on the functional composition and the identity of the dominant species in the mix, but also on the abiotic factors such as nutrient availability, climatic conditions and soil type. Indeed, when we used the tree model to explore which variable most influenced NEP in our study, it was clear that soil parameters like K concentration were splitting the database along sites. Comparing both sites, WICST has more resources available for plant growth (soils with higher O.M., TC and TN content as well as higher water holding capacity) and these differences help explain the stronger relationship of the major components of the C cycle to increasing C4 abundance at that site. While our study did not reveal a relationship between BNPP with plant cover at BR Ranch, a higher proportion of biomass was allocated belowground at the Ranch than at WICST. Using regression trees we can clearly see that aboveground production drives C dynamics at WICST, while at BR Ranch the driver was the belowground production. Others have shown that belowground resource limitation causes plants to invest a higher proportion of their biomass belowground (Reich et al., 2001).

Soil resources may not be the only limiting factor for a higher NEP at BR Ranch. It is known that the amount of SOM retained by grassland soils is highly influenced by management (Jones et al., 2006). Cutting for hay exports a large part of the primary production from the pasture and nutrient removal has to be compensated since net sequestration is a matter of balancing C inputs and outputs. For instance, Franzluebbers et al. (2009) estimated that the removing and redistributing the forage on the land to feed the cattle elsewhere could result in a total of 0.1 Mg of C per hectare per year that is lost from the original land (this was not a complete life cycle analysis where CO_2 emissions resulting from cutting, baling, and transporting operations were discounted).

Conclusions

Several quantitative observations in this study reveal that NEP and ANPP has the potential to positively change with increasing C4 grass cover, but these relationships appeared to be driven by a single species, *Andropogon gerardii*. The relationships between C parameters (NEP, NPP, and Rs) and C4 cover were modified by site, where C dynamics were driven by BNPP at the low-resource site and ANPP at the high-resource site, but more replication along a gradient of resources availability is needed to determine whether this effect is general.

There are several conclusions in this project that can guide land managers and policy makers regarding mixed C4-C3 grasslands. At the management level, the July C4 grass cover can guide the land managers in assessing the productivity of the grassland before the end of the season when the grasses are very tall and the heat strong. It seems also that low-diversity grasslands that are mainly dominated by productive warm-season grasses, such as the CRP

lands, may prove to be a great alternative to improve SOC. At the same token, a low cover of cool-season grasses in restored prairies may not threaten the potential of the restoration to rebuilt SOC if the C4 grasses still the dominating grass. Our results also show that the higher C sequestration in consequence of a higher cover of warm-season grasses is not general across sites and nutrient-poor permanent grasslands may need to be moderately intensified either by increasing organic carbon input or moderate fertilization (Soussana et al., 2004). In a positive note, many forage species such as *Panicum virgatum* L. have been studied as good sources of bioenergy and according to our study, more attention could also be given to the potential of *Andropogon gerardii*. This project shows that research at the farm level, across various soil types and management still necessary if the C sequestered by mixed C4-C3 grasslands is to be considered as an effective strategy to long-term C storage and a key part to climate stabilization.

LITERATURE CITED

AWON - UW Automated Weather Observation Network. *Uw-Awon Data Retrieval* WI-MN Cooperative Extension Agricultural Weather Page, [cited March, 6, 2009. Available from http://www.soils.wisc.edu/wimnext/awon/SelectReport.html.

Baer, S. G., D J Kitchen, J M Blair, and C W Rice. "Changes in Ecosystem Structure and Function Along a Chronosequence of Restored Grasslands." *Ecological Applications* 12, no. 6 (2002): 1688-701.

Bruce, J. P., M. Frome, E. Haites, H. Janzen, R. Lal, and K. Paustian. "Carbon Sequestration in Soils." *Journal of Soil and Water Conservation* 54, no. 1 (1999): 382-89.

Brye, K. R., S. T. Gower, J. M. Norman, and L. G. Bundy. "Carbon Budgets for a Prairie and Agroecosystems: Effects of Land Use and Interannual Variability." 12, no. 4 (2002): 962-79.

Burke, Ingrid C., William K. Lauenroth, and Debra P. Coffin. "Soil Organic Matter Recovery in Semiarid Grasslands: Implications for the Conservation Reserve Program." *Ecological Applications* 5, no. 3 (1995): 793-801.

Buttel, Frederick. H. "Envisioning the Future Development of Farming in the USA: Agroecology between Extinction and Multifunctionality?" In *New Directions in Agroecology Research and Education*. Madison: UW-Madison, 2003.

Camill, P., M. J. McKone, S. T. Sturges, W. J. Severud, E. Ellis, J. Limmer, C. B. Martin, R. T. Navratil, A. J. Purdie, B. S. Sandel, S. Talukder, and A. Trout. "Community- and Ecosystem-Level Changes in a Species-Rich Tallgrass Prairie Restoration." 14, no. 6 (2004): 1680-94.

Chapin, F.S., P. A. Matson, and H. A. Mooney. *Principles of Terrestrial Ecosystem Ecology*. New York: Springer, 2002.

Chou, Wendy W. , Whendee L. Silver, Randall D. Jackson, Andrew W. Thompson, and Barbara Allen-Diaz. "The Sensitivity of Annual Grassland Carbon Cycling to the Quantity and Timing of Rainfall." *Global Change Biology* 14, no. 6 (2008): 1382-94.

CIAS - Center for Integrated Agricultural Systems. *The Wisconsin Beef Cattle Industry: A Snapshot.* UW- Madison Center for Integrated Agricultural Systems, 2008 [cited 2009]. Available from http://www.cias.wisc.edu/crops-and-livestock/the-wisconsin-beef-cattle-industry-a-snapshot/.

Craine, J. M., D. A. Wedin, and F. S. Chapin. "Predominance of Ecophysiological Controls on Soil Co2 Flux in a Minnesota Grassland." *Plant and Soil* 207, no. 1 (1999): 77-86.

Dijkstra, F. A., S. E. Hobbie, and P. B. Reich. "Soil Processes Affected by Sixteen Grassland Species Grown under Different Environmental Conditions." *Soil Science Society of America Journal* 70, no. 3 (2006): 770-77.

Elliot, E. T., J. W. Heil, E. F. Kelly, and H. C. Monger. "Soil Structural and Other Physical Properties. ." In *Standard Soil Methods for Long-Term Ecological Research.*, edited by D. C. Coleman G. P. Robertson, C. S. Bledsoe and P. Sollins., 74. New York: Oxford University Press., 1999.

Fahey, T. J., C. S. Bledsoe, F. P. Day, R. W. Ruess, and A. J. M. Smucker. "Fine Root Production and Demography." In *Standard Soil Methods for Long-Term Ecological Reserach*, edited by D. C. Coleman G. P. Robertson, C. S. Bledsoe and P. Sollins., 437. New York: Oxford University Press., 1999.

Fahey, Timothy J., and Jeffrey W. Hughes. "Fine Root Dynamics in a Northern Hardwood Forest Ecosystem, Hubbard Brook Experimental Forest, Nh." *The Journal of Ecology* 82, no. 3 (1994): 533-48.

Farber, S., R. Costanza, D. L. Childers, J. Erickson, K. Gross, M. Grove, C. S. Hopkinson, J. Kahn, S. Pincetl, A. Troy, P. Warren, and M. Wilson. "Linking Ecology and Economics for Ecosystem Management." *Bioscience* 56, no. 2 (2006): 121-33.

Follett, R.F., E.G. Pruessner, S.E.Samson-Liebig, J.M. Kimble, and S.W. Waltman. "Carbon Sequestration under the Conservation Reserve Program in the Historic Grasslands Soils of the United States of America." In *Soil Carbon Sequestration and the Greeenhouse Effect.*, 27-40. Madison: Soil Science Society of America 2001.

Franzluebbers, A. J., and J. A. Stuedemann. "Soil-Profile Organic Carbon and Total Nitrogen During 12 Years of Pasture Management in the Southern Piedmont USA." *Agriculture Ecosystems & Environment* 129, no. 1-3 (2009): 28-36.

Gebhart, D. L., H. B. Johnson, H. S. Mayeux, and H. W. Polley. "The Crp Increases Soil Organic-Carbon." 49, no. 5 (1994): 488-92.

Gibson, David J. "Grassland Loss." In *Grasses and Grassland Ecology*, 1-20. New York: Oxford University Press, 2009.

Gill, R. A. "Using Simple Environmental Variables to Estimate Belowground Productivity in Grasslands." *Global Ecology & Biogeography* 11 (2002): 79-86.

Gill, R. A., and R. B. Jackson. "Global Patterns of Root Turnover for Terrestrial Ecosystems." 147, no. 1 (2000): 13-31.

Gotelli, Nicholas J , and Aaron M. Ellison. *A Primer of Ecological Statistics*. Sunderland, Mass.: Sinauer Associates, Inc. Publishers., 2004.

Heady, Harold F., R.P. Gibbens, and R.W. Powell. "A Comparison of the Charting, Line Intercept, and Line Point Methods of Sampling Shrub Types of Vegetation." *Journal of Range Management* 12 (1959): 180-88.

Hilderbrand, R. H., A. C. Watts, and A. M. Randle. "The Myths of Restoration Ecology." *Ecology and Society* 10, no. 1 (2005).

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer, and D. A. Wardle. "Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge." *Ecological Monographs* 75, no. 1 (2005): 3-35.

Hurlbert, S.H. "Pseudoreplication and the Design of Ecological Experiments." *Ecology* 54 (1984): 187-211.

Jackson, R. B., H. A. Mooney, and E. D. Schulze. "A Global Budget for Fine Root Biomass, Surface Area, and Nutrient Contents." *Proceedings of the National Academy of Sciences of the United States of America* 94, no. 14 (1997): 7362-66.

Jarrell, W.M., D.E. Armstrong, D.F. Grigal, E.F. Kelly, H.C. Monger, and D.A. Wedin. "Soil Water and Temperature Status." In *Standard Soil Methods for Long-Term Ecological Reserach*, edited by D. C. Coleman G. P. Robertson, C. S. Bledsoe and P. Sollins. New York: Oxford University Press, 1999.

Jobbagy, E. G., and R. B. Jackson. "The Vertical Distribution of Soil Organic Carbon and Its Relation to Climate and Vegetation." 10, no. 2 (2000): 423-36.

Johnson, J. M. F., D. C. Reicosky, R. R. Allmaras, T. J. Sauer, R. T. Venterea, and C. J. Dell. "Greenhouse Gas Contributions and Mitigation Potential of Agriculture in the Central USA." *Soil and Tillage Research* 83, no. 1 (2005): 73-94.

Jones, M. B., and Alison Donnelly. "Carbon Sequestration in Temperate Grassland Ecosystems and the Influence of Management, Climate and Elevated Co2." *New Phytologist* 164, no. 3 (2004): 423-39.

Jones, S. K., R. M. Rees, D. Kosmas, B. C. Ball, and U. M. Skiba. "Carbon Sequestration in a Temperate Grassland; Management and Climatic Controls." 22, no. 2 (2006): 132-42.

Kindscher, K., and P. V. Wells. "Prairie Plant Guilds - a Multivariate-Analysis of Prairie Species Based on Ecological and Morphological Traits." *Vegetatio* 117, no. 1 (1995): 29-50.

Knops, Johannes M. H., and David Tilman. "Dynamics of Soil Nitrogen and Carbon Accumulation for 61 Years after Agricultural Abandonment." *Ecology* 81, no. 1 (2000): 88-98.

Kucharik, C. J., K. R. Brye, J. M. Norman, J. A. Foley, S. T. Gower, and L. G. Bundy. "Measurements and Modeling of Carbon and Nitrogen Cycling in Agroecosystems of Southern Wisconsin: Potential for Soc Sequestration During the Next 50 Years." 4, no. 3 (2001): 237-58.

Kuzyakov, Y. V., and A. A. Larionova. "Contribution of Rhizomicrobial and Root Respiration to the Co2 Emission from Soil (a Review)." 39, no. 7 (2006): 753-64.

Lal, R. "Offsetting Global Co2 Emissions by Restoration of Degraded Soils and Intensification of World Agriculture and Forestry." *Land Degradation & Development* 14, no. 3 (2003): 309-22.

Luo, Yiqi, Robert B. Jackson, Christopher B. Field, and Harold A. Mooney. "Elevated Co_2 Increases Belowground Respiration in California Grasslands." *Oecologia* 108, no. 1 (1996): 130-37.

Mahaney, W. M., K. A. Smemo, and K. L. Gross. "Impacts of C-4 Grass Introductions on Soil Carbon and Nitrogen Cycling in C-3-Dominated Successional Systems." *Oecologia* 157, no. 2 (2008): 295-305.

Matamala, R., J. D. Jastrow, R. M. Miller, and C. T. Garten. "Temporal Changes in C and N Stocks of Restored Prairie: Implications for C Sequestration Strategies." *Ecological Applications* 18, no. 6 (2008): 1470-88.

McLauchlan, K. K., S. E. Hobbie, and W. M. Post. "Conversion from Agriculture to Grassland Builds Soil Organic Matter on Decadal Timescales." *Ecological Applications* 16, no. 1 (2006): 143-53.

Nelson, C. Jerry, and J C Burns. "Fifty Years of Grassland Science Leading to Change." *Crop Science* 46, no. 5 (2006): 2204-17.

NOAA - National Oceanic and Atmospheric Administration. *Historical Climate Data* United States Department of Commerce, [cited March 15 2009]. Available from http://www.aos.wisc.edu/~sco/clim-history/stations/470308.html and http://www.aos.wisc.edu/~sco/clim-history/stations/473405.html

Norman, J. M., R. Garcia, and S. B. Verma. "Soil Surface Co-2 Fluxes and the Carbon Budget of a Grassland." 97, no. D17 (1992): 18845-53.

NRCS - Natural Resources Conservation Service. *Web Soil Survey* United States Department of Agriculture, 2006 [cited March 5 2009]. Available from http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx

Paine, Laura K., Dan Undersander, and Michael D. Casler. "Pasture Growth, Production, and Quality under Rotational and Continuous Grazing Management." *Journal of Production Agriculture* 12, no. 4 (1999): 569-77.

Post, W. M., R. C. Izaurralde, J. D. Jastrow, B. A. McCarl, J. E. Amonette, V. L. Bailey, P. M. Jardine, T. O. West, and J. Z. Zhou. "Enhancement of Carbon Sequestration in Us Soils." *Bioscience* 54, no. 10 (2004): 895-908.

Reeder, J. D., G. E. Schuman, and R. A. Bowman. "Soil C and N Changes on Conservation Reserve Program Lands in the Central Great Plains." *Soil & Tillage Research* 47, no. 3-4 (1998): 339-49.

Reich, P. B., D. Tilman, J. Craine, D. Ellsworth, M. G. Tjoelker, J. Knops, D. Wedin, S. Naeem, D. Bahauddin, J. Goth, W. Bengtson, and T. D. Lee. "Do Species and Functional Groups Differ in Acquisition and Use of C, N and Water under Varying Atmospheric Co2 and N Availability Regimes? A Field Test with 16 Grassland Species." *New Phytologist* 150, no. 2 (2001): 435-48.

Rhemtulla, J. M., D. J. Mladenoff, and M. K. Clayton. "Regional Land-Cover Conversion in the Us Upper Midwest: Magnitude of Change and Limited Recovery (1850-1935-1993)." *Landscape Ecology* 22 (2007): 57-75.

Robertson, G. P., and S. M. Swinton. "Reconciling Agricultural Productivity and Environmental Integrity: A Grand Challenge for Agriculture." 3, no. 1 (2005): 38-46.

Samson, F., and F. Knopf. "Prairie Conservation in North America." *Bioscience* 44 no. 6 (1994): 418-21.

Seastedt, T. R., C. C. Coxwell, D. S. Ojima, and W. J. Parton. "Controls of Plant and Soil Carbon in a Semihumid Temperate Grassland." *Ecological Applications* 4, no. 2 (1994): 344-53.

Simonsen, Katie. "Investigations of Composition, Germination, Structure and Physiognomy in Three Southern Wisconsin Tallgrass Prairies." MSc Thesis, University of Wisconsin, 2004.

Six, J., R. T. Conant, E. A. Paul, and K. Paustian. "Stabilization Mechanisms of Soil Organic Matter: Implications for C-Saturation of Soils." *Plant and Soil* 241, no. 2 (2002): 155-76.

Smith, J., S. G. Potts, B. A. Woodcock, and P. Eggleton. "The Impact of Two Arable Field Margin Management Schemes on Litter Decomposition." *Applied Soil Ecology* 41, no. 1 (2008): 90-97.

Smith, P. "Soils as Carbon Sinks: The Global Context." *Soil Use and Management* 20 (2004): 212-18.

Soussana, J. F., P. Loiseau, N. Vuichard, E. Ceschia, J. Balesdent, T. Chevallier, and D. Arrouays. "(Carbon Cycling and Sequestration Opportunities in Temperate Grasslands." *Soil Use and Management* 20 (2004): 219-30.

Taylor, J. , and J. Foltz. "Grazing Int He Dairy State: Pasture Use in the Wisconsin Dairy Industry, 1993-2003." Madison, WI: Univeristy of Wisconsin - Madison 2006.

Tilman, D. "The Resource-Ratio Hypothesis of Plant Succession." 125, no. 6 (1985): 827-52.

Tilman, D., and J. A. Downing. "Biodiversity and Stability in Grasslands." 367, no. 6461 (1994): 363-65.

Tilman, D., Jason Hill, and Clarence Lehman. "Carbon-Negative Biofuels from Low-Input High-Diversity Grassland Biomass." *Science* 314, no. 5805 (2006): 1598-600.

Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. "The Influence of Functional Diversity and Composition on Ecosystem Processes." 277, no. 5330 (1997): 1300-02.

Vogt, Kristiina A., Charles C. Grier, Stith T. Gower, Douglas G. Sprugel, and Daniel J. Vogt. "Overestimation of Net Root Production: A Real or Imaginary Problem?" *Ecology* 67, no. 2 (1986): 577-79.

Wedin, David A., and David Tilman. "Species Effects on Nitrogen Cycling: A Test with Perennial Grasses." *Oecologia* 84, no. 4 (1990): 433-41.

Western, D. . "Human-Modified Ecosystems and Future Evolution." 5458-65.: National Academy of Sciences of the United States of America, 2001.

White, R., S Murray, and M. Rohweder. *Pilot Analysis of Global Ecosystems: Grasslands Ecosystems Technical Report.* Washington, D.C.: World Resources Institute, 2000.

Woodis, Julie Elizabeth. "An Agroecological Approach to Incorporating Native Warm-Season Grasses into Wisconsin Farms." Doctor of Philosophy, University of Wisconsin, 2008.