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### Influence of Nitrogen and Phosphorus on Ecosystem CO<sub>2</sub> Exchange in a Restored Temperate Grassland

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Influence of Nitrogen and Phosphorus on Ecosystem CO<sub>2</sub> Exchange in a Restored  
Temperate Grassland

By

Lynn M. Socha

An Abstract of a Thesis  
in  
Biology

Submitted in Partial Fulfillment  
Of the Requirements  
For the Degree of

Master of Arts

December 2012

State University of New York  
College at Buffalo  
Department of Biology

## ABSTRACT OF THESIS

### Influence of Nitrogen and Phosphorus on Ecosystem CO<sub>2</sub> Exchange in a Restored Temperate Grassland

Nitrogen (N) and phosphorus (P) affect the structure and function of grasslands by altering plant competitive interactions, shifting patterns of above- and belowground biomass allocation, and by increasing net primary production. However, the influence of N and P on net ecosystem productivity is poorly understood. In the context of a field-based factorial N- and P-addition experiment, I measured soil moisture, leaf area index and component fluxes of ecosystem CO<sub>2</sub> exchange throughout the growing season in a restored temperate grassland near Buffalo, New York. I predicted that N-addition would enhance ecosystem CO<sub>2</sub> uptake (GEE) while P-addition would stimulate ecosystem respiration ( $R_e$ ). As predicted, N-addition increased GEE and correspondingly amplified net ecosystem CO<sub>2</sub> exchange (NEE) to increase ecosystem CO<sub>2</sub> uptake. In contrast, P-addition did not significantly increase  $R_e$ . However, N- and P-addition interacted to significantly reduce NEE in comparison with plots that received N alone. Moreover, water limitation and phenological constraints during the middle and late growing season appear to limit autotrophic responses to nutrient addition. These results suggest that influences of N- and P-addition on ecosystem processes are seasonally dynamic and that the availability of N and P in soils may interact to weaken the strength of the terrestrial carbon sink.

State University of New York  
College at Buffalo  
Department of Biology

Influence of Nitrogen and Phosphorus on Ecosystem CO<sub>2</sub> Exchange in a Restored  
Temperate Grassland

A Thesis in  
Biology

By

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## Introduction

Anthropogenic climate change, species introductions, changing patterns of land-use and shifting patterns of nutrient cycling are altering ecosystem structure and function worldwide (Vitousek *et al.* 1997, Arnell 1999, Walther *et al.* 2002, Weltzin *et al.* 2003). Terrestrial ecosystems have both above- and belowground components, which, though linked through litter inputs and the rhizosphere, respond differently to environmental alterations (Wardle *et al.* 2004, Kardol and Wardle 2010). For example, nitrogen deposition has increased greatly due to a combination of anthropogenic factors associated with the burning of fossil fuels and the use of industrial fertilizers in agriculture (Vitousek *et al.* 1997). Nitrogen deposition may alter species richness, increase photosynthesis or alter aboveground net primary productivity (Vitousek *et al.* 1997, Stevens *et al.* 2004, Stevens *et al.* 2009). In turn, these changes may modify the cycling of other soil nutrients, especially phosphorus (Stewart and Tiessen 1987).

Nitrogen (N) availability limits primary productivity in temperate grasslands (Chapin *et al.* 1987, Tilman 1987). However, in contrast with the role of N in limiting primary productivity in temperate grasslands, phosphorous (P) mainly limits heterotrophic activity, such as the abundance of soil microbes (Sundareshwar *et al.* 2003). The effect of P on heterotrophs in temperate grasslands may in turn affect autotrophs by altering root to shoot ratios (Marschner *et al.* 1994). Moreover, N and P may co-limit temperate grasslands because they affect ecosystems differently (Morecroft *et al.* 1994, Craine *et al.* 2003, Niinemets and Kull 2005). In isolation, increased N or P may not have a large effect on plant activity, however, at least in some grasslands, N and



P in combination may increase aboveground net primary productivity (Craine *et al.* 2003).

These two limiting nutrients, N and P, influence autotrophs in several ways. N-addition is known to increase leaf photosynthesis (Gulmon 1981) whereas P-addition can indirectly increase shoot length in plants (Marshner *et al.* 1994). Plants may allocate resources to aboveground productivity rather than to root growth if P is present in significant quantities in the soil (Marschner *et al.* 1994). N-addition increases the concentration of ribulose-1, 5-bisphosphate carboxylase oxygenase (Rubisco), the enzyme responsible for primary carboxylation in C<sub>3</sub> photosynthesis, thereby increasing leaf level photosynthesis (Evans 1989). In practice, this usually means that the concentration of Rubisco increases with increasing N-availability (Warren *et al.* 2002). Plants generally allocate additional N to photosynthetic apparatuses, such as the antenna complex (Evans 1989). As the concentration of Rubisco increases, the maximum rate of photosynthesis also increases (Quick *et al.* 1991).

Likewise, N and P may influence soil microbial communities in complex ways. For example, P-addition has been shown to increase microbial respiration in soils where P is in short supply (Amador and Jones 1993). N- and P-addition may alter microbial community composition and biomass, thereby altering microbial respiration (Amador and Jones 1993, Bardgett *et al.* 1999, Piceno and Lovell 2000, Kennedy *et al.* 2004). In long-term studies, N and P in combination have been shown to decrease diversity in microbial community composition (Piceno and Lovell 2000). Likewise, Kennedy *et al.* (2004) demonstrated that soil N content had a greater influence on microbial community composition than plant community composition or other plant-mediated characteristics of

the rhizosphere. However, Bardgett *et al.* (1999) observed that changes in plant productivity along with N-addition altered microbial biomass and community composition in the short term.

Several studies have demonstrated the influence of N and P availability on the structure and function of grassland ecosystems (Tilman 1987, Wilson *et al.* 1995, Gulis and Suberkropp 2003). Through a structural change, such as increased canopy development, ecosystem functions that effect ecosystem CO<sub>2</sub> exchange may also be altered. N and P influence the components of ecosystem CO<sub>2</sub> exchange, photosynthesis and respiration as well (Evans 1989, Piceno and Lovell 2000, Sundareshwar *et al.* 2003). Temperate grasslands are typically considered as a net carbon sink (Scurlock and Hall 1998). However, N and P-addition might differentially influence the components of ecosystem CO<sub>2</sub> exchange in turn altering the source-sink dynamics of the carbon cycle. Thornley and Cannell (1997) demonstrated that additional CO<sub>2</sub> can increase the strength of the carbon sink in a grassland as long as the grasses are able to continually photosynthesize more. Although researchers have shown the ways in which N positively influences photosynthetic rates (Evans 1989) and that increased P availability may increase microbial respiration (Amador and Jones 1993), how these nutrients influence ecosystem carbon balance on their own and in combination with one another is understood less.

Measurements of ecosystem CO<sub>2</sub> exchange taken before 2003 were usually conducted using tower-based eddy covariance measurements requiring expensive instrumentation and infrastructure and large (> 1 ha), topographically uniform sites. Understandably, research emphasized broad-scale, long-term observational studies rather

than manipulative experiments (Xu and Baldocchi 2003). Moreover, often the most reliable data from these studies are measurements of daytime net ecosystem CO<sub>2</sub> exchange, rather than rates of photosynthesis or respiration (Baldocchi 2003). Eddy covariance data collected from towers are reliable when weather conditions are calm and the area being studied is homogenous, but are less accurate in real world situations that include high wind, changing weather, intricate landscapes or conditions that change over the course of time (Baldocchi 2003).

To address some of the shortcomings of tower-based methods, Arnone and Obrist (2003) created a portable chamber in which to measure ecosystem CO<sub>2</sub> exchange on small (< 9 m<sup>2</sup>) plots. Through the advent of a portable means to measure the component fluxes of ecosystem CO<sub>2</sub> exchange, researchers can now manipulate small experimental plots and measure ecosystem CO<sub>2</sub> exchange with accuracy. The original static chamber made by Arnone and Obrist (2003) has become a template for many other small scale manipulation experiments such as in the context of comparing burned and unburned sections of shrub land (Prater *et al.* 2006), CO<sub>2</sub> enrichment experiments (Jasoni *et al.* 2005) and rainfall manipulation experiments (Huxman *et al.* 2004b, Potts *et al.* 2006a, Potts *et al.* 2012).

Many of the manipulation experiments done using the tent based CO<sub>2</sub> exchange method have been done in arid or semi-arid regions (Arnone and Obrist 2003, Huxman *et al.* 2004a, Huxman *et al.* 2004b, Jasoni *et al.* 2005, Yopez *et al.* 2005, Potts *et al.* 2006a and 2006b, Prater *et al.* 2006, Carbone and Trumbore 2007, Harpole *et al.* 2007, Patrick *et al.* 2007, Nakano *et al.* 2008). Few studies have been focused outside of arid regions (Risch and Frank 2006, Carbone *et al.* 2007). For example, Risch and Frank (2006) used

a portable chamber to measure grazing and topographic effects on seasonal patterns of CO<sub>2</sub> exchange in a temperate grassland in Yellowstone National Park.

My objective was to determine how N- and P-addition influence seasonal patterns of shallow soil moisture, canopy development, ecosystem CO<sub>2</sub> exchange and above ground net primary productivity (ANPP). In the context of a N- and P-addition experiment in a restored temperate grassland, I predicted that N-addition would stimulate canopy development and, in turn, draw down shallow soil moisture. Similarly, I predicted that N-addition would increase canopy photosynthesis and, in turn, increase net ecosystem CO<sub>2</sub> exchange (NEE). In contrast, by stimulating microbial respiration, I predicted that P-addition would increase mid-day ecosystem respiration  $R_e$  and thus decrease NEE. Finally, I predicted that the contrasting effects of N- and P-addition on net ecosystem CO<sub>2</sub> exchange would offset one another in experimental plots that received simultaneous N- and P-addition.

## Materials and Methods:

### *Site Description*

This research was conducted at Tifft Nature Preserve (TNP) in the city of Buffalo, New York (42.87°N 78.87°W; elev. 181 m). Located on a former industrial site south of downtown Buffalo on the shore of Lake Erie, TNP is managed by the Buffalo Museum of Science as a nature preserve encompassing wetlands, riparian forest and grassland areas. The experimental site was located on the gently sloping east face of a former municipal landfill that was capped in 1973. Soils at the experimental site were shallow (~ 45 cm deep) and were situated on top of an impermeable layer of bentonite clay. Soil at the site originated as pond dredging during excavation of surrounding wetlands. This organic-rich, silty-clay soil was subsequently compacted during the capping of the landfill (David Spiering, personal communication).

The site has a humid, continental- type climate influenced by the presence of the Great Lakes. The nearest climate data are recorded approximately 16 km away at the Buffalo Niagara International Airport in Cheektowaga, NY (42.56° N, 78.43° W, elev. 222 m) with a mean annual temperature of 9 ° C and a mean annual precipitation of 924 mm. Precipitation for the period April 2010–November 2010 was 617.98 mm (Figure 1A).

The site was seeded in 1973 with a mix of non-native grasses and forbs. Presently, the plant community is dominated by the cool-season grasses *Festuca rubra* (red fescue) and *Bromus inermis* (smooth brome). Other, less abundant species include the cool-

season grass, *Agrostis gigantea* (red top), and the non-native forbs, *Coronilla varia* (crown vetch) and *Lotus corniculatus* (bird's foot trefoil).

### *Experimental Design*

Five experimental blocks, each containing four, 1 m x 1 m plots were delineated in May 2009. Block locations were selected based on similar slope position, proximity to one another and similar, representative vegetation. Within each experimental block, a 1 m aisle separated experimental plots to facilitate access and to provide a buffer between experimental treatments. An aisle approximately 3 m long separated each block. Plots corners were demarcated using short lengths of ½-inch PVC pipe and were randomly assigned as a control (C), nitrogen-addition (N), phosphorus-addition (P) or nitrogen and phosphorus-addition (N+P) plots. The plots were fertilized for two years beginning in 2009; nutrients were applied on April 1, June 14, August 1 and September 14. Nitrogen was applied by hand in the form of calcium nitrate ( $\text{CaNO}_3$ ) pellets at a rate of  $10\text{g NO}_3/\text{m}^2/\text{yr}$  and phosphorus was applied by hand in the form of triple super phosphate (TSP) pellets at a rate of  $8\text{g PO}_4/\text{m}^2/\text{yr}$ . The use of these fertilizers at these application rates is consistent with similar nutrient addition experiments (Baddeley *et al.* 1994, Phoenix *et al.* 2003, Harpole *et al.* 2007).

### *Measurements of Soil Moisture, Canopy Development*

Volumetric soil moisture ( $\theta$ ) was measured every seven to ten days using a portable meter fit with 12 cm probes (Hydrosense Campbell Scientific, Logan, UT)

between April 22 and October 8, 2010. Probes were inserted vertically into the soil in three, representative locations in each plot and measurements of  $\theta$  were averaged. Seasonal patterns of leaf area index (LAI) were estimated by measuring canopy interception of photosynthetically active radiation (PAR) using a line ceptometer (Accupar, Decagon Devices, Pullman, WA) every seven to ten days between April 22 and October 8, 2010 during the midday under clear sky conditions. For above-canopy measurements of PAR, the line ceptometer was oriented level and positioned 25 cm above the canopy, facing south. For below-canopy measurements, three measurements of PAR were made at 25 cm intervals, positioned level above the soil litter layer, facing south and averaged. Leaf area index was calculated from measurements of canopy light interception using the line ceptometer's built-in algorithm.

#### *Measurements of Ecosystem CO<sub>2</sub> Exchange*

A tent-based method of collecting CO<sub>2</sub> exchange data was used to observe the effects of nutrient addition on the component fluxes of ecosystem CO<sub>2</sub> exchange. This method of collecting CO<sub>2</sub> exchange data is ideal for working in the context of experimentally manipulated field plots (Arnone and Obrist 2003). The tent-based method of CO<sub>2</sub> exchange has been used in similar manipulation experiments (Huxman *et al.* 2004b, Potts *et al.* 2006a, Harpole *et al.* 2007, Patrick *et al.* 2007).

Measurements of midday ecosystem CO<sub>2</sub> exchange were made using a portable, static chamber measuring 1.0 m by 1.0 m by 1.5 m, constructed of PVC piping, and covered by a tightly-sewn, translucent polyethylene cover (Durashield 6000, Thor Tarp, Oconomowoc, WI). These measurements were made eight times over the course of the

2010 growing season (May 10, May 25, June 18, July 2, July 22, August 7, August 29 and September 26) under clear sky conditions between the hours of 11:00-13:00. To measure net ecosystem CO<sub>2</sub> exchange (NEE), the chamber was positioned over a plot and secured to the ground by a heavy chain to minimize leaks. Inside the chamber, two 23 cm diameter, electric fans mounted on a portable tripod mixed the chamber atmosphere while a pump connected to flexible tubing cycled chamber atmosphere to and from an infrared gas analyzer (Li-840, Licor Environmental, Lincoln, NE) positioned outside the tent. After an initial mixing period of 30 seconds, changes in CO<sub>2</sub> concentration inside the tent were logged to a portable computer for 90 seconds.

To measure ecosystem respiration ( $R_e$ ), the chamber was ventilated, reseated and the heavy chain was repositioned. Then, an opaque cover was placed over the chamber, the chamber was allowed to mix for 30 seconds, and the increase in chamber CO<sub>2</sub> concentration was logged for 90 seconds. Because temperature influences gas molecule density, air temperature inside the chamber was recorded with a fine-wire thermocouple attached to a portable reader (Fluke 51-54 Series II Thermometer, Everett, WA) at the beginning and end of each measurement of NEE and  $R_e$ . During 120 seconds that would elapse during a typical measurement of NEE, air temperature would increase ~2°C over ambient. In addition, light conditions inside the chamber were recorded with a photosynthetically active radiation (PAR) sensor connected to a bubble-level and attached to a portable tripod (Decagon Devices, Pullman WA) during each measurement. I calculated NEE and  $R_e$  using air temperature and change in CO<sub>2</sub> concentration with time according to Jasoni *et al.* (2005). I estimated gross ecosystem CO<sub>2</sub> exchange (GEE) as:



$$NEE = GEE - R_e$$

where NEE is net ecosystem CO<sub>2</sub> exchange, GEE is gross ecosystem CO<sub>2</sub> exchange and R<sub>e</sub> is ecosystem respiration. Leaf area within plots varied greatly throughout the growing season and between experimental treatments. To better understand seasonal- and treatment-mediated shifts in GEE per unit leaf area, I standardized GEE measurements with LAI measurements to calculate leaf area adjusted GEE (GEE<sub>A</sub>) as:

$$GEE_A = GEE / LAI$$

where LAI was taken within +/- 2 days of the ecosystem CO<sub>2</sub> exchange measurements.

#### *Measurements of Aboveground Net Primary Productivity*

I estimated aboveground net primary productivity (ANPP) and litter abundance by clipping a 10 cm x 100 cm strip in each experimental plot during the second week of October 2010. Clipped biomass was sorted in the field as grasses, forbs and litter, returned to the laboratory, oven dried for 48 hours at 50°C and weighed. I report ANPP as the sum of area-adjusted live grass and forb biomass and expressed on a per square meter basis.

#### *Statistical Analysis*

Data were examined to see if they met the normality assumption of parametric statistics. In the case of ANPP, data were log transformed to meet this assumption. A two-factor, repeated measures ANOVA (JMP, SAS Institute, Cary, NC) was used to test for the significance of N-addition, P-addition, time and their interactions using NEE, GEE, R<sub>e</sub>, θ and LAI as response variables. I used a two-factor ANOVA to test the effect

of N-addition, P-addition and their interaction on ANPP. To better understand the effects of N- and P-addition on the linkage between above- and below-ground processes, I plotted average GEE and average  $R_e$  on all dates using linear regression and tested for separate slopes.

## Results:

Across nutrient addition treatments, volumetric soil moisture ( $\theta$ ) reflected seasonal patterns of precipitation (Figure 1A-B). Early in the growing season, frequent rainfall resulted in greater  $\theta$ . As the growing season progressed, smaller, less frequent storms were associated with declining  $\theta$  across treatments (Table 1, Time). Throughout the growing season, N-addition influenced a decline in  $\theta$  (Table 1, N), however, this effect was minimized during the driest portions of the growing season (Table 1, N x Time). In contrast, P-addition did not influence  $\theta$ .

Beginning in mid-April and continuing through early October, continuous grassland canopy development was reflected in increasing leaf area index (LAI) throughout the growing season (Figure 2; Table 1, Time). Similar to  $\theta$ , N-addition increased LAI throughout the growing season (Table 1, N). The positive effect of N-addition on LAI was reflected in the significant positive effect of N-addition on ANPP (Figure 3). In contrast, P did not significantly increase ANPP nor did the positive effect of N-addition depend on the addition of P (Figure 3).

Net ecosystem CO<sub>2</sub> exchange (NEE) varied throughout the growing season in a saddle-shaped pattern (Figure 4). The greatest rates of midday net CO<sub>2</sub> uptake (indicated by large, negative values of NEE) occurred during the early growing season. As the growing season progressed, midday NEE became less negative (indicating a weakening of the ecosystem as a midday C-sink) and became more negative again during the late-growing season.

Consistent with my prediction, N-addition produced increasingly negative values of NEE (Table 2; N). The effect of N-addition was greatest during the early-growing

season and declined as the growing season progressed (Figure 5; Table 2, Time x Nitrogen). In contrast, P-addition did not influence NEE (Figure 4). However, N and P in combination were associated with a weakening of the ecosystem as a midday CO<sub>2</sub> sink (as indicated by values of NEE closer to zero) compared to those that received only N-addition (Table 2, NxP).

Seasonal patterns of ecosystem respiration ( $R_e$ ) mirrored the saddle-shaped dynamics of NEE (Table 2, Time). During the early growing season,  $R_e$  increased rapidly (larger positive values indicating increased respiratory losses of CO<sub>2</sub> by plants and soil microbes) before declining during July. Later,  $R_e$  increased for a second time during August and declined during the last measurement in late September. Contrary to my prediction, P-addition did not significantly increase ecosystem respiration ( $R_e$ ; Figure 5). Similar to NEE, the influence of N-addition on  $R_e$  was seasonally dynamic such that the positive influence of N on  $R_e$  was greatest during the earliest part of the growing season (Table 2, N x Time).

Similar to ecosystem respiration, N-addition significantly increased gross ecosystem CO<sub>2</sub> exchange (GEE) as predicted (Table 2, N). The treatment effect of N on GEE was seasonally dynamic, being pronounced in the early portion of the growing season and later declining (Figure 6; Table 2, N x Time). Consistent with other components of ecosystem CO<sub>2</sub> exchange I measured, P-addition did not influence GEE. Moderate temperatures and abundant soil moisture during the early growing season created an ideal environment for C<sub>3</sub> photosynthesis (Figure 1B). However, in the middle portion of the growing season, high temperatures and low soil moisture (Figure 1B) may explain the decline in photosynthesis (Figure 6). The most negative GEE values occurred

in the early growing season (May 10, May 25, June 18) and the greatest differences between treatments also occurred at these times (Figure 6). Interestingly, although GEE was greatest during the early growing season, LAI was at its lowest (Figure 2).

To better understand the influence of N- and P-addition on the relationship between GEE and  $R_e$ , I used least squares linear regression to compare treatment averaged GEE and  $R_e$  across sampling dates (Fig. 7). Regardless of treatment, increasingly positive  $R_e$  (indicating increasing  $\text{CO}_2$  efflux) was correlated with increasingly negative GEE (indicating increasing  $\text{CO}_2$  uptake by the ecosystem; Fig. 7). However, the 95% confidence interval of around the slope of the best-fit line does not form a one-to-one ratio, suggesting that throughout the growing season, changes in midday GEE are consistently matched by changes in  $R_e$  of the same magnitude (mean = -1.16, 95% CI = -1.37—-0.96,  $n = 32$ ). Finally, treatment-specific regressions did not explain significant additional variance, suggesting that nutrient addition does not alter the fundamental relationship between these principal component fluxes of ecosystem  $\text{CO}_2$  exchange.

In striking contrast with seasonal patterns of GEE,  $\text{GEE}_A$  declined exponentially throughout the growing season (Fig. 8; Table 1,  $\text{GEE}_A$ ). Although N-addition plots had greater LAI than other plot types,  $\text{GEE}_A$  was most negative in the control plots. Moreover, large negative values of  $\text{GEE}_A$  in control plots suggest that on a per unit leaf area basis, control plots were more efficient at canopy photosynthesis than those that received supplemental nitrogen.

## Discussion:

Consistent with my first prediction, N-addition stimulated canopy development during the early portion of the growing season (Fig. 2) and was accompanied by a decrease in shallow soil moisture (Fig. 1B). Differences in leaf area index (LAI) between N-addition and control plots increased rapidly in the early growing season. However, later in the growing season, plants in the N-addition plots were not able to continually increase leaf area because they were likely constrained by phenology or water limitation (Begonia and Begonia 2007, Harpole *et al.* 2007). Indeed, during the latter portions of the growing season, water limitation might limit the effects of N-addition on ecosystem CO<sub>2</sub> exchange (Harpole *et al.* 2007).

In addition to nitrogen availability, water limitation may limit temperate grassland ANPP (Burke *et al.* 1997; Knapp *et al.* 2001). In the present study, a decline in soil moisture during the middle growing season was associated with less negative midday NEE (Fig. 1B, 4). In fact, during the middle and late growing season, NEE declined to rates similar to those observed in a Chihuahuan desert grassland (Patrick *et al.* 2007). A mid-season decline in midday NEE is attributable to a decline in GEE (values closer to zero) associated with water limitation and high midday temperatures leading to high rates of photorespiration in this plant community dominated by the C<sub>3</sub> photosynthetic pathway (Sharkey 1988). While several studies have experimentally established the linkage between soil moisture and ecosystem CO<sub>2</sub> exchange in semi-arid (Potts *et al.* 2006a, Patrick *et al.* 2007) and Mediterranean-type grasslands (Harpole *et al.* 2007; Potts *et al.* 2012), much remains to be learned regarding the role of seasonal water deficit in

constraining ecosystem CO<sub>2</sub> exchange in ecosystems not typically associated with water limitation (Weltzin *et al.* 2003; Xia *et al.* 2009).

Whereas middle growing season water limitation may have reduced NEE, N-addition increased NEE (Fig. 5). This increase in the strength of the ecosystem as a midday carbon sink was supported by increased LAI and more negative GEE in N-addition plots in comparison with other treatments. Whereas Flanagan *et al.* (2002) observed close correlation between changes in GEE and changes in LAI in a Canadian shortgrass steppe, I observed the most negative GEE during the early growing season, long before LAI peaked (Fig. 6 and 2 respectively). However, the LAI values observed by Flanagan *et al.* (2002) were relatively low ( $LAI < 1$ ) whereas in the present study, LAI reached a maximum of approximately 7 (Fig. 2). Increasing light limitation of photosynthesis with increasing LAI may help to explain the weak linkage between LAI and GEE that I observed. Indeed, canopy light limitation has been implicated in altering the structure of meadow communities (Hautier *et al.* 2009) though its influence on grassland CO<sub>2</sub> exchange remains poorly studied.

To better understand the CO<sub>2</sub> exchange implications of increasing LAI associated with N-addition, I calculated leaf area adjusted GEE ( $GEE_A$ ). Over the course of the growing season,  $GEE_A$  declined rapidly as GEE became less negative and LAI increased (Fig. 8). While the influence of supplemental nitrogen on leaf-level photosynthesis is well documented (Evans 1989), few studies have attempted to document the effects of supplemental N on GEE (Harpole *et al.* 2007; Niu *et al.* 2010). In the context of a factorial N-addition and free air CO<sub>2</sub> enrichment study, Lee *et al.* (2001) observed that supplemental N did not increase leaf photosynthesis. Instead, plants responded to

increased N availability by increasing leaf area. In a similar fashion, I observed that N-addition was associated with a decline in  $GEE_A$  suggesting that grasses in these plots allocated N to produce more leaves, rather than increasing the nitrogen content and hence photosynthetic capacity, of existing leaves.

Surprisingly, in addition to positively influencing GEE, N-addition positively influenced  $R_e$ . Enhanced  $R_e$  in N-addition plots may be explained in part by the greater plant biomass that these plots supported (Potts *et al.* 2008; Xia *et al.* 2009). In addition to this increase in  $R_e$  associated with an increase in plant biomass, by increasing plant productivity, N-addition may have indirectly increased soil microbial respiration through the increased availability of labile carbon in the rhizosphere (de Graaff *et al.* 2010). The close association between GEE and  $R_e$  across experimental treatments is consistent with the idea that these important ecosystem functions are tightly coupled to one another through plant productivity (Fig. 7; Metcalfe *et al.* 2011).

Labile carbon limitation by soil microbes may also help explain the fact that, contrary to my prediction, P-addition had little influence on  $R_e$  and NEE. Instead, the effect of P-addition on ecosystem  $CO_2$  exchange depended on nitrogen availability (Table 2, N x P). By stimulating plant productivity, N-addition may have indirectly increased labile carbon supply to the soil through enhanced root activity and increased root exudates (Högberg and Read 2006) in turn shifting microbial activity from carbon limitation to P-limitation. However, while this explanation is supported by the response of NEE, the interactive effects of N- and P-addition on  $R_e$  are less consistent suggesting the possibility that this interactive effect is mediated by other environmental conditions such as temperature or soil moisture. Alternatively, a lack of  $R_e$  response to P-addition



may be related to a decrease in plant allocation to fine roots and root exudates with increased P-availability (Marschner *et al.* 1996). By reducing below ground allocation of carbon by plants, increasing microbial labile carbon limitation may have offset P-mediated increases in soil microbial respiration.

Differential responses of above- and belowground components of grassland ecosystems to N- and P-addition influence ecosystem CO<sub>2</sub> exchange, and therefore ecosystem carbon balance. Moreover, these responses are seasonally dynamic reflecting plant phenology and allocation plasticity as well as the limitation of temperature and soil moisture on photosynthesis and soil microbial activity. Driven by increasing LAI, N-addition significantly increased growing season GEE, R<sub>e</sub> and NEE. In contrast, the effect of P-addition on NEE depended on the availability of N and influenced a weakening of the ecosystem as a carbon sink. The significant interaction of these factors reinforces the critical role of plant-mediated labile carbon allocation to the rhizosphere (Metcalf *et al.* 2011) and the close coupling of nitrogen and phosphorous availability in controlling carbon balance in this restored temperate grassland (Kardol and Wardle 2010).

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Figure 1(A): Daily precipitation during the 2010 growing season. (B) Mean  $\pm$  SE volumetric soil moisture ( $\Theta$ ) taken using a 12cm soil moisture probe in control (C), N-addition (N), P-addition (P) and NP-addition (NP) plots during the 2010 growing season in a restored, temperate grassland near Buffalo, NY.

Figure 1

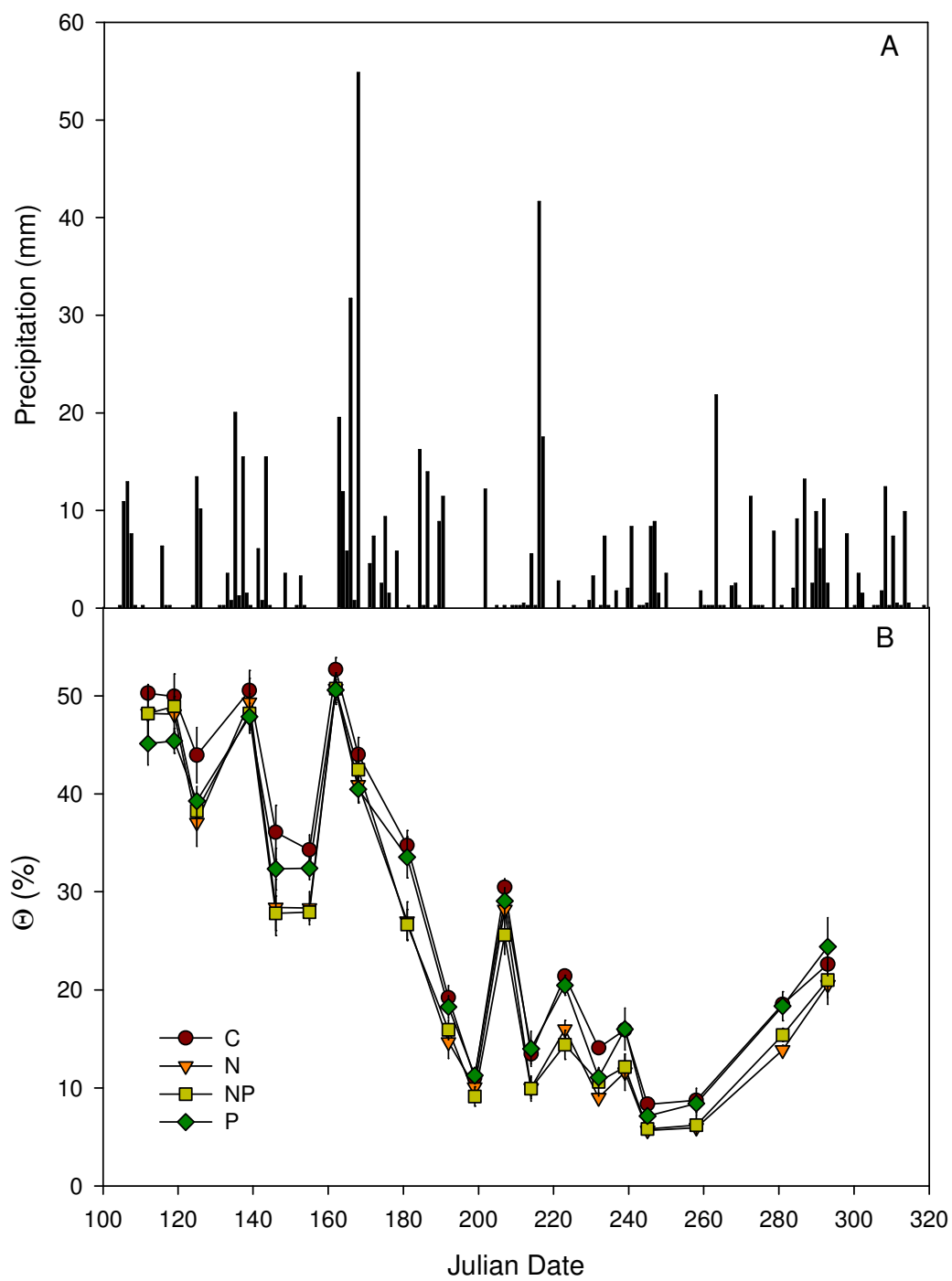


Figure 2: Mean  $\pm$  SE leaf area index (LAI) in control (C), N-addition (N), P-addition (P) and NP-addition (NP) plots during the 2010 growing season in a restored, temperate grassland near Buffalo, NY.

Figure 2

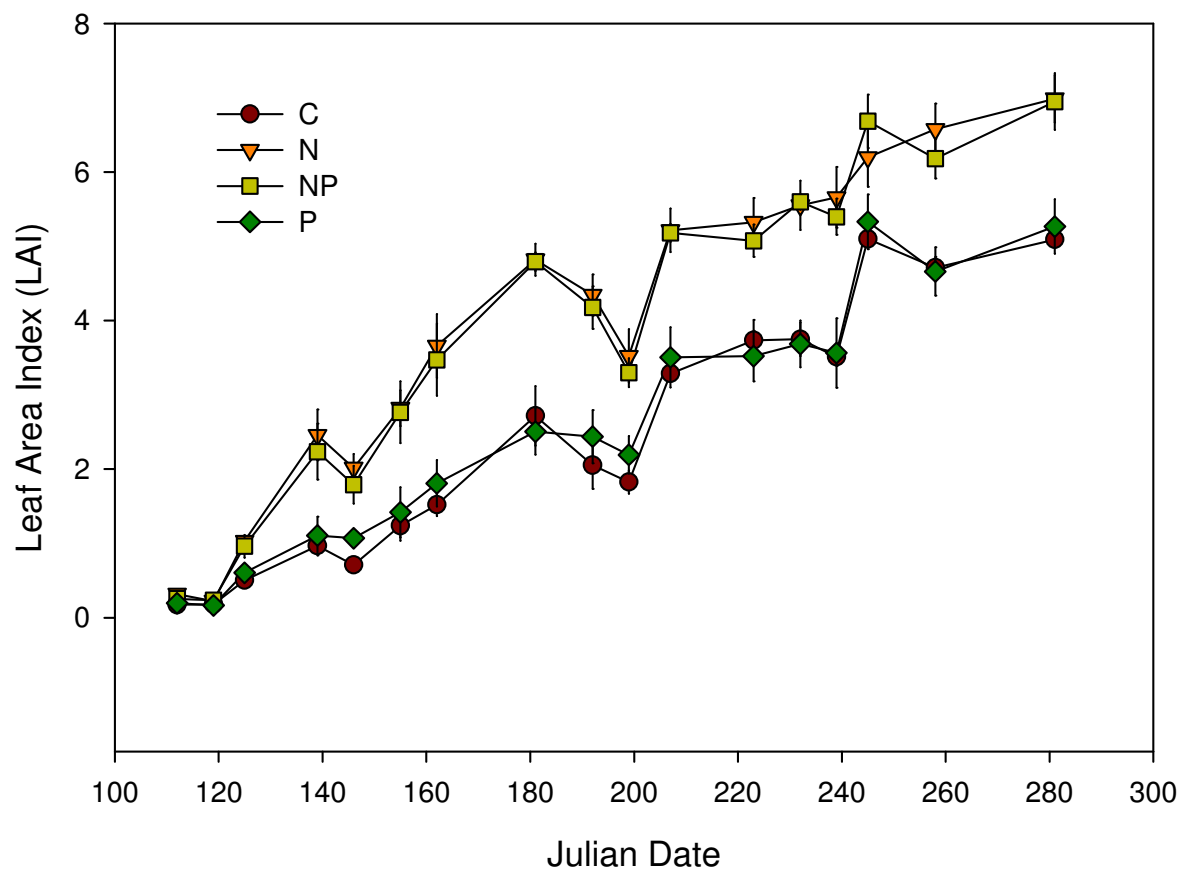


Figure 3: Aboveground net primary productivity (ANPP;  $\text{g/m}^2$ ) in control (C), N-addition (N), P-addition (P) and NP-addition (NP) plots in a restored, temperate grassland near Buffalo, NY. Error bars indicate SE.

Figure 3

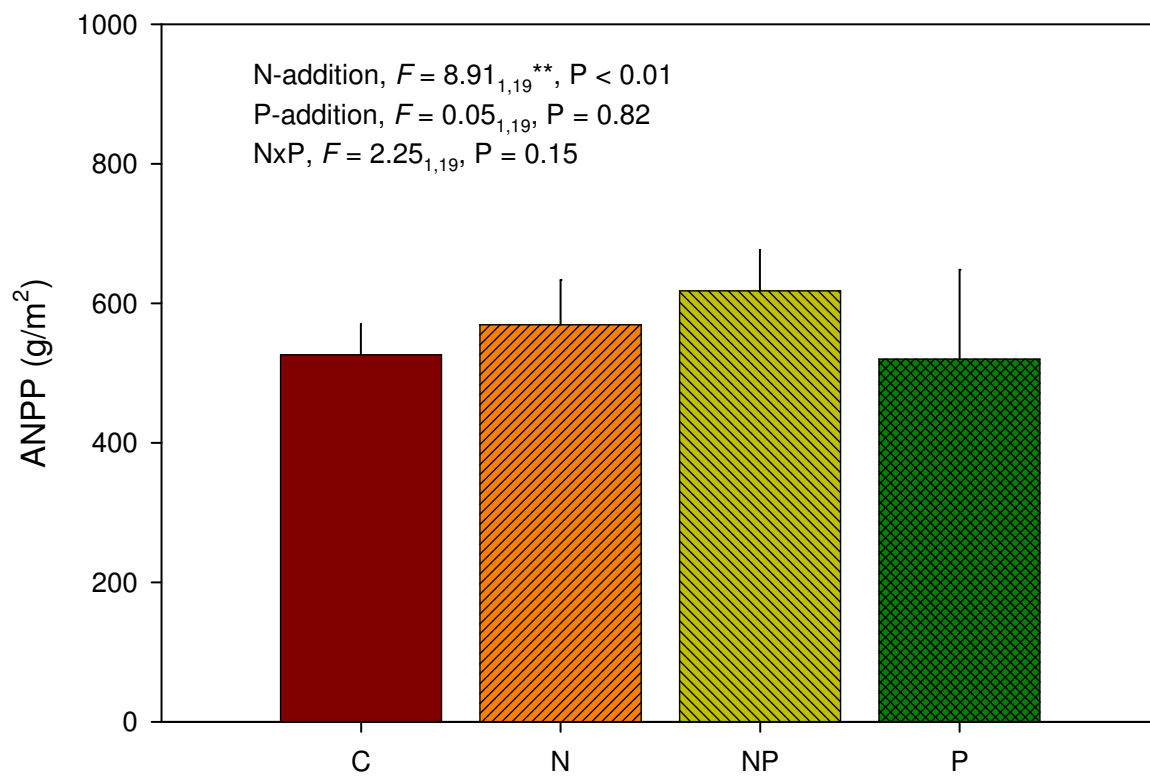




Figure 4: Mean midday net ecosystem CO<sub>2</sub> exchange (NEE;  $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ ) in control (C), N-addition (N), P-addition (P) and NP-addition (NP) during the 2010 growing season in a restored, temperate grassland near Buffalo, NY. Error bars indicate SE. Increasingly negative values indicate increasing ecosystem CO<sub>2</sub> assimilation.

Figure 4

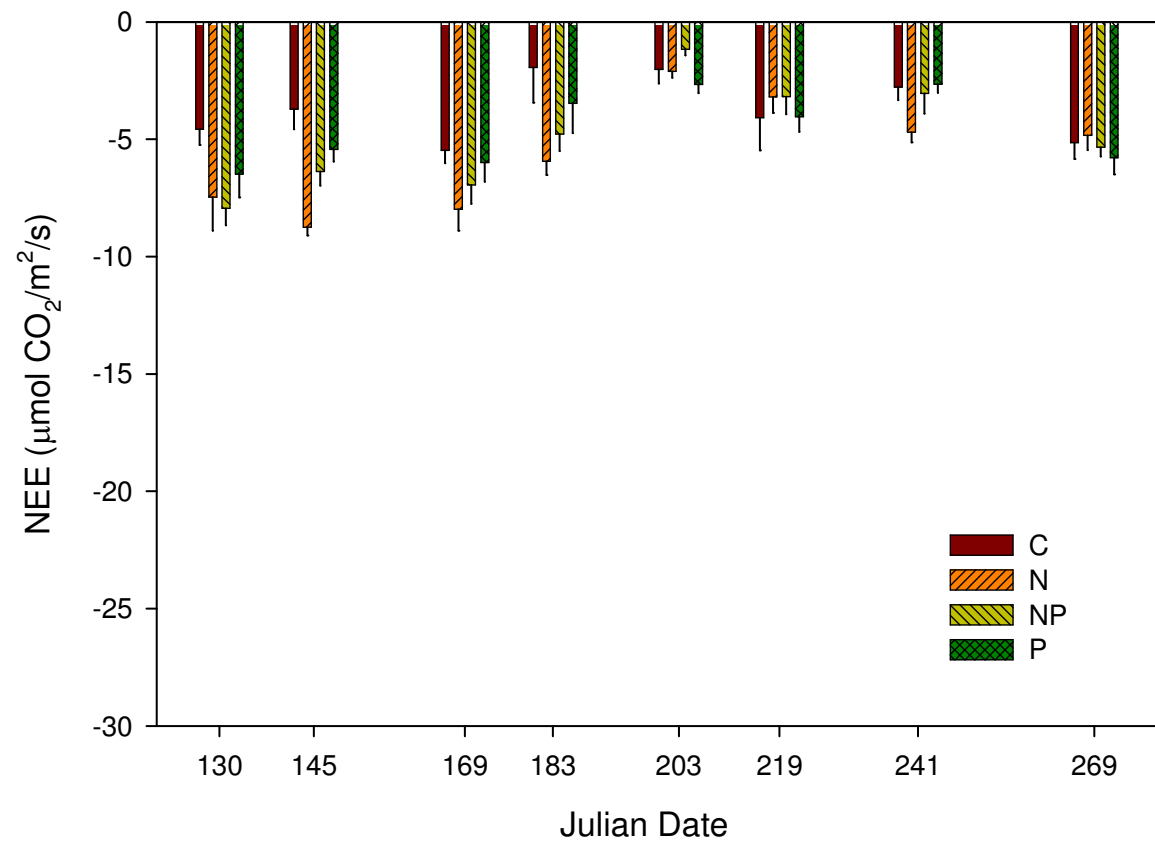


Figure 5: Mean midday ecosystem respiration ( $R_e$ ;  $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ ) in control (C), N-addition (N), P-addition (P) and NP-addition (NP) during the 2010 growing season in a restored, temperate grassland near Buffalo, NY. Error bars indicate SE.

Figure 5

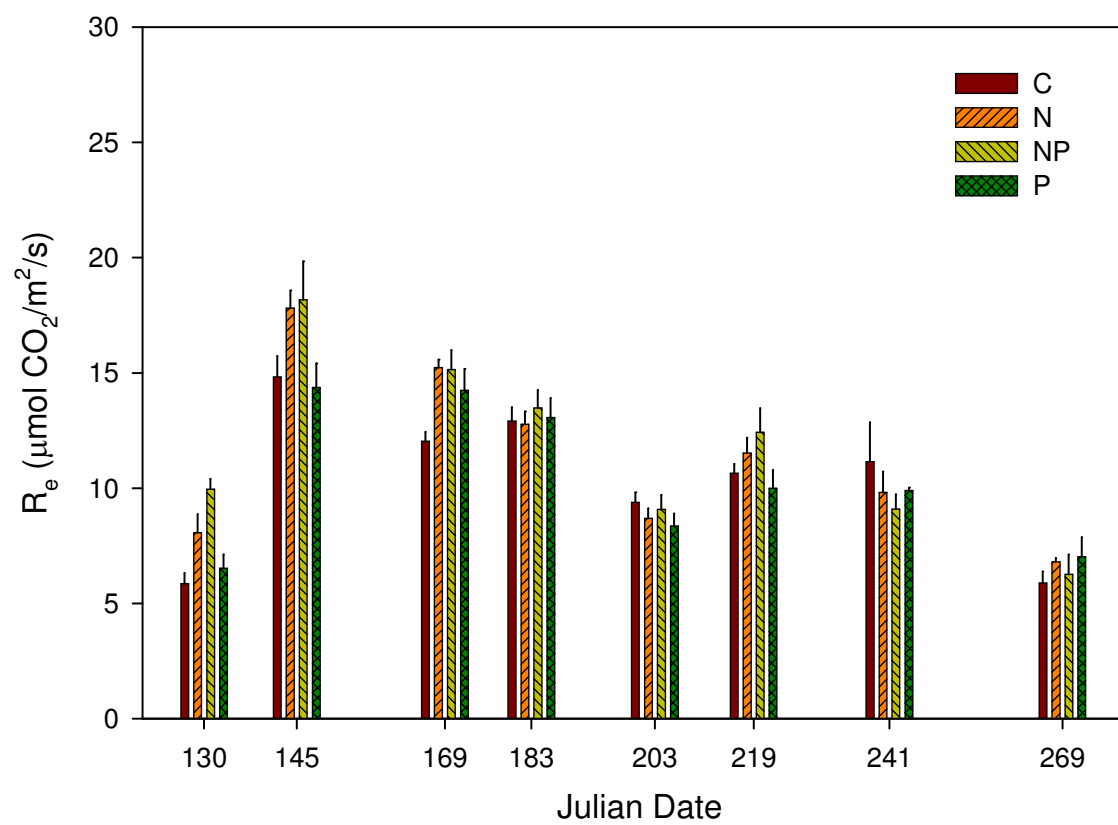


Figure 6: Mean midday gross ecosystem CO<sub>2</sub> exchange (GEE;  $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ ) in control (C), N-addition (N), P-addition (P) and NP-addition (NP) during the 2010 growing season in a restored, temperate grassland near Buffalo, NY. Error bars indicate SE. Negative values indicate increasing ecosystem CO<sub>2</sub> assimilation.

Figure 6

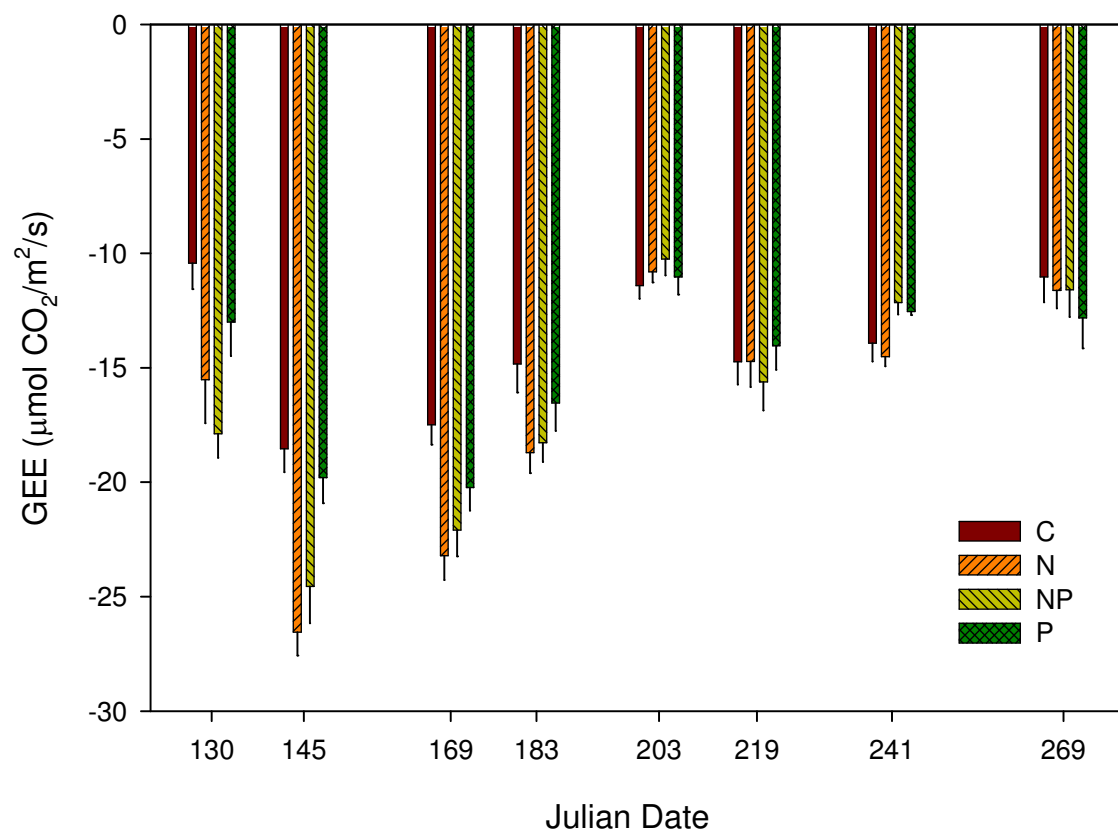


Figure 7: Midday gross ecosystem CO<sub>2</sub> exchange (GEE;  $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ ) versus midday ecosystem respiration ( $R_e$ ;  $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ ) for all sampling days in control (C), N-addition (N), P-addition (P) and NP-addition (NP) during the 2010 growing season in a restored, temperate grassland near Buffalo, NY. Symbols follow Fig. 1B. Increasing negative values of GEE note increasing ecosystem CO<sub>2</sub> assimilation.

Figure 7

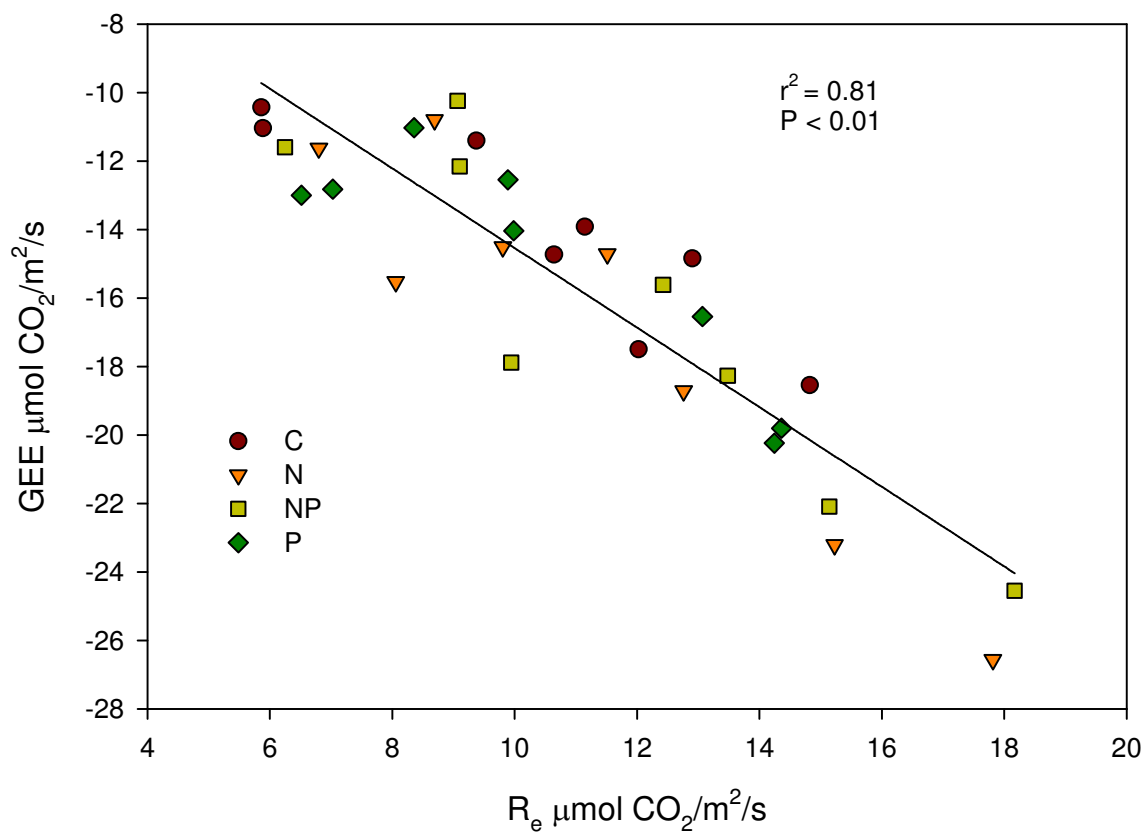




Figure 8: Leaf area adjusted midday gross ecosystem CO<sub>2</sub> exchange (GEE<sub>A</sub>;  $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ ) in control (C), N-addition (N), P-addition (P) and NP-addition (NP) during the 2010 growing season in a restored, temperate grassland near Buffalo, NY. Error bars indicate SE. Increasing negative values note increasing uptake of CO<sub>2</sub> by the ecosystem.

Figure 8

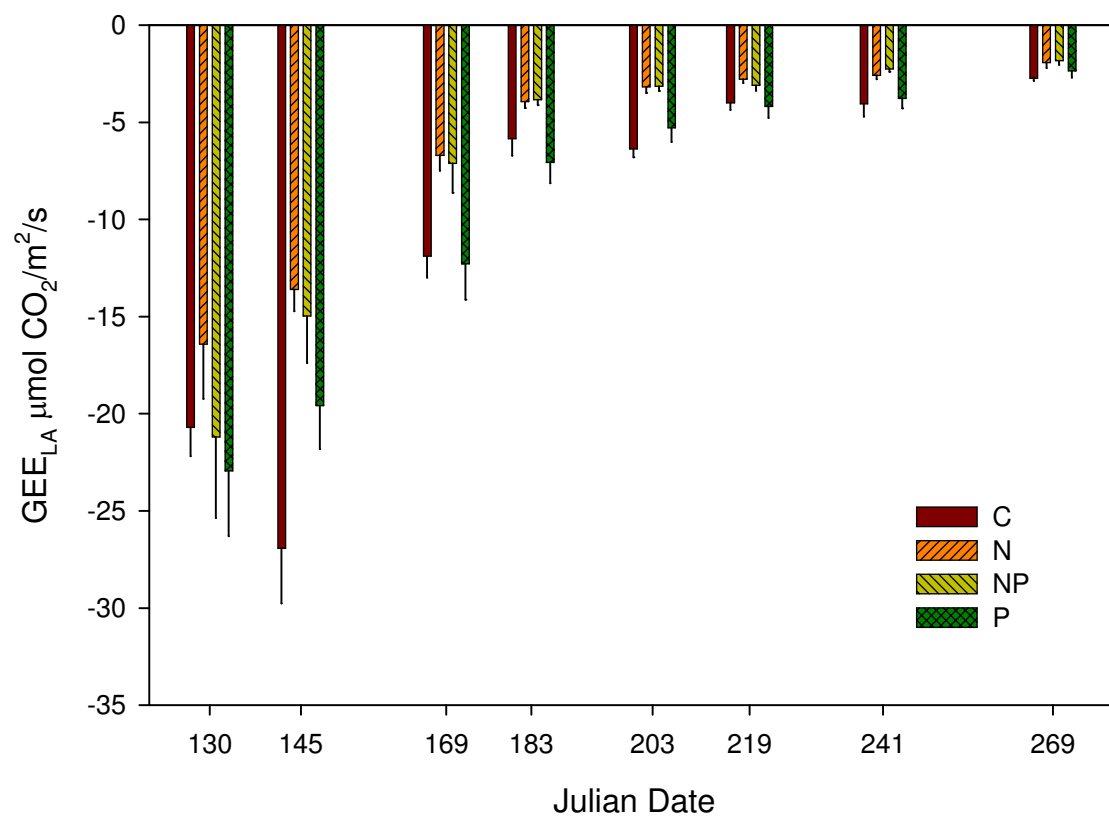


Table 1: Degrees of freedom (*df*) and *F*-statistics from the repeated measures ANOVA on the effect of N-addition, P-addition and time on volumetric soil moisture ( $\Theta$ ), leaf area index (LAI) and leaf area adjusted-GEE ( $GEE_a$ ) in a restored temperate grassland near Buffalo, New York.  $\Theta$ , volumetric soil moisture; LAI, leaf area index; N, nitrogen-addition; P phosphorus-addition; \*\*,  $P < 0.05$

Factors	<i>df</i>	$\Theta$	LAI
N	1, 16	1.37**	59.74**
P	1, 16	0.07	0.001
Time	16, 1	25713.71**	77177.89**
N x P	1, 16	0.079	0.0217
N x Time	16, 1	5256.66**	176.160
P x Time	16, 1	22.641	133.296
N x P x Time	16, 1	161.231	194.381

**Table 1:** *df*, degrees of freedom;  $\Theta$ , volumetric soil moisture; LAI, leaf area index; N, nitrogen-addition; P phosphorus-addition; \*\*,  $P < 0.05$

Table 2: Degrees of freedom (*df*) and *F*-statistics from the repeated measures ANOVA on the effect of N-addition, P-addition and time on the components of ecosystem CO<sub>2</sub> exchange in a restored temperate grassland near Buffalo, New York. NEE, net ecosystem CO<sub>2</sub> exchange; GEE, gross ecosystem CO<sub>2</sub> exchange; R<sub>e</sub>, respiration; N, nitrogen-addition; P, phosphorus-addition; \*, *P* < 0.1; \*\*, *P* < 0.05

Factors	<i>df</i>	NEE	GEE	R <sub>e</sub>	GEE <sub>A</sub>
N	1, 16	8.61**	17.24**	10.34**	16.84**
P	1, 16	0.01	0.25	0.43	0.77
Time	7, 10	32.22**	47.86**	113.82**	42.32**
N x P	1, 16	4.73**	1.60	0.14	0.06
N x Time	7, 10	10.69**	4.12**	3.08*	5.99**
P x Time	7, 10	0.94	2.12	1.05	2.65
N x P x Time	7, 10	1.87	0.58	1.13	1.02

**Table 2:** *df*, degrees of freedom; NEE, net ecosystem CO<sub>2</sub> exchange; GEE, gross ecosystem CO<sub>2</sub> exchange; R<sub>e</sub>, respiration; GEE<sub>A</sub>, leaf area adjusted-GEE; N, nitrogen-addition; P, phosphorus-addition; \*, *P* < 0.1; \*\*, *P* < 0.05



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Appendix A: Ecosystem CO<sub>2</sub> exchange data organized by date collected. Values are recorded as  $\mu\text{mol CO}_2/\text{m}^2/\text{s}$

5/10/2010

Treatment/Block	R <sub>e</sub>	NEE	GEE
C/1	4.17	-2.14	-6.31
C/2	6.31	-4.52	-10.83
C/3	5.75	-4.67	-10.43
C/4	6.09	-5.31	-11.41
C/5	6.95	-6.19	-13.15
N/1	8.50	-8.51	-17.02
N/2	6.50	-5.78	-12.28
N/3	8.59	-12.51	-21.11
N/4	6.10	-4.32	-10.42
N/5	10.57	-11.15	-21.72
NP/1	8.20	-6.89	-15.10
NP/2	10.63	-10.50	-21.14
NP/3	10.73	-8.21	-18.94
NP/4	10.01	-7.84	-17.85
NP/5	10.15	-6.21	-16.36
P/1	4.97	-2.55	-7.52
P/2	6.29	-7.21	-13.51
P/3	6.00	-7.07	-13.07
P/4	6.66	-7.77	-14.44
P/5	8.63	-7.79	-16.43

5/25/2010

Treatment/Block	R <sub>e</sub>	NEE	GEE
C/1	13.755	-2.97	-16.73
C/2	16.64	-5.39	-22.03
C/3	14.03	-2.44	-16.47
C/4	12.59	-6.14	-18.73
C/5	17.36	-1.66	-19.03
N/1	15.11	-7.70	-22.81
N/2	18.23	-8.31	-26.55
N/3	18.33	-8.66	-27.00
N/4	17.71	-9.78	-27.49
N/5	19.69	-9.27	-28.96
NP/1	15.43	-4.75	-20.18
NP/2	24.09	-5.23	-29.32
NP/3	18.95	-6.75	-25.71
NP/4	14.65	-6.66	-21.31
NP/5	17.70	-7.90	-25.61
P/1	10.74	-5.08	-15.82
P/2	14.58	-6.80	-21.39
P/3	16.66	-3.76	-20.43
P/4	14.89	-5.60	-20.50
P/5	16.24	-5.98	-22.23

6/18/2010

Treatment/Block	R <sub>e</sub>	NEE	GEE
C/1	11.95	-4.48	-16.43
C/2	12.21	-6.52	-18.74
C/3	12.27	-4.48	-16.76
C/4	13.10	-7.07	-20.18
C/5	10.59	-4.78	-15.38
N/1	16.17	-10.81	-26.98
N/2	15.43	-5.31	-20.74
N/3	14.18	-8.83	-23.02
N/4	14.80	-6.97	-21.78
N/5	15.55	-7.98	-23.54
NP/1	14.32	-8.74	-23.06
NP/2	17.51	-6.34	-23.86
NP/3	13.51	-4.25	-17.76
NP/4	13.57	-8.38	-21.96
NP/5	16.79	-7.03	-23.82
P/1	13.44	-6.67	-20.12
P/2	17.16	-3.67	-20.84
P/3	11.50	-5.50	-17.01
P/4	14.49	-5.42	-19.92
P/5	14.60	-8.68	-23.29

7/2/2010

Treatment/Block	R <sub>e</sub>	NEE	GEE
C/1	11.56	-4.71	-16.27
C/2	11.43	-3.53	-14.96
C/3	13.22	-1.99	-15.21
C/4	14.22	-3.27	-17.49
C/5	14.06	3.82	-10.24
N/1	12.61	-6.88	-19.49
N/2	12.20	-4.22	-16.42
N/3	14.33	-5.30	-19.64
N/4	11.04	-5.79	-16.83
N/5	13.61	-7.53	-21.14
NP/1	14.71	-6.54	-21.26
NP/2	12.32	-6.01	-18.33
NP/3	14.45	-3.48	-17.93
NP/4	11.01	-5.06	-16.07
NP/5	14.90	-2.85	-17.76
P/1	12.95	-5.45	-18.41
P/2	10.41	-6.06	-16.47
P/3	15.72	-2.80	-18.53
P/4	12.95	1.04	-11.91
P/5	13.29	-4.06	-17.36

7/22/2010

Treatment/Block	R <sub>e</sub>	NEE	GEE
C/1	9.27	-1.35	-10.63
C/2	8.02	-3.67	-11.70
C/3	10.50	-3.04	-13.54
C/4	9.01	-1.74	-10.75
C/5	10.08	-0.30	-10.38
N/1	10.10	-2.13	-12.24
N/2	8.53	-1.07	-9.60
N/3	7.54	-2.46	-10.01
N/4	8.94	-2.35	-11.29
N/5	8.33	-2.51	-10.84
NP/1	7.36	-1.59	-8.96
NP/2	9.93	-1.53	-11.46
NP/3	8.76	-1.26	-10.03
NP/4	10.96	-1.29	-12.25
NP/5	8.32	-0.17	-8.50
P/1	7.91	-2.01	-9.93
P/2	7.27	-1.93	-9.20
P/3	9.60	-3.89	-13.49
P/4	7.28	-3.05	-10.34
P/5	9.70	-2.45	-12.15



8/7/2010

Treatment/Block	R <sub>e</sub>	NEE	GEE
C/1	10.78	-4.25	-15.04
C/2	10.87	-3.88	-14.75
C/3	10.72	-3.43	-14.16
C/4	9.16	-8.77	-17.93
C/5	11.67	-0.10	-11.78
N/1	12.63	-3.42	-16.05
N/2	10.77	-2.99	-13.76
N/3	13.30	-5.14	-18.44
N/4	9.47	-3.58	-13.06
N/5	11.38	-0.87	-12.26
NP/1	10.39	-1.07	-11.46
NP/2	13.38	-4.68	-18.07
NP/3	10.77	-5.05	-15.83
NP/4	16.05	-2.12	-18.18
NP/5	11.52	-2.99	-14.52
P/1	9.40	-2.34	-11.75
P/2	10.63	-5.23	-15.86
P/3	10.96	-5.60	-16.57
P/4	11.74	-2.80	-14.55
P/5	7.17	-4.25	-11.42

8/29/2010

Treatment/Block	R <sub>e</sub>	NEE	GEE
C/1	10.36	-3.67	-14.04
C/2	8.46	-4.10	-12.57
C/3	12.45	-2.74	-15.19
C/4	7.41	-0.89	-8.312
C/5	17.04	-2.43	-19.48
N/1	11.30	-4.05	-15.35
N/2	6.64	-5.18	-11.82
N/3	11.41	-4.28	-15.69
N/4	9.00	-3.81	-12.81
N/5	10.68	-6.18	-16.86
NP/1	8.16	-2.82	-10.99
NP/2	10.60	-6.05	-16.66
NP/3	9.57	-1.45	-11.02
NP/4	9.96	-1.35	-11.32
NP/5	7.19	-3.58	-10.77
P/1	9.98	-1.37	-11.35
P/2	10.28	-2.46	-12.75
P/3	9.62	-2.66	-12.28
P/4	9.91	-3.27	-13.19
P/5	9.65	-3.50	-13.15

9/26/2010

Treatment/Block	R <sub>e</sub>	NEE	GEE
C/1	7.69	-6.88	-14.57
C/2	7.41	-6.89	-14.31
C/3	6.51	-5.71	-12.22
C/4	6.99	-6.18	-13.18
C/5	4.80	-5.41	-10.22
N/1	6.78	-3.88	-10.66
N/2	7.85	-8.10	-15.96
N/3	7.56	-5.84	-13.40
N/4	6.03	-5.79	-11.83
N/5	6.48	-3.24	-9.73
NP/1	9.82	-5.58	-15.40
NP/2	5.94	-4.21	-10.15
NP/3	5.81	-4.93	-10.74
NP/4	6.61	-4.58	-11.20
NP/5	4.90	-3.68	-8.59
P/1	7.74	-5.89	-13.64
P/2	5.09	-2.72	-7.81
P/3	6.70	-5.51	-12.22
P/4	6.04	-5.86	-11.90
P/5	2.99	-4.57	-7.57

Appendix B: Volumetric soil moisture ( $\Theta$ ) data recorded as a percentage. Data are organized by date collected.

4/22/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	41.3	40.3	39.0	39.6
Block 2	50.6	48.0	42.0	50.6
Block 3	54.3	51.3	45.3	57.3
Block 4	54.3	53.6	51.6	44.6
Block 5	50.6	47.6	47.6	48.6
Mean	50.2	48.2	45.1	48.2
Standard Error	2.3	2.2	2.1	2.9

4/29/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	45.0	42.6	42.0	44.6
Block 2	48.3	45.3	44.0	50.3
Block 3	57.0	51.0	44.3	53.6
Block 4	53.3	52.3	48.6	49.6
Block 5	46.0	49.3	48.0	46.3
Mean	49.9	48.1	45.4	48.9
Standard Error	2.2	1.8	1.2	1.5

5/5/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	35.0	30.3	37.3	34.0
Block 2	42.6	34.3	37.3	41.0
Block 3	49.6	43.6	39.0	43.6
Block 4	50.3	41.3	45.0	36.0
Block 5	42.0	35.6	37.6	36.6
Mean	43.9	37.1	39.2	38.2
Standard Error	2.8	2.4	1.4	1.7

5/17/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	43.3	43.0	45.0	44.0
Block 2	50.6	50.0	46.6	48.3
Block 3	56.0	49.6	46.6	55.6
Block 4	52.0	57.6	53.0	47.3
Block 5	50.6	46.3	48.0	45.6
Mean	50.5	49.3	47.8	48.2
Standard Error	2.0	2.4	1.3	2.0

5/26/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	29.6	22.0	28.6	22.6
Block 2	29.3	25.0	29.0	27.6
Block 3	41.0	30.0	31.3	33.3
Block 4	42.3	38.6	40.3	29.3
Block 5	38.0	26.3	32.3	26.0
Mean	36.1	28.4	32.3	27.8
Standard Error	2.7	2.8	2.1	1.7

6/04/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	32.3	27.3	31.3	29.0
Block 2	30.3	25.3	34.0	27.0
Block 3	37.3	28.6	31.3	30.0
Block 4	38.3	34.6	36.0	25.0
Block 5	33.0	25.6	29.3	28.6
Mean	34.2	28.3	32.4	27.9
Standard Error	1.5	1.6	1.1	0.8

6/11/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	51.0	49.6	51.0	53.6
Block 2	53.6	51.6	50.3	49.6
Block 3	57.0	54.6	51.3	55.3
Block 4	51.3	51.6	53.3	47.3
Block 5	50.3	46.0	47.0	47.6
Mean	52.6	50.7	50.6	50.7
Standard Error	1.2	1.4	1.0	1.6

6/17/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	42.3	39.6	41.0	42.0
Block 2	39.6	37.0	41.6	39.6
Block 3	48.0	43.0	42.3	47.0
Block 4	48.3	46.6	42.3	47.0
Block 5	41.6	38.3	35.0	36.6
Mean	44.0	40.9	40.4	42.4
Standard Error	1.7	1.7	1.3	2.0

6/30/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	36.0	30.6	34.6	31.3
Block 2	31.6	22.6	37.6	25.0
Block 3	38.3	24.0	31.6	26.0
Block 4	37.0	32.6	37.3	28.6
Block 5	30.6	25.0	26.3	22.33
Mean	34.7	27.0	33.5	26.6
Standard Error	1.5	1.9	2.1	1.5

7/11/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	21.3	18.3	20.0	19.6
Block 2	20.6	13.0	21.6	15.3
Block 3	21.0	11.3	16.3	14.0
Block 4	18.3	19.0	17.6	16.3
Block 5	14.6	11.6	15.6	14.3
Mean	19.2	14.6	18.2	15.9
Standard Error	1.2	1.6	1.1	1.0

7/18/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	13.3	11.0	12.0	12.3
Block 2	10.0	8.3	13.3	10.0
Block 3	11.6	9.3	10.0	7.6
Block 4	10.6	12.3	12.0	9.0
Block 5	9.3	9.3	9.0	6.6
Mean	11.0	10.1	11.2	9.1
Standard Error	0.7	0.7	0.7	0.9

7/26/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	32.3	31.0	32.6	33.0
Block 2	32.3	28.3	31.3	24.6
Block 3	30.6	27.3	28.0	25.6
Block 4	28.6	28.3	28.3	23.0
Block 5	28.3	26.0	25.0	21.6
Mean	30.4	28.2	29.1	25.6
Standard Error	0.8	0.8	1.3	1.9

8/02/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	17.0	13.6	18.6	15.0
Block 2	14.0	10.6	18.0	9.3
Block 3	11.0	7.0	10.6	8.0
Block 4	13.3	9.3	12.0	9.0
Block 5	12.0	9.3	10.6	8.3
Mean	13.4	10.0	14.0	9.9
Standard Error	1.0	1.1	1.7	1.2

8/11/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	22.6	15.6	22.0	19.6
Block 2	22.6	14.6	23.3	14.0
Block 3	22.3	13.6	19.0	11.3
Block 4	19.6	18.6	20.3	15.0
Block 5	19.6	17.3	17.6	12.0
Mean	21.4	16.0	20.5	14.4
Standard Error	0.7	0.9	1.0	1.5

8/20/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	15.6	9.3	14.3	14.3
Block 2	13.6	9.6	10.3	11.3
Block 3	14.6	7.0	8.0	6.0
Block 4	12.33	9.6	11.0	9.3
Block 5	14.0	9.3	11.6	12.0
Mean	14.1	9.0	11.1	10.6
Standard Error	0.6	0.5	1.0	1.4

8/26/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	18.3	17.6	23.3	16.0
Block 2	13.6	11.6	18.3	13.0
Block 3	16.0	11.6	13.3	10.3
Block 4	15.0	11.0	12.0	8.3
Block 5	16.6	6.0	13.0	13.0
Mean	15.9	11.6	16.0	12.1
Standard Error	0.8	1.9	2.1	1.3

9/02/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	9.0	5.3	6.3	6.3
Block 2	8.6	6.0	8.0	5.0
Block 3	7.3	4.0	5.3	4.3
Block 4	7.6	7.6	8.6	6.3
Block 5	9.0	5.3	7.3	7.0
Mean	8.3	5.6	7.1	5.8
Standard Error	0.3	0.6	0.6	0.5

9/15/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	13.3	8.0	12.0	10.0
Block 2	6.0	6.0	9.3	6.0
Block 3	8.6	4.6	7.3	4.3
Block 4	7.6	6.6	6.3	6.0
Block 5	8.0	4.3	7.0	4.6
Mean	8.7	5.9	8.4	6.2
Standard Error	1.2	0.7	1.0	1.0

10/01/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	19.3	15.0	23.6	18.0
Block 2	18.3	15.0	18.0	15.3
Block 3	18.6	13.3	16.0	14.3
Block 4	18.6	13.3	15.3	15.0
Block 5	17.6	12.6	18.6	14.3
Mean	18.5	13.9	18.3	15.4
Standard Error	0.3	0.5	1.5	0.7

10/08/2010

Treatment:	Control	Nitrogen	Phosphorus	N and P
Block 1	25.3	23.0	34.6	27.3
Block 2	20.0	24.3	27.0	21.6
Block 3	24.3	15.6	19.3	20.3
Block 4	24.0	24.0	22.3	17.0
Block 5	19.3	15.6	18.6	18.6
Mean	22.6	20.5	24.4	21.0
Standard Error	1.2	2.0	3.0	1.8

Appendix C: LAI measurements over the 2010 growing season (This is measured as a ratio and is a unitless number.) These data are organized by treatment: C, control; N, nitrogen; P, phosphorus; NP, nitrogen and phosphorus

	Block 1 C	Block 2 C	Block 3 C	Block 4 C	Block 5 C
4/22/2010	0.14	0.30	0.11	0.13	0.18
4/29/2010	0.19	0.35	0.10	0.16	0.08
5/5/2010	0.36	0.64	0.46	0.50	0.55
5/19/2010	0.63	1.35	0.75	1.12	0.98
5/26/2010	0.77	0.77	0.82	0.52	0.67
6/4/2010	0.91	1.99	1.28	1.08	0.91
6/11/2010	1.02	1.91	1.45	1.74	1.47
7/1/2010	2.11	4.28	2.62	2.22	2.34
7/11/2010	1.34	3.19	1.94	1.59	2.18
7/18/2010	1.45	2.36	1.90	1.62	1.79
7/26/2010	3.26	3.54	3.15	3.39	3.09
8/11/2010	4.17	4.50	2.95	3.65	3.39
8/20/2010	3.84	4.59	3.46	3.33	3.52
8/27/2010	3.49	3.64	3.41	3.86	3.14
9/2/2010	5.19	5.33	4.87	4.97	5.12
9/15/2010	4.63	5.02	5.02	4.66	4.24
10/8/2010	5.22	5.15	4.86	5.40	4.82
	Block 1 N	Block 2 N	Block 3 N	Block 4 N	Block 5 N
4/22/2010	0.40	0.38	0.24	0.34	0.23
4/29/2010	0.35	0.16	0.23	0.13	0.25
5/5/2010	1.11	0.96	1.11	1.12	0.85
5/19/2010	1.42	3.05	2.18	2.28	3.37
5/26/2010	1.27	2.25	2.06	2.14	2.35
6/4/2010	2.23	2.51	3.63	3.06	2.68
6/11/2010	3.10	2.60	4.35	4.93	3.30
7/1/2010	4.63	4.85	4.79	5.58	4.25
7/11/2010	3.58	5.02	4.49	4.79	3.82
7/18/2010	3.44	2.36	4.26	4.30	3.25
7/26/2010	5.52	4.18	5.53	5.83	5.01
8/11/2010	6.18	4.36	5.54	4.82	5.71
8/20/2010	6.10	4.36	5.88	6.10	5.31
8/27/2010	5.66	4.41	6.86	6.09	5.26
9/2/2010	5.18	5.67	7.48	6.61	6.04
9/15/2010	6.76	5.30	6.74	7.41	6.66
10/8/2010	7.03	5.92	7.17	7.91	6.91



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	Block 1 P	Block 2 P	Block 3 P	Block 4 P	Block 5 P
4/22/2010	0.19	0.20	0.17	0.13	0.28
4/29/2010	0.21	0.17	0.16	0.16	0.12
5/5/2010	0.50	0.53	0.39	0.58	1.01
5/19/2010	0.54	0.83	1.02	1.09	2.05
5/26/2010	0.99	0.85	0.82	1.29	1.38
6/4/2010	1.03	0.93	0.97	1.43	2.73
6/11/2010	1.45	1.12	1.61	1.92	2.94
7/1/2010	2.33	1.66	2.21	2.83	3.50
7/11/2010	1.34	2.38	2.13	2.88	3.46
7/18/2010	1.82	1.87	1.68	2.67	2.91
7/26/2010	2.87	2.66	3.21	3.88	4.90
8/11/2010	3.12	2.78	3.06	4.08	4.57
8/20/2010	2.88	3.71	3.30	3.76	4.77
8/27/2010	2.01	3.20	4.02	3.77	4.82
9/2/2010	4.91	4.77	5.29	4.91	6.77
9/15/2010	4.20	4.21	4.14	4.94	5.82
10/8/2010	5.01	4.50	5.04	5.12	6.66
	Block 1 NP	Block 2 NP	Block 3 NP	Block 4 NP	Block 5 NP
4/22/2010	0.21	0.26	0.27	0.28	0.25
4/29/2010	0.20	0.23	0.26	0.18	0.31
5/5/2010	0.42	0.91	0.99	1.30	1.19
5/19/2010	1.15	1.53	2.60	3.01	2.88
5/26/2010	0.88	1.64	1.98	2.11	2.34
6/4/2010	1.45	2.26	3.08	3.15	3.89
6/11/2010	1.77	3.68	3.41	3.74	4.76
7/1/2010	4.35	4.71	4.86	5.03	5.03
7/11/2010	3.77	5.20	3.53	4.10	4.28
7/18/2010	2.65	3.64	3.68	3.07	3.46
7/26/2010	5.22	5.01	5.10	4.95	5.63
8/11/2010	5.33	4.83	4.53	5.78	4.90
8/20/2010	5.42	5.81	5.37	5.88	5.51
8/27/2010	4.81	5.88	4.81	5.79	5.70
9/2/2010	5.72	6.16	7.17	6.62	7.75
9/15/2010	5.95	6.08	5.42	7.04	6.4
10/8/2010	6.57	7.50	5.68	7.85	7.15

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Appendix D: Live, litter and forb biomass (g/m<sup>2</sup>)

Treatment/Block	Live biomass	Litter biomass	Forb biomass
C/1	520	77	
C/2	582	153	0.1
C/3	365	170	
C/4	626	125	
C/5	429	114	
N/1	455	620	
N/2	551	166	0.4
N/3	643	92	
N/4	688	33	
N/5	656	138	
NP/1	589	28	1.3
NP/2	989	100	
NP/3	524	105	0.5
NP/4	753	60	
NP/5	684	114	0.2
P/1	185	365	0.1
P/2	470	156	0.3
P/3	402	137	
P/4	413	89	
P/5	648	93	

