

State University of New York College at Buffalo - Buffalo State College Digital Commons at Buffalo State

Biology Theses

Biology

12-2012

Influence of Nitrogen and Phosphorus on Ecosystem CO₂ Exchange in a Restored Temperate Grassland

Lynn M. Socha

State University of New York College at Buffalo, lmsocha@gmail.com

Advisor

Dr. Daniel L. Potts

First Reader

Dr. Christopher Pennuto

Second Reader

Dr. Edward Standora

Department Chair

Dr. Gregory Wadsworth

To learn more about the Biology Department and its educational programs, research, and resources, go to <http://biology.buffalostate.edu/>.

Recommended Citation

Socha, Lynn M., "Influence of Nitrogen and Phosphorus on Ecosystem CO₂ Exchange in a Restored Temperate Grassland" (2012). *Biology Theses*. Paper 4.

Follow this and additional works at: http://digitalcommons.buffalostate.edu/biology_theses



Part of the [Biology Commons](#), and the [Plant Sciences Commons](#)

Influence of Nitrogen and Phosphorus on Ecosystem CO₂ 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 CO₂ 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 CO₂ exchange throughout the growing season in a restored temperate grassland near Buffalo, New York. I predicted that N-addition would enhance ecosystem CO₂ uptake (GEE) while P-addition would stimulate ecosystem respiration (R_e). As predicted, N-addition increased GEE and correspondingly amplified net ecosystem CO₂ exchange (NEE) to increase ecosystem CO₂ 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 CO₂ Exchange in a Restored
Temperate Grassland

A Thesis in
Biology

By

Lynn M. Socha

Submitted in Partial Fulfillment
Of the Requirements
For the Degree of

Master of Arts
December 2012

Approved by:

Daniel L. Potts, Ph.D.
Assistant Professor of Biology
Chairperson of the Committee/Thesis Adviser

Gregory Wadsworth, Ph.D.
Chair and Associate Professor of Biology

Kevin Railey, Ph.D.
Associate Provost and Dean of the Graduate School

Table of contents

List of Figures.....	v
List of Tables.....	v
Introduction.....	1
Methods.....	6
Results.....	12
Discussion.....	15
Acknowledgements.....	19
Figures 1-8.....	20
Tables 1-2.....	36
Literature Cited	39
Appendix A: Ecosystem CO ₂ exchange data.....	47
Appendix B: Volumetric soil moisture (Θ) data.....	52
Appendix C: Leaf Area Index data.....	57
Appendix D: Live grass, forb and litter biomass data.....	59

List of Figures

Figure 1, Volumetric soil moisture (Θ) and precipitation over the course of the 2010 growing season

Figure 2, Leaf area index (LAI) over the course of the 2010 growing season

Figure 3, Live and litter biomass taken in October 2010

Figure 4, Net ecosystem CO_2 exchange (NEE) over the course of the 2010 growing season

Figure 5, Ecosystem respiration (R_e) over the course of the 2010 growing season

Figure 6, Gross ecosystem CO_2 exchange (GEE) over the course of the 2010 growing season

Figure 7, GEE plotted against R_e over the course of the 2010 growing season

Figure 8, GEE_A over the course of the 2010 growing season

List of Tables

Table 1, Statistical model results of the effects of nutrient addition and time on volumetric soil moisture and leaf area index.

Table 2, Statistical model results of the effects of nutrient addition and time on the component fluxes of ecosystem CO_2 exchange.

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 C₃ 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 CO₂ exchange may also be altered. N and P influence the components of ecosystem CO₂ 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 CO₂ exchange in turn altering the source-sink dynamics of the carbon cycle. Thornley and Cannell (1997) demonstrated that additional CO₂ 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 CO₂ 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 CO₂ 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 CO₂ exchange on small (< 9 m²) plots. Through the advent of a portable means to measure the component fluxes of ecosystem CO₂ exchange, researchers can now manipulate small experimental plots and measure ecosystem CO₂ 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), CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 Tiff 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 (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 (θ) 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 θ 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 CO₂ Exchange

A tent-based method of collecting CO₂ exchange data was used to observe the effects of nutrient addition on the component fluxes of ecosystem CO₂ exchange. This method of collecting CO₂ exchange data is ideal for working in the context of experimentally manipulated field plots (Arnone and Obrist 2003). The tent-based method of CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ concentration with time according to Jasoni *et al.* (2005). I estimated gross ecosystem CO₂ exchange (GEE) as:

$$NEE = GEE - R_e$$

where NEE is net ecosystem CO₂ exchange, GEE is gross ecosystem CO₂ exchange and R_e 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_A) as:

$$GEE_A = GEE / LAI$$

where LAI was taken within +/- 2 days of the ecosystem CO₂ 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_e, 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 (θ) reflected seasonal patterns of precipitation (Figure 1A-B). Early in the growing season, frequent rainfall resulted in greater θ . As the growing season progressed, smaller, less frequent storms were associated with declining θ across treatments (Table 1, Time). Throughout the growing season, N-addition influenced a decline in θ (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 θ .

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 θ , 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 CO₂ exchange (NEE) varied throughout the growing season in a saddle-shaped pattern (Figure 4). The greatest rates of midday net CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 C₃ 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 CO_2 efflux) was correlated with increasingly negative GEE (indicating increasing 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 CO_2 exchange.

In striking contrast with seasonal patterns of GEE, GEE_A declined exponentially throughout the growing season (Fig. 8; Table 1, GEE_A). Although N-addition plots had greater LAI than other plot types, GEE_A was most negative in the control plots. Moreover, large negative values of 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 CO₂ 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 C₃ photosynthetic pathway (Sharkey 1988). While several studies have experimentally established the linkage between soil moisture and ecosystem CO₂ 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 CO₂ 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 CO₂ exchange remains poorly studied.

To better understand the CO₂ 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 CO₂ 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 CO₂ 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_e 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).

Acknowledgements:

D. Huff, M. Socha, J. Hirtreiter, J. Louie, E. Snyder, N. Wood and J. Wuerstle assisted in the field and in the laboratory. D. Speiring and his staff kindly provided access to the experimental site at Tifft Nature Preserve. Buffalo State College provided additional equipment for this experiment.

Figure 1(A): Daily precipitation during the 2010 growing season. (B) Mean \pm SE volumetric soil moisture (Θ) 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

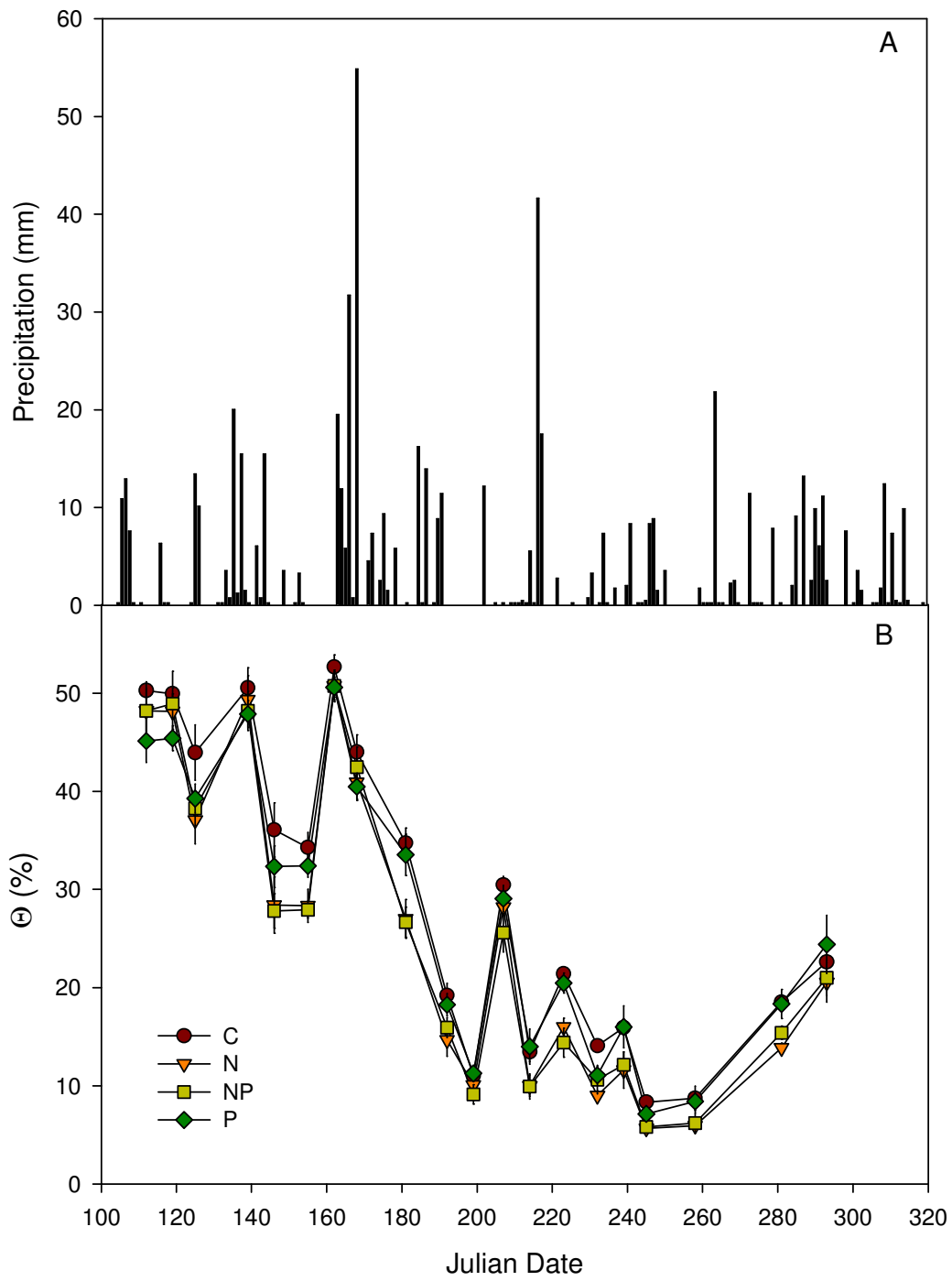


Figure 2: Mean \pm SE leaf area index (LAI) in control (C), N-addition (N), P-addition (P) and NP-addition (NP) plots during the 2010 growing season in a restored, temperate grassland near Buffalo, NY.

Figure 2

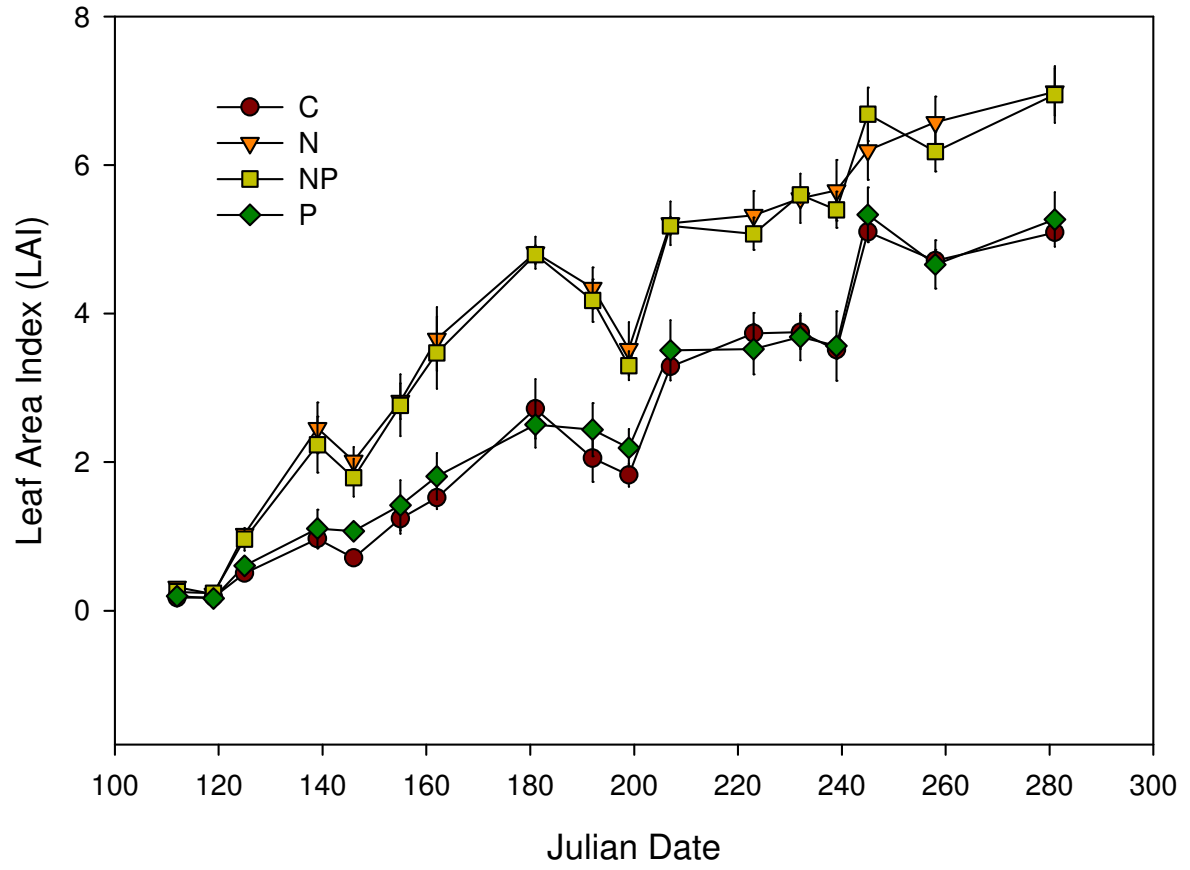


Figure 3: Aboveground net primary productivity (ANPP; g/m^2) in control (C), N-addition (N), P-addition (P) and NP-addition (NP) plots in a restored, temperate grassland near Buffalo, NY. Error bars indicate SE.

Figure 3

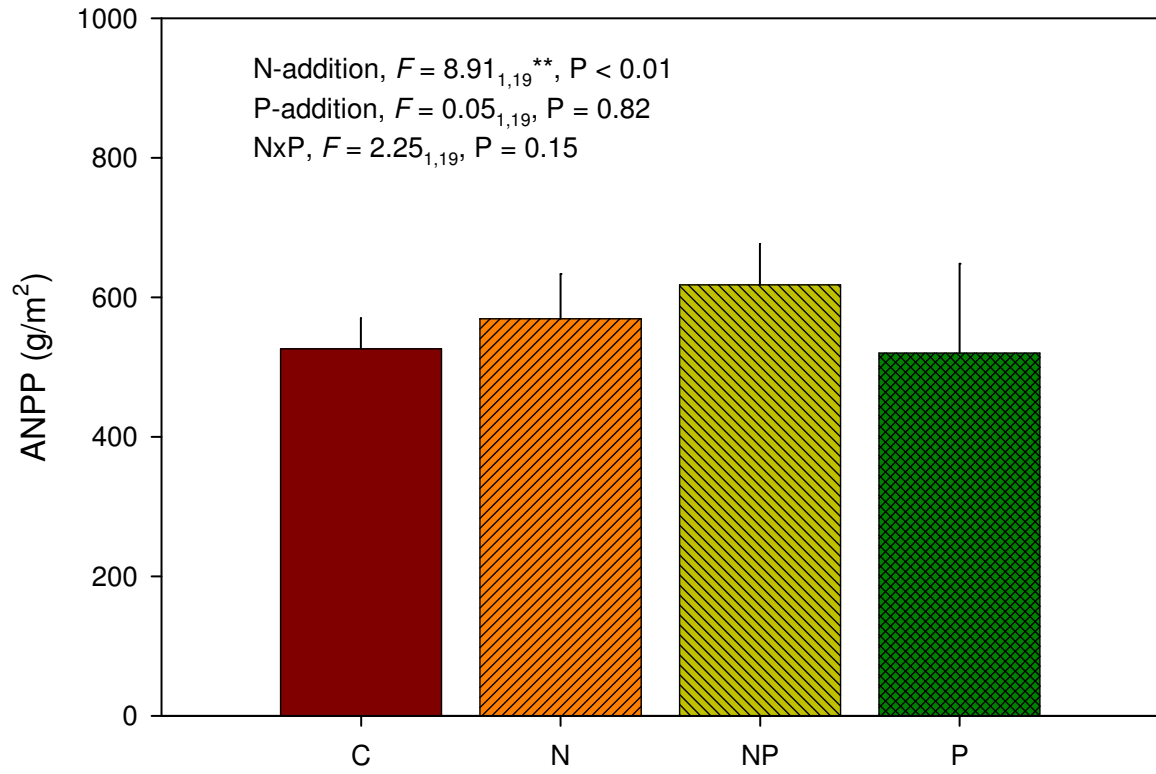


Figure 4: Mean midday net ecosystem CO₂ exchange (NEE; $\mu\text{mol CO}_2/\text{m}^2/\text{s}$) in control (C), N-addition (N), P-addition (P) and NP-addition (NP) during the 2010 growing season in a restored, temperate grassland near Buffalo, NY. Error bars indicate SE. Increasingly negative values indicate increasing ecosystem CO₂ assimilation.

Figure 4

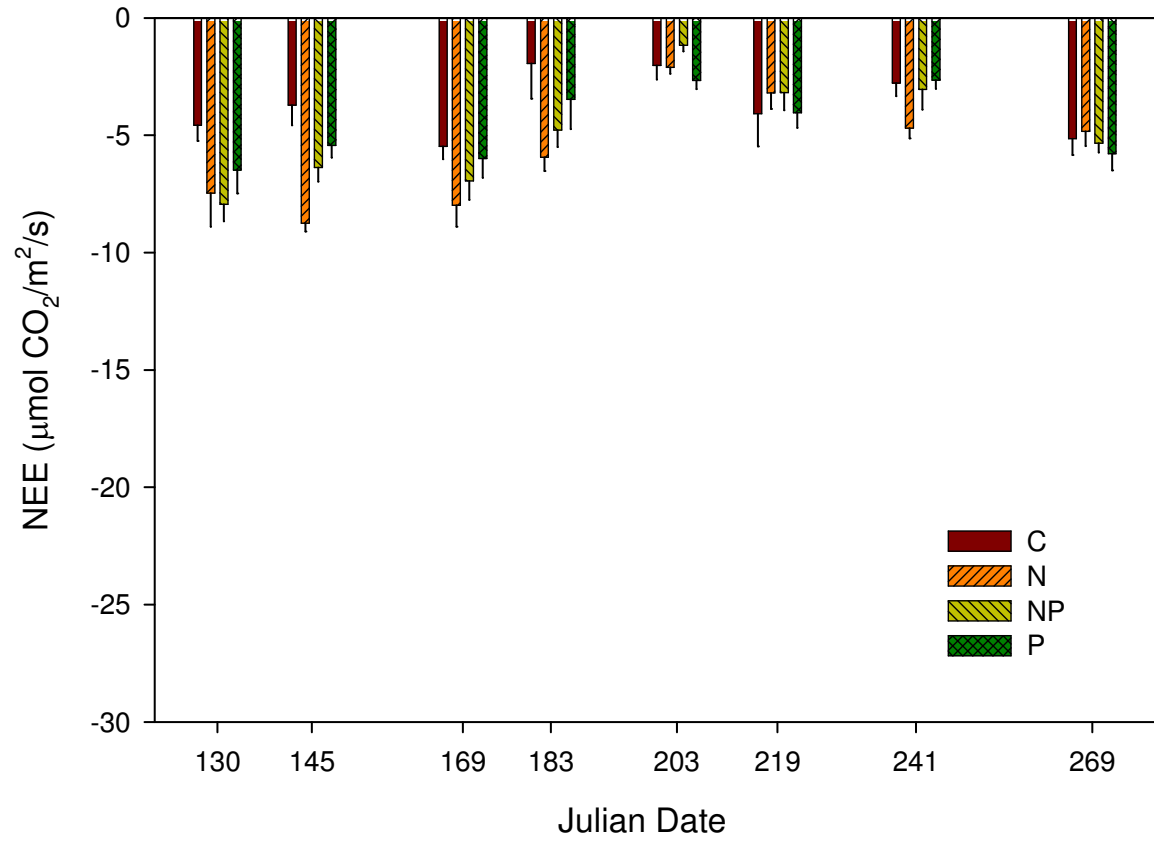


Figure 5: Mean midday ecosystem respiration (R_e ; $\mu\text{mol CO}_2/\text{m}^2/\text{s}$) in control (C), N-addition (N), P-addition (P) and NP-addition (NP) during the 2010 growing season in a restored, temperate grassland near Buffalo, NY. Error bars indicate SE.

Figure 5

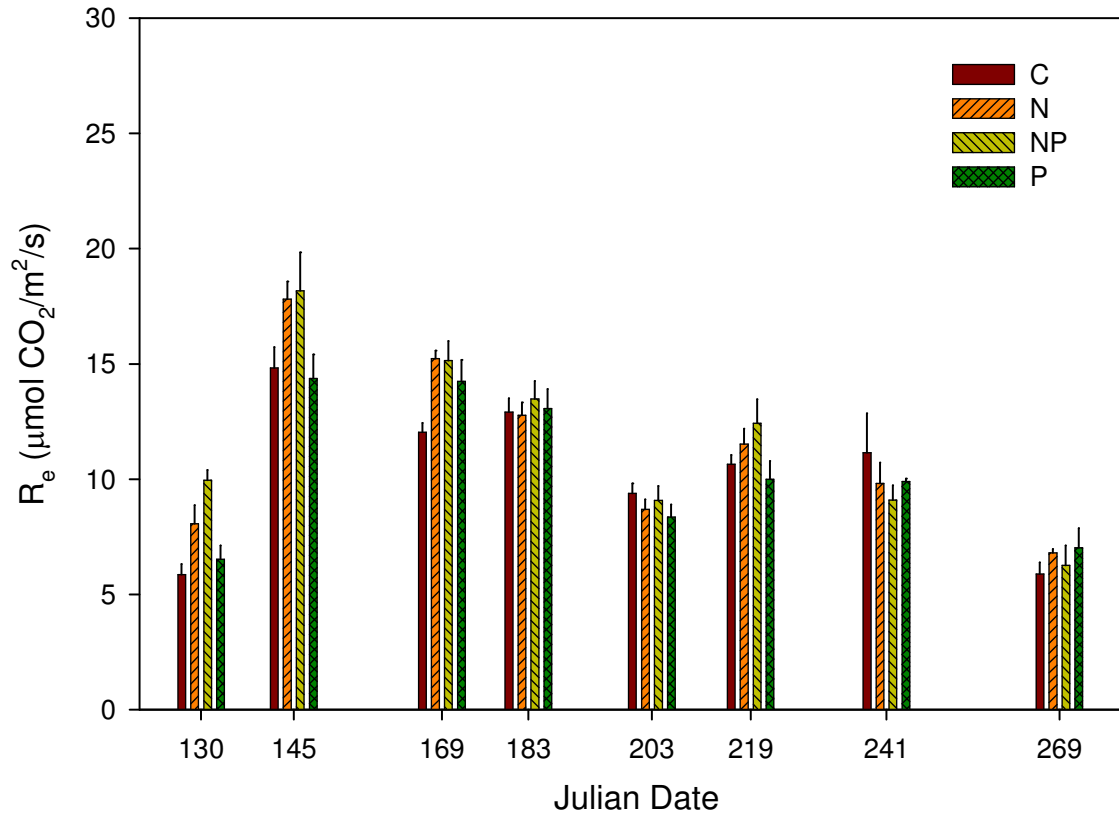


Figure 6: Mean midday gross ecosystem CO₂ exchange (GEE; $\mu\text{mol CO}_2/\text{m}^2/\text{s}$) in control (C), N-addition (N), P-addition (P) and NP-addition (NP) during the 2010 growing season in a restored, temperate grassland near Buffalo, NY. Error bars indicate SE. Negative values indicate increasing ecosystem CO₂ assimilation.

Figure 6

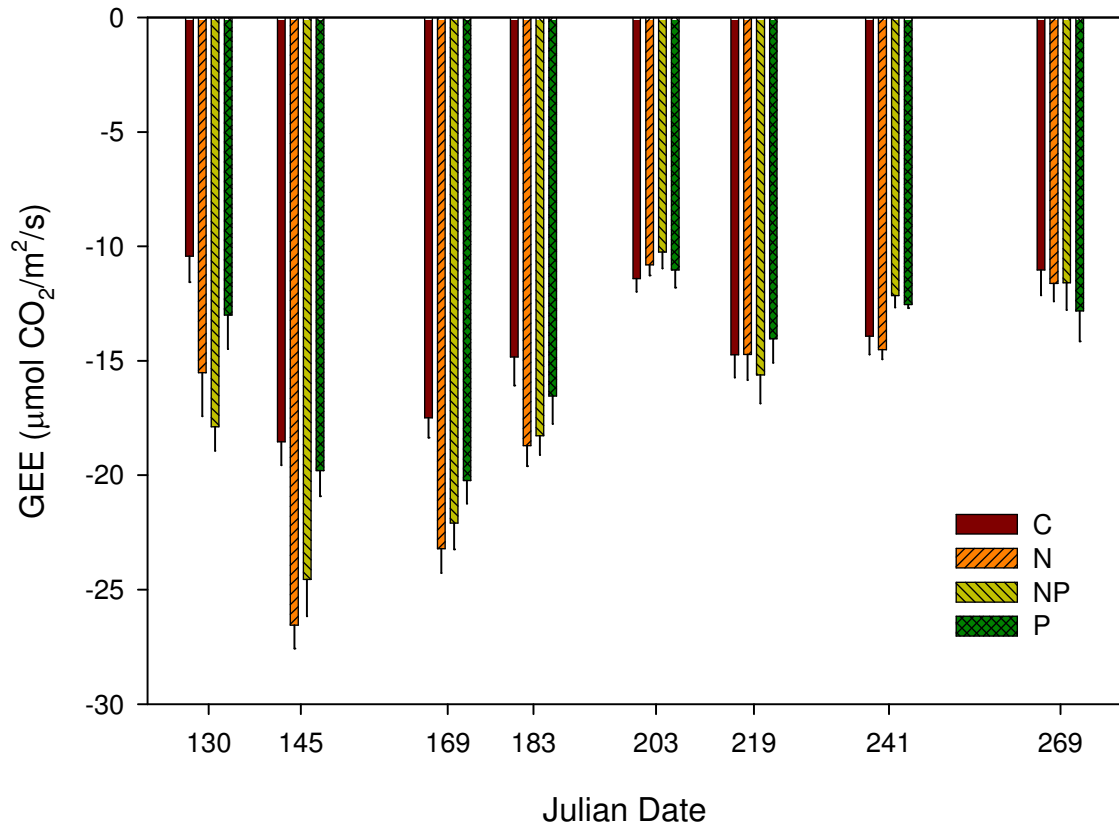


Figure 7: Midday gross ecosystem CO₂ exchange (GEE; $\mu\text{mol CO}_2/\text{m}^2/\text{s}$) versus midday ecosystem respiration (R_e ; $\mu\text{mol CO}_2/\text{m}^2/\text{s}$) for all sampling days in control (C), N-addition (N), P-addition (P) and NP-addition (NP) during the 2010 growing season in a restored, temperate grassland near Buffalo, NY. Symbols follow Fig. 1B. Increasing negative values of GEE note increasing ecosystem CO₂ assimilation.

Figure 7

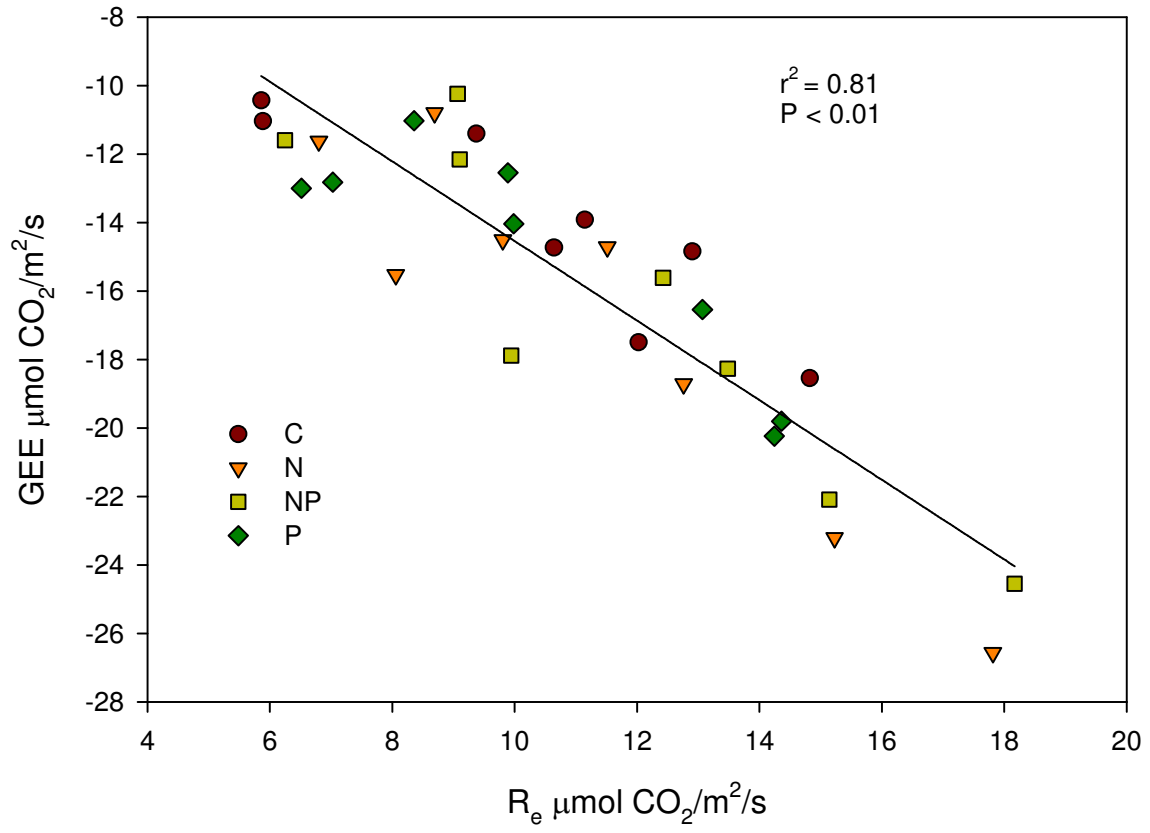


Figure 8: Leaf area adjusted midday gross ecosystem CO₂ exchange (GEE_A; $\mu\text{mol CO}_2/\text{m}^2/\text{s}$) in control (C), N-addition (N), P-addition (P) and NP-addition (NP) during the 2010 growing season in a restored, temperate grassland near Buffalo, NY. Error bars indicate SE. Increasing negative values note increasing uptake of CO₂ by the ecosystem.

Figure 8

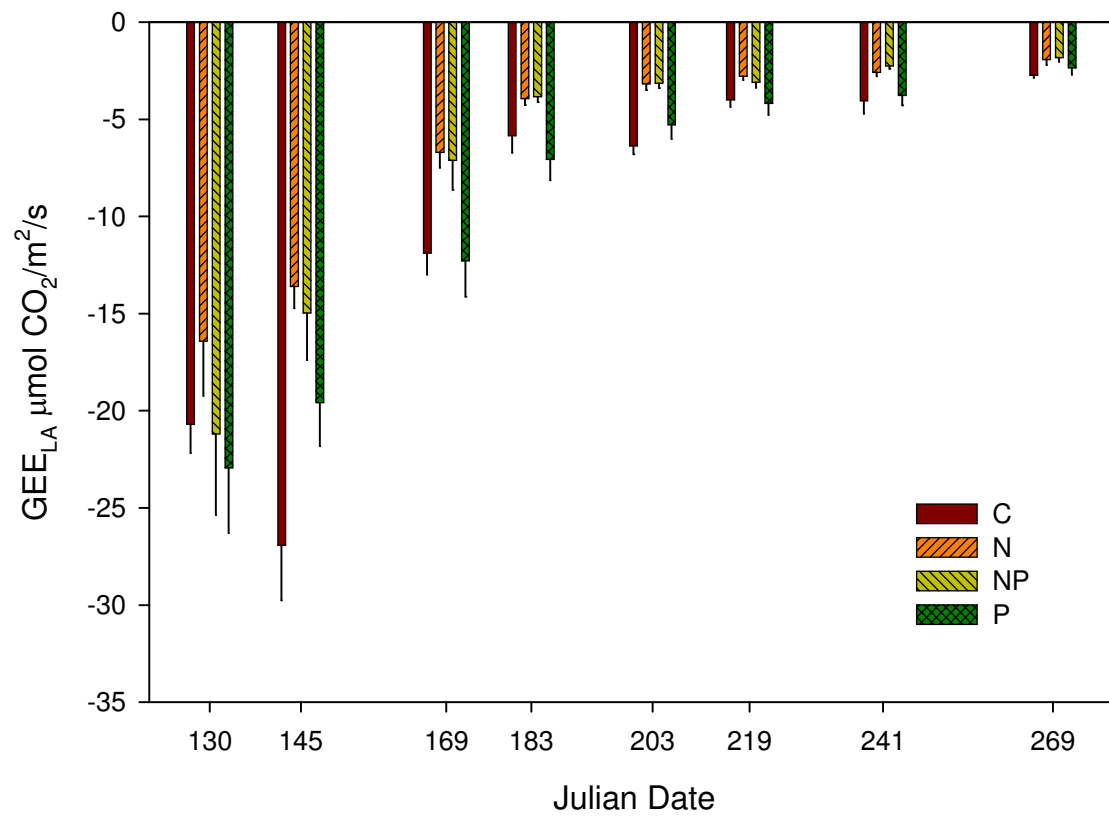


Table 1: Degrees of freedom (*df*) and *F*-statistics from the repeated measures ANOVA on the effect of N-addition, P-addition and time on volumetric soil moisture (Θ), leaf area index (LAI) and leaf area adjusted-GEE (GEE_a) in a restored temperate grassland near Buffalo, New York. Θ , volumetric soil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

Factors	<i>df</i>	Θ	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; Θ , 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 CO₂ exchange in a restored temperate grassland near Buffalo, New York. NEE, net ecosystem CO₂ exchange; GEE, gross ecosystem CO₂ exchange; R_e, respiration; N, nitrogen-addition; P, phosphorus-addition; *, P < 0.1; **, P < 0.05

Factors	<i>df</i>	NEE	GEE	R _e	GEE _A
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 CO₂ exchange; GEE, gross ecosystem CO₂ exchange; R_e, respiration; GEE_A, leaf area adjusted-GEE; N, nitrogen-addition; P, phosphorus-addition; *, P < 0.1; **, P < 0.05

Literature Cited

Amador JA, Jones RD (1993) Nutrient Limitations on Microbial Respiration in Peat Soils with Different Total Phosphorus Content. *Soil Biology and Biochemistry* **25**:793-801

Arnell NJ (1999) Climate Change and Global Water Resources. *Global Environmental Change* **9**:31-49

Arnone III JA, Ohrsit D (2003) A Large Daylight Geodesic Dome for Quantification of Whole-Ecosystem CO₂ and Water Vapor Fluxes in Arid Shrublands. *Journal of Arid Environments* **55**: 629-643

Baddeley JA, Woodin SJ, Alexander IJ (1994) Effect of Increased Nitrogen and Phosphorus Availability on the Photosynthesis and Nutrient of Three Arctic Dwarf Shrubs from Svalbard. *Functional Ecology* **8**:676-685

Baldocchi DD (2003) Assessing the Eddy Covariance Technique for Evaluating Carbon Dioxide Exchange Rates of Ecosystems: Past, Present and Future. *Global Change Biology* **9**:1-14

Bardgett RD, Mawdsley JL, Edwards S, Hobbs PJ, Rodwell JS, Davies WJ (1999) Plant Species and Nitrogen Effects on Soil Biological Properties of Temperate Upland Grasslands. *Functional Ecology* **13**:650-660

Begonia GB, Begonia MT (2007) Plant Photosynthetic Production as Controlled by Leaf Growth, Phenology, and Behavior. *Photosyntheica* **45**: 321-333

Bolton JK, Brown RH (1980) Photosynthesis of Grass Species Differing in Carbon Dioxide Fixation Pathways. *Plant Physiology* **66**:97-100

Breshears DD, Barnes FJ (1999) Interrelationships Between Plant Functional Types and Soil Moisture Heterogeneity for Semiarid Landscapes Within the Grassland/Forest Continuum: a Unified Conceptual Model. *Landscape Ecology* **14**:465-478

Burke IC, Yonkers C, Parton WJ, Cole CV, Flach K, Schimel DS (1989) Texture, Climate, and Cultivation Effects on Organic Matter in U.S. Grassland Soils. *Soil Science Society of America Journal* **53**:800-805

Burke IC, Lauenroth WK, Parton WJ (1997) Regional and Temporal Variation in Net Primary Production and Nitrogen Mineralization in Grasslands. *Ecology* **78**:1330-1340

Carbone MS, Czimczik CI, McDuffee KE, Trumbore SE (2007) Allocation and Residence Time of Photosynthetic Products in a Boreal Forest Using a Low-Level ¹⁴C Pulse-Chase Labeling Technique. *Global Change Biology* **13**:466-477

- Carbone MS, Trumbore SE (2007) Contribution of New Photosynthetic Assimilates to Respiration by Perennial Grasses and Shrubs: Residence Times and Allocation Patterns. *New Phytologist* **176**:124–135
- Chapin FS, Vitousek PM, Van Cleve K (1985) The Nature of Nutrient Limitation in Plant Communities. *American Naturalist* **127**:48-58.
- Chapin FS, Bloom AJ, Field CB, Waring RH (1987) Plant Responses to Multiple Environmental Factors. *BioScience* **37**:49-57
- Craine JM, Morrow C, Stock WD (2008) Nutrient Concentration Ratios and Co-Limitation in South African Grasslands. *New Phytologist* **179**:829-836
- de Gaffe M, Classen AT, Castro HF, Schadt CW (2010) Labile Soil Carbon Inputs Mediate the Soil Microbial Community Composition and Plant Residue Decomposition Rates. *New Phytologist* **188**: 1055-1064
- DeMiranda JCC, Harris PJ (1994) Effects of Soil Phosphorus on Spore Germination and Hyphal Growth of Arbuscular Mycorrhizal Fungi. *New Phytologist* **128**:103-108
- Ellsworth DS, Reich PB (1992) Leaf Mass Per Area, Nitrogen Content and Photosynthetic Carbon Gain in *Acer saccharum* Seedlings in Contrasting Forest Light Environments. *Functional Ecology* **6**: 423-435
- Evans JR (1989) Photosynthesis and Nitrogen Relationships in Leaves of C₃ Plants. *Oecologia* **78**:9-19
- Fenn MA, Haeuber R, Tonnesen GS, Baron JS, Grossman-Clarke S (2003) Nitrogen Emissions, Deposition and Monitoring in the Western United States. *BioScience* **53**:391-403
- Flanagan LB, Wever LA, Carlson PJ (2002) Seasonal and Interannual Variation in Carbon Dioxide Exchange and Carbon Balance in a Northern Temperate Grassland. *Global Change Biology* **8**:599-615
- Field C, Mooney HA (1986) The Photosynthesis-Nitrogen Relationship in Wild Plants. On The Economy of Plant Form and Function Cambridge University Press 25-54
- Gulis V, Suberkropp K (2003) Leaf Litter Decomposition and Microbial Activity in Nutrient-Enriched and Unaltered Reaches of a Headwater Stream. *Freshwater Biology* **48**:123-134
- Gulmon SL, Chu CC (1981) The Effects of Light and Nitrogen on Photosynthesis, Leaf Characteristics, and Dry Matter Allocation in the Chaparral Shrub, *Diplacus aurantiacus*. *Oecologia* **49**:207-212

- Harpole WS, Potts DL, Suding KN (2007) Ecosystem Responses to Water and Nitrogen Amendment in a California Grassland. *Global Change Biology* **13**:2341–2348
- Harpole WS, Tilman D (2007) Grassland Species Loss Resulting from Reduced Niche Dimension. *Nature* **446**:791-793
- Hautier Y, Niklaus PA, Hector A (2009) Competition for Light Causes Plant Biodiversity Loss After Eutrophication. *Science* **324**:636-638
- Hecky RE, Kilham P (1988) Nutrient Limitation of Phytoplankton in Freshwater and Marine Environments: A Review of Recent Evidence on the Effects of Enrichment. *Limnology and Oceanography* **33**:796-822
- Högberg P, Read DJ (2006) Towards a More Plant Physiological Perspective on Soil Ecology. *Trends in Ecology and Evolution* **21**: 548-554
- Huxman TE, Turnipseed AA, Sparks JP, Harley PC, Monson RK (2003) Temperature as a Control Over Ecosystem CO₂ Fluxes in a High-Elevation, Subalpine Forest. *Oecologia* **134**:537–546
- Huxman T, Snyder KA, Tissue D, Leffler AJ, Ogle K, Pockman WT, Sandquist DR, Potts DL, Schwinning S (2004a) Precipitation Pulses and Carbon Fluxes in Semiarid and Arid Ecosystems. *Oecologia* **141**:254-268
- Huxman TE, Cable JM, Ignace DD, Eilts JA, English NB, Weltzin J, Williams DG (2004b) Response of Net Ecosystem Gas Exchange to a Simulated Precipitation Pulse in a Semi-Arid Grassland: the Role of Native Versus Non-Native Grasses and Soil Texture. *Oecologia* **141**: 295-305
- Huxman TE, Wilcox BP, Breshears DD, Scot RL, Snyder KA, Small EE, Hultine K, Pockman WT, Jackson RB (2005) Ecohydrological Implications of Woody Plant Encroachment. *Ecology* **86**:308-319
- Jasoni RL, Smith SD, Arnone III JA (2005) Net Ecosystem CO₂ Exchange in Mojave Desert Shrublands During the Eighth Year of Exposure to Elevated CO₂. *Global Change Biology* **11**:749-756
- Johnson D, Vandenkoornhuyse PJ, Leakey JR, Gilbert L, Booth RE, Grime JP, Young JPW, Reak DJ (2003) Plant Communities Affect Arbuscular Mycorrhizal Fungal Diversity and Community Composition in Grassland Microcosms. *New Phytologist* **161**: 503-515
- Kardol P, Wardle DA (2010) How Understanding Aboveground–Belowground Linkages Can Assist Restoration Ecology. *Trends in Ecology and Evolution* **25**:670-679

Keeler BL, Hobbie SE, Kellog LE (2009) Effects of Long-Term Nitrogen-Addition on Microbial Enzyme Activity in Eight Forested and Grassland Sites: Implications for Litter and Soil Organic Matter Decomposition. *Ecosystems* **12**:1-15

Knapp AK, Briggs JM, Koelliker JK (2001) Frequency and Extent of Water Limitation to Primary Production in a Mesic Temperate Grassland. *Ecosystems* **4**:19-28

Knapp AK, Beier C, Briske DD, Classen AT, Luo Y, Reichstein M, Smith MD, Smith SD, Bell JE, Fay PA, Heisler JL, Leavitt SW, Sherry R, Smith B, Weng E (2008) Consequences of More Extreme Precipitation Regimes for Terrestrial Ecosystems. *BioScience* **58**:1-11

Lee TD, Tjoelker MG, Ellsworth DS, Reich PB (2001) Leaf Gas Exchange Responses of 13 Prairie Grassland Species to Elevated CO₂ and Increased Nitrogen Supply. *New Phytologist* **150**:405-418

Lieth HFH (1978) Patterns of Primary Productivity in the Biosphere. *Hutchinson Ross* 342

Marschner H, Dell B (1994) Nutrient Uptake in Mycorrhizal Symbiosis. *Plant and Soil* **159**:89-102

Marschner H, Kirkby EA, Cakmak T (1996) Effect of Mineral Nutritional Status on Shoot-Root Partitioning of Photoassimilates and Cycling of Mineral Nutrients. *Journal of Experimental Botany* **47**: 1255-1263

Metcalf DB, Fisher RA, Wardle DA (2011) Plant Communities as Drivers of Soil Respiration: Pathways, Mechanisms, and Significance for Global Change. *Biogeosciences* **8**:2047-2061

Monnin E, Indermühle A, Dällenbach A, Flückiger J, Stauffer B, Stocker TF, Raynaud D, Barnola JM (2001) Atmospheric CO₂ Concentrations Over the Last Glacial Termination. *Science* **291**:112-114

Morecroft MD, Sellers EK, Lee JA (1994) An Experimental Investigation into the Effects of Atmospheric Nitrogen Deposition on Two Semi-Natural Grasslands. *Journal of Ecology* **82**:475-483

Nakano T, Nemoto M, Shinoda M (2008) Environmental Controls on Photosynthetic Production and Ecosystem Respiration in Semi-Arid Grasslands of Mongolia. *Agricultural and Forest Meteorology* **148**:1456-1466

Niinemets U, Kull K (2005) Co-limitation of Plant Primary Productivity by Nitrogen and Phosphorus in a Species-Rich Wooded Meadow on Calcareous Soils. *Acta Oecologica* **28**:345-356

- Niu S, Wu M, Han Y, Xia J, Zhang Z, Yang H, Wan S (2010) Nitrogen Effects on Net Ecosystem Carbon Exchange in a Temperate Steppe. *Global Change Biology* **16**: 144-155
- Novick KA, Stoy PC, Katul GG, Ellsworth DS, Siqueira MBS, Juang J, Oren R (2004) Carbon Dioxide and Water Vapor Exchange in a Warm Temperate Grassland. *Oecologia* **138**:259-274
- Orchard VA, Cook FJ (1983) Relationship Between Soil Respiration and Soil Moisture. *Soil Biological Biochemistry* **15**:447-453
- Patrick L, Cable J, Potts D, Ignace D, Barron-Gafford G, Griffith A, Alpert H, Van Gestel N, Robertson T, Huxman TE, Zak J, Loik ME, Tissue D (2007) Effects of an Increase in Summer Precipitation on Leaf, Soil, and Ecosystem Fluxes of CO₂ and H₂O in a Sotol Grassland in Big Bend National Park, Texas. *Oecologia* **151**:704-718
- Piceno YM, Lovell CR (2000) Stability in Natural Bacterial Communities: I. Nutrient Addition Effects on Rhizosphere Diazotroph Assemblage Composition. *Microbial Ecology* **39**:32-40
- Prater MR, Obrist D, Arnone III JA, DeLucia EH (2006) Net Carbon Exchange and Evapotranspiration in Postfire and Intact Sagebrush Communities in the Great Basin. *Oecologia* **146**:595-607
- Phoenix GK, Booth RE, Leake JR, Read DJ, Grime P, Lee JA (2003) Effects of Enhanced Nitrogen Deposition and Phosphorus Limitation on Nitrogen Budgets of Semi-Natural Grasslands. *Global Change Biology* **9**:1309-1321
- Potts DL, Huxman TE, Cable JM, English NB, Ignace DD, Eilts JA, Mason MJ, Weltzin JF, Williams DG (2006a) Antecedent Moisture and Seasonal Precipitation Influence the Response of Canopy-Scale Carbon and Water Exchange to Rainfall Pulses in a Semi-Arid Grassland. *New Phytologist* **170**:849-860
- Potts DL, Huxman TE, Enquis BJ, Weltzin JF (2006b) Resilience and Resistance of Ecosystem Functional Response to a Precipitation Pulse in a Semi-Arid Grassland. *Journal of Ecology* **94**:23-30
- Potts DL, Harpole WS, Goulden ML, Suding KN (2008a) The Impact of Invasion and Subsequent Removal of an Exotic Thistle, *Cynara cardunculus*, on CO₂ and H₂O Vapor Exchange in a Coastal California Grassland. *Biological Invasions* **10**:1073-1084
- Potts DL, Scott RL, Cable JM, Huxman TE, Williams DG (2008b) Sensitivity of Mesquite Shrubland CO₂ Exchange to Precipitation in Contrasting Landscape Settings. *Ecology* **89**:2900-2910

- Potts, DL, Suding, KN, Winston, GC, Rocha, AV, Goulden, ML. 2012. Ecological effects of experimental drought and prescribed fire in a southern California coastal grassland *Journal of Arid Environments* **81**:59-66
- Quick WP, Schurr U, Fichtner K, Schulze ED, Rodermel SR, Bogorad L, Stitt M (1991) The Impact of Decreased Rubisco on Photosynthesis, Growth, Allocation and Storage in Tobacco Plants Which Have Been Transformed With Antisense *rbcS*. *The Plant Journal* **1**:51-58
- Reich PB (2009) Elevated CO₂ Reduces Losses of Plant Diversity Caused by Nitrogen Deposition. *Science* **326**:1399-1402
- Risch AC, Frank DA (2006) Carbon Dioxide Fluxes in a Spatially and Temporally Heterogeneous Temperate Grassland. *Oecologia* **147**:291:302
- Sala OE, Parton WJ, Joyce LA, Lauenroth WK (1988) Primary Production of the Central Grassland Region of the United States. *Ecology* **69**:40-45
- Schlesinger WH, Tilman DG (1997) Human Alteration of the Global Nitrogen Cycle: Sources and Consequences. *Ecological Applications* **7**:737-750
- Scurlock JMO, Hall DO (1998) The Global Carbon Sink: a Grassland Perspective. *Global Change Biology* **4**:229-233
- Sharkey TD (1988) Estimating the Rate of Photorespiration in Leaves. *Physiologia Plantarum* **73**:147-152
- Spiering D (2009) Tiff Nature Preserve Management Plan. 7-14
- Sterner RW, Elser JJ (2002) Ecological Stoichiometry. *Princeton University Press* 190-197
- Stevens CJ, Dise NB, Mountford JO, Gowing DJ (2004) Impact of Nitrogen Deposition on the Species Richness of Grasslands. *Science* **303**:1876-1879
- Stevens CJ, Maskell LC, Smart SM, Caporn SJM, Dise NB, Gowing DJG (2009) Identifying Indicators of Atmospheric Nitrogen Deposition Impacts in Acid Grasslands. *Biological Conservation* **142**:2069-2075
- Stewart JWB, Tiessen H (1987) Dynamics of Soil Organic Phosphorus. *Biogeochemistry* **4**:41-60
- Sundareshwar PV, Morris JT, Koepfler EK, Fornwalt B (2003) Phosphorus Limitation of Coastal Ecosystem. *Processes Science* **299**:563-565

- Thornley JHM, Cannell MGR (1997) Temperate Grassland Responses to Climate Change: an Analysis Using the Hurley Pasture Model. *Annals of Botany* **80**:205-221
- Tilman D (1982) Resource Competition and Community Structure. Princeton University Press 12-16
- Tilman D (1987) Secondary Succession and the Pattern of Plant Dominance Along Experimental Nitrogen Gradients. *Ecological Monographs* **57**:189-214
- Van der Heijden MGA, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, Wiemken A, Snaders IR (1998) Mycorrhizal Fungal Diversity Determines Plant Biodiversity, Ecosystem Variability and Productivity. *Nature* **396**:69-72
- Vitousek PM, Howarth RW (1991) Nitrogen Limitation on Land and in the Sea: How Can it Occur? *Biogeochemistry* **13**:87-115
- Vitousek PM, Turne DR (1995) Foliar Nutrients During Long-Term Soil Development in Hawaiian Montane Rain Forest. *Ecology* **76**:712-720
- Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG (1997) Human Alteration of the Global Nitrogen Cycle: Sources and Consequences. *Ecological Applications* **7**:737-750
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological Responses to Recent Climate Change. *Nature* **416**:389-395
- Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten WH, Wall DH (2004) Ecological Linkages Between Aboveground and Belowground Biota. *Science* **304**:629-1633
- Warren CR, Dreyer E, Adams MA (2003) Photosynthesis-Rubisco Relationships in Foliage of *Pinus sylvestris* in Response to Nitrogen Supply and the Proposed Role of Rubisco and Amino Acids as Nitrogen Stores. *Trees* **17**:359-366
- Weltzin JF, Loik ME, Schwinning S, Williams DG, Fay PA, Haddad BM, Harte J, Huxman TE, Knapp AK, Lin G, Pockman WT, Shaw MR, Small EE, Smith MD, Smith SD, Tissue DT, Zak JC (2003) Assessing the Response of Terrestrial Ecosystems to Potential Changes in Precipitation. *BioScience* **53**:941-952
- Wilson EJ, Wells TCE, Sparks TH (1995) Are Calcareous Grasslands in the UK Under Threat from Nitrogen Deposition? – An Experimental Determination of a Critical Load. *Journal of Ecology* **83**:823-832

Xia J, Niu S, Wan S (2009) Response of Ecosystem Carbon Exchange to Warming and Nitrogen Addition During Two Hydrologically Contrasting Growing Seasons in a Temperate Steppe. *Global Change Biology* **15**: 1544-1556

Xu L, Baldocchi DD (2004) Seasonal Variation in Carbon Dioxide Exchange Over a Mediterranean Annual Grassland in California. *Agricultural and Forest Meteorology* **123**:79-96

Yezpe EA, Huxman TE, Ignace DD, English NB, Weltzin JF, Castellanos AE, Williams DG (2005) Dynamics of Transpiration and Evaporation Following a Moisture Pulse in a Semiarid Grassland: A Chamber-Based Isotope Method for Partitioning Flux Components. *Agricultural and Forest Meteorology* **132**:359–376

Appendix A: Ecosystem CO₂ 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 _e	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 _e	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 _e	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 _e	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 _e	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 _e	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 _e	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 _e	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 (Θ) 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

	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

Appendix D: Live, litter and forb biomass (g/m²)

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	

