Nonlinear responses to nitrogen and strong interactions with nitrogen and phosphorus additions drastically alter the structure and function of a high arctic ecosystem

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[1] Significant changes in ecosystem CO₂ exchange and vegetation characteristics were observed following multiple additions of nitrogen (N) and factorial additions of N and phosphorus (P) to prostrate dwarf-shrub, herb tundra in Northwest Greenland. Ecosystem CO₂ exchange and vegetation cover and composition were very sensitive to low rates of N inputs (0.5 g m⁻² y⁻¹), indicating that even low rates of atmospheric N deposition may alter high arctic ecosystem structure and function. Increasing N addition from 1 to 5 g N m⁻² y⁻¹ did not alter CO₂ exchange or vegetation characteristics, suggesting the ecosystem had become N saturated. Factorial additions of both N and P released the ecosystem from N saturation and dramatically increased gross ecosystem photosynthesis (+500%) and ecosystem respiration (+250%), such that the ecosystem switched from a small source of CO₂ to a small sink for CO₂ at midday during the 2005 growing season. Changes in the component fluxes of CO₂ exchange were largely explained by a doubling of the normalized difference vegetation index, a 100% increase in vascular plant cover and dramatic increases in the abundance of several previously rare grass species. Our results clearly demonstrate that high arctic prostrate dwarf-shrub, herb tundra is highly sensitive to low levels of N addition and that future increases in N deposition or N mineralization will likely lead to change in carbon cycling and vegetation characteristics, but the magnitude of the response will be constrained by P availability.


1. Introduction

[2] Experimental manipulations have shown that Arctic ecosystems can be limited by temperature, light, water and/or nutrient availability [e.g., Billings, 1974; Chapin, 1983; Chapin et al., 1986; Welker et al., 1993, 1997]. Nutrient additions, independently or in combination with water or warming, have generally caused the greatest increase in aboveground vascular plant biomass and/or the most dramatic changes in species composition [e.g., Dormann and Woodin, 2002; van Wijk et al., 2003a]. Prostrate dwarf-shrub, herb tundra, the most common high arctic ecosystem [CAVM Team, 2003], may be predisposed to rapid and dramatic changes in structure and function because extensive areas of bare ground allow for both the horizontal expansion of existing plants and seedling recruitment [Wookey and Robinson, 1997]. Low soil temperatures and shallow organic horizons typically lead to low nitrogen (N) and phosphorus (P) availability in high arctic ecosystems [Dowding et al., 1981; Robinson et al., 1995]. Previous studies in high arctic tundra on Svalbard and in northern Canada showed that live vegetation biomass increased by nearly 100% and plant cover increased by 30% following moderate nutrient additions (5 g N m⁻² y⁻¹), with plant species composition shifting from a prostrate dwarf-shrub, herb community to one more dominated by forbs after three to five years [Henry et al., 1986; Robinson et al., 1998].

[3] Productivity in many ecosystems is not limited by a single resource, but by several. Liebig [1841] introduced the concept of nutrient colimitations, and his Law of the Minimum states that addition of nutrients (or any other resource) will stimulate plant growth only with addition of the nutrient in scarest supply. Ecosystem CO₂ exchange, aboveground biomass, total plant cover and photosynthesis have generally shown positive responses to N additions in arctic ecosystems, but the strongest responses have most often occurred with the combined addition of N and P [Shaver and Chapin, 1980; Henry et al., 1986; Baddeley et al., 1994; Shaver and Chapin, 1995; Shaver et al., 1998]. Strong interactions between N and P were observed in
several arctic fertilization experiments [Shaver and Chapin, 1980; Henry et al., 1986; Shaver and Chapin, 1995] and additions of high concentrations of NP or NPK fertilizer is a common technique to study plant or ecosystem responses to the alleviation of most all nutrient limitations [Parsons et al., 1994; Chapin et al., 1995; Robinson et al., 1998].

Temperature induced increases in net N mineralization and deposition of atmospheric N will likely increase N availability in high arctic ecosystems [e.g., Nadelhoffer et al., 1991; Hodson et al., 2005], but the availability of P is likely to be less affected by global change as it is very tightly conserved and largely determined by mobilization from mineral horizons [Robinson and Wookey, 1997]. Air temperatures between April and October from 1971 to 2000 in Pituffik (Thule), Greenland show a warming trend of 0.8°C per decade [Sullivan et al., 2008b]. Warmer temperatures may increase rates of net N mineralization and total plant available N. N mineralization in low arctic soils was relatively insensitive to changes in temperature below 9°C, but increased by more than a factor of two when temperatures were increased from 9°C to 15°C [Nadelhoffer et al., 1991]. With predicted temperature changes of 4 to 8°C in the Arctic by 2100 [Intergovernmental Panel on Climate Change (IPCC), 2007], soil temperatures in many arctic regions will likely cross temperature thresholds that lead to substantial increases in N mineralization [Nadelhoffer et al., 1991]. Emission of nitrous oxides, through the burning of fossil fuels, has led to extensive deposition of N in natural ecosystems around the world [Fenn et al., 2003; Matson et al., 2002]. Anthropogenic N deposition may stimulate plant growth and ecosystem productivity in N-limited ecosystems, but long-term N addition experiments in temperate forests showed that chronic, high rates of N addition eventually caused a decline in net ecosystem photosynthesis and even tree mortality [Aber et al., 1989; McNulty et al., 1996]. N deposition impacts even remote high arctic regions with atmospheric N deposition in arctic regions varying from 0.1 to 0.5 g m⁻² y⁻¹ [Woodin, 1997]. Over a two year period, Hodson et al. [2005] observed 0.03–0.11 g m⁻² y⁻¹ of N deposition in two small watersheds on Svalbard. Although the amount of anthropogenic N deposition is lower in remote arctic regions, even small annual increases in N availability may be significant as N mineralization rates on Svalbard were observed at 0.2 g N m⁻² y⁻¹ [Robinson et al., 1995].

General effects of nutrient addition on arctic ecosystems have been well established, but most studies have employed either a single treatment of NPK fertilizer [e.g., Shaver and Chapin, 1980; Wookey et al., 1995; Robinson et al., 1998] or relatively high factorial additions of N and P [e.g., Henry et al., 1986; Shaver and Chapin, 1995]. In this study, we sought to understand how CO₂ exchange and vegetation characteristics in a high arctic prostrate dwarf-shrub, herb tundra respond to small N additions and to determine if and at what point N ceases to be the most limiting resource. By using three levels of N additions, including a low 0.5 g m⁻² y⁻¹ application rate, we tested the sensitivity to N and examined the functional form of the response to increasing levels of N addition. Factorial additions of N and P were used to test for potential colimitations. Measurements of ecosystem CO₂ exchange were made to investigate changes in ecosystem function, while measurements of the community composition and cover were made to examine change in ecosystem structure and to help explain potential changes in CO₂ exchange.

2. Materials and Methods

2.1. Site Description and Experimental Design

The study was conducted near Pituffik (Thule), Greenland (76°29′N, 68°26′W; elevation 245 m asl) in a prostrate dwarf-shrub, herb tundra. Prostrate dwarf-shrub, herb tundra occupies approximately 8% of the ice-free arctic land surface [CAFM Team, 2003]. Between 1978 and 2004, mean annual air temperature and precipitation for the site were −11.4°C and 12.5°C respectively. Over the same period, growing season (June, July and August) air temperatures averaged 3.8°C and approximately 50% of precipitation fell between October and April as snow. The soil surface of the study site was approximately 40% covered by vascular plants and 60% unvegetated. Dominant vascular plants include the deciduous dwarf-shrub Salix arctica, the graminoid Carex rupestris and the wintergreen dwarf-shrub Dryas integrifolia. Subdominant vascular plant species include the graminoids Carex nardina, Festuca brachyphylla and Poa arctica, and the forbs Cerastium alpinum, Cochlearia officinalis var. groenlandica, Sagina intermedia and Papaver radicatum. The unvegetated areas vary from completely bare to partial cover by a cryptogamic crust.

A partially factorial randomized complete block design was established in 2004 to test the effects of five levels or combinations of nutrient additions. Eighteen 2.0 m² plots were established at 2.0 m intervals along one linear transect perpendicular to a southwest-facing slope in each of the two blocks. Two blocks were established to account for variability in soil temperatures and soil moisture. Plots were evenly distributed across the two blocks, one of which had consistently lower soil moisture, higher soil temperatures and lower plant cover. Six control plots (CTL) and six replicates of the following nutrient treatments were split evenly across the blocks and randomly assigned to plots: 0.5 g m⁻² yr⁻¹ nitrogen (N0.5), 1.0 g m⁻² yr⁻¹ nitrogen (N1.0), 5.0 g m⁻² yr⁻¹ nitrogen (N5.0), 2.5 g m⁻² yr⁻¹ phosphorus (P2.5) and 2.5 g m⁻² yr⁻¹ phosphorus + 5.0 g m⁻² yr⁻¹ nitrogen (N + P). Nutrient additions were made twice during the growing seasons of 2004, 2005 and 2006 by evenly spreading the appropriate amount and combination of dry NH₄NO₃ and/or triple super phosphate commercial fertilizer. In all years, fertilizer was applied approximately one week after snowmelt and again in the first week of July.

2.2. CO₂ Exchange

Net ecosystem exchange (NEE), ecosystem respiration (ER) and gross ecosystem photosynthesis (GEP) were measured on 10 dates in 2005 and 13 dates 2006 during June–August using a passive, closed chamber technique [Vourlitis et al., 1993]. A LI-COR-6200 portable photosynthesis system (LI-COR, Inc., Lincoln, Nebraska, USA) was attached to a custom-made 20 cm × 40 cm × 20 cm clear acrylic chamber, equipped with a small fan to ensure proper mixing. Soils at the site are very rocky and prohibit the installation of permanent chamber bases. The CO₂ flux
chamber was, therefore, fit with a foam-lined aluminum flange that was sealed to the soil surface using steel weights. Exact locations for CO$_2$ flux measurements were chosen by the following criteria: proper seal between the chamber and soil surface and presence of the three dominant plant species, *S. arctica*, *D. integrifolia* and *C. rupestris*. The location of CO$_2$ flux measurements were permanently marked using colored nails. NEE was measured over a 30 s period after allowing 15 s for mixing. The chamber was vented to the atmosphere after each NEE measurement. ER was measured using the same method as above, but the chamber was covered with an opaque cloth. GEP was calculated as the difference between NEE and ER. All CO$_2$ flux measurements were taken within two hours of the solar maximum on both sunny and cloudy days. All CO$_2$ fluxes are reported from the ecosystem perspective where a negative flux represents a net release of CO$_2$ to the atmosphere, while a positive CO$_2$ flux represented net uptake.

Belowground respiration was measured in each plot during June–August of 2004–2006 using a LI-6400 portable photosynthesis system equipped with a LI-6400-09 soil respiration chamber (LI-COR, Inc., Lincoln, Nebraska, USA). Belowground respiration was defined as the efflux of CO$_2$ from the soil in the absence of live aboveground vascular plant tissue. Locations in each plot that were devoid, or nearly devoid, of live aboveground vascular plant tissue were selected and 10.0 cm diameter PVC collars were permanently installed 5 cm into the soil. Two consecutive measurements of belowground respiration were made in each plot within two hours of the solar maximum in conjunction with NEE and ER measurements.

2.3. Normalized Difference Vegetation Index (NDVI)

Cover of green biomass in a subset of each plot was measured using a multispectral digital camera (Tetracam ADC, Chatsworth, CA, USA) sensitive to green, red, and near-infrared spectral bands that was mounted on a tripod 80 cm above the soil surface. Images captured with the multispectral camera were used to calculate the normalized difference vegetation index (NDVI). NDVI is a vegetation index that is correlated with the presence of photosynthetically active vegetation and derived from the reflectance of red (R) and near-infrared light (NIR) [Rouse et al., 1973] as follows:

\[
\text{NDVI} = \frac{(\text{NIR} - R)}{(\text{NIR} + R)},
\]

where NIR is reflectance at 750–900 nm and R is reflectance at 620–750 nm. NDVI images were captured for all plots on 6 dates in 2005 and 6 dates in 2006 simultaneous with CO$_2$ flux measurements. Images of a Teflon card (Tetracam, Chatsworth, CA, USA), which reflects all light wavelengths, were captured to correspond with each NDVI image and used to correct for changes in light intensity. Plot NDVI was calculated for the 20 × 40 cm area where CO$_2$ flux measurements were taken and all images were captured within 2 h of the solar maximum.

2.4. Plant Community Composition

Plant species composition was recorded for each plot around the time of peak vascular plant biomass (the middle of July) during 2006 using the point interception technique (Jonasson, 1988). Each point interception frame was 80 cm × 120 cm and contained 99 points, defined by the intersection of monofilament lines. For each plot, a 30 cm pin was dropped vertically from each point in the frame. Due to the development of a canopy in N + P plots, every pin hit between the point frame and the ground was recorded for CTL and N + P plots and the first pin hit was recorded in all other plots. Vascular plants were identified to species. Nonvascular plants were identified as moss or lichen. Pin hits identified as bare ground were areas of rock, bare soil, or litter. The Shannon index for diversity (H) was used to calculate species diversity in CTL and N + P plots and was defined as:

\[
H = \sum_{i=1}^{S} p_i \ln p_i
\]

where S is the total number of species in plot and $p_i$ is the proportion of the $i$th species [Pielou, 1975]. Species richness was also calculated for CTL and N + P plots.

2.5. Leaf Chemistry

*S. arctica*, *D. integrifolia*, *C. rupestris*, *F. brachyphylla* and *P. arctica* leaves were collected every other week during the 2006 growing season. Leaf samples were stored in coin envelopes, oven-dried at 60°C for 24 h, and ground into a fine powder with mortar, pestle and liquid nitrogen. All leaf samples were analyzed for C, N and $\delta^{13}$C using a Costech 4010 Elemental Analyzer (Costech Analytical, Valencia, CA) interfaced with a Thermo-Finnigan Delta Plus XP continuous-flow stable isotope ratio mass spectrometer (Thermo Electron Corp., Waltham, MA).

2.6. Statistical Analysis

Data presented did not deviate significantly from assumptions of normality or equality of variance. Differences in CO$_2$ flux, belowground respiration, NDVI, leaf N, and leaf $\delta^{13}$C across treatments were tested using a Factorial Repeated Measures Analysis of Variance (ANOVA) in the Mixed Model procedure of SAS 9.1 (SAS Institute, Cary, NC). The primary factors in the statistical model were date, N, P, block and interactions between block, N and P. Each level of N and P addition was treated as a quantitative level which corresponded to the level of fertilization. Residuals were attributed to an autocorrelation structure that resulted in the lowest Akaike Information Criteria (AIC) value and comparisons across treatments were made using Tukey’s Honestly Significant Difference (HSD). Block significantly affected measurements of CO$_2$ exchange (except 2005 GEP), NDVI and 2004 belowground respiration with p < 0.01 in all cases of significance. Significant interactions between block, N and P; however, only occurred in measurements of belowground respiration in 2004 and NEE in both 2005 and 2006. Differences in plant community composition across treatments were tested using ANOVA in the General Linear Model procedure of SAS 9.1. Comparisons were, again, made using Tukey’s HSD. Correlations between NDVI, GEP, ER and NEE were examined using a quadratic polynomial regression in SigmaPlot 9.0 (Systat Software, Inc., San Jose, CA). Each data point in the regression represents the mean of six sampling dates of paired NDVI
and ecosystem CO₂ exchange measurements during 2005 and 2006.

3. Results

3.1. CO₂ Exchange

3.1.1. Multiple Levels of Nitrogen Addition

[14] NEE, GEP and ER showed a nonlinear, saturating response to increasing levels of N addition, with the largest response observed in N1.0 plots and a decrease or no further increase of response in N5.0 plots (Figure 1). The response of GEP and ER to N additions was qualitatively similar in 2005 and 2006 and both fluxes were very sensitive to small N additions (N0.5 plots) with a 96% and 90% increase in rates of GEP and a 91% and 82% increase in rates of ER in 2005 and 2006, respectively, compared to CTL plots. In 2005 and 2006, all levels of N addition decreased rates of NEE (greater CO₂ source) such that rates of NEE were 79% and 73% lower in N0.5 plots compared to CTL plots in 2005 and 2006, respectively.

3.1.2. Factorial Nitrogen and Phosphorus Additions

[15] Additions of N (N5.0) and P (P2.5) alone stimulated GEP and ER, but the combined addition of N and P (N + P) caused the greatest response. In 2005, N + P addition increased GEP by 474%, as a result of a significant interaction between N and P (F = 163.27, p < 0.01) (Figure 1). In 2006, GEP in N + P plots increased by 618% over CTL plots with a significant interaction between N and P (F = 109.98, p < 0.01). ER measurements showed a qualitatively similar response to N and P additions, but again, N + P addition elicited the greatest response, enhancing ER by 266% and 289% over CTL plots in 2005 and 2006, respectively, and there was a significant interaction between N and P in both 2005 (F = 39.81, p < 0.01) and 2006 (F = 47.63, p < 0.01). Amendments of N and P alone and N and P combined affected NEE in opposite directions. Measurements of midday growing season NEE demonstrated that the CTL plots were a small net source of CO₂ in both years of the study. In 2005, NEE was significantly decreased (greater CO₂ source) by additions of N5.0 and both N5.0 and P2.5 treatments tended to decrease NEE in 2006. N + P addition had an opposite effect, increasing NEE in 2005, but there was no difference in NEE between CTL and N + P plots in 2006.

3.2. Belowground Respiration

[16] Additions of N alone generally did not affect belowground respiration in 2004 and 2005 (Figure 2). Additions of P stimulated belowground respiration by 23% in 2004 and 2005, and there was a strong trend toward higher belowground respiration in P2.5 plots during 2006. N + P addition did not affect belowground respiration in 2004, but caused a 54% and 111% increase in 2005 and 2006, respectively, compared to CTL plots. There was a significant interaction between N and P in both 2005 (F = 9.35, p < 0.01) and 2006 (F = 18.72, p < 0.01).

3.3. Normalized Difference Vegetation Index (NDVI)

3.3.1. Multiple Levels of Nitrogen Addition

[17] As observed in measurements of CO₂ exchange, NDVI also showed a nonlinear, saturating response to increasing levels of N addition, such that the largest NDVI response occurred in N1.0 plots and no further increase was observed in N5.0 plots (Figure 3). N addition significantly affected NDVI in 2005 (F = 128.54, p < 0.01) and 2006 (F = 118.64, p < 0.01) and NDVI in all N addition plots was greater than in CTL plots. The highest NDVI values occurred in N1.0 plots, where NDVI was 60% greater than CTL plots during 2005 and 2006.
3.3.2 Factorial Nitrogen and Phosphorus Additions

N and P alone and in combination increased plot-level NDVI in both years of the study. NDVI increased by 29% in 2005 and 25% in 2006 in P2.5 plots, while NDVI in N5.0 plots increased by 54% in 2005 and 57% in 2006 compared to CTL plots (Figure 3). Again, additions of N + P led to the greatest response and caused a 126% and 117% increase in NDVI of N + P plots compared to CTL plots during 2005 and 2006, respectively. NDVI was correlated to GEP during 2005 ($r^2 = 0.81$, $F = 74.23$, $p < 0.01$) and 2006 ($r^2 = 0.88$, $F = 127.53$, $p < 0.01$) (Figure 4). NDVI was also strongly correlated with ER during 2005 ($r^2 = 0.89$, $F = 70.00$, $p < 0.01$) and 2006 ($r^2 = 0.80$, $F = 69.20$, $p < 0.01$). Weaker correlations between NDVI and NEE were found in both 2005 ($r^2 = 0.12$, $F = 3.45$, $p = 0.04$) and 2006 ($r^2 = 0.22$, $F = 5.86$, $p < 0.01$).

3.4 Plant Community Composition

3.4.1 Multiple Levels of Nitrogen Addition

High variability in the extent and type of cover prevented the detection of statistically significant differences between treatments. Variability was in part due to inherent differences in plant cover between CTL plots of the two blocks ($t = 1.65$, $p = 0.05$) and differences in plant cover of all plots between blocks ($t = 2.27$, $p = 0.04$). Data were condensed into four categories for comparison by cover types. C. rupestris, D. integrifolia and S. arctic were considered dominant vascular plants, while all other vascular plants were considered subdominant. Nonvascular plants included all species of moss and lichen excluding crustose lichen. The bare ground category includes bare soil, rock and litter. The greatest cover of dominant vascular plants was observed in N1.0 plots and represented a 60% increase over CTL plots (Figure 5). Cover of subdominant vascular plants increased slightly with increasing rates of N addition from 3% in CTL plots to 8% in N5.0 plots, where there was a marginally significant increase in the cover of Papaver radicatum ($p = 0.06$). Notable changes in cover of plant functional groups included a 41% increase in deciduous shrubs in N0.5 plots, a 97% increase in graminoids in N1.0 plots and a 296% and 740% increase in forbs in N1.0 and N5.0 plots, respectively, compared to CTL plots.

3.4.2 Factorial Nitrogen and Phosphorus Additions

Addition of N and P radically changed plant community composition with change driven by a significant increase in the graminoid F. brachyphylla ($p < 0.01$) (Table 1). Subdominant plant cover increased from 3% in
CTL plots to 38% of cover in N + P plots (p < 0.01) and bare ground decreased from 64% in CTL plots to 28% in N + P plots (p = 0.01). There was no change in the cover of deciduous shrubs or evergreen shrubs with N + P addition, but significant increases in cover of forbs (p = 0.05) and graminoids (p < 0.01) were observed. Increases in vascular plant cover with N + P addition led to the development of a multilayered canopy. Canopy development in N + P plots was characterized by recording every hit as a pin was dropped vertically from a point-intercept frame to the ground in CTL and N + P plots. A plant community with a single-layered canopy and only 1 hit per pin drop would have 99 total hits. A greater number of hits was recorded in N + P plots when compared to CTL plots (p < 0.01, t-test, df = 10) with a mean of 143 hits in N + P plots and 109 hits in CTL plots. Comparisons between the number of hits recorded for selected plant species in CTL and N + P plots were made using the multiple hit point frame data set to include understory species (Table 1). Changes in species composition in N + P plots manifested as an increase in vascular plant species richness and diversity. Species richness increased from 8 in CTL plots to 13 in N + P plots, while the Shannon Diversity index in CTL plots was 1.47 compared 1.92 in N + P plots.

3.5. Leaf Chemistry

3.5.1. Multiple Levels of Nitrogen Addition

[21] N addition significantly affected foliar δ¹³C of C. rupestris (F = 9.26, p < 0.01), with a significant increase in foliar δ¹³C in N5.0 plots (t = −4.51, p < 0.01) and a marginally significant increase in foliar δ¹³C in N1.0 plots (t = −2.39, p = 0.09). N treatment did not have a significant effect on foliar δ¹³C any other plant species. Foliar N concentration was significantly higher in N5.0 plots compared to CTL plots for C. rupestris (t = −8.75, p < 0.01), D. integrifolia (t = −7.87, p < 0.01), S. arctica (t = −5.97, p < 0.01) and F. brachyphylla (t = −10.23, p < 0.01).

3.5.2. Factorial Nitrogen and Phosphorus Additions

[22] With the exception of C. rupestris, factorial amendments of N and P did not affect foliar δ¹³C of measured plant species. Additions of P alone did not affect foliar N concentrations. Addition of N and P significantly increased foliar N concentrations relative to CTL plots in C. rupestris (t = −6.74, p < 0.01), S. arctica (t = −3.28, p < 0.01), F. brachyphylla (t = −9.53, p < 0.01) and P. arctica (t = −7.66, p < 0.01), but foliar N was generally lower in N + P plots than observed in N5.0 plots.

4. Discussion

4.1. Multiple Levels of Nitrogen Addition

[23] Our results show that prostrate dwarf-shrub herb tundra in Northwest Greenland is very sensitive to small N additions, as CO₂ exchange and NDVI were significantly altered in N0.5 plots. Although 0.5 g m⁻² y⁻¹ of N addition is small compared to other fertilization studies, it represents a doubling of the annual net N mineralization of 0.2 g N m⁻² y⁻¹ observed in a polar semi-desert on Svalbard [Robinson et al., 1995]. Rates of GEP (greater plant uptake of CO₂) and ER (greater CO₂ efflux) showed high sensitivity to N0.5 addition as both increased by a nearly a factor of two compared to CTL plots. NEE was significantly reduced (greater CO₂ source) in N0.5 plots resulting in a 70–80% increase in net CO₂ efflux to the atmosphere as determined during midday measurements. Similarities in the functional form of response to N additions in measurements of ecosystem CO₂ exchange, NDVI and plant cover, coupled with strong correlations between GEP, ER and NDVI suggest increases in vascular plant cover and biomass largely explain increases in rates of GEP and ER. To our knowledge, no other study has assessed the impact of low

Figure 4. Correlations between NDVI and GEP, NDVI and ER and NDVI and NEE during 2005 and 2006. Each point on the curve represents the mean six sampling dates for each plot in 2005 and 2006.
levels of N addition on CO2 exchange in arctic ecosystems, and increasing industrialization in the Arctic will likely lead to rates of atmospheric N deposition that exceed those of 0.1 g m^{-2} y^{-1} observed on Svalbard [Hodson et al., 2005].

[24] Foliar N responded linearly to N additions with the highest foliar N concentrations in N5.0 plots for C. rupestris, D. integrifolia, and S. arctica, indicating that plants allocated some of the additional N to leaf material. The observed higher leaf N concentrations may have been stored for future use [van Wijk et al., 2003b], or used immediately to support photosynthesis [Baddeley et al., 1994]. Measurements of C. rupestris foliar δ13C revealed a marginally significant increase in foliar δ13C in N1.0 plots and a significant increase in foliar δ13C in N5.0 plots. Increases in foliar δ13C generally reflect a decrease in leaf intercellular CO2 concentrations, which may arise through either a reduction in stomatal conductance or an increase in photosynthesis [Farquhar et al., 1989]. It seems likely that increases in foliar δ13C in N1.0 and N5.0 plots were caused by an increase in photosynthesis of C. rupestris, given that increases in foliar N were observed, while there was no evidence of a change in soil water contents with N addition and studies of plant water relations near Pitufik have found limited signs of water stress [Sullivan and Welker, 2007]. Increased photosynthetic rates of C. rupestris may have contributed to the increase in GEP observed in N1.0 and N5.0 plots.

[25] The functional form of the response to increasing levels of N addition was nearly identical in CO2 exchange and NDVI measurements and followed a nonlinear pattern such that the greatest response occurred with 1.0 g m^{-2} y^{-1} of N addition with a saturating or decreasing response at higher levels of N addition. A trend toward decreasing GEP, ER and NDVI in N5.0 plots suggested that ecosystem, or vegetation, N saturation began to occur between 1.0 and 5.0 g m^{-2} y^{-1} of N addition [Aber et al., 1989]. N saturation is defined as the point at which ammonium and nitrate availability exceed plant and microbial demands for N [Aber et al., 1989]. Prior to N saturation, tree growth, leaf N and net primary production typically increase with additional N [McNulty et al., 1996], but as N saturation occurs, it can cause reductions in net ecosystem photosynthesis and net primary production [Aber et al., 1989]. While the suite of measurements collected prevent quantitatively detecting ecosystem N saturation, the addition of multiple levels of N to our site gave rise to several responses similar to those observed in N saturated temperate forests. Foliar N concentration progressively increased with increasing rates of N addition in C. rupestris, D. integrifolia and F. brachyphylla with a trend toward increasing foliar N in S. arctica [Arens, 2007]. A concurrent increase in GEP and NDVI of

![Figure 5. Percent cover by (a) cover type and (b) functional group in 2006. Each bar represents the mean of six plots for each treatment.](image)

### Table 1. Mean Number of Hits Observed for Select Vascular Plant, Bryophyte, and Lichen Species (1SE)^a

<table>
<thead>
<tr>
<th>Species/Cover Type</th>
<th>Control</th>
<th>N + P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carex rupestris</td>
<td>13.3 (4.9)</td>
<td>18.5 (3.6)</td>
</tr>
<tr>
<td>Dryas integrifolia</td>
<td>13.3 (4.9)</td>
<td>8.7 (1.6)</td>
</tr>
<tr>
<td>Salix arctica</td>
<td>4.5 (1.3)</td>
<td>13.8 (3.7)*</td>
</tr>
<tr>
<td>Carex nardina</td>
<td>2.0 (1.1)</td>
<td>3.8 (2.1)</td>
</tr>
<tr>
<td>Cerastium alpinum</td>
<td>0.2 (0.2)</td>
<td>4.8 (0.2)***</td>
</tr>
<tr>
<td>Cochlearia officinalis</td>
<td>0</td>
<td>2.3 (1.5)</td>
</tr>
<tr>
<td>Drosera nivalis</td>
<td>0</td>
<td>1.8 (1.2)</td>
</tr>
<tr>
<td>Festuca brachyphylla</td>
<td>1.3 (0.6)</td>
<td>43.8 (12.0)***</td>
</tr>
<tr>
<td>Papaver radicum</td>
<td>0</td>
<td>2.1 (1.1)</td>
</tr>
<tr>
<td>Poa arctica</td>
<td>0</td>
<td>6.5 (3.4)*</td>
</tr>
<tr>
<td>Sagina intermedia</td>
<td>0</td>
<td>2.5 (1.7)</td>
</tr>
<tr>
<td>Saxifraga oppositifolia</td>
<td>0.8 (0.3)**</td>
<td>0</td>
</tr>
<tr>
<td>Silene acaulis</td>
<td>0</td>
<td>0.3 (0.2)</td>
</tr>
<tr>
<td>Bryophytes</td>
<td>3 (1.2)</td>
<td>10.7 (3.2)***</td>
</tr>
<tr>
<td>Lichens</td>
<td>8.2 (2.7)**</td>
<td>2.3 (1.1)</td>
</tr>
<tr>
<td>Bare ground</td>
<td>53.5 (11.6)**</td>
<td>17.5 (2.4)</td>
</tr>
</tbody>
</table>

^aSignificant differences between CTL and N + P plots are denoted by *p < 0.1, **p < 0.05, ***p < 0.01.
N0.5 and N1.0 plots occurred in both years, but, as predicted by the final stage of N saturation, GEP declined and NDVI tended to be lower in N5.0 plots compared to N1.0 plots despite very high foliar N in N5.0 plots. Strong positive responses of CO$_2$ exchange and NDVI to small additions of N demonstrate that prostrate dwarf-shrub, herb tundra was primarily limited by N, but a decrease or saturation of response in those variables with high levels of N addition suggest ecosystem, or vegetation N saturation.

4.2. Factorial Nitrogen and Phosphorus Additions

[26] Factorial additions of N and P shed light on a secondary limitation to ecosystem productivity. Combined N and P addition radically altered GEP, ER, NEE, NDVI, and plant community composition, releasing the system from apparent N saturation, suggesting that a strong colimitation with P arose between N additions of 1 and 5 g m$^{-2}$ yr$^{-1}$. Ecosystem CO$_2$ exchange was highly sensitive to N, but showed the greatest magnitude of response to combined addition of N and P. N and P interacted very strongly to increase GEP five to sixfold and enhanced ER by 250% over CTL plots. Addition of N stimulated both GEP and ER more than P. Unlike our results, factorial addition of N, P and K to wet sedge tundra in Alaska, showed that P stimulated CO$_2$ flux more than N and there was only a small interaction between N and P [Shaver et al., 1998]. The positive synergistic effect of N and P addition on CO$_2$ exchange stimulated GEP slightly more than ER resulting in significant NEE increases during 2005. Higher rates of NEE in 2005 compared to 2006 may be the result of either a warmer 2005 growing season or the diminished response of CO$_2$ exchange to fertilization by 2006.

[27] Changes in CO$_2$ flux due to multiple levels of N and N + P addition can largely be explained by changes in plot-level NDVI and plant community composition. N and P interacted significantly to increase NDVI from 0.3 in CTL plots to 0.6 in N + P plots. NDVI in N + P plots in Pituffik was greater than that observed in unaltered Alaskan wet sedge tundra [Boelman et al., 2003] and similar to that measured in a highly productive fen near Pituffik [Sullivan et al., 2008a]. NDVI increases in N + P plots were due to large decreases in bare ground, a shift in species composition and development of a multilayered canopy. Over two years of measurement, NDVI was significantly correlated to CO$_2$ exchange, explaining 81 to 88% of variation in GEP and 80% of variation in ER. Correlations between NDVI, GEP and ER were also observed in wet sedge tundra [Boelman et al., 2003], but were weaker than those observed at our site.

[28] Measurements of belowground respiration in 2004 showed that neither N nor combined N and P addition directly limited microbial respiration, similar to results from a study in eastern Greenland [Illeris et al., 2003]. Belowground respiration in N + P plots increased progressively during each year of this study. Such a response could be caused by stimulation of microbial respiration through greater inputs of higher quality litter (including root exudates) or through large increases in plant root respiration. Although litter input was not quantified, NDVI measurements indicate large increases in aboveground biomass by 2005. Increases in foliar N with N + P addition were observed in nearly all measured plant species. Increases in litter quantity and quality may have stimulated microbial respiration by relieving limitations associated with C quality [Hobbie and Chapin, 1996; Hobbie et al., 2000] as substrate quality is one of the primary controls of decomposition [Heal et al., 1981].

[29] High N addition resulted in a small, nonsignificant decrease in bare ground, but N + P addition decreased bare ground from over 60% to less than 20%. Superimposed on changes to plant cover in N + P plots was an inherent difference in plant cover between blocks. We hypothesize that differences in plant cover were largely responsible for the significant effect of block on CO$_2$ exchange, belowground respiration and NDVI. Establishment of graminoids, principally *F. brachyphylla*, was the primary reason for the reduction of bare ground. Colonization of bare ground by vascular plants subjected to N and P additions has also been observed in polar semi-desert [Robinson et al., 1998] and alpine tundra [Heer and Körner, 2002]. *F. brachyphylla* constituted only 1% of cover in CTL plots, but, after two years of N + P addition, it became the dominant vascular plant species, comprising over 40% of the total cover in N + P plots. Significant interactions between block, N and P were present only in NEE measurements. Graminoids were the most responsive functional group in our study and have shown a strong positive response to combined N and P fertilization in many tundra ecosystems, including alpine tundra [Heer and Körner, 2002], low arctic tundra [Chapin and Shaver, 1985; Gough et al., 2002; Gough and Hobbie, 2003], and high arctic tundra [Henry et al., 1986; Robinson et al., 1998]. The strength of the graminoid response at our site appears to be unique within the High Arctic, as other nutrient additions to similar landscapes showed a comparatively weaker graminoid response with forbs and deciduous shrubs responding most strongly and establishing more often on bare ground areas [Henry et al., 1986; Baddeley et al., 1994; Robinson et al., 1998].

[30] Increases in species richness and diversity accompanied dramatic increases in graminoid cover. Forbs, bryophytes and the deciduous shrub *S. arctica* all increased cover in response to N + P fertilization. Total forb cover in N + P plots increased nearly twenty-fold compared to CTL plots, with most of that increase from vascular plants not present in CTL plots. The effects of fertilization on species richness and diversity in the Arctic vary from complete dominance by a single species, reducing species richness and diversity [Chapin et al., 1995], to situations in which richness and diversity have increased [Robinson et al., 1998] to others where richness and diversity have remained unchanged [Gough and Hobbie, 2003]. The only fertilization studies to observe increases in species richness and diversity were in the High Arctic where open canopy ecosystems dominate [Robinson et al., 1998]. In a Svalbard polar semi-desert, after three years NPK addition, previously unobserved forbs characteristic of bird cliff communities, established in bare ground areas [Robinson et al., 1998]. The mechanism and type of change to species composition in Svalbard was very similar to changes observed at our site, but the speed and magnitude of changes in Pituffik were substantially greater.

[31] In our study, prostrate dwarf shrub, herb tundra responded strongly to small N inputs and showed a magnitude and speed of response to factorial N and P additions.
not previously observed. Significant changes to ecosystem CO$_2$ exchange and NDVI in response to low levels of N addition suggest that future atmospheric N deposition, even at relatively low rates, may alter both vegetation characteristics and net rates of CO$_2$ efflux as N0.5 addition caused a 70% decrease in NEE (greater net CO$_2$ efflux). After N + P addition, ecosystem and vegetation characteristics more closely resembled characteristics of ecosystems one subzone further south [CAVM Team, 2003], or those fertilized for centuries by nesting sea birds [Robinson et al., 1998].

Also unique to our study is the rapidity of ecosystem and community level responses to N and P additions. Changes in plant species composition began to occur after only one year of nutrient addition. Our observations contribute to a growing body of evidence that suggests a strongly divergent response to nutrient additions in ecosystems of the High and Low Arctic. Nutrient additions to low arctic tundra have almost always led to reductions in species diversity and richness, while elevating codominant species to dominance [Chapin et al., 1995]. Nutrient additions in the High Arctic have generally led to increases in species diversity and richness through a strong stimulation of rare subdominant plant species [Henry et al., 1986; Robinson et al., 1998]. Increases in plant available N, due to atmospheric N deposition or warming-induced increases in net N mineralization, will likely alter carbon cycling and vegetation characteristics of prostrate dwarf-shrub, herb tundra, but the magnitude of the response will be constrained by P availability.

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