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Authors: Dagg, Jennifer, and Lafleur, Peter

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Vegetation Community, Foliar Nitrogen, and Temperature Effects on Tundra CO₂ Exchange across a Soil Moisture Gradient

Jennifer Dagg* and
Peter Lafleur†

*Corresponding author: Environmental
and Life Sciences Program,
Trent University, Peterborough, Ontario,
K9J 7B8, Canada
jenniferdagg@trentu.ca

†Department of Geography,
Trent University, Peterborough, Ontario,
K9J 7B8, Canada
plafleur@trentu.ca

Abstract

Soil moisture has both direct and indirect effects on carbon dioxide (CO₂) exchange in tundra vegetation. It directly affects vegetation distribution and functioning, thus CO₂ exchange at the leaf level, and it controls microbial decomposition influencing soil respiration. In this study we investigated CO₂ exchange on a heterogeneous tundra landscape in the Canadian low arctic with the primary purpose of exploring the relationship between moisture variability and community level fluxes. CO₂ exchange was measured with a portable chamber system, along with soil and air temperature. Biomass, leaf area, and foliar nitrogen were determined from harvested vegetation. Fluxes were compared in birch, tussock, heath, and sedge communities under different moisture regimes. Respiration and productivity were typically highest in wet or mesic groups, with fewer differences in net CO₂ exchange. Across the soil moisture gradient, productivity and net CO₂ exchange per unit leaf area and foliar nitrogen showed a significant negative linear trend. Respiration was limited in very dry and saturated soil, and soil temperature effects on respiration were seen only in mesic moisture conditions. These findings indicate that nutrient and temperature affects on fluxes can be at least partially explained within the framework of soil moisture availability.

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Introduction

Arctic ecosystems play a critical role in the global carbon cycle because up to 50% of the global belowground organic carbon pool is stored in northern permafrost regions (Tarnocai et al., 2009). This accumulation of soil organic matter is due to greater carbon dioxide (CO₂) uptake via photosynthesis than CO₂ release through respiration over the preceding millennia. Changes in the rates of CO₂ storage and release are of great interest because release of stored carbon as CO₂ (or methane) into the atmosphere could create positive feedbacks to global warming (Callaghan et al., 2004; Chapin et al., 2008). There is growing evidence that tundra ecosystems are changing dramatically (Post et al., 2009). Climate change will likely lead to decreased soil moisture availability (Hinzman et al., 2005), increased shrub distribution (Tape et al., 2006), and increased nitrogen (N) availability (Hobbie et al., 2002). These changes will have large impacts on the arctic CO₂ cycle (Mack et al., 2004; Post et al., 2009).

Soil moisture is an important variable in controlling tundra soil respiration (Sjögersten et al., 2006). Several studies that have examined CO₂ exchange across moisture gradients in the arctic have found that differences in moisture strongly affect responses to simulated climate change (Welker et al., 2000, 2004; Oberbauer et al., 2007). Net CO₂ exchange in tundra environments has been strongly linked to soil moisture at both the plot level (Nobrega and Grogan, 2008; Sjögersten et al., 2006) and the landscape level (Lafleur et al., 2001; Harazano et al., 2003; Kwon et al., 2006). In saturated soils, ecosystem respiration is limited by low oxygen concentrations, and respiration increases when wet soils are dried (Johnson et al., 1996). Conversely, in very dry soils respiration is limited by low soil water content (Sjögersten and Wookey, 2004; Illeris et al., 2003) and may be further decreased if soil moisture is

reduced (Illeris and Jonasson, 1999). The relationship between soil moisture and productivity, however, is less clear (McFadden et al., 2003; Welker et al., 2004; Oberbauer et al., 2007) because productivity is highly limited by N in northern latitudes (Jonasson et al., 1999; van Wijk et al., 2003). Foliar nitrogen has been shown to be a strong constraint on canopy-level photosynthesis (Williams and Rastetter, 1999; Williams et al., 2001) and shows a strong positive relationship with leaf area (van Wijk et al., 2005). Because soil moisture directly limits the rate of N mineralization, with saturated soils having less available N for uptake by vegetation during the growing season (Nadelhoffer et al., 1992; Arndal et al., 2009), soil moisture indirectly affects CO₂ exchange through nitrogen dynamics.

CO₂ flux is also directly impacted through vegetation community. Subarctic tundra is composed of a mosaic of vegetation communities that are distributed along a gradient of soil moisture. Tundra ecosystems can be generally grouped as dry, where there is limited soil moisture and little vegetation; mesic, which is more thickly vegetated, and may undergo periods of higher soil moisture; and wet, where standing or flowing water is present for the extent of the growing season (Welker et al., 2004). Tundra vegetation is also highly variable; ranging from highly diverse communities of ericaceous herbs to almost uniform graminoid fields, and this variability is often seen over a small spatial scale (Walker et al., 1994; Shaver et al., 1996; Williams and Rastetter, 1999). Small-scale variability seen in both biotic and abiotic factors can affect the uptake and release of CO₂ by tundra in different ways (Soegaard et al., 2000), such that the effects on net CO₂ exchange are not easily predicted. Yet, such knowledge is necessary to predict spatial carbon dynamics in a warming climate (McGuire et al., 2002).

The goal of this study was to examine small-scale spatial patterns and controls on CO₂ exchange in common vegetation groups in subarctic tundra in central Canada, with an aim of improving our understanding of biotic and abiotic controls on CO₂ exchange. The first objective of this study was to investigate differences in fluxes between similar vegetation communities that differ in soil moisture regime. The second objective was to explore relationships between CO₂ exchange and environmental variables; specifically between net CO₂ exchange and gross photosynthesis and plant biomass, light availability, and foliar nitrogen and between temperature (soil and air) and respiration.

Methodology

STUDY AREA

The study was conducted during the 2008 growing season near the Tundra Ecosystem Research Station at Daring Lake, Northwest Territories (NWT) (64°52'N, 111°34'W), located 300 km northeast of Yellowknife, NWT, and approximately 70 km north of the treeline. The region is classified as low-arctic shrub tundra, which is broken up by frequent eskers and hydrologic features. Local elevation ranges from 414 to 470 m above sea level. Soils in the region typically have a thin surface organic horizon in drier areas (less than 0.1 m) and a thicker organic horizon in wetter areas (up to 0.45 m), overlying a coarse mineral layer (Nobrega and Grogan, 2007, 2008). The area is underlain by continuous permafrost with an active layer typically ranging from 0.3 to 1.0 m. Climate in this region is characterized by long cold winters with a short growing season (mid-June to early September). The mean annual temperature ranges from −10.0 °C to −12.5 °C, and mean total annual precipitation ranges between 200 and 300 mm (Lafleur and Humphreys, 2008). Climate records for 1997–2008 from the Daring Lake weather station indicate growing season (June–August) daily mean temperature is 10.5 (±2.8) °C, with average precipitation of 31.2 (±24.0) mm month^{−1} and daily mean solar radiation of 222.3 (±51.1) W m^{−2}.

CO₂ EXCHANGE MEASUREMENTS

An infrared gas analyzer (LICOR 840, Lincoln, Nebraska) and a custom-built, closed-flow portable chamber system were used to measure CO₂ and H₂O concentrations. The clear acrylic chamber (0.4 × 0.4 × 0.4 m = 64 L) was fitted with a small fan to continually mix the air inside the chamber and 2 handles for ease of transport. Air from the chamber was drawn into the gas analyzer at a rate of 0.9 L minute^{−1} by a pump (model UN89, KNF Neuberger, Trenton, New Jersey) and was returned to the chamber through a port at the top of the chamber. The lip of the chamber was lined with 5-mm-thick foam, and the chamber was held in place with 4 small clamps on aluminum collars (0.4 m × 0.4 m) that were inserted into the soil. Air temperature inside the chamber (T_{cham}) was measured with a 0.35 mm copper-constantan thermocouple mounted on the inside of the chamber. CO₂, H₂O concentrations, and T_{cham} were recorded every 2 s for 150 s with a CR21X datalogger (Campbell Scientific, Logan, Utah). The first 10 s of data were discarded due to the disturbance of the placement of the chamber. Sampling took place first under ambient light conditions, then under reduced incident sunlight, under three successive layers of netting, then in complete darkness using a thick black plastic shroud, for a total of 5 measurements per collar. Following each measurement the chamber was lifted and turned into the wind for ~20 s to restore ambient conditions.

Net ecosystem CO₂ exchange (NEE) was calculated according to the following equation, after Shaver et al. (2007):

$$NEE = ([p * V] * [A^{-1}]) * (\Delta C * \Delta t^{-1}) \quad (1)$$

where p is air density (mol m^{−3}), calculated with the Ideal Gas Law, using average H₂O vapor concentration and average T_{cham} during the 140 s sampling period, V is the effective chamber volume (m³), calculated by summing the chamber volume and the volume contributed by the offset of the ground surface to the top of the collar, which was calculated by averaging 20 depth measurements taken from the top of the collar to the ground surface (the volume of tubes and the internal volume of the IRGA were considered negligible in comparison to the overall volume), A is the surface area of the collar (0.16 m²) and $\Delta C \Delta t^{-1}$ is the change in CO₂ concentration over time (μmol mol^{−1} s^{−1}), determined by calculating the linear slope of the CO₂ concentration versus time.

Samples taken in full darkness were assumed to represent ecosystem respiration (ER). ER values were subtracted from NEE values (samples taken under ambient light) to determine gross ecosystem productivity (GEP). Throughout this paper, the micrometeorological sign convention is used, where flux from atmosphere to tundra is negative and flux from the tundra to the atmosphere is positive.

Photosynthetic photon flux density (PPFD, μmol m^{−2} s^{−1}) was detected with a quantum sensor (Kipp and Zonen PAR-LITE, Campbell Scientific, Logan, Utah). To prevent this sensor from blocking radiation entering the chamber, it was mounted on a small wooden platform ~0.4 m in height placed within 1 m of the chamber and logged every 2 s during sampling on the CR21X datalogger. The platform and sensor were covered with shade cloths identical to those covering the chamber during the light reduction sampling. Additionally, because the Plexiglas chamber reduced PPFD reaching vegetation by ~7%, measured PPFD values were reduced to reflect this shading effect. Light response curves were fitted to the data according to the following equation:

$$GEP = (\alpha * PPFD * P_{max}) * ([\alpha * PPFD - P_{max}]^{-1}) \quad (2)$$

where α is the quantum efficiency (μmol CO₂ μmol^{−1} photon) and P_{max} is the rate of photosynthesis at infinite PPFD (μmol m^{−2} s^{−1}).

Supporting measurements included air temperature (T_{air}), which was measured with a 0.35 mm copper-constantan thermocouple inside a radiation shield, mounted on the same platform as the quantum sensor and logged every 2 s on the CR21X. Volumetric soil water content (VWC) was measured with a SMC probe (Hydrosense, Campbell Scientific Inc., Logan, Utah). To avoid repeated probing of the soil inside the collar, 4 soil moisture measurements were taken just outside the collar and the results were averaged. Copper-constantan thermocouples were inserted 5 cm deep into the soil in the center of each plot and soil temperature (T_{soil}) was measured with a digital thermocouple thermometer (model HH501, Omega Engineering, Stamford, Connecticut). Prior to the start of sampling, all thermocouples employed in the study ($n = 40$) were intercompared and no significant differences were found ($p = 0.886$).

Forty plots were established in vegetation communities defined by the most abundant plant species or family and by soil moisture regime. Due to logistical restrictions, sample sizes were not equal for all groups. Collars were inserted into the soil by cutting a slot with a serrated knife in the soil around the outer edge of the collar, and pressing it 6–10 cm into the soil organic layer. CO₂ flux sampling did not begin until 2 days after collars were inserted to allow CO₂ released from disturbance of the soil to

TABLE 1

Soil characteristics of seven tundra vegetation groups at Daring Lake, Northwest Territories (NWT), from 5 July to 13 August, 2008. The minimum-maximum of all data points is presented in parentheses. *N*-values indicate the number of CO₂ sampling sessions. Common superscripts indicate no significant difference between groups (Tukeys HSD, $p < 0.05$). VWC = volumetric soil water content.

	Mean soil water content (VWC %)	Mean soil temperature at 5 cm (°C)
Dry birch ($n = 21$)	15 ^a (6–24)	13.4 ^a (11.3–17.1)
Mesic birch ($n = 30$)	35 ^b (22–51)	10.6 ^b (3.7–12.7)
Dry tussock ($n = 25$)	25 ^{a,b} (13–53)	12.7 ^{a,b} (7.7–17.9)
Wet tussock ($n = 30$)	79 ^{c,d} (39–100)	13.2 ^{a,b} (6.5–16.5)
Dry heath ($n = 40$)	9 ^a (4–16)	15.4 ^a (9.6–20.8)
Mesic heath ($n = 21$)	37 ^b (21–46)	10.5 ^b (5.5–12.9)
Wet sedge ($n = 45$)	97 ^d (90–100)	12.7 ^{a,b} (6.1–17.6)

dissipate. Plots were sampled in a random order, with all plots sampled every 5–6 days, for a total of 8 sample sessions for each collar. CO₂ sampling occurred between 5 July and 12 August 2008, between 10:00 and 16:00 M.D.T., in all weather conditions except precipitation events. Vegetation groups (n = number of collars) were defined as follows (see Table 1 for further vegetation and soil characteristics):

- (1) Dry birch plots ($n = 3$) were dominated by *B. glandulosa* (Michx) with a negligible moss layer and an average soil moisture of <30% VWC.
- (2) Mesic birch plots ($n = 6$) were also dominated by *Betula glandulosa* (Michx) and showed a well-developed moss layer and an average soil moisture of >30% VWC.
- (3) Dry tussock plots ($n = 5$) were dominated by *E. vaginatum* (L.) tussocks that were highly colonized by *Vaccinium uliginosum* (L.), *Vaccinium vitis-idaea* (L.) and lichens, with an average soil moisture of <30% VWC.
- (4) Wet tussock plots ($n = 6$) were also dominated by the characteristic tussock formations of *Eriophorum vaginatum* (L.), with scattered *Andromeda polifolia* (L.) and *Ledum decumbens* (Ait.), and an average soil moisture of >70% VWC.
- (5) Mesic heath plots ($n = 3$) were composed of vegetation from the family Ericaceae (*L. decumbens* (Ait.), *Arctostaphylos alpina* (L.), *V. vitis-idaea* (L.), *V. uliginosum* (L.)), with a moderately thick moss layer and an average soil moisture of >30% VWC.
- (6) Dry heath plots ($n = 8$) were dominated by similar ericaceous species as mesic heath, but with a negligible moss layer and an average soil moisture of <10% VWC.
- (7) Wet sedge plots ($n = 9$) were composed entirely of *Carex* spp. (L.), and the soil was highly saturated at all sampling sessions (>95% VWC).

VEGETATION ANALYSIS

After the flux sampling was completed, all above-ground biomass, including the top green layer of moss, was harvested from the collars. Non-living matter was removed, vascular plant material (leaves and stems) was sorted by species and non-vascular plant material was divided in mosses or lichens. Biomass was dried in a plant press and later dried again at 100 °C for 48 hours before mass was determined to the nearest 0.001 g. To determine leaf area index (LAI (m²leaf^{−2} m²ground^{−2}), additional vegetation plots ($n = 10$) were harvested throughout the sampling period. All leaf

material was harvested from a 0.4 m × 0.4 m plot and sorted by species. Leaf material was laid flat and traced on 1 mm² graph paper, total area per unit ground area was summed, and material was dried later in a 100 °C oven for 48 hours before mass was determined to the nearest 0.001 g. Three (3) samples of dry leaf material of the dominant species for each group (listed in Table 1) were powdered and combusted with tungsten in a Macro Elemental Analyzer (Elementar Americas, Inc, St Laurel, New Jersey) to determine nitrogen content by mass (g N g leaf^{−1}). Average species-specific nitrogen content values were calculated with specific leaf area (m²leaf^{−2} g^{−1}leaf mass^{−1}) and LAI (m²leaf^{−2} m²ground^{−2}) to obtain total foliar nitrogen (TFN; [g N m²(ground)^{−2}]).

STATISTICAL METHODS

Statistical analyses for CO₂ flux were performed for T_{cham} and T_{air} , soil moisture, biomass, leaf N content, LAI, and plant community as independent variables. Differences in the normally distributed soil and vegetation characteristics data were determined with an ANOVA and Tukeys post-hoc test. CO₂ flux data were normalized with log transformations, and the results presented below have been back-transformed and to the original units. The unbalanced sampling design (different number of collars between groups) necessitated taking an average of the flux measurements. All flux data were analyzed for linear relationships with sampling date and no significant trends were found. Hence, data for each vegetation community were pooled and compared. Differences in flux between groups were determined with a generalized *F*-test (Weerahandi, 1995) due to heteroscedastic variance. Linear regressions were performed for all other analyses. GEP and NEE were estimated at 500 μmol m^{−2} s^{−1} PPFD using the fitted parameter estimates found in Equation 2 (above). All statistical analysis was performed using STATISTICA (Statsoft, 2007) software.

Results

ENVIRONMENTAL CONDITIONS

Daily temperature and daily solar radiation during June to August 2008 were close to the 10-year average (10.4 [±3.3 standard deviation] °C and 203.7 [±59.5] W m^{−2}, respectively). The same period was slightly drier than normal, with an average precipitation of 19.8 (±11.8) mm month^{−1}. During the sampling period (5 July to 12 August) the average daily temperature was 14.4 °C, with a maximum of 27.5 °C and a minimum of 2.5 °C. Total precipitation during the sampling period was 33.6 mm.

Across the sampling period soil moisture ranged from 4% VWC in dry heath to saturated (100% VWC) in the wet sedge, with wet tussock showing the greatest variability (Table 1). Mean soil moisture was significantly different between comparative groups (between dry and mesic birch, dry and wet tussock, mesic and dry heath) and soil moisture in wet sedge was significantly higher than all other groups except wet tussock (Table 1). Soil temperature in mesic birch and mesic heath was significantly lower than dry birch and dry heath (Table 1).

Total biomass was variable, ranging from 223 g dry mass m^{−2} in the wet sedge plots to more than two and a half times greater (580 g dry mass m^{−2}) in the dry tussock plots (Table 2). Vascular biomass and LAI showed a similar trend, with the lowest values in wet sedge and highest in dry and mesic birch (Table 2). Moss biomass ranged widely across vegetation groups, from negligible in dry birch to a thick layer that was equivalent to the vascular biomass in dry and wet tussock and wet sedge (Table 2).

TABLE 2

Vegetation characteristics of seven tundra vegetation groups at Daring Lake, NWT, from destructive harvest on 13–15 August 2008. Values presented in parentheses are standard error of the mean. *N*-values indicate the number of collars in each group. Common superscripts indicate no significant difference between groups (Tukeys HSD, $p < 0.05$).

	Total biomass (g mass m ⁻²)	Vascular biomass (g mass m ⁻²)	Lichen biomass (g mass m ⁻²)	Moss biomass (g mass m ⁻²)	Dominant plant species (in order of decreasing abundance)
Dry birch (<i>n</i> = 3)	414.7 ^{a,b,c} (53.2)	335.7 ^a (33.2)	94.4 ^a (21.0)	0 ^a	<i>B.glandulosa</i> (Michx.) <i>A. alpina</i> (L.) <i>L. decumbens</i> (Ait.) <i>V. vitis-idaea</i> (L.) <i>V. uliginosum</i> (L.)
Mesic birch (<i>n</i> = 6)	455.2 ^{a,b} (36.5)	304.6 ^a (42.4)	53.1 ^{a,b} (21.9)	105.3 ^b (47.4)	<i>B.glandulosa</i> (Michx.) <i>A. polifolia</i> (L.) <i>Carex</i> spp. <i>V. vitis-idaea</i> (L.) <i>V. uliginosum</i> (L.)
Dry tussock (<i>n</i> = 5)	578.8 ^a (85.9)	213.5 ^a (29.6)	98.8 ^{a,c} (23.7)	280.3 ^{a,b} (124.4)	<i>E. vaginatum</i> (L.) <i>A. polifolia</i> (L.) <i>L. decumbens</i> (Ait.) <i>V. uliginosum</i> (L.) <i>V. vitis-idaea</i> (L.)
Wet tussock (<i>n</i> = 6)	284.3 ^c (33.5)	80.3 ^b (8.3)	16.5 ^b (9.8)	192.0 ^b (32.7)	<i>E. vaginatum</i> (L.) <i>A. polifolia</i> (L.) <i>L. decumbens</i> (Ait.) <i>A. alpina</i> (L.) <i>E. nigrum</i> (L.)
Dry heath (<i>n</i> = 8)	277.9 ^a (24.0)	210.5 ^a (34.5)	57.6 ^{a,b} (13.5)	9.8 ^a (9.8)	<i>L. decumbens</i> (Ait.) <i>A. alpina</i> (L.) <i>E. nigrum</i> (L.) <i>L. decumbens</i> (Ait.) <i>V. uliginosum</i> (L.)
Mesic heath (<i>n</i> = 3)	413.1 ^{a,b,c} (100.4)	180.6 ^a (50.7)	169.4 ^c (29.4)	63.1 ^a (21.1)	<i>V. vitis-idaea</i> (L.) <i>L. decumbens</i> (Ait.) <i>V. vitis-idaea</i> (L.) <i>V. uliginosum</i> (L.) <i>A. alpina</i> (L.)
Wet sedge (<i>n</i> = 9)	223.4 ^a (39.1)	35.3 ^c (5.6)	1.7 ^b (1.7)	186.3 ^b (35.7)	<i>Carex</i> spp. <i>A. polifolia</i> (L.)

AMBIENT-LIGHT CO₂ EXCHANGE

Mean ambient-light GEP was greatest in mesic birch and lowest in the dry heath (Fig. 1). Similarly, the greatest NEE was also in mesic birch and lowest in dry heath and dry tussock (Fig. 1). Mean ER was greatest in wet tussock and lowest in wet sedge (Fig. 1). Comparisons of mean fluxes between hydrologically distinct groups with similar vegetation showed that ER was more variable within groups than GEP and NEE (Fig. 1). In the wet or mesic groups ER was significantly higher than in their dry counterparts (i.e., mesic birch ER was greater than dry birch, wet tussock ER was greater than dry tussock, and mesic heath ER was greater than dry heath) (Fig. 1). GEP and NEE in mesic birch were significantly higher than in dry birch. In wet tussock GEP was significantly higher than dry tussock, but NEE was not significantly different. Though GEP and NEE in mesic heath were larger than for dry heath, they were not significantly different (Fig. 1). Wet sedge plots were considered to be unique due to constantly saturated soil conditions and their distinct vegetative growth form, and thus were not compared with other groups.

LIGHT-ADJUSTED CO₂ EXCHANGE

GEP estimated at 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD (GEP₅₀₀), ranged from -2.5 in wet tussock to -0.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in dry heath. NEE estimated at 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD (NEE₅₀₀), ranged from -1.3 in mesic birch to -0.38 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in dry heath (Table 3). Neither NEE₅₀₀ or GEP₅₀₀ showed a significant relationship with

leaf area or with soil moisture. However, when fluxes were adjusted for leaf area across the range of soil moisture there was a significant negative linear relationship (Fig. 2), indicating that CO₂ uptake per unit leaf was greater with higher soil moisture.

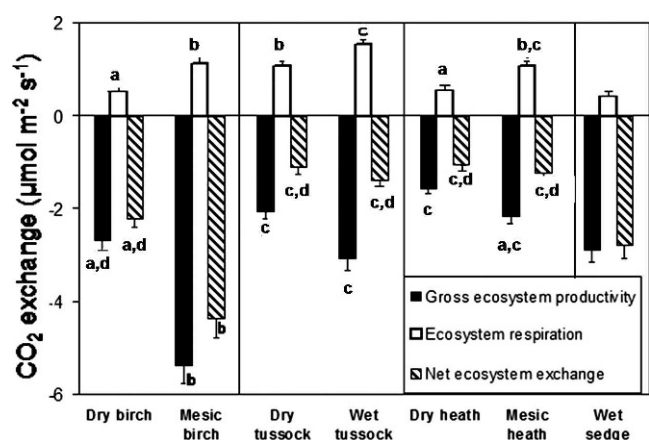


FIGURE 1. Mean ambient-light carbon dioxide (CO₂) exchange for tundra vegetation groups for 5 July to 12 August 2008. Filled bars indicate gross ecosystem productivity, unfilled bars indicate ecosystem respiration, and hatched bars indicate net ecosystem CO₂ exchange ($\mu\text{mol m}^{-2} \text{s}^{-1}$). Whiskers indicate standard deviations. Common superscripts indicate no significant difference between vegetation groups ($n = 230\text{--}249$; Games-Howell test, $p < 0.05$).

TABLE 3

Parameter estimates of the rectangular hyperbola light response curve between gross ecosystem productivity and light availability using non-linear, least-squares regressions with the Quasi-Newton method (custom loss set as $[(\text{OBS}-\text{PRED})^2 + (\text{P}_{\text{max}} > 0)*100 + (\alpha < 0)*100]$ and start values set at 0.1). NEE_{500} and GEP_{500} indicate gross ecosystem productivity and net ecosystem CO_2 exchange ($\mu\text{mol m}^{-2} \text{s}^{-1}$) at $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ light, and P_{max} indicates the maximum rate of photosynthesis.

	<i>N</i>	α	P_{max}	GEP_{500}	Variance of GEP explained (%)	NEE_{500}	Variance of NEE explained (%)
All data	703	0.0060 (0.0007)	-4.29 (0.45)	-1.76	31.0	-0.94	15.0
Dry birch	53	0.0031 (0.0003)	-8.83 (1.05)	-1.33	73.8	-0.87	72.5
Mesic birch	116	0.0050 (0.0007)	-25.29 (1.23)	-2.27	52.8	-1.30	44.8
Dry tussock	93	0.0089 (0.0029)	-2.90 (0.53)	-1.76	34.0	-0.70	26.8
Wet tussock	99	0.0137 (0.0030)	-3.95 (0.44)	-2.50	36.7	-0.89	24.5
Dry heath	125	0.0024 (0.0005)	-3.71 (1.18)	-0.90	55.8	-0.38	48.5
Mesic heath	60	0.0122 (0.0037)	-2.70 (0.39)	-1.87	37.3	-0.80	37.3
Wet sedge	157	0.0032 (0.0004)	-12.73 (0.94)	-1.44	50.5	-1.07	49.5

There was a significant negative linear relationship between TFN and soil moisture ($F_{1,6} = 15.37$, $R^2 = 0.755$, $p = 0.01$; Fig. 3a) and a significant positive relationship between leaf N concentration and soil moisture ($F_{1,6} = 6.55$, $R^2 = 0.466$, $p = 0.05$; Fig. 3b). Thus, despite the higher concentration of N in foliage at the upper end of the soil moisture gradient, the total N in foliage was low, because the quantity of foliage was small. When fluxes were adjusted for TFN and compared across the range of soil moisture, it was found that GEP_{500} showed a significant negative linear relationship ($F_{1,6} = 16.22$, $R^2 = 0.764$, $p = 0.01$; Fig. 3c), but no trend was found for NEE_{500} ($F_{1,6} = 1.06$, $p = 0.34$; Fig. 3d).

TEMPERATURE AND MOISTURE EFFECTS ON RESPIRATION

T_{air} and T_{cham} were significantly correlated for all samples ($n = 242$, $r = 0.778$, $p < 0.001$) and even more strongly correlated for ER measurements (samples taken in darkness) ($n = 224$, $r = 0.852$, $p < 0.001$); thus air temperature was not treated as a significant variable because of this co-linearity. ER dependence on temperature was found only in the dry and mesic groups. This suggests an interactive effect between temperature and moisture up to a threshold level. Once soils were saturated (85% VWC or higher), no significant temperature effects were found. There was a significant exponential relationship between T_{cham} and ER in dry soil types (dry heath: $F_{1,43} = 12.516$, $R^2 = 0.220$, $p = 0.02$; dry birch: $F_{1,17} = 14.318$, $R^2 = 0.252$, $p = 0.02$; dry tussock: $F_{1,31} = 8.622$, $R^2 = 0.129$, $p = 0.04$). The effects of T_{soil} were also found in mesic soil moisture conditions (mesic birch: $F_{1,34} = 6.564$, $R^2 = 0.153$, $p = 0.018$; mesic heath: $F_{1,21} = 7.31$, $R^2 = 0.122$, $p = 0.037$).

When ER was adjusted with residual analysis to remove the effects of temperature mentioned above, there was a non-linear trend across the range of soil moisture (Fig. 4). The impact of vegetation type on ER was evident, particularly in tussock groups. ER in wet tussock was higher and more variable than ER in wet sedge around 90% VWC, and ER in dry tussock was more variable than other groups in the same moisture range (Fig. 4).

Discussion

In this assessment of the spatial patterns of CO_2 exchange across a range of soil moisture and vegetation groups in typical subarctic tundra we found few straightforward relationships between CO_2 fluxes and environmental variables, either within or between the tundra vegetation groups. This simple finding reflects the importance of the interaction effects of factors that determine CO_2 fluxes. For example, across the soil moisture gradient there was a significant negative relationship between light-adjusted CO_2 exchange per unit LAI and unit N. Although soil moisture was found to be important in determining gross differences in CO_2 exchange between similar vegetation types, it was not a factor in determining variations in flux within individual vegetation communities. Temperature-adjusted ER followed a non-linear trend across the range of soil moisture, which suggests that soil moisture controls may be more important at the landscape level compared to the plot scale.

The magnitude of measured GEP and NEE was comparable to other recent investigations in similar vegetation communities (La Puma et al., 2007; Nobrega and Grogan, 2008). Respiration was slightly lower (in mesic birch, wet sedge, and dry heath in particular) than has been found in some other studies (Oberbauer

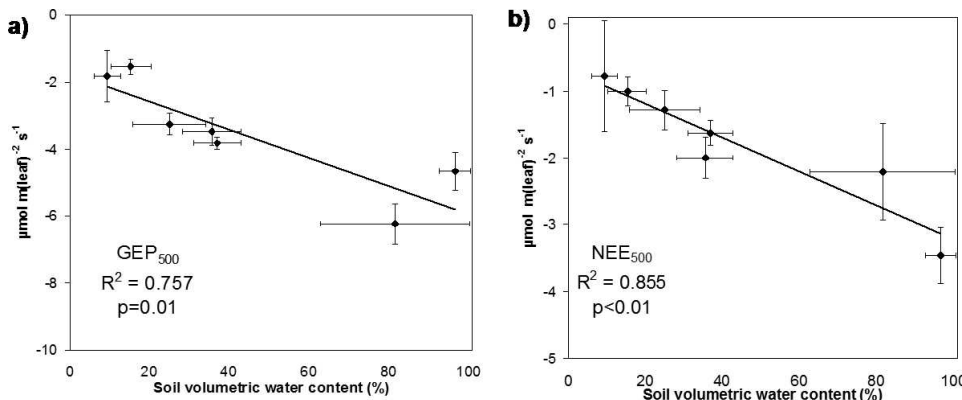


FIGURE 2. Linear regressions between mean soil volumetric water content (%) and (a) gross ecosystem productivity at $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ of light ($F_{1,6} = 15.59$, $R^2 = 0.757$, $p = 0.01$), and (b) net ecosystem CO_2 exchange at $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ of light ($F_{1,6} = 36.35$, $R^2 = 0.855$, $p < 0.01$) for all vegetation groups. CO_2 exchange values were adjusted for leaf area ($\mu\text{mol m[leaf]}^{-2} \text{s}^{-1}$). Whiskers indicate standard error of the mean.

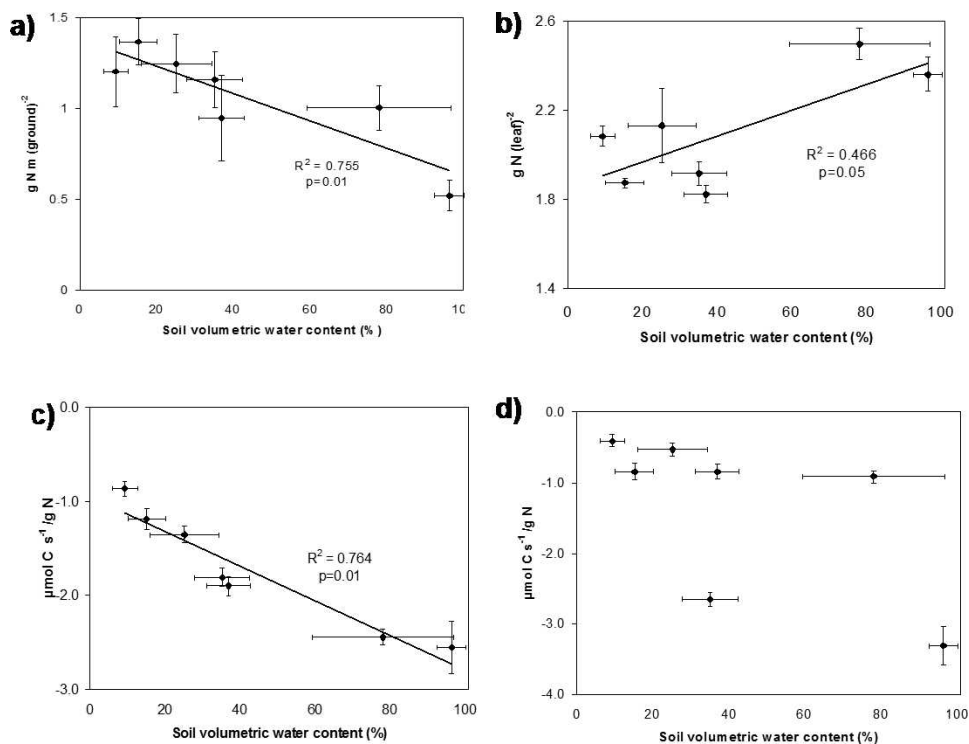


FIGURE 3. Linear regressions between mean soil volumetric water content (%) and (a) mean total foliar nitrogen (TFN) ($\text{g N m}^{-2} \text{ground}^{-2}$); (b) mean leaf N concentration ($\text{g N m}^{-2} \text{leaf}^{-2}$); (c) GEP_{500} adjusted for mean TFN ($\mu\text{mol C s}^{-1} \text{g N}^{-1}$); and (d) NEE_{500} adjusted for mean TFN ($\mu\text{mol C s}^{-1} \text{g N}^{-1}$), for all vegetation groups. Whiskers indicate standard error of the mean.

et al., 1996; Nobrega and Grogan, 2008), but it was well within the range of published values for arctic sites. Biomass values and leaf nitrogen concentrations presented here were comparable to findings from other tundra sites (Oberbauer et al., 1996; Williams and Rastetter, 1999; Campioli et al., 2009).

CO₂ EXCHANGE BETWEEN VEGETATION GROUPS

Comparisons among vegetation groups of similar biomass and species composition, but different soil moisture regimes, showed that while GEP and ER were generally larger in wet and mesic tundra types, mean NEE was significantly different between mesic and dry plots for only one vegetation type (birch; Fig. 1). Higher productivity in the wet or mesic groups as compared to the dry groups may be partly attributed to the presence of the thick moss layer, which was not present in the dry plots. Although this was not evident from visual inspection, the dry groups are found in conditions that are drier than optional for these specific

communities, which can frequently lead to water stress (Illeris et al., 2004). Further, dry groups tend to be found at higher topographic positions where snow cover is lower and vegetation is exposed to the wind, leading to foliar damage during winter, which can decrease summer productivity (Shaver and Chapin, 1991). The limited variability in NEE between groups is due to the covariance of GEP and ER. Increased ER has been associated with stimulated GEP under both greenhouse warming and fertilization treatments (Shaver et al., 1998; Boelman et al., 2003) and is often attributed to the large contribution of plant respiration to ER at peak season (Johnson et al., 2000). Others have suggested that increased biomass is correlated with a higher rate of litter production, leading to a higher heterotrophic respiration component of ER (Boelman et al., 2003).

The pattern in wet sedge CO₂ exchange was anomalous compared to the other groups. Wet sedge exhibited a high mean NEE due to a high GEP and relatively low ER, similar to findings of Shaver et al. (2007) and Nobrega and Grogan (2008). The high GEP per unit leaf area (Fig. 2a) may be explained by the high leaf N concentration (Fig. 3a). The low ER is expected in saturated soils because CO₂ production is limited by low oxygen concentration in the soil (Oechel and Billings, 1992).

CO₂ EXCHANGE ACROSS THE SOIL MOISTURE GRADIENT

The effects of both soil moisture and vegetation community can be seen in the trends of CO₂ exchange across all tundra vegetation communities. Across groups, NEE and GEP were both significantly related to soil moisture only after adjusting for leaf area, with NEE showing somewhat greater explained variance (Fig. 2). This finding is consistent with other studies that found moisture was important in explaining the variation in CO₂ exchange after accounting for differences in LAI (Street et al., 2007) or biomass (Shaver et al., 1996; Welker et al., 2004). Such a result likely underscores by the fact that the distribution of vegetation types is ultimately a response to long-term differences

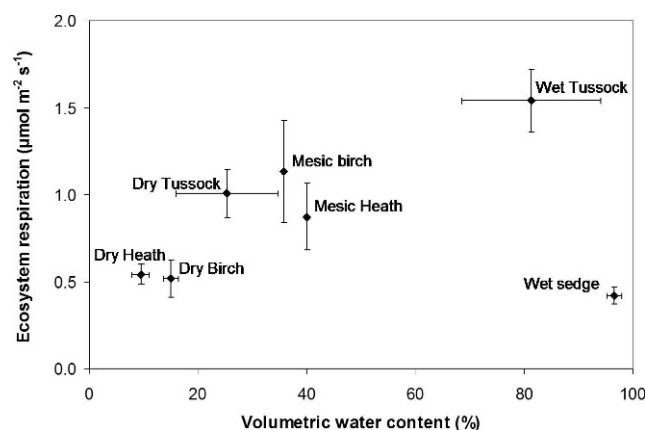


FIGURE 4. Temperature-adjusted ecosystem respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and soil moisture (%VWC) for all vegetation groups (Spearman's $r = 0.45$, $p = 0.038$).

in soil moisture driven by topographic differences, which control establishment and persistence of tundra communities. This gives rise to the observed close associations in soil moisture and community both at the local level (Walker et al., 1994) and across the arctic region (Walker, 2000). However, carbon flux responds to the vegetative expression in each of these communities (translated as either LAI or biomass) and these differences must be accounted for before flux-soil moisture relationships emerge.

Total foliar nitrogen reflects the interaction between plant community composition and nitrogen constraints on growth because it is the product of leaf area and mass and leaf N concentration. Because LAI had a weak significant (negative) relationship with soil moisture ($F_{1,6} = 5.213$, $p < 0.10$; data not shown), the negative TFN-soil moisture relationship (Fig. 3a) suggests that the nitrogen constraints on growth (represented by the distribution of LAI) affect TFN more strongly than the relative differences in N uptake capacity (represented by leaf N concentration). Effects of physiological differences in N-uptake between vegetation groups can be seen in Figure 3b, where high leaf N concentrations are seen at high moisture levels. The wet tussock and wet sedge community are dominated by *E. vaginatum* and *Carex* spp., which have a greater N uptake capacity than most arctic species (McKane et al., 2002), allowing them to exist in N-poor environments. While it has been suggested that TFN could be used to predict NEE through the strong correlation between LAI and TFN (van Wijk et al., 2005; Campioli et al., 2009), our results produced a significant linear relationship between GEP per unit N, but not with NEE per unit N, due to the confounding effects of ER.

The temperature-ER relationship in arctic ecosystems has been the subject of considerable debate in the literature. Temperature is the greatest control on ER at a very broad scale (Raich and Schlesinger, 1992). Within a given vegetation community, greenhouses and other warming manipulations have led to increased soil temperature and increased respiration (e.g. Grogan and Chapin, 2000; Dorrepaal et al., 2009). However, the temperature-ER relationship is not straightforward, as moisture conditions play a large role in determining the temperature sensitivity of ER (Illeris et al., 2004; Kwon et al., 2006). In some cases substrate quality has been found to be of greater importance than temperature in predicting ER (Flanagan and Van Cleve, 1983; Hobbie, 1996). We found significant soil temperature-ER relationships only in mesic moisture conditions. This was surprising because in general the mesic groups exhibited a low mean and range in T_{soil} (Table 1), whereas it would be expected that relationships would be revealed in ecosystems that exhibited a greater range in T_{soil} . Similar to findings here, Nobrega and Grogan (2008) found that the birch ecosystems with the lowest soil temperature had the highest ER and soil respiration, indicating that temperature is not the primary control in comparisons across the range of soil moisture conditions.

The findings of this study emphasize the importance of strong moisture control at the highest and lowest soil moisture conditions. Soil respiration in saturated ecosystems has been shown to be insensitive to increased temperature (Johnson et al., 1996, 2000), likely due to oxygen limitation. In dry arctic ecosystems, lack of moisture has been found to be a greater limiting factor than temperature on ER (Illeris and Jonasson, 1999; Welker et al., 2000) because water stress limits microbial growth and root respiration (Illeris et al., 2003). These findings are consistent with those from other dry ecosystems where the primary control on variation in ER was moisture input, and no relationships between ER and soil temperature were found (e.g., Chimner and Welker, 2005; Knapp et al., 2002).

While soil moisture and temperature together create a non-linear trend in ER across the landscape (Fig. 4), other factors contribute to the variability seen in this relationship. Vegetation community plays a role in determining ER, through control on the quality of litter inputs to the soil (Hobbie, 1996; Christensen et al., 1999) and because of vegetation structure. In particular, tussock tundra demonstrated the most variable ER, especially wet tussock at high soil moisture content. Johnson et al. (1996) found no significant difference between ER in tussock and intertussock spaces, although within the intertussock group, ER was reduced in saturated conditions versus ER at field capacity. In a comparison of hummock and hollows, Sullivan et al. (2008) found that ER was much lower in hollows due to limitations imposed by the water table. Variations in ER in wet tussock may be at least partly influenced by the highly variable soil moisture, which may be due to the vertical structure of the tussock (which can reach heights of 0.5 m). Soil moisture may temporarily increase after a precipitation event, but this moisture quickly drains due to gravitational flow. While dry tussock did not exhibit the same variability in soil moisture, the deep layer of organic matter and the high root density found under tussocks (Chapin et al., 1979) may allow the vegetation greater access to the soil carbon, leading to increased ER.

Conclusions

The results of this study highlight the importance of soil moisture as a factor in the spatial patterns of CO_2 dynamics in high-latitude terrestrial ecosystems. Soil moisture conditions create variability in CO_2 flux in similar vegetation communities. The impact of nitrogen availability, soil temperature, and vegetation community distribution on CO_2 exchange can all be considered within the framework of soil moisture distribution across the landscape. Predicting CO_2 exchange under future climatic conditions will be complicated by changes in soil moisture availability due to melting permafrost and increasing active layer depth. A better understanding of the distribution of soil moisture across the tundra landscape and how it interacts with temperature and nutrient status will allow better predictions of CO_2 flux in the changing arctic ecosystem.

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