Landscape and Ecosystem-Level Controls on Net Carbon Dioxide Exchange along a Natural Moisture Gradient in Canadian Low Arctic Tundra

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ABSTRACT

Our understanding of the controls and magnitudes of regional CO_2 exchanges in the Arctic are limited by uncertainties due to spatial heterogeneity in vegetation across the landscape and temporal variation in environmental conditions through the seasons. We measured daytime net ecosystem CO_2 exchange and each of its component fluxes in the three major tundra ecosystem-types that typically occur along natural moisture gradients in the Canadian Low Arctic biweekly during the full snow-free season of 2004. In addition, we used a plant-removal treatment to compare the contribution of bulk soil organic matter to total respiratory CO_2 loss among these ecosystems. Net CO_2 exchange rates varied strongly, *but not consistently*, among ecosystems in the spring and summer phases as a result of ecosystem-specific and differing responses of gross photosynthesis and respiration to temporal variation in environmental conditions. Overall, net carbon gain was largest in the wet sedge ecosystem and smallest in the dry heath. Our measures of CO_2 flux variation within each eco-

system were frequently most closely correlated with air or soil temperatures during each seasonal phase. Nevertheless, a particularly large rainfall event in early August rapidly decreased respiration rates and stimulated gross photosynthetic rates, resulting in peak rates of net carbon gain in all ecosystems. Finally, the bulk soil carbon contribution to total respiration was relatively high in the birch hummock ecosystem. Together, these results demonstrate that the relative influences of moisture and temperature as primary controls on daytime net ecosystem CO_2 exchange and its component fluxes differ in fundamental ways between the landscape and ecosystem scales. Furthermore, they strongly suggest that carbon cycling responses to environmental change are likely to be highly ecosystem-specific, and thus to vary substantially across the low arctic landscape.

Key words: carbon; soil; plant; temperature; moisture; heath; birch; sedge; hummock; vegetation; Canada; climate change.

INTRODUCTION

The Arctic plays a crucial role in Earth's climate system because its prolonged snowcover exerts strong albedo effects, and because its soils have the potential to release significant amounts of

carbon-based greenhouse gases (Shaver and others 1992; Lashof and others 1997; Chapin and others 2000; Shaver and others 2000; ACIA 2005). Thus, there is keen interest in characterizing carbon cycling in the arctic region (Chapin and others 2000; ACIA 2005), and in understanding potential changes in snowcover and vegetation that affect albedo (Chapin and others 2005).

At the *regional* scale, the distribution of ecosystem types and their associated patterns of biogeochemical cycling are governed by at least five independent controls or 'state factors' (climate, parent material, topography, potential biota, and time) (Jenny 1994; Chapin and others 2002). Tundra ecosystems across a region can vary substantially in their mid-summer rates of daytime net CO_2 exchange (NEE) due primarily to differences in leaf area index (McFadden and others 2003; Shaver and others 2007). At the *landscape* scale (that is, within a common climatic zone), topography as it affects soil hydrological regime is the primary control on the distribution of ecosystem types in the Arctic (Bliss and Matveyeva 1992; Walker 2000). Tundra ecosystems also vary in their summertime rates of net CO_2 exchange at this scale (Jones and others 1998; Oechel and others 2000; Welker and others 2004; Williams and others 2006; Oberbauer and others 2007), but as yet we do not have an adequate understanding of why these differences occur, whether these differences are maintained consistently across the snow-free season, and which of the component carbon fluxes contributing to NEE is most variable among ecosystems (Oberbauer and others 1996). For example, the influence of hydrology on ecosystem carbon gain is unclear. It is a curious paradox that although deeper soil organic accumulation is generally found in the more moisture-saturated ecosystems across the Arctic (Heal and others 1981; Ping and others 1997), several major comparative studies of summer NEE among tundra ecosystems have found no correlation between wetter hydrological regimes and larger net carbon gain (Mc Fadden and others 2003; Welker and others 2004; Oberbauer and others 2007). As a result of our limited understanding of these issues, local topographic variation has not been included in current regional models of land–atmosphere carbon exchange, and the two recent syntheses of our understanding of arctic responses to climate change (Chapin and others 2000; ACIA 2005) have highlighted this shortfall as a critical research gap.

Net ecosystem CO_2 exchange (NEE) is the result of two opposing CO_2 fluxes: gross carbon gain via photosynthesis (GEP) and respiratory carbon losses from plants and soils [ecosystem respiration (ER)]. Regional variation in arctic ecosystem NEE during mid-summer has been attributed to differences in daytime net CO_2 uptake due to photosynthesis rather than differences in ER (McFadden and others 2003). Furthermore, a very recent study across a large arctic latitudinal transect suggests that summer GEP and ER (and NEE) vary more *among* adjacent hydrologically distinct ecosystems, than *between* similar ecosystems at different latitudes (Oberbauer and others 2007). Thus, landscape-scale variation in NEE appears to exert strong control on regional level carbon cycling in tundra.

To quantify regional carbon exchange, and predict its responses to environmental change, we need to better understand the patterns and controls on GEP and ER among adjacent dry, mesic, and wet tundra ecosystems. Furthermore, we need to include the shoulder spring and fall parts of the growing season when GEP and ER might be more differentially affected by environmental factors such as light availability, temperature, and soil flooding at thaw. Could either GEP or ER be the principal driver of patterns of NEE within these ecosystems when considered over the full snow-free season, or do the component fluxes vary independently of each other? Can the differences in seasonal NEE rates among these ecosystems be attributed primarily to variation in GEP or to ER? Although tundra plant species can vary substantially in rates of gross photosynthesis at the leaf level (Semikhatova and others 1992; Oberbauer and others 1996), and GEP has been measured in several tundra studies (Hobbie and Chapin 1998; Illeris and others 2004), data comparing GEP among arctic vegetation types are not common (Welker and others 2004; Grogan and Jonasson 2006; Sjogersten and others 2006; Oberbauer and others 2007). By contrast, it is well established that ecosystem and soil respiration (SR) can vary significantly among tundra ecosystems of differing hydrological regimes (Giblin and others 1991; Oberbauer and others 1996; Grogan and Jonasson 2005). Furthermore, lab incubation studies demonstrate fundamental differences in soil biogeochemical cycling among tundra ecosystems (Nadelhoffer and others 1991; Neff and Hooper 2002; Weintraub and Schimel 2003). It is unclear, however, if these differences in incubated SR rates, measured under constant temperature and moisture conditions and in the absence of growing plants, are manifested in the field throughout the growing season to the extent that they can explain the overall differences in net CO_2 exchange (or ER) observed among ecosystems. Of the field studies

cited above that include ecosystem CO_2 component fluxes, all were of low temporal frequency (ranging from 1 to 10 sampling dates during the growing season). Here, we characterize both GEP and ER rates every 3–4 days in three hydrologically distinct ecosystem-types through the snow-free season. In addition, we made simultaneous measures of several environmental and biogeochemical variables in each plot to identify and compare the controls on CO_2 fluxes *among* those ecosystems with the principal controls on CO_2 fluxes *within* those ecosystems. To the best of our knowledge, this is the first study to directly contrast frequent and simultaneous measures of NEE and its component fluxes (GEP and ER) among and within adjacent, but hydrologically very distinct, tundra ecosystem-types through spring, summer, and fall.

Air temperatures in the Arctic have risen at almost twice the rate of the rest of the world in the past few decades (ACIA 2005). Arctic terrestrial ecosystems encompass 7% of the global terrestrial surface, yet they contain 14% of the global soil carbon reserve to 1 m soil depth (Post and others 1982). This large belowground carbon stock could provide a significant positive feedback to atmospheric CO_2 levels and global warming if changes in climate enhance bulk soil organic matter decomposition (Shaver and others 1992, 2000). The magnitude of this release will be determined by changes in soil temperature and moisture that we have not yet characterized, especially at the landscape and decadal or longer timescales (Churkina and Running 1998; Hobbie and others 2000; Hinzman and others 2005). Landscape (and therefore regional) patterns of bulk soil carbon release, and the potential effects of climate change, cannot be determined without answers to the following questions: Does hydrological regime determine the proportions of bulk SR to total ER among ecosystems? Is either bulk soil or total ER inversely related to the landscape pattern of long-term (that is, post-glacial) soil carbon accumulation? Does hydrology drive ecosystem differences in bulk soil carbon turnover rates? To address these questions, we used a plant removal treatment (Boone and others 1998; Grogan and Jonasson 2005) to characterize carbon release from the bulk soil component of each ecosystem as well as differences in turnover rates.

This study focuses on the dry heath lichen, mesic birch hummock, and wet sedge meadow ecosystem types that represent approximately 6, 40, and 16% of the total Arctic land mass, respectively (Bliss and Matveyeva 1992). These ecosystem types are the principal ones occurring along topographically determined moisture gradients within a common tundra landscape that extends thousands of kilometers from the MacKenzie River delta across Canada to the Hudson Bay (Porsild and Cody 1980). We tested the following hypotheses over the 2004 snow-free season:

1. Daytime net CO_2 exchange rate differences among adjacent wet, mesic, and dry ecosystems are consistent throughout the snow-free season.
2. Ecosystem differences in gross photosynthetic carbon gain rates, and ER rates, are consistent through the snow-free season.
3. Wetter ecosystems along a natural moisture gradient have larger rates of net carbon gain when considered over the full snow-free season. This pattern corresponds with either larger rates of gross photosynthetic carbon gain or smaller rates of ER.
4. The relative contribution of bulk SR to total ER rates through the snow-free season is similar among these adjacent ecosystems.

METHODS

Study Area

This study was conducted during the 2004 growing season at the Tundra Ecological Research Station (TERS), Daring Lake, Northwest Territories, Canada (64°E 50′N, 111°E 38′W), which is located approximately 300 km northeast of Yellowknife within the Coppermine River drainage basin, close to the geographic center of the western continental Arctic. The region is underlain by continuous permafrost and is characterized by numerous Canadian shield outcrops and occasional eskers that were formed toward the end of the most recent glaciation (that is, ~12,000 years ago) (Rampton 2000). Climate records from the Daring Lake weather station indicate a mean annual air temperature of −9.0°C, and mean snow-free season (~125 days) air temperature of 8.6°C and rainfall of 146 mm (1997–2004; B. Reid, unpublished data). Detailed vegetation mapping of the area as part of the Ecological Monitoring and Assessment Network (S. Matthews, personal communication) indicates a hydrologically driven mosaic of tundra vegetation types including dry heath, dwarf birch, and inundated wet sedge. This local area is an important habitat for various wildlife species including the Bathurst Caribou herd (*Rangifer tarandus*) which migrates through in large numbers (~1000s) in the spring and fall of many years (including 2004).

Our study was conducted at three tundra eco-systems that varied in soil moisture and plant species composition. The dry heath lichen tundra site was located on a wind exposed upland area with a slope less than 3° next to the side of an esker (472710°E, 7194082°N). The vegetation consisted of mat-forming evergreen shrubs [*Ledum decumbens* (Ait.), *Vaccinium vitis-idaea* (L.), *Empetrum nigrum* (L.), *Loiseleuria procumbens* (L.), and *Arctostaphylos alpina* (L.)], deciduous dwarf shrubs [*Betula glandulosa* (Michx.) and *Vaccinium uliginosum* (L.)], graminoids (*Carex* spp.), significant lichen cover [*Cetraria nivalis* (L.), *Briocaulon divergens* (Ach.), *Cladina mitis* (Sandst.), *Cladina rangiferina* (L.)], and a moss layer that is not well-developed. The surface organic horizon is thin (ranging from 2 to 5 cm) and lies above a coarse sandy loam mineral layer.

The mesic dwarf birch [*B. glandulosa* (Michx.)] hummock site was located on lowland tundra with a slope less than 3° (472797°E, 7194015°N) approximately 60 m south-east and downslope of the dry heath site. The vegetation was dominated by hummocks and hollows containing *Eriophorum vaginatum* (L.) alongside *L. decumbens* (Ait.), *V. vitis-idaea* (L.), *V. uliginosum* (L.), *Andromeda polifolia* (L.), *Carex* spp. A well-developed moss layer composed largely of *Sphagnum* spp. and *Aulacomnium turgidum* (Wahlenb.) with lichen cover [*Alectoria ochroleuca* (Hoffm.), *C. nivalis* (L.), *B. divergens* (Ach.), *C. rangiferina* (L.), and *Masonhalea richardsonii* (Hook.)] occurred on both the hummocks and hollows. In contrast to the acidic tussock tundra of N. Alaska, the hummocks are smaller and not necessarily dominated by graminoids, and willows (*Salix* spp.) are scarce. The organic surface horizon (ranging from 4 to 8 cm in thickness) was generally moist throughout the snow-free season and lies above mineral soils of relatively fine texture (silts and loams).

The wet sedge meadow was located approximately 50 m north-east and downslope of the birch hummock site and 100 m east of the dry heath site in a low depression (472842°E, 7194051°N) surrounded by large moss-dominated hummocks. This vegetation occurs in low-lying flat areas and is generally inundated with surface water for a substantial part of the growing season. Sedges (*Carex* spp. and *Eriophorum* spp.) predominate above a thick moss layer composed largely of *Sphagnum* spp., and occasional *A. polifolia* (L.), *L. decumbens* (Ait.) and algae. Excavations in a nearby wet sedge patch of similar peak active layer depth (~50 cm) but larger size than our site indicated a full organic horizon of approximately 45 cm depth (E. Humphreys, personal communication). Point frame quadrats (0.25 m^2) were used at randomly selected areas in each of the three major ecosystem-types to provide estimates of vegetation cover and leaf area index ($n = 6$) (Warren Wilson 1958).

Experimental Treatment

On June 7 and June 8, 2004, we chose 12 plots (1–15 m apart) within the dry heath and mesic birch hummock ecosystems. At the heath site, plot selection was random. At the birch site, we selected plots within hollows that contained at least one mature dwarf birch plant. Six of the experimental plots in each ecosystem were randomly assigned to a 'plant removal' treatment, aimed at substantially reducing the respiratory contribution from plants and from carbon directly associated with plants (that is, rhizosphere exudates and fresh litter). All aboveground vegetation including the green moss layer and as much of the coarse (and attached fine roots) as possible were carefully pulled out by hand from the surface of 50 × 50 cm plots, while minimizing disturbance to the underlying soil. Any senesced leaf litter was replaced on the soil surface. The much higher water content (and therefore specific heat capacity) of the wet sedge meadow soils meant that they remained frozen solid for longer in the spring, even though the soil temperature was relatively warm and only just below zero. Therefore, the plant removal treatment could not be achieved on 6 of the 12 randomly located plots in that ecosystem until later in the spring (June 23, 2004), when the soil finally thawed. Very occasional re-growth of shoots that occurred through the growing season in the treatment plots of all ecosystem types was manually removed more than 1 day prior to flux measurement. The plant removal treatment resulted in an approximate 30% decrease in total root biomass per unit volume ($n = 6$) in August 2004, and no change in soil microbial biomass (see below). Thus, as in previous similar studies (Grogan and Jonasson 2003, 2005; Nobrega and Grogan 2007), this treatment removed all sources of shoot respiration, but the significant root biomass remaining implies that the plant-associated component of respiration had been substantially diminished, rather than eliminated. Enhanced labile C inputs arising from increased root mortality and exudation following treatment may also have influenced plot CO_2 efflux. To determine the timing of such 'disturbance' effects, CO_2 exchange measurements were conducted every 30 min on two test plots in the birch hummock tundra for 5 h immediately after plant removal and over the subsequent four days. Respiration rates were initially high, but rapidly

decreased over the following 5 h. Rates on subsequent days were indistinguishable from birch hummock study plots treated weeks earlier, suggesting a significant initial disturbance flush effect that dissipated within one day and therefore well before the flux measures reported below.

Permanent collars (PVC SDR-35 sewer pipe, IPEX, Mississauga, Ontario; inner diameter 29.9 cm, height 12 cm) were inserted into the soil at each sampling plot several days prior to the initial flux measurements according to the following procedure. All enclosed rooted vegetation was guided up through each collar before cutting a slot with a serrated knife in the soil around the outer edge of the collar, and pressing it down 6–10 cm into the soil organic layer.

Ecosystem CO_2 Exchange Measurements

Regular measurement of CO_2 fluxes began on June 16, 2004, at the heath and birch hummock sites and on June 24 at the sedge meadow, and were continued approximately twice weekly on 21 sampling dates until August 18 and once on September 11. On each sampling day, flux measures were begun early in the morning and took 2–3 h per ecosystem, meaning that they were not completed until well into the evening. The order in which ecosystem-types were measured was randomized for each flux sampling date so that the seasonal set of fluxes from each plot consists of measurements made at a wide variety of times during the day. Furthermore, this randomization was necessary to preclude diurnal variation in solar radiation input (that affects PPFD and air and soil temperatures) from confounding our statistical analyses of flux differences among ecosystems for successive sampling days over each phase of the snow-free season.

CO_2 fluxes were measured using an infrared gas analyzer (LI-COR 6400, Lincoln, Nebraska, USA) attached in 'closed system' mode to a custom-built transparent acrylic (Plexiglass) cylinder-shaped chamber (30 cm height; 697.5 cm^2 area; 21 l). The chamber was fitted with two small circulation fans and a pressure equilibration vent (1-mm diameter). To achieve an adequate seal, the top of each collar contained a circular water-filled channel into which the cylindrical gas sampling chamber fitted securely. Net ecosystem CO_2 exchange (NEE) rates were measured with the transparent chamber on control plots every 5 s over 2 min after an initial equilibration period of more than 15 s. Afterwards, the chamber was lifted for approximately 20 s to restore ambient conditions, replaced on the same plot and covered with an opaque plastic sheet, and

ER was measured after a dark equilibration period of approximately 15 s. GEP was calculated as the difference between NEE and ER.

We tested the precision of our flux measurement protocol by repeating ten plot flux measurements (ER and SR) at the end of the sampling visit at each ecosystem (that is, 30 min to 5 h after the initial measurements). Initial and repeat measures were very closely correlated (R^2 = 0.96; Slope = 0.92; n = 10), indicating close precision in the measurement protocol. To quantify the sensitivity of the equipment to low fluxes, we placed the chamber on a plastic sheet and made successive blank measurements (mean ± 95% confidence intervals: 0.017 ± 0.010 μmol CO_2 m^2 s^{-1}; SD = 0.013; n = 7).

Environmental Measurements

Soil temperatures at 2, 5, and 10 cm depths into the soil organic layer (that is, below the moss green-brown transition layer in all vegetation types) were recorded simultaneously with each CO_2 flux at three random locations outside the perimeter of each chamber collar using handheld temperature probes (TD32, Omega, Stanford, Connecticut, USA). Mean soil thaw depth was determined by inserting a steel rod three times around each plot. Soil volumetric water contents (n = 3) for each plot were determined using a 'Hydrosense' (Campbell Scientific Inc., Logan, Utah, USA) with 12 cm probes. Mean photosynthetic photon flux density (PPFD) was measured by an external quantum sensor (LI-COR, Lincoln, Nebraska, USA) attached to the top of the gas sampling chamber.

Soil temperatures were also measured continuously every half hour at 2, 5, and 10 cm (n = 2) throughout the growing season in each ecosystem (except the sedge where the 2 and 10 cm records began on July 18) using copper-constantan thermocouples (T type, OMEGA, Stamford, Connecticut, USA) and three dataloggers (CR10X, Campbell Scientific, Logan, Utah, USA). Soil volumetric water contents were also recorded continuously at the three sites with 30 cm probes (CS616 Campbell Scientific) inserted at an angle to provide an integrated measure of moisture in the surface 10 cm of the soil. Probe measurements (n = 2–3) within each site were very similar (0.01 SD), indicating close precision in soil moisture measurements.

Biological and Chemical Analyses

Dry bulk density of the soil was determined from volume (measured directly in the field) and oven dry mass of the soil in the sample (that is, not including the root mass). Live roots were distinguished on the

basis of color and elasticity, and separated into coarse (>1-mm diameter) and fine categories for drying (70°C). Soil pH was determined by shaking 10 g fresh mass in 50 ml water for 1 min and allowing the solution to stand for 10 min prior to measurement (AB15 pH meter; Fisher Scientific). Soil sub-samples were dried and ground with a ball mill for total C, N, and S analysis by combustion (CNS-2000, LECO, St. Joseph, Michigan, USA).

Soil microbial biomass C and N were determined by the chloroform-fumigation direct-extraction technique (Brookes and others 1985) on samples that were collected in mid-August, transported in a cooler to Kingston, and processed within 5 days. A 10 g (15 g for the wet sedge) sample of sorted soil (that is, roots removed) was either immediately extracted in 50 ml 0.5 M K_2SO_4 or fumigated over 24 h with ethanol-free chloroform ($\sim$25 ml) in a darkened desiccation jar under vacuum. All extracts were shaken for 1 h and then allowed to stand for 1 h before vacuum filtration through a G4 glass fiber filter (Fisher Scientific) and freezing until analyses. Blanks were included to detect contamination.

Total dissolved organic C (TOC) and total dissolved N (TN) in the fumigated and non-fumigated extracts were determined on a TOC-TN analyzer (Shimadzu, Kyoto, Japan). Microbial biomass C and N were calculated as the differences between fumigated and non-fumigated extracts, having divided by 0.35 (k_C) and 0.4 (k_N), respectively (Jonasson and others 1996), to account for C and N not released by chloroform.

Data Processing and Statistical Analyses

The use of a regression approach to 'back calculate' the flux at the initial ambient headspace CO_2 concentration is strongly recommended if the rate of increase in CO_2 concentration is being inhibited by the rising headspace concentration (Livingston and others 2006). An extensive examination of our data indicated that there was no evidence for inhibition of ER over each measurement period. As a result, the fluxes reported here for NEE and its components in each plot are means of the flux values for each 5-s interval over the 2-min measurement period.

We used repeated-measure analysis of variance (JMP 5.1, SAS Institute 2005; Cary, North Carolina, USA) to investigate the influence of ecosystem-type ('between subjects') and time (nominal sampling date—'within subjects') on all CO_2 flux components (NEE, GEP, ER, and SR) during the spring, summer, and fall phases of the snow-free season. Post-hoc multiple comparisons were analyzed using the Tukey Kramer HSD test to determine significant differences among the tundra ecosystems in each phase. CO_2 flux data were transformed using either $\log_{10}$ or Box-Cox Power to reduce skewness and improve variance homogeneity. Total CO_2 fluxes for the snow-free season were estimated by linearly interpolating the flux rate from each plot ($n = 6$) between sample dates, yielding six independent estimates from which a mean and standard error were calculated.

Multiple linear regression models were created for each ecosystem-type to examine the relationships between the individual CO_2 fluxes for each plot and associated environmental variables (but not their interactions). In general, fluxes were more closely correlated to air and soil temperatures using linear rather than exponential relationships, and to light (PPFD) using linear rather than asymptotic relationships. We used the least-square step-wise selection technique based on the adjusted R^2 and Mallow's C_p values, and significance levels of 0.10 and 0.15 for entering and removing terms, respectively. We tested for collinearity (that is, correlation between model predictor variables) by evaluating the variance inflation factors (inverse of tolerance) and found no significant associations.

By including all plot measures across all sampling days within the multiple regression for each ecosystem, we are assuming that the relationships between fluxes and environmental variables for each plot were independent of those from neighboring plots, and from that same plot later in time. Autocorrelation through time might be expected for soil moisture and thaw depth because these variables are obviously influenced by the microscale topography and soil texture of each plot. In fact, however, air and surface soil temperatures (2 cm depth) contributed by far the most explanatory power, strongly suggesting that autocorrelation did not affect the conclusions from this analysis.

The soil properties and microbial biomass data for each ecosystem were assessed separately using one-way analysis of variance (ANOVA) and post-hoc Tukey Kramer HSD tests. Transformations ($\log_{10}$) were performed on values when necessary to meet normality and homogeneity of variance assumptions (Shapiro–Wilk test).

RESULTS

Environmental Conditions among Ecosystems

Diel mean air and soil temperatures suggested three distinct phases within the 2004 snow-free season
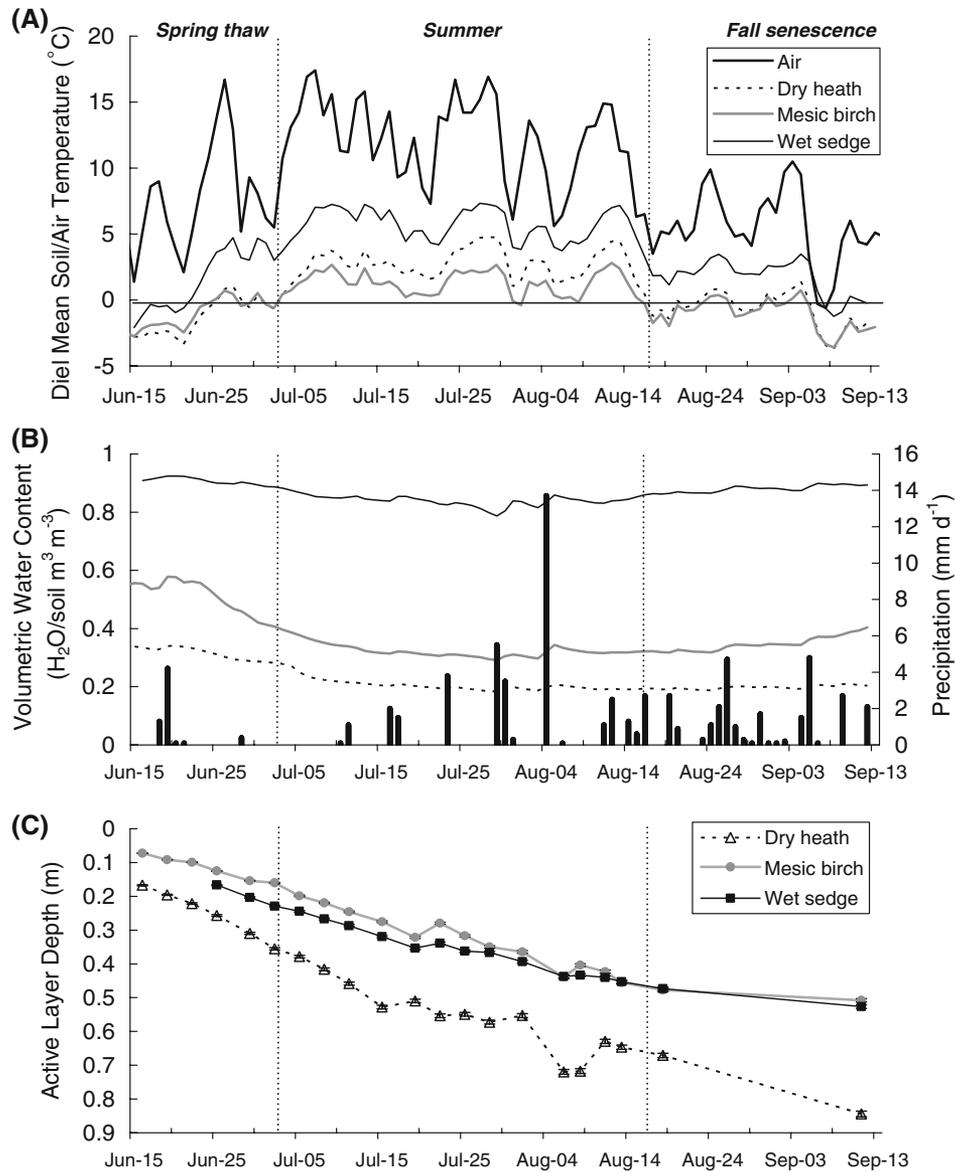
Figure 1. (**A**) Diel mean air and soil temperature (5 cm depth); (**B**) diel precipitation (columns) and diel mean soil moisture; and (**C**) mean active layer depth ($n = 36$ for each data point) at the dry heath lichen, mesic birch hummock, and wet sedge meadow ecosystems through the 2004 snow-free season at Daring Lake, NWT.

(Figure 1A). The spring thaw phase (June 11–July 2) was characterized by thawing soils as a result of rising air temperatures (Figure 1A) and peak solar radiation. Warm air temperatures and high solar radiation maintained soil temperatures above 0°C in all vegetation types between July 3 and August 16 (summer). The fall phase (August 17 to end of study, September 13) was characterized by decreasing mean diel soil temperatures (often below 0°C) due to lowering air temperatures and light availability.

Diel mean soil temperatures (at 5 cm depth) generally reflected the major fluctuations in air temperature pattern but often with a short time lag (~2 days) for most of the snow-free season (Figure 1A), and differed significantly among the adjacent ecosystem types. Soils in the wet sedge meadow at 5 cm depth were consistently at least 3°C warmer than either the birch hummock or heath ecosystems throughout the snow-free season (Figure 1A). Our handheld temperature probe data for the 5 and 10 cm depths that was collected simultaneously with each flux measurement also exhibited the same consistent pattern (data not shown). Finally, although there were no significant differences in soil temperatures between the heath

and birch sites during spring and fall, the former was consistently approximately 2°C warmer during the summer phase (Figure 1A).

Throughout the snow-free season soils in the wet sedge meadow were wettest (inundated with standing water for most of the season) and the heath ecosystem was driest (Figure 1B). Peak diel soil moisture values were recorded in the spring thaw period in all ecosystem types due to snow melt. Substantial individual precipitation events increased soil moisture in early August and during the fall senescence phase in all ecosystem types (Figure 1B). Depth to frozen soil (that is, active layer depth) increased through the growing season and was deepest at the dry heath lichen tundra (Figure 1C), suggesting that its elevated topographic position and coarse mineral soils resulted in better drainage and larger summer-time ground heat fluxes down the soil profile. The sharp increase in heath active layer depth immediately following a major rainfall event on August 6, 2004 (Figure 1B, C), is consistent with this hypothesis because it suggests that a substantial input of rainwater can quickly percolate to the frozen base layer, causing rapid thawing followed by re-freezing. Together, these results indicate significant differences in soil temperature and moisture regimes among the ecosystems, the sedge meadow site being warm and very wet, the birch hummock cool and mesic, and the heath moderately warm (at least in summer) and relatively dry.

Table 1. Plant Species Composition, Vascular Leaf Area Index, Relative Cover, Total Biomass and Root Biomass in the Three Major Tundra Ecosystems of the Daring Lake Region

	Dry heath lichen	Mesic birch hummock	Wet sedge meadow
Dominant plant species (in order of decreasing relative cover)	*Ledum decumbens* (Ait.), *Vaccinium vitis-idaea* (L.), *Empetrum nigrum* (L.), *Loiseleuria procumbens* (L.), *Betula glandulosa* (Michx.), *Carex* spp. (L.), *Vaccinium uliginosum* (L.), *Arctostaphylos alpina* (L.)	*Betula glandulosa* (Michx.), *Ledum decumbens* (Ait.), *Vaccinium vitis-idaea* (L.), *Vaccinium uliginosum* (L.), *Andromeda polifolia* (L.), *Carex* spp. (L.), *Eriophorum vaginatum* (L.) tussocks, *Sphagnum* spp. (L.)	*Carex* spp. (L.), *Eriophorum* spp. (L.) *Andromeda polifolia* (L.), *Sphagnum* spp. (L.)
Leaf area index			
Live leaf area per unit ground (m^2 m^{-2})	0.8 (0.09)[a]	0.9 (0.05)[a]	0.5 (0.04)[b]
Vascular plant cover (%)	81.0 (10.0)[a]	86.7 (7.9)[a]	59.5 (15.0)[a]
Moss cover (%)	12.5 (8.4)[a]	18.5 (8.3)[a]	99.3 (0.3)[b]
Lichen cover (%)	67.3 (9.6)[a]	41.2 (13.5)[a]	0
Plant biomass[1] (g dry mass m^{-2})			
Vascular	450.7 (47.7)[a]	620.3 (26.5)[b]	63.4 (13.6)[c]
Non-vascular (mosses, lichens)	997.1 (71.7)[a]	1237.5 (73.3)[b]	257.8 (51.3)[c]
Total	1447.8 (60.2)[a]	1857.8 (87.5)[b]	321.2 (64.0)[c]
Root biomass[2] (g dry mass m^{-2})			
Fine roots (≤ 1 mm diameter)	86.0 (14.5)[a]	162.0 (24.6)[a]	111.7 (39.4)[a]
Coarse roots (>1 mm diameter)	27.5 (10.5)[a]	86.1 (36.2)[a]	Not detected
Total roots (coarse and fine)	113.4 (13.2)[a]	248.1 (39.6)[b]	111.7 (39.4)[a]

Parentheses indicate standard error (n = 6–10). Values for each variable that do not share superscript letters in common indicate significant differences among ecosystems (Tukey's HSD, P < 0.05).

[1]*Biomass was estimated from the harvested material during the establishment of the plant removal plots and therefore includes all aboveground material and most of the belowground stems and rhizomes in the uppermost soil surface layer (~1–2 cm).*

[2]*Root biomass was measured by sorting soil cores as described in the section ''Methods''. Sampling depths for the heath, birch, and sedge ecosystems were 3.5, 6.3, and 7.5 cm, respectively.*

Vegetation Properties among Ecosystems

Plant species differed strongly in dominance among the three ecosystems (Table 1). Vascular plant leaf area index values were significantly lower at the wet sedge meadow reflecting the predominance of sedge growth forms (*Carex* and *Eriophorum* spp.) in this ecosystem. As expected, lichen cover was largest at the heath ecosystem whereas moss cover was particularly extensive in the sedge meadow as a result of the thick layer of *Sphagnum* spp. Plant biomass differed significantly among the three ecosystems, the biomasses of both vascular and non-vascular species recorded being smallest in the wet sedge meadow and largest in the birch hummock ecosystem (Table 1). Note that our estimates of plant biomass were based on tissues collected during the plant removal treatment and therefore include much but not all of the belowground component. Our separate soil core estimates indicated no significant differences in fine root biomass

among ecosystems, but twice as much total root biomass in the birch hummock ecosystem compared to the others (Table 1).

Soil and Microbial Properties among Ecosystems

The pH and total carbon (C), nitrogen (N), and sulfur (S) concentrations of the soil organic horizon and C:N ratios at each ecosystem were not significantly different among ecosystem types (Table 2). The soil bulk density of the organic horizon, however, differed significantly among ecosystems, the dry heath being approximately two times larger than the mesic birch hummock and approximately three times larger than the wet sedge (Table 2). Thus, although carbon concentrations did not vary significantly, the strong gradient in soil bulk density resulted in a similarly strong gradient in carbon content per unit soil volume (Table 2). Overall, the heath and birch systems had similar total soil car-

Table 2. Soil Characteristics of the Three Tundra Ecosystems

	Dry heath lichen	Mesic birch hummock	Wet sedge meadow
Bulk density of organic horizon (g dry mass soil cm^{-3})	0.29 (0.02)[a]	0.17 (0.02)[b]	0.089 (0.01)[c]
pH	4.8 (0.1)[a]	4.9 (0.1)[a]	5.2 (0.1)[a]
Elemental concentration of organic horizon (% dry mass)			
C	37.4 (2.7)[a]	40.6 (0.6)[a]	39.9 (1.0)[a]
N	1.3 (0.1)[a]	1.4 (0.1)[a]	1.4 (0.2)[a]
S	0.1 (0.01)[a]	0.1 (0.01)[a]	0.1 (0.02)[a]
C:N	29.5 (0.8)[a]	28.8 (2.1)[a]	31.4 (4.1)[a]
Soil depth horizons (cm) (June 30, 2004)			
Organic H1 (live plant/moss)	2	3	4
Organic H2	3	5	>18[1]
Mineral (cm)	>26	>15	Not detected
MBC (g m^{-2})	118.5[a] (7.4)	141.7[a] (23.0)	119.5[a] (15.5)
MBN (g m^{-2})	9.3[a,b](1.0)	9.7[a,b] (1.5)	4.1[b] (0.6)
MBC:MBN	13.2[a] (1.0)	14.6[a] (0.7)	31.2[b] (3.7)
TOC (g m^{-2})	4.4[a] (0.6)	7.6[a,b] (0.8)	11.5[b] (1.2)
TN (g m^{-2})	0.3[a] (0.04)	0.6[b] (0.1)	1.6[c] (0.2)
Carbon content in organic horizon (g cm^{-3})	0.105[a] (0.006)	0.070[b] (0.007)	0.035[c] (0.005)
[2]Total organic horizon carbon stock (g m^{-2})	3682[a] (213)	4510[a] (424)	15851[b] (2277)

Parentheses indicate standard error (n = 6). Soil microbial biomass carbon (MBC) and nitrogen (MBN) and total dissolved organic carbon (TOC) and total dissolved nitrogen (TN) were measured on August 17, 2004, and represent means (n = 6) for sample depths as reported in Table 1 footnote. Values for each variable that do not share superscript letters in common indicate significant differences among ecosystems (Tukey's HSD, P < 0.05).

[1]Excavation in a nearby similar wet sedge site indicated that the full organic horizon can extend down ∼45 cm, almost to the base of the full active layer (E. Humphreys, personal communication).

[2]Total carbon stocks in the organic horizons of the heath and birch ecosystems were calculated using mean organic horizon depths of 3.5 (SE = 0.4) and 6.4 cm (SE = 0.7), respectively, that were measured after full thaw of the organic layers (n = 6). Estimates of total carbon stocks in the wet sedge system are based on a mean soil organic depth of 45 cm, and assume constant soil bulk density down the profile.

bon stocks calculated over their entire organic soil horizons. By contrast, we estimate that the wet sedge meadow organic soils contained about four times as much carbon in total (Table 2).

Microbial biomass carbon was not significantly different among the ecosystems (Table 2). Carbon-to-nitrogen ratios in the microbial biomass in the heath and birch hummock ecosystems were similar, whereas the sedge meadow was approximately 2.5 times larger due to significantly less nitrogen within the microbial biomass (Table 2). By contrast, total extractable dissolved nitrogen in mid-August was significantly larger in the wet sedge meadow soils than in the other two ecosystems. Total extractable dissolved organic carbon was also significantly higher at the wet sedge meadow compared to the heath, although not significantly different from the mesic birch hummock. The plant removal treatment had no significant effects on any of the above properties in any of the ecosystem types. Furthermore, this treatment did not significantly affect soil temperature (at 2, 5, or 10 cm), soil moisture, or active layer depth (data not shown).

Net Ecosystem CO_2 Exchange Rates among Ecosystems Through the Snow-free Season

The pattern of carbon dioxide fluxes during the snow-free season reflected the changes in temperatures and solar radiation availability that characterized the three seasonal phases (above). In almost all cases, both ecosystem type and sampling time were highly significant factors in explaining the variation in rates of net ecosystem CO_2 exchange (NEE) and each of its component fluxes during each of the three phases (see Appendix 2, http://www.springerlink.com). Furthermore, in most cases, the effect of ecosystem type significantly interacted with sampling time within each phase of the snow-free season (Appendix 2, http://www.springerlink.com), indicating that ecosystem differences in carbon cycling occurred on some but not all sampling days. For example, the spring-thaw phase was generally characterized by *net* CO_2 releases to the atmosphere (source activity) from all three tundra ecosystems (Figure 2A), but the sedge meadow responded particularly rapidly to the thawing conditions, becoming a net carbon sink by the end of June. Over summer, the wet sedge meadow was the strongest CO_2 sink at almost all sampling times, whereas the birch hummock sink strength was more variable, and the dry heath lichen ecosystem frequently alternated from being a

net CO_2 sink to a source (Appendix 2, http://www.springerlink.com; Figure 2A). Post-hoc tests indicated that summer NEE rates were significantly larger in the sedge meadow than in the heath, and that birch hummock rates were not significantly different from either. By contrast, ecosystem type was not significant during the fall (Appendix 2, http://www.springerlink.com), when solar radiation levels were lower (Appendix 1, http://www.springerlink.com) and many of the vascular plants were in senescence, resulting in net CO_2 exchange rates close to zero for all ecosystems by mid-September (Figure 2A).

Component CO_2 Flux Rates among Ecosystems Through the Snow-free Season

We made simultaneous measures of the CO_2 flux components contributing to *net* carbon gain to understand the seasonal NEE patterns among ecosystems. Gross ecosystem photosynthetic carbon gain (GEP) rates increased dramatically as thaw progressed, presumably reflecting regenerating leaf photosynthetic capacities and new leaf growth as well as increasing temperatures and peak photoperiod. Likewise, ER rates were also substantial during spring thaw, although sedge ER was significantly lower than the other two ecosystems (Appendix 2, http://www.springerlink.com; Figure 2C). The flux rates in the plant-removal treatment strongly suggest that respiration derived mainly from the bulk soil pool (SR) started well before soil thaw in each of the ecosystems, and continued at very similar rates throughout the snow-free season (Figure 2D). Furthermore, the ratios of mean bulk soil to total respiration were highest when the soil was frozen in the heath and birch ecosystems, indicating that SR almost completely dominated ER initially. As thaw progressed, the ratios declined rapidly, suggesting that plant-associated respiration rates increased rapidly in the approximately 10 days leading up to soil thaw (Figure 3). The wet sedge meadow SR/ER exhibited a similar pattern but with a lag of about 2 weeks, presumably due to prolonged solid frozen conditions due to much higher soil ice content in this ecosystem (see section ''Methods'').

Summertime GEP rates at the birch hummock were significantly larger than the dry heath but not significantly different from the wet sedge ecosystem (Appendix 2, http://www.springerlink.com; Figure 2B). These high rates of gross C gain were, however, counteracted by correspondingly high rates of ER (and SR) during the summer phase
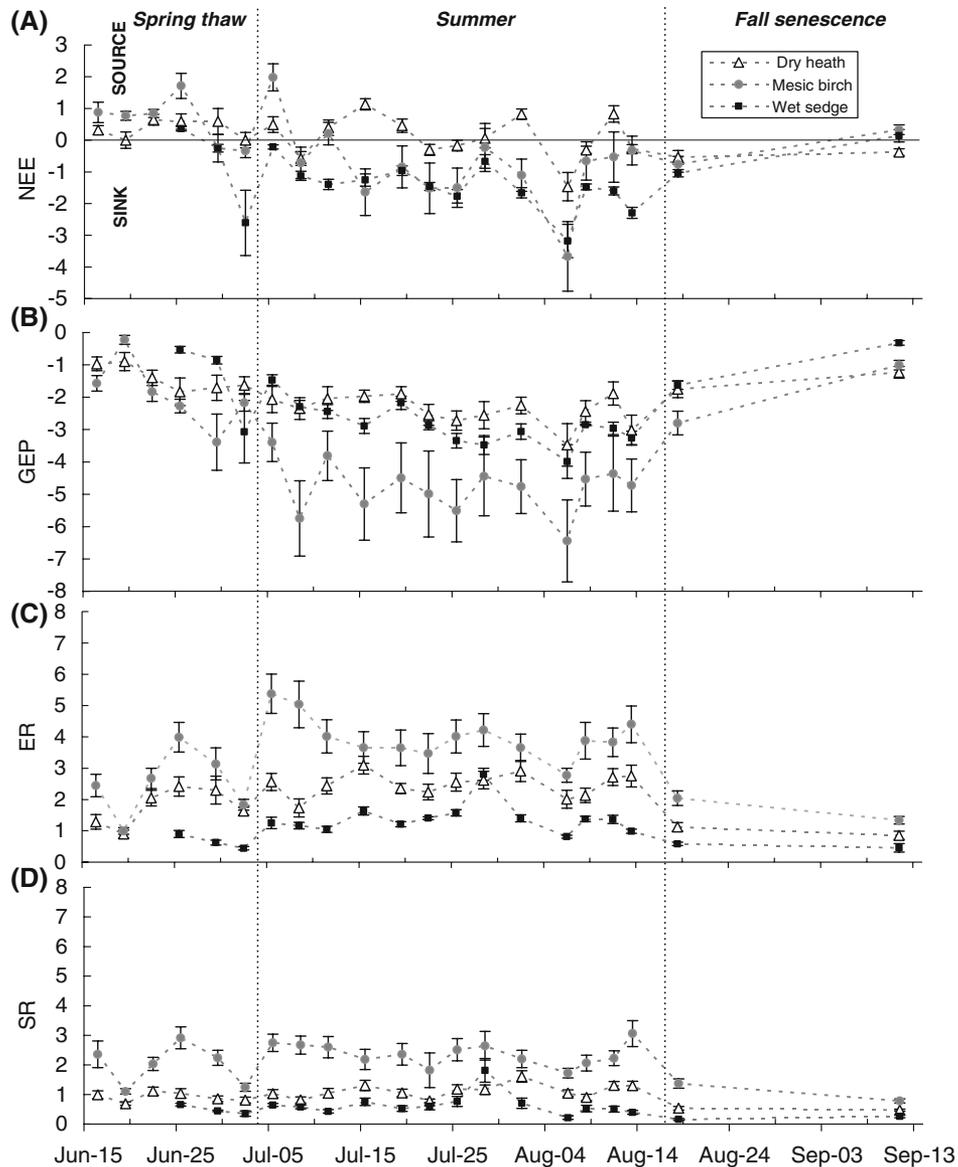
Figure 2. Mean daytime rates of (**A**) net ecosystem CO_2 exchange (NEE), (**B**) gross ecosystem photosynthesis (GEP), (**C**) ecosystem respiration (ER), and (**D**) soil respiration (SR) for the dry heath lichen, mesic birch hummock, and wet sedge meadow ecosystems (units = μmol CO_2 m^{-2} s^{-1}; bars = standard errors). Positive CO_2 exchange rates indicate CO_2 loss to the atmosphere, whereas negative values indicate ecosystem CO_2 gain. *Dashed lines* between measurements assist with comparing CO_2 exchange patterns through the season among ecosystems and do not indicate actual CO_2 fluxes between sample dates.

(Figure 2C, D), resulting in NEE rates that did not differ significantly from the sedge (Appendix 2, http://www.springerlink.com; Figure 2A). The birch component fluxes in particular were characterized by strong spatial variability among plots for each sampling date, especially for GEP (Figure 2B) but also for ER (Figure 2C), probably reflecting a combination of relatively high plot variation in the biomass and photosynthetic activity of particular plant species within this vegetation type.

Our simultaneous measures of NEE and its component fluxes following a single major rainfall event on August 4, 2004 (Figure 1b), provided important insights into the mechanistic controls on net ecosystem carbon gain in this landscape. Our measures of seasonal NEE rates peaked for each of the ecosystems at the next sampling date (2 days later). GEP rates also peaked at the same time, indicating potential moisture limitation on landscape-level photosynthesis rates (Figure 2B).
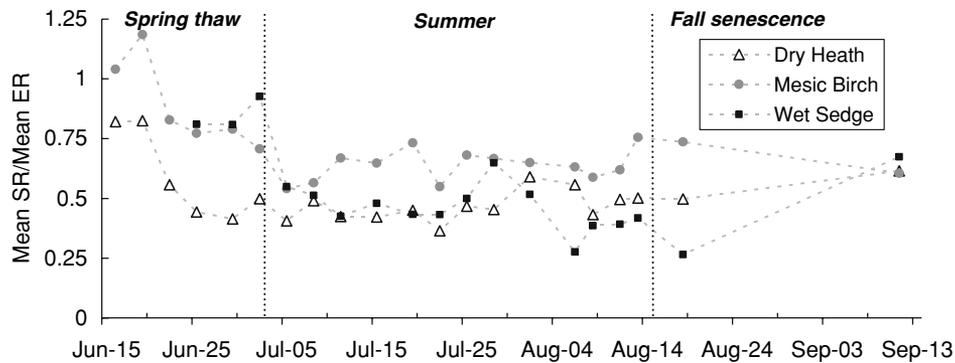
Figure 3. Mean bulk soil respiration as a proportion of the mean total ecosystem respiration for the dry heath lichen, mesic birch hummock, and wet sedge meadow ecosystems during the 2004 snow-free season. *Dashed lines* between measurements assist with comparing CO_2 exchange patterns through the season among ecosystems and do not indicate actual CO_2 fluxes between sample dates.

Simultaneous measures of ER indicate that C loss rates were reduced to summertime minimum levels in the birch and sedge ecosystems. Likewise SR rates were minimized in these ecosystems at this time while the ratios of SR/ER did not change at the birch and heath sites (Figure 3), strongly suggesting that respiration from both bulk soil and plant-associated sources were equally moisture-inhibited by the inundation. By contrast, the decline in both SR and SR/ER in the wet sedge ecosystem immediately after this rainfall event (Figures 2D and 3) suggests that the reduction in C losses was primarily due to inhibited CO_2 production from the bulk soil (or physically restricted CO_2 efflux) due to rapid wetting at the surface (Figure 1B). Thus, these substantial rains immediately raised GEP and simultaneously lowered ER, resulting in peak NEE rates for the entire snow-free season in each of the three vegetation types at this time.

GEP, ER, and SR rates in all ecosystems decreased rapidly once temperatures began to severely decline after August 13 at the end of the summer phase (Figure 2B–D), but continued to differ significantly among ecosystem types through the fall season sampling dates (Appendix 2, http://www.springerlink.com). Although the birch hummock system with its larger vascular biomass and larger complement of evergreen species (Table 1) had higher GEP rates at this time, total respiratory rates were also high, resulting in no ecosystem differences in NEE rates then or at the end of the fall period (Figure 2A). SR rates also declined rapidly in all ecosystems at the end of summer (Figure 2D). As in the previous phases, SR in the sedge was not higher than in the other ecosystems

despite the approximately 3°C warmer soil temperatures at this time, presumably reflecting an ongoing low oxygen constraint on microbial activity due to the relatively wet soil conditions (Figure 1B).

CO_2 Flux Interpolations Over the Full Snow-free Season among Ecosystems

To facilitate relative comparisons among ecosystems, we linearly interpolated each plot's seasonal set of 18–21 individual flux rates, which had been measured at a wide variety of times during daylight hours (see section ''Methods''). The dry heath, mesic birch hummock and wet sedge meadow ecosystems differed strongly in their estimated overall net carbon gains during the full 2004 snow-free season (Figure 4). Even though it had the smallest total plant biomass (Table 1) and shortest photosynthetically active growing season (Figure 2B), the sedge meadow had the largest net carbon gain relative to the other ecosystem types. By contrast, the birch hummock system had the largest plant biomass and significantly higher GEP compared to the two other ecosystem types, but also had significantly larger ER (and SR) losses (Figure 4). Thus, the high GEP at the birch site was offset by high respiration losses resulting in relatively low net carbon gain over the entire snow-free season compared to the sedge meadow (Figure 4).

Sensitivity of CO_2 Flux Rates to Environmental Variables

The above results and conclusions relate to landscape-level controls (that is, *among* ecosystems) on components of NEE during each phase of the
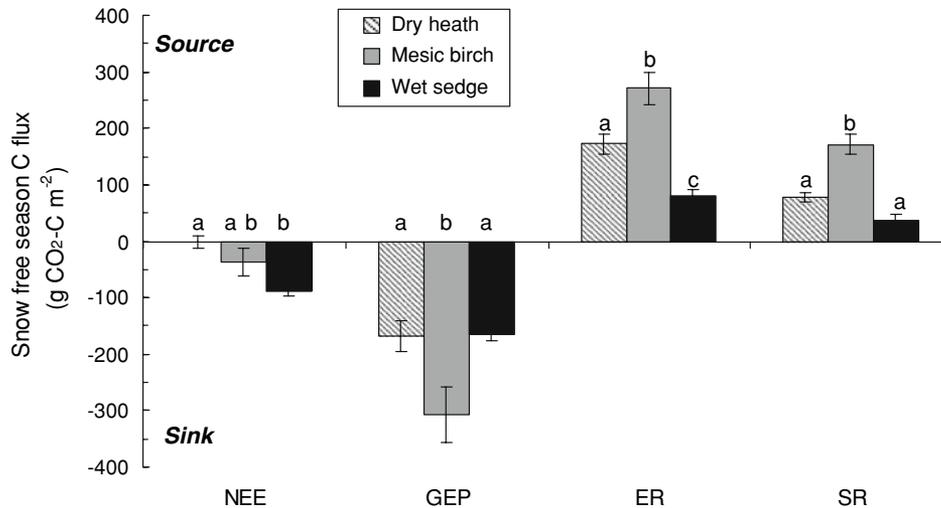
Figure 4. Interpolated estimates of daytime ecosystem CO_2 fluxes (±SE) for the snow free season (June 16–September 11, 2004) in the three principal tundra ecosystems at Daring Lake, NWT, Canada [$n = 6$; net ecosystem exchange (NEE), gross ecosystem photosynthesis (GEP), ecosystem respiration (ER), and soil respiration (SR)]. Positive numbers indicate net carbon loss to the atmosphere and negative numbers indicate net carbon gain. Significant differences ($P < 0.01$) among tundra ecosystems for each component flux are indicated by columns that do not share letters in common.

snow-free season. To characterize the controls on NEE rates *within* ecosystems, we used multiple linear regressions to relate the component fluxes from each sampling plot (made at different times on each of the sampling days) to simultaneous measures of several environmental variables. Air and soil temperatures, soil volumetric water content, active layer depth, and light (PPFD) together explained between 11 and 86% of the variation in NEE rates during the snow-free phases of 2004 (Table 3). Air temperature was generally the strongest predictive variable to explain NEE rates within each of the ecosystems during spring and summer (Table 3). Reduced rates of net carbon uptake were generally associated with relatively warm days during spring and summer in each ecosystem (Table 3; Figures 1A and 2A).

High levels of PPFD were associated with stimulated GEP rates in each ecosystem during summer (Table 3), and warmer air or soil temperatures were generally correlated with decreased GEP rates. Surprisingly, however, these factors explained little of the total variation (except in the wet sedge; $R^2 = 0.42$) even though both PPFD and temperature varied substantially (by a factor of seven) between GEP measurement dates (Appendix 1, http://www.springerlink.com; Figure 1). By contrast, low GEP rates in the fall were closely associated with low PPFD and relatively warm air temperatures in the wet sedge ($R^2 = 0.95$), and with decreasing (sub-zero) soil temperatures in the

dry heath ($R^2 = 0.42$) and mesic birch sites ($R^2 = 0.77$).

Rates of ER loss within each ecosystem were strongly positively correlated with temperature in the spring and summer phases (Table 3), explaining 20–56% of the total variation. Thus, ER was highest in plots that were warm relative to their neighbors within each ecosystem and/or on sampling days that were relatively warm. An almost identical pattern held for SR, accounting for 18–55% of variation, except that the regression for the dry heath in spring was not statistically significant. Likewise, heath ER or SR fluxes in the fall were not correlated with the environmental variables, suggesting either that there were time lags or that other ecosystem-specific variables such as organic layer depth, soil carbon, or litter quality were more important. In contrast to the heath, both ER and SR fluxes from the birch hummock plots during fall were closely related to the measured environmental variables, explaining 68 and 70% of the total variation, respectively (Table 3). Birch ecosystem carbon loss was lower in relatively wet plots and/or on wetter sampling days, whereas birch SR was lower in relatively cool plots and/or on cooler days. Together, these regression analyses strongly suggest that day-to-day and/or plot-to-plot variation in NEE within each of these ecosystems was determined mainly by the effects of temperature on ecosystem and bulk soil respiration.

Table 3. Multiple Linear Regression Analyses of Net CO_2 Exchange and its Component Fluxes in Relation to Environmental Variables [Air temperature, T_a (°C); soil temperature at 2 cm depth[1], T_s (°C); soil volumetric water content, VWC (H_2O/soil m^3 m^{-3}); photosynthetic photon flux density, PPFD (μmol photons m^{-2} s^{-1}); and active layer thaw depth, Thaw (cm)] for Three Tundra Ecosystems during the Three Phases of the 2004 Snow-Free Season at Daring Lake, NWT.

	Ecosystem	Model	df	F	R^2
Net ecosystem exchange					
Spring Thaw	Dry heath lichen	$(T_a \times 0.04) - 0.3$	1, 34	4.3	0.11
	Mesic birch hummock	$-(\text{Thaw} \times 0.1) + (T_a \times 0.2) - (T_s \times 0.1) - (\text{PPFD} \times 0.0007) + 1.1$	4, 31	7.0	0.48
	Wet sedge meadow	$(T_a \times 0.2) - 4.9$	1, 14	15.4	0.52
Summer	Dry heath lichen	$(T_a \times 0.1) - (\text{PPFD} \times 0.0008) + (\text{VWC} \times 0.03) + (T_s \times 0.06) - 3.7$	4, 72	19.3	0.52
	Mesic birch hummock	$(T_a \times 0.2) - (\text{PPFD} \times 0.001) + (T_s \times 0.1) - 5.7$	3, 74	15.7	0.39
	Wet sedge meadow	$(T_a \times 0.1) - (\text{Thaw} \times 0.05) - (\text{PPFD} \times 0.0006) - 2.2$	3, 73	44.0	0.64
Fall Senescence	Dry heath lichen	$(\text{Thaw} \times 0.1) - 2.4$	1, 9	4.6	0.34
	Mesic birch hummock	$-(T_s \times 0.2) + 0.6$	1, 10	14.2	0.59
	Wet sedge meadow	$(\text{Thaw} \times 0.2) - 11.1$	1, 10	62.6	0.86
Gross ecosystem photosynthesis					
Spring Thaw	Dry heath lichen	$-(\text{PPFD} \times 0.0008) - 0.6$	1, 34	8.2	0.19
	Mesic birch hummock	$-(T_s \times 0.2) - 0.5$	1, 34	16.6	0.33
	Wet sedge meadow	$(T_a \times 0.19) - 5.0$	1, 14	12.0	0.46
Summer	Dry heath lichen	$(T_a \times 0.09) - (\text{PPFD} \times 0.0008) - 3.7$	2, 73	8.0	0.18
	Mesic birch hummock	$(T_a \times 0.2) + (\text{Thaw} \times 0.06) - (\text{PPFD} \times 0.001) - 11.1$	3, 74	5.5	0.18
	Wet sedge meadow	$-(\text{Thaw} \times 0.06) - (\text{PPFD} \times 0.0007) + (T_s \times 0.05) + (\text{VWC} \times 0.007) - 1.4$	4, 72	13.1	0.42
Fall Senescence	Dry heath lichen	$-(T_s \times 0.6) + 2.6$	1, 9	6.5	0.42
	Mesic birch hummock	$-(T_s \times 0.3) + (\text{Thaw} \times 0.03) - 1.9$	2, 9	15.2	0.77
	Wet sedge meadow	$(T_a \times 0.5) - (\text{PPFD} \times 0.0009) - 5.3$	2, 9	95.1	0.95
Ecosystem respiration					
Spring Thaw	Dry heath lichen	$(T_a \times 0.1) - (\text{Thaw} \times 0.03) + 0.6$	2, 33	15.8	0.49
	Mesic birch hummock	$(T_a \times 0.1) + 0.5$	1, 34	38.3	0.53
	Wet sedge meadow	$(T_s \times 0.07) - 0.1$	1, 16	20.7	0.56
Summer	Dry heath lichen	$(T_s \times 0.1) + 0.7$	1, 75	19.1	0.20
	Mesic birch hummock	$-(\text{Thaw} \times 0.05) + (T_s \times 0.08) + (\text{VWC} \times 0.02) + 3.3$	3, 74	8.9	0.27
	Wet sedge meadow	$(T_a \times 0.08) - (\text{VWC} \times 0.01) + 0.6$	2, 75	46.4	0.55
Fall Senescence	Dry heath lichen	Not significant			
	Mesic birch hummock	$-(\text{VWC} \times 0.04) - (\text{Thaw} \times 0.02) + 4.7$	2, 9	9.8	0.68
	Wet sedge meadow	Not significant			
Soil respiration					
Spring Thaw	Dry heath lichen	Not significant			
	Mesic birch hummock	$(T_a \times 0.1) + (\text{VWC} \times 0.02) - 0.7$	2, 33	15.1	0.48
	Wet sedge meadow	$(T_s \times 0.04) - 0.04$	1, 16	19.3	0.55
Summer	Dry heath lichen	$(T_s \times 0.09) - (T_a \times 0.04) + 0.5$	2, 75	8.0	0.18
	Mesic birch hummock	$(T_s \times 0.2) - (T_a \times 0.1) - (\text{Thaw} \times 0.02) + 2.7$	3, 74	11.7	0.32
	Wet sedge meadow	$(T_a \times 0.06) - (\text{VWC} \times 0.009) - 0.03$	2, 75	22.7	0.38
Fall Senescence	Dry heath lichen	Not significant			
	Mesic birch hummock	$(T_s \times 0.09) - (\text{Thaw} \times 0.02) + 1.5$	2, 9	10.6	0.70
	Wet sedge meadow	$(T_a \times 0.03) - 0.2$	1, 10	5.5	0.35

Parameters are listed in order of explanatory power within each model. All models presented were statistically significant ($P < 0.0001$). Negative model outputs indicate CO_2 uptake by the system.

[1]*Flux rates throughout this study were generally more closely and significantly related to soil temperatures at 2 cm depth than to soil temperatures at 5 or 10 cm depth. Note that soil temperatures at 2 cm were generally below 0°C (that is, negative) for the heath and birch heath ecosystems during the spring and fall phases.*

DISCUSSION

At the landscape scale (that is, within a common climatic zone), the low Arctic typically consists of a variety of ecosystem types whose distribution is determined primarily by topography and parent material as they affect hydrological drainage patterns (Bliss and Matveyeva 1992; Walker 2000). As expected, we found that the principal tundra ecosystem-types along a natural moisture gradient in the Canadian low Arctic differed very strongly in their daytime net ecosystem CO_2 exchange (NEE) rates with the atmosphere at least during the spring and summer phases of the snow-free season (Appendix 2, http://www.springerlink.com; Figure 2A). Our study demonstrates, however, that these NEE differences among ecosystems were not consistent between sampling dates (statistically significant interaction—Appendix 2), refuting Hypothesis 1. Thus, particular ecosystems differed in their NEE flux rates on some days within each seasonal phase, but not on others (Figure 2A), presumably due to differing sensitivities to environmental variability among ecosystem types. Furthermore, differences in NEE rate within an ecosystem between sampling dates were often as large as differences among ecosystem-types (Figure 2A). Similar conclusions apply to GEP and ER (Appendix 2; Figure 2B, C), refuting Hypothesis 2. We conclude that the rates of growing season net carbon gain across the landscape were strongly influenced not just by the distribution of ecosystem types, but also by the individualistic (that is, ecosystem-specific) and differing responses of GEP and ER to daily variation in environmental conditions.

Secondly, our study of the simultaneous rates of GEP carbon inputs and ER outputs that comprise NEE demonstrates very different patterns of component contributions among ecosystems. The wet sedge system consistently exhibited moderate rates of gross photosynthetic carbon gain but low respiratory losses, resulting in the highest rates of net carbon gain across the landscape at many of the sampling times (Figure 2A), and strongly suggesting the largest overall net carbon gain throughout the snow-free season (Figure 4). By contrast, the mesic birch hummock system consistently had high photosynthetic rates but also high respiratory losses, resulting in moderate rates of net carbon gain (Figures 2A–C and 4). The dry heath had moderate photosynthetic carbon gains and almost equivalent respiratory carbon losses (Figure 2B, C), resulting in zero rates of net carbon gain (Figure 4). Thus,

the pattern of NEE rates among ecosystems across the full snow-free season correlated with the hydrological gradient—overall net carbon gain was consistently larger in the wetter ecosystems, supporting Hypothesis 3. A similar pattern occurred across a small-scale moisture gradient within a high Arctic vegetation-type (Sjogersten and others 2006), but moisture regime and net carbon gain were not correlated in several larger scale comparisons among tundra ecosystems (McFadden and others 2003; Welker and others 2004; Oberbauer and others 2007), perhaps because they were confined to summer rather than the full snow-free season. However, as in the other studies cited above, the pattern of net carbon gain among ecosystems that we observed did not match that of gross photosynthetic carbon gain. Furthermore, in contrast to some studies at least (Giblin and others 1991; Welker and others 2004), we found no consistent pattern of declining ER from the dry heath through to the wet sedge ecosystems along our moisture gradient. Thus, both GEP and ER were largest in the mesic ecosystem-type, indicating that these two flux components were inhibited by both the *high* and *low* moisture conditions, that are characteristic of the other two ecosystems along the moisture gradient.

Thirdly, our estimates of the bulk SR component of ER suggest substantial ecosystem differences in the turnover rates for carbon within the bulk soil and plant-associated (that is, recently fixed photosynthate within shoot, root, fresh litter, and rhizosphere exudate) pools. The birch hummock ecosystem consistently exhibited the highest rates of both gross photosynthetic carbon gain and total respiratory losses in the summer phase at least (Figure 2B, C). Furthermore, almost two-thirds of the total respired carbon in the birch hummock ecosystem were derived from bulk soil, in contrast to just under half in the wet sedge and heath lichen ecosystems (Figures 3 and 4), refuting Hypothesis 4. Thus, respiratory carbon losses in the birch system were relatively large and dominated by bulk soil sources, suggesting a higher turnover rate for bulk soil carbon, and by implication a slower turnover rate for plant-associated carbon in the birch hummock system. We conclude that the consistently moderate and therefore more favorable moisture conditions in the mesic birch hummock as compared to the dry heath and wet sedge ecosystems (Figure 1B) promoted relatively fast decomposition of bulk soil carbon during the summer phase.

Differences in CO_2 Exchange among Tundra Ecosystems

Although several environmental conditions clearly varied among the tundra ecosystems, differences in hydrology seem to have been the most important driver of CO_2 flux differences among ecosystems. For example, soil temperatures at 5 cm depth at all sites were similar at the end of winter, but were at least approximately 3°C warmer in the wet sedge throughout the growing season (Figure 1A). The wet sedge meadow was located at the base of a gentle slope in a depression that retained water throughout the snow-free season. Infiltration of water during the spring melt can result in substantial heat transfer (Kane and others 2001), and may have raised soil temperatures relatively quickly in the wet sedge compared to the other two ecosystems. Once warmed, the relatively high heat capacity of water-saturated, *Sphagnum*-dominated sedge soils (Fuchs and Hadas 1972) may have resulted in higher mean diel soil temperatures (that is, greater thermal buffering) at this depth in spring and fall. In addition, the larger plant biomasses and leaf area indices at the birch hummock and heath sites (Table 1) may have resulted in canopy shading effects that restricted soil temperature increases (Callaghan and Jonasson 1995) in spring and summer. Nevertheless, by July 18 (when we also have datalogger records at 2 and 10 cm for all sites), the mean diel soil temperatures close to the surface (2 cm) were very similar in the heath and sedge ecosystems but relatively low in the birch, indicating that the very dry conditions associated with heath permitted substantial warming. The pattern of significantly higher soil temperatures in the sedge meadow at 5 cm, however, also occurred at 10 cm (data not shown). Thus, site-specific interactions between vegetation cover and high or low soil moisture contents mediated differences in the magnitudes and depth profiles of soil temperature that these adjacent ecosystems experienced. We conclude that hydrological differences at least contributed to these ecosystem differences in soil temperatures, and that because the coldest site at all depths measured (that is, birch hummock) had the highest ER and SR fluxes, soil temperature was clearly not the primary control on respiration differences among ecosystems (Figures 1A, 2C, D). Soil incubation studies have demonstrated that temperature and moisture can interact to control respiratory activity, and that respiration responds positively to moisture at low levels, but negatively at saturating levels because of oxygen limitation (Flanagan and Bunnell 1980; Johnson and others

1996). These mechanistic data and our results together strongly suggest that site-specific moisture regimes restricted respiratory activity at the heath and sedge systems (too dry and too wet respectively), but were relatively favorable in the birch hummock, resulting in the largest ER and SR rates among ecosystems at all sampling times throughout the snow-free season (Figure 2C, D). We conclude that soil moisture was the dominant control on the patterns of SR and ER among ecosystems across the moisture gradient.

The importance of soil moisture as a control on CO_2 exchange in these ecosystems was further exemplified by the responses to rainfall. A particularly large precipitation event in early August rapidly decreased SR and ER and stimulated GEP, resulting in peak seasonal NEE rates in all ecosystems (Figure 2A). These rapid responses to substantial increases in soil moisture over 0–10 cm depth (Figure 1B) strongly suggest that landscape-level net carbon gain had become moisture-limited at this time in the growing season. Total snow-free precipitation for 2004 was 120 mm which was well within the normal inter-annual range (90–220 mm over 1997–2004; mean 146 mm, SD 59; B. Reid, unpublished data), indicating that moisture limitation on net primary production in the ecosystems of this region may be a common occurrence.

Apart from moisture, some of the differences in vegetation properties among ecosystems strongly influenced CO_2 fluxes. The GEP rates were highest in the birch hummock, where leaf area index and vegetation cover were also largest. Phenology and plant species effects, however, were also clearly important determinants of the patterns of CO_2 fluxes at particular stages of the snow-free season. For example, our measures of respiration from the bulk soil component (Figure 2D), and the ratio of SR to total ER (Figure 3), clearly indicate that wet sedge ER at the end of the spring phase (July 2nd) was low relative to the other vegetation types (Figure 2C) not because of differences in SR but because respiration directly associated with plants was relatively low (Figure 3). In contrast to the heath and birch ecosystems, the sedge meadow is phenologically adapted to rapidly produce a completely new set of leaves after winter snowmelt. Respiration associated with perennial shoots, 'standing dead' leaves and litter was minimal because these pools are generally small and submerged at this time of year. Thus, although the sedge meadow plants were taking up C at similar rates to the other ecosystem types (Figure 2B), and bulk SR rates were similar (Figure 2D), non-photosynthetically active tissue was minimal resulting

in relatively low total ecosystem C losses (Figure 2C), and therefore strong net C sink activity at this time (Figure 2A). Furthermore, toward the end of the growing season (August 18), the proportion of ER derived from the bulk soil pool in the wet sedge ecosystem declined substantially from summertime levels (Figure 3). By contrast, although ER from the birch and heath sites also declined with cooling temperatures in mid-August (Figure 2C), the proportions of respiration from the bulk soil and plant-associated pools in these more evergreen ecosystems were not affected (Figure 3). These data strongly suggest that sedge ecosystem CO_2 losses at this time became dominated by aboveground respiration associated with senescing plant leaf tissue in this relatively deciduous vegetation type. Together, these spring and fall patterns indicate that the higher growth rates and faster tissue turnover of the deciduous sedge species (Hobbie 1996) resulted in markedly different patterns of seasonal carbon dynamics compared to the evergreen-dominated birch hummock and heath lichen systems.

Our study investigated whether differences in soil organic carbon stores among tundra ecosystems are driven not just by differences in soil moisture that affect decomposition and SR, but also by differences in GEP. We estimated that the total carbon stock per unit area was at least four times larger in the wet sedge compared to the other ecosystems (Table 2). Both the sedge and heath systems had similar moderate rates of gross carbon gain throughout the snow-free season (Figure 2B), but the former had by far the highest seasonal net carbon gain (Figures 2B and 4). Thus, the inundated conditions of the wet sedge system consistently resulted in the lowest rates of bulk soil (and ecosystem) respiration throughout the 2004 snow-free season (Figure 2C, D), and correspondingly, over the longer term, have led to the largest soil carbon accumulation across the landscape (Table 2). We conclude that at the landscape scale, soil carbon accumulation tends to be largest in the sedge systems because decomposition is restricted, and not because GEP carbon inputs are particularly high.

Controls on CO_2 Exchanges within and among Ecosystems

High NEE rates within each ecosystem along the moisture gradient were generally most closely associated with lows in air temperature, at least in the spring and summer phases (Table 3). As in several previous studies (Oberbauer and others 1996; Grogan and Jonasson 2005), this pattern was strongly influenced by temperature effects on respiratory carbon loss. Here, air and soil temperatures were generally the closest correlates (positive) to both ER and SR, in many cases explaining at least half the seasonal variation in respiration rates. By contrast, the among ecosystem comparisons described in previous sections and other studies (Jones and others 1998; Oechel and others 2000; Welker and others 2004; Williams and others 2006; Oberbauer and others 2007) indicate that soil moisture can exert strong control on landscape-scale variation in growing season NEE rates. Hydrological regime determines the distribution of ecosystem-types across the landscape (Bliss and Matveyeva 1992; Walker 2000). Our study demonstrated that hydrologically distinct ecosystems differ in NEE rates at some times but not others during the growing season, probably because individual ecosystems vary substantially in their GEP and ER responses to changes in environmental conditions. Together, these results strongly suggest that the primary controls on daytime rates of net ecosystem CO_2 exchange and its component fluxes during the snow-free season differ in fundamental ways between the landscape (that is, among ecosystem) and plot (that is, within ecosystem) scales in the low Arctic.

Interpolated Carbon Fluxes for the Full Snow-free Season

Interpolated flux estimates for the full 2004 snow-free season suggest that the wet sedge was a strong net carbon sink, the birch ecosystem was a moderate sink, and that the heath ecosystem was neutral. Because these interpolations rely on daytime data only, albeit randomized in order among ecosystems from morning to evening for each day's set of measures, our values probably overestimate the actual magnitudes of both component fluxes (GEP and ER). The main conclusions of this study are based on statistical analyses of flux rates among ecosystems on individual sampling days, and therefore apply most directly to daytime conditions. The interpolations facilitate comparisons of individual flux components over the full snow-free season among ecosystems, and therefore assume that low light and cool temperatures at night reduce GEP rates to similar extents in each of the ecosystems, and likewise for ER. This assumption is intuitively very reasonable for GEP (because instantaneous rates are strongly regulated by PPFD), but diel variation in ER seems to be significantly larger in dry heath tundra (Illeris and others 2004), than in moist tussock tundra (Hobbie and Chapin 1998; Grogan and Chapin 2000), or wet

sedge (Johnson and others 2000) ecosystems (presumably because soil water buffers diel temperature dynamics). Thus, interpolated ER may have been overestimated most in the heath and least in the sedge meadow. Nevertheless, we expect that the pattern of significant differences in seasonal NEE among ecosystem types reported here would be upheld even if it had been based on diel 'round the clock' data. First, the pattern is totally consistent with biomass harvest data from Alaskan tundra, indicating that plant net carbon gain (both above-ground and total) during the full growing season was smallest in heath tundra, largest in birch tussock tundra, and moderate in sedge tundra (Shaver and Chapin 1991). Plant net carbon gain [that is, net primary production (NPP)] differs from growing season NEE in that it includes only respiration directly associated with plants. We estimated NPP at our sites [by subtracting interpolated plant-associated carbon losses (that is, ER − SR) from GEP] to be 73, 208, and 122 g C m^{-2} for the heath, birch, and sedge ecosystems, respectively. Not only does the pattern of differences in estimated total NPP among our ecosystems match that of similar Alaskan tundras, but also the absolute numbers are very similar (Shaver and Chapin 1991). Furthermore, our estimates of mean seasonal NEE for the heath, birch, and sedge ecosystem types (−1, 37, and 88 g CO_2-C m^{-2}, respectively; Figure 4) are entirely consistent in magnitude with eddy covariance data that indicated an overall net carbon accumulation of approximately 32 g CO_2-C m^{-2} from May 15 to August 31st, 2004, for a footprint that included all three of our sites but that was dominated by heath and birch (Lafleur and Humphreys 2008). Overall, the strong *relative* differences indicated by these interpolation results indicate substantial seasonal variation in CO_2 exchange and its component fluxes among adjacent but hydrologically very different ecosystems, and therefore suggest that tundra carbon cycling responses to environmental change (warming, increasing precipitation, and effects of permafrost melting on soil moisture) are also likely to vary substantially across the landscape. A recent study of tundra CO_2 fluxes across latitudinal and moisture gradients that reported strong ecosystem-specific GEP and ER responses to experimental warming (Oberbauer and others 2007) supports this final conclusion.

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