

## TUNDRA CO<sub>2</sub> FLUXES IN RESPONSE TO EXPERIMENTAL WARMING ACROSS LATITUDINAL AND MOISTURE GRADIENTS

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**Abstract.** Climate warming is expected to differentially affect CO<sub>2</sub> exchange of the diverse ecosystems in the Arctic. Quantifying responses of CO<sub>2</sub> exchange to warming in these ecosystems will require coordinated experimentation using standard temperature manipulations and measurements. Here, we used the International Tundra Experiment (ITEX) standard warming treatment to determine CO<sub>2</sub> flux responses to growing-season warming for ecosystems spanning natural temperature and moisture ranges across the Arctic biome. We used the four North American Arctic ITEX sites (Toolik Lake, Atqasuk, and Barrow [USA] and Alexandra Fiord [Canada]) that span 10° of latitude. At each site, we investigated the CO<sub>2</sub> responses to warming in both dry and wet or moist ecosystems. Net ecosystem CO<sub>2</sub> exchange (NEE), ecosystem respiration (ER), and gross ecosystem photosynthesis (GEP) were assessed using chamber techniques conducted over 24-h periods sampled regularly throughout the summers of two years at all sites.

At Toolik Lake, warming increased net CO<sub>2</sub> losses in both moist and dry ecosystems. In contrast, at Atqasuk and Barrow, warming increased net CO<sub>2</sub> uptake in wet ecosystems but increased losses from dry ecosystems. At Alexandra Fiord, warming improved net carbon uptake in the moist ecosystem in both years, but in the wet and dry ecosystems uptake increased in one year and decreased the other. Warming generally increased ER, with the largest increases in dry ecosystems. In wet ecosystems, high soil moisture limited increases in respiration relative to increases in photosynthesis. Warming generally increased GEP, with the notable exception of the Toolik Lake moist ecosystem, where warming unexpectedly decreased GEP >25%. Overall, the respiration response determined the effect of warming on ecosystem CO<sub>2</sub> balance. Our results provide the first multiple-site comparison of arctic tundra CO<sub>2</sub> flux responses to standard warming treatments across a large climate gradient. These results indicate that (1) dry tundra may be initially the most responsive ecosystems to climate warming by virtue of strong increases in ER, (2) moist and wet tundra responses are dampened by higher water tables and soil water contents, and (3) both GEP and ER are responsive to climate warming, but the magnitudes and directions are ecosystem-dependent.

**Key words:** carbon balance; climate warming; ecosystem respiration; High Arctic; International Tundra Experiment, ITEX; Low Arctic; net ecosystem exchange; soil moisture; tundra; water table.

### INTRODUCTION

Climate warming in the Arctic is expected to strongly affect the carbon balance of tundra ecosystems, and some studies suggest that the carbon balance of these ecosystems is already changing (Oechel et al. 1993, 1995, 2000, ACIA 2005). Of great concern is that the very large stores of carbon present as peat in arctic

ecosystems may be released as the Arctic warms and dries (Billings 1987, Oechel and Billings 1992, Shaver et al. 1992). However, the Arctic encompasses a wide range of tundra ecosystems with differing productivity that are arrayed along bioclimatic gradients (Webber 1974, Gilmanov and Oechel 1995). Furthermore, within a bioclimatic zone, different tundra ecosystems are positioned along topographic gradients in response to different soil moisture and nutrient regimes (Billings 1973, Bliss 2000). Ridgetops typically have low-growing dry vegetation dominated by dwarf shrubs and lichens,

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while low areas may have lush graminoid stands. Small differences in topography may lead to large differences in ecosystem type. As a result, tall, shrub-dominated ecosystems may be separated from short, moss-dominated ecosystems by only a few decimeters.

Responses of carbon balance to warming may differ substantially among the array of arctic ecosystems (Jones et al. 1998, Shaver et al. 1998, Arft et al. 1999, Welker et al. 2000). High-latitude, lower-temperature ecosystems might be expected to have greater responses to warming than warmer, lower-latitude ecosystems (Welker et al. 1997, Arft et al. 1999, Shaver et al. 2000). Moist and wet ecosystems likely will not respond to warming in the same way as drier ecosystems because of the potential for soil anoxia in wet systems (Shaver et al. 2000). Currently, researchers are not only interested in the magnitudes of carbon exchange in the Arctic, but also in developing models that can predict the magnitudes and direction of carbon exchange under future climates (McGuire et al. 2000). However, to accurately predict the effects of warming on the carbon exchange of tundra systems, a mechanistic and ecosystem-specific understanding of the manner in which warming affects tundra ecosystems from different moisture and temperature regimes is needed.

The International Tundra Experiment (ITEX) is a network of more than 20 sites in polar and alpine locations around the world conducting a standardized, small-scale, plot-level, passive-warming experiment using small open-top chambers (OTCs; Marion et al. 1997). The OTCs typically increase mean air temperatures by 1–2°C. The experiment takes advantage of the small stature of tundra ecosystems that allows whole-ecosystem manipulations and measurements at the level of <1 m<sup>2</sup>. The ITEX approach has been validated by tundra responses at the plot level (Hollister and Webber 2000), and results have been consistent with large-scale vegetation changes (Sturm et al. 2001, Walker et al. 2006).

Although originally applied to evaluate warming effects on phenology and growth of individual plants and later to responses of plant communities (Hollister et al. 2005, Wahren et al. 2005, Walker et al. 2006), the ITEX treatments offer an exceptional opportunity to evaluate the effects of climate warming on the CO<sub>2</sub> fluxes of different tundra ecosystems under standard protocols.

Net ecosystem CO<sub>2</sub> exchange (NEE) represents the balance between the respiratory losses from plants and soil (ecosystem respiration, ER) and gross ecosystem photosynthesis (GEP), each of which may be affected differently by warming. Increases in GEP can result from increased leaf area and/or increased leaf-level photosynthesis. Warming by OTCs has accelerated growth and increased leaf area in many tundra sites (Arft et al. 1999). In response to experimental warming, plants at Toolik Lake, Alaska, USA, also increased leaf-level photosynthetic rates (Chapin and Shaver 1996).

Because dry ecosystems tend to be more strongly nutrient-limited than wet ecosystems (Shaver and Chapin 1991), the photosynthetic response to warming may be weakest in dry sites because leaf area and photosynthesis can only increase if nutrients are available to support them. On the other hand, high leaf area and photosynthetic rates are typically associated with high maintenance respiratory costs. Furthermore, not all dry sites in the Arctic will respond alike because of differences in the dominant species. For example, dry tundra at Alexandra Fiord, Canada, is dominated by a deciduous dwarf shrub, *Salix arctica*, that can have high photosynthetic rates (Jones et al. 1997), whereas dry tundra at Toolik Lake is dominated by an evergreen subshrub, *Dryas octopetala*, that has low rates of leaf photosynthesis (Baddeley et al. 1994). Warming should also increase respiration rates of plant tissue and soil biota directly through increased enzyme activity. In wet ecosystems, however, high soil moisture and therefore low soil oxygen levels may inhibit soil respiration rates, regardless of the temperature (Oberbauer et al. 1992). The net balance of a warmed ecosystem will thus depend on the interactive responses of all of these components (Shaver et al. 2000, Marchand et al. 2004).

As part of the North American Tundra Experiment (NATEX) program (the North American participants in ITEX), we conducted measurements of ecosystem CO<sub>2</sub> fluxes at four ITEX sites in northern Alaska and Canada that represent maritime and continental climate regimes in the High and Low Arctic. At all sites we investigated the responses of dry and moist or wet ecosystems to similar levels of warming using the same methodology. The objective of our study was to assess the effect of warming on the CO<sub>2</sub> fluxes (NEE, GEP, and ER) of different tundra ecosystems spanning natural temperature and moisture gradients. Given the sometimes-independent responses of ER and GEP, we hypothesized that: (1) warming will increase GEP, with the greatest increases in ecosystems with the strongest temperature limitation, i.e., wetter and cooler; (2) warming will increase ER, with the greatest increases in dry ecosystems where anoxia is not strongly limiting to below-ground respiration; and (3) warming will not strongly affect NEE because increases in GEP will be offset by increases in ER.

## METHODS

### *Study sites and warming treatments*

The OTC warming and CO<sub>2</sub> exchange measurements were conducted at the four North American Arctic ITEX sites: Alexandra Fiord on Ellesmere Island in Canada and Barrow, Atqasuk, and Toolik Lake in Alaska, USA (Fig. 1). These sites span a range of climate zones from High to Low Arctic, with substantial variation in temperature and precipitation (Table 1). At each site, the effects of soil moisture were evaluated by sampling two or more ecosystems of contrasting

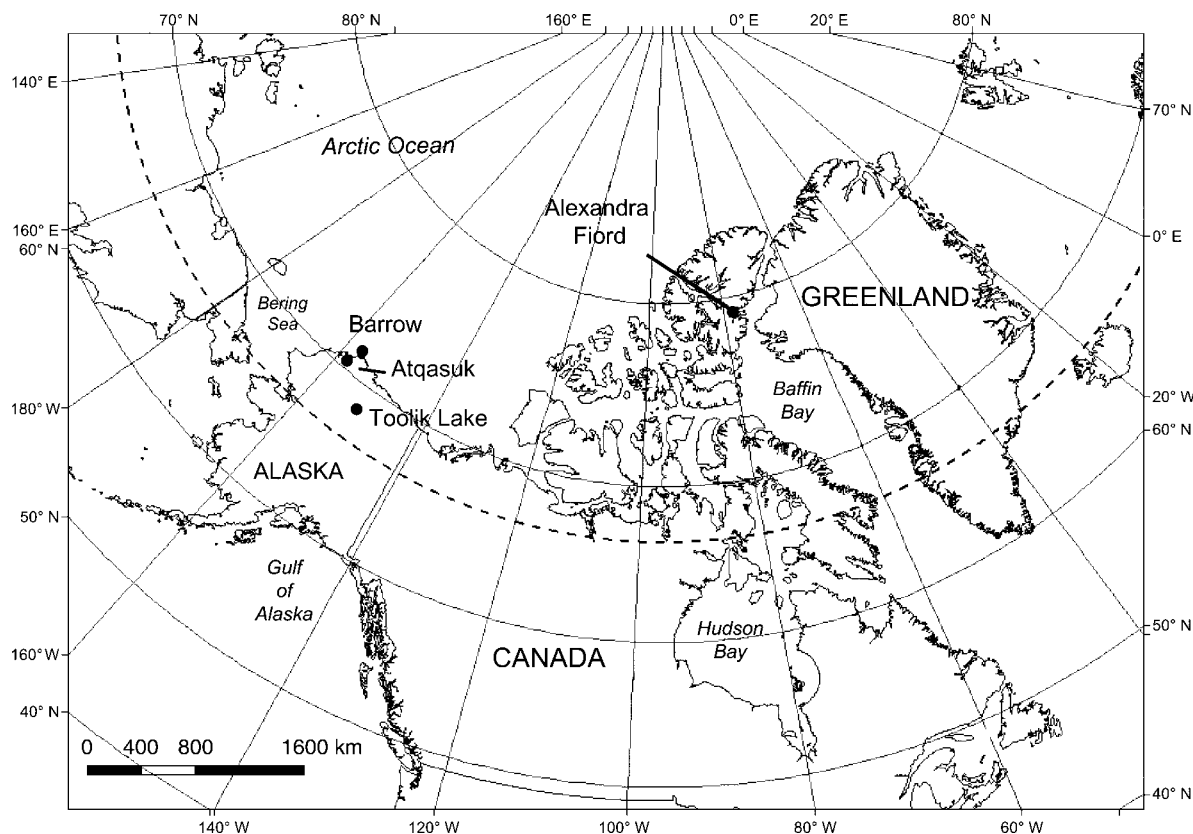


FIG. 1. Location of the four North American International Tundra Experiment (ITEX) sites (solid circles).

moisture regimes (wet, moist, dry) and biomass (Table 2).

The study plots were warmed using hexagonal ITEX OTCs (Marion 1993, 1997, Molau and Mølgaard 1996). At all sites except Alexandra Fiord, the OTCs were installed immediately upon snowmelt in the spring and were left until the end of August. At Alexandra Fiord, the chambers were left in place year-round because of the extreme remoteness of the site. The duration of warming treatments at the time of CO<sub>2</sub> flux measurement also differed among the sites, with the longest warming treatments measured at Alexandra Fiord and the shortest warming treatments measured at Toolik Lake (Table 2). Ideally, the warming manipulations

would have begun simultaneously and CO<sub>2</sub> exchange measurements would have been taken after the same period of treatment, but because of asynchrony among funding cycles, we were unable to do so. However, we believe our analysis is robust and informative.

At each study site the warmed and control plots were established as a completely randomized design with one treatment factor (warming). The designation of control or experimental plot was randomly determined after all plots were located. Air temperatures at canopy height within the OTCs and controls were recorded in all ecosystems with Hobo temperature loggers (Onset Computer, Bourne, Massachusetts, USA). At Alexandra Fiord, air temperatures were collected from all three

TABLE 1. Location and climatic characteristics of the four North American International Tundra Experiment (ITEX) sites.

Site	Longitude, latitude	Elevation (m asl)	Annual temperature (°C)	July temperature (°C)	Summer precipitation (mm)	Thaw days
Alexandra Fiord, Canada	78°53' N, 75°55' W	10	-14.6	5	trace†	439
Barrow, Alaska, USA	71°18' N, 156°40' W	3	-12.6	3.7	57	369
Atqasuk, Alaska, USA	70°27' N, 157°24' W	30	-11.9	9	55	618
Toolik Lake, Alaska, USA	68°38' N, 149°34' W	740	-8.6	11.6	180	905

*Notes:* Values are means for annual and July temperature, summer precipitation, and thaw days. The value for growing-season thaw degree-days represents the cumulative sum of daily mean air temperature for days with daily mean air temperature >0°C. Summer precipitation includes precipitation in June, July, and August.

† Summer precipitation is very infrequent.

TABLE 2. Experimental characteristics of the study ecosystems.

Site	Ecosystem	Biomass (g/m <sup>2</sup> ) <sup>†</sup>	Year started	Sample years	N <sup>‡</sup>	Sample dates
Alexandra Fiord	wet	132 <sup>1</sup>	1992	2000	3	19, 27 Jun; 24 Jul; 18 Aug
Alexandra Fiord	moist	190 <sup>1</sup>	1992	2000	3	12, 24, 30 Jun; 8, 15, 21, 29 Jul; 4 Aug
Alexandra Fiord	dry	71 <sup>1</sup>	1992	2000	3	19, 27 Jun; 25 Jul; 9 Aug
Barrow	wet	84 <sup>2</sup>	1995	2000	3	27 Jun; 11 Jul; 6 Aug
Barrow	dry	85 <sup>2</sup>	1994	2000	3	19, 27 Jun; 24 Jul; 1 Aug
Atqasuk	wet	54 <sup>3</sup>	1996	2000	3	12, 24, 30 Jun; 8, 15, 21, 29 Jul; 4 Aug
Atqasuk	dry	45 <sup>3</sup>	1996	2000	3	21, 25 Jun; 8, 11, 18, 20, 26, 29, 31 Jul
Toolik	moist	708 <sup>4</sup>	1995	2000	5	25 Jun; 2, 17, 23, 30 Jul; 6 Aug
Toolik	dry	319 <sup>4</sup>	1995	2000	5	14, 21, 25 Jun; 8, 11, 18, 20, 26, 29, 31 Jul
				2001	5	11, 18, 25 Jun; 2, 17, 23, 30 Jul; 6 Aug
				2001	5	18 Jun; 15, 23 Jul; 5 Aug
				2001	5	16, 28 Jun; 12, 26 Jul; 9 Aug
				2001	5	18 Jun; 15, 23 Jul; 5 Aug
				2001	5	4, 16, 28 Jun; 12, 26 Jul; 9 Aug
				1997	3	9, 16 Jun; 14, 29 Jul
				1998	3	27 May, 2, 8, 12, 15, 21, 30 Jun; 7, 14 Jul; 25 Aug
				1997	3	24 May; 2, 10, 23 Jun; 9, 21 Jul; 5, 30 Aug
				1998	3	27 May; 2, 8, 12, 15, 21, 30 Jun; 7, 14 Jul; 25 Aug

<sup>†</sup> Sources: 1, Muc et al. (1994c); 2, Webber (1978); 3, S. F. Oberbauer (*unpublished data*); 4, Shaver and Chapin (1991).

<sup>‡</sup> The sample size represents the number of plots measured for each treatment (warmed or control) within each ecosystem.

ecosystems in 2001 but were only collected from the dry site in 2000. Consequently, temperatures for the moist and wet sites for 2000 were estimated based on the relationships between dry site temperatures and those of the moist and wet sites in 2001.

*Alexandra Fiord*.—Although Alexandra Fiord is by far at the highest latitude (78° N), it is a polar oasis (Svoboda and Freedman 1994), situated in a warm lowland on the east-central side of Ellesmere Island, Nunavut, Canada. This relatively small (8-km<sup>2</sup>) lowland site is well-vegetated compared to the surrounding polar desert and semi-desert that is more typical of high-arctic vegetation (Muc et al. 1994a). Adiabatic warming of descending air from upslope and heat trapping and reflected radiation from surrounding cliffs increase the temperatures compared to those of the surrounding island. Skies are often clear and albedos are low in the lowland, also increasing temperatures. Growing-season temperatures are as much as 0.5°C above those on the opposite side of Ellesmere Island and are higher than those at Barrow (Table 1). Precipitation at Alexandra Fiord is 10–20 cm/yr, with almost all falling during the winter. Hydrologic variability is extreme across this polar oasis lowland, and moisture status determines the nature of the plant communities (Muc et al. 1994a, c). Runoff from accumulated snow and glacial melt provide a steady moisture supply during the growing season to the well-vegetated lowland areas. Winds average 2–3 m/s over the growing season. The snow-free period is variable, only 2–3 months long (Labine 1994). The vascular flora consists of ~96 species, with a highly diverse lichen flora of >119 species (Freedman et al. 1994).

At Alexandra Fiord, oversize ITEX OTCs (0.5 m tall, 1.5 and 2.0 m between parallel sides at the top and bottom, respectively; Marion et al. 1997) were installed in three ecosystems that differed in hydrology and plant

species composition: wet meadow, moist meadow, and dry heath. Hydric sedge-dominated meadows cover ~30% of the landscape in the Alexandra Fiord lowland and are generally found on relatively undeveloped soils consisting of a shallow (0–15 cm thick) organic layer on parent material of alluvial sands and gravels. The soils are classified as Pergelic Cryochrepts (Gleysolic Static Cryosols; Muc et al. 1994b). The maximum thaw depth is 50–70 cm. These ecosystems typically have flowing surface water most of the growing season. Vegetation is dominated by *Eriophorum angustifolium*, *Carex stans*, and *C. membranacea*, with cushion plants and dwarf shrubs restricted to the drier tops of the hummocks that emerge above the water level (Muc et al. 1994a). The moist tundra ecosystem we studied is typically found on outwash plains and seepage slopes drier than the wet sedge ecosystems. The soils in this ecosystem are typically damp throughout the growing season. The vegetation was a variation of the dwarf shrub-cushion plant type (Muc et al. 1994a), with *Dryas integrifolia*, *Cassiope tetragona*, *Eriophorum angustifolium* subsp. *triste*, and *Arctagrostis latifolia* as major constituents. This ecosystem covers ~20% of the Alexandra Fiord lowland. The soil is a relatively well-drained Pergelic Cryorthent (Orthic Static Cryosol; Muc et al. 1994b) with a shallow litter plus organic layer (0–10 cm) over a variably thick Bm horizon (1–15 cm). The maximum active-layer depth ranges from 55 to 70 cm. At the other end of the soil moisture spectrum are relatively xeric ecosystems near the banks of streams and along the terraces of slopes. These ecosystems are characterized by minimal snow deposition, relatively early snowmelt, and deep early-season active layer depth. Soils are classified as Pergelic Cryochrepts (Brunosolic Static Cryosols), with a silty-loam texture and relatively organic-rich A and B horizons (Muc et al. 1994b). The maximum active layer depth is typically 35–70 cm. These ecosystems

cover ~35% of the Alexandra Fiord lowland and are dominated by *Salix arctica*, *Dryas integrifolia*, *Saxifraga oppositifolia*, and a few graminoid and lichen species.

**Barrow.**—Both Barrow and Atqasuk lie within the Alaskan Arctic Coastal Plain, a relatively flat region bordered on the north by the Arctic Ocean and on the south by the North Slope foothill region. Barrow lies on the most northern point on the Coastal Plain. The climate is strongly influenced by proximity to the Arctic Ocean and is characterized by long, cold winters and short, cool summers during which the temperature can fall below 0°C on any given day. Summers are typically cloudy or foggy, cool, wet, and windy (Brown et al. 1980). The snow-free period is variable, but generally begins in early June and continues until early September during which time an average of 369 thaw degree-days (cumulative sum of average daily air temperature for days with temperature >0°C) are accrued (Brown et al. 1980). The shallow thaw (30–50 cm) of the active layer (seasonally thawed soils) and the low relief of the Coastal Plain create an environment where differences of <50 cm in elevation can have dramatically different soil water regimes and vegetation composition. Sedges and grasses dominate the vegetation. The vascular plant flora consists of ~120 species (Murray and Murray 1978). The low diversity likely results from the relatively harsh climate and low habitat diversity of the area.

Standard ITEX open-top chambers (0.35 m tall, 0.6 and 1.03 m between parallel sides at the top and bottom, respectively; Marion et al. 1997) were installed at Barrow in both a wet meadow and a dry heath. The wet meadow is located on the edge of a thaw lake basin and is dominated by graminoids, in particular *Carex aquatilis/stans*. Standing water is frequently present at the wet ecosystem. Soils are Histic Pergelic Cryaquepts. The vegetation at the Barrow dry ecosystem is dominated by a dwarf deciduous shrub, *Salix rotundifolia*, with evergreen shrubs (e.g., *Cassiope tetragona*) and graminoids (e.g., *Luzula* spp., *Arctagrostis latifolia*). Soils at the Barrow dry ecosystem are Pergelic Cryaquepts on silt, sand, and gravel on a raised beach ridge (Hollister et al. 2006). The dry ecosystem typically thaws a week or more in advance of the wet meadow ecosystem and maximum thaw depth is nearly twice as great (84 vs. 46 cm, respectively; Hollister et al. 2006).

**Atqasuk.**—Atqasuk lies 100 km south of Barrow, approximately in the middle of the Coastal Plain beyond the marine influence, and is warmer than would be expected based on its location (Table 1). Unlike Barrow, low clouds and fog typically dissipate by early afternoon in Atqasuk. The climate of Atqasuk consists of long, cold winters and short, moderate summers during which the temperature can fall below zero on any given day, but daily maximums may also exceed 20°C. The snow-free period is variable, but generally begins in late May and continues until early September over which an average of 618 thaw degree-days are accrued (Haugen and Brown 1980). The vascular plant flora consists of

~250 species (Komárková and Webber 1980). The higher diversity relative to Barrow is primarily a consequence of the greater landscape heterogeneity and warmer climate at Atqasuk (Komárková and Webber 1980).

Standard ITEX open-top chambers were installed at Atqasuk in both a wet meadow and a dry heath ecosystem. The wet meadow at Atqasuk is located on the edge of a thaw lake basin and is dominated by *Carex aquatilis/stans*. Standing water is present throughout most of the summers in this ecosystem. Soils at the wet ecosystem are Histic Pergelic Cryaquepts. Soils at the dry ecosystem are Pergelic Cryopsammets on aeolian sand of a stabilized sand dune. Vegetation at the dry ecosystem is dominated by the dwarf evergreen shrubs *Ledum palustre*, *Cassiope tetragona*, and *Vaccinium vitis-idaea* and the graminoids *Hierochloa alpina* and *Luzula confusa*. Heavy grazing by reindeer in this ecosystem in 1999 reduced much of the aboveground biomass. Snow melt in the dry ecosystem precedes that at the wet meadow by a week or more.

**Toolik Lake.**—Toolik Field Station, Alaska, is located on the shores of Toolik Lake in the northern foothills of the Brooks Range. The terrain of the foothill province is highly variable, with elevation ranging from 180 m to >1050 m. Elevation in the vicinity of Toolik Lake ranges between 650 and 850 m (Walker et al. 1994). The terrain where the study was conducted is located within the Ikillik I formation that was deglaciated ~60 000 years ago (Hamilton 1986). The climate is continental arctic with cold winters and relatively warm summers (Chapin and Shaver 1985). The snow-free period is highly variable, with snowmelt occurring between mid-May to early June. Persistent fall snow cover initiation is also highly variable, commencing as early as mid-September or as late as December. However, snowfall may occur on any given day in the summer. The period of temperatures suitable for plant growth is usually 9–12 weeks. The vascular flora in the vicinity of Toolik Lake and nearby Imnavait Creeks consists of ~300 species (Walker and Walker 1996).

At Toolik Lake, standard ITEX OTCs were installed in both dry heath and moist tussock tundra ecosystems (Jones et al. 1998, Walker et al. 1999). The dry heath is dominated by *Dryas octopetala*, *Salix phlebophylla*, *Arctous alpina*, and fruticose lichens located on Pergelic Cryumbrepts. Thaw depth may attain 1 m or more, but is often difficult to determine because of the rocky soils. The moist tussock ecosystem consists of dwarf tundra dominated by the graminoids *Eriophorum vaginatum* and *Carex bigelowii*, the deciduous shrubs *Betula nana* and *Salix pulchra*, and the evergreens *Ledum palustre* and *Vaccinium vitis-idaea*. The dominant plant at the site is *Eriophorum vaginatum*, a sedge that forms tussocks or raised mounds with the current years growth, persisting on top of the previous years growth. Soils are Pergelic Cryaquepts with thaw depths attaining 50–60 cm.

### *CO<sub>2</sub> flux measurements*

We used techniques similar to those described by Bartlett et al. (1989), Whiting et al. (1991), Vourlitis et al. (1993), and Tenhunen et al. (1995). Rapid, transient measurements of ecosystem CO<sub>2</sub> exchange are made using a portable transparent acrylic chamber attached to a base permanently installed in the soil. Carbon dioxide concentration changes were measured with a LI-6200 portable photosynthesis system (LI-COR, Lincoln, Nebraska, USA). For each measurement, three 30-s incubation periods were recorded. If the values of the sequential readings differed substantially or showed a strong directional trend, the process was repeated until a steady value was obtained. Measurements were conducted every 4 h over 24-h periods at regular intervals during the course of the growing season (Table 2).

For ecosystem dark respiration, the flux chamber was covered with an opaque black cloth during measurement. At Alexandra Fiord and Toolik Lake a dark measurement was made each sample interval. However, at Barrow and Atqasuk the larger number of plots precluded measurement of ER on each plot every 4-h sample period, so all plots were measured for both NEE and ER at only one sample period (04:00 hours). At all other sample periods, all plots were measured for NEE but only one reference plot of each treatment was measured for ER. The ratio of ER of the reference plot to ER of each of the other sample plots at 04:00 hours was used to scale ER of the reference plot at each sample period to calculate ER for the other sample plots. Effectively, the reference plot was used to determine the temperature response of respiration for that treatment during the course of the day, and that response was applied to the dark respiration of the other plots measured at 04:00 hours to calculate respiration rates for all plots and sample periods. Gross ecosystem photosynthesis was then calculated for each plot as NEE minus ER. This procedure was very effective at the wet sites. At the Barrow dry site, out-gassing of CO<sub>2</sub> occurred on rare occasions from individual plots during a sample period in response to unknown causes, resulting in unusually high CO<sub>2</sub> effluxes. These events resulted in negative GEP estimates, in which case the GEP data were discarded. Flux data are presented from the ecosystem perspective rather than the atmospheric perspective, that is, fluxes from the ecosystem are treated as negative and fluxes into the system (photosynthetic uptake) are treated as positive.

At Alexandra Fiord, flux chamber bases were installed in three warmed and three control plots of each of the dry, moist, and wet ecosystems the year prior to measurements. Bases consisted of welded aluminum. The flux chamber was 75 × 75 × 30 cm (w × w × h), made of transparent acrylic. At Barrow and Atqasuk, bases for gas flux measurements were also installed the year prior to initiation of flux measurements. Bases consisted of 30 cm deep sections of 45 cm diameter polyvinyl chloride pipe sunk nearly level with the soil

surface. Five bases were installed in warmed and control plots in both the wet and dry ecosystems. The flux chambers consisted of a 45 cm diameter and 70 cm tall transparent acrylic cylinder that was sealed to the polyvinyl chloride base. At Toolik the bases consisted of welded polypropylene installed in May of 1995 measuring 30 × 30 cm and 20 cm deep. Three bases were installed in warmed and control plots of both the dry and moist ecosystems. The flux chamber was 30 × 30 × 30 cm, made of transparent acrylic plastic. Because of their remoteness, the number of data sets obtained from Atqasuk and Alexandra Fiord were fewer than at Barrow and Toolik, but spanned the majority of the growing season (Table 2).

### *Data analysis*

The mean of the last two of the three CO<sub>2</sub> flux observations were used as the final data for each plot. For a variety of reasons, including severe weather and operator error, a small number of data points were not collected or were lost or discarded. For the purpose of calculating seasonal mean fluxes, when possible, these missing data were estimated (gap-filled) using one of three procedures. The standard procedure was to fit a simple model to the light response for the other data points for that plot and use light data for the missing data point (either measured by the LI-6200 or from a nearby weather station) to estimate the missing flux data. Missing dark respiration measurements were estimated from relationships between flux and temperature measurements. If no light or temperature data were available, the point was taken as the mean of points before and after the missing value.

The individual values of flux parameters (NEE, ER, and GEP) were evaluated for the effects of treatment in a separate ANOVA for each study site, ecosystem, and year after testing for normality and homogeneity of variances (Zar 1998). The effects of year, ecosystem (wet, moist, dry), and location (study site) on mean July canopy air temperature and seasonal mean flux components of all the study sites were evaluated in a three-way ANOVA. We also extracted the highest mean daily GEP found over the season (GEP<sub>max</sub>) to reflect the maximum potential uptake for a given ecosystem. Pearson correlations were used to evaluate relationships between air temperature at canopy height and flux parameters. Statistical analyses were conducted using the SAS 9.0 software package (SAS Institute, Cary, North Carolina, USA).

## RESULTS

### *Canopy air temperature*

Mean July canopy-level air temperatures increased 1°–2°C over control temperatures in response to the OTCs (Fig. 2). The lowest control temperatures were found in Barrow (3.5°–4°C) and highest at Toolik Lake (15.5°–16.5°C). Analysis of July air temperatures across location, ecosystem, and treatment revealed significant

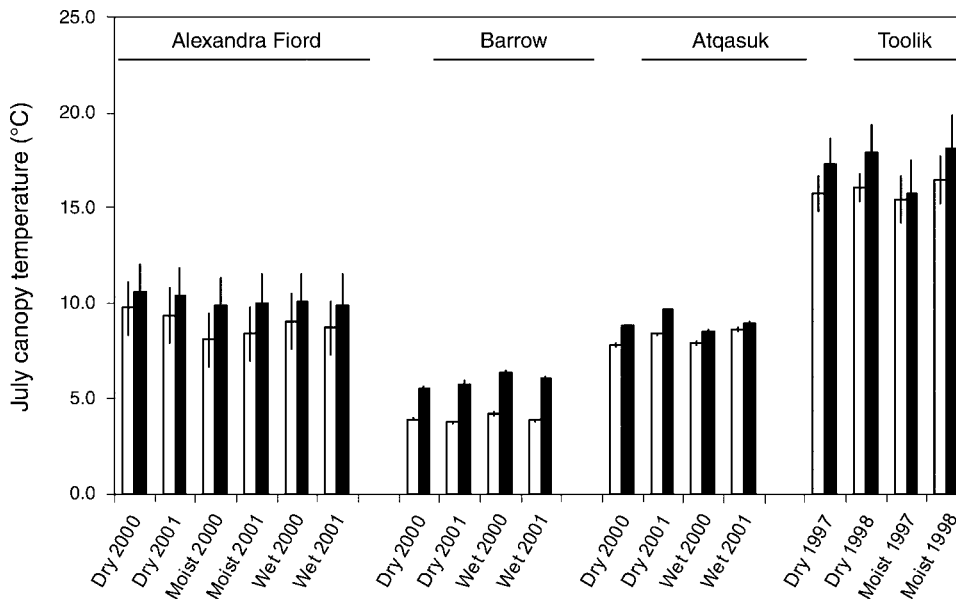


FIG. 2. July canopy air temperature (mean  $\pm$  SE) within controls (open bars) and open-top chambers (OTCs; shaded bars) for the four study locations. Abscissa variables indicate ecosystem type and years of measurement.  $N = 3$  for Alexandra Fiord and Toolik, and  $N = 4-7$  for Barrow and Atqasuk. The sample size represents the number of plots measured for each treatment (warmed or control) within each ecosystem.

effects of location, ecosystem, treatment, year, and a location  $\times$  treatment interaction (Table 3).

*Net ecosystem exchange*

The effect of OTC warming treatments on NEE depended on both ecosystem and location (Fig. 3, Tables 4 and 5). The Toolik Lake moist ecosystem showed increased carbon losses with warming in both years, with the difference close to significance in 1998. Even larger declines were seen at the Toolik Lake dry heath, which also showed increased losses with warming in both years. At both Atqasuk and Barrow, warming significantly increased carbon losses in dry ecosystems and increased carbon uptake in wet ecosystems. The increase in carbon losses at the Barrow dry ecosystem was large (seasonal mean NEE decrease of 0.5–1.0  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ; Fig. 3) and similar in magnitude to the losses in response to warming at the Toolik Lake dry site. At Alexandra Fiord, warming did not significantly affect NEE in any of the ecosystems, and for the dry plots, results reversed between years. The NEE of wet-ecosystem warming and control plots were almost identical in one of the two sample years and warming decreased NEE in the other year. In the moist ecosystem, which lost carbon over the growing season, the mean carbon loss tended to be reduced by the warming treatment in both years. However, after combining the data of the two growing seasons shown here into a single exemplar season for statistical analysis, Welker et al. (2004) reported a significant increase in CO<sub>2</sub> uptake in the dry and moist sites and a significant reduction in the wet site at Alexandra Fiord.

When seasonal mean NEE values of all the locations and ecosystems were compared in a three-way ANOVA, we found significant effects of ecosystem, year, and the location  $\times$  ecosystem interaction (Table 5). The interaction between location and treatment was marginally significant ( $P = 0.094$ ; Table 5).

*Ecosystem respiration*

Ecosystem respiration generally increased with warming in all ecosystems, with the exception of the Atqasuk wet and the Toolik Lake moist plots, both of which had slight decreases with treatment (Fig. 3). Increases were significant in all dry ecosystems and for all years except the dry ecosystem at Alexandra Fiord in 2000 (Table 4, Fig. 3). Differences between OTC treatments and controls were not significant for any of the wet or moist ecosystems (Table 4, Fig. 3).

Comparison of seasonal means from all locations and ecosystems revealed significant effects of location, ecosystem, and location  $\times$  ecosystem and treatment  $\times$

TABLE 3. Results of three-way ANOVA for the effects of location (study site), ecosystem, year, and interactions for mean July canopy-level air temperature.

Factor	df	F	P
Location	2, 19	330.5	<0.001
Ecosystem	2, 19	3.9	0.036
Treatment	1, 19	100.2	<0.001
Year	2, 19	7.7	0.032
Location $\times$ treatment	3, 19	3.2	0.042
Location $\times$ ecosystem	3, 19	2.3	0.102
Treatment $\times$ ecosystem	2, 19	0.12	0.881

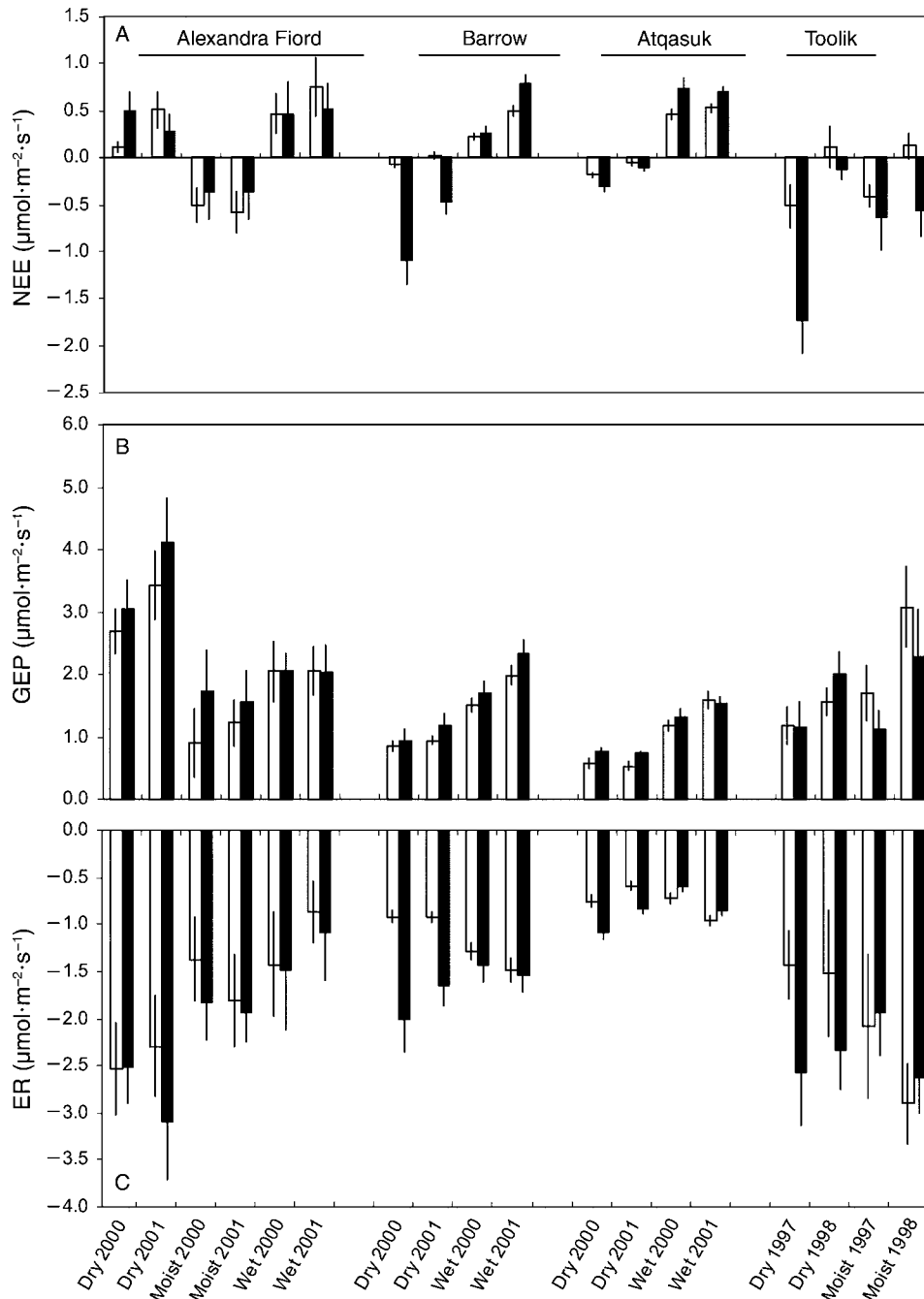


FIG. 3. (A) Net ecosystem CO<sub>2</sub> exchange (NEE), (B) gross ecosystem photosynthesis (GEP), and (C) ecosystem respiration (ER) for the four study locations (seasonal mean  $\pm$  SE). Abscissa variables indicate ecosystem type and years of measurement. Open bars represent controls; shaded bars represent open-top chamber warming treatments.  $N = 3$  for Alexandra Fiord and Toolik, and  $N = 5$  for Barrow and Atqasuk. The sample size represents the number of plots measured for each treatment (warmed or control) within each ecosystem.

ecosystem interactions (Table 5). Notable were the high respiration values found at the dry ecosystem at Alexandra Fiord. Seasonal mean values from the controls ( $-2$  to  $-2.5$   $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) were more negative than the values from the Toolik Lake dry site and similar to those of the Toolik Lake moist ecosystem.

#### Gross ecosystem photosynthesis

Similar to ER, seasonal mean GEP was unchanged or increased in response to warming for all sites, with the exception of the Toolik Lake moist ecosystem (Fig. 3). Significant increases were only found for the Atqasuk dry ecosystem, but near-significant values were found



TABLE 4. Results from one-way ANOVA for effects of open-top chamber (OTC) warming on net ecosystem CO<sub>2</sub> exchange (NEE), ecosystem respiration (ER), and gross ecosystem photosynthesis (GEP) of the four individual International Tundra Experiments (ITEX).

Site and ecosystem	df	Year	P		
			NEE	ER	GEP
<b>Alexandra Fiord</b>					
Wet	1, 4	2000	0.998	0.842	0.995
Wet	1, 4	2001	0.380	0.139	0.952
Moist	1, 4	2000	0.418	0.190	0.305
Moist	1, 4	2001	0.432	0.667	0.593
Dry	1, 4	2000	0.431	0.899	0.617
Dry	1, 4	2001	0.610	0.001**	0.087†
<b>Barrow</b>					
Wet	1, 8	2000	0.572	0.993	0.603
Wet	1, 8	2001	0.002**	0.763	0.197
Dry	1, 8	2000	0.004**	0.016*	0.829
Dry	1, 8	2001	0.003**	0.001**	0.291
<b>Atqasuk</b>					
Wet	1, 8	2000	0.058†	0.117	0.395
Wet	1, 8	2001	0.063†	0.215	0.847
Dry	1, 8	2000	0.062†	0.009**	0.057†
Dry	1, 8	2001	0.395	0.007**	0.043*
<b>Toolik Lake</b>					
Moist	1, 4	1997	0.672	0.661	0.394
Moist	1, 4	1998	0.070†	0.252	0.111
Dry	1, 4	1997	0.001**	0.001**	0.926
Dry	1, 4	1998	0.907	0.001**	0.057†

\*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; †  $P \leq 0.1$ .

for single years for the dry sites at Toolik Lake and Alexandra Fiord (Table 4). Again, after combining the data of the two growing seasons shown here into a single exemplar season, Welker et al. (2004) reported significant increases in GEP for the dry and moist sites at Alexandra Fiord.

Comparison of seasonal GEP across region and ecosystems revealed significant effects of location, ecosystem, year, and a location × ecosystem interaction (Table 5). Somewhat surprising but in accord with the ER values was the finding of high GEP values for the Alexandra Fiord dry site (controls, 2.6–3.4  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ; warmed, 3.1–4.2  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ).

We identified the highest mean daily gross ecosystem production (GEP<sub>max</sub>) among all sample dates over the season to facilitate comparisons of the maximum carbon

uptake potential for each ecosystem. The pattern among sites and treatments was essentially the same as that for seasonal mean GEP, with the exception that values of the Alexandra Fiord dry site were similar to rather than greater than those of the Toolik moist site. For the lowest temperature sites, Barrow and Atqasuk, greatest peak photosynthetic potential were found for the warming plots, with the lone exception of the Atqasuk wet ecosystem in 2001. As with mean GEP, GEP<sub>max</sub> values were higher for wet ecosystems than for dry ecosystems. On control plots, the wet ecosystems had approximately double the GEP<sub>max</sub> of the dry ecosystems for both Barrow and Atqasuk. Contrary to our expectations, GEP<sub>max</sub> of both wet and dry ecosystems were greater at Barrow, the cooler, more northerly site, than at Atqasuk in both years. At Alexandra Fiord, the highest GEP<sub>max</sub> values were found for dry ecosystems with the moist and wet ecosystems similar. At Toolik Lake, the moist ecosystem generally had higher GEP than the dry ecosystems. However, for the moist ecosystem in both years, GEP<sub>max</sub> unexpectedly decreased in response to warming. In one of the two years, GEP<sub>max</sub> also decreased at the dry ecosystem.

*Relationship between temperature and flux variables*

We tested for correlations between CO<sub>2</sub> flux components and July canopy temperatures across all sites and ecosystems (Fig. 4). For the controls, relationships between canopy temperature and CO<sub>2</sub> flux components were significant for GEP<sub>max</sub> and ER. Maximum gross ecosystem photosynthesis increased with increased temperature, while both NEE and ER became more negative with increased temperature. Compared to the temperature-flux relationships for control plots, warming by OTCs decreased the slope of GEP and NEE with temperature toward greater carbon losses as a result of the declines in GEP at the Toolik Lake moist site (Fig. 4). Only the relationship between ER and canopy temperature was significant for the warmed plots ( $P = 0.03$ ).

To examine further the response to OTC warming on maximum photosynthetic potential, we plotted the change in GEP<sub>max</sub> in response to warming vs. mean July canopy temperature (Fig. 5). Overall responses to warming were greater in dry sites than in moist or wet

TABLE 5. Results of three-way ANOVA for the effects of location (study site), ecosystem, year, and interactions for seasonal mean CO<sub>2</sub> flux components, net ecosystem CO<sub>2</sub> exchange (NEE), ecosystem respiration (ER), and gross ecosystem photosynthesis (GEP).

Factor	df	NEE		ER		GEP	
		F	P	F	P	F	P
Location	2, 19	1.8	0.199	22.4	<0.001	42.2	<0.001
Ecosystem	2, 19	27.5	<0.001	5.1	0.016	7.9	0.003
Treatment	1, 19	0.1	0.708	0.1	0.787	0.11	0.746
Year	2, 19	5	0.002	0.1	0.957	6.7	0.006
Location × treatment	3, 19	2.4	0.094	0.1	0.976	1.8	0.170
Location × ecosystem	3, 19	6.2	0.004	7.0	0.002	28.8	<0.001
Treatment × ecosystem	2, 19	1.7	0.217	5.6	0.013	0.98	0.393

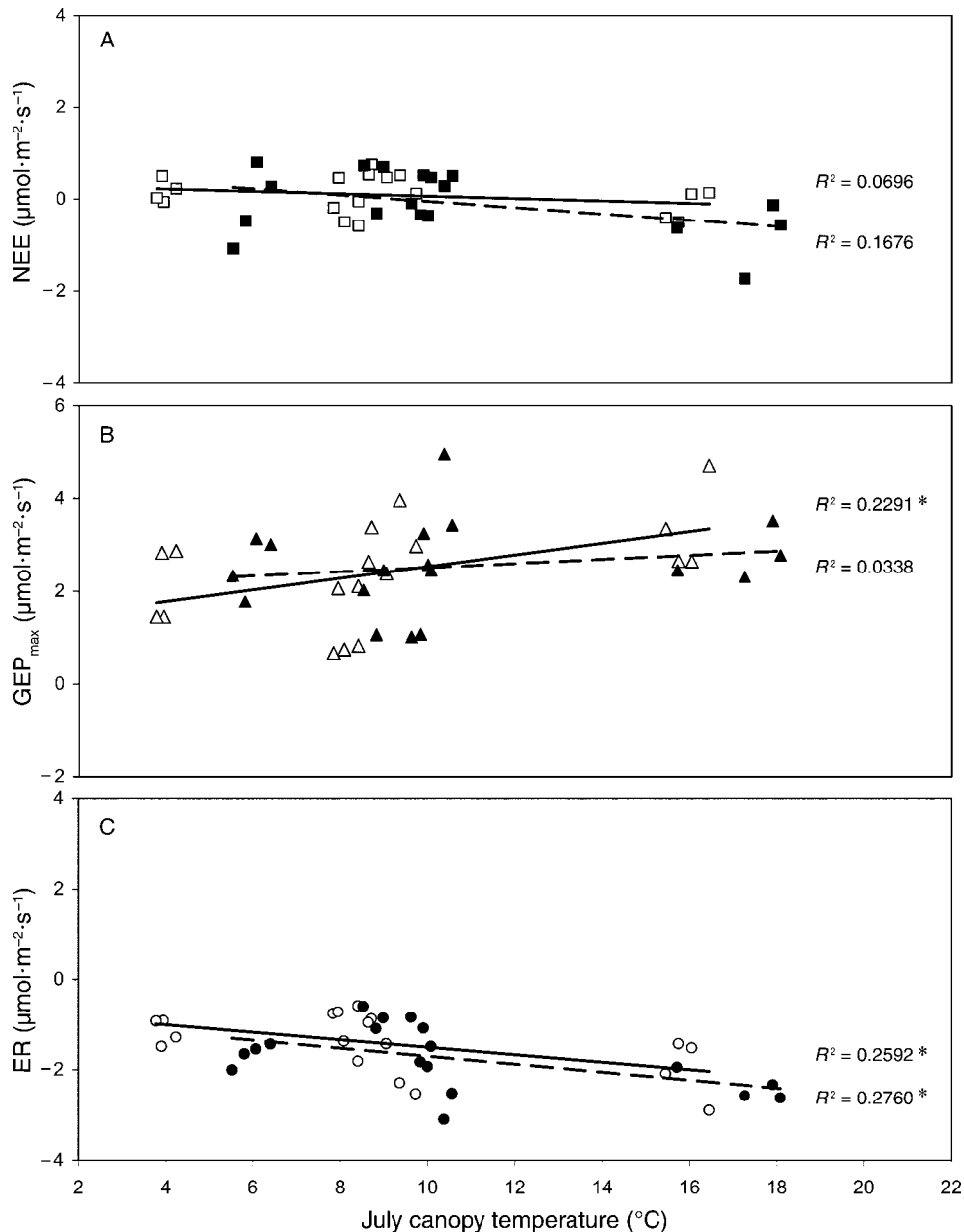


FIG. 4. (A) Net ecosystem CO<sub>2</sub> exchange (NEE), (B) maximum gross ecosystem photosynthesis ( $\text{GEP}_{\text{max}}$ ), and (C) seasonal mean ecosystem respiration (ER) vs. mean July air temperature for the four study locations. Linear correlations for controls are represented by solid lines and open symbols, while those for warmed plots are represented by dashed lines and solid symbols. An asterisk indicates a significant correlation at  $P < 0.05$ . Note the shift in the ordinate scale in (B).

sites. Three out of the four ecosystem–year combinations at Toolik showed declines in  $\text{GEP}_{\text{max}}$  in response to warming.

#### DISCUSSION

While a number of prior studies of CO<sub>2</sub> flux in response to warming have been conducted for individual ecosystems and in a few cases for different ecosystems within a single site, this study represents the first multiple-site comparison of ecosystem CO<sub>2</sub> flux respons-

es to a standard warming experiment across a large climate gradient. Furthermore, incorporation of a soil moisture gradient within the study allowed for the first time simultaneous testing of warming responses to both climate and soil moisture effects and their interactions. Previous studies of CO<sub>2</sub> flux responses to warming have focused on wet or moist tundra. Our inclusion of dry tundra ecosystems within each study site helps fill an important gap in the knowledge base available for the warming responses of these relatively understudied

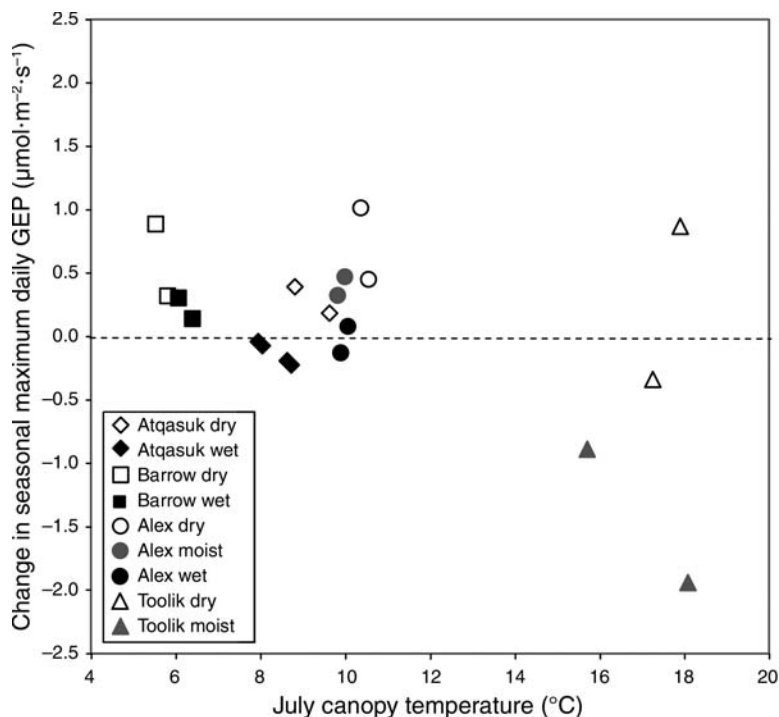


FIG. 5. Change in maximum gross ecosystem photosynthesis ( $GEP_{max}$ ) with open-top chamber (OTC) warming vs. mean July air temperature within OTCs for the four study locations.

ecosystems. Below we consider the effects of climate, soil moisture, OTC warming, and their interactions within the framework of this study and in consideration of previous studies.

*Effects of location (study site)*

Our study sites spanned  $>10^\circ$  of latitude and an annual mean temperature range of  $6^\circ\text{C}$ . However, because Alexandra Fiord is a polar oasis, it was intermediate in growing-season temperatures despite its location  $7^\circ$  north of Barrow. As a result, the range of growing-season temperatures measured in this study was smaller than would be expected based on latitude alone. Nevertheless, we found highly significant effects of location for all the components of  $\text{CO}_2$  exchange and temperature. We also found a trend of higher  $GEP_{max}$  and ER on control plots with higher July temperatures (Fig. 4). Because both GEP and ER increased with temperature, NEE did not show a significant relationship with July canopy temperatures. This pattern of GEP and ER reflects the general pattern of high biomass and production in warm arctic ecosystems (Bliss 2000) and in this case is largely driven by the high GEP and ER at Toolik Lake. Toolik Lake had by far the greatest biomass for both moist/wet and dry sites, whereas the site with the lowest biomass was Atqasuk (S. F. Oberbauer, unpublished data), which also had low overall GEP. The ratio of maximum daily GEP to biomass revealed contrasting patterns for wet and dry sites (Fig. 6); GEP per biomass decreased with

increasing latitude for wet sites and increased for dry sites. Decreasing GEP per unit biomass with increasing latitude, as seen for the wet sites, might be expected given the less-favorable conditions for photosynthesis at high latitudes. The opposite pattern, seen for dry ecosystems, likely reflects the greater proportion of woody biomass at low-latitude sites compared to high-latitude sites.

We had hypothesized that the increases in GEP and ER with warming would be greatest for ecosystems at

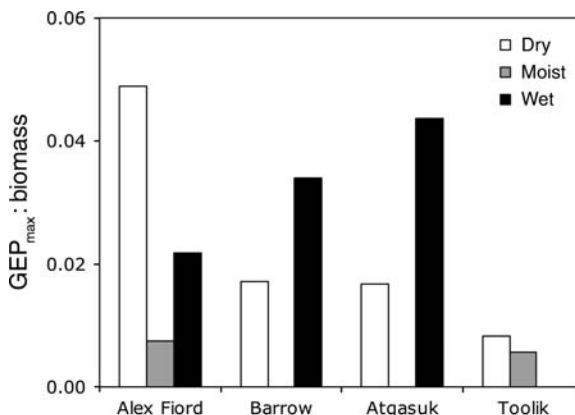


FIG. 6. Ratio of maximum gross ecosystem photosynthesis ( $GEP_{max}$ ) to biomass for control plots in dry, moist, and wet ecosystems in the four study locations.  $GEP_{max} : \text{biomass}$  values are in  $\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$ .

the lowest temperature because temperature limitation would be the largest (Callaghan et al. 2004). When we expressed the response to warming for the CO<sub>2</sub> flux components as a percentage of the control values, we found that the proportional response of GEP<sub>max</sub> to warming significantly declined with increasing temperature ( $P = 0.03$ ) as predicted. The pattern was largely driven by the decline of GEP with warming at Toolik Lake rather than strong increases at Barrow. The relative response of ER, however, did not change significantly with warming because wet ecosystems showed no relationship between the increase in ER and July air temperature. In a regional study of ecosystem fluxes of different tundra types, McFadden et al. (2003) also reported no relationship between ER and temperature. The absolute differences between warmed plots and controls for CO<sub>2</sub> flux components were not significant, although for both GEP<sub>max</sub> and ER, the tendency was for increasing magnitudes with increased temperatures. The declines in GEP and ER with warming found at the Toolik Lake moist site weakened the relationships substantially.

#### *Effects of soil moisture*

As might be expected, differences among the ecosystems were significant for all components of CO<sub>2</sub> flux and temperature. Although a comparison among equivalent ecosystems at each study site would have been ideal, the ecosystems included within our moisture categories represent a continuum of moisture conditions. Even so, the effects of high water tables on soil anoxia and consequently soil respiration were clearly evident at the wet ecosystems. For example, at the two regions that were most alike, Barrow and Atqasuk, we found similar patterns of positive NEE for wet ecosystems and negative NEE for dry ecosystems and higher GEP for wet ecosystems than for dry ecosystems. The wet meadow at Atqasuk represents the extreme on the wet end of the continuum, with standing water above the soil surface nearly the entire growing season, whereas the wet ecosystem at Barrow had infrequent standing water. The wet ecosystem at Alexandra Fiord was similar in physiognomy to those at Barrow and Atqasuk and had positive carbon balances during the summer, though unlike those at Barrow and Atqasuk, it had lower GEP than the Alexandra Fiord dry ecosystem. The effects of moisture are less clear in the intermediate ecosystems.

Similar to the wet meadows at Barrow and Atqasuk, the carbon balance of the moist ecosystem at Alexandra Fiord responded positively to warming, but unlike the wet systems at Barrow and Atqasuk, it was negative over both growing seasons. The moist ecosystem at Alexandra Fiord was somewhat anomalous, however, because a glacial outwash stream suddenly changed course during the growing season of the first year of CO<sub>2</sub> exchange measurements (2000), increasing water flow over the plots. The sudden change in water flow caused the hydrologic conditions to become more similar to

those of wet sites while the vegetation remained typical of a moist site. At the Toolik Lake moist ecosystem, where the water table was variable over the growing season, GEP was highest, but NEE was similar among moist and dry ecosystems during the two measurement years. Dry ecosystems were consistently carbon sources or carbon neutral during the growing season, except at Alexandra Fiord. That ecosystem was structurally somewhat similar to the Toolik Lake dry heath, but had very high GEP. Because it is a streamside environment with relatively good soils (Muc et al. 1994a), the nutrient and water regimes may have been more favorable than those at the Toolik Lake dry heath.

#### *Effect of OTC warming*

The overall analysis comparing seasonal means of CO<sub>2</sub> exchange components for all locations and ecosystems showed no effect of OTC warming ( $P = 0.708$ ; Table 5). Such a result is not surprising given the divergent responses to warming across all locations and ecosystems and the low power of the analysis for testing treatment effects. The power for testing effects of OTC warming was in the individual location tests (Table 4). We found two consistent patterns of ecosystem CO<sub>2</sub> fluxes in response to simulated climate warming. First, mean ER and GEP tended to increase in most ecosystems in response to OTC warming. Second, increases in ER at dry ecosystems were greater than those at wet ecosystems. This latter difference is likely a result of the different controls on below- and above-ground respiration (Oberbauer et al. 1996a, b, Callaghan et al. 2004, Marchand et al. 2004). At the wet ecosystems, warming increased aboveground biomass and ecosystem respiration, but low soil aeration likely limited belowground respiration. At dry ecosystems, soil aeration was not limiting and increases in soil temperature likely increased both respiration of belowground biomass and decomposition rates.

The exceptions to these patterns were the Alexandra Fiord wet site, where GEP was unaffected by warming, the Atqasuk wet site, where GEP was unaffected and ER declined with warming, and the Toolik Lake moist site, where both GEP and ER declined with warming. An important consideration is that the treatment effects at the time of exchange measurements represent the cumulative ecosystem response to warming over the entire duration of the experiments, and responses earlier in the experiment may determine the treatment effects in later years (Hollister et al. 2005). For example, at the Atqasuk wet meadow, increased growth in response to warming in the early years of the experiment resulted in large accumulations of standing litter that effectively shaded the soil and standing water (Hollister et al. 2005, 2006). As a result, soil temperatures in the OTCs on these plots during the years of this study were lower than those of the controls, and we saw lowered ER as a result.

The cause for the surprising and strong decline in GEP at the Toolik Lake moist ecosystem in response to

warming is unclear. Vegetation was taller in the OTCs than in the control plots (Wahren et al. 2005) and therefore was likely greater in biomass, so presumably at some time earlier in the experiment GEP was greater in the OTCs than in controls. Although July air temperature in 1997 was similar to the long-term mean, the mean in 1998 was much warmer, 2.6°C higher. Temperatures within the flux chambers, which sometimes exceed air temperature during measurements, may have exceeded the photosynthetic optimum, resulting in lower estimated GEP. However, because the OTCs were removed during flux measurements, any effect would have been seen in the controls as well as warmed plots. Why respiration did not increase and why the GEP decline occurred on the moist tundra but not on the dry tundra is unknown. Measurements of tissue  $\delta^{13}\text{C}$  suggest that plants within the OTCs may have experienced greater water stress than in the controls (J. M. Welker, unpublished data). A data set from these plots from the year prior to the current study (1996) showed higher peak respiration and highest peak GEP on the warmed plots early in the season but a reversal toward lower GEP in the warmed plots later in the season (Jones et al. 1998).

For our comparisons of maximum GEP with temperature, we used mean July temperatures because peak biomass typically occurs in July. However, timing of bud break and rate of leaf expansion are controlled by temperatures earlier in the season, particularly in warmed plots (Oberbauer et al. 1998, Pop et al. 2000). Peak GEP may be determined by temperatures prior to July, and if July temperatures do not reflect the temperatures during the majority of leaf production, the strength of the relationships between GEP and temperature would be weakened. Furthermore, early-season warming accelerates growth within OTCs over that of the controls, and they may attain peak GEP earlier than the controls. In the remote sites where we were only able to sample infrequently, we could have missed the absolute peak GEP of OTCs, while hitting those of the controls by measuring at "normal" peak season. However, Toolik Lake, the site with the unexpectedly lower GEP with warming, had good seasonal coverage of sampling.

One consideration when comparing OTC warming responses is that OTC warming may not be equally effective at all sites. Cloudiness, wind, soil moisture, and vegetation type may affect warming by OTCs, and all may differ from year to year (Marion et al. 1997, Hollister and Webber 2000, Hollister et al. 2006). For example, as a result of large amounts of standing water with a high specific heat, OTC warming may be less effective in wet ecosystems than dry ecosystems (Marion et al. 1997). However, in this study we did not find a significant treatment  $\times$  ecosystem interaction for canopy temperature (Table 3). We did find that air temperatures differed significantly across ecosystems, and a significant location  $\times$  treatment interaction indicates that some

differences found in this study may be partially the result of differences in the warming treatments. Warming also differed among years. We found significant effects of year for both GEP and NEE. Interannual variation effects can be as strong as warming treatments (Hollister and Webber 2000) and may cause summer carbon balance of sites to vary considerably or even switch from source to sink (Lafleur et al. 2001, Lloyd 2001, Harazono et al. 2003, Rennermalm et al. 2005).

#### *Comparisons with other studies*

Flux responses to a variety of warming methods applied to ecosystems ranging from wet to dry tundra are largely, but not entirely, in agreement with what we report here. Below we consider these studies for wet, moist, and dry tundra.

*Wet tundra.*—Using wet sedge tundra microcosms from Barrow, Billings et al. (1982) found decreased NEE at 8°C relative to 4°C, which they attributed to increased ER. No GEP data were collected in that study. Oechel et al. (1998) found only a slight increase in GEP in the second of two years of warming treatment in wet sedge tundra at Prudhoe Bay, Alaska. They attributed the lack of warming response to the treatment not yet having a significant effect (a lag in response to soil warming) and microbial immobilization of nutrients released from warming, although soil temperatures did not measurably increase in response to their treatment. In the same study, experimentally lowering the water table combined with warming reduced GEP significantly, a response that they attributed to water stress. In wet sedge tundra at Toolik Lake, Shaver et al. (1998) found significant increases in aboveground biomass, GEP, ER, and NEE in response to warming. In their analysis, changes in CO<sub>2</sub> fluxes were a result of both increases in aboveground biomass and changes in CO<sub>2</sub> flux per unit biomass that were, in most cases, decreases. That is, biomass increased more than CO<sub>2</sub> flux, suggesting increased importance of shading in the higher biomass plots or reduction in photosynthetic capacity per unit leaf area. In another study at the same sites, Johnson et al. (2000) found only slight increases in GEP and ER in one of two sites of wet sedge tundra that were subjected to a very strong warming (mean of 5.6°C over eight growing seasons). These measurements, however, were only taken on one or two days at peak season and do not provide a representation of the seasonal variation for these treatments. They concluded that most of the increases were a result of phenological shifts toward earlier maturity in the warmed plots.

*Moist tundra.*—The long history of ecosystem research on tussock tundra near Toolik Lake has produced the most comprehensive data sets on responses of tundra to experimental warming. Oechel et al. (1994) found that with warming in a closed, null-balance system, elevated CO<sub>2</sub> plots had increased carbon uptake and warmed plots did not show the down-regulation of GEP seen at ambient temperatures. Long-term green-

house warming treatments within moist tussock tundra at Toolik Lake have shown increases in biomass production relative to control plots (Chapin and Shaver 1996, Shaver and Jonasson 1999). Chapin and Shaver (1996) also found increased photosynthesis in response to temperature for three of the four dominant species tested and an increase in shoot mass in all four species. In a similar study at Toolik Lake, Hobbie and Chapin (1998) found increased GEP and ER with 4°C warming in tussock tundra. Biomass in response to warming changed little, but the community shifted toward more productive deciduous shrubs. Johnson et al. (1996) used growth chambers and tussock tundra microcosms to study the combined effects of warming and soil moisture manipulation. They found a large increase in GEP with a temperature increase from 7° to 15°C under both saturated and field capacity soils. In response to flooding they found no effects on GEP but did find a large reduction in ER. At a moist site in Greenland, Marchand et al. (2004) found increased GEP and ER in response to warming. Increases were a result of both increased biomass and the direct physiological response to warming.

*Dry tundra.*—Few data exist on the effects of warming on the CO<sub>2</sub> exchange of dry tundra. Jones et al. (1998) found warming increased losses in 1996 at the same dry heath at Toolik used in the current study. Both GEP and ER increased in response to warming, but the increase in ER was greatest. Welker et al. (1999) found that warming in dry alpine tundra in Colorado shifted the tundra from a sink to a source during the growing season, with ER increased in response to warming early in the season and GEP enhanced in three of the four samplings. Two studies at Abisko, Sweden, have produced similar results; in moss-dominated heath Christensen et al. (1997) found that the ecosystem was a CO<sub>2</sub> source during the growing season and warming increased CO<sub>2</sub> losses by increasing ER with only a slight, nonsignificant increase in GEP. Also at Abisko, Illeris et al. (2004b) found slight but nonsignificant enhancements in ER and GEP in a dry heath site in response to a relatively strong (3.9°C) long-term (11-year) warming treatment.

*Meta-analyses.*—Several meta-analyses have been conducted on the ecosystem-level responses to warming that have included tundra sites. Dormann and Woodin (2002) found that tundra biomass increases to warming were not significant, though on average biomass of warmed plots was 125% of that of controls. However, physiological responses increased significantly with warming (>40%). Similarly, in a meta-analysis of climate change experiments conducted in Alaska and Sweden, van Wijk et al. (2004) found significant increases in biomass of individual species, but not overall biomass for warming treatments. They suggested that perhaps soil is not warmed sufficiently in the small warming manipulations or the soil is cooled by shading from increased leaf area and litter. They also suggested

that warming treatments might induce water stress in poikilohydric plants. Arft et al. (1999) reported increased growth of individual tundra plants in response to ITEX OTC warming during the first three years of treatment, but did not evaluate whole-plot biomass. Plant community structure and composition changes occurred in response to ITEX warming, with increases in canopy height greatest in moist tundra compared to wet and dry tundra and in the Low Arctic compared to alpine and High Arctic (Walker et al. 2006). In a meta-analysis of soil moisture, nitrogen mineralization, soil respiration, and aboveground plant productivity of four terrestrial biomes including high and low tundra, Rustad et al. (2001) reported decreased soil moisture and increased N mineralization in most tundra sites tested. Soil respiration increased in response to warming in most of the arctic and alpine tundra ecosystems with one exception (Rocky Mountain Biological Station). The greatest increase was reported for the Toolik tussock dry heath site reported here. Plant production was increased in most tundra sites. The greatest production responses were found in low-temperature, low-precipitation regions. Unfortunately, very few of the tundra sites were measured for all four parameters.

#### *Integrated responses to warming*

Effects of warming on carbon fluxes can occur through both direct and indirect mechanisms, with different rate constants for change (Shaver et al. 2000). Effects of warming are also expected to differ among ecosystems starting from different initial temperature, moisture, and nutrient regimes (Callaghan et al. 2004). The responses to warming treatments in the present study are the result of many of the processes conceptualized by Shaver et al. (2000) acting interactively. Gross ecosystem photosynthesis increased through increased production per unit biomass. Such changes can occur through changes in physiological capacity or changes in community composition, i.e., replacement of less-productive species with more-productive species. These changes are largely supported through relaxation of the temperature limitation on physiology both above and below ground (Marchand et al. 2004, Starr et al. 2004). As temperature increases become large, however, optimum temperatures may be exceeded and photosynthesis decreases. Gross ecosystem photosynthesis also increases through increased photosynthetic biomass resulting from a reduction of the temperature limitation on growth and increases in nutrient availability from increased decomposition rates (Hobbie et al. 2002), although such nutrients may be rapidly immobilized by increased activity of microbes (Oechel et al. 1998). Greater biomass and accumulation of standing dead material increase shading within the canopy, lowering photosynthesis per unit biomass. Increased shading of the soil potentially lowers soil temperature and reduces nutrient availability (Callaghan and Jonasson 1995). Ecosystem respiration increases as a result of the

increases in plant biomass, both above- and below-ground, and from increased physiological activity of that biomass, as well as from increases in the activity of microbial enzymes to temperature. In areas of high soil water tables, soil anoxia limits the belowground component of ecosystem respiration and also potentially limits nutrient availability (Hobbie et al. 2002). Areas of intermediate moisture may occasionally be limited by anoxia, and under those limitations, increases in temperature have small effects (Illeris et al. 2004a). Oberbauer et al. (1992) found that with the depth to the water table >10 cm, the primary driver on respiration in riparian tundra was temperature. In dry ecosystems, soil anoxia rarely limits belowground respiration, but physiological activity of both above- and belowground components may be limited by soil moisture. Moist and particularly dry tundras have important biomass contributions from poikilohydric plants, with photosynthetic and respiratory rates strongly determined by moisture content (Green and Lange 1995, Oberbauer et al. 1996a, b). With increased evaporation from warming, depth to the water table may increase, inducing water stress in vascular species from moist sites. Changes in the quality of litter resulting from plant responses to warming affect decomposition rates, but these changes may take several years to develop. We have found, however, that warming and deeper snow may increase the leaf nitrogen of important species such as *Betula* in moist tussock tundra which, in turn, may have a positive feedback on growth, carbon gain, and NEE (Welker et al. 1997, 2004). Given that responses of ecosystem components to warming occur at different rates, the results from this study must be viewed as representative of the responses in what must be a transitory phase of warming of sites starting from different initial conditions (Walker et al. 2006).

#### *Implications for future carbon balances*

The findings of this study have important implications for predictions of future climate scenarios for the Arctic. The finding that wet ecosystems accumulate additional carbon in response to warming scales to a fairly large increase in sink strength for the Coastal Plain of Alaska, where such systems account for a large area. However, these systems could become drier in response to warming, with greater evaporation, permafrost melting, and thermokarst lowering the soil water level. Evidence is accumulating that drying is already occurring in northern Alaska (Hinzman et al. 2005). With drying and warming, increased GEP made possible by greater nutrient availability may be partially offset by increased respiratory losses. For the High Arctic of Greenland, Soegaard and Nordstroem (1999) suggested, based on measurements and modeling, that increased temperatures will cause the site to become a carbon source. Moist tussock tundra such as that near Toolik Lake covers large areas of the Low Arctic. The findings that these sites lost additional carbon with warming and were

already losing carbon or were nearly carbon neutral supports the suggestion that these ecosystems are already carbon sources when winter losses are considered (Oechel et al. 1993, Oechel and Vourlitis 1994, Fahnestock et al. 1998, 1999, Jones et al. 1998) and may become greater sources in the future. However, as mentioned previously, other studies of tussock tundra show increases rather than decreases in GEP in response to warming, so the results reported here may be specific to the conditions during the growing seasons of 1997 and 1998. Corradi et al. (2005), based on comparisons of Siberian tussock tundra measurements and other studies, suggest that with warming the tundra will become a sink rather than a source. Complicating the situation is the recent finding that with long-term fertilization of this ecosystem, soil carbon has dramatically declined (Mack et al. 2004).

Dry tundra and polar deserts cover large areas of the Low and especially the High Arctic. Our sample design did not include true polar desert representative of vast areas of the High Arctic. However, the dry tundra examined in this study represents large areas of the Low Arctic and should also provide indications of the responses of polar desert. These ecosystems were currently CO<sub>2</sub> sources or neutral during the growing season and were undoubtedly CO<sub>2</sub> sources annually when winter losses are considered. Warming dramatically increased growing-season CO<sub>2</sub> losses, pointing toward further losses from these ecosystems in the future. Growing-season thaw depths at these sites preclude any soil anoxia effects on respiration. Dry ecosystems are relatively low in production and at Toolik Lake and other areas are exporters of nutrients through windblown litter and winter grazing by caribou. These systems in the Low Arctic are more strongly nutrient-limited than water-limited (Oberbauer and Dawson 1992). All of the dry sites increased GEP in response to warming and overall tended to have greater increases than the wet sites. Whether losses of carbon from these ecosystems will continue with warming after the labile carbon is depleted is not clear. The Barrow and Atkasuk dry sites were in years 7 and 5 of treatment, respectively, when these measurements were started. The polar desert is drier than Low Arctic dry ecosystems, and it may be that in polar deserts increases in carbon uptake will not occur without changes in the moisture regime.

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