

Responses of High Arctic wet sedge tundra to climate warming since 1980

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Abstract

The global climate is changing rapidly and Arctic regions are showing responses to recent warming. Responses of tundra ecosystems to climate change have been examined primarily through short-term experimental manipulations, with few studies of long-term ambient change. We investigated changes in above- and belowground biomass of wet sedge tundra to the warming climate of the Canadian High Arctic over the past 25 years. Aboveground standing crop was harvested from five sedge meadow sites and belowground biomass was sampled from one of the sites in the early 1980s and in 2005 using the same methods. Aboveground biomass was on average 158% greater in 2005 than in the early 1980s. The belowground biomass was also much greater in 2005: root biomass increased by 67% and rhizome biomass by 139% since the early 1980s. Dominant species from each functional group (graminoids, shrubs and forbs) showed significant increases in aboveground biomass. Responsive species included the dominant sedge species *Carex aquatilis stans*, *C. membranacea*, and *Eriophorum angustifolium*, as well as the dwarf shrub *Salix arctica* and the forb *Polygonum viviparum*. However, diversity measures were not different between the sample years. The greater biomass correlated strongly with increased annual and summer temperatures over the same time period, and was significantly greater than the annual variation in biomass measured in 1980–1983. Increased decomposition and mineralization rates, stimulated by warmer soils, were likely a major cause of the elevated productivity, as no differences in the mass of litter were found between sample periods. Our results are corroborated by published short-term experimental studies, conducted in other wet sedge tundra communities which link warming and fertilization with elevated decomposition, mineralization and tundra productivity. We believe that this is the first study to show responses in High Arctic wet sedge tundra to recent climate change.

Keywords: climate change, Ellesmere Island, High Arctic, tundra ecosystems, wetlands

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Introduction

Arctic regions are showing strong responses to recent climate warming due to a complex of feedback processes (Maxwell, 1997; Hughen *et al.*, 2000; Serreze *et al.*, 2000; Polyakov *et al.*, 2002; Michelutti *et al.*, 2003; ACIA, 2004). Arctic plants, limited by temperature and nutrient availability, respond directly and indirectly to climate change. Indirect effects caused by changes in soil temperature, including changes in active layer depth and nutrient availability, and changes in precipitation affecting soil moisture are usually found to be more important than direct effects of climate on tundra plants (Tinker & Ineson, 1990; Chapin *et al.*, 1992; Schmidt *et al.*, 1999; Johnson *et al.*, 2000). Species composition and abundance in Arctic tundra ecosystems have been responsive to prehistoric and historic climate fluctuations, as measured through pollen analysis (Kaakinen &

Eronen, 2000; Gajewski & Atkinson, 2003). Current warming trends have caused dramatic responses in a variety of Arctic systems measurable over the past 10–30 years with remote and direct measurement techniques (Serreze *et al.*, 2000; Hinzman *et al.*, 2005; Welker *et al.*, 2005; Rayback & Henry, 2006; Hudson & Henry, 2009). An understanding of the magnitude of changes taking place in the Arctic will enable more accurate prediction of changes expected in the near future.

Responses of tundra vegetation to real and simulated climate warming have been studied across a broad range of plant communities and spatial scales. A common thread found among all such studies is the non-linear nature of tundra species responses to climate change over time (Phoenix & Lee, 2004). Time-lag effects on nutrient cycling processes were often cited as the cause of this notable response (Billings *et al.*, 1984; Chapin & Shaver, 1985; Oechel & Billings, 1992; Chapin *et al.*, 1995; Shaver *et al.*, 2001; Phoenix & Lee, 2004). Multifactor experiments have consistently shown tundra systems to be more responsive to additions of

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nitrogen and phosphorus than to changes in temperature, light, or CO₂ (Chapin *et al.*, 1995; Hobbie & Chapin, 1998; Shaver *et al.*, 1998; van Wijk *et al.*, 2003). If warming only influenced tundra species directly, responses would likely be much smaller than those recorded or experimentally induced. However, elevated temperature has been shown to indirectly enhance growth and productivity by enhancing decomposition and mineralization (Chapin *et al.*, 1995; Robinson *et al.*, 1995; Rustad *et al.*, 2001; Schmidt *et al.*, 2002; Welker *et al.*, 2004; Walker *et al.*, 2006). Increases in productivity through fertilization or warming were most pronounced in deciduous dwarf shrubs, including *Betula nana* (Low Arctic) and *Salix arctica* (High Arctic), and graminoids including *Carex* and *Eriophorum* spp. (Henry *et al.*, 1986; Carlson & Callaghan, 1994; Chapin *et al.*, 1995; Shaver & Chapin, 1995; Shaver *et al.*, 1998; Arft *et al.*, 1999; Jones *et al.*, 1999; van Wijk *et al.*, 2003; Walker *et al.*, 2006; Sullivan *et al.*, 2008). Results from warming experiments have supported: (i) the similar response of control plots to ambient climate warming (Chapin *et al.*, 1995); (ii) increases in NDVI between 1980 and 1990 as found through analysis of satellite imagery (Myneni *et al.*, 1997; Stow *et al.*, 2004); and (iii) the increasing shrub cover over the last 50 years in the northwestern North American Arctic (Sturm *et al.*, 2001; Tape *et al.*, 2006).

Despite the relatively large number of temperature and/or fertilization experiments in tundra systems, most span less than a few years and very few have been maintained for longer than 10 years (Chapin *et al.*, 1995; Hobbie & Chapin, 1998; Shaver *et al.*, 1998; Arft *et al.*, 1999; Johnson *et al.*, 2000; van Wijk *et al.*, 2003; Mack *et al.*, 2004; Welker *et al.*, 2004; Walker *et al.*, 2006). Additionally, most manipulation experiments have been conducted in the Low Arctic, primarily in Alaska (Chapin *et al.*, 1995; Phoenix & Lee, 2004) or in northern alpine systems (e.g. van Wijk *et al.*, 2003). Using a dynamic vegetation model, Epstein *et al.* (2004) predict that a minimum of two decades are needed before ecosystem response to natural climate change can be effectively measured. This has been echoed by many researchers conducting experimental studies who have identified the need for longer-term studies to validate short-term experimental results (Chapin *et al.*, 1995; Arft *et al.*, 1999; Shaver *et al.*, 2001; Phoenix & Lee, 2004; Walker *et al.*, 2006). While continuous long-term studies are rare, remeasuring sites that had been studied in the past allows an examination of responses that may have resulted from recent climate change. Hudson & Henry (2009) provide an example of this approach and show that High Arctic evergreen shrub tundra has increased in biomass over the past 25 years.

Between 1980 and 1984, Henry (1987) and Henry *et al.* (1990) studied wet sedge meadow ecosystems at Alex-

andra Fiord (AF), Ellesmere Island, Nunavut, establishing one of Canada's oldest comprehensive Arctic tundra studies (Svoboda & Freedman, 1994). Warming experiments were established a decade later at the site as part of the International Tundra Experiment (ITEX) (<http://www.geog.ubc.ca/itex>), creating one of the most appropriate sites to study long-term tundra responses to ambient climate change. We hypothesized that the warming climate over the last two decades has enhanced growth and productivity of wet sedge tundra species at AF. We assumed that precipitation changes spanning the duration of the study (25 years) had no effect on soil moisture in the saturated sedge meadows. Our objective was to compare above- and belowground biomass, species responses, active layer depth, and soil characteristics between the early 1980s and 2005. Comparisons were made at both the site scale, to determine the extent of sedge meadow responses and at the species scale in order to understand responses influencing sedge meadow community structure.

Materials and methods

Definitions

Biomass refers to all live above- or belowground plant tissue. Standing crop refers to all live and attached dead plant material, above- or belowground. Litter is unattached aboveground dead plant material.

Study site

The coastal lowland at AF (78°53'N, 75°55'W) is an 8 km² glacial sandur and is ca. 90% vegetated, 20% of which is dominated by sedge meadows with wet or wet-mesic organic soils (Muc *et al.*, 1989). The lowland is bounded by the coast and outlet glaciers in the north and south, and by steep cliffs (500–700 m a.s.l.) on the west and east. Moisture is supplied by snow and glacial melt water, with occasional precipitation events throughout the growing season, and the lowland is drained by one large river and three smaller streams. Overland flow, through a network of hummocks and hollows, also occurs in most wet sedge meadows. The soils of these communities are usually saturated throughout the growing season and as a result, the relatively high net primary production and associated low decomposition rates have allowed thick litter and organic layers to accumulate. Litter accumulation is also due to the lack of large herbivores at the site (Henry *et al.*, 1986; Henry, 1998; Elliott & Henry, 2010). These nutrient deficient cryosols typically have more than 90% of total nitrogen complexed with organic compounds, which limits plant growth and development (Henry *et al.*, 1986; Henry, 1987; Rolph, 2003). Additional site details can be found in Henry (1987, 1998), Henry *et al.* (1990), and Svoboda & Freedman (1994).

Climate analysis

Regional mean daily air temperature data were obtained from the Meteorological Service of Canada for Resolute Bay, Cornwallis Island and Eureka, Ellesmere Island between 1970 and 2005. These stations have operated since the early 1950s and are the closest meteorological stations to AF. Local average daily air temperature at 1.5 m was measured at an automatic climate station at AF, established in a wet sedge tundra area in 1989 (AF Meadow Station). Soil temperature at 10 cm depth was also measured at the AF Meadow Station. Temperatures were measured continuously using thermistors attached to a data logger (equipment from Campbell Scientific Canada Corp., Edmonton, AB, Canada). Temperature trends were analyzed using linear regressions of spring and summer (Day 90–270), fall and winter (Day 271–89), and annual averages of daily temperature against time. All climate data series were tested for sphericity using the Durbin–Watson statistic and no autocorrelation was found.

In addition to the continuous temperature data since 1989 at the AF Meadow Station, daily climate variables have been recorded at another automatic station at the site since 1980 (Labine, 1994). The station is located adjacent to coast near the research camp at Alexandra Fiord (AF Camp Station), and air temperature and precipitation were measured for most of the summer season between 1980 and 1983. Data from this station were used to compare the sample years.

Biomass and soil sampling

The wet sedge tundra sites were analyzed for long-term response to climate change by comparing above- and below-ground biomass harvests and soil samples taken in 1980–1983 (Henry, 1987; Henry *et al.*, 1990) with repeated measurements using the same methods at five of the same sites in 2005. Site A was the largest meadow community on the lowland (~50 ha), sloped at 1% grade to the coast and had 50% hummock cover. Site B was smaller (~3 ha), ~600 m south of site A, and had similar site conditions to site A. Site C was located on a plateau, 20–30 m above the lowland, sloped south at 2–3%, and had slightly smaller hummock features. The conditions of Sites A–C were similar to those given in Henry (1987). Site D, located on a small sandy floodplain of one of the smaller streams, has experienced multiple flood events in the past 25 years, with one large event in 2001. Site E was on a sandy delta formed by a tributary stream draining into the SW part of the lowland. In the late 1980s overland flow that used to pass through Site E became diverted into channels, which now circumscribe the site.

In the early 1980s, (Henry, 1987; Henry *et al.*, 1990) sampled the sedge meadows with a random design. Above- and below-ground standing crop was collected from five randomly located quadrats per site per sample period. In Site A, the quadrats were sampled from within five randomly located permanent areas (5 m × 5 m), whereas in the other sites quadrats were sampled from systematic locations along 30 m transects randomly located in visually homogeneous areas of the wet sedge communities. In 2005, 30 m transects were randomly

established in the same part of the site sampled in the 1980s. Site A was intensively sampled using four transects whereas each of the Sites B, C, D, and E were sampled with only one transect and are referred to as the extensive sites. Eight samples were taken from each transect in Site A and six samples were taken from Sites B, C, D, and E.

In all sites, aboveground (AG) standing crop was sampled between July 28 and August 3, which corresponds to the time of maximum aboveground biomass. The AG standing crop was harvested from a 20 cm × 50 cm (0.1 m²) quadrat by clipping all plant material at the surface, using the same methods as Henry *et al.* (1990). When the quadrat-contained moss, the upper green portion was collected by clipping at approximately 2–3 cm below the moss surface. The aboveground material was sorted by species and then into live green tissue (Gr) and attached dead (Att). In order to reduce identification error and increase statistical power, *Carex* was analyzed as a genus (labeled *Carex* spp.) with the exception of *Carex misandra*, which was easily distinguishable. Essentially all of the *Carex* spp. consisted of *C. membranacea* and *C. aquatilis stans* (Henry *et al.*, 1990). Samples were dried at ~30–40 °C for 24–48 h in the field laboratory and again at 60 °C in a drying oven for 24 h before weighing in the lab at the University of British Columbia (UBC) (± 0.001 g).

Belowground biomass was extracted in Site A in late July or early August using the same methods as (Henry, 1987; Henry *et al.*, 1990). In both the early 1980s and in 2005, two soil cores were taken with a corer (20 cm in depth and 6 cm diameter) from each of the aboveground harvest quadrats, 2 days after the aboveground biomass was harvested. The samples were washed to remove inorganic sediment, shipped in coolers to the lab at UBC. The washed samples were kept at 3–4 °C and sorted into live and dead roots, live and dead rhizomes, and shrub roots.

In order to compare soil pH and soil organic carbon between the 1980s and 2005, soil samples were extracted from plots in Site A with the same methodology as belowground biomass. Soil samples were washed and the majority of roots were removed, dried at 50–60 °C in the field laboratory and again at 60 °C in a drying oven at UBC, pulverized by hand, and sieved through a 2 mm screen. An estimation of soil organic carbon was determined by loss on ignition of dried soil samples at 750 °C for 2 h. In 2005, soil pH was measured with a glass electrode in a 1 : 5 soil to distilled water solution. Measurement of soil pH was the only method that may have differed between this study and Henry (1987) due to an unknown ratio of soil to solution.

Active layer depths were determined using a graduated steel probe in both the 1980s and in 2005. Depths were taken every 6 m along the 30 m transect established for biomass sampling in each site. The active layer depths in Site A in the 1980s were measured along a permanent 30 m transect established to follow the rate of permafrost melting.

Statistical analysis

The data from each quadrat in Henry's (1987) study and the current study were entered using the same format and grouped into the same categories. The 2005 biomass data for

Site A were averaged for each of the transects ($n = 4$) in order to more closely match the sample size ($n = 5$) used in each of the years of the earlier study. For the belowground data, the values for the two cores in each quadrat were averaged to give the biomass per quadrat. Most data conformed to the assumptions for parametric analysis (ANOVA). In instances where the data could not be transformed to these assumptions, we used nonparametric analysis (Wilcoxon's/Kruskal–Wallis test). We only tested for changes between time periods in each site rather than differences among sites, as Henry *et al.* (1990) clearly showed there were spatial differences in net primary production of these wet tundra sites. Our preliminary analysis also showed differences among sites in both sample years and a year \times site interaction for nearly all of the variables tested. An α -value of 0.05 was used for all tests. ANOVAs or Wilcoxon's/Kruskal–Wallis tests were used to compare values of above- and belowground components between sample years within each site using JMP 8 (SAS, 2008). For most comparisons between the sample periods, we used values from 1981 in Henry's (1987) original study, as biomass harvests were made at all of the sites and at the nearly the same dates as in 2005.

Principal components analysis (PCA) was used to visually display and summarize the relationships between plots, species, and time. PCA was used in this case as the gradients within the data were small: a preliminary DCA showed gradient lengths of only 1.4SD units. ter Braak (1995) recommends use of PCA only when gradients are less than 2SD units. All quadrat data from each of the sample periods were used in the PCA ($n = 40$ in 1980s; $n = 56$ in 2005). The PCA was conducted with PC-ORD 5 (McCune & Mefford, 1999). Diversity measures were also calculated in PC-ORD 5 for comparison between the sample periods.

Results

Climate analysis

Air temperature records at Resolute and Eureka depict a warming trend in the Canadian High Arctic over the last 30+ years (Fig. 1). Trends at AF were similar, but winters warmed much more than summers during the 1990s (Fig. 2). The annual air temperature record at AF correlates strongly ($r = 0.93$) with the record at Eureka, which shows a significant warming of $0.8^\circ\text{C}/\text{decade}$ since 1970 (Fig. 1). Soil temperature (10 cm depth) recorded at AF Meadow Station (at Site B) also showed annual and winter warming ($P < 0.05$) to be significantly stronger than summer warming ($P > 0.05$) (Fig. 3).

General climatic conditions during the sampling years 1980–1983 were variable. Mean daily air temperature (\pm SD) in July varied from 5.8°C (± 2.2) in 1983 to 7.3°C (± 2.2) in 1981 (Henry *et al.*, 1990; Labine, 1994). In 2005, mean July air temperature was similar to 1983: 5.5°C (± 2.0). During the 1980s, July precipitation varied from 0.8 mm in 1981 to 11.7 mm in 1982 (Henry *et al.*,

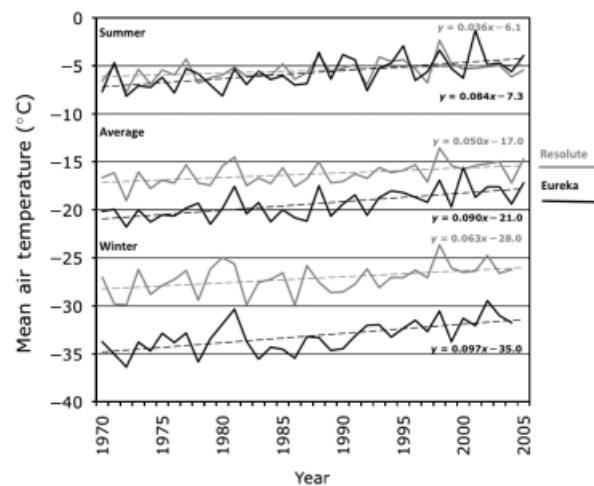


Fig. 1 Summer, annual, and winter mean daily air temperature from Resolute Bay, Cornwallis Island and Eureka, Ellesmere Island, Nunavut, Canada, from 1970 to 2005. Significant linear regressions represented with dashed lines and the corresponding regression equation ($P < 0.05$).

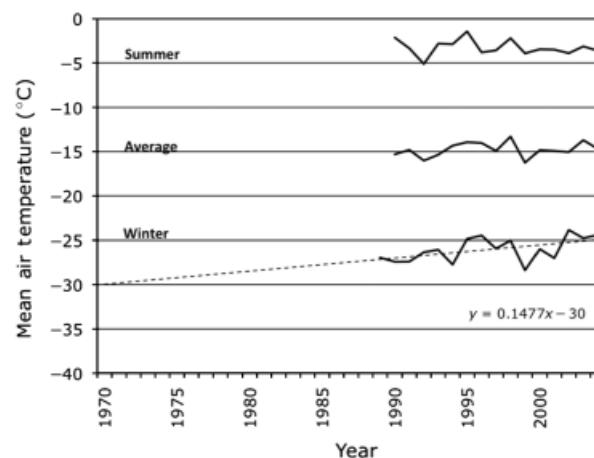


Fig. 2 Summer, annual, and winter mean daily air temperature from Alexandra Fiord Meadow climate station from 1990 to 2003. Significant linear regressions represented with dashed lines and the corresponding regression equation ($P < 0.05$).

1990; Labine, 1994). Precipitation in July 2005 was considerably greater, with 27.9 mm of rain.

Soil responses

Differences between the sample years (1980s mean \pm SE, 2005 mean \pm SE) were analyzed for estimated soil organic carbon ($14.7 \pm 4.2\%$, $21.7 \pm 4.3\%$), active layer depths (76.8 ± 8.1 , 76.1 ± 10.6 cm), and soil pH (6.3 ± 0.4 , 6.1 ± 0.2). Only pH was found to be significantly different ($P < 0.05$). However, with means differing by a pH of 0.2, there is unlikely to be any

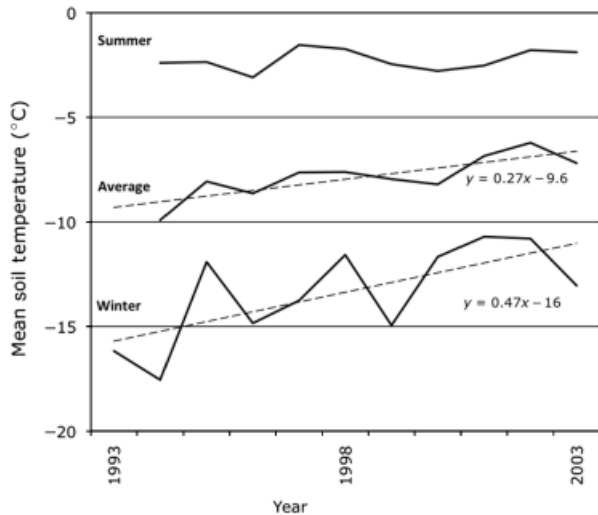


Fig. 3 Summer, annual and winter mean daily soil temperature measured continuously at 10 cm depth at Alexandra Fiord in a sedge meadow near Site B, from 1993 to 2003. Significant linear regressions represented with dashed lines and the corresponding regression equation ($P < 0.05$).

ecologically meaningful effect (H. Schrier, personal communication, 2005).

Belowground biomass response

There was a very strong increase in belowground biomass between the 1980s and in 2005 (Fig. 4): biomass was significantly greater in 2005 ($P < 0.05$) in live roots (64%), live rhizomes (138.5%), and dead roots (348.7%).

Aboveground responses: site level

There was no significant annual variability in mean aboveground biomass for the major species or for all vascular plant combined in the early 1980s ($P > 0.05$) despite variable climate conditions, including significantly different mean annual surface temperatures and active layer depths ($P < 0.05$) (Henry, 1987; Henry *et al.*, 1990).

Green (leaf) biomass was 60–184% greater in all sites in 2005 compared with the 1981 harvests (Fig. 5a; Table 1). These increases were significant at all sites ($P < 0.05$). Site E was the only site to show significant ($P < 0.001$) increases in litter and attached dead with a greater than fivefold increase from $84.0 \pm 17.5 \text{ g m}^{-2}$ in the 1980s to $496 \pm 74 \text{ g m}^{-2}$ in 2005; Site A also showed a positive response although it was nonsignificant ($P = 0.06$) (Fig. 5b). No consistent pattern in litter and attached dead was seen in the responses at the other Sites, although litter at Site D was significantly less in 2005 than in 1981

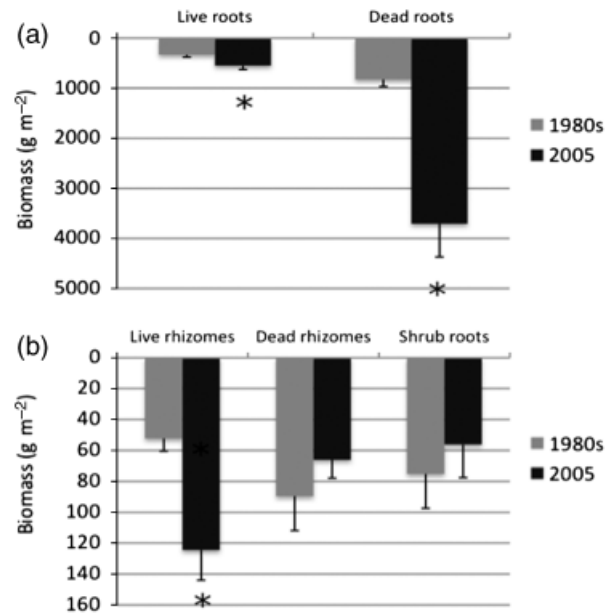


Fig. 4 Belowground biomass and standing crop in late July at Site A in the early 1980s ($n = 20$) and 2005 ($n = 24$), of (a) live roots and dead roots and (b) live rhizomes, dead rhizomes, and shrub roots. Data are means with SE bars. *Significant differences ($P < 0.05$).

(Table 1). A similar trend of greater values in 2005 was observed for total standing crop (Fig. 5c), with significant increases only at Site A, $186 \pm 24 \text{ g m}^{-2}$ (1980s) and $270 \pm 25 \text{ g m}^{-2}$ (2005) and Site E, $106 \pm 23 \text{ g m}^{-2}$ (1980s) and $546 \pm 75 \text{ g m}^{-2}$ (2005).

Community- and species-level responses

Table 1 shows mean biomass values for the major species in the five wet sedge tundra sites at AF in 1981 and 2005. There were significant changes in biomass and total standing crop at all sites between the sample years; however, there were difference among sites as to which species had changed. Overall, the dominant species in each functional group were the most responsive (Table 1). *Carex* spp. showed a consistent increase across all sites in both live biomass and total standing crop, with significant increases found in two sites. *Eriophorum angustifolium* also showed increases in biomass across all sites, although there were statistically significant increases only in two sites. Mean total standing crop of *E. angustifolium* was also greater in 2005 in all sites, but was only significant in Site D. Aboveground biomass of the deciduous dwarf shrub *S. arctica* was also greater in all sites in 2005, with significant differences found in three sites (Table 1). Although a minor component of the biomass at each

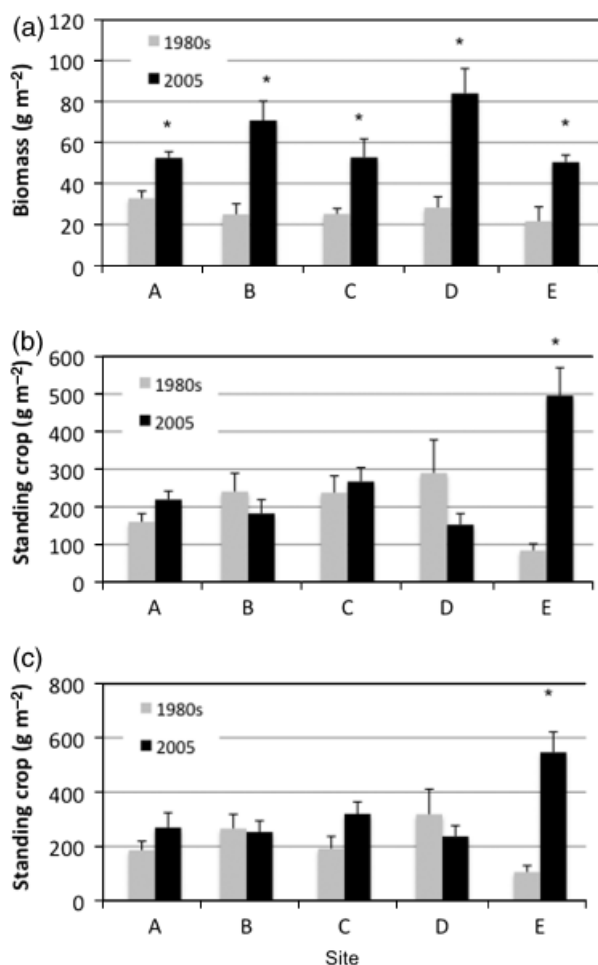


Fig. 5 Aboveground site-level comparisons, between 1981 ($n = 5$) and 2005 ($n = 4$ Site A; $n = 6$ in all other sites) of (a) live biomass, (b) litter and attached dead, and (c) total standing crop. Data are means with SE bars. *Significant differences ($P < 0.05$) between time periods.

site, the forb *Polygonum viviparum* also had significantly greater biomass values in 2005 in four of the five sites. Interestingly, mean biomass values for the dwarf shrub *Dryas integrifolia* were nonsignificantly greater in 2005 than 1981 in four of the five sites, but were significantly lower in Site E ($P < 0.05$) (Table 1).

Biomass values for moss were also generally greater in 2005 than 1981 in four sites and were significantly greater in two of them (Table 1). However, moss biomass was much lower in 2005 in Site E.

The PCA of species biomass showed a shift in position of plots in 2005 relative to those from the early 1980s (Fig. 6). The spread of the 2005 plots around the 1980s cluster is described primarily by the main eigenvectors of the dominant species *E. angustifolium*, *Carex* spp., *P. viviparum*, *S. arctica* and *D. integrifolia* (Fig. 6). These species were the main actors in the community

wide biomass response (Table 1). The first four axes accounted for 54.4% of the variance and a randomization test showed the PCA represents a significant percent of the variability ($P < 0.05$) within the data set (Table 2).

Discussion

Our results show that High Arctic wet sedge meadows have likely responded to recent climate warming, with increased biomass in all sites and dominant species. This conclusion is in opposition to the hypothesis that infertile grasslands are resistant to climate change (Grime *et al.*, 2008).

Climate change

The air temperature increases in the Canadian High Arctic match trends predicted by global climate models and observations made at other Arctic locations (Serreze *et al.*, 2000; ACIA, 2004). Climate monitoring at the meadow site at AF began in the late 1980s, resulting in nonsignificant temperature trends when compared with trends at Eureka and Resolute, which have records extending back to the 1970s. Despite the lack of significance, the strong correlation between AF and Eureka gave us the confidence to assume the warming trend at AF extended back to the early 1980s when this study began. Hudson & Henry (2009) found similar significant air temperature increases for the Canadian High Arctic. The strong winter soil warming trend recorded at AF was likely nonlinear, given that the slope of the linear regression line ($4.5\text{ }^{\circ}\text{C}/10$ years) was more than double that of longer-term soil warming trends from other coastal Arctic locations (Majorowitz *et al.*, 2004; Osterkamp, 2005).

Belowground response

The recorded increase in soil temperature, including winter soil temperature, has likely been a major cause of the significant increase in belowground biomass in the wet sedge tundra site at AF. The combination of increased substrate availability with the direct and indirect effects of increased temperature, created improved conditions for decomposition and mineralization (Pendall *et al.*, 2004; Schimel *et al.*, 2004). This likely led to greater nutrient availability in the soils (Schimel *et al.*, 2004), which in turn supported the increased growth of the tundra plant species, both below- and aboveground. The accumulation of dead roots in the soils of these systems is a clear record of the increased growth belowground over the 25 years. Pendall *et al.* (2004) make special note of the elevated biomass and mortality of

Table 1 Biomass (g) and total standing crop (t) (g m^{-2}) of the major wet sedge tundra species, moss and litter at five sites at Alexandra Fiord in 1981 and 2005

| Species | Site A | | Site B | | Site C | |
|-------------------------------------|-----------------|----------------------|-----------------|-----------------------|-----------------|-----------------------|
| | 1981 (n = 5) | 2005 (n = 4) | 1981 (n = 5) | 2005 (n = 6) | 1981 (n = 5) | 2005 (n = 6) |
| <i>Carex</i> spp. (g) | 15.12 ± 5.03 | 24.18 ± 2.20 | 9.77 ± 4.28 | 44.34 ± 7.76 | 11.26 ± 2.39 | 24.04 ± 6.12 |
| <i>Carex</i> spp. (t) | 40.10 ± 10.75 | 58.65 ± 9.02 | 42.38 ± 19.40 | 111.35 ± 15.25 | 41.78 ± 9.69 | 87.26 ± 27.03 |
| <i>Carex misandra</i> (g) | 0.57 ± 0.44 | 2.17 ± 0.40 | 2.43 ± 1.12 | 0 | 0.58 ± 0.38 | 1.33 ± 0.48 |
| <i>Carex misandra</i> (t) | 3.80 ± 2.93 | 16.38 ± 3.49 | 19.23 ± 10.60 | 0 | 3.77 ± 2.29 | 10.38 ± 2.89 |
| <i>Eriophorum angustifolium</i> (g) | 8.81 ± 1.26 | 17.25 ± 1.90 | 7.99 ± 2.25 | 11.22 ± 2.92 | 4.26 ± 1.41 | 15.14 ± 5.13* |
| <i>Eriophorum angustifolium</i> (t) | 33.30 ± 5.66 | 49.15 ± 8.21 | 26.9 ± 8.43 | 27.83 ± 7.04 | 11.60 ± 2.76 | 56.30 ± 20.72* |
| <i>Kobresia</i> spp. (g) | 0.51 ± 0.51 | 0.41 ± 0.20 | 0.38 ± 0.19 | 0 | 0.04 ± 0.02 | 0.69 ± 0.31 |
| <i>Kobresia</i> spp. (t) | 3.40 ± 3.40 | 2.07 ± 0.83 | 2.09 ± 0.89 | 0 | 0.17 ± 0.09 | 3.78 ± 1.79 |
| <i>Arctagrostis latifolia</i> (g) | 0.04 ± 0.04 | 0.54 ± 0.22 | 0.95 ± 0.47 | 0.41 ± 0.36 | 0.57 ± 0.38 | 1.65 ± 1.17 |
| <i>Arctagrostis latifolia</i> (t) | 0.04 ± 0.04 | 1.03 ± 1.08 | 2.46 ± 1.26 | 0.80 ± 0.67 | 0.86 ± 0.58 | 2.90 ± 2.14 |
| <i>Juncus biglumis</i> (g) | 0.15 ± 0.14 | 0.41 ± 0.10 | 0.03 ± 0.02 | 0.07 ± 0.04 | 0 | 0.10 ± 0.07 |
| <i>Juncus biglumis</i> (t) | 0.28 ± 0.27 | 0.95 ± 0.20* | 0.10 ± 0.08 | 0.22 ± 0.12 | 0 | 0.22 ± 0.14 |
| <i>Polygonum viviparum</i> (g) | 0.08 ± 0.05 | 0.42 ± 0.04 | 0.61 ± 0.33 | 1.17 ± 0.33 | 0.05 ± 0.05 | 0.64 ± 0.14 |
| <i>Polygonum viviparum</i> (t) | 0.08 ± 0.05 | 0.76 ± 0.14 | 0.61 ± 0.33 | 1.87 ± 0.57 | 0.05 ± 0.05 | 1.21 ± 0.30 |
| <i>Equisetum</i> spp. (g) | 0.03 ± 0.03 | 0.39 ± 0.37 | 0.44 ± 0.25 | 0.03 ± 0.02 | 0.12 ± 0.12 | 0.06 ± 0.06 |
| <i>Dryas integrifolia</i> (g) | 2.26 ± 1.05 | 6.44 ± 2.44 | 2.33 ± 1.33 | 6.31 ± 3.72 | 2.30 ± 1.04 | 8.18 ± 3.47 |
| <i>Dryas integrifolia</i> (t) | 26.10 ± 11.52 | 47.22 ± 17.64 | 25.02 ± 14.27 | 22.26 ± 12.91 | 33.57 ± 18.14 | 58.20 ± 23.79 |
| <i>Salix arctica</i> (g) | 0.07 ± 0.07 | 0.34 ± 0.10 | 0 | 7.21 ± 3.55 | 0.07 ± 0.07 | 0.34 ± 0.10 |
| <i>Salix arctica</i> (t) | 0.22 ± 0.22 | 0.85 ± 0.32* | 0 | 12.43 ± 5.26 | 1.23 ± 0.72 | 2.36 ± 2.32 |
| Total vascular (g) | 27.65 ± 10.46 | 52.55 ± 6.91 | 24.95 ± 5.18 | 70.76 ± 9.47 | 19.22 ± 2.27 | 52.69 ± 9.06 |
| Total vascular (t) | 107.36 ± 8.99 | 177.62 ± 38.00* | 119.26 ± 27.53 | 176.78 ± 20.49 | 93.15 ± 25.08 | 222.67 ± 33.83 |
| Moss | 18.59 ± 9.42 | 81.48 ± 17.54 | 28.15 ± 9.03 | 223.98 ± 86.90* | 11.30 ± 7.75 | 121.18 ± 41.99 |
| Litter | 78.68 ± 25.38 | 91.69 ± 18.86 | 146.21 ± 39.56 | 76.17 ± 27.86 | 103.12 ± 23.91 | 97.12 ± 26.69 |

| Species | Site D | | Site E | | Average Site | |
|-----------------------|-----------------|-----------------|-----------------|---------------------|------------------|---------------------|
| | 1981 (n = 5) | 2005 (n = 6) | 1981 (n = 5) | 2005 (n = 6) | 1981 (n = 25) | 2005 (n = 28) |
| <i>Carex</i> spp. (g) | 13.79 ± 3.67 | 25.50 ± 4.44* | 18.05 ± 5.77 | 43.47 ± 4.27 | 13.59 ± 9.71 | 32.88 ± 2.97 |

| | | | | | | |
|-------------------------------------|----------------|----------------------|----------------|-----------------------|----------------|-----------------------|
| <i>Carex</i> spp. (t) | 51.12 ± 13.32 | 57.78 ± 9.99 | 41.50 ± 12.02 | 152.43 ± 13.44 | 43.37 ± 5.56 | 95.98 ± 9.87 |
| <i>Carex misandra</i> (g) | 0.17 ± 0.17 | 0 | 0 | 0 | 0.75 ± 0.29 | 0.60 ± 0.19 |
| <i>Carex misandra</i> (t) | 0.60 ± 0.60 | 0 | 0 | 0 | 5.48 ± 2.51 | 4.56 ± 1.42 |
| <i>Eriophorum angustifolium</i> (g) | 1.57 ± 1.23 | 14.48 ± 3.66 | 0.35 ± 0.25 | 1.09 ± 0.37 | 4.60 ± 0.90 | 11.45 ± 1.79 |
| <i>Eriophorum angustifolium</i> (t) | 5.90 ± 5.02 | 29.62 ± 6.18 | 0.68 ± 0.47 | 5.12 ± 1.75* | 15.68 ± 3.32 | 32.49 ± 5.82 |
| <i>Kobresia</i> spp. (g) | 0 | 0 | 0 | 0.002 ± 0.002 | 0.19 ± 0.11 | 0.21 ± 0.09 |
| <i>Kobresia</i> spp. (t) | 0 | 0 | 0 | 0.07 ± 0.07 | 1.13 ± 0.70 | 1.12 ± 0.48 |
| <i>Arctagrostis latifolia</i> (g) | 1.10 ± 1.09 | 1.76 ± 1.26 | 0.45 ± 0.45 | 0.51 ± 0.18 | 0.62 ± 0.25 | 1.00 ± 0.37* |
| <i>Arctagrostis latifolia</i> (t) | 1.37 ± 1.34 | 2.61 ± 1.60 | 0.59 ± 0.59 | 1.19 ± 0.39 | 1.06 ± 0.40 | 1.75 ± 0.58 |
| <i>Juncus biglumis</i> (g) | 0.01 ± 0.01 | 0.01 ± 0.01 | 0.04 ± 0.04 | 0 | 0.05 ± 0.03 | 0.10 ± 0.03 |
| <i>Juncus biglumis</i> (t) | 0.06 ± 0.04 | 0.02 ± 0.02 | 0.04 ± 0.04 | 0 | 0.10 ± 0.06 | 0.23 ± 0.07 |
| <i>Polygonum viviparum</i> (g) | 0.10 ± 0.10 | 2.41 ± 1.07 | 0 | 0.06 ± 0.06 | 0.17 ± 0.08 | 0.97 ± 0.28 |
| <i>Polygonum viviparum</i> (t) | 0.10 ± 0.10 | 4.16 ± 1.99 | 0 | 0.11 ± 0.11 | 0.17 ± 0.08 | 1.68 ± 0.50 |
| <i>Equisetum</i> spp. (g) | 0.12 ± 0.08 | 8.07 ± 1.64 | 0 | 0 | 0.14 ± 0.06 | 1.80 ± 0.71 |
| <i>Dryas integrifolia</i> (g) | 5.28 ± 3.37 | 14.26 ± 4.37 | 0.88 ± 0.37 | 0.02 ± 0.02 | 2.61 ± 0.77 | 7.08 ± 1.64* |
| <i>Dryas integrifolia</i> (t) | 61.19 ± 42.47 | 39.75 ± 13.19 | 1.98 ± 0.83 | 0.12 ± 0.12 | 29.57 ± 9.87 | 32.53 ± 7.54 |
| <i>Salix arctica</i> (g) | 6.12 ± 1.74 | 17.50 ± 4.95* | 1.82 ± 0.94 | 5.29 ± 1.32 | 1.61 ± 0.60 | 6.66 ± 1.74 |
| <i>Salix arctica</i> (t) | 37.29 ± 13.82 | 44.66 ± 8.58 | 7.34 ± 2.27 | 27.01 ± 8.17* | 9.22 ± 3.88 | 18.65 ± 4.11 |
| Total vascular (g) | 28.24 ± 2.28 | 83.98 ± 12.10 | 21.58 ± 6.97 | 50.42 ± 3.42 | 24.33 ± 3.80 | 62.76 ± 3.59 |
| Total vascular (t) | 157.74 ± 51.62 | 186.66 ± 26.08 | 52.12 ± 13.93 | 186.04 ± 11.07 | 105.93 ± 12.92 | 190.83 ± 12.20 |
| Moss | 47.72 ± 14.71 | 128.81 ± 36.65* | 156.23 ± 66.04 | 31.49 ± 23.07* | 52.40 ± 16.70 | 111.95 ± 24.60 |
| Litter | 160.56 ± 41.22 | 49.67 ± 15.83 | 53.43 ± 12.71 | 360.00 ± 76.57 | 108.4 ± 14.90 | 138.02 ± 28.55 |

Data are means ± SE. Significant differences between 1981 and 2005 means within sites shown in bold ($P < 0.05$). Differences at $P < 0.10$ are shown with *.

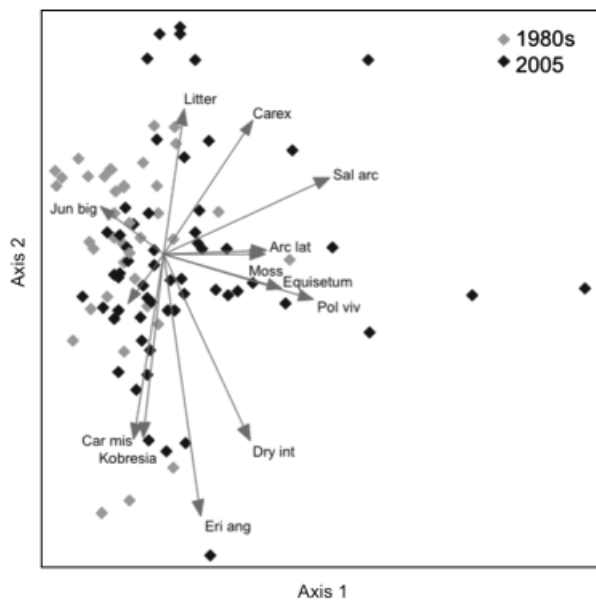


Fig. 6 Principal components analysis biplot of live biomass by species for all plots in all sites for both sampling periods: early 1980s ($n = 40$) and 2005 ($n = 48$). The species are shown as eigenvectors and the codes are as follows: Carex, *Carex* spp. (*C. membranacea* + *C. aquatilis stans*); Sal arc, *Salix arctica*; Arc lat, *Arctagrostis latifolia*; Pol viv, *Polygonum viviparum*; Equisetum, *Equisetum* spp. (*E. variegatum*, *E. arvense*); Dry int, *Dryas integrifolia*; Eri ang, *Eriophorum angustifolium*; Kobresia, *Kobresia* spp. (*K. myosuroides*, *K. simpliciuscula*); Car mis, *C. misandra*; Jun big, *Juncus biglumis*. See Table 2 for ordination statistics.

Table 2 Results of principal components analysis on species biomass values in sedge meadow plots measured in the early 1980s and again in 2005 at Alexandra Fiord, Ellesmere Island

| Axis | Eigenvalue | % Variance | Cumulative % variance | Randomization test (P -value) |
|------|------------|------------|-----------------------|----------------------------------|
| 1 | 2.550 | 19.62 | 19.62 | 0.002 |
| 2 | 1.934 | 14.88 | 34.50 | 0.001 |
| 3 | 2.347 | 11.15 | 45.65 | 0.044 |
| 4 | 2.044 | 8.70 | 54.35 | 0.996 |

fine roots (<2 mm in diameter) in decade scale responses to temperature-induced decomposition of soil organic matter.

In their experimental studies, Shaver *et al.* (1998) found no effect of warming on belowground biomass (rhizomes) after 6–9 years of treatment in wet sedge tundra, and the only significant increases occurred with the addition of phosphorus. Passive warming in another Alaskan wet sedge meadow resulted in increased near-surface air temperatures which likely resulted in increases in early season root production (Sullivan &

Welker, 2005). Interestingly, root production declined earlier in warmed plots, likely because the available nutrient pool may have been consumed by early season productivity (Sullivan & Welker, 2005). This nonlinear response of biomass to temperature has been documented in a number of experimental studies (Chapin *et al.*, 1995; Arft *et al.*, 1999; van Wijk *et al.*, 2003). In addition, comparisons between grazed and ungrazed wet sedge tundra have shown that grazed systems have significantly greater belowground biomass than ungrazed meadows (Elliott & Henry, 2010). The constant removal of leaves stimulates the production of roots and rhizomes in many of the wet sedge species. The greater belowground biomass serves both to increase nutrient absorption and as a store of nutrients for regrowth of the aboveground tissue. The soils of grazed meadows have increased nutrient availability as a result of the activities of the herbivores (muskoxen) (Henry, 1998), and this likely contributed to the greater biomass of roots and rhizomes. However, the wet sedge meadows at AF are not grazed (Elliott & Henry, 2010). Hence, the effect of the warming over the past 25 years on nutrient availability was likely a major factor in the greatly elevated root biomass and standing crop in the wet sedge tundra at AF.

Aboveground response

There was no significant annual variation in maximum biomass of all vascular plants combined or the major species, or in net annual primary production at Site A during 1980–1983, despite variable climate conditions, including significantly different mean annual surface temperatures and active layer depths (Henry, 1987; Henry *et al.*, 1990). Thus, it can be effectively assumed that biomass production in these sedge meadow sites is relatively insensitive to short-term changes in environmental conditions, and one season of sampling in 2005 can accurately represent the short-term stable state of sedge wetlands at AF. Chapin & Shaver (1985) showed this same relative compensatory stability (despite variability among species) in Alaskan sedge meadows. In support of this short-term stability at AF, the initial 5 years of passive warming [1–2 °C during the growing season (Marion *et al.*, 1997)] with open top greenhouses did not induce changes in sedge meadow aboveground biomass at AF (G. H. R. Henry, unpublished results).

The most consistent trend observed was increased biomass at all Sites and in all dominant species. This is consistent with trends of increasing Arctic terrestrial productivity and biomass documented with proxy measurements such as aerial photography and NDVI (Myneni *et al.*, 1997; Zhou *et al.*, 2001; Stow *et al.*, 2004; Tape *et al.*, 2006; Verbyla, 2008). Numerous short-term

experiments conducted in Arctic plant communities have induced responses in aboveground productivity (Henry *et al.*, 1986; Chapin *et al.*, 1995; Shaver *et al.*, 1998; Arft *et al.*, 1999; Johnson *et al.*, 2000; van Wijk *et al.*, 2003; Mack *et al.*, 2004; Welker *et al.*, 2004; Walker *et al.*, 2006). Temperature and nutrient availability are the most commonly manipulated ecosystem variables. Multifactor experiments show that the influence of temperature is minor in comparison with nutrient additions (Chapin *et al.*, 1995; van Wijk *et al.*, 2003; Phoenix & Lee, 2004). In a meta-analysis of warming experiments throughout the Arctic, Arft *et al.* (1999) found that the initial increase in graminoid productivity was not sustained after 4 years. Rolph (2003) showed that 10 years of passive warming was needed to stimulate mineralization necessary for sustained productivity. Many authors cited the need for long-term studies of the effects of ambient climate change to validate the results of short-term experiments and proxy measurements. Our study clearly shows an increase in biomass and standing crop over the 25-year period, most likely due to the indirect effects of increased temperature on nutrient availability and nutrient acquisition via increased root growth.

Our results are consistent with the only other long-term assessment of change in High Arctic tundra, conducted at the same site in an evergreen dwarf shrub heath community (Hudson & Henry, 2009). On average, the aboveground biomass of the sedge meadow communities is now 2.6 times the mean biomass in the early 1980s. Hudson & Henry (2009) found a similar increase (2.6) in a mesic dwarf shrub heath at the same site. Hence, both wet and mesic community types appear to be responding to the general warming of the past 25 + years with increased productivity.

As expected, there was substantial variability among the sites in the biomass responses to recent climate change. Site D, located on a creek bank, had greater biomass but lower amounts of attached dead standing crop and litter 2005. The lower standing crop was most likely caused by recurring large floods, with the most recent in 2001 which covered nearly all aboveground vegetation with 2–10 cm of sediment. Despite this disturbance there was greater biomass in 2005 than during the early 1980s.

Site E contained four times more peak season biomass, two times more leaf biomass and five times more total standing crop in 2005 when compared with 1981, largely due to significantly greater mass of *Carex* spp. In 2005, litter standing crop was 6.8 times greater than in 1981. This response was likely exacerbated by a changing flood disturbance regime in the late 1980s when glacial melt water was diverted, channeling water around Site E instead of flowing through it. The change of flood regime and reduction in the local water table

may have initiated drying and aeration of the soil, which could have stimulated increases in productivity and standing crop in addition to increases associated with climate warming. Hence, geomorphic and hydrologic changes in the landscape, perhaps in response to climate change, have important implications for ecological responses.

Species- and community-level responses

Dominant sedge meadow species, including *Carex* spp. (*C. membranacea* and *C. aquatilis stans*) and *E. angustifolium*, were the most responsive of all species. The deciduous dwarf shrub *S. arctica* also showed strong increases in biomass between the two sampling periods. This observation supports a meta-analysis of community-level responses in warming experiments across tundra sites which found the strongest response to be greater cover (biomass) of deciduous shrubs and graminoids (Walker *et al.*, 2006). Shaver *et al.* (1998) studied warming and fertilization of wet sedge tundra for 6–9 years at Toolik Lake, Alaska, where ecosystem productivity and the dominant graminoid (*C. cordorhizza*) responded to fertilization positively, significantly, and similarly to the dominant graminoids at AF. Despite dominant species becoming more dominant, diversity was not affected at Toolik Lake (Shaver *et al.*, 1998) or at AF due to consistent community wide responses.

Synthesis: carbon balance implications

Multifactor experiments show that the influence of temperature is minor in comparison with nutrient additions (Chapin *et al.*, 1995; van Wijk *et al.*, 2003; Phoenix & Lee, 2004). Warming at AF has likely affected the sedge meadows mainly indirectly through a suite of nutrient enhancing factors including increased decomposition and mineralization rates and/or duration, and enhanced nutrient pools (Shaver *et al.*, 2001; Rolph, 2003; Sullivan *et al.*, 2008). The increase in biomass that we measured indicates that the long-term ambient warming has stimulated the accumulation of carbon in this system. Carbon fluxes were not measured as part of this study and the long-term natural changes remain unknown. However, ecosystem CO₂ exchange was measured at Site A after 9 years of experimental warming and showed continued strong sink activity despite the relatively stronger stimulation of ecosystem respiration than photosynthesis (Welker *et al.*, 2004). Much of the increased respiration was likely due to greater decomposition rates and root growth (Welker *et al.*, 2004). Elevated aboveground productivity at AF appears to have been balanced by elevated litter decomposition rates, as litter standing crops were not

significantly different between the sample periods except at Site E, as explained above. However, the strong increase in belowground standing crop, especially dead roots indicates that decomposition rates in the soil, at least for the larger roots and rhizomes, have not increased in step with root and rhizome production. This is likely due to the cooler temperatures with depth in these permafrost soils.

Conclusions

Sedge meadows at Site A were experimentally warmed with open top greenhouses as part of the ITEX network (Henry, 1997). Over the initial 5-year period, warming showed no significant changes in plant cover in any meadow functional group, including graminoids (Walker *et al.*, 2006; G. H. R. Henry, unpublished results). However, the long-term (25 years) nature of our ambient change study showed increased productivity at the site and species scale, contributing information that could not be obtained from short-term experimentation. These results should stimulate the search for sites and data sets that can be revisited and resampled, such as those established during the International Biological Program in the early 1970s (Bliss, 1977; Michelutti *et al.*, 2003).

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