Arctic and Alpine Research, Vol. 30, No. 4, 1998, pp. 373–380

Carbon Dioxide Fluxes in Moist and Dry Arctic Tundra during the Snow-free Season: Responses to Increases in Summer Temperature and Winter Snow Accumulation

M. H. Jones,*,‡
J. T. Fahnestock,*
D. A. Walker,†
M. D. Walker,† and
J. M. Welker*

*Department of Renewable Resources, University of Wyoming, Laramie, Wyoming 82071, U.S.A.
†Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado 80309, U.S.A.
‡Present address: Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, Columbus, Ohio 43210, U.S.A.
jones.1436@osu.edu

Abstract

Climate-induced environmental changes are likely to have pronounced impacts on CO_2 flux patterns in arctic ecosystems. We initiated a long-term experiment in 1994 in moist tussock and dry heath tundra in arctic Alaska in which we increased summer air temperature (ca. 2°C) and increased winter snow accumulation (shortening the growing season approximately 4 wk). During the 1996 snow-free season, we measured ecosystem CO_2 flux weekly in order to quantify net carbon gain or loss from these systems. Over the duration of the snow-free season, both dry heath and moist tussock tundra exhibited a net loss of carbon to the atmosphere, ranging from 12 to 81 g C m^{-2} depending upon experimental treatment. Elevated summer temperatures accelerated net CO_2 loss rates over ambient temperatures in both deep and ambient snow treatments, and increased the total amount of carbon emitted during the snow-free season by 26 to 38% in ambient snow plots and by 112 to 326% in deep snow plots. Increased snow accumulation had less impact on CO_2 flux than did warming, and snow effects on total carbon loss were not consistent between the two temperature regimes. Ecosystem respiration exceeded assimilation on most sampling dates throughout the season. These data, coupled with winter carbon losses recently demonstrated in the same ecosystems, indicate that the moist and dry arctic ecosystems we examined are currently net sources of atmospheric carbon on an annual basis, and that anticipated global warming may increase carbon losses from these systems.

Introduction

One of the concerns about the response of arctic ecosystems to climate changes involves whether tundra systems will sequester carbon or whether it will be respired to the atmosphere. Globally, arctic tundra contains some 250 to 455 Pg of carbon in permafrost and the active layer (Oechel and Billings, 1992). In arctic Alaska, soil carbon ranges from 16 to 94 kg m^{-3} (Michaelson et al., 1996). Release of this stored carbon to the atmosphere could have a positive feedback on global warming (Oechel and Vourlitis, 1994), particularly since global CO_2 emissions from soils may be exceeding terrestrial net primary production (Raich and Potter, 1995). Over the past century, carbon storage has probably fluctuated in the Arctic (McKane et al., 1997a), but there is concern that arctic tundra is now a source of CO_2 to the atmosphere during the summer (Oechel et al., 1993, 1995) as well as during winter (Fahnestock et al., 1997; Oechel et al., 1997; Jones et al., 1999). Recent modeling has demonstrated that much of the carbon stored in tundra soils could be volatized at rapid rates, depending upon the nature of climate change (McKane et al., 1997b).

Several studies have examined arctic ecosystem CO_2 fluxes and controls in unmanipulated ecosystems during the growing season (Billings et al., 1982; Poole and Miller, 1982; Nadelhoffer et al., 1991; Oberbauer et al., 1991, 1992, 1996; Oechel et al., 1993, 1995). Many factors affecting CO_2 uptake and release have been identified, including community composition, leaf area, soil and air temperature, nutrient availability and turnover, active-layer and water-table depths, and soil quality (Oberbauer et al., 1996). Although a number of studies have examined the effects of simulated climate changes on tundra species' growth responses (e.g., Jones et al., 1997; Welker et al., 1997), few have examined the effects of climate change manipulations on arctic tundra ecosystem CO_2 flux (Billings et al., 1982; Grulke et al., 1990; Oechel and Vourlitis, 1994; Christensen et al., 1997). Moreover, we are aware of no published studies that have examined effects of winter snow manipulations on arctic ecosystem CO_2 flux.

Here we present the results of a summer-long study of ecosystem CO_2 flux in dry heath and moist tussock tundra in arctic Alaska in response to experimental increases in winter snow accumulation and summer temperature. Increased snow accumulation is a potential consequence of global climate change, and could lead to a reduction in the duration of the summer snow-free season (Maxwell, 1992). Summer air temperatures will also likely increase with global warming, perhaps as much as 5°C in arctic systems (Maxwell, 1992). The effects of coupled changes in winter snow cover and summer temperature on CO_2 flux are important since independent alteration of either factor is unlikely (Gates et al., 1992). The purpose of this paper is to describe how increased winter snow accumulation (subsequently reducing growing season length) and increased growing season air and soil temperature affect CO_2 fluxes and net carbon gain or loss in moist tussock and dry heath tundra in the Alaskan arctic. This study is being conducted as part of the International Tundra Experiment (ITEX), a collaboration of researchers examining effects of summer warming on arctic and alpine tundra (Henry and Molau, 1997).

0004-0851/98 $7.00

Methods

STUDY SITES

This research was conducted in dry and moist tundra at Toolik Lake, Alaska (68°38′N, 149°38′W, 760 m elevation) in the northern foothills of the Brooks Range. The dry tundra site is an old gravel outwash plain with sparse prostrate vegetation composed primarily of *Dryas octopetala, Arctostaphylos alpina, Loiseleuria procumbens,* and many lichens. Rock, bare soil, and litter cover more than 25% of the surface. Soils are primarily mineral and freely draining. Winter snow accumulation is typically 30 cm or less, and the site becomes snowfree relatively early in the season, usually by mid-May. The moist site is acidic tussock tundra dominated by *Eriophorum vaginatum, Betula nana,* mosses, and lichens. Soils are saturated, with a shallow organic horizon. Winter snow accumulation is typically 50 to 80 cm, and this site becomes snow free later than the dry site, usually late-May.

EXPERIMENTAL DESIGN

In July 1994, one 60 m long by 3 m high Wyoming-style snow fence was erected at each site, perpendicular to prevailing winter winds. The purpose was to increase winter snow accumulation, simulating one potential environmental alteration expected to accompany climate change (Maxwell, 1992). Snowdrifts reached maximum depths of 3 m, extending downwind ca. 25 to 35 m before diminishing to ambient snow depths ca. 50 to 60 m from the fence. Drift depth and cover gradually declined with the onset of summer.

In late June 1995, six plots were established in areas of deepest snow accumulation behind each fence, and six in nearby areas of ambient snow accumulation. At each plot, square bases were installed in the tundra to provide a seal for CO_2 flux measurements. These bases were open-ended polyethylene tubes (30 cm × 30 cm × 20 cm high with a 5 cm horizontal lip), set 10 to 20 cm into the tundra. Polyethylene was used to minimize heat transfer. In the dry site, bases were carefully placed around clones of the dominant vegetation, *D. octopetala,* which covered 34 to 67% of each base area. In the moist site, plots were selected to uniformly include the dominant vascular plant species in this tundra type, primarily *E. vaginatum, B. nana,* and *Vaccinium vitis-idaea.*

Three of the six plots in each snow treatment were randomly selected for enhanced summer warming. Air temperature was elevated using small open-top chambers, 1 m diameter × 40 cm tall conical hexagons constructed of translucent fiberglass (SunLite HP, Solar Components Corp., Manchester, NH). Open-top chambers are the standard experimental warming treatment used by ITEX researchers; they raise summer air temperatures 2 to 5°C throughout most of the growing season (Henry and Molau, 1997; Marion et al., 1997). In 1995, open-top chambers were placed over the selected plots immediately after the bases were installed, and were removed in mid-August. In 1996, open-top chambers were placed over the bases as soon as 50% of each plot became snow free. Air (20 cm) and soil (−5 cm) temperature were measured in the center of three open-top chamber and three unwarmed plots in each site from the end of May through mid-August. A single 1.5-m air temperature was also measured in each site. Temperature was recorded every 48 min using Hobo temperature logging devices (Onset Computer Corporation, Pocasset, MA). To summarize the CO_2 flux experimental design, each tundra site had two snow treatments (deep and ambient) and two summer temperature treatments (warmed and ambient), with three plots in each of these treatment combinations.

CO_2 MEASUREMENTS

Carbon dioxide flux was measured using a system similar to that described by Vourlitis et al. (1993). A 30 cm × 30 cm × 30 cm Plexiglas chamber was clamped and sealed to the chamber bases, and a closed-system infrared gas analyzer (LiCor 6200, Lincoln, NE) was used to quantify CO_2 flux. A small fan mixed the air enclosed in the chamber. Once CO_2 concentrations stabilized (typically within 1–2 min), three flux determinations were made at ca. 20-s intervals for each plot. These were subsequently averaged to give a mean flux measurement for each plot. If these three measurements were not within a narrow range of one another (indicating temperature or pressure changes within the chamber during the 60 s measurement period), then the chamber was removed for a short time (ca. 2 min) and the procedure repeated.

Diurnal measurements were made in each plot every 4 h for a 24-h period, and were repeated at approximately weekly intervals at each site beginning 2 June in the dry site and 5 June in the moist site. Final diurnal measurements were made on 29 August in the moist site (n = 12) and 3 September in the dry site (n = 13). In both sites, the first two diurnal measurements were made only on plots in the ambient snow depth zone, since the plots in the deep snow zones were still snow covered.

During the first 6 wk, we measured only net ecosystem CO_2 flux (defined in this paper as the sum of ecosystem-level photosynthetic uptake and respiratory losses). Beginning with week 7 in each site (mid-July), we also measured whole ecosystem dark respiration (defined as ecosystem CO_2 loss to the atmosphere). Ecosystem respiration measurements were made on a subset of plots (1 plot of each treatment type) during each measurement period, using an opaque blanket to prevent light from reaching the plot. From the net flux and respiration measurements we subsequently calculated whole ecosystem assimilation (defined as ecosystem CO_2 uptake only).

STATISTICAL ANALYSIS

Repeated measures analysis of variance was used to test for effects of the snow and warming treatments on each set of CO_2 flux data (net flux, whole ecosystem assimilation, whole ecosystem respiration) because we measured the same plots repeatedly during the snow-free season. We followed procedures given by von Ende (1993) and used SAS statistical software (SAS Institute, 1989). Each tundra type was analyzed separately. We note that because we had only one snow fence in each tundra type, our snow treatment was pseudo-replicated. Erecting a minimum of six snow fences in each tundra type was prohibitive for experimental and logistical reasons. Consequently, we treated each open-top chamber or control plot in the deep snow or ambient snow areas of each site as replicates in our statistical analyses.

The fixed effects in our models were the snow and warming treatments, with week the repeated factor. Within-subjects effects were tested using the Huyhn-Feldt correction for sphericity. Profile transformation contrasts were used to compare the mean response measured one week with that measured the week prior in order to test for abrupt changes in CO_2 flux. We did not analyze the data in a doubly-repeated fashion (von Ende, 1993); i.e., we did not test for diurnal effects within weekly effects, since the principal interest of the study was the seasonal, rather than diurnal, change in CO_2 flux under the experimental treatments.

TABLE 1

Air and soil temperatures from the dry and moist tundra sites at Toolik Lake, Alaska

			Dry Tundra Site					Moist Tundra Site				
	Sample	Treatment	N	Mean	SE	Min	Max	N	Mean	SE	Min	Max
June	1.5 m Air	ref	900	7.74	0.19	−4.29	23.32	900	7.68	0.19	−4.29	22.58
	Plot Air	warmed	900	11.09	0.25	−2.93	33.80	900	10.96	0.27	−3.18	34.47
	Plot Air	unwarmed	900	8.67	0.21	−3.79	25.23	900	8.87	0.22	−3.79	26.81
	Plot Soil	warmed	900	11.10	0.15	1.70	25.39	900	8.27	0.17	−0.19	23.37
	Plot Soil	unwarmed	900	9.61	0.14	0.43	22.96	900	6.57	0.13	−0.31	18.20
July	1.5 m Air	ref	899	11.32	0.18	−2.81	26.01	899	11.24	0.18	−2.56	26.41
	Plot Air	warmed	899	14.07	0.23	−2.50	34.47	899	13.95	0.25	−3.86	35.70
	Plot Air	unwarmed	899	12.13	0.19	−2.97	28.18	899	12.16	0.20	−4.04	29.90
	Plot Soil	warmed	899	14.20	0.13	4.98	25.24	899	10.97	0.15	1.45	23.25
	Polt Soil	unwarmed	899	12.85	0.13	3.33	23.85	899	8.89	0.11	0.69	18.60
August[a]	1.5 m Air	ref	404	8.31	0.26	−1.81	20.11	403	8.42	0.28	−2.06	23.32
	Plot Air	warmed	404	10.72	0.37	−1.75	31.36	403	10.79	0.42	−3.24	35.75
	Plot Air	unwarmed	404	9.15	0.30	−2.06	23.95	403	9.21	0.32	−3.13	26.82
	Plot Soil	warmed	404	10.94	0.20	2.73	20.46	403	8.26	0.20	0.68	18.22
	Polt Soil	unwarmed	404	9.67	0.18	1.96	18.32	403	6.95	0.17	0.52	14.95

[a] 1 August through 14 August only.

Net ecosystem CO_2 flux was analyzed for the entire snow-free season, with the following exceptions. Since repeated measures analysis of variance does not permit missing values, data from the first two diurnal measurements in early June in each site were excluded from the analyses since plots in the deep snow areas were still snow covered. In addition, the last measurement in the dry site (3 September) was excluded from the analyses because of equipment failure during the final measurement. Whole ecosystem assimilation and respiration, measured during weeks 7 to 12, were analyzed in a manner identical with that for net CO_2 flux. Data from all measurement periods are shown in the figures.

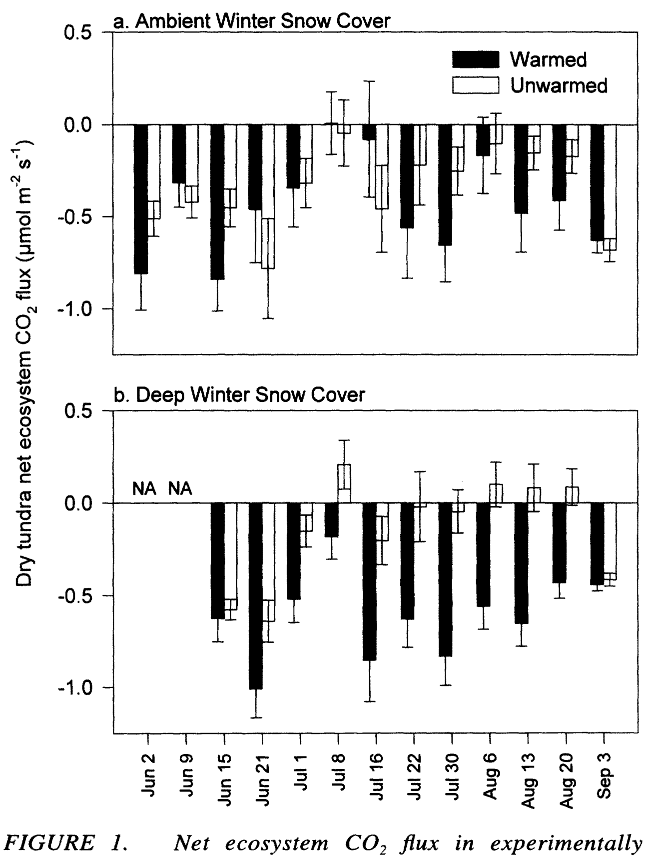

FIGURE 1. Net ecosystem CO_2 flux in experimentally warmed and ambient temperature plots in dry heath tundra with (a) ambient snow and (b) increased snow. Data are from the 1996 snow-free season at Toolik Lake, Alaska. Bars represent means (± SE); n *= 18. All flux figures in this paper retain the following convention: positive values represent carbon uptake, negative values represent carbon loss to the atmosphere.*

Results

SNOW DEPTH AND AIR TEMPERATURE

Ambient snow accumulation in both sites melted by mid-May in 1995, and, in 1996, by 23 May in the dry site and 29 May in the moist site. The last of the snow from the deepest part of both experimental drifts melted by 8 June in 1995 and by 20 June in 1996. Consequently, the growing season in the deep snow zone in each site was delayed (and reduced) by ca. 4 wk each year. In both sites, mean air and soil temperatures in open-top chambers were ca. 2°C higher than temperatures in unmanipulated plots from June through mid-August (Table 1). Soil temperatures were generally ~2 to 3°C lower in the moist site than in the dry.

SEASONAL CO_2 FLUX

Net CO_2 flux occurred principally as loss to the atmosphere in both dry heath (Fig. 1) and moist tussock (Fig. 2) tundra throughout the growing season; there were few dates on which either dry or moist tundra were net sinks for carbon, regardless of experimental treatment. Even at the peak of the growing season (mid-July), net ecosystem CO_2 flux was negative. Carbon dioxide flux rates changed significantly from the beginning to the end of the season for both tundra types (effect of week, $P = 0.0001$, Table 2a), but the contrasts indicated no statistically significant week-to-week changes in net CO_2 flux. Moreover, there were no strong seasonal patterns apparent in the weekly net flux data (Figs. 1, 2).

Generally, net CO_2 fluxes were more negative in the moist tundra than the dry tundra (Figs. 1, 2), but variability was more pronounced in the dry site. Moist tundra had ecosystem CO_2

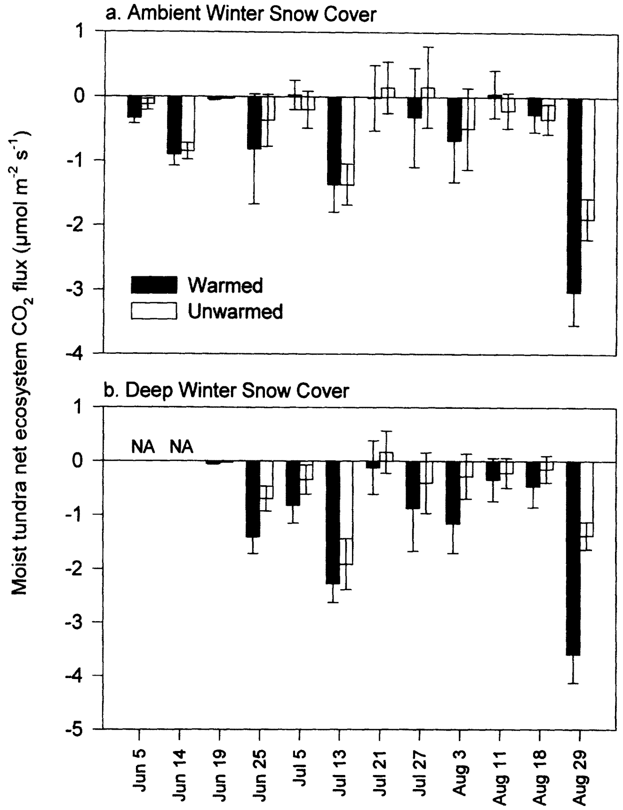

FIGURE 2. Net ecosystem CO_2 flux in experimentally warmed and ambient temperature plots in moist tussock tundra with (a) ambient snow and (b) increased snow. Data are from the 1996 snow-free season at Toolik Lake, Alaska. Bars represent means (± SE); n = *18.*

assimilation rates approximately double those of dry tundra ecosystems (Figs. 3, 4). Ecosystem respiration rates were similar for both tundra types (Figs. 3, 4), with the exception of respiration in the moist tundra deep snow plots, which was roughly twice that of the other treatment/tundra combinations.

The experimental warming treatment had a strong negative effect on net ecosystem carbon flux in dry tundra. Net CO_2 flux was significantly more negative (i.e., more CO_2 efflux to the atmosphere) in warmed plots than those under ambient temperature conditions (week × warming, $P = 0.0163$, Table 2a). Net carbon gain in dry tundra occurred only in those plots which received the deep snow and ambient temperature treatments (Fig. 1b). Over the season as a whole, ecosystem assimilation was significantly greater in the deep snow than in the ambient snow plots (snow × warming, $P = 0.0319$, Table 2b; Fig. 3), but ecosystem respiration did not differ between snow treatments. Ecosystem assimilation changed significantly during the season (effect of week, $P = 0.0001$, Table 2b), and dropped off sharply during the last measurement period in early September (Fig. 3). Respiration was unaffected by either the warming or snow treatments in dry tundra, and tended to decline steadily and significantly as the growing season ended (effect of week, $P = 0.0001$, Table 2c).

In moist tundra, net ecosystem CO_2 flux (Fig. 2) was also significantly more negative (i.e., more CO_2 loss) in experimentally warmed plots over the course of the summer than in unwarmed plots (week × warming, $P = 0.0215$, Table 2a). There was no significant effect of the snow treatment on net CO_2 flux. However, ecosystem assimilation (Fig. 4) was significantly greater in the deep snow plots (week × snow, $P = 0.0321$, Table 2b), where warming had a positive but nonsignificant effect. Gross ecosystem respiration (Fig. 4) was significantly greater in warmed and deep snow plots for the season as a whole (between subjects effects of warming, $P = 0.0090$, and snow, $P = 0.0001$, Table 2c). However, respiration did not vary significantly among weeks in moist tundra (Table 2c).

ECOSYSTEM CARBON LOSS

We estimated the net amount of CO_2-C respired to the atmosphere for the 12- to 13-wk snow-free season by assuming that the mean daily flux rate measured during any one diurnal sampling period was the same for all days until the next measurement period, then summing these daily flux estimates (Table 3). In both tundra types, the seasonal carbon loss was greater in the experimentally warmed plots than those which experienced ambient temperatures in both snow treatment regimes. In contrast, the effects of the snow drifts depended upon the warming treatment. Under ambient temperature conditions, plots in the deep snow treatment had less total carbon loss than ambient snow plots. In experimentally warmed plots, the opposite occurred; deep snow plots exhibited greater total carbon loss than plots in the ambient snow treatment. In dry tundra, net growing season carbon loss ranged from 11.5 to 33.2 g CO_2-C m^{-2} for unwarmed tundra, and 41.7 to 49.0 g CO_2-C m^{-2} for experimentally warmed plots. In moist tundra, net carbon loss was more pronounced. Unwarmed plots ranged from 38.2 to 40.3 g CO_2-C m^{-2}, while warmed plots ranged from 55.7 to 80.8 g CO_2-C m^{-2}.

DIURNAL FLUX PATTERNS

Representative diurnal patterns for dry tundra are shown in Figure 5. Measurements made on 15 June showed net CO_2 loss in both ambient and deep snow treatments for the entire diurnal period. In the ambient snow plots, net carbon loss was greatest during the midnight hours, but this pattern was less evident for deep snow plots. Effects of the warming treatment were more pronounced in the ambient snow plots. Mid-season measurements (16 July) showed some net carbon uptake in the late afternoon and morning hours (< 1.5 μmol m^{-2} s^{-1}), but net loss the remainder of the day. Greater net gain occurred in the ambient snow plots during mid-season, but there was little difference between the warming treatments at this time. By late season (20 August), however, the effects of warming again became apparent, with more positive net carbon flux in the deep snow plots than the ambient snow plots.

Patterns in the moist site were similar to those in the dry site (Fig. 6). No net carbon gain occurred early in the season (19 June) in any of the treatments. However, in contrast to the dry site, the effects of experimental warming were more pronounced in the deep snow than in the ambient snow plots. Mid-season (21 July) diurnal patterns were similar for all treatments, and exhibited positive net CO_2 fluxes (≤ 2 μmol m^{-2} s^{-1}) for about half of the diurnal period. By late season (29 August), net CO_2 fluxes were again negative throughout the diurnal period, and the warming treatment increased the amount of carbon loss from these systems. Overall, diurnal patterns were affected little by the snow accumulation treatment.

Discussion

The net ecosystem carbon loss from both dry heath and moist tussock tundra at Toolik Lake, Alaska, during the 1996

TABLE 2

Repeated measures analysis of variance for CO_2 flux variables for moist and dry tundra. Probability (P) is adjusted for the Huyhn-Feldt correction for sphericity[a]

	Dry Tundra				Moist Tundra			
	Between-subjects effects				Between-subjects effects			
Source	MS	df	F	P>F	MS	df	F	P>F
a. Net Ecosystem CO_2 Flux								
Snow	0.12	1	0.04	0.8519	12.98	1	0.72	0.3991
Warming	13.33	1	3.93	0.0526	26.87	1	1.49	0.2263
Snow × Warming	2.61	1	0.77	0.3842	7.23	1	0.04	0.5287
	Within-subjects effects				Within-subjects effects			
Source		df	F	P>F		df	F	P>F
Week		9	11.45	0.0001		9	28.53	0.0001
Week × Snow		9	1.03	0.4020		9	0.80	0.5452
Week × Warming		9	2.82	0.0163		9	2.75	0.0215
Week × Snow × Warming		9	1.58	0.1650		9	0.32	0.8904
		Huyhn-Feldt Epsilon =		0.5614		Huyhn-Feldt Epsilon =		0.5175
	Between-subjects effects				Between-subjects effects			
Source	MS	df	F	P>F	MS	df	F	P>F
b. Ecosystem Assimilation								
Snow	0.07	1	0.23	0.6596	17.38	1	1.52	0.2322
Warming	1.91	1	5.78	0.0741	4.10	1	0.36	0.5557
Snow × Warming	3.45	1	10.45	0.0319	10.76	1	0.94	0.3437
	Within-subjects effects				Within-subjects effects			
Source		df	F	P>F		df	F	P>F
Week		6	9.31	0.0001		5	18.55	0.0001
Week × Snow		6	0.13	0.9919		5	3.09	0.0321
Week × Warming		6	0.46	0.8335		5	0.74	0.5377
Week × Snow × Warming		6	1.56	0.2011		5	1.33	0.2724
		Huyhn-Feldt Epsilon =		1.0024		Huyhn-Feldt Epsilon =		0.6229
	Between-subjects effects				Between-subjects effects			
Source	MS	df	F	P>F	MS	df	F	P>F
c. Ecosystem Respiration								
Snow	1.07	1	3.53	0.1335	28.33	1	66.75	0.0001
Warming	1.82	1	6.00	0.0704	3.59	1	8.47	0.0090
Snow × Warming	0.32	1	1.07	0.3589	1.66	1	3.91	0.0628
	Within-subjects effects				Within-subjects effects			
Source		df	F	P>F		df	F	P>F
Week		6	11.50	0.0001		5	16.49	0.0001
Week × Snow		6	0.18	0.9508		5	1.58	0.1981
Week × Warming		6	1.18	0.3552		5	1.14	0.3429
Week × Snow × Warming		6	0.90	0.4914		5	0.41	0.7710
		Huyhn-Feldt Epsilson =		0.6935		Huyhn-Feldt Epsilon =		0.6914

[a] MS = mean square, df = degrees of freedom, F = group MS/error MS, P = probability of effect caused by random chance.

snow-free season was significant. Total carbon losses ranged from 12 to 81 g CO_2-C m^{-2} for the 12- to 13-wk snow-free season, and occurred in all treatment combinations. Weekly measurements demonstrated that net CO_2 efflux occurred throughout the season, and that net carbon gain was positive during few sampling periods. Net CO_2 flux from the moist tussock tundra was greater than from dry heath tundra, possibly because of larger soil carbon stocks and differences in quality of soil organic matter (Nadelhoffer et al., 1991; Schimel and Clein, 1996). The carbon losses we measured in moist tundra were somewhat lower than those reported by Oechel et al. (1993) for studies conducted from 1983 to 1990, which were years of record high temperature. Net ecosystem CO_2 flux and respiration rates in late July in both dry and moist tundra in Alaska were similar to those we measured in high arctic polar desert and semidesert ecosystems near Thule, Greenland, during the same time of year (Jones et al., unpublished data).

Significantly, net carbon loss occurred in plots under current (ambient) summer temperature and snow regimes in both tundra types. Growing season carbon losses from these tundra ecosystems (this study; Oechel et al. 1993), coupled with winter CO_2 losses (Fahnestock et al., 1997; Grogan and Chapin, 1997;

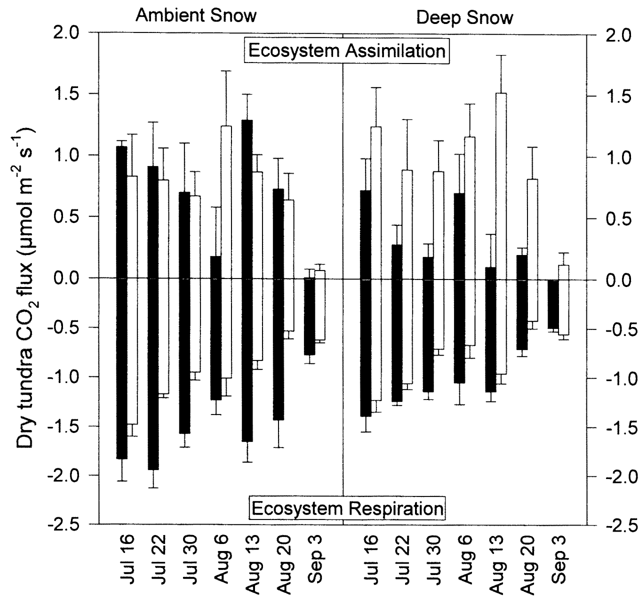

FIGURE 3. Dry heath tundra ecosystem assimilation and ecosystem respiration in warmed (solid bars) and unwarmed plots (open bars) under ambient and deep snow experimental treatments. Bars represent means (± SE); n = *6.*

Oechel et al., 1997; Jones et al., 1999), indicate that the sites examined in this study are currently a source, rather than a sink, of atmospheric carbon, with potential annual carbon losses ranging from 20 g CO_2-C m^{-2} to as much as 500 g CO_2-C m^{-2}. Over the past century, large transient losses of soil carbon (50–180 g C m^{-2} yr^{-1}) have probably occurred in moist tussock tundra in arctic Alaska, with relatively large losses suggested for 1988 to 1990 (McKane et al., 1997a; Oechel et al., 1993). Our data suggest that this apparent trend has not abated.

Experimentally warming the air and soil significantly increased CO_2 emissions from moist tussock and dry heath tundra relative to unwarmed plots, regardless of the snow treatment.

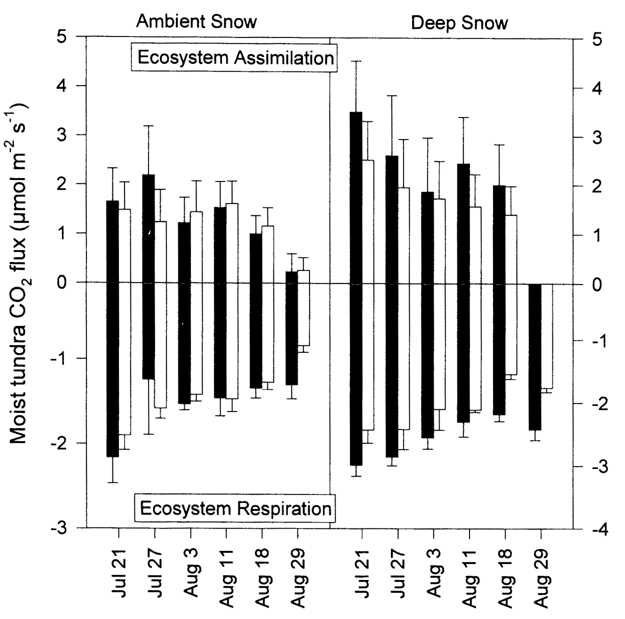

FIGURE 4. Moist tussock tundra ecosystem assimilation and ecosystem respiration in warmed (solid bars) and unwarmed plots (open bars) under ambient and deep snow experimental treatments. Bars represent means (± SE); n = *6.*

TABLE 3

Estimated carbon loss (g CO_2-C m^{-2}) from moist tussock and dry heath tundra during the 1996 snow-free season at Toolik Lake, Alaska

	Dry Tundra		Moist Tundra	
	Ambient snow	Deep snow	Ambient snow	Deep snow
Unwarmed	33.2	11.5	40.3	38.2
Warmed	41.7	49.0	55.7	80.8

Elevated summer temperatures increased the total amount of carbon emitted during the season by 26 to 38% in ambient snow plots and by 112 to 326% in deep snow plots. In contrast, the effects of increased snow accumulation on CO_2 flux varied with summer temperature. With experimental warming, season-long ecosystem carbon losses were greater from the deep snow plots than from those with ambient snow conditions. However, under ambient temperatures, carbon loss to the atmosphere was lower in the deep snow plots than ambient snow plots (Table 3).

The increase in carbon loss from warmer plots is consistent with other field studies in both manipulated (Christensen et al., 1997) and unmanipulated arctic ecosystems (Oberbauer et al., 1991, 1992). Nadelhoffer et al. (1991) found that microbial respiration was insensitive to temperature below 9°C, but that temperatures from 9 to 15°C resulted in pronounced increases in respiration. Under the field conditions of this study, soil temperatures ranged from ca. 1 to 25°C, with monthly means ranging from ca. 7 to 14°C, sufficient for temperature to have a significant effect on CO_2 flux. Other factors are likely involved,

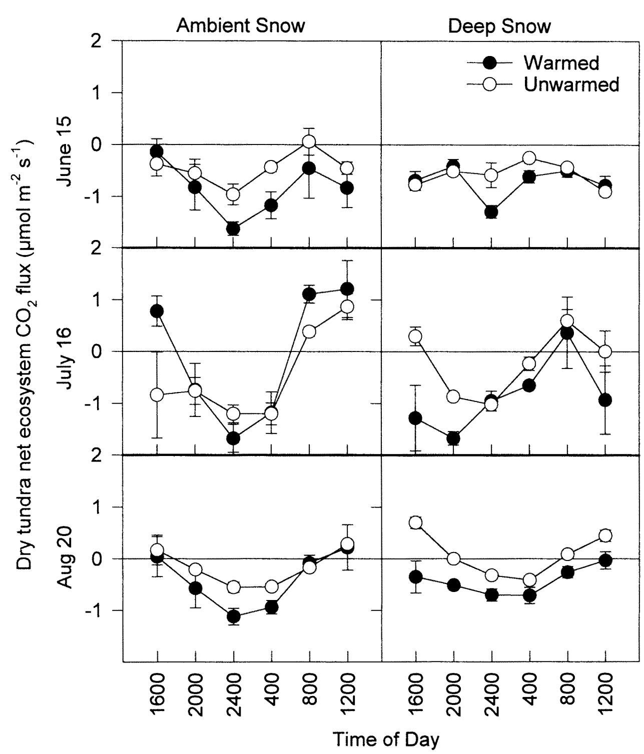

FIGURE 5. Diurnal patterns of net ecosystem CO_2 flux in dry heath tundra under ambient and increased temperature and snow treatments. Circles represent means (± SE); n = *18. The figures show representative patterns from early, mid-, and late in the growing season.*

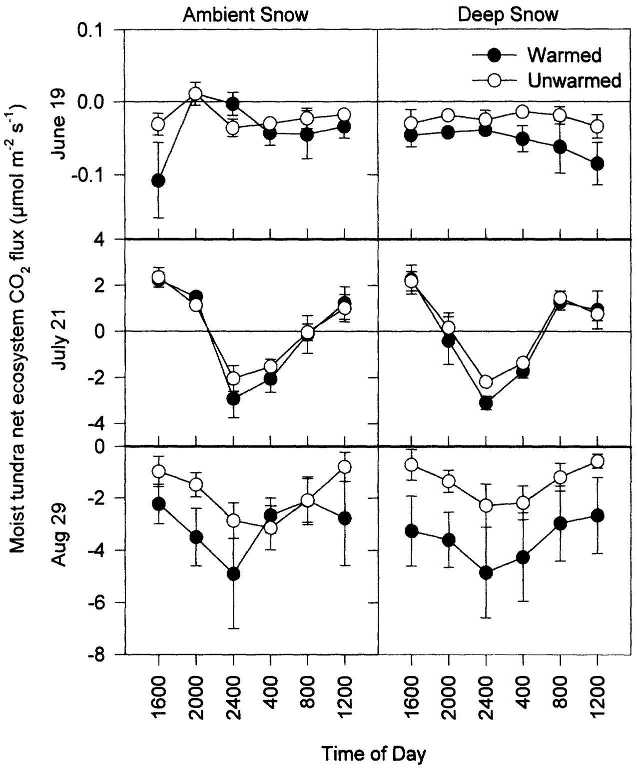

FIGURE 6. Diurnal patterns of net ecosystem CO_2 flux in moist tussock tundra under ambient and increased temperature and snow treatments. Circles represent means (± SE); n = *18. The figures show representative patterns from early, mid-, and late in the growing season. Note different scales on the vertical axis.*

however. Nadelhoffer et al. (1991) and Schimel and Clein (1996) found that soil carbon quality was more important than temperature in regulating microbial respiration, which may help account for the differences we measured between sites. In tundra microcosms examined in controlled environments, Johnson et al. (1996) found that increased temperature led to greater heterotrophic respiration, but that this CO_2 loss was offset by enhanced ecosystem assimilation. In the tundra ecosystems we examined in the field, ecosystem assimilation did not compensate for increased ecosystem respiration.

The differing effects of the snow treatment on total carbon loss under the two warming regimes may be related more to the potential effects of the artificial snowdrifts on soil moisture than growing season length. In tussock tundra similar to that at Toolik Lake, Oberbauer et al. (1992) found that high water tables and low soil temperatures inhibited microbial respiration, and that individual rainfall events were sufficient to reduce CO_2 efflux. In a study involving irrigation of arctic tundra, Oberbauer et al. (1989) found that adding water to an already-moist system increased photosynthesis in three species. We do not know why ecosystem assimilation was strongly reduced by experimental warming in the deep snow plots in dry heath tundra; assimilation rates were well below those for warmed plots under ambient conditions. Since *D. octopetala* was the primary species in these plots, strong effects on this one species could have had a major impact on ecosystem-level fluxes relative to the moist tundra, in which several species were present.

The week-to-week variation apparent in the net CO_2 flux measurements reflects relatively greater variability in ecosystem assimilation than in ecosystem respiration. Variability in ecosystem assimilation was particularly apparent in the dry site, and was probably related to the predominance of *D. octopetala* in those plots. Although the magnitude differed with experimental regime, ecosystem respiration in both dry and moist tundra exhibited a steady decline from mid-July to late August. These patterns suggest that ecosystem assimilation is more sensitive to daily weather (e.g., temperature, irradiance) than respiration, and that ecosystem respiration may be relatively more sensitive to season-long climate phenomena. If this holds true over multiple years, then long-term climate patterns may be more important in influencing whether arctic ecosystems are net sources or sinks of carbon, whereas variability in seasonal weather may be more important in determining the magnitude of weekly fluxes.

Studies of high-latitude ecosystems have shown that during the growing season most ecosystem carbon flux values are small, oscillating around a null balance, and are the result of large values for carbon acquisition offset by large respiration components. Small errors of 1 μmol CO_2 m^{-2} s^{-1} in measured net flux can translate to roughly 400 g C m^{-2} when fluxes are modeled on an annual basis (McGuire, pers. comm., 1997). Ecosystem CO_2 flux estimates made using surface chambers may be as much as 40% greater than those using eddy covariance towers (Ryan, 1997). Thus, there is some uncertainty about the magnitude or possibly the sign of carbon flux in ecosystem studies, including the data reported here, and extrapolations should be cautious. Some models suggest that while global warming may enhance decomposition and soil carbon loss, nutrient release (particularly nitrogen) will stimulate canopy growth and carbon uptake (McKane et al., 1997b; M. Walker et al., unpublished). These models emphasize the dynamic nature of nutrient-limited arctic ecosystems.

The net growing season carbon losses in the moist tussock and dry heath ecosystems we examined reflect an inability to sequester carbon via photosynthesis faster than it is respired by soil heterotrophs and roots. Summer and winter carbon efflux patterns indicate that these particular ecosystems are now sources of CO_2 to the atmosphere, and that global warming could increase carbon loss. However, climatic changes could lead to different seasonal effects. During the summer growing season, increased winter snow accumulation and a shorter growing season, in the absence of warmer summer temperatures, could result in less carbon loss than is now occurring. This could be offset by increased winter carbon efflux from under deep snow. We found greater CO_2 efflux and warmer soil temperatures under the artificial snowdrifts of this experiment than from tundra under ambient snow accumulations (Welker et al., unpublished data). Similarly, natural communities which accumulated snow earlier in the season also had higher CO_2 efflux during the winter (Fahnestock et al., 1997; Jones et al., 1999). These findings warrant investigation of a potential carryover effect from winter to summer respiration in this experiment. We are currently examining the effects of the snow and warming treatments on a number of environmental and biotic variables, including microbial biomass, soil carbon, and soil moisture, in order to elucidate potential mechanisms for the carbon flux patterns we observed in this study.

Acknowledgments

This research was supported by the National Science Foundation (OPP-9321730, OPP-9617643, and OPP-930083). Logistical support was provided by the Toolik Field Station, University of Alaska Fairbanks, and the Polar Ice Coring Office, University of Nebraska, Lincoln. We gratefully acknowledge the assistance of K. Povirk, A. Parsons, S. Oberbauer, G. Starr, and E.

Pop. The manuscript benefited from the comments of Laura Gough and one anonymous reviewer.

References Cited

Billings, W. D., Luken, J. O., Mortensen, D. A., and Peterson, K. M., 1982: Arctic tundra: a source or sink for atmospheric carbon dioxide in a changing environment? *Oecologia,* 53: 7–11.

Christensen, T. R., Michelsen, A., Jonasson, S., and Schmidt, I. K., 1997: Carbon dioxide and methane exchange of a subarctic heath in response to climate change related to environmental manipulations. *Oikos,* 79: 34–44.

Fahnestock, J. T., Jones, M. H., Brooks, P. D., Walker, D. A., and Welker, J. M., 1997: Winter and early spring CO_2 efflux from tundra communities of northern Alaska. *Journal of Geophysical Research,* In Press.

Gates, W. L., Mitchell, J. F. B., Boer, G. J., Cubasch, U., and Meleshko, V. P., 1992: Climate modelling, climate prediction and model validation. *In* Houghton, J. T., Callander, B. A., and Varney, S. K. (eds.), *Climate Change 1992: The Supplementary Report to the IPCC Scientific Assessment.* Cambridge: Cambridge University Press, 97–134.

Grogan, P. and Chapin, F. S., III, 1997: Belowground CO_2 flux in Alaskan tundra: effects of climate and vegetation-type with regional extrapolation. *Bulletin of the Ecological Society of America,* 78: 99.

Grulke, N. E., Riechers, G. H., Oechel, W. C., Hjelm, U., and Jaeger, C., 1990: Carbon balance in tussock tundra under ambient and elevated atmospheric CO_2. *Oecologia,* 83: 485–494.

Henry, G. H. R. and Molau, U., 1997: Tundra plants and climate change: the International Tundra Experiment (ITEX). *Global Change Biology,* 3 (Suppl. 1):1–9.

Johnson, L. C., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J., Rastetter, E. R., Laundre, J. A., and Murray, G. L., 1996: Effects of drainage and temperature on carbon balance of tussock tundra microcosms. *Oecologia,* 108: 737–748.

Jones, M. H., Bay, C., and Nordenhall, U., 1997: Effects of experimental warming on arctic willows (*Salix* spp.): a comparison of responses from the Canadian High Arctic, Alaskan Arctic, and Swedish Subarctic. *Global Change Biology,* 3 (Suppl. 1): 55–60.

Jones, M. H., Fahnestock, J. T., and Welker, J. M., 1999: Early and late winter CO_2 efflux from arctic tundra in the Kuparuk River watershed, Alaska, U.S.A. *Arctic, Antarctic, and Alpine Research.* 31 (in press).

Marion, G. M., Henry, G. H. R., Freckman, D., Johnstone, J., Jones, G., Jones, M. H., Lévesque, E., Molau, U., Molgaard, P., Parsons, A. N., Svoboda, J., and Virginia, R. A., 1997: Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology,* 3 (Suppl. 1): 20–32.

Maxwell, B., 1992: Arctic climate: potential for change under global warming. *In* Chapin, F. S., III, Jeffries, R. L., Reynolds, J. F., Shaver, G. R., and Svoboda, J. (eds.), *Arctic Cosystems in a Changing Climate: An Ecophysiological Perspective.* San Diego: Academic Press, 11–34.

McGuire, D., 1997: Personal communication. U.S. Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, University of Alaska, Fairbanks, Alaska.

McKane, R. B., Rastetter, E. B., Shaver, G. R., Nadelhoffer, K. J., Giblin, A. E., Laundre, J. A., and Chapin, F. S., III, 1997a: Reconstruction and analysis of historical changes in carbon storage in arctic tundra. *Ecology,* 78: 1188–1198.

McKane, R. B., Rastetter, E. B., Shaver, G. R., Nadelhoffer, K. J., Giblin, A. E., Laundre, J. A., and Chapin, F. S., III, 1997b: Climatic effects on tundra carbon storage inferred from experimental data and a model. *Ecology,* 78: 1170–1187.

Michaelson, G. J., Ping, C. L., and Kimble, J. M., 1996: Carbon storage and distribution in tundra soils of arctic Alaska, U.S.A. *Arctic and Alpine Research,* 28: 414–424.

Nadelhoffer, K. J., Giblin, A. E., Shaver, G. R., and Laundre, J. A., 1991: Effects of temperature and substrate quality on element mineralization in six arctic soils. *Ecology,* 72: 242–253.

Oberbauer, S. F., Hastings, S. J., Beyers, J. L., and Oechel, W. C., 1989: Comparative effects of downslope water and nutrient movement on plant nutrition, photosynthesis, and growth in Alaskan tundra. *Holarctic Ecology,* 12: 324–334.

Oberbauer, S. F., Tenhunen, J. D., and and Reynolds, J. F., 1991: Environmental effects on CO_2 efflux from water track and tussock tundra in arctic Alaska, U.S.A. *Arctic and Alpine Research,* 23: 162–169.

Oberbauer, S. F., Gillespie, C. T., Cheng, W., Gebauer, R., Sala Serra, A., and Tenhunen, J. D., 1992: Environmental effects of CO_2 efflux from riparian tundra in the northern foothills of the Brooks Range, Alaska, USA. *Oecologia,* 92: 568–577.

Oberbauer, S. F., Cheng, W., Gillespie, C. T., Ostendorf, B., Sala, A., Gebauer, R., Virginia, R. A., and Tenhunen, J. D., 1996: Landscape patterns of carbon dioxide exchange in tundra ecosystems. *In* Reynolds, J. F. and Tenhunen, J. D. (eds.), *Landscape Function and Disturbance in Arctic Tundra.* Berlin: Springer-Verlag, 223–256.

Oechel, W. C. and Billings, W. D., 1992: Effects of global change on the carbon balance of arctic plants and ecosystems. *In* Chapin, F. S., III, Jeffries, R. L., Reynolds, J. F., Shaver, G. R., and Svoboda, J. (eds.), *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective.* San Diego: Academic Press, 139–168.

Oechel, W. C. and Vourlitis, G. L., 1994: The effects of climate change on land-atmosphere feedbacks in arctic tundra regions. *Trends in Ecology and Evolution,* 9: 324–329.

Oechel, W. C., Hastings, S. J., Vourlitis, G., Jenkins, M., Riechers, G., and Grulke, N., 1993: Recent change of arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature,* 361: 520–523.

Oechel, W. C., Vourlitis, G. L., Hastings, S. J., and Bochkarev, S. A., 1995: Change in arctic CO_2 flux over two decades: effects of climate change at Barrow, Alaska. *Ecological Applications,* 5: 846–855.

Oechel, W. C., Vourlitis, G., and Hastings, S. J., 1997: Cold season CO_2 emission from arctic soils. *Global Biogeochemical Cycles,* 11: 163–172.

Poole, D. K. and Miller, P. C., 1982: Carbon dioxide flux from three arctic tundra types in north-central Alaska, U.S.A. *Arctic and Alpine Research,* 14: 27–32.

Raich, J. W. and Potter, C. S., 1995: Global patterns of carbon dioxide emissions from soils. *Global Biogeochemical Cycles,* 9: 23–36.

Ryan, M., 1997: Autotrophic respiration in BOREAS. SIMS Workshop, The role of high latitude ecosystems in the global carbon cycle. 12–14 October 1997, Edgartown, MA.

SAS Institute, 1989: *SAS/Stat User's Guide, Version 6, Fourth Edition, Vol. 2.* Cary, NC: SAS Institute, Inc. 846 pp.

Schimel, J. P. and Clein, J. S., 1996: Microbial response to freeze-thaw cycles in tundra and taiga soils. *Soil Biology and Biochemistry,* 28: 1061–1066.

von Ende, C. N., 1993: Repeated-measures analysis: growth and other time-dependent measures. *In* Scheiner, S. M. and Gurevitch, J. (eds.), *Design and Analysis of Ecological Experiments.* New York: Chapman and Hall, 113–137.

Vourlitis, G. L., Oechel, W. C., Hastings, S.J., and Jenkins, M. A., 1993: A system for measuring in situ CO_2 and CH_4 flux in unmanaged ecosystems: an arctic example. *Functional Ecology,* 7: 369–379.

Welker, J. M., Molau, U., Parsons, A. N., Robinson, C. H., and Wookey, P. A., 1997: Responses of *Dryas octopetala* to ITEX environmental manipulations: a synthesis with circumpolar comparisons. *Global Change Biology,* 3 (Suppl. 1): 61–73.

Ms submitted October 1997