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Initial effects of experimental warming on above- and belowground components of net ecosystem CO_2 exchange in arctic tundra

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Abstract The Arctic contains extensive soil carbon reserves that could provide a substantial positive feedback to atmospheric CO_2 concentrations and global warming. Evaluation of this hypothesis requires a mechanistic understanding of the in situ responses of individual components of tundra net ecosystem CO_2 exchange (NEE) to warming. In this study, we measured NEE, total ecosystem respiration and respiration from below ground in experimentally warmed plots within Alaskan acidic tussock tundra. Soil warming of 2–4°C during a single growing season caused strong increases in total ecosystem respiration and belowground respiration from moss-dominated inter-tussock areas, and similar trends from sedge-dominated tussocks. Consequently, the overall effect of the manipulation was to substantially enhance net ecosystem carbon loss during mid-summer. Components of vascular plant biomass were closely correlated with total ecosystem respiration and belowground respiration in control plots of both microsites, but not in warmed plots. By contrast, in the warmed inter-tussock areas, belowground respiration was most closely correlated with organic-layer depth. Warming in tussock areas was associated with increased leaf nutrient pools, indicating enhanced rates of soil nutrient mineralisation. Together, these results suggest that warming enhanced net ecosystem CO_2 efflux primarily by stimulating decomposition of soil organic matter, rather than by increasing plant-associated respiration. Our short-term experiment provides field evidence to support previous growth chamber and modelling studies indicating that arctic soil C reserves are relatively sensitive to warming and could supply an initial positive feedback to rising atmospheric CO_2 concentrations/changing climate.

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Introduction

Warming effects on net carbon balance in the Arctic may be of crucial importance in understanding links between terrestrial carbon cycling, rising atmospheric CO_2 concentrations and future global warming. Arctic ecosystems contain extensive soil carbon reserves in the active and upper permafrost layers (Post et al. 1982; Ping et al. 1997) that could provide a substantial positive feedback to climate warming (Lashof 1989). In addition, general circulation models of CO_2-induced global climate change predict that Arctic ecosystems will undergo the most rapid increases in air temperature (Kattenberg et al. 1996). Recent trends in high-latitude temperature records are consistent with these projections, suggesting that warming in the Arctic may already have begun (Chapman and Walsh 1993; Serreze et al., in press).

The effects of warming on net carbon balance in arctic ecosystems have been predicted from biogeochemical theory (Shaver et al. 1992) and from models validated with experimental field data on the response of plant primary production to warming (McKane et al. 1997). These models indicate that increases in air temperature will result in an initial stimulation of net ecosystem C release, but that the longer-term effect of warming would be to increase primary production and C storage through enhanced availability of growth-limiting nutrients. Actual field measurements of CO_2 flux in Arctic ecosystems have focussed on characterising net ecosystem CO_2 exchange (NEE) using chamber and eddy correlation techniques (Oberbauer et al. 1991, 1992, 1996; Oechel et al. 1993; Christensen et al. 1997; Aurela et al. 1998; Hobbie and Chapin 1998; Jones et al. 1998; Shaver et al. 1998; Soegaard and Nordstroem 1999; Vourlitis and Oechel 1999; Welker et al. 1999). However, NEE is the balance between two opposing and relatively large fluxes: C uptake (gross ecosystem photosynthesis, GEP) and C losses

due to respiration derived from both plant and soil organic matter source pools (ecosystem respiration, ER). Decadal warming in the Arctic during the 1980s may have enhanced tundra net ecosystem CO_2 release (Oechel et al. 1993), but whether this response was due to stimulated respiration associated with plants, or stimulated decomposition of soil organic matter is not clear. This distinction is critical, since it is the warming response of the vast stores of soil organic C in tundra that make the Arctic important in the context of feedbacks to global climate change. Thus, models linking the response of tundra net C balance to future climate require a mechanistic understanding of the impact of warming on each of the components of NEE, as well as the source pools affected.

In this study, we distinguished the initial responses of GEP, ER and belowground respiration to an experimental warming manipulation that elevated soil temperature in Alaskan acidic tussock tundra. We placed plastic tents over tundra at snow melt and made diel CO_2 flux measurements of above- and belowground components of NEE at the height of the growing season. In addition, we measured treatment effects on above- and belowground components of plant biomass/nutrient content. This study differs from previous studies on the effects of warming on C balance in mesic/moist tundra (Chapin et al. 1995; Christensen et al. 1997; Hobbie and Chapin 1998; Jones et al. 1998; Jonasson et al. 1999) in several major ways. First, it is a short-term study requiring a destructive harvest to determine the initial warming responses not just of GEP and ER, but also of respiration from belowground. Second, by measuring above- and belowground plant biomass and nutrients in the same plots, we can relate fluxes, and the effects of treatment, directly to potential driving variables at the ecosystem level. This approach was designed to identify the controls on above- and belowground components of NEE and their initial responses to warming. Third, this study of acidic tussock tundra differentiates sedge-dominated tussocks from moss-dominated inter-tussock areas in order to evaluate the potential importance of these markedly different microsites in determining spatial and temporal responses to increased temperature. The aim of our study was to test the hypothesis that the initial response of tundra NEE to soil warming is enhanced net CO_2 flux to the atmosphere due to stimulated decomposition of soil organic matter.

Materials and methods

Study site

This study was conducted in upland acidic tussock tundra at the Long-Term Ecological Research site in Toolik Lake, Alaska (68°38′ N, 149°34′ W, elevation 760 m). Acidic tussock tundra consists of tussocks dominated by *Eriophorum vaginatum* surrounded by inter-tussock moss-dominated zones that comprise approximately 80% of the total ground area (D. Hooper, personal communication). Dwarf evergreen and deciduous shrubs are common in both tussock and inter-tussock areas (Shaver et al. 1992). Tussock soils at the site have deeper organic layers (16.1 cm from the base of the green moss horizon; SE=1.3, n=18) and slightly higher bulk densities (0.11 g cm^{-3}, SE=0.01, n=18) compared to those in inter-tussock areas (10.9 cm, SE=1.1, n=18; and 0.09 g cm^{-3}, SE=0.01, n=18, respectively). On 9 May 1997, at the beginning of snow melt, we placed three A-shaped wooden tent frames (2×5 m at the base, 1 m high at the apex) 20–50 m apart on a uniform region of gently sloping tundra close to where long-term (9-year) warming experiments had been conducted using similar methodology (Chapin et al. 1995). A continuous sheet of 0.15-mm-thick ("6-mil") polyethylene transparent plastic (Weatherall; T.R.M., La Mirada, Calif.) was fixed to each frame. On 5 July 1997, plastic collars (20 cm internal diameter) were placed over three randomly located tussock and inter-tussock areas within each of the tents (i.e. n=9 in total for each vegetation type). In addition, collars were placed over three randomly located tussock and inter-tussock control areas adjacent to each of the tents. Since tussocks were generally smaller in diameter than the collars, some inter-tussock vegetation was present in many of the tussock plots. We used a bread knife to cut a slot approximately 5 cm deep into the soil (i.e. below the green moss horizon) around the edge of each collar. The collars were pushed down into the soil and held in place by screwing them to two wooden stakes that were driven into the soil on opposite sides of the outer circumference of each collar.

Flux measurements

Ecosystem CO_2 fluxes were measured in each plot on 12–13 July 1997 using a Plexiglas cylindrical "top-hat"-shaped chamber fitted with two circulation fans and a pressure equilibration tube. The chamber (internal volume 10.6 l, basal area 324 cm^2) had a flat flange ring fixed to the open end that could be clamped with spring clips to a 20-cm-diameter plastic pipe flange that fitted over the collars. The pipe flange joints to the chamber flange and the collar were sealed with rubber "O" rings. CO_2 concentrations in the chamber were measured with a LI-COR 6200 infrared gas analyser (LI-COR Instruments, Lincoln, Neb.) attached by hoses to the chamber wall.

We measured CO_2 flux on each plot five times during a diel cycle, each time measuring first under ambient light conditions and then under darkness (by covering with several layers of black plastic sheeting). For the light measurements, we waited 15 s after clamping the chamber in position, to allow equilibration before beginning to record CO_2 changes. After each light measurement, the chamber was lifted to equilibrate CO_2 concentrations and temperatures with ambient conditions. Dark measurements were initiated at least 30 s after replacing the chamber and covering it with black sheeting. Preliminary measurements indicated that this was a sufficient period for acclimation to darkness. During the night period at photosynthetically active radiation (PAR) levels <50 µmol m^{-2} s^{-1} and air temperatures <9°C, we found no differences between dark and light flux measurements, and discontinued the light measurements. Fluxes were measured over six consecutive 20-s intervals and later averaged for statistical analyses. We recorded the height of tussock and inter-tussock vegetation within each collar and adjusted the LI-COR flux output data to account for differences among plots in sampling volume within the chamber headspace.

Fluxes under ambient light (net ecosystem CO_2 exchange, NEE) are the balance between gross photosynthesis, plant-associated respiration (by shoots, roots, mycorrhizae, rhizosphere-associated microbes and microbial decomposition of standing dead/fresh surface litter material) and respiration derived from the microbial decomposition of soil organic matter. Flux measurements in the dark represent the sum of plant-associated and soil organic matter-derived respiration (ecosystem respiration, ER). Gross ecosystem photosynthesis (GEP) is estimated by adding the absolute value of ER to the measured value of NEE for each plot. Both ends of each tent were opened prior to making treatment flux measurements in order to determine all ecosystem CO_2 fluxes at ambient air temperature. Where the CO_2 concentrations inside the tents became elevated due to human breathing, we temporarily va-

cated the tent so that the initial chamber CO_2 concentration at the beginning of each flux measurement was always less than 380 µl l^{-1}. On the evening of 13 July, having finished the NEE flux measures, we clipped all aboveground tissue including the green moss layer and surface litter from within each collar. Clipping was carried out with considerable care to minimise damage to roots and rhizomes.

Belowground CO_2 fluxes from the clipped surfaces were measured in each plot five times during a diel cycle on 15–16 July 1997 (i.e. at least 36 h after the last set of NEE flux measures). This timing interval was based on a preliminary growth chamber study with tussocks that indicated a small flush of CO_2 from the soil surface over the first 24 h after clipping of aboveground vegetation, followed by a slow decline in respiration rates over succeeding days. We measured belowground CO_2 flux using a protocol similar to that for NEE measurements described above. However, the chamber CO_2 concentration was initially drawn down approximately 10 µl l^{-1} below ambient by switching in the soda lime CO_2 scrubber line for 20 s, in order to facilitate mixing within the sampling chamber. We waited a further 20 s to allow equilibration before beginning to record the change in chamber headspace CO_2 concentration.

Environmental parameters

Air temperature and relative humidity in the chamber were measured by the LI-COR sensor head. A quantum sensor (LI-190SA; LI-COR Instruments) fixed to the top of the chamber recorded PAR concurrent with CO_2 flux measurements. Soil temperatures during the course of both sets of diel measurements were recorded at 5 cm below the junction of the green moss and brown organic horizons at the centre of each plot. We constructed probes using temperature transducers (AD 592; Analog Devices, Norwood, Mass.) sealed within waterproof heat-shrink tubing (3M, Austin, Tex.). The data were averaged every 5 min and recorded every 30 min using CR10 dataloggers (Campbell Scientific, Logan, Utah).

Plant and soil harvest

The entire aboveground harvest of each inter-tussock area and subsamples (approximately 30%) of the harvest from each tussock area were sorted into the following categories: vascular plant leaves, vascular plant stems and non-green shoot/tiller tissue, green moss tissue, and standing dead/surface litter material. The leaf area of vascular plants was determined using a leaf area meter (LI-3000A, LI-COR Instruments) fitted with a conveyor belt accessory. Following the belowground CO_2 flux measurements, total organic layer depth for all plots was measured from the base of the green moss horizon. We cut out the complete organic soil core from beneath each collar to 10 cm depth or to the mineral soil horizon where the organic layer was <10 cm deep. Approximately one quarter of each core was used to determine gravimetric moisture content. The remainder was cut up into small chunks, homogenised and randomly subsampled. Approximately 5% of the total core was subsampled and sorted into the following categories: live roots <1.5 mm in diameter, rhizomes and belowground stems, and soil. All harvested material was dried for >96 h in a fan-assisted oven (65°C). Vascular leaf and root nitrogen and phosphorus contents were analysed colorimetrically by the indophenol-salicylate and molybdenum blue methods, respectively (Kedrowski 1983) after sulphuric acid/selenium digestion of a maximum of 0.1 g of ground plant material.

Statistical analyses

We estimated mean diel fluxes of NEE, ER, GEP and belowground respiration by interpolating the flux rates between sampling intervals within each diel measurement cycle and normalising the interpolations to a 24-h period. The effects of the experimental manipulation on mean diel fluxes, environmental parameters, plant biomass components, litter pools, allocation patterns and tissue nutrient contents were analysed using individual two-factor analyses of variance (ANOVAs) with block (i.e. tent) as a separate factor. Data that failed Cochran's test of homogeneity of variances (Winer 1971) were log-transformed prior to analysis. We recognise that the plots within each treated block were not completely independent of each other because they were covered by the same tent (pseudoreplication). However, because the plots were relatively small compared to the area enclosed by each tent, we do not expect any interactions between plots within a tent and their response to treatment.

Mean diel values of environmental parameters were calculated by interpolating the data between sampling intervals across the full diel measurement cycle. We used Spearman's pairwise rank correlation test to evaluate relationships between mean diel fluxes and ecosystem properties/environmental parameters. As the number of correlation variables increases, the probability of obtaining a significant correlation by chance alone also increases (Zar 1996). However, lowering α (the probability of a type 1 error) to counteract this effect decreases the power to detect real differences (Winer et al. 1991; Underwood 1997), especially with a low number of replicates. In the discussion of our results, we focus only on correlations that are significant at an α less than 0.05, and emphasise consistency in the patterns of these correlations across microsites and/or treatments. Aboveground environmental parameters during flux measurements (Table 2) were calculated from means (120-s averages) for air temperatures and PAR, and from initial values (20 s averages) for relative humidities and CO_2 concentrations. All statistical analyses were conducted using Systat 5.2 (SPSS, Chicago, Ill.).

Results

Environmental parameters

Above- and belowground environmental parameters in mid-summer were significantly altered by the plastic tents. Mean diel soil temperatures in tussock and moss-dominated inter-tussock areas were elevated 2–4°C by the manipulation (Fig. 1, Table 1). In contrast, soil moisture levels were not altered by the manipulation (Table 1), presumably because of lateral water flow on the sloped site. Air temperatures during the CO_2 flux measurements were unaffected by the treatment (Table 1) because each tent was opened at both ends during the measuring interval. Nevertheless, the strong soil-warming effect indicates that air temperatures must have been substantially elevated beneath the tents during the 2-month period prior to flux measurement. As in similar previous manipulations (Chapin et al. 1995; Hobbie and Chapin 1998), the plastic tenting reduced mean diel PAR by 25–30% (Table 1). Atmospheric CO_2 concentration and relative humidity inside the tents at the time of flux measurement were significantly increased (Table 1). However, the magnitudes of these increases were relatively small and are unlikely to be biologically significant (Billings et al. 1984; Tissue and Oechel 1987; Grulke et al. 1990; Chapin et al. 1995).

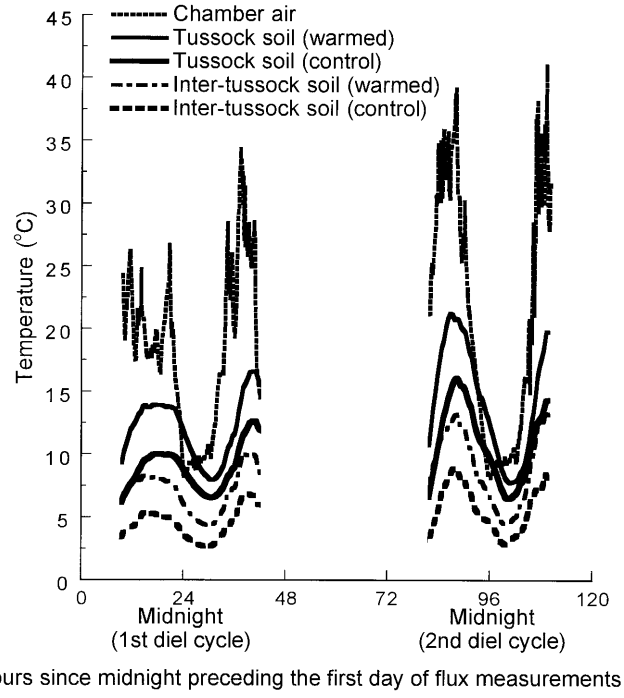

Fig. 1 Air and soil temperatures in tussock and inter-tussock areas during the diel measurement cycles of net ecosystem CO_2 exchange and belowground respiration. Air temperatures are presented for all plots as the mean internal chamber values during each individual flux measurement. The soil temperature data are 1/2-hourly means at 5 cm depth (n=8–9; SEs<1.0°C)

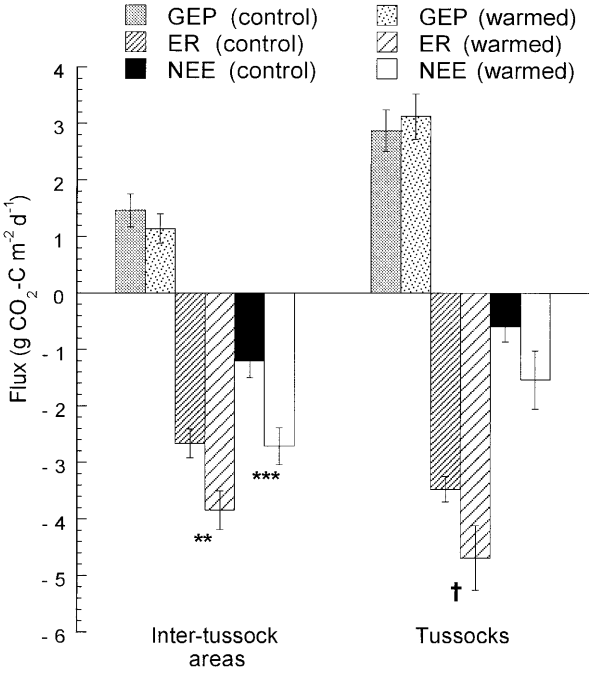

Fig. 2 Ecosystem CO_2 fluxes in inter-tussock and tussock areas in response to experimental warming (*GEP* gross ecosystem photosynthesis, *ER* ecosystem respiration, *NEE* net ecosystem exchange). Each value is the mean diel CO_2 flux measured at ambient air temperature on 12–13 July 1997 (n=9, *bars* SEs). Positive values indicate CO_2 flux into the ecosystem (sink), negative values indicate flux to the atmosphere (source) ($^{\dagger}P$<0.10, $^{**}P$<0.01, $^{***}P$<0.001

Table 1 Environmental parameters during flux measurements of net ecosystem CO_2 exchange/ecosystem respiration (day 1) and belowground respiration (day 4). Soil temperature data are presented as mean values of 1/2-hourly data through each diel flux measurement cycle. Soil moisture was measured gravimetrically at the end of the experiment. Aboveground environmental data were collected at the time of individual flux measurements, and have been pooled from both microsites within each series of block measurements for analysis. Data for each parameter were analysed by separate two-factor ANOVAs ('treatment', 1 *df*; 'block', 2 *df*) for each microsite-type (n=9). Effects of 'block' were rarely statistically significant and are not reported (*PAR* photosynthetically active radiation)

		Net ecosystem exchange (12–13 July 1997)				Belowground respiration (15–16 July 1997)			
		Control	Warmed	*F*-ratio	*P*-value	Control	Warmed	F-ratio	*P*-value
Soil temperature (°C)	Tussocks	8.9	11.9	26.363	*0.001*	10.9	14.7	20.071	*0.001*
	Inter-tussocks	4.5	7.0	8.392	*0.012*	5.7	8.6	4.839	*0.045*
Soil moisture (%)	Tussocks	Not measured	Not measured			487	487	0.001	0.997
	Inter-tussocks	Not measured	Not measured			361	418	0.477	0.501
Air temperature (°C)		18.3	19.1	0.583	0.446	24.2	24.2	0.003	0.956
Light (PAR, µmol photons m^{-2} s^{-1})		533.3	375.0	7.318	*0.008*	724.1	550.3	5.791	*0.017*
CO_2 (µl l–1)		354.3	376.5	41.842	*0.001*	368.2	383.7	28.633	*0.001*
Relative humidity (%)		63.2	66.9	5.371	*0.022*	56.14	58.37	0.959	0.329

Ecosystem CO_2 fluxes

Diel net ecosystem CO_2 exchange mid-way through the growing season was strongly influenced by the experimental manipulation. In inter-tussock areas, the treatment significantly increased total ecosystem respiration (Fig. 2; treatment: P=0.006, block: P=0.10), but did not affect GEP C gain (Fig. 2). Consequently, the overall effect of the manipulation on inter-tussock areas was to significantly enhance net ecosystem C loss (Fig. 2; treatment: P=0.001, block: P=0.07). In tussocks, ER was higher in tented plots (treatment: P=0.06, block:

P=0.60), and gross photosynthetic C gain was unaltered, resulting in a trend towards increased net ecosystem C loss (treatment: *P*=0.13, block: *P*=0.90). Thus, the pattern of tussock flux responses was identical to that of inter-tussock areas described above (Fig. 2), although greater variability in fluxes from tussocks resulted in mean differences of lower statistical significance.

Diel belowground CO_2 release 36 h after clipping and removing shoot and surface litter material was significantly enhanced within warmed inter-tussock areas (Fig. 3; treatment: *P*=0.017, block: *P*=0.58), and tended towards an increase in warmed tussocks (Fig. 3; treatment: *P*=0.11, block: *P*=0.45). Mean values for belowground respiration (day 4; Fig. 3) were generally greater than those for mean total ecosystem respiration (day 1; Fig. 2) reflecting substantially higher air and soil temperatures during the diel cycle of belowground efflux measurements (Fig. 1, Table 1). A wound or disturbance response to shoot clipping may also have contributed to the higher fluxes observed on day 4. In any event, individual diel measures of total ER and belowground respiration were closely correlated (Fig. 4), indicating that CO_2 release from each microcosm was consistent across

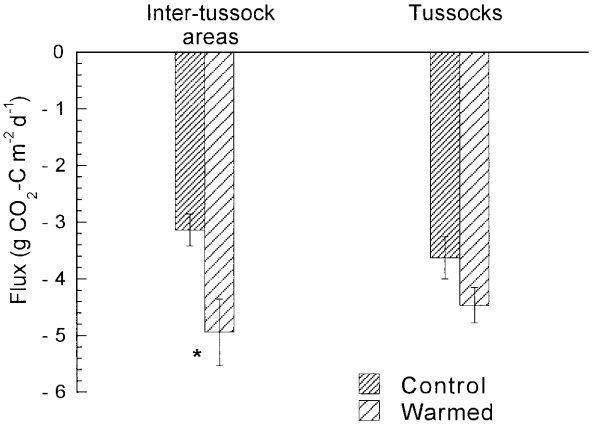

Fig. 3 Belowground respiration in inter-tussock and tussock areas in response to warming. Each value is the mean diel CO_2 flux measured at ambient air temperature on 15–16 July 1997 (*n*=9, *bars* SEs) (**P*<0.05)

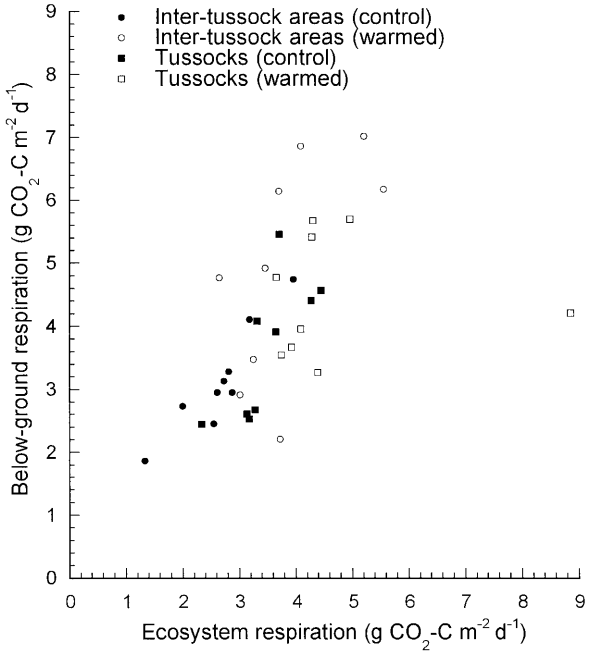

Fig. 4 Relationship between diel measures of total ecosystem respiration (day 1) and belowground respiration (day 4) for inter-tussock and tussock areas (Spearman's correlation test: *r*=0.69, *P*<0.001, *n*=36). The outlying data point has been included in all statistical analyses. This plot had consistently high values of ecosystem respiration (relative to all other plots at each flux measurement time) that could not be explained by any anomalous values of biomass or environmental parameters

Table 2 Plant biomass, litter pools and allocation patterns in response to treatment (g m^{-2}). SEs of the means are indicated in *parentheses* (*n*=8–9). Data for each component were analysed by separate two-factor ANOVAs ('treatment', 1 *df*; 'block', 2 *df*) for each microsite type. Effects of 'block' were rarely statistically significant and are not reported. Belowground stems of shrubs were included with rhizomes. The small difference between mean total plant biomass and the sum of individual component means for inter-tussock controls occurs because the aboveground harvested samples from one of the plots were mislaid, resulting in eight replicates for total plant and aboveground biomass values, and nine replicates for belowground biomass

	Inter-tussock areas				Tussock areas			
	Control	Warmed	*F*-ratio	*P*-value	Control	Warmed	*F*-ratio	*P*-value
Aboveground:								
Vascular plant leaves	43 (10)	42 (12)	0.001	0.99	157 (19)	245 (42)	3.915	0.07
Vascular plant stems	80 (12)	129 (41)	0.294[a]	0.60	110 (21)	179 (25)	3.966	0.07
Mosses	1,303 (225)	1,242 (85)	0.014[a]	0.91	544 (153)	103 (35)	2.722[a]	0.12
Belowground:								
Vascular plant roots	682 (141)	527 (143)	0.674	0.43	325 (87)	208 (34)	1.672[a]	0.22
Vascular plant rhizomes	509 (145)	1052 (311)	0.389[a]	0.54	624 (156)	429 (130)	0.919	0.35
Total plant biomass	2,523 (395)	2,990 (414)	0.545	0.47	1,760 (292)	1,165 (150)	3.302[a]	0.09
Standing dead and surface litter	20 (6)	58 (24)	1.375[a]	0.262	946 (122)	1,079 (126)	0.574	0.46
Leaf area index	0.35 (0.07)	0.35 (0.14)	0.038	0.85	1.16 (0.14)	1.91 (0.33)	2.776[a]	0.12
Leaf/root ratio	0.12 (0.03)	0.16 (0.05)	1.391	0.26	0.71 (0.17)	1.93 (0.47)	6.559[a]	*0.02*

[a] Variance of the data significantly heterogeneous (Cochran's test) and log-transformed prior to analysis

Table 3 Leaf and root nutrient contents of vascular plants in response to treatment. Tissue concentrations are presented in mg g^{-1}, pool sizes in g m^{-2}. SEs are indicated in parentheses (n=8–9). Data were analysed as described in Table 2. Effects of 'block' were rarely statistically significant and are not reported

	Inter-tussock areas				Tussock areas			
	Control	Warmed	*F*-ratio	*P*-value	Control	Warmed	*F*-ratio	*P*-value
Aboveground:								
Leaf N concentration	19.94 (0.39)	18.77 (0.40)	4.379	*0.05*	18.63 (0.45)	18.48 (0.31)	0.107	0.75
Leaf N pool	0.85 (0.17)	0.79 (0.23)	0.006	0.94	2.93 (0.37)	4.53 (0.75)	3.837	0.07
Leaf P concentration	1.22 (0.04)	1.00 (0.08)	7.724	*0.02*	1.21 (0.09)	1.36 (0.11)	1.614	0.23
Leaf P pool	0.05 (0.01)	0.05 (0.01)	0.218	0.65	0.19 (0.03)	0.33 (0.06)	5.753	*0.03*
Belowground:								
Root N concentration	16.92 (0.31)	16.28 (0.33)	2.153	0.16	15.28 (0.21)	16.14 (0.58)	1.877	0.19
Root N pool	11.74 (2.51)	8.62 (2.31)	0.954	0.35	4.96 (1.33)	3.51 (0.46)	0.583[a]	0.46
Root P concentration	0.92 (0.04)	0.83 (0.04)	2.015	0.18	0.74 (0.05)	0.80 (0.08)	0.464	0.51
Root P pool	0.63 (0.14)	0.43 (0.12)	1.328	0.27	0.22 (0.05)	0.18 (0.03)	0.349	0.57

[a] Variance of the data significantly heterogeneous (Cochran's test) and log-transformed prior to analysis

both days of measurement (i.e. before and after clipping), and suggesting that clipping did not influence the response of belowground CO_2 release to the warming manipulation. Together, our results indicate that the significant treatment effects on total ER/NEE were driven by effects of warming on respiration from belowground.

Plant biomass and nutrient contents

Plant biomass pools in inter-tussock and tussock areas responded differently to the treatment. In inter-tussock areas, the manipulation had no significant impacts on above- or belowground biomass (Table 2). By contrast, tussock vascular plant leaf biomass and aboveground stem biomass tended to be increased by the treatment (Table 2). In addition, the biomass ratio of tussock vascular leaves to fine roots (Table 2) was significantly enhanced in warmed plots. Since the treatment had no significant effect on tussock root or rhizome biomass, these results suggest that the manipulation caused a shift in tussock plant allocation towards greater aboveground tissue production. The increase in vascular plant tissue aboveground was counteracted by a reduction in green moss biomass, resulting in an overall trend towards decreased total plant biomass in warmed tussock areas (Table 2).

Tussock and moss-dominated inter-tussock areas also differed in the effect of treatment on vascular plant tissue nutrient contents. In inter-tussock areas, the manipulation lowered leaf nitrogen (N) and phosphorus (P) concentrations, but had no effect on leaf nutrient pools (Table 3) because of high variability in biomass relative to nutrient concentrations (Tables 2, 3). By contrast, leaf N and P pools in tussock areas were substantially increased in the tented plots (Table 3). The absence of a treatment effect on tissue N and P concentrations indicates that the increases in tussock leaf biomass (Table 2) were associated with enhanced nutrient uptake and/or allocation to leaves by tussock vascular plants.

Ecosystem CO_2 flux components in relation to ecosystem properties

Ecosystem diel gross photosynthetic C gain (GEP) in control and warmed inter-tussock areas was most closely correlated with leaf biomass and leaf nutrient pool sizes (Table 4). These results suggest that vascular plant leaves were the principal photosynthetic C sink in inter-tussock areas. By contrast, tussock GEP was not significantly correlated with either leaf or stem biomass, or with mean diel environmental parameters (Table 4). Together, our results suggest that mean diel CO_2 fluxes were not limited by light availability in any of the plots. First, there were no significant correlations between mean diel GEP and PAR in either microsite (Table 4). Second, the considerable reduction in incoming light due to the tenting (Table 1) did not result in significant treatment effects on mean diel GEP (Fig. 2).

ER was closely correlated with root plus rhizome biomass in control inter-tussock areas, and with leaf biomass and leaf nitrogen pools in control tussocks (Table 5), suggesting that plant-associated respiration was the principal source of ecosystem CO_2 release in unmanipulated plots. The disruption of these highly significant biomass correlations by warming (Table 5) suggests that plant-associated respiration was replaced by soil organic matter decomposition as the dominant source of ecosystem CO_2 release in manipulated plots. Our flux measurements after clipping away the aboveground tissue consistently support this interpretation. Belowground respiration was closely correlated with root plus rhizome biomass in unmanipulated inter-tussock areas only (Table 5). By contrast, belowground respiration in warmed inter-tussock areas was significantly correlated with organic layer depth (Table 5), suggesting that soil organic matter content became the principal determinant of CO_2 release in manipulated plots.

Table 4 Spearman rank correlation coefficients for ecosystem properties in relation to mean diel gross photosynthesis (n=8–9)

	Gross photosynthesis			
	Inter-tussock areas		Tussock areas	
	Control	Warmed	Control	Warmed
Leaf biomass	0.71†	0.77*	0.47	0.10
Leaf area index	0.69†	0.68†	0.40	0.02
Moss biomass	0.19	–0.60†	–0.40	0.58
Stem biomass	0.62	0.20	0.40	0.23
Leaf N pool	0.74*	0.77*	0.52	0.10
Leaf P pool	0.93**	0.57	0.43	–0.03
Mean diel PAR	–0.03	0.35	–0.08	0.43
Mean diel air temperature	–0.43	–0.02	–0.12	0.18
Mean diel soil temperature	–0.10	0.58	0.03	0.52

†P<0.10, *P<0.05, **P<0.01

Table 5 Spearman rank correlation coefficients for ecosystem properties in relation to mean diel total ecosystem respiration (day 1) and belowground respiration (day 4), (n=7–9; – indicates no data)

	Ecosystem respiration				Belowground respiration			
	Inter-tussock areas		Tussock areas		Inter-tussock areas		Tussock areas	
	Control	Warmed	Control	Warmed	Control	Warmed	Control	Warmed
Leaf biomass	0.45	0.12	*0.82**	–0.30				
Leaf area index	0.57	–0.12	*0.72**	–0.32				
Moss biomass	0.67†	–0.07	–0.47	0.40				
Stem biomass	0.36	–0.15	0.42	–0.22				
Dead/surface litter	–0.17	–0.28	0.35	0.10				
Leaf N pool	0.53	0.18	*0.85***	–0.30				
Leaf P pool	0.57	–0.23	0.67†	–0.13				
Root biomass	0.58	0.27	–0.10	0.48	0.55	0.23	–0.27	0.05
Rhizome biomass	0.58	0.50	0.15	–0.02	0.62†	0.60†	–0.02	0.33
Root+rhizome biomass	*0.95****	0.45	0.15	0.08	*0.97****	0.50	–0.02	0.13
Organic layer depth	0.14	0.57	–0.07	0.30	0.30	*0.75**	–0.18	0.26
Root N pool	0.60†	0.23	–0.10	0.43	0.60†	0.20	–0.27	–0.17
Root P pool	0.53	0.17	0.01	0.67†	0.52	0.22	–0.17	0.12
Mean diel air temperature	0.12	–0.35	–0.37	0.60†	0.15	0.05	0.68†	0.00
Mean diel soil temperature	–0.42	0.13	–0.12	*0.74**	–0.10	0.15	0.07	0.29
Soil moisture	–	–	–	–	0.43	0.50	–0.10	–0.15

†P<0.10, *P<0.05, **P<0.01, ***P<0.001

Discussion

Effects of the manipulation

Our experimental warming manipulation enhanced ER with little effect on GEP, resulting in a strong increase in net ecosystem CO_2 release to the atmosphere. The identical treatment effects on belowground respiration, and the patterns of correlation between gas exchange and potential controlling variables indicate that increased soil temperature was the primary cause of the enhanced CO_2 efflux from manipulated plots. Previous growth chamber and field studies of mesic/moist tundra in which both air and soil temperatures were elevated (at ambient light levels) also identified ER as the most sensitive component of tundra NEE to warming (Johnson et al. 1996; Jones et al. 1998; Welker et al. 1999). Our study is novel in that we included a follow-up clipping treatment, demonstrating in the field that warming enhances net ecosystem CO_2 release principally by stimulating belowground CO_2 efflux. Furthermore, we observed strong correlations between ER/belowground respiration and components of plant biomass in control plots that were not apparent in warmed plots. Conversely, belowground CO_2 efflux became significantly correlated with organic matter depth in warmed plots (Table 5), suggesting that the enhanced CO_2 release in moss-dominated inter-tussock areas (which comprise 80% of the ground area of acidic tussock tundra) was due to warming effects on the decomposition of soil organic matter. Together, these results provide strong field evidence suggesting that the first effect of a warmer climate would be to enhance tundra net ecosystem CO_2 release by stimulating soil organic matter breakdown, potentially causing an initial positive feedback to atmospheric CO_2 concentrations and "greenhouse" warming.

Tussock/inter-tussock differences in response to treatment

The greater response of aboveground vascular plant biomass to warming in tussock than inter-tussock areas

(Table 2) may be the result of sedge dominance in the tussocks and/or warmer tussock soil microclimate. Sedges are the only growth form in acidic tussock tundra that increased dramatically (by a factor of nine) within 1 year of fertiliser addition (Shaver and Chapin 1986). The ability of sedges to markedly increase the size of existing leaves, to develop additional leaves without forming new buds, and to tiller readily, permits rapid production responses to increased resource availability (Shaver et al. 1997). By contrast, the deciduous and evergreen shrubs of inter-tussock areas are slower to respond, but ultimately have the highest potential resource uptake and growth rates, leading to their increasing dominance after 3 and more years of fertilisation (Chapin et al. 1995; Bret-Harte et al., in press).

Soil temperatures are generally warmer in tussock than inter-tussock areas (Table 1; Chapin et al. 1979). Long-term warming and fertilisation studies indicate that tundra ecosystems are more responsive to increased nutrient availability than to warmer temperatures (Chapin et al. 1995; Jonasson et al. 1999). Consequently, the strong nutrient limitation at our site (Chapin et al. 1995) suggests that the enhanced tussock leaf nutrient pools (Table 3) and vascular plant primary production in manipulated tussocks resulted from higher soil nutrient availability associated with warming of tussock soils. The absence of vascular plant biomass or leaf nutrient pool responses to warming in inter-tussock areas (Tables 2, 3), despite significant treatment increases in ecosystem and belowground respiration (Figs. 2, 3), suggests that nutrient fluxes differed between microsites in response to warming. First, inter-tussock vascular plants may not have had the capacity to respond as quickly as the tussock sedges within the short time frame of the experiment. Second, in contrast to the manipulated tussocks, the colder microclimate within inter-tussock areas (Fig. 1, Table 1) and/or higher total N and microbial biomass in inter-tussock soils (Cheng and Virginia 1993) may have favoured microbial net nutrient immobilisation rather than mineralisation, resulting in unaltered plant-available nutrient pools. Regardless of the causes, our experiment suggests that tussock and inter-tussock areas differ in the initial effects of warming on plant production and/or nutrient availability to plants, with more pronounced effects in relatively warm, sedge-dominated tussocks than in cooler moss-dominated inter-tussocks.

Controls on ecosystem CO_2 fluxes

A comparison of our results with those of other field studies at Toolik Lake suggests that the net effect of warming on plant-associated and soil organic matter contributions to ecosystem CO_2 exchange depends on the duration of the increase in soil temperature, and/or ecosystem type. In an experiment that manipulated only air temperature, both GEP and ER were enhanced to a similar extent, resulting in no overall effect of warmer air temperatures on NEE (Hobbie and Chapin 1998). Furthermore, aboveground biomass and mean diel ER were strongly correlated across all plots in that study, consistent with our conclusion that plant-associated respiration is the principal source of ER under ambient soil temperatures. Similarly, NEE measured in ten tundra sites by eddy covariance correlated closely with vascular plant leaf area and leaf nitrogen pools, and showed no significant relationship to moss biomass or soil organic matter (Williams et al., in press). In an arctic wet sedge ecosystem that was warmed for 5–9 years before measurement (Shaver et al. 1998), most of the treatment effects on ecosystem CO_2 fluxes were due to changes in plant biomass, although there were additional, smaller effects on CO_2 fluxes per unit biomass and nutrient contents. In that long-term warming study, immediate increases in CO_2 efflux such as we observed may have been counteracted by increased sink activity due to enhanced plant growth (Shaver et al. 1992; McKane et al. 1997). Alternatively, the waterlogged, relatively anaerobic conditions in wet sedge soils may result in relatively low sensitivity of decomposition to temperature, and a prevailing influence of plant-associated respiration in warmed wet sedge ecosystems.

A surprising aspect of our study was the absence of significant relationships between ecosystem CO_2 fluxes (GEP, ER, belowground respiration) and air or soil temperatures for either microsite. Only mean diel ER in the warmed tussock plots and mean diel soil temperature were significantly correlated (Table 5). Furthermore, the individual ecosystem CO_2 fluxes measured five times within each diel cycle were also only weakly correlated with instantaneous values of air or soil temperatures (data not shown), despite strong variations in temperature through each diel cycle (Fig. 1). Together, these results suggest that the treatment effects on ecosystem CO_2 release were due to an acclimated/altered microbial community with inherently higher rates of soil organic matter decomposition, rather than to direct stimulation of microbial decomposer activity by elevated temperatures.

Conclusions

This short-term field study demonstrates that the initial effects of warming on ecosystem net CO_2 exchange in acidic tussock tundra are driven by strong increases in belowground respiration. A comparison of the relationships between CO_2 fluxes and ecosystem properties in the same plots suggests that the enhanced carbon release with warming is derived primarily from stimulated decomposition of soil organic matter in relatively cold inter-tussock microsites. Models predict that the duration of this initial warming response on NEE will be constrained by the size of the labile, readily decomposible fraction within the tundra soil organic matter pool (Liski et al. 1999), and by the response of plant GEP to increased nutrient availability (McKane et al. 1997). Our short-term experiment provides strong field evidence supporting previous growth chamber and modelling results indicating that the initial effects of increased summer temperatures at high latitudes could be to mineralise extensive soil C stocks in the

Arctic and provide a substantial positive feedback to greenhouse warming. Further field research is required to evaluate longer-term dynamics of the effects of warming on net ecosystem CO_2 exchange in the Arctic.

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