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Arctic Soil Respiration: Effects of Climate and Vegetation Depend on Season

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ABSTRACT

Arctic ecosystems are important in the context of global climate change because the most rapid rises in air temperature are expected at high northern latitudes during winter. The presence of extensive soil carbon reserves in the Arctic suggests that substantial feedbacks to CO_2-induced climate change could occur if warming alters carbon cycling belowground. Characterization of the controls on regional patterns of belowground CO_2 release through the annual cycle is an important step towards evaluating potential feedbacks from arctic ecosystems to climate change. In this study, we assess seasonal control over the influences by climate and vegetation-type on CO_2 efflux from belowground in the Alaskan tundra. Our results indicate that climate had strong effects on belowground CO_2 release in both seasons. By contrast, vegetation-type had little impact on CO_2 efflux from belowground in winter but was the principal control in summer. Together, these results demonstrate that seasonality is a critical factor regulating climate and vegetation-type effects on belowground CO_2 release, which should be included in regional models of net carbon balance in arctic ecosystems.

Key words: Arctic; soil respiration; carbon dioxide; soda lime; climate; vegetation.

INTRODUCTION

Models of global climate change predict that regional increases in air temperature in response to rising atmospheric CO_2 will be most rapid at high northern latitudes during winter (Kattenberg and others 1996). Arctic tundra soils contain 14% of the global soil carbon pool (Post and others 1982) and could provide a substantial positive feedback to climate change if warming were to stimulate CO_2 release from belowground because of enhanced decomposition of soil organic matter (Lashof 1989). Assessment of the global impact of changes in the net carbon balance of arctic ecosystems requires an understanding of controls on belowground CO_2 efflux at appropriate spatial and temporal scales. Do the primary controls on regional patterns of CO_2 release from the soil surface differ seasonally?

Small-scale variation in temperature and moisture within a site is critical in explaining microsite differences in belowground CO_2 release in the field (Oberbauer and others 1991, 1992). Heterogeneity in CO_2 release patterns at the ground surface is also a function of plant species differences in litter quality for decomposition (Nadelhoffer and others 1991; Hobbie 1996) as well as root production (Wielgolaski and others 1981) and root respiration (Billings and others 1977; Chapin and Tyron 1982; Limbauch and others 1982). However, there have been few studies examining the relationship of belowground respiration to broad patterns of climate and vegetation—information that is essential

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to understanding controls on ecosystem net carbon balance at a regional scale. Furthermore, although most studies of net carbon exchange in arctic ecosystems have been conducted in the growing season (Oechel and others 1993; Oberbauer and others 1996; Hobbie and Chapin 1998; Vourlitis and Oechel 1999), recent evidence suggests that winter respiration is a significant component of the annual carbon balance (Zimov and others 1996; Oechel and others 1997) and that nearly all litter mass loss occurs during winter (Hobbie and Chapin 1996). These results indicate that models of regional net carbon balance linking arctic ecosystem processes to climate change must incorporate controls by climate, vegetation-type, and season. We investigated these ecosystem-level controls by choosing an experimental design that allowed separation of the influences of climate and vegetation-type on arctic soil respiration. Here, we contrast summer and winter CO_2 efflux measurements to evaluate the effect of season on climate and vegetation-type influences over regional patterns of belowground CO_2 release in the Arctic.

Methods

To examine the effects of climate (and its seasonal variation) on belowground CO_2 efflux from a specific vegetation-type, we selected acidic tussock tundra vegetation (Bliss and Matveyeva 1992) plots along a 500-km transect from northern to central Alaska at Sagwon (69.42°N, 148.70°W), Toolik (68.63°N, 149.56°W), and at a muskeg site containing black spruce (*Picea mariana*) near Fairbanks (64.75°N, 148.25°W). These sites span the latitudinal range of acidic tussock tundra in Alaska. To investigate the influence of vegetation-type on seasonal belowground CO_2 release, we selected sites in dry heath and shrub tundra communities at Toolik and in wet sedge tundra [see Shaver and Chapin (1991) for a full description of above vegetation types] and non-acidic tundra (Walker and others 1994) at Galbraith (68.50°N, 149.49°W), which is 15 km south of Toolik and experiences a similar climate (Haugen 1982). CO_2 efflux from the soil surface was measured gravimetrically using soda lime over 24 h periods three to four times during summer and continuously through an entire winter. Because the soda lime method tends to underestimate CO_2 efflux (Ewel and others 1987; Nay and others 1994), all CO_2 data reported here have been converted from soda lime to equivalent infra-red gas analysis values using a logarithmic calibration curve (Grogan 1998).

Summer Flux Measurements

Growing season belowground CO_2 release was measured at all vegetation-type/latitude sites in June 1996, August 1996, May 1997 (except tussock tundra at Toolik and Sagwon), and July 1997. Acidic tussock tundra consists of tussocks dominated by *Eriophorum vaginatum* surrounded by intertussock zones of mosses and deciduous shrubs. We measured fluxes from tussocks and from intertussock areas dominated by the feather mosses *Hylocomium splendens* and *Pleurozium schreberii.* Total efflux was estimated using the proportional cover of tussock and intertussock vegetation at each site. Intertussock zones comprise approximately 82% of the area at each of the three acidic tussock tundra sites in this study (D. Hooper, personal communication). Our protocol was to clip aboveground vegetation including the green moss layer from a patch just larger than the sampling area (625 cm^2). Clipping was conducted with care to minimize damage to roots and rhizomes. A preliminary growth chamber study with tussocks suggested that removal of aboveground vegetation results in a small flush of CO_2 from the soil surface over the first 24 h after clipping followed by a slow decline in respiration rates over succeeding days. Accordingly, we waited 24 h after clipping before making diel flux measurements and prepared fresh plots each time. Jars of oven-dried soda lime (35 g) were opened and placed on mesh baskets above the soil surface (Edwards 1982). Chambers (20 l) were immediately installed over the sample area and pressed into the soil (1–3 cm). The chambers were held firmly in place by taut elastic cords stretched between stakes driven into the surrounding tundra. After 24 h exposure, we lifted the chambers, re-sealed the jars, and transported them to the lab for oven drying (24 h at 100°C). Blank controls ($n = 3$) were included to account for CO_2 adsorption during collection in the field and oven drying. Respiration rates were estimated as dry weight gain over the sampling period after correcting for water formed as soda lime adsorbs CO_2 (Grogan 1998).

We differentiated the seasons by defining the growing season as the period when diel mean soil temperatures at 5 cm depth in intertussock zones were above 0°C. Precipitation, air, and soil temperature records indicate that the growing seasons of 1996 and 1997 were similar at each site (J. Laundre and L. Hinzmann, personal communication). Total efflux for a growing season was calculated by combining the measurements from both years and interpolating the flux rates between monthly sampling intervals. Flux rates at the beginning and end of the growing season were assumed to be equal to the mean diel flux rates during winter (see below). Our primary purpose in this study was to contrast the influence of latitude (and vegetation-type) on CO_2 release in summer as opposed to winter seasons. Our approach was not designed to yield accurate estimates of seasonal belowground CO_2 release during a specific year but rather to provide a consistent basis for relative comparisons across latitudes (and vegetation-types) in each season.

Soil temperatures at 5 cm depth were logged within and outside plots at each site. We constructed probes using temperature transducers (AD 592; Analog Devices, Norwood, MA, USA) sealed within waterproof heatshrink tubing (3M, Austin, TX, USA). The data were averaged every 5 min and recorded every 30 min using CR10 dataloggers (Campbell Scientific, Logan, UT, USA). On the warmest sampling date, the heat trapping effect of the chambers raised mean diel soil temperature by 3°C.

Winter Flux Measurements

Wintertime CO_2 efflux from belowground was measured continuously from late August/early September 1996 through to late April/early May 1997. Plots were prepared as in summer except that slots (4–8 cm deep) were cut into the soil surface around the circumference of the sample area to be able to press the chambers well down into the soil column and achieve a good seal. For dry heath vegetation, the junctions between the chambers and the rocky ground surface were sealed with strips of plastic sheeting held in place by a ring of stones. After at least 3 d, oven-dried soda lime (400 g) was poured onto plates (22.5 cm in diameter) that had been fixed on mesh baskets above the sample area. In a laboratory study, we observed that CO_2 adsorption efficiency by soda lime at freezing temperatures (-18°C) is lowered by 40% unless the soda lime has been moistened initially. Accordingly, for our winter measures, we added water (150 ml) to the soda lime samples before installing and fixing the chambers. At the time of collection, most chambers were frozen into the tundra indicating a good seal with the soil. After chipping out the chambers, the soda lime samples were transferred to canning jars (1 l), sealed, and brought to the lab for oven drying (at least 36 h at 100°C in a fan-assisted oven). Blank controls (five per latitude) consisted of similar quantities of moistened soda lime on plates contained within upright chambers sealed with airtight lids.

The effect of using soda lime for respiration measurements over a prolonged exposure period may have been to overestimate CO_2 flux. Depletion of chamber headspace CO_2 by soda lime most likely promoted CO_2 diffusion from the soil beneath. We tested the impact of this draw-down effect by using similar large quantities of soda lime to measure diel efflux during the growing season. The CO_2 efflux measured over the first 24-h period was approximately four times the mean site efflux value. However, succeeding diel efflux values on the same plot were similar to the mean site efflux value suggesting that the error associated with an initial change in CO_2 diffusion gradient may be negligible over a 200–250 d measuring period. Nevertheless, the enhanced diffusion gradient resulting from the use of large quantities of soda lime for long-term flux measurements may have increased the effective soil volume sampled, leading to an overestimation of efflux per unit area. However, because this bias was present at all our sites, these methodological considerations do not affect the validity of this study's major conclusions, which are based on comparisons of relative fluxes across latitudes or among vegetation-types within each season.

Soil temperatures were recorded both beneath and outside chambers every 6 h at 2 and 5 cm depth within the organic horizon in tussock and intertussock zones (by using the apparatus described above). The seasonal temperature profiles were similar at both soil depths in all plots, suggesting that the temperature transducers performed accurately. No significant differences between mean diel winter soil temperatures beneath and outside chambers were observed at Sagwon or Toolik. At Fairbanks, a period of particularly cold air temperatures occurred before complete snow cover of the chambers in early November. The tops of the chambers protruded above the snow during this period resulting in lowered mean diel temperatures in both tussock and intertussock soils beneath the chambers as compared with outside the chambers. For example, mean diel soil temperatures in intertussock areas (which predominate this vegetation-type) were lowered by 0.7°C (5 cm depth) during this period. By contrast, during the remainder of the winter, the presence of the chambers raised diel mean soil temperatures in intertussock areas by approximately 4.6°C (5 cm depth) at the Fairbanks site. The warming effect of the chambers occurred only in the intertussock zones during this interval. Tussocks occupied a particularly large volume of the chamber headspace at Fairbanks (approximately 66%) suggesting that the chamber warming effect in intertussock areas could have been related to the insulating properties of a greater enclosed air volume. The net result of these chamber effects on soil temperature may have been to overestimate Fairbanks winter efflux. However, they do not affect our conclusions that are focused on relating the pattern of winter efflux across latitudes to the soil temperature regime measured directly beneath the chambers.

For the winter CO_2 efflux measures, the chambers were installed as late as logistically possible in the preceding growing season. The datalogger temperature records indicated that a considerable period of time (13–24 d) elapsed before the diel mean soil temperature beneath the chambers dropped below 0°C. Furthermore, there was a period of 5 d at the end of the Fairbanks winter soda lime measures when the diel mean soil temperatures had risen above 0°C. To estimate flux during the period when diel mean soil temperatures at 5 cm depth in intertussock areas were below 0°C (our definition of winter), we corrected our measured soda lime flux values to account for respiration during these "winter transition" periods. This correction is necessary to compare winter effluxes across sites that varied in total winter length and in soil temperature during the winter transition period.

The appropriate corrections for each site were estimated using the soil temperature records from the time of chamber installation and a generalized relationship between temperature and soil respiration derived from field soil incubations. We incubated 10 fresh, local soil samples in buried canning jars (1 l) in the field at each latitude and vegetation-type in June and August 1996. CO_2 accumulation in the jar headspace after 24 h was measured by injecting samples (10 ml) into an infra-red gas analysis system (LI-COR 6200, Lincoln, NE, USA). Incubation temperatures were measured using the apparatus described above. Means of CO_2 efflux rate and temperature were used to develop a generalized relationship between temperature and soil respiration for Alaskan arctic vegetation. Respiration from the soils of each vegetation-type (and possibly from each latitude) is likely to also have been influenced by inherent differences in soil organic matter quality, microbial community composition, and soil moisture. We calibrated our use of the generalized soil temperature/respiration to estimate efflux during the winter transition periods at each latitude/vegetation-type as follows. To use the generalized relationship with field soil temperature records to estimate efflux, we needed a site-specific conversion factor from CO_2 release per gram of dry weight (field incubations) to CO_2 release per square meter (field belowground CO_2 efflux measures). We used the August 1996 set of diel field measurements of CO_2 and diel mean soil temperature to calculate a conversion factor for each site. Effectively, these field data and the incubation relationship were used to calculate individual site-specific values for the mass of respiring soil per square meter at each latitude/vegetation-type. Finally, estimates of total diel flux over the interval from chamber installation until the mean soil temperature dropped below 0°C were determined using the incubation relationship, the mass of respiring soil per unit area, and the soil temperature record for each site.

Winter fluxes (that is, CO_2 release during the period of diel mean soil temperatures below 0°C) for each vegetation-type/latitude were calculated by subtracting the estimated cumulative CO_2 release while mean diel soil temperatures were above 0°C from the measured soda lime values for the entire sampling period. This adjustment was greatest at Fairbanks where it represented 24% of the total measured winter flux. Winter fluxes for dry heath, shrub, and non-acidic tundra vegetation types were calculated using intertussock temperatures from Toolik. No over-winter data are reported for the wet sedge site because the soda lime samples were contaminated by floodwater.

Statistical Analysis

The CO_2 efflux data were analyzed separately for each season by using analyses of variance (ANOVA) with Systat 5.2 (SPSS, Chicago, IL, USA). The effect of latitude on winter efflux from tussock and intertussock areas of acidic tussock tundra was assessed using a two-way ANOVA. Latitudinal effects on growing season efflux from tussock and intertussock areas of acidic tussock tundra was assessed using a three-way ANOVA with time of season when sampling took place as an independent factor. Latitude and time of season during the growing season were treated as categorical variables. Similar analyses were performed to investigate the effect of vegetation-types (including tussock and intertussock areas of acidic tussock tundra) on CO_2 efflux during each season.

Results

Climate strongly influenced belowground CO_2 efflux from acidic tussock tundra vegetation in both seasons. Winter CO_2 release varied markedly among tussock tundra sites of different latitudes (Table 1), with Toolik having substantially higher fluxes than the other sites (Figure 1). The pattern of variation in winter efflux reflected site differences in the soil thermal regime during early winter rather than over the entire winter (Table 2 and Figure 2). First, the initial time interval while mean diel soil temperatures remained above -5°C correlated with winter CO_2 release patterns across latitudes (Table 2 and Figure 1). Second, total degree-days above -5°C at each site (that is, summed diel mean soil temperature increment above -5°C) was dominated by the

Table 1. Statistical Significance of Site Effects on Belowground CO_2 Efflux in Each Season

	Winter			Growing Season		
	df	MS	F	df	MS	F
Tussock tundra sites across latitudes						
Latitude	2	22879	5.87**	2	6.332	5.63**
Tussock/inter-tussock	1	1067	0.27	1	9.985	8.87**
Time in season				2	33.569	29.82***
Lat. × T/IT	2	2688	0.69	2	1.254	1.11
Lat. × time in season				4	16.822	14.94***
T/IT × time in season				2	4.140	3.68*
Lat. × T/IT × time in season				4	1.124	1.00
Error	36	3897		158	1.126	
Vegetation-types within Toolik area						
Vegetation type	4	4065	0.85	5	64.03	19.6***
Time in season				2	355.35	108.7***
Vegetation-type × time in season				10	45.68	14.0***
Error	40	4795		159	3.27	

n = 4–10 plots per site at each sampling time.
**P < 0.05; **P < 0.01; ***P < 0.001.*
Tussock and intertussock fluxes (T/IT) from acidic tussock tundra were treated separately in the analyses. No diel flux measurements were made in acidic tussock tundra at Toolik or Sagwon in May. Accordingly, the May data have been omitted from the analyses of growing season fluxes to assess interactions between effects of vegetation-type and time of season in which the fluxes were measured.

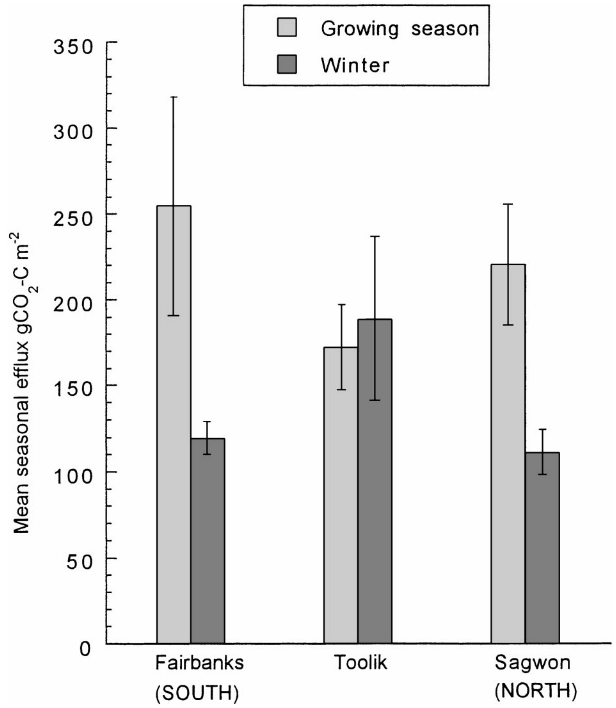

Figure 1. Seasonal belowground CO_2 efflux from acidic tussock tundra in northern Alaska. The sites occur along a latitudinal transect from Fairbanks north to Sagwon. Values are means and standard errors (n = 4–10).

Table 2. Soil Characteristics in Intertussock Areas at Different Latitudes in Winter 1996–97

	Fairbanks	Toolik	Sagwon
Latitude	64.75°N	68.63°N	69.42°N
Initial winter period with temperature >−5°C (days)	26	115	69
Total degree-days >−5°C			
Early winter	291	373	252
Late winter	50		
Snow depth at time of chamber installation (cm)	0	7	0
Total winter length (days)	209	246	237
Mean winter temperature	−4.2	−5.3	−8.7

Winter is defined as the period when diel mean soil temperatures (5 cm depth) were below 0°C. Mean winter temperature (°C) was computed from four measurements per day beneath the CO_2 sampling chambers. Degree-days are calculated from the summed diel mean soil temperature increments above −5°C (5 cm soil depth).

early winter period and was also correlated with latitudinal CO_2 efflux patterns (Table 2 and Figure 1). During the growing season, there was also significant variation in belowground CO_2 release among tussock tundra sites (Table 1 and Figure 1). As might be expected, time of sampling within the growing season was highly significant (Table 1) reflecting substantial differences in soil temperature, soil moisture, and changes in plant phenology through the summer season at each site (Table 3). Nevertheless, the pattern of variation in interpolated growing season CO_2 efflux across sites broadly reflected trends in diel mean soil temperature (Figure 1 and Table 3). Fairbanks had the largest total growing season efflux (Figure 1) and experienced consistently higher soil temperatures relative to the more northerly sites (Table 3). Toolik had the lowest total growing season efflux (Figure 1) and experienced the coolest soil temperatures at the time of peak plant physiological activity in mid-July (Table 3). Together, these data indicate that climatic variation associated with differences in latitude resulted in

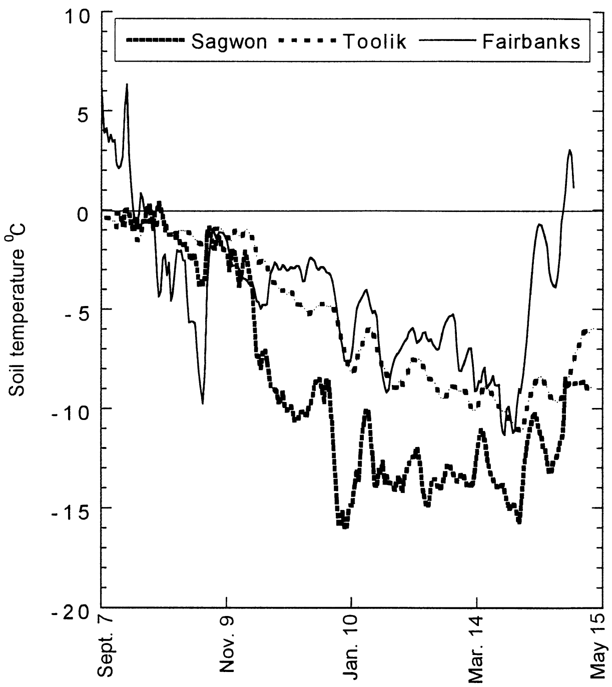

Figure 2. Winter soil temperature in intertussock moss mats at three different latitudes in northern Alaska in 1996–97. Temperatures are diel means at 5 cm soil depth beneath the chambers.

Table 3. Tussock Tundra CO_2 Efflux at Different Latitudes during the Growing Seasons of 1996 and 1997 and Corresponding Soil Characteristics in Intertussock Areas

	Fairbanks	Toolik	Sagwon
Latitude	64.75°N	68.63°N	69.42°N
Mean diel efflux ($gC\ m^{-2}\ d^{-1}$)			
May 1997	0.17 (0.19)	N.D.	N.D.
June 1996	2.23 (0.41)	1.33 (0.21)	1.88 (0.26)
July 1997	1.66 (0.81)	3.05 (0.51)	4.13 (0.86)
Aug. 1996	2.38 (0.48)	0.82 (0.12)	1.15 (0.22)
Mean diel temperature (°C)			
May 1997	0.9 (0.2)	N.D.	N.D.
June 1996	9.0 (0.5)	5.3 (1.0)	3.4 (0.4)
July 1997	16.6 (0.9)	3.1 (0.2)	6.2 (0.9)
Aug. 1996	7.9 (0.2)	5.0 (0.3)	2.3 (0.2)
Mean moisture content (%)			
June 1996	379 (46)	200 (37)	545 (54)
July 1997	178 (25)	N.D.	355 (42)
Aug. 1996	278 (22)	135 (35)	132 (51)

Data are means and standard errors (parens) (n = 3–10). Soil temperatures are at 5 cm depth except in June 1996 (10 cm). Soil moisture contents were determined on cores of 10 cm depth and are expressed as percentage of dry weight. N.D. = No data.

significant differences in CO_2 release from belowground during both summer and winter seasons.

The effect of vegetation-type on belowground CO_2 efflux strongly depended on season. Within the common climatic zone at Toolik, variation in belowground efflux across a range of vegetation-types was highly significant in summer but not in winter (Table 1 and Figure 3). Similarly, belowground CO_2 release from tussock and intertussock areas within acidic tussock tundra vegetation was significantly different during the growing season but not over winter (Table 1). Our data also indicate that vegetation-type had a greater impact than latitude on the magnitude of belowground CO_2 release in summer (Figures 1 and 3). These results suggest that shifts in vegetation distribution may be more important than direct effects of warming in determining the effect of changing climate on regional patterns of belowground CO_2 release during summer.

Soil Incubations

Our field incubation data reflect strong temperature control on soil respiration from a range of arctic vegetation types (Figure 4). A logarithmic function described the relationship between mean 24-h flux and mean incubation temperature [Ln (Respiration) = 0.12 × (Soil Temperature) - 0.87; µmol CO_2 $gdw.^{-1}\ h^{-1}$; $r^2 = 0.60$; $P < 0.002$; $n = 13$]. The computed Q_{10} factor (ratio of activities over a 10°C change) of 3.3 is similar to the previously reported range for tundra soils (1.9–5) (Flanagan and Veum 1974; Flanagan and Bunnell 1980).

Discussion

We have demonstrated that season exerts strong control on the influence of climate and vegetation-type over CO_2 release from belowground in arctic tundra. Our results suggest that regional patterns of belowground CO_2 efflux in the Arctic during winter are dominated by differences in climate. Vegetation-type had little effect on wintertime CO_2 release suggesting that climate change–induced shifts in vegetation distribution may have relatively little impact on carbon cycling in winter. By contrast, our results suggest that regional patterns of belowground CO_2 efflux in summer are controlled principally by the distribution of vegetation-types and secondarily by climatic differences. These results are important to regional models of annual net C balance in the Arctic because they indicate that the relative importance of climate and vegetation-type as controls on belowground CO_2 release depends on season.

This study supports recent conclusions that CO_2 release in the Arctic during winter is substantial

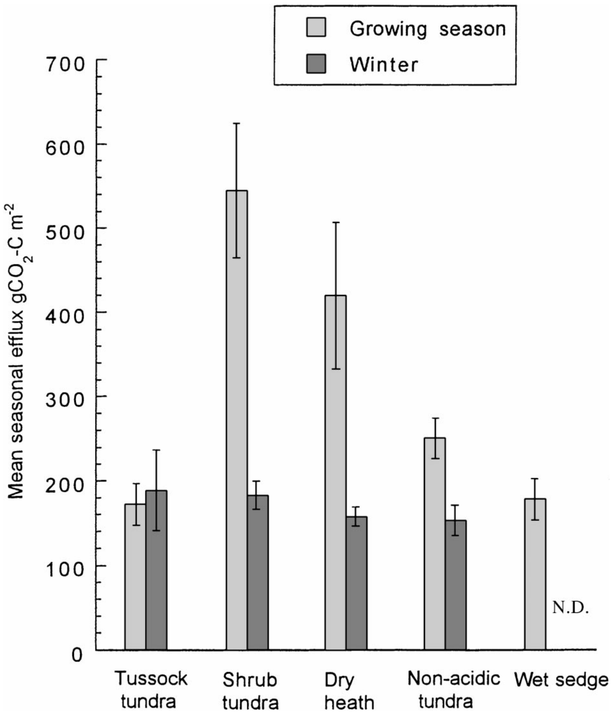

Figure 3. Seasonal belowground CO_2 efflux from different vegetation-types at Toolik in northern Alaska. Values are means and standard errors (*n* = 8–10). N.D. = No data.

(Zimov and others 1996; Oechel and others 1997) and therefore should be taken into account in predictions of the effect of changes in climate on ecosystem net carbon balance. Our estimates of winter efflux (111–189 g C m^{-2} y^{-1}) are somewhat higher than rates estimated for forest tundra in northern Russia (89 g C m^{-2} y^{-1}) (Zimov and others 1996) and for tussock tundra at Toolik Lake in the winter of 1993–94 (69 g C m^{-2} y^{-1}) (Oechel and others 1997). Fahnestock and others (1998) estimated an over-winter flux of 2 g C m^{-2} y^{-1} for acidic tussock tundra in northern Alaska in 1995–96. Interestingly, although the fluxes in that study were relatively low, the authors reported some significant differences in winter flux rates between vegetation-types not measured by us. However, these differences were not consistent across measurement times, and hence the underlying cause is unclear. Methodological issues as well as inter-annual variation are the most likely causes of differences in estimates of winter CO_2 release between studies. In our case, the soda lime method for extended soil respiration measurements probably overestimated total efflux (see methods). Nevertheless, our study is important because it compares relative differences in winter efflux across latitudes demonstrating for the first time that regional differences in climate exercise strong influence on belowground CO_2 release in winter.

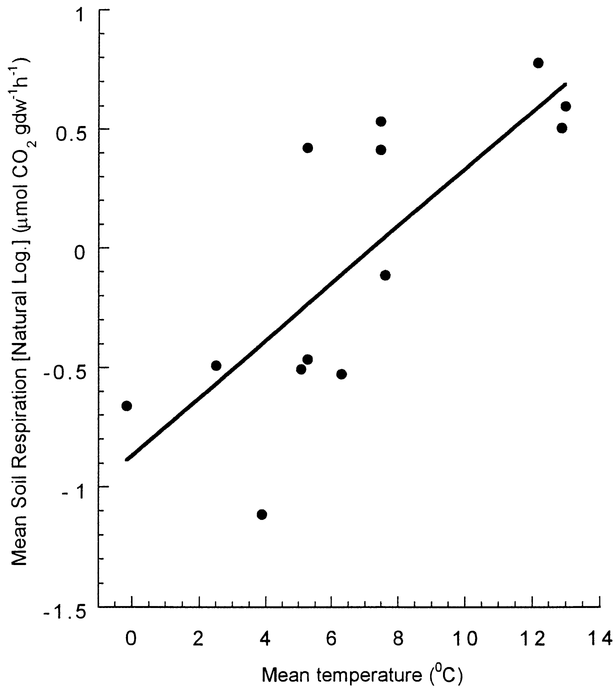

Figure 4. The relationship between mean CO_2 release and mean temperature in 24-h incubations of soils from a range of arctic vegetation types.

Winter CO_2 release from belowground in tussock tundra across latitudes appears to have been closely associated with characteristics of the soil thermal regime in early winter. Mean soil temperatures over the entire winter period decreased with increasing latitude (Table 2). Sagwon (the most northern site) experiences the coolest winter air temperatures because of its proximity to the Arctic ocean (Zhang and others 1996). However, CO_2 release from tussock tundra sites in winter showed no relationship to latitude, mean winter soil temperature, or total winter length (Table 2 and Figure 1). Instead, the high efflux at Toolik (the central site along the latitudinal transect) was associated with substantial early snowfall (Table 2) and a particularly long period of relatively warm soil temperatures in early winter (Figure 2). The nature and concentration of solutes in most soil solutions frequently result in the presence of liquid water at temperatures well below 0°C (Edwards and Cresser 1992; Boike 1997). We expect that the clipping treatment to remove aboveground tissue at the beginning of the winter flux measures would have disrupted plant root respiration during winter. Substantial microbial respiration has been recorded from soils at 0°C, but activity decreases rapidly as soil temperatures descend towards -5°C (Flanagan and Bunnell 1980; Coxson and Parkinson 1987; Clein and Schimel 1995). Freeze–thaw incubations indicate that approximately 30% of the viable microbial population may be killed when soils are completely frozen for the first time (-7°C) (Skogland and others 1988). Cycling of arctic soils through a series of freeze–thaw events (±5°C) resulted in an increasingly damaged microbial community and progressively lowered respiratory activity (Schimel and Clein 1996). Toolik experienced the greatest number of degree-days above -5°C (Table 2), the longest initial period above -5°C (Table 2), and few temperature fluctuations (Figure 2), indicating a relatively favorable thermal environment for microbial respiration in early winter. Measurements of tundra CO_2 release rates through winter consistently indicate highest efflux in October/November (Zimov and others 1996; Oechel and others 1997) supporting our contention that the majority of cold season CO_2 release occurs during the initial phase of slow decline in soil temperature in early winter. Climatologists expect warming in the Arctic to be greatest during winter and to be accompanied by increased snowfall (Kattenberg and others 1996). Our study suggests that winter biological activity belowground will be sensitive to changes in the timing and thermal-insulating properties of local snow cover and thus that alterations in cold season climate may have substantial effects on regional net carbon balance in arctic ecosystems.

Vegetation-type exercised strong influence on CO_2 release patterns during summer but had little effect during winter. There are several possible reasons why season may regulate the impact of vegetation-type on belowground CO_2 efflux. First, roots account for the majority of belowground respiration in Alaskan boreal forests (Reuss and others 1996) and wet sedge tundra (Billings and others 1977) during summer, suggesting that high root/rhizosphere respiration could explain the sensitivity of belowground CO_2 efflux to vegetation-type during the growing season. Second, biogeochemical effects of litter quality on soil organic matter decomposition in tundra (Nadelhoffer and others 1991; Cheng and Virginia 1993; Hobbie 1996) probably contributed to the differences in belowground respiration between vegetation-types during the growing season. However, the absence of significant differences during winter suggests that these biogeochemical effects are regulated by seasonal soil temperature patterns. Third, growing season belowground respiration may also have varied with vegetation-type due to biophysical effects of plant growth form on microsite soil temperature and moisture during summer. Ultimately, tundra vegetation distribution is closely associated with landscape drainage patterns (Walker and others 1994), suggesting that topographical variation may exercise primary control on belowground CO_2 efflux in summer. In each of these mechanisms, climate during the growing season may interact with vegetation-type to determine summertime CO_2 release from belowground. For example, field manipulations of summer air temperature (Chapin and others 1995) and paleo-reconstruction of vegetation changes that occurred during the Holocene thermal maximum (Brubaker and others 1995) suggest that climate warming may convert tussock tundra to shrub tundra in arctic Alaska. The high rates of belowground CO_2 efflux that we observed in shrub tundra during the growing season (Figure 3) indicate that shifts in vegetation distribution due to warming will strongly influence regional patterns of belowground CO_2 release during summer.

The effect of warming on CO_2 release from belowground is an important component in predicting the overall response of net carbon balance in arctic ecosystems to climate change. This study demonstrates that the relative influence of climate and vegetation-type on belowground CO_2 release is strongly regulated by season. CO_2 efflux from belowground is the sum of respiration from roots and rhizosphere microbes and respiration associated with the decomposition of soil organic matter. Assessment of the impact of climate change on annual net carbon balance will require: (a) characterization of the controls on individual CO_2 source pools belowground; (b) coupling of above- and belowground components of carbon cycling during the growing season; (c) incorporation of winter fluxes; and (d) integration of these parameters to develop regional models of net annual CO_2 exchange.

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