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Vegetation and climate controls on potential CO_2, DOC and DON production in northern latitude soils

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Abstract

Climatic change may influence decomposition dynamics in arctic and boreal ecosystems, affecting both atmospheric CO_2 levels, and the flux of dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) to aquatic systems. In this study, we investigated landscape-scale controls on potential production of these compounds using a one-year laboratory incubation at two temperatures (10° and 30 °C). We measured the release of CO_2, DOC and DON from tundra soils collected from a variety of vegetation types and climatic regimes: tussock tundra at four sites along a latitudinal gradient from the interior to the north slope of Alaska, and soils from additional vegetation types at two of those sites (upland spruce at Fairbanks, and wet sedge and shrub tundra at Toolik Lake in northern Alaska). Vegetation type strongly influenced carbon fluxes. The highest CO_2 and DOC release at the high incubation temperature occurred in the soils of shrub tundra communities. Tussock tundra soils exhibited the next highest DOC fluxes followed by spruce and wet sedge tundra soils, respectively. Of the fluxes, CO_2 showed the greatest sensitivity to incubation temperatures and vegetation type, followed by DOC. DON fluxes were less variable. Total CO_2 and total DOC release were positively correlated, with DOC fluxes approximately 10% of total CO_2 fluxes. The ratio of CO_2 production to DOC release varied significantly across vegetation types with Tussock soils producing an average of four times as much CO_2 per unit DOC released compared to Spruce soils from the Fairbanks site. Sites in this study released 80–370 mg CO_2-C g soil C^{-1} and 5–46 mg DOC g soil C^{-1} at high temperatures. The magnitude of these fluxes indicates that arctic carbon pools contain a large proportion of labile carbon that could be easily decomposed given optimal conditions. The size of this labile pool ranged between 9 and 41% of soil carbon on a g soil C basis, with most variation related to vegetation type rather than climate.

Keywords: arctic soils, boreal soils, DOC, DON, decomposition, climate, vegetation

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Introduction

Alaskan ecosystems have warmed significantly in the past 100 years and are projected to continue warming through the next century (Chapman & Walsh, 1993; Washington & Meehl, 1997; Serreze *et al*., 2000). These warming trends may trigger changes in vegetation cover, primary productivity and carbon exchange (Keeling *et al*., 1996; Zimov *et al*., 1996; Chapin & Starfield, 1997; Randerson *et al*., 1999). Northern latitude soils contain large quantities of soil organic matter (SOM) (Billings, 1987) that accumulate and persist due to low mean temperatures (Hobbie *et al*., 2000). Decomposition processes generally increase with temperature in both field and laboratory settings (Peterjohn *et al*., 1994; Anisimov & Shiklomanov, 1997; Jones *et al*., 1998; Kätterer *et al*., 1998) raising the possibility of significant carbon release from northern latitude soils under future climatic regimes. Even under conditions of adequate temperature and moisture, however, decomposition of these organic rich soils is likely to be highly heterogeneous. Arctic ecosystems contain a variety of vegetation and soil

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types that vary widely in organic matter quality and biogeochemical flux rates (Giblin *et al.*, 1991; Nadelhoffer *et al.*, 1991; Hobbie, 1996). Both *in situ* and laboratory measurements of inorganic N and C fluxes demonstrate that carbon quality and biological activity can vary substantially across vegetation types (Nadelhoffer *et al.*, 1991; Cheng *et al.*, 1998; Christensen *et al.*, 1999). Furthermore, differences in climatic regimes may lead to variability in the fraction of labile soil carbon, although whether arctic soils differ in their decomposability along climatic gradients is unknown.

Although most C flux studies focus on gaseous forms of C, fluxes of dissolved organic matter are an important transfer of carbon and nutrients out of arctic and boreal soils. Dissolved organic carbon (DOC) leaching accounts for as much as 20% of total C fixation in tussock tundra microcosm studies (Johnson *et al.*, 1996) and in boreal peatlands (Waddington & Roulet, 1997). Dissolved organic nitrogen (DON) flux through soils may play an important role in the nutrition of boreal forests and arctic vegetation (Kielland, 1994; Nasholm *et al.*, 1998) and could function as an important loss of N from terrestrial ecosystems (e.g. Hedin *et al.*, 1995). In comparison to the decomposition processes that control CO_2 release from northern soils, the mechanisms that result in dissolved organic matter (DOM) production remain poorly understood.

To understand the geographic heterogeneity in labile organic matter pools in tundra soils, and the potential for decomposition-mediated carbon release with warmer temperatures, we examined CO_2 and DOM production potentials from a variety of soil types in a controlled laboratory setting. Specifically, we investigated CO_2, DOC and DON fluxes from soils collected at several different arctic and boreal vegetation types from across a natural climatic gradient in Alaska. We hypothesized that soils from the more northerly sites would be more decomposable (on a per gram soil basis) due to temperature-limited decomposition processes. In addition, we examined differences among vegetation types with the hypothesis that large variation in the decomposability of litter across vegetation types (e.g. Hobbie *et al.*, 2000) is matched belowground by variation in the decomposability of SOM.

Methods

Site description

Soils used in this experiment came from a north–south transect that runs along the Dalton highway from Fairbanks in the south to Sagwon (100 km south of Prudhoe Bay) in the north. This transect covers a broad gradient in climate and includes a mosaic of vegetation types (Table 1). Along this transect, we chose four sites: Sagwon (the northern extent of tussock tundra), Toolik Lake (in the northern foothills of the Brooks Range), Chandalar (in the southern foothills of the Brooks Range) and Fairbanks. Mean average daily high and low temperatures increase from north to south (Table 1). Tussock tundra occurs at all sites. This vegetation type is composed of roughly equal cover of a tussock-forming sedge (*Eriophorum vaginatum*), dwarf shrubs, and moss mats and is the dominant vegetation type on moderately drained mid-slope microhabitats with moist, highly organic soils (Walker, 1985). At Fairbanks, this community is found in the floodplain of the Tanana River and also contains scattered black spruce (Muskeg), but because of the similarity in groundcover, we refer to this site as a tussock site. Our cross-latitude comparison takes advantage of these similar vegetation communities in sites characterized by different temperature regimes (Table 1). This component of the experiment is referred to as the climate treatment. For this same set of sites (tussocks from the four sites), we carried out laboratory incubations at 10 °C and 30 °C and refer to this experiment as the temperature treatment. Finally, we carried out two comparisons of vegetation type within sites at Fairbanks and Toolik. The Fairbanks vegetation comparison included an upland white spruce (*Picea glauca*) forest and tussock tundra; the Toolik vegetation comparison included tussock tundra, wet lowland sites dominated by the sedge *Carex aquatilis* (referred to as wet sedge), and sites dominated by dwarf shrubs (*Salix spp.* and *Betula nana*) in water tracks that drain the hill slopes (referred to as shrub tundra). Each site was underlain by permafrost at approximately 30–50 cm, except in the Fairbanks spruce sites where permafrost was > 50 cm deep.

Soils collection

We collected soils from the top 10 cm of soil in late August 1996 and froze the samples until the following spring when we begun the laboratory incubation. The top 10 cm of these soils correspond to the Oi–Oe layers in the US soil system and contain a mix of roots, dead moss and humified organic matter, but little to no mineral soil content. In spring 1997, we thawed the cores, removed roots > 2 mm by hand and began the incubation experiment.

Incubation design

We added 10 g of soil to Nalgene filter units with upper and lower chambers separated by Whatman GF-F glass fibre filters (0.7 μ pore size) and glass wool (Nadelhoffer *et al.*, 1991). Five replicates (10 g each) from each site/

Table 1 Climate data (A) and soil characteristics (B) for the study sites. Mean average daily low (Mean Low T) and high (Mean High T) temperatures (°C) for Fairbanks, Chandalar and Sagwon are from http://www.wrcc.dri.edu/summary/climsmak.html. There is no climate station at the Chandalar site so we show weather data from Bettles, AK, which is approximately 74 miles to the South-east. Data for Toolik are calculated from the LTER database at http://www.mbl.edu/html/ECOSYSTEMS/lterhtml/arc_Generalhtml. Values for soil data are means (± Standard Error) for samples taken from the top 10 cm of soil (Oi–Oe horizons in the US soil system)

(A) Site Climate	Lat/Long	Mean Low T	Mean High T
Fairbanks	64°52.06′N 147°47.16′W	− 8.4	2.7
Chandalar	67°39.24′N 149°43.09′W	− 10.6	− 0.5
Toolik Lake	69°40.92′N 149°4. 15′W	− 13.7	− 4.6
Sagwon	70°14.39′N 148°29.73′W	− 14.8	− 7.7

(B) Site soil characteristics	Vegetation type	%C (SE)	%N (SE)	C:N Ratio (SE)
Fairbanks	Spruce	43.65 (0.50)	0.79 (0.01)	52.6 (2.2)
	Tussock	44.62 (0.63)	1.06 (0.04)	39.7 (2.8)
Chandalar	Tussock	43.85 (0.92)	1.35 (0.02)	31.8 (0.9)
Toolik Lake	Tussock	43.14 (0.54)	1.33 (0.03)	33.7 (1.2)
	Shrub	41.26 (0.89)	1.35 (0.04)	29.4 (2.0)
	Wet sedge	37.04 (0.87)	1.69 (0.05)	22.4 (0.3)
Sagwon	Tussock	44.64 (0.68)	1.28 (0.05)	34.9 (1.8)

vegetation treatment were used in the incubation. Tussock cores were incubated at 10 °C and 30 °C. The vegetation comparison experiments were carried out at 30 °C. The high temperature incubations were designed to cause rapid decomposition of the active (most labile) fraction of the soil organic matter, while the low temperature incubations more closely resemble actual summer soil temperatures at these sites. Although much higher than normal temperatures in these sites, the high temperature incubations provide the most direct indication of potential decomposability of these soils under optimal conditions. The soils were maintained at field capacity (determined gravimetrically) throughout the incubations and the soils were periodically leached with de-ionized water to remove DOC and DON. During these leachings, the soils were saturated with 100 mL of water for 30 min and then suctioned until 100 mL of leachate was collected. Suctioning was necessary because these highly organic soils drain exceptionally slowly. We leached soils approximately every two weeks for the first two months and then at roughly monthly intervals thereafter.

Prior to leaching soils, we measured CO_2 production from the samples by placing the sample cups in sealed one liter mason jars and measuring CO_2 accumulation in the headspace of the jar over a 24 h period. Air samples (8 mL) were taken at time 0 and at 24 h by syringe through a septum in the Mason jar lid, and injected into a sealed jar attached to the LI-COR 6200 Infrared gas analyser (LI-COR Inc., Lincoln, Nebraska, USA). Carbon dioxide concentration in the Mason jar was then calculated from the increase in CO_2 concentration in the LI-COR and attached jar. We calculated cumulative CO_2 flux from the soils over the course of the incubation by interpolating fluxes between successive measurement times.

Analytical measurements

We measured DOC by high temperature oxidation of DOC to CO_2 followed by detection with an infrared gas analyser (Shimadzu Instruments, Columbia, Maryland, USA). The minimum detection limits for DOC were approximately $1\,\mathrm{mg\,C\,L^{-1}}$. We determined DON concentrations by difference between inorganic N concentrations before and after persulphate oxidations (Solorzano & Sharp, 1980). The minimum detection limit for DON was $0.050\,\mathrm{mg}$ DON-N $\mathrm{L^{-1}}$. We had intended to follow DON concentrations through the course of the experiment; however, after the first 40 days, many of the soils began to mineralize considerable amounts of inorganic N. Against these background concentrations ($>20\,\mathrm{mg}$ DIN-N $\mathrm{L^{-1}}$), it became impossible to measure DON concentrations, which averaged between 0.5 and 2 mg DON-N L^{-1}. While there were measurable values of DON in some of the incubation samples for considerably longer than 40 days, the difficulty of measuring DON in samples with high inorganic N would have biased the DON analysis toward samples with low inorganic N concentrations. For this reason, we present DON results for only the first 40 days of the incubation.

Statistical analyses

We compared initial (up to 40 days) and cumulative (352 days) fluxes of DOC, DON and CO_2, and DOC : DON ratios across sites (climate treatment) and vegetation types. For the tussock vegetation samples (common to all sites), we compared across the sites with a two-way analysis of variance (ANOVA) of incubation temperature × site. To separate site differences, we then carried out *a priori* comparisons of site differences in fluxes for the high and low temperature incubations separately. For the vegetation comparisons, we examined the Fairbanks and Toolik sites individually. Differences in fluxes from vegetation types were examined with a one way ANOVA at Fairbanks and with one-way ANOVA combined with Tukey *posthoc* comparisons at Toolik. We examined the relationship between DOC and CO_2 fluxes and DOC/SOM C:N ratios using regression analysis. In most cases, we log transformed flux data prior to analysis by ANOVA in order to achieve homogeneity of variance. All analyses were carried out with the Statistica software package (Statsoft, Tulsa, OK, USA).

Estimating DOM fluxes

The complicated mechanisms that underlie DOM production make it impossible to estimate field fluxes of DOM from a laboratory experiment. At issue are the quantities of DOM removed at each leaching, the simultaneous production and consumption of DOM in soils, the dependence of actual field fluxes on the amount and timing of rainfall, and, in this case, the potential for DOM leached from the organic soil layers to be stabilized in underlying mineral soil. Several different incubation approaches have been tried. Most studies indicate that leaching with water removes a substantial portion of the DOM pool (Kaiser *et al*., 1996; McDowell & Likens, 1988). In this study, approximately 65–90% of the measured DOC was removed on the first leaching. Under these conditions, it is most reasonable to describe DOM fluxes in the context of a potentially soluble fraction of the organic matter at a point in time (as opposed to a flux per unit time) and we follow this approach in our comparisons of CO_2 and DOC fluxes. While summing the flux of DOM during leaching events across time is a useful exercise for comparing across treatments, the flux of DOM should be interpreted with caution relative to field flux values because higher or lower frequency leaching regimes would lead to differences in flux values. We follow this convention in our presentation of data in tables and figures.

Table 2 Initial fractional loss of C and N in tussock tundra soils. Values are shown as the cumulative percentage of soil carbon respired (CO_2), or leached (DOC) at high (30° C) and low (10° C) temperatures by 40 days. Dissolved organic nitrogen fluxes are expressed as the fraction (%) of soil nitrogen lost to DON leaching and DOC:DON ratios are expressed on a per gram soil basis. *A priori* contrasts are shown for each flux or ratio (CO_2, DOC, DON or DOC:DON) within a column. Significant differences at the $P < 0.05$ level are shown by contrasting letters. Values for soil data are means (± Standard Error)

	Percent C or N loss or DOC:DON Ratio	
Site	30 °C Incubation	10 °C Incubation
CO_2 fluxes		
Fairbanks	4.03 (0.02) A	0.81 (0.07) A, B
Chandalar	5.93 (0.02) B	1.24 (0.10) A, B
Toolik	5.84 (0.03) B	1.36 (0.07) A
Sagwon	3.80 (0.03) A	0.67 (0.07) B
DOC fluxes		
Fairbanks	0.12 (0.001) A	0.23 (0.05) A
Chandalar	0.15 (0.02) A	0.18 (0.03) A
Toolik	0.16 (0.03) A	0.19 (0.02) A
Sagwon	0.27 (0.02) B	0.15 (0.02) A
DON fluxes		
Fairbanks	1.33 (0.19) A	1.49 (0.43) A
Chandalar	1.21 (0.14) A	1.01 (0.08) A
Toolik	1.25 (0.17) A	1.05 (0.06) A
Sagwon	1.31 (0.28) A	0.95 (0.10) A
DOC:DON ratio		
Fairbanks	12.52 (2.13) A	20.47 (2.78) A
Chandalar	12.27 (0.91) A	17.47 (3.09) A
Toolik	15.09 (4.76) A	18.57 (2.65) A
Sagwon	24.05 (3.64) B	16.69 (2.35) A

Results

Temperature and latitudinal effects on fluxes

Not surprisingly, incubation temperature had a substantial effect on CO_2 fluxes at all the tussock vegetation sites at 40 days into the incubation, with 4–5 fold larger fluxes at the higher vs. the lower temperatures ($F = 790.9$, $P < 0.001$) (Table 2). Approximately 4–6% of soil carbon was lost in the first 40 days of the incubation at the higher temperature (Table 2). Carbon losses differed significantly among sites ($F = 26.3$, $P < 0.001$), but did not monotonically follow average temperatures at the site of soil origin. The largest fluxes at the higher temperature were from the Chandalar and Toolik sites with lower fluxes from Fairbanks and Sagwon (Table 2). This pattern was similar at the low incubation temperature as well (i.e. there was no significant site by temperature interaction; $F = 1.1$, $P = 0.381$). Initial DOC fluxes were insensitive to site differences ($F = 0.503$, $P = 0.683$) and temperature ($F = 0.192$, $P = 0.664$), but did show a significant site by temperature interaction ($F = 3.684$, $P = 0.022$) (Table 2). The interaction resulted from a pattern of high DOC fluxes from the Sagwon site at high temperatures that did not occur at low incubation temperatures. Initial DON fluxes were unaffected by site ($F = 0.593$, $P = 0.624$), temperature ($F = 1.698$, $P = 0.202$) or by the combination of site and temperature ($F = 0.259$, $P = 0.854$).

Dissolved organic carbon : Dissolved organic nitrogen ratios ranged between 16 and 20 at low temperature, with no significant differences among sites ($F = 1.140$, $P = 0.348$). Ratios were generally lower (12–15) at high temperature, but not significantly so ($F = 2.285$, $P = 0.141$) because of a substantially higher value at Sagwon (weak site by temperature interaction, $F = 2.259$, $P = 0.101$). Initial DOM C:N ratios were much lower than SOM C : N ratios which generally varied between 30 and 50 (Tables 1 and 2).

By the end of the one year incubation, substantial amounts of carbon had been lost as both CO_2 and DOC fluxes (Table 3). Across the tussock sites, an average of 26% of soil carbon was respired in the high temperature incubations with slightly less than two percent of soil carbon lost as DOC fluxes. At low temperatures, about 11% of soil carbon was lost through respiration and less than one percent as DOC. The overall ratio of CO_2 to DOC loss was relatively insensitive to temperature. Cumulative one year fluxes of CO_2 varied across the four sites ($F = 15.7$, $P < 0.001$) but without a north to south trend. As with the initial fluxes, temperature had a large effect on cumulative CO_2 loss ($F = 326.5$, $P < 0.001$), and there was a significant site by temperature interaction ($F = 11.8$, $P < 0.001$). The largest fluxes of CO_2 from tussock tundra at high temperatures were from the Toolik site where an average of 28.7% of soil carbon was lost during the incubation and the lowest were from the Chandalar site with a carbon loss of 24.0% (Table 3). At low temperatures, Toolik also had the largest fluxes of CO_2 but the other three sites did not follow the same pattern as in the high temperature incubations. The lowest CO_2 carbon losses at low temperatures were from the Fairbanks and Sagwon sites. Dissolved organic carbon fluxes at one year were 2–3 times higher at 30 °C than at 10 °C ($F = 51.42$, $P < 0.001$, Table 3). At high temperature, soils from the Toolik site had significantly greater DOC flux than the other sites ($F = 16.89$, $P < 0.001$). Patterns in DOC fluxes at high and low temperature were somewhat different (Interaction effect, $F = 4.52$, $P = 0.009$) with a smaller increase in DOC production at Fairbanks with elevated temperature than at Chandalar or Sagwon. In general however, DOC and CO_2 fluxes had similar patterns across the four tussock sites with the highest fluxes of carbon from Toolik (Table 3).

The temporal trends in CO_2 and DOC flux through the one-year incubation markedly differed. At high temperatures, DOC concentrations from most soils were constant through the course of the incubations, although soils from the Toolik site had substantially higher concentrations later in the incubation (Fig. 1). In contrast, CO_2 fluxes from all sites declined substantially from the beginning to the end of the incubation. As a result, the ratio of CO_2 flux to DOC concentration for individual leaching measurements declined from 1 to 2 at the beginning of the experiment to around 0.5 by 1 year (Fig. 1). The strongest decline in CO_2:DOC flux was in soils from Toolik. At low temperatures, DOC concentrations were again constant for soils from all sites except Toolik, which increased from day 53. Low temperature CO_2 fluxes changed little during the incubation for all soils (Fig. 2). Because of declines in flux rates through time at high temperatures, the low temperature fluxes were greater than or equal to high temperature fluxes by the end of the incubation.

Vegetation effects on fluxes

Differences in vegetation communities played a major role in determining carbon fluxes in the experiment.

Table 3 Total fractional loss of C in tussock tundra soils. Values are expressed as the cumulative percentage of soil carbon respired (CO_2), or leached (DOC) at high (30 °C) and low (10 °C) temperatures by one year. *A priori* contrasts are shown for each flux (CO_2 or DOC) within a column. Significant differences at the $p < 0.05$ level are shown by contrasting letters. Values for soil data are means (± Standard Error)

	Percent C Loss	
Treatment Site	30° C Incubation	10° C Incubation
CO_2 fluxes		
Fairbanks	26.48 (2.68) A, B	8.37 (0.86) A
Chandalar	24.03 (1.44) A	12.15 (0.36) B
Toolik	28.74 (1.33) B	16.96 (0.46) C
Sagwon	26.58 (1.35) A, B	8.14 (0.79) A
DOC fluxes		
Fairbanks	0.9 (0.02) A	0.69 (0.08) A, B
Chandalar	1.2 (0.02) A, B	0.57 (0.03) A
Toolik	3.1 (0.03) C	0.97 (0.03) B
Sagwon	1. 5 (0.01) B	0.71 (0.04) A, B

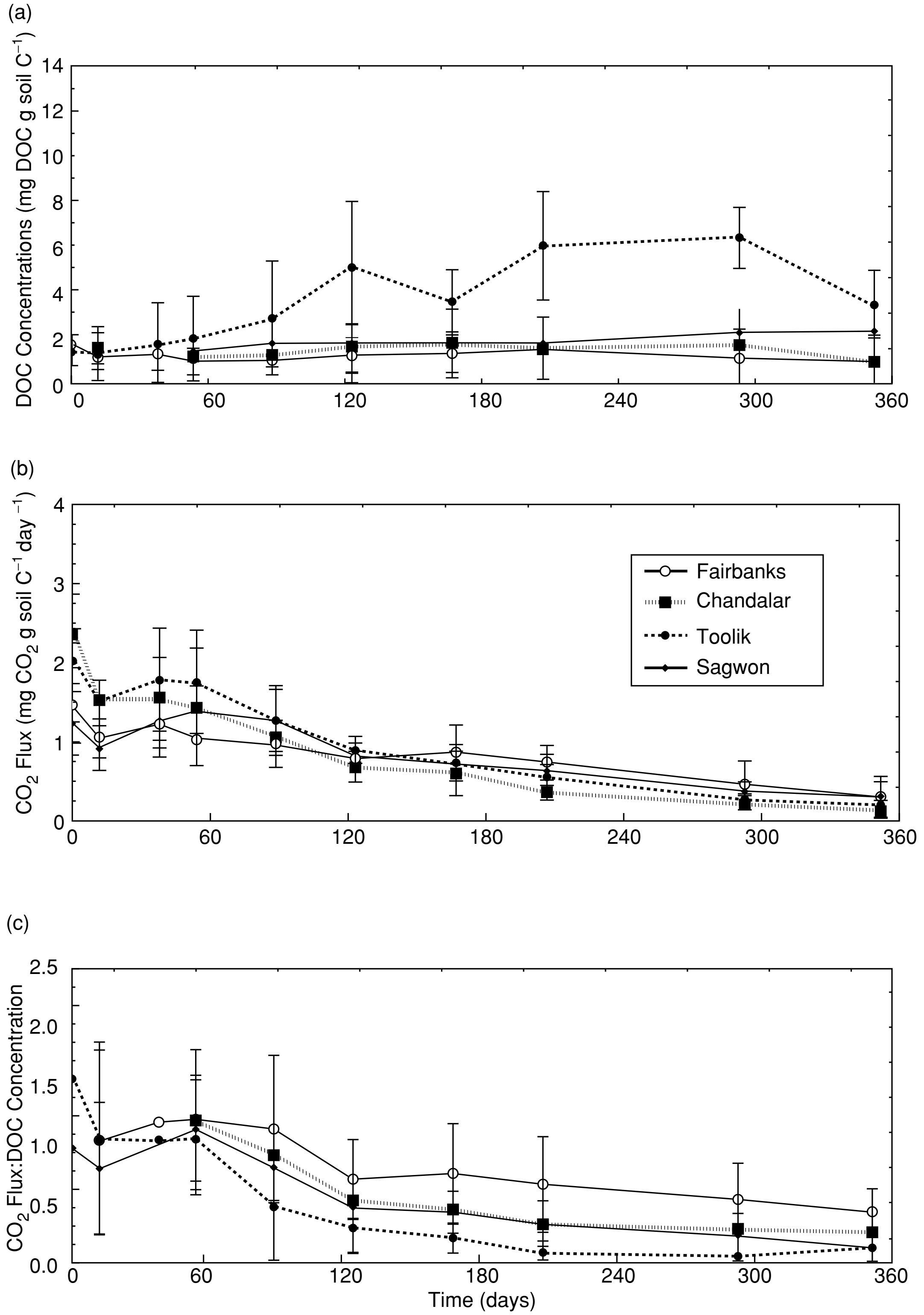

Fig. 1 CO_2 and DOC fluxes from tussock tundra soils incubated at 30 °C. (a) DOC concentrations (mg DOC-C• g soil C^{-1}) at each sampling point. (b) CO_2 flux (mg CO_2-C• g soil C^{-1} day^{-1}). (c) The ratio of CO_2 flux (CO_2-C• g soil C^{-1} day^{-1}) to DOC concentration (mg DOC – C• g soil C^{-1}) for the leaching carried out on the same day. Values are means (± Standard Error).

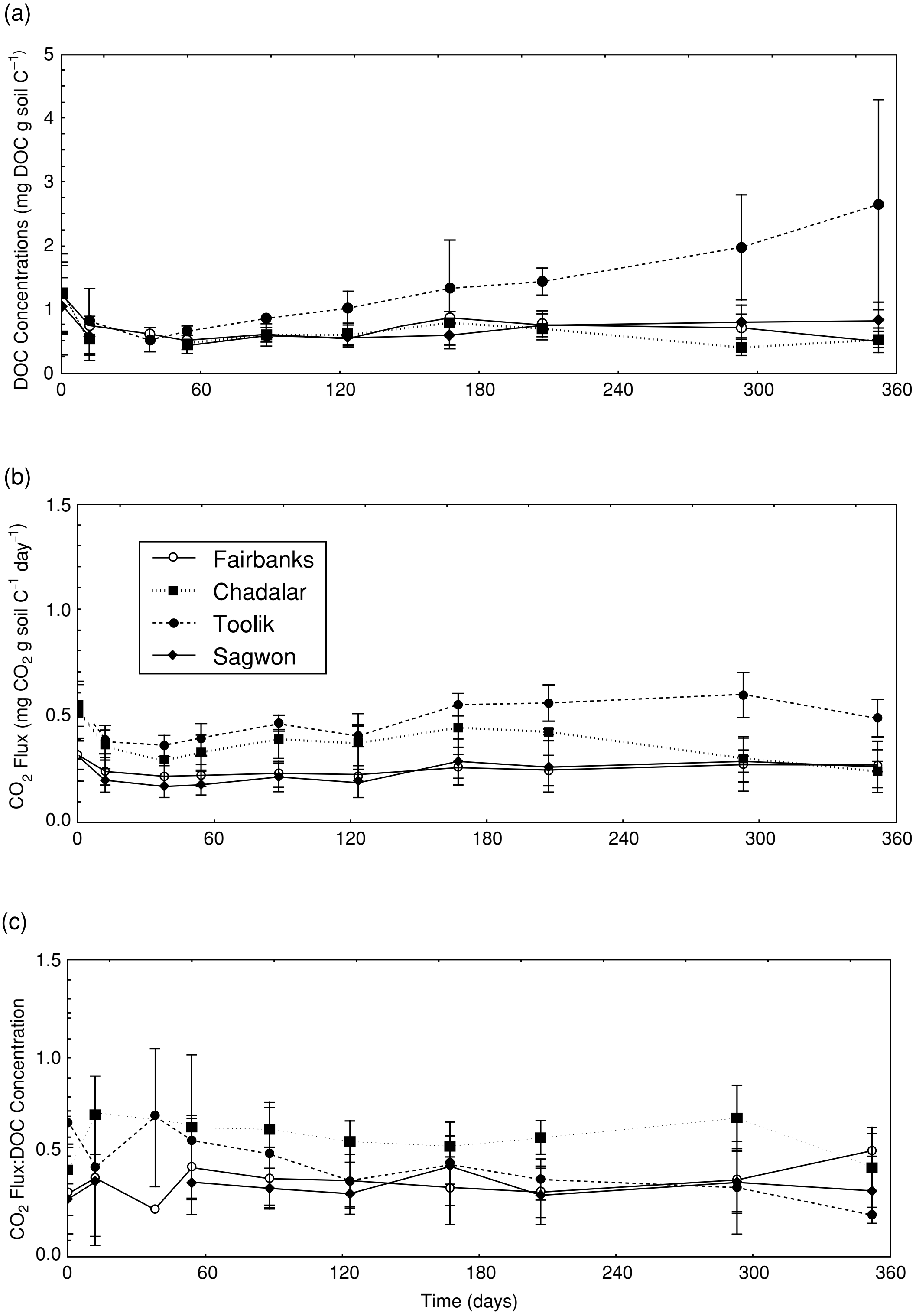

Fig. 2 CO_2 and DOC fluxes from tussock tundra soils incubated at 10 °C. (a) DOC concentrations (mg DOC-C• g soil C^{-1}) at each sampling point. (b) CO_2 flux (mg CO_2-C• g soil C^{-1} day^{-1}). (c) The ratio of CO_2 flux (CO_2-C• g soil C^{-1} day^{-1}) to DOC concentration (mg DOC– C• g soil C^{-1}) for the leaching carried out on the same day. Values are means (± Standard Error).

Table 4 Initial fractional loss of C or N from soils from differing vegetation types. Values are expressed as the cumulative percentage of soil carbon respired (CO_2), or leached (DOC) by 40 days. Dissolved organic nitrogen fluxes are expressed as the fraction (%) of soil nitrogen lost to DON leaching and DOC:DON ratios are calculated on a per gram soil basis. *A priori* contrasts are shown for each flux or ratio (CO_2, DOC, DON or DOC:DON) within a column. Significant differences at the $P < 0.05$ level are shown by contrasting letters. Values for soil data are means ($\pm$ Standard Error)

Fairbanks Vegetation	Percent C or N loss or DOC:DON Ratio	Toolik Lake Vegetation Types	Percent C or N loss or DOC:DON Ratio
CO_2 fluxes			
Tussock	4.03 (0.30) A	Tussock	5.84 (0.35) A
Spruce	2.94 (0.14) B	Shrub	8.87 (0.64) B
		Wet sedge	2.93 (0.25) C
DOC fluxes			
Tussock	0.12 (0.01) A	Tussock	0.18 (0.02) A, B
Spruce	0.41 (0.09) B	Shrub	0.25 (0.05) A
		Wet sedge	0.13 (0.02) B
DON fluxes			
Tussock	1.33 (0.24) A	Tussock	0.12 (0.18) A
Spruce	1.02 (0.09) A	Shrub	0.89 (0.09) A, B
		Wet sedge	0.68 (0.08) B
DOC:DON ratio			
Tussock	12.5 (0.22) A	Tussock	15.09 (4.76) A
Spruce	10.17 (0.09) A	Shrub	24.66 (4.16) A
		Wet sedge	28.36 (7.44) A

At Fairbanks, initial CO_2 fluxes were affected by vegetation type ($F = 17.79$, $P = 0.003$) with approximately 25% higher fluxes from tussock than from spruce soils (Table 4). In contrast, DOC fluxes at Fairbanks followed an opposite pattern to CO_2 with three-fold higher carbon loss from spruce compared to tussock soils at 40 days ($F = 13.15$, $P = 0.008$). At Toolik, CO_2 flux from shrub soils was about three times that of the wet sedge soils ($F = 72.28$, $P < 0.001$). Forty-day cumulative DOC fluxes followed similar patterns but with less variation between vegetation types ($F = 3.011$, $P = 0.087$). Organic N leaching was unaffected by vegetation type at Fairbanks ($F = 1.695$, $P = 0.229$), but did vary at Toolik Lake ($F = 6.023$, $P = 0.015$) where the lowest DON fluxes occurred in the wet sedge vegetation type and the highest from the tussock vegetation (Table 4). Despite a wide range of DOC:DON ratios across the different vegetation types, differences among vegetation types were not significant at either Fairbanks ($F = 0.903$, $P = 0.374$) or Toolik Lake ($F = 2.960$, $P = 0.090$) because of high variability within sites. The highest average DOM C:N ratios (28) in this incubation were from the wet sedge vegetation type at Toolik Lake which had the lowest SOM C:N ratio (22) in the experiment (Table 1).

By one year, vegetation type continued to exert an influence over CO_2 and DOC fluxes at both Fairbanks (CO_2: $F = 22.00$, $P = 0.002$; DOC: $F = 17.70$, $P = 0.003$) and Toolik (CO_2: $F = 72.28$, $P < 0.001$; DOC: $F = 108.8$, $P < 0.001$) (Fig. 3). Both DOC and CO_2 fluxes at Toolik had similar patterns with substantially higher fluxes from the shrub vegetation, followed by the tussocks. CO_2 fluxes from shrub soils were 2.5 times larger than from the wet sedge soils, whereas DOC fluxes from shrub soil were almost eight times larger than DOC fluxes from the wet sedge (Table 5). In Fairbanks, however, CO_2 fluxes were greatest in the tussock vegetation, but DOC fluxes were greatest in the spruce. In all vegetation types, CO_2 fluxes decreased most strongly between days 52 and 120 of the incubation. Dissolved organic carbon fluxes showed varied patterns, however, with stable, increasing (Toolik tussock), or peaked (Toolik shrub) loss rates through the course of the incubation (Fig. 3).

Flux relationships

We examined the relationship between DOC and CO_2 production at two intervals during the experiment. During the first 40 days of the incubation, there was no correlation between DOC and CO_2 fluxes across all sites and vegetation types (Regression analysis, $F = 0.190$, $P = 0.669$, $r^2 = 0.003$). By one year, however, there was a moderately strong relationship between the two fluxes (Regression analysis, $F = 79.08$, $P < 0.001$, $r^2 = 0.59$) (Fig. 4). Dissolved organic carbon flux rates (per gram

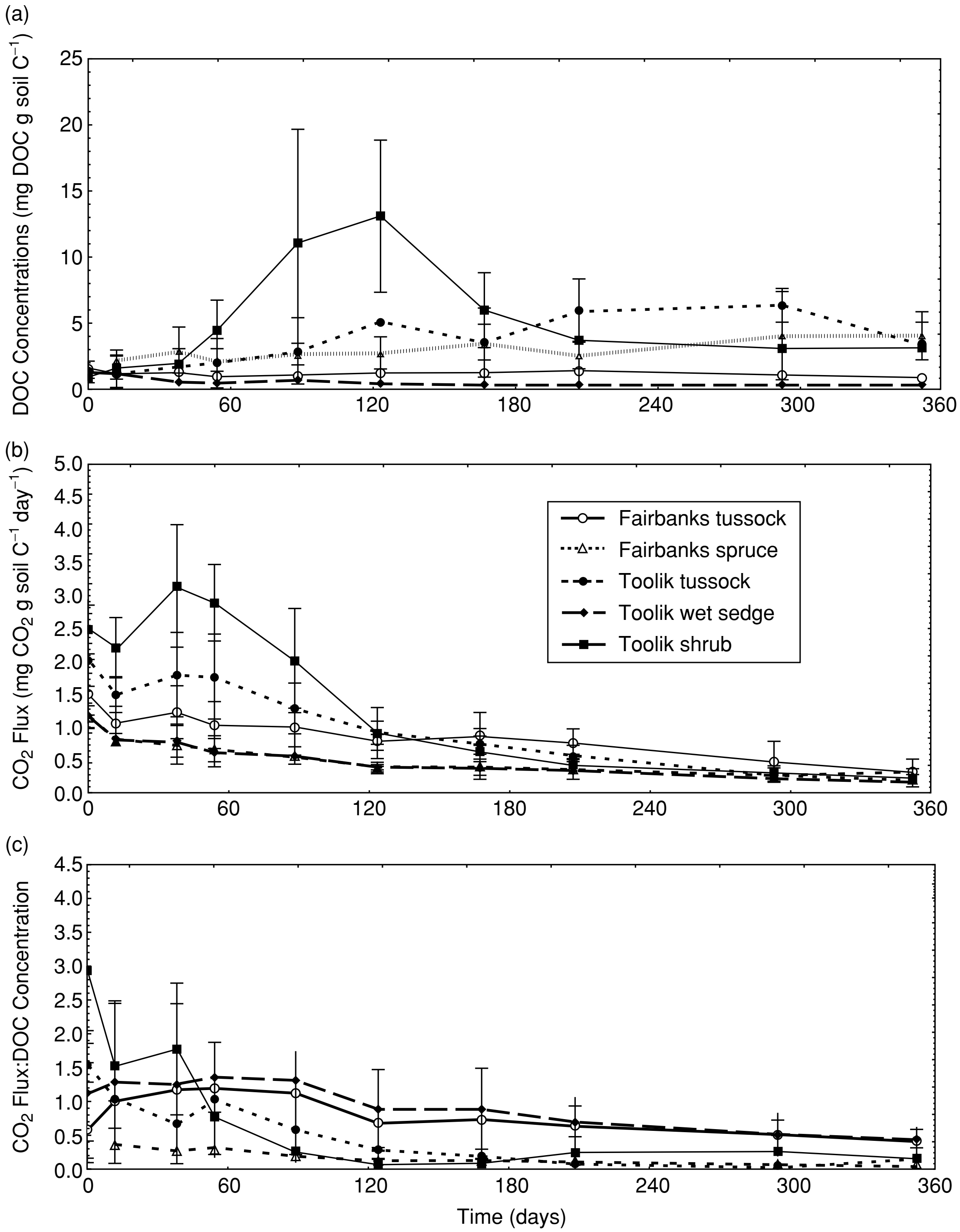

Fig. 3 CO_2 and DOC fluxes from soils from differing vegetation types incubated at 30 °C. (a) DOC concentrations (mg DOC-C• g soil C^{-1}) at each sampling point. (b) CO_2 flux (mg CO_2-C• g soil C^{-1} day^{-1}). (c) The ratio of CO_2 flux (CO_2-C• g soil C^{-1} day^{-1}) to DOC concentration (mg DOC– C• g soil C^{-1}) for the leaching carried out on the same day. Values are means (± Standard Error).

soil) were not related to SOM C content for either the initial (Regression analysis, $F = 0.421$, $P = 0.520$, $r^2 = 0.013$) or cumulative fluxes (Regression analysis, $F = 2.972$, $P = 0.094$, $r^2 = 0.082$). However, carbon content was uniformly high (37–45%) across the suite of soils investigated (Table 1). In this study, initial DOC fluxes (per gram soil) were only weakly proportional to SOM C:N ratio (Regression analysis, $F = 3.91$, $P = 0.05$, $r^2 = 0.11$), and cumulative (1 year)

DOC fluxes were not related to SOM C:N at all (Regression analysis, $F = 0.26$, $P = 0.61$).

Discussion

The decomposability of northern soils

Alaskan tundra soils contain a large proportion of labile carbon. The product of soil organic matter stocks and the biologically labile fraction of organic matter set an upper limit on the potential carbon release due to decomposition. In many tropical and temperate soils, there is a relatively small pool of SOM that disappears in the first days to weeks of an experimental incubation (e.g. Townsend *et al*., 1997; Holland *et al*., 2000). These data are used in ecological models (e.g. Parton *et al*., 1987) to partition carbon into SOM pools of varied residence times with labile (active) fractions that are generally only 2–3% of total soil carbon. While this experiment is not representative of normal arctic field conditions, our results indicate that as much as 40% of soil carbon is potentially decomposable over short time scales; a fraction that is substantially higher than temperate or tropical soils and more analogous to the light fraction of temperate soils (Whalen *et al*., 2000). If soils in boreal and arctic regions warm in the coming decades, the response of decomposition could be less constrained by the biological availability of organic matter than temperate or tropical systems.

Table 5 Total fractional loss of C from soils from differing vegetation types. Values are expressed as the cumulative percentage of soil carbon respired (CO_2), or leached (DOC) by one year. *A priori* contrasts are shown for each flux (CO_2 or DOC) within a column. Significant differences at the $P < 0.05$ level are shown by contrasting letters. Values for soil data are means (± Standard Error)

Fairbanks	Percent C Loss	Toolik Lake	Percent C Loss
CO_2 fluxes			
Tussock	26.48 (2.68) A	Tussock	28.74 (1.33) A
Spruce	15.45 (0.84) B	Shrub	37.01 (1.86) B
		Wet sedge	14.97 (1.02) C
DOC fluxes			
Tussock	0.91 (0.22) A	Tussock	3.12 (0.34) A
Spruce	2.62 (0.33) B	Shrub	4.64 (0.49) B
		Wet sedge	0.58 (0.04) C

Climatic and vegetation controls on decomposition

Tundra soil decomposability appears to be highly variable with patterns that follow differences in vegetation and landscape characteristics. Alaskan tundra and boreal ecosystems span a range of vegetation types and macroclimatic regimes. Of these two factors, our results

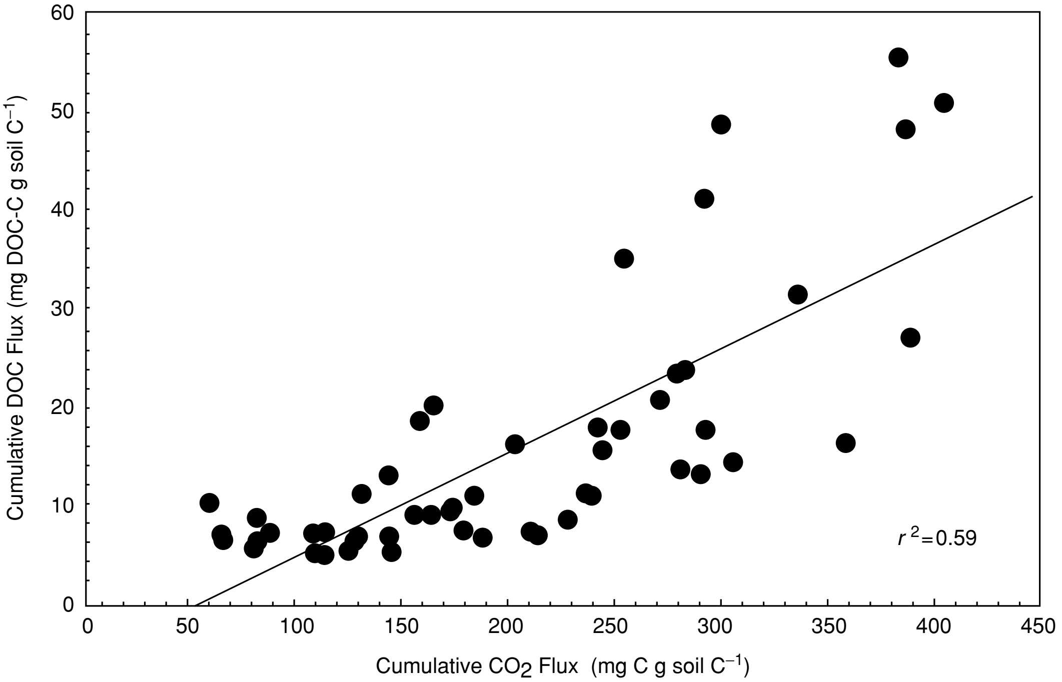

Fig. 4 The relationship between DOC and CO_2 fluxes for soils incubated at 30 °C. The regression line is based on a linear regression of cumulative (to one year) DOC (mg DOC• g soil C^{-1}) and CO_2 fluxes (mg CO_2-C• g soil C^{-1}).

indicate that vegetation type plays the dominant role in regulating the decomposability of soil organic matter. There are three potential factors that may influence variation in SOM decomposability across vegetation types. First, there may be direct biochemical properties of vegetation that influence the decomposability of soils. Studies of litter decomposition clearly indicate variation in decomposition rates across vegetation types (Hobbie, 1996; Shaver *et al*., 1997) driven by variation in plant chemistry (Coulson & Butterfield, 1978; Coley *et al*., 1985; Verhoeven & Toth, 1995). In a literature review of chemistry and decomposition across a range of arctic and boreal ecosystems, Hobbie *et al*. (2000) found that growth form explained a substantial portion of variation in decomposition rates. Notably, the decomposition of mosses in wet, lowland systems such as most of the systems examined here was consistently slow and appeared to be related to some aspect of litter chemistry rather than soil physical environment (Hobbie *et al*., 2000). Second, vegetation may covary with properties such as soil drainage, aspect or microclimate that influence carbon storage on the landscape scale (Harden *et al*., 2000). Third, microbial decomposer communities may vary across vegetation types. While there are few data on microbial communities at the three northern sites in this experiment, studies at the Fairbanks site indicate that the soils beneath spruce and tussock vegetation types have markedly different microbial communities. Of the two communities, the tussock site has a larger pool of microbial biomass and a larger fungal contribution to the overall biomass pool (Balser and Firestone, unpublished results). Whatever the proximate mechanism, these results, combined with previous studies indicate that vegetation composition and/or microclimatic conditions influence not only litter decomposition rates (e.g. Hobbie, 1996) but also the subsequent decomposability of SOM.

Because of cooler temperatures and slower decomposition, we expected greater available pools of carbon at higher latitudes (Fairbanks < Chandalar < Toolik < Sagwon). However, while Toolik tussock soils consistently had the greatest fluxes of both DOC and CO_2 after one-year, regardless of temperature, soils from Sagwon (the most northern and coldest site) were more similar to the Fairbanks tussock soils (the most southerly site), than they were to Toolik. Based on these results, it appears that other site characteristics outweigh mean climate as the driving control over the fraction of total C that is labile in a given site. Another significant factor that influences carbon fluxes from these sites is the size of the soil organic matter pool. While these results suggest that climate has little influence on the fractional decomposability of SOM, they do not address potential climatic controls over the size of the SOM pool. In the tussock tundra sites that make up our latitudinal transect, there are differences in the seasonal thaw depth from north to south (Hooper *et al*., unpublished results) and likely variation in the overall size of the organic matter pool. A full accounting of latitudinal/climatic controls over soil carbon fluxes would need to address both the decomposability of carbon as described here and the influence of climate on the accumulation and availability of organic matter pools.

Gaseous and soluble element fluxes

Both DOC and CO_2 are vectors of potential carbon loss from terrestrial ecosystems. Northern rivers typically have higher DOC loads than temperate or tropical rivers (Hope *et al*., 1994) and DOC losses may be a larger contributor to terrestrial net ecosystem productivity than in temperate or tropical systems (Randerson *et al*., unpublished results). There are multiple pathways of DOM production and stabilization including both physical and biological processes (see Neff & Asner, 2001 for a review). The results from this study and others suggest that DOM production is not directly related to SOM turnover (Gödde *et al*., 1996). Evidence for this conclusion includes the opposite patterns of DOC and CO_2 release from spruce and tussock vegetation types at Fairbanks, the weak correlation of DOC and CO_2 in the initial (40 days) stages of this incubation experiment, and overall differences in the time-courses of DOC and CO_2.

The behaviour of DOM in relation to CO_2 raises several issues in relation to the dynamics of DOM under changing climate. Previous work on DOM leaching from soils indicates that DOM fluxes are sensitive to temperature, but the combination of those studies and this work suggest that the control of temperature on DOM flux is not as strong as the temperature regulation of CO_2 release (Christ & David, 1996; Gödde *et al*., 1996; Moore & Dalva, 2001). In addition to temperature, DOM flux is closely related to moisture content and leaching intensity. In general, the proportional contribution of DOC to carbon loss ($DOC + CO_2$) increases with soil moisture content and the frequency of leaching events (Christ & David, 1996; Gödde *et al*., 1996; Moore & Dalva, 2001). These results highlight the apparent trade off between CO_2 and DOC production in soil carbon release. Correlations between soil respiration and water-soluble organic matter indicate that DOM is a likely substrate for microbial growth (Zsolnay & Steindl, 1991; Jandl & Sollins, 1997) as well as a by-product of microbial activity (Burford & Bremner, 1975; Brooks *et al*., 1999). As a result, the bioavailability of DOC will play a large role in determining whether carbon is lost through leaching or as CO_2 following decomposition. This balance is shown in previous modelling analyses that suggest that the intensity of leaching competes with both DOM sorption and microbial decomposition (of DOC to CO_2) to determine the balance between carbon stabilization, CO_2 loss or DOC loss to groundwater or streams (Currie & Aber, 1997; Neff & Asner, 2001). If arctic and boreal soils warm in coming decades, DOC production has the potential to increase, but whether these increased production rates translate into elevated DOC fluxes from ecosystems will depend on the balance between leaching regime and the response of decomposer communities to increased DOC generation.

Conclusions

At the landscape scale, differences in vegetation type and/or correlated differences in microenvironment conditions (e.g. soil moisture, drainage) appear to more strongly influence the decomposability of arctic and boreal soils than do regional macroclimatic differences. Of the possible forms of carbon loss from soils, CO_2 fluxes were more sensitive to differences across vegetation types than were DOC fluxes. Although DON fluxes were affected by vegetation type, their responses were much smaller than for CO_2 fluxes. The fluxes of CO_2, DOC and DON, normalized to SOM C or N content, showed little relationship to site climatic characteristics, even when vegetation type was held constant. This result suggests that, across landscapes, differences in vegetation types are likely to be better predictors of SOM lability than indirect effects of climate on SOM quality (at least over the scales investigated here). Therefore, resolving landscape scale patterns of vegetation distribution will be an important component of modelling attempts to understand regional fluxes of CO_2. This experiment also suggests that as arctic and boreal soils warm, decomposition rates are unlikely to be immediately limited by the decomposability of arctic soils. Rather, a substantial fraction of SOM may be relatively easily converted into CO_2 and DOC under favourable climatic conditions.

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