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Abstract

Soil organic matter distributions, reservoirs, and mineralization rates in tundra soils are important factors for understanding biogeochemical carbon cycling. This study focuses on spatial trends and environmental controls of soil carbon distribution and microbial soil respiration in 4 tundra vegetation communities in an arctic valley in NE-Greenland (74°N), including Dryas and Cassiope heaths, Salix snow bed, and fen vegetation. Measured total soil organic carbon in the upper 50 cm averaged ($\pm$SD) 11.0 ± 1.5 kg C m^{-2} with spatial variations strongly affected by vegetation, hydrology, and buried organic layers. Observed soil CO_2 concentrations and effluxes were simulated with a steady-state diffusion model using laboratory measured CO_2 productions as input. Simulated CO_2 profiles and CO_2 effluxes (up to 3 µmol CO_2 m^{-2} s^{-1}) agreed with field observations and revealed the importance of both vegetation- and depth-specific CO_2 production and CO_2 diffusion for understanding the spatial variation in near-surface soil CO_2 gas dynamics. These results confirm that molecular diffusion dominates gas transport in the studied soils; but also that the complexity of CO_2 production/transport coupled to soil heterogeneity (in particular the litter layer) complicates the application of soil-diffusion models to estimate seasonal trends of soil gas effluxes.

Introduction

Soil carbon and nutrient cycling within the terrestrial arctic regions is an important topic (e.g., Coyne and Kelley, 1974; Oberbauer et al., 1996; Burkins et al., 2001) as these landscapes hold about 14% of the world's organic carbon (Post et al., 1982) and may be some of the most sensitive ecosystems with respect to climatic changes (Oechel et al., 1993, 1998; Maxwell, 1997). The decomposition of soil organic carbon results in a release of several greenhouse gasses to the atmosphere of which the release of carbon dioxide (CO_2) is considered the most important (Oechel et al., 1993). CO_2 is being produced primarily by near-surface respiration in living roots (Billings et al., 1977) and by heterotrophic soil microorganisms (Buchmann, 2000). Consequently, gas-filled pores in soils typically have CO_2 concentrations 10 to 100 times higher than the atmosphere (Welles et al., 2001), resulting in a net CO_2 flux from the soil to the atmosphere. The transport of near-surface gases such as CO_2 has long been considered mainly as a result of diffusion (e.g., Lundegärdh, 1927; De Jong and Schappert, 1972) driven by concentration gradients and limited by the decrease in continuous air-filled soil pores with increasing water content. The decomposition of soil organic matter is sensitive to several site-specific environmental conditions including the quality, abundance, and redistribution of carbon substrates (Van Cleve, 1974; Nadelhoffer et al., 1991, Fahnestock et al., 2000) and climatic factors, in particular soil temperature (Fang and Moncrieff, 2001), water content (Howard and Howard, 1993; Kirschbaum, 1995), and snow (Welker et al., 2000). Availability of oxygen, types of microorganisms present, as well as faunal abundance and activity are additional factors influencing soil microbial respiration processes (Lomander et al., 1998).

The spatial and temporal variability of such conditions in the field results in substantial variations in rates of soil organic carbon mineralization, soil CO_2 production, and effluxes between tundra vegetation types (e.g., Evans et al., 1989; Oberbauer et al., 1991, 1992; Hobbie, 1996; Grogan and Chapin, 1999).

Striking changes in arctic plant communities and concurrent soil CO_2 effluxes have been observed over small distances due to microtopography, which seemed related primarily to hydrology (Oberbauer et al., 1996). Consequently, changes in plant community structure, composition, and distribution in the landscape will be an additional feedback mechanism for long-term climate changes (Zimov et al., 1996). This feedback is not limited to the plants, but also involves the complex interactions between plants, the soil organic matter pools, and the soil organic matter mineralization, which, again, is closely related to the availability of nutrients for plants and microorganisms competing in nutrient-limited arctic ecosystems (Oberbauer et al., 1991).

Reported data for the arctic show that less attention has been given to the well-drained and drier upland tundra areas where the vegetation cover is limited and dominated by heath vegetation (Welker et al., 1999; 2000). This is despite the facts that the drier tundra is more widespread toward the most northern dry arctic regions, e.g., most of northern Greenland north of 74°N (Bay, 1992), and that these soils show the greatest thaw depths (Oberbauer et al., 1996).

For these reasons, the assessment of present carbon cycling and long-term trends of net carbon balance in arctic regions requires not only improved understanding of specific controls on below-ground CO_2 dynamics at appropriate spatial and temporal scales (Grogan and Chapin, 1999), but also improved understanding of the interacting processes at a landscape scale including soil types, soil water distribution, vegetation types, soil organic matter quality, and soil gas transport.

While it is still debatable to what extent the arctic region will act as a source or a sink for atmospheric carbon in the future, the net loss or gain in carbon is expected to result in significant changes in the total ecosystem pools. However, future estimates of changes in pools require detailed information on total and depth distribution of existing soil carbon. So far, very little has been reported on plant community–controlled variations in the amount of soil organic carbon and on the

TABLE 1

Soil physical and biogeochemical properties of major soil/vegetation types in Zackenberg, Greenland (± one standard deviation)

Vegetation type	Dry Dryas heath	Moist Cassiope heath	Salix snow bed	Wet Eriophorum fen
% Water saturation range (0–5 cm)	40–60	60–80	65–90	90–100
Area below 200 m a. s. l. (km^2)	4.36 ± 0.5	4.09 ± 0.6	3.17 ± 0.3	4.87 ± 0.6
[1]Approximate % of total area	26	25	19	30
Total soil C (0–20 cm) (kg C m^{-2})	4.1 ± 0.4	6.3 ± 3.0	10.5 ± 1.8	5.6 ± 3.2
Total soil C (0–50 cm) (kg C m^{-2})	6.1 ± 1.1	8.5 ± 2.6	21.2 ± 4.1	11.3 ± 3.8
Vegetation C:N	35	43	28	31
Vegetation-C (g C m^{-2})	327 ± 73	360 ± 73	80 ± 39	[1]134 ± 19
[1]Plant cover (%)	65	65	80	88
Litter-C (g C m^{-2})	13 ± 7	21 ± 6	36 ± 10	nd[3]
Root-C (g C m^{-2})	155 ± 25	123 ± 10	nd[3]	nd[3]
Belowground debris-C (g C m^{-2})	265 ± 150	423 ± 121	877 ± 156	nd[3]
Above-below ground biomass ratio	0.81	0.70	nd[3]	nd[3]
[2]Soil Temperature (5 cm) (°C)	9.13 ± 3.8	5.49 ± 1.8	7.59 ± 3.8	7.59 ± 3.8
[2]Soil CO_2 efflux (µmol m^{-2} s^{-1})	0.836 ± 0.2	0.52 ± 0.1	1.22 ± 0.3	2.48 ± 0.5
Maximum thaw in August (cm)	80	65	45	40

Horizon	Dry Dryas heath			Moist Cassiope heath				Salix snow bed					Wet Eriophorum fen				
	A	B/C	C	A	B/C	A_b	C	A	B_1	B_2	A_b	B/C	A	B_1	B_2	A_b	B/C
Depth (cm)	0–2	2–35	>35	0–5	5–17	17–22	>22	0–2	2–6	6–20	20–22	>22	0–10	10–50	50–80	80–87	>87
[4]pH-H_2O	5.9	6.4	7.0–7.2	5.7	6.0	5.5	6.6–7.1	5.1	5.2	5.3	5.0	5.9	5.4	6.7	7.6	6.0	7.2
[4]Bulk density (g cm^{-3})	0.8	1.5	1.6	0.8	1.3	1.5	1.6	0.6	1.2	1.5	0.8	1.6	0.6	0.8	1.1	1.3	1.3
[4]C (%)	3.9	0.6	0.5	6.7	2.1	4.9	0.4	15.4	3.7	3.2	14.2	1.8	3.8	1.8	1.0	3.3	1.4
[4]N (%)	0.2	0.1	<0.1	0.4	0.1	0.2	<0.1	0.9	0.2	0.2	0.9	0.2	0.4	0.2	0.1	<0.1	<0.1
[4]C/N	16.3	11.5	nd[3]	16.2	17.3	20.4	nd[3]	17.3	17.6	16.8	15.6	11.3	10.9	9.0	10.0	nd[3]	nd[3]
[4]P (total) (mg kg^{-1})	357	341	300	510	299	466	250	1240	612	751	1220	460	680	660	nd[3]	nd[3]	nd[3]
[4]P (uorg) (mg kg^{-1})	99	72	50	188	156	109	240	803	202	334	778	93	371	587	nd[3]	nd[3]	nd[3]

[1] Modified from Bay (1998) and Soegaard et al. (2000).

[2] Average of hourly readings in July August 2001.

[3] Not determined.

[4] Values given for each horizon represent the average of samples taken with 5 cm increments within each horizon (3 replicates).

potentials for future shifts in the distribution of plant communities as a result of climate changes.

The present study was designed to (1) evaluate spatial trends and environmental controls of soil carbon reservoirs and mineralization rates during a growing season of 4 characteristic vegetation types found within an arctic valley in NE-Greenland, where all plant communities were subject to similar above-ground climatic conditions; (2) quantify the importance of soil horizons in terms of storing organic carbon and releasing CO_2 produced by organic matter mineralization; and (3) discuss the effects of climatic changes on vegetation patterns and corresponding soil CO_2 dynamics.

Material and Methodology

STUDY SITES

The study sites are situated in the Zackenberg Valley near the Zackenberg Research Station in NE-Greenland (74°28′N, 20°34′W). The sites were selected to represent major plant communities which again reflected the hydrological regimes present in the valley. Vegetation types were identified in the field by topographic position, vegetation, and soils. This classification was confirmed by an aerial photo that previously had been used to quantify the area distribution (Table 1) of all major vegetation zones (Bay, 1998; Søgaard et al., 2000). The abrasion plateaus represent the most exposed and driest areas in the valley. Here, the snow cover is thin or absent throughout winter, resulting in early and fast development of the active layer during spring. The sparse vegetation cover is dominated by Dryas sp. (including D. integrifolia). Flat low-lying areas receiving the average amount of snow

(0.5–1 m yr^{-1}) were typically free of snow by late June and remained moist but aerated during most of the growing seasons (1998–2001). Cassiope tetragona dominates these areas, although other heath species such as Vaccinium uliginosum are found in patches. The variety of heath vegetation covers more than 30% of the valley below 200 m above sea level (asl.) and is the most dominant vegetation type found in the valley. Areas receiving water from persistent snow drifts (snow beds) remain moist or wet throughout the growing season and are dominated by Salix arctica. Fen vegetation dominated by graminoids is found in undrained landscape depressions and other low lying areas receiving substantial amounts of water from snow melt throughout the summer. Arctagrostis latifolia and Eriophorum triste are key species found in less-wet parts, whereas Eriophorum scheuchzeri and Dupontia pilosantha dominate the wetter parts. The four studied vegetation types, referred to as the Dryas, Cassiope, Salix, and Eriophorum sites, were selected within an area of 3 km^2. These four types represent a simplification of vegetation types previously reported for the Zackenberg Valley (Bay, 1998), including also grassland, saltmarsh, vaccinium, abrasion plateau, and fell-fields. In this study, grassland areas were split into Eriophorum and Salix sites, depending on the dominance of Salix sp., while abrasion plateaus dominated by Dryas sp. were included in the Dryas group. Small areas consisting of salt marsh, fell-fields, lakes, and rivers representing less than 10% were not included.

SOILS

The Zackenberg Valley is a generally flat valley dominated by noncalcareous sandy fluvial sediments. The present soil development is weak and has been classified as Typic Psammoturbels (Elberling and

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Jakobsen, 2000). A relict A-horizon (buried old surface layer, A_b) of 1–5 cm thickness was found in most soil profiles at depths between 15 and 30 cm and was in places associated with a well-developed Podzol. Previous datings of these buried horizons have shown that they represent a soil development during the Holocene Climate Optimum starting at least 5000 yr ago (Christiansen et al., 2002).

CLIMATE

A climate station located within the study area was established in 1995. The station is operated by the Danish Polar Centre (DPC) as part of the Zackenberg ZERO (Zackenberg Ecological Research Operation), GeoBasis Programme. Based on data from that station, the mean annual temperature is about −10°C, and the annual precipitation varies from 150 to 200 mm (Caning and Rasch, 2000). Minimum air temperatures during winter are close to –40°C, and temperatures 2.5 cm below the soil surface are below −18°C for about 4 months per year. During the period 1997–2001, temperatures at 2.5 cm depths were positive for an average of 124 days per year (on average 4.3°C). Climate data used in this study include precipitation, air temperatures (at 2 m above ground), and snow thickness (using Campbell model SR 50 sonic distance measuring probes).

SOIL CO₂ EFFLUXES

Ecosystem CO_2 efflux (microbial and root respiration) measurements were made using a LiCor infrared (nondispersive) gas analyzer (LiCor 6400-09/6262 Soil CO_2 Flux Chamber, LiCor, Lincoln, U.S.A.). The CO_2 analyzer was attached to a portable chamber, functioning as a dark and closed soil-flux chamber when placed on top of pre-installed open collards (9 cm long and 10 cm inside diameter). The measuring procedure is described in Elberling (2003) and modified from Welles et al. (2001) and Buchmann (2000). The final flux reported is the flux observed at ambient chamber CO_2 concentrations and is the average flux based on at least 10 replicate collards per site (in most cases 17 replicates). Flux measurements were made during 2 weeks in August 1999 as well as throughout July and August 2001. Measurements were made at least every second day at the Cassiope site, weekly at the Dryas and Salix sites, and three times at the Eriophorum site. Additionally, measurements were made at the Dryas and Cassiope sites without vegetation (more than 20 cm to the nearest plant). Such barren areas could not be found at the Salix and Eriophorum sites. In addition, measurements were carried out on sites where the litter layer (0–2 cm) and the A-horizon (5–7 cm) were removed. Measurements made on the first 2 days after the removal of material were not included due to short-term effects of disturbance.

Soil gas was withdrawn from pre-installed passive gas samplers holding 250 mL, and concentrations of O_2 and CO_2 were measured on-site using a portable dual wavelength precision CO_2 analyzer (GasData PCO₂, Gas Data Ltd., England). Soil gas was extracted at least every second week in the summers of 2000 and 2001 from depths of 5, 10, 15, 20, 25, 40, and 60 cm. The O_2 and CO_2 concentrations were measured to an accuracy of 500 and 20 μL L^{-1}, respectively. To evaluate spatial variations in soil gas composition, soil gas was also extracted from various depths by connecting the gas analyzer to a soil probe (Dräger Sicherheits-tecnik GmbH, Germany), which was pushed vertically into the soil at intervals of 5 cm. These detailed profile measurements were followed immediately by measurements of the temperature and soil water contents at these depths. On 30 July and 3 August 1999, a survey of the spatial variation in soil CO_2 concentrations and water content in 10 and 25 cm depths was performed in a 4 × 4 m grid (n = 16) at a Cassiope and a Dryas site. Soil gas measurements were not possible at all at Eriophorum sites due to high water content.

The volumetric soil water content was monitored using handheld and automatic logging instruments responding to changes in the apparent dielectrical constant (Theta Probe, Soil Moisture sensors, ML2x, Delta-T Devices Ltd., Cambridge, UK). Water content measurements were logged at seven depths at the Cassiope site on an hourly basis throughout the summer of 2001. Additional manual readings (at least 3 replicates) of near-surface water contents (0–5 cm) were made at the same time as the soil CO_2 efflux measurements. Air and ground temperatures at 2 cm depth were logged at all sites on an hourly basis using TinyTag loggers (Gemini Data Loggers Ltd., Chichester, UK). Manual temperature readings were taken by pre-installed thermistors at a minimum of five depths. The depth of thawing was determined manually throughout the growing season using a graduated stainless steel rod inserted vertically into the soil until frozen soil was encountered.

CHEMICAL ANALYSES

Intact depth-specific and volume-specific (100 cm³) soil samples (3–5 replicates) were collected at 5 cm depth intervals within each horizon in late July or August and stored in the dark at maximum 4°C until analyzed in the laboratory (a total of 6 replicate profiles). Samples stored for more than a few days were stored at temperatures as close to 0°C as possible. Samples were collected from 1998 to 2001.

Soil pH was measured in distilled water at a soil-solution ratio of 1:2.5. Total inorganic C (TIC) and total organic C (TOC) were measured using a Total Organic Carbon Analyzer (Dohrmann DC-190). Measurements of decarbonated samples revealed that carbonate minerals were absent from all samples. Total nitrogen was measured by the Kjeldahl method (Bremner and Mulvaney, 1982); Al and Fe were determined by atomic absorption after acid-oxalate extraction (McKeague and Day, 1966); exchangeable bases (Ca, Mg, Na, and K) were analyzed by AAS (atomic absorption spectrophotometry) after extraction with $NaOOCCH_3$ and NH_4OOCCH_3 (Jakobsen, 1991), and exchangeable H and Al were determined by titration after extraction with 1.0M KCl (Sims, 1996). Inorganic P and total P (after 1 h at 550°C) were determined by colorimetry with ascorbic acid after 6.0M sulfuric acid extractions (Kuo, 1996). Air-filled porosity was calculated from the grain-size distribution (determined by sieving and hydrometer), total volume, weight, porosity, and solid bulk density.

Above-ground biomass was quantified by harvesting all vegetation in 0.25 m² plots (5 replicates) Litter material was collected from the same plots. Below-ground biomass was quantified by wet separation of dead and live roots (visual inspection of color and appearance) and organic debris from soil samples. Samples were subsequently ground, homogenized, and analyzed for soil organic C and N.

CO₂ PRODUCTION EXPERIMENTS

CO_2 production rates were measured in the laboratory from soil samples that had been stored in polyethylene bags at 0°C to 4°C for a maximum of 1 week. Prior to measurements, soil samples were carefully split to remove roots and stones. After an initial pre-incubation of 48 h, weighed soil samples (equivalent to 2–3 g dry soil) were transferred to 12 mL Venoject tubes, left for 2 h pre-incubation, and out-gassed with air free of CO_2. Soil respiration in depth-specific soil samples was subsequently measured by monitoring the linear ($r^2 > 0.95$) increase of headspace CO_2 concentrations during a 6–8 h period by gas chromatography, using either a Hewlett Packard (HP-6890) or a MicroLab (ML-GC8212) equipped with a Porapack Q-column kept at 30°C and a TCD detector operated at 200°C and a flow rate of 25 mL He min^{-1}. These measurements are referred to as BSR (basal soil respiration) measurements below.

Additional experiments made with samples after various degrees of reworking indicated that sample splitting had only little influence on

CO$_2$ production rates, whereas gentle mixing increased short-term rates by up to 20%. CO$_2$ production rate measurements on material from A-horizons from the four vegetation types were made at constant temperatures (± 1°C) at 0 °C, 7°C, 21°C, and 26°C. Additional samples were partly air-dried and subsequently rewetted (about 5% and 10% relative to in-situ moisture content) before being incubated at 26°C to test whether the availability of water influenced the measured rates. Substrate limitation was tested by gently mixing soil material with a powder mixture containing glucose (1.2 mg glucose-C g^{-1} soil) and talc (Anderson and Domsch, 1978). Results are referred to as substrate-induced soil respiration (SIR-measurements) and compared with samples mixed with talc only. All CO$_2$ production measurements were made with 3 replicates. Manipulated soil samples were all prepared from soil samples air dried for a few hours, followed by sieving (2 mm) and subsequently rewetted to specific water contents and thoroughly mixed to ensure homogenous samples. Control incubations with empty Venoject tubes showed that CO$_2$ diffusion into the tubes was negligible. Repeated incubation experiments revealed that the results were independent of the experimental time.

MODELLING

Assuming steady-state conditions and neglecting the effect of water movement, the relationship between one-dimensional diffusion and production of CO$_2$ in soils can be described by Fick's second law:

$$\frac{d}{dx}\left(D_e \frac{dC}{dx}\right) + R = 0 \qquad (1)$$

where C is the CO$_2$ concentration, x is the depth, D_e is the effective diffusion coefficient, and R is the production rate per unit volume of soil. Depth variations of D_e and R were observed in the studied soils, which prevented any analytical solutions to Equation 1. Consequently, Equation 1 was solved numerically using a control volume approach as described by Berg et al. (1998). In short, the soil columns were divided into N horizontal layers, so-called control volumes, each with a grid point located in the center. The numerical solution allowed us to calculate CO$_2$ concentrations for each grid point and also fluxes across each boundary between the control volumes based on known or estimated values of D_e and R. A value of $N = 100$ was used, which guaranteed precise numerical solutions to Equation 1, which have been successfully tested against analytical solutions (Berg et al., 1998). The effective diffusion coefficient (D_e) in Equation 1 was estimated as

$$D_e = \frac{D_a \, a^{10/3}}{\varphi^2} \qquad (2)$$

where D_a is the diffusivity in free air [equal to $0.139 \times (T/273)^2$ cm^2 s^{-1}; where T is the temperature (°K) reported by De Jong and Schappert (1972)], a is the air-filled porosity, and ϕ is the porosity. Equation 2 was originally suggested by Millington (1959) for relating the effective diffusion in soil to the fraction of "continuous" air-filled pore volume. The equation was later shown to be suitable for a variety of sandy soils (Jin and Juri, 1996). Values of R were derived from measured CO$_2$ productions rates and used with calculated effective diffusion coefficients as input to the model after being temperature-corrected. The model was calibrated using observed soil CO$_2$ efflux and subsequently used to compute the corresponding CO$_2$ concentration profile for model verification.

Results

SOIL CHARACTERISTICS AND RESERVOIRS

Soil characteristics of replicate profiles from the four vegetation types are summarized in Table 1. All sites were slightly acidic to neutral (pH range 5.0 to 7.2) with pH generally increasing with depth. Most sites were more or less cryoturbated which were noted as discontinuous soil horizons. The maximum active layer depth was observed by the end of August (1999–2001) and varied from 40 cm at Eriophorum sites to 80 cm at Dryas sites. The highest proportion of fine material and less-sorted sediments was found at Salix sites (25% finer that 2 μm; $d_{50} = 15$ μm); larger grain sizes and greater degree of sorting was found in Eriophorum (20% finer than 2 μm; $d_{50} = 75$ μm), Cassiope (10% finer than 2 μm; $d_{50} = 150$ μm), and Dryas (5% finer than 2 μm; $d_{50} = 360$ μm). The grain size distribution, drainage conditions, and the distribution of snow drifts determined a variation in near-surface water saturation from about 40% at Dryas sites to 100% at Eriophorum sites. Litter layers were noted to be very irregularly distributed at Cassiope and Salix sites (in the range of 0–2 cm, on average 0.8 cm, n = 17) and almost absent at Dryas and Eriophorum sites. However, layers of peat were detected at Eriophorum sites. These layers contain substantial mineral material and are consequently considered to be part of the mineral soil profile.

Soil profiles had maximum concentration of carbon (C) and nitrogen (N) near the surface and decreasing concentrations with depth (Table 1, Figs. 1 and 2) with the exception of buried organic-rich layers, which were found in most profiles. These layers occurred at different depths and revealed varying thicknesses and carbon contents both between replicate sites at each vegetation type (Fig. 1B) and between vegetation types. The greatest difference in buried layers was observed between Cassiope and Eriophorum sites (Fig. 2). At Eriophorum sites the buried organic layer was observed within the permafrost. Single plant remains (birch leaves) were found in all buried organic layers.

Soil bulk densities increased with depth from about 0.8 g cm^{-3} to values near 1.6 g cm^{-3}. Variations in soil bulk densities within each vegetation type were on the same order of magnitude as observed between vegetation types, except for the consistently lower densities observed at the Eriophorum site.

For each soil layer, the total amount of soil organic carbon was calculated by multiplying the average concentration of the element by the average soil density and thickness of the layer. The total amount of soil organic matter within the upper 20 cm, 50 cm (Table 1), and 100 cm was obtained by adding the sum of these layers and is referred to as the soil carbon reservoir to a certain depth. One standard deviation for bulk density, percent soil organic carbon, and carbon reservoirs are
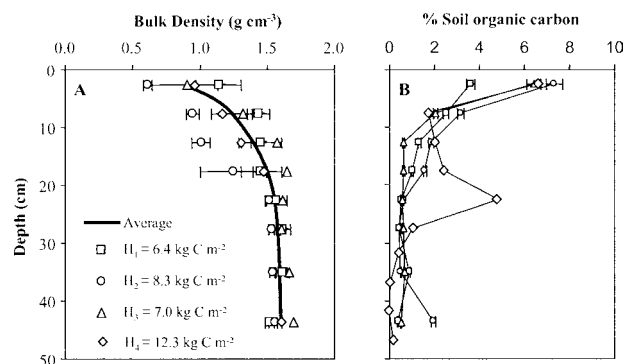

FIGURE 1. *Profiles (replicates) of soil bulk density and soil organic content at four Cassiope sites showing the maximum spatial variation observed in Zackenberg within a single vegetation type. One standard deviation ($\pm$) of 3 replicates per depth is shown as horizontal lines. The total amount of soil organic carbon is calculated to a depth of 50 cm.*

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given in Table 1, indicating that although large variations are observed between profiles of each vegetation type, variations between different vegetations were larger. Maximum variations within a single vegetation type were observed for Cassiope sites (Fig. 1), consistent with an irregular distribution of the buried A_b-horizon.

The depth used for these stock estimates is critical for both absolute stock values reported and for comparisons between vegetation sites. It can be seen (Fig. 2B) that using 50 cm as the depth for stock estimates includes only 55% of the soil organic carbon found in the upper 1 m at Eriophorum sites, whereas 92% is included at Cassiope sites. In contrast, the 50 cm depth stock value represents 100% of the carbon found within the active layer at Eriophorum sites (maximum thaw depth about 40 cm) but 95% at Cassiope sites (maximum thaw depth about 65 cm). If buried surface layers are found near the total depth for estimates, the standard deviations become relatively large (e.g., Cassiope sites, Fig. 1).

The resulting C-reservoirs estimated to depths of 20 and 50 cm (Table 1) indicate that Dryas had the lowest carbon stock within the upper 50 cm (6.1 kg soil-C m^{-2}), followed by Cassiope (8.5 kg soil-C m^{-2}), Eriophorum (11.3 kg soil-C m^{-2}), and Salix (21.2 kg soil-C m^{-2}); the last contains 2–3 times as much as Dryas sites. The vegetation-specific differences in C stock were only slightly affected (less than 10%) when calculated without taking buried A_b-horizons into account. Only the reservoir estimate for 20 cm at Cassiope sites was reduced up to 25%. Taking the area distribution of each vegetation type in the valley into account (see Table 1), the average ($\pm$SD) amount of soil organic C to a depth of 50 cm is 11.0 ± 2.2 kg soil-C m^{-2} or 110 tonne soil-C ha^{-1}, of which 37% was found at Salix sites, 30% at Eriophorum sites, 19% at Cassiope sites, and 14% at Dryas sites. Compared to other fractions of ecosystem carbon pools (vegetation, litter, debris, and roots), the soil organic pools represent more than 94% of the total ecosystem organic carbon (Table 1).

CONTROLS ON SOIL CO_2 PRODUCTION OBSERVED IN THE LABORATORY

The amounts of CO_2 being released from depth-specific soil samples per unit weight revealed that the release from the two A-horizons at Cassiope sites (A and A_b) was not significantly different (p < 0.05) and that these A-horizons produced about 3–5 times as much CO_2 as underlying B- and C-horizons. The same was noted for the other vegetation types. Calculating CO_2 production per dry weight soil-C at optimum conditions provided a measure of the relative differences in reactivity of the soil organic matter or organic matter quality (Fig. 3A). These reactivity numbers revealed that the reactivity of A_b was higher than the near-surface A-horizon at the Cassiope sites, that the opposite was noted at Salix sites, that CO_2 production rates unit soil organic-C in near-surface layers (A-horizons) were the same for Dryas and Salix but 40% higher than for A-horizon material at Cassiope sites and that reactivity increases from A-horizons to underlying B/C-horizons (Fig. 3A).

CO_2 production rates in samples after air drying and rewetting revealed no significant changes in rates, except for the Dryas A-horizon and the Dryas B/C-horizon, which increased by factors of 1.6 and 1.2, respectively, after a 5% increase in the water content (data not shown). This indicates that Dryas sites are the only sites being partly limited by the availability of water.

The production of CO_2 increased significantly (p < 0.05) in all samples after glucose addition, suggesting that soil respiration is also limited by the availability of easily-degradable carbon substrates (Fig. 3B). A maximum increase in CO_2 production after glucose addition was observed in A material from the Cassiope site increasing by a factor of 2 (Fig. 3B).

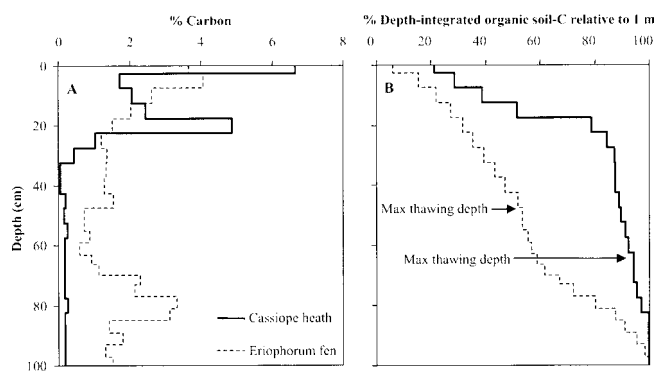C:N ratios have previously been used to relate carbon substrate

FIGURE 2. Concentrations and distribution of soil organic carbon in Cassiope and Eriophorum sites; given as (A) percent C at various depths and (B) accumulated organic C to a certain depth in percent of the total amount of organic carbon within the upper 1 m.

quality to decomposition, including Van Cleve (1974), who showed that C:N ratios were negatively correlated with organic matter decomposition (measured as percent weight loss over 2 yr) for a range of circumpolar tundra sites. C:N ratios in A-horizon material collected at Dryas, Cassiope, and Salix sites (Table 1) were similar (16.2 to 17.3), with the lowest value being observed at Cassiope sites (Fig. 4). Consequently, the C:N ratios alone cannot explain the lower activity of carbon sources at Cassiope sites. In contrast, C:N ratios of vegetation and litter at Cassiope sites were the highest detected of all vegetations types investigated (Fig. 4). The control of plant species on litter decomposition has previously been reported from Alaskan tundra (Hobbie, 1996), who showed that decomposition rates were more related to carbon quality than to nitrogen concentrations.

The temperature dependency of microbial soil respiration at Cassiope sites in Zackenberg has been investigated previously (Elberling and Brandt, 2002). In these studies, an exponential increase in soil respiration was observed with increasing temperature and was
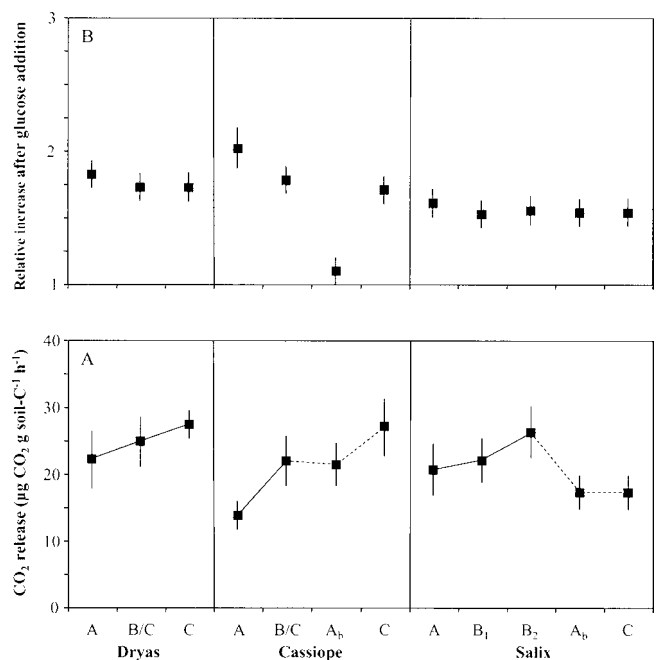

FIGURE 3. (A) CO_2 production rates per unit organic soil-C (at 26EC) as observed in individual soil horizons at Dryas, Cassiope, and Salix sites, and (B) the relative increase in CO_2 production rate after glucose addition. One standard deviation ($\pm$) of 3 replicates per horizon is shown as vertical lines.
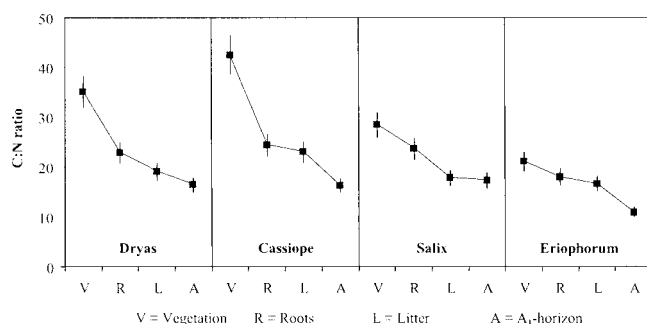
FIGURE 4. *C:N ratio for vegetation, litter, roots, and near-surface organic horizons (A-horizons) at the four vegetation sites.*

described using an Arrhenius-type equation. The increase in reaction rate per 10°C (Q_{10}) equaled 2.1 ($r^2 = 0.99$) for the A-horizon for the entire temperature range studied (–5°C to 27°C). For the temperature range most relevant for this study (0–10°C), the Q_{10} value equals 2.5. Results from the present study reveal that Q_{10} values estimated from rates observed at 0°C, 7°C, 21°C, and 26°C could not prove any significant deviations from the previously reported Q_{10} values. Consequently, it is assumed that CO_2 production rates observed in the laboratory for different vegetation types and depth intervals can be converted to in-situ rates by reducing the rate according to the observed Q_{10} value.

Additional CO_2 production rates were obtained from incubated litter material from Cassiope and Salix sites. Variations in production rates per volume sample were on the order of 100%; average rates were

7 and 7.5 times higher than measured rates in A-horizon material from Cassiope and Salix, respectively.

SOIL RESPIRATION AND CO_2 EFFLUXES DURING THE 2001 GROWING SEASON

Temporal trends in observed soil CO_2 effluxes, active layer depths, water contents, and soil temperatures during the 2001 growing season (Fig. 5) indicate that efflux variations during the 2-month period correlated relatively well with near-surface soil temperature (Fig. 6). Q_{10} estimates based on field observed soil temperatures at 2 cm and observed CO_2 effluxes show Q_{10} values equal to 3.3 ($r^2 = 0.8$) for Cassiope sites, 1.9 ($r^2 = 0.7$) for Dryas sites, and 2.7 ($r^2 = 0.7$) for Salix sites. The few measurements at Eriophorum sites did not allow Q_{10} estimates.

Significant variations in soil CO_2 effluxes were observed between plant communities (Table 1), with minimum effluxes observed at Cassiope sites (on average 0.52 ± 0.1 µmol CO_2 m^{-2} s^{-1}) and maximum effluxes observed at Eriophorum sites (on average 2.48 ± 0.5 µmol CO_2 m^{-2} s^{-1}). The range of these CO_2 fluxes is comparable with previously reported soil CO_2 effluxes in High Arctic Greenland (Christensen et al., 1998; Jones et al., 2000). Observed effluxes normalized to a temperature of, e.g., 10°C (Fig. 6) indicate that overall effluxes from Cassiope and Dryas are approximately the same, but a factor of 2 less than effluxes at Salix sites. In turn, effluxes at Salix sites are a factor of 2 less than effluxes from Eriophorum sites (Table 1).

Soil CO_2 efflux measurements on barren ground and manipulated sites after the removal of litter and the A-horizon were only possible for
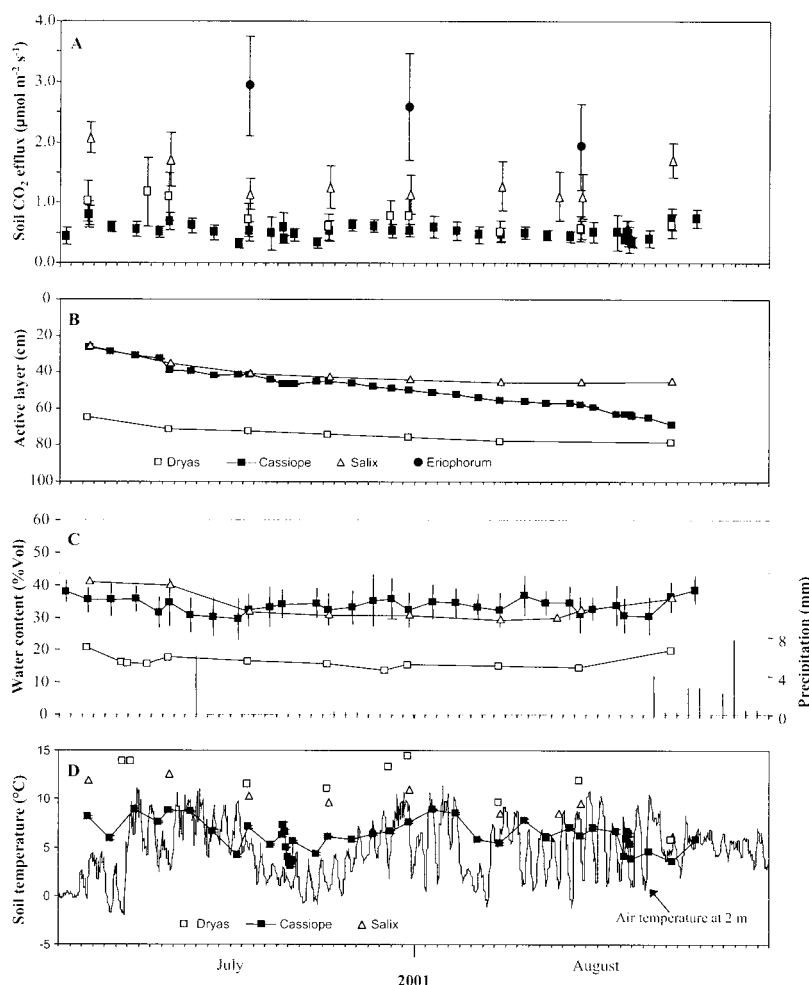

FIGURE 5. *Field observations during the 2001 growing season (July and August) including (A) average soil CO_2 effluxes shown as marks for each of the four vegetation types and one standard deviation ($\pm$) shown as vertical lines, (B) active layer depths, (C) precipitation and near-surface water contents with one standard deviation ($\pm$) shown for replicates at Cassiope sites (n = 17), and (D) air and soil temperatures.*
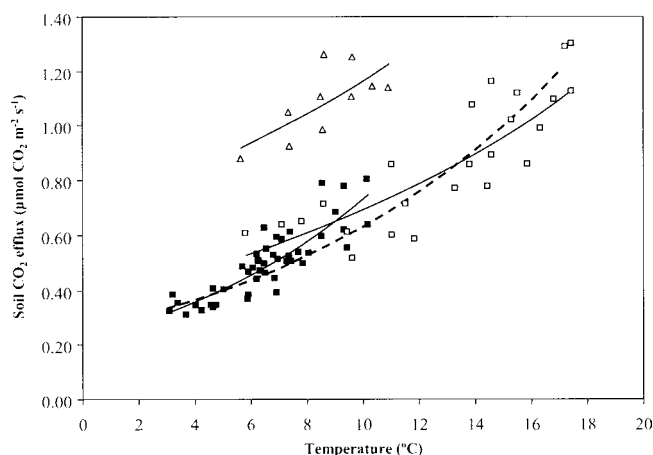
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FIGURE 6. *Observed soil CO_2 effluxes versus soil temperatures (at a depth of 2 cm). Exponential regression lines are shown as solid lines for Cassiope (solid squares, $0.2203e^{0.1196x}$; $r^2 = 0.8$; $Q_{10} = 3.3$, $R_{10} = 0.73$), Dryas (open squares, $0.3553e^{0.0662x}$, $r^2 = 0.7$; $Q_{10} = 1.9$; $R_{10} = 0.69$) and Salix (solid triangles, $0.4648e^{0.1013x}$; $r^2 = 0.7$; $Q_{10} = 2.7$; $R_{10} = 1.28$). The dashed line is based on laboratory studies previously reported for Cassiope (Elberling and Brandt, 2002).*

some of the vegetation types. Patches of barren ground large enough for measurements were not found at Salix and Eriophorum sites, and a litter layer in the proper sense was not detected at Dryas and Eriophorum sites. Soil CO_2 efflux measurements on nonvegetated sites at Dryas and Cassiope sites were 94% and 70% of ambient rates, respectively (Fig. 7). Removing the litter layer at Cassiope and Salix sites reduced the soil respiration rates to 70–75% compared to rates from ambient soils. Removing the litter layer and the A-horizon material reduced the rates to about 50% at Eriophorum sites and 18–20% at Cassiope and Dryas sites (Fig. 7). Standard deviations were generally much lower for manipulated sites, especially after the removal of litter material from the surface. This suggests that most of the variation observed in ambient replicates represents spatial variation in the actual amount of carbon available for decomposition in the litter layer.

SOIL CO_2 AND O_2 CONCENTRATIONS

Subsurface concentrations of CO_2 as observed from gas samplers were about 10–20 times that of atmospheric concentrations throughout the growing season, and concentrations generally increased with depth (Figs. 8 and 9). However, toward the permafrost boundary, CO_2 concentrations tended to decline. This decline throughout the growing seasons of 2000 and 2001 (Fig. 8) indicates that the concentrations are not representing true steady-state conditions. However, steady state seems to be a reasonable assumption in the upper part of the profiles. Concurrent oxygen profiles (data not shown) indicated that near-atmospheric O_2 concentrations always existed throughout the entire active layer (19–21%). However, it is worth noting that these gas concentrations represent the bulk concentrations in the larger air-filled pores, whereas smaller pores may have locally much higher or lower concentrations.

Discussion

LABORATORY VERSUS FIELD OBSERVED CO_2 PRODUCTION

During steady-state conditions, soil CO_2 effluxes observed in the field represent the combined effects of soil microbial and root respiration, whereas CO_2 production observed during laboratory incubations represent only soil microbial respiration. As reported by

Buchmann (2000), the ratio between the two respiration components is site-specific and may vary between 1:9 and 9:1. Comparing soil CO_2 effluxes from nonvegetation patches with ambient fluxes may indicate to what extent root respiration influences observed soil respiration rates. For nonvegetated sites within the Cassiope heath, effluxes were reduced to 70% compared to sites nearby with an average vegetation cover. However, when nonvegetated sites were compared to vegetated sites after the removal of litter material at both types of sites, the differences in rates were not significant (n = 5). Litter was almost absent at Dryas sites and effluxes from nonvegetated patches were about 95% compared to ambient condition. This suggests that microbial respiration dominated (>95%) the total soil CO_2 efflux as observed using dark chamber measurements at Cassiope and Dryas sites. However, the discussion on microbial versus plant-associated respiration is controversial because estimates of the importance of microbial respiration are partly related to the methodology used. It remains uncertain to what extent root respiration (and plant respiration in the chamber) is actually reduced during short-term dark chamber measurements. Using different methods, Billings et al. (1977) found root respiration to account for 66–90% of the total soil respiration in arctic soils dominated by Carex sp. and Eriophorum sp., whereas Oberbauer et al. (1992) concluded that microbial respiration accounted for a major portion of soil respiration in a similar site. The dominance of microbial respiration at the two dry sites in Zackenberg adds to a more general debate on the importance of microbial respiration versus plant-associated respiration, particularly in the context of a warming climate. Field experiments have shown that artificial warming enhances net ecosystem CO_2 efflux, primarily by stimulating microbial-driven decomposition of organic matter rather than by increasing plant-associated respiration (Welker et al., 1999; Grogan and Chapin, 2000). Thus, the high correlation between near-surface temperatures and effluxes observed in this study confirms the dominance of microbial respiration during short-term dark chamber measurements, but cannot be used to conclude that microbial respiration dominates in general.

The apparent dominance of microbial respiration at Cassiope and Dryas sites makes it possible to compare actual depth-specific soil respiration results obtained in the laboratory with field observation of total CO_2 effluxes from the soil surface. Salix sites are included in this comparison even though the assumed dominance of microbial respiration may not be valid. The relative importance of soil layers to producing CO_2 is evaluated assuming steady-state conditions, which implies that the flux at the permafrost table is zero and, consequently, that the total production of CO_2 in the profile equals the efflux of CO_2 to the atmosphere for a certain period of time. For that purpose, CO_2
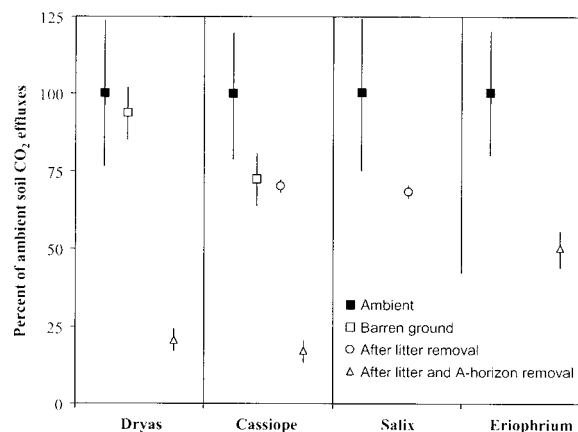

FIGURE 7. *Observed soil CO_2 effluxes at Dryas and Cassiope sites without vegetation (more than 20 cm to the nearest plant) and after the removal of the litter layer (0–2 cm) and the A-horizon (5–7 cm).*
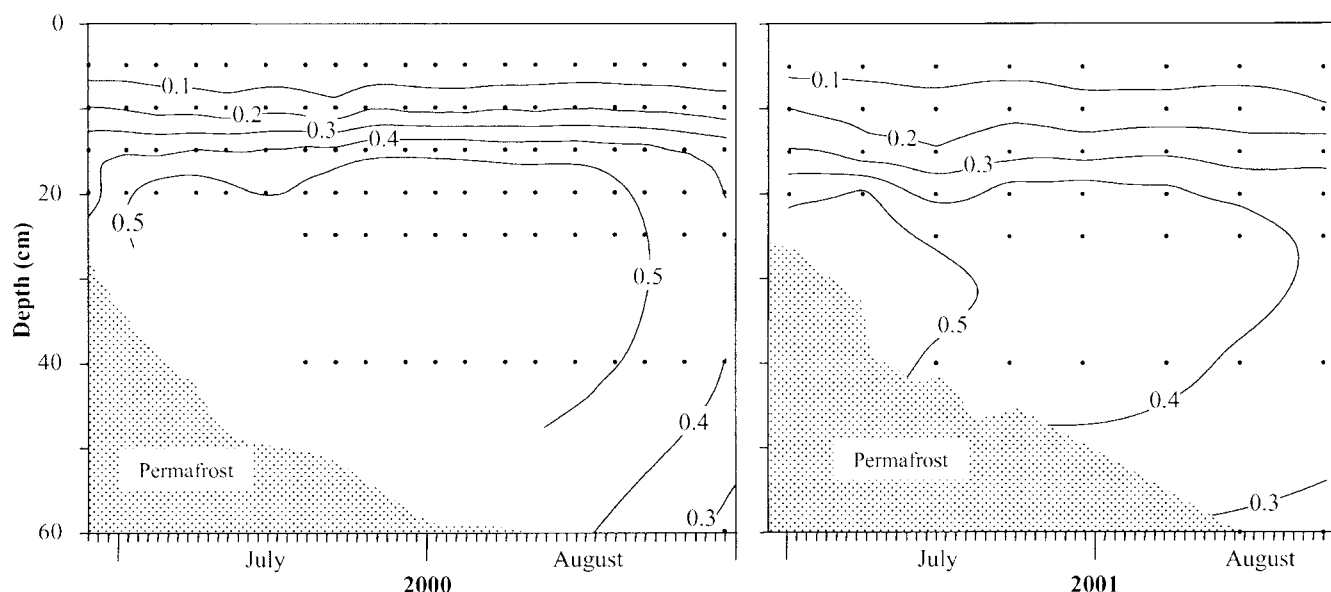
FIGURE 8.   Observed soil pore gas CO_2 concentrations (%) in a Cassiope soil profile during the 2000 and 2001 growing seasons (measurements are shown as dots).

production rates observed from soil samples have been expressed per volume soil (Fig. 9E) and adjusted to field-observed temperatures (Fig. 9D). Assuming steady-state conditions, the total CO_2 production from the surface to the permafrost boundary can be estimated as the integrated CO_2 production profile. Taking into account the fraction of soil respiration in the litter layer to the total soil respiration, 0% for Dryas sites and 30% for Cassiope and Salix sites, CO_2 production profiles can be constructed. However, the CO_2 distribution within the soil profile is not only a result of CO_2 production but also of soil diffusivity being a function of the water content (Fig. 9C) and porosity, among other parameters (Eqation 2). In order to evaluate the relationship between observed CO_2 concentration profiles, measured

CO_2 production profiles, and soil CO_2 effluxes, the diffusion model given by Equations 1 and 2 was used.

SIMULATING SOIL CO_2 CONCENTRATION PROFILES AND EFFLUXES

Simulated results shown in Figs. 9A and 9B are based on data collected on 2 August 1999. Only steady-state CO_2 concentration profiles are simulated, which explains why attempts to simulate the entire CO_2 concentration profile, including observations below 30 cm, failed for Cassiope and Salix sites. It is assumed that low CO_2 concentrations near the permafrost boundary reflect a non-steady-state
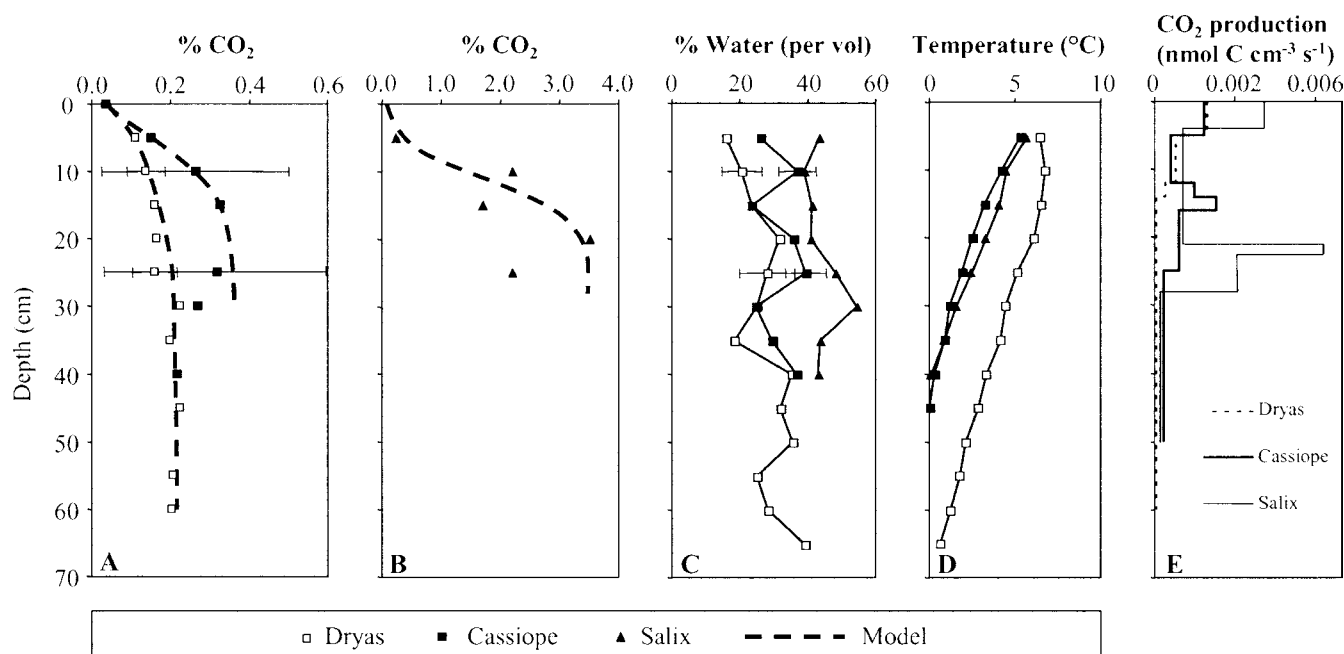

FIGURE 9.   Field measurements of (A and B) soil CO_2 concentration profiles, (C) water contents, and (D) soil temperatures at Dryas, Cassiope, and Salix sites as observed on 2 August 1999. CO_2 production profiles (E) as observed in the laboratory have been used as input to a diffusion model, and the resulting model outputs are shown as solid lines for Dryas and Cassiope (A) and Salix (B). One standard deviation (±) based on 16 replicates of CO_2 concentrations and water contents observed at two depths at Dryas and Cassiope sites is shown as horizontal lines (A).

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situation where CO_2 diffuses throughout the growing season from soil layers above as the soil profile thaws. But predicted concentrations within the upper 30 cm agree well the observed concentrations ($r^2 = 0.88$ for Cassiope sites, 0.98 for Dryas sites, and 0.72 for Salix sites). Thus, it is concluded that CO_2 production profiles (Fig. 9E) provide reliable estimates of the relatively depth-dependent soil CO_2 production. It should be noted further (Fig. 9E) that CO_2 production in the buried A_b horizon represents up to 20% of the total active layer of CO_2 production in August. However, most of the time the decomposition within the buried layer is probably further limited by temperature and higher water content as compared to the surface A-horizon. Also the A_b horizon must have been subject to very slow decomposition rates since deposited a few thousand years ago (Christiansen et al., 2002), and the present situation is therefore unlikely to represent long-term steady-state conditions.

The simulated total CO_2 production integrated to a depth of 40 cm was within 1 standard deviation (SD) of observed effluxes during the first week of August 1999. However, the definition of the litter layer is quite uncertain because the thickness and reactivity were highly variable in the field. In the modeling, the litter layer was included with the average thickness observed, a reactivity seven times that of the A-horizon and a high diffusion coefficient only limited by the actual volume of air-filled porosity. Allowing the litter thickness and reactivity to vary within the 1 SD of observations, a perfect match between simulated and observed effluxes could be obtained. Excluding litter layers in the modeling had very little effect on soil CO_2 concentrations but caused reduced CO_2 effluxes (to about 70%). This important ecological significance of litter is consistent with other studies from the arctic (e.g., Fahnestock et al., 2000). This reduction was consistent with field observations at manipulated sites (Fig. 7) and in agreement with an expected high diffusivity coefficient of litter material. This further explains why the litter layer in some vegetation types (Cassiope and Salix) is important for the overall release of CO_2 to the atmosphere without having a similar importance for soil CO_2 concentration profiles. This also explains general problems associated with applying 1-D soil-diffusion-models to estimate soil gas effluxes and that attempts to simulate temporal trends in soil CO_2 effluxes in the present study failed (simulations not shown). As shown in Fig. 8, the CO_2 concentration profile remained fairly constant in the upper 20 cm throughout the growing season despite of pronounced seasonal trends in soil CO_2 effluxes (Figs. 5 and 6).

CARBON RESERVOIRS IN THE ARCTIC REGION—ACTIVE AND INACTIVE POOLS

In most arctic ecosystems, easily decomposable organic materials are found in near-surface horizons (Van Cleve, 1974), and the high proportion of organic carbon stored in the upper part of the soil profile has been noted for a range of high-latitude tundra soils (Post et al., 1982). However, the importance of carbon in both A- and A_b-horizons found in this study is probably a more site-specific characteristic, although it may also apply to other soils. A comparison of substrate quality and CO_2 production rates in A- and A_b-horizons is complex. The source of carbon in buried layers was most likely different from the plant types found at specific sites today as indicated by abundant birch leaves found in the A_b-horizon of previously described Podzols (Christiansen et al., 2002). It is worth noting that A_b-material at Cassiope sites seems significantly more reactive than material in present-day near-surface A-horizon, whereas the opposite seems to be the case for Salix sites (Fig. 3).

For evaluating the organic carbon reservoirs distributed within the Zackenberg valley it is important to evaluate the controls on organic matter decomposition for several organic carbon reservoirs: active, potential, and inactive pools of which some seem closely linked to specific plant communities and hydrological conditions. This study only allows a descriptive evaluation but is important to show the interacting parameters that may determine whether an ecosystem (soil-plant system) will become a future net source or sink for organic carbon. Furthermore, it illustrates that changes due to climate changes are unlikely to be uniform across the arctic tundra landscape (Welker et al., 2000).

Dryas sites contain a small amount of the total ecosystem organic C (Table 1), and respiration rates are limited by the C-substrate, temperatures, and probably also water in some periods. Compared to Dryas, respiration rates at Cassiope sites are more limited by the quality of C-substrate (Fig. 3) and more limited by temperature (Fig. 6) due to a higher water content. But because of the larger quantities of organic matter at Cassiope sites compared to Dryas sites (thicker A-horizon), the overall soil CO_2 efflux at these two sites at a given temperature is almost the same (Fig. 6). Decreasing water contents and increasing temperatures will likely lead to a positive feedback in terms of near-surface soil respiration at Cassiope sites, whereas the net effect on Dryas sites is more uncertain. Increasing temperatures will provide a positive feedback, but the lack of water can be a limiting factor as discussed by Welker et al. (2000). Cassiope sites store large quantities of organic carbon in potential pools of easily degradable C below the present A-horizon (Fig. 1), which is presently only contributing less than 20% of the soil effluxes. The effects of global warming and a thicker active layer on soil CO_2 effluxes, e.g., from Cassiope sites, can be expected to be even higher than predicted using only the temperature sensitivity relationship (Fig. 6), because CO_2 production from the decomposition of carbon stored in buried A-horizons will be an additional source of CO_2. Salix sites are also substrate-limited and hold very large quantities of organic matter (Table 1), giving rise to high effluxes (Fig. 6) and maximum soil CO_2 concentrations (Fig. 9B). Decomposition of potential pools is sensitive to the water content, as decreasing water contents are likely to increase both the availability of oxygen and soil temperatures and thereby increase decomposition. In that respect, Eriophorum sites are more extreme, holding an active carbon pool of the most reactive C-source and presently giving rise to maximum soil effluxes throughout the growing season (Fig. 5). As Eriophorum sites are partly water saturated throughout the growing season, increasing air temperatures will enhance soil respiration directly but may also indirectly (and in combination with changes in water balance) influence the depth to the water table and thereby change soil redox conditions. A shift from anaerobic to aerobic conditions stops the production of methane but generally increases CO_2 production rates (Chapman and Thurlow, 1996; Blodau and More, 2003). Finally, changes in the hydrological regime are closely related to changes in winter precipitation, snow redistribution, and the overall wind regime (Zimov et al., 1996; Fahnestock et al., 1998, 1999).

From the discussion above it appears that temperature, water content, and substrate quality are all crucial parameters controlling the presently observed spatial variation in CO_2 dynamics in Zackenberg. Changes in these parameters will rather quickly and directly affect the active soil carbon pool and therefore the soil carbon dynamics. Indirect and more slowly responding effects may also have a significant impact on the soil carbon pool. Such effects are likely to be the result of changes on a landscape scale, e.g., changing wind pattern, snow distribution, draining, and formation of thermo casts (Evans et al., 1989; Hobbie et al., 2000). A final indirect and more slowly responding climatic effect is the shift/transition in plant community structure and area distribution of vegetation types (Oberbauer et al., 1996; Grogan and Chapin, 2000). It is worth noting that the most important effects may be the slowly responding and indirect effects which are poorly described for the arctic and which presently make it difficult to provide reliable long-term estimates for global change feedback in the arctic.

CONCLUSIONS

Several biogeochemical and physical factors and their interactions affect soil organic carbon reservoirs and mineralization. This study has focused on the interactions between depth-specific distribution and reactivity of carbon substrate and vegetation types. From laboratory and field observations as well as modeling, the following conclusions can be made. More than 95% of total ecosystem-C was found as potentially reactive soil organic carbon pools. Sampling in order to quantify total C reservoirs requires a procedure that takes into account site-specific active layer development, e.g., the occurrence of buried surface layers. The simulated CO_2 activity profiles suggest that buried old surface layers (A_b) are presently important for the overall soil CO_2 dynamics. Decomposition within the litter layer influences strongly on total soil CO_2 fluxes observed, contributing up to 30% of the total CO_2 fluxes to the atmosphere but without having the equivalent importance on the subsurface CO_2 distribution. Furthermore, the spatial distribution of litter material seems to be responsible for most of the spatial variations of observed soil CO_2 effluxes.

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