Oecologia (1992) 92:568–577

Oecologia

Environmental effects on CO_2 efflux from riparian tundra in the northern foothills of the Brooks Range, Alaska, USA

S.F. Oberbauer[1], C.T. Gillespie[2], W. Cheng[2], R. Gebauer[2], A. Sala Serra[2], and J.D. Tenhunen[3]

[1] Department of Biological Sciences, Florida International University, Miami, FL 33199, USA
[2] Systems Ecology Research Group, College of Sciences, San Diego State University, San Diego, CA 92182, USA
[3] Bayreuther Institut für Ökosystemforschung (BITÖK), Universität Bayreuth, W-8580 Bayreuth, Federal Republic of Germany

Received February 2, 1992 / Accepted in revised form July 6, 1992

Summary. Carbon dioxide efflux and soil microenvironmental factors were measured diurnally in *Carex aquatilus*- and *Eriophorum angustifolium*-dominated riparian tundra communities to determine the relative importance of soil environmental factors controlling ecosystem carbon dioxide exchange with the atmosphere. Measurements were made weekly between 18 June and 24 July 1990. Diurnal patterns in carbon dioxide efflux were best explained by changes in soil temperature, while seasonal changes in efflux were correlated with changes in depth to water table, depth to frozen soil and soil moisture. Carbon dioxide efflux rates were lowest early in the growing season when high water tables and low soil temperatures limited microbial and root activity. Individual rainfall events that raised the water table were found to strongly reduce carbon dioxide efflux. As the growing season progressed, rainfall was low and depth to water table and soil temperatures increased. In response, carbon dioxide efflux increased strongly, attaining rates late in the season of approximately 10 g CO_2 m^{-2} day^{-1}. These rates are as high as maxima recorded for other arctic sites. A mathematical model is developed which demonstrates that soil temperature and depth to water table may be used as efficient predictors of ecosystem CO_2 efflux in this habitat. In parallel with the field measurements of CO_2 efflux, microbial respiration was studied in the laboratory as a function of temperature and water content. Estimates of microbial respiration per square meter under field conditions were made by adjusting for potential respiring soil volume as water table changed and using measured soil temperatures. The results indicate that the effect of these factors on microbial respiration may explain a large part of the diurnal and seasonal variation observed in CO_2 efflux. As in coastal tundra sites, environmental changes that alter water table depth in riparian tundra communities will have large effects on ecosystem CO_2 efflux and carbon balance.

Key words: Arctic tundra – Depth of thaw – Ecosystem carbon exchange – Permafrost – Soil respiration

Correspondence to: S.F. Oberbauer

Although riparian communities occupy only a small proportion of the foothill tundra north of the Brooks Range in arctic Alaska, these communities are extremely important from the perspective of landscape processes. While most tundra communities obtain nutrients primarily from decomposition and atmospheric deposition, streamside communities also receive nutrients in runoff from upslope areas (Kummerow et al. 1987). Riparian areas are the last terrestrial filter for nutrients before they are lost to the aquatic system. Nutrient uptake by mass flow is facilitated as compared to other tundra communities because plants are frequently rooted in flowing water (Chapin et al. 1988). Furthermore, the transfer of thermal energy from flowing water results in greater thaw depths, hence larger rooting volumes, than found in other moist tundra communities. Riparian communities in foothill tundra are similar to coastal wet tundra in that the belowground microenvironment is dominated by water tables close to the surface. Consequently, soils are frequently anaerobic and decomposition limited.

Water table appears to be one of the primary controls on CO_2 losses in wet tundra and bog systems (Billings et al. 1982, 1983; Peterson et al. 1984; Luken and Billings 1985; Moore 1989). For example, Billings et al. (1983), in a study using tundra microcosms from Barrow, Alaska, estimated an annual net gain of 119 g CO_2 m^{-2} when the water table was at the surface, but an annual net loss of 476 g CO_2 m^{-2} when the water table was 10 cm below the surface. As a result of high water tables, wet tundra and bog areas have a potential for lower carbon losses than drier tundra communities. Thus, given similar productivities (Shaver and Chapin 1991), the potential for carbon storage is greater in riparian areas than in drier, upland tundra.

Considerable effort has been made to assess the carbon exchange from tundra and bog systems because of the large amounts of stored carbon in these systems and the implications of release of this carbon for global climate (Billings et al. 1977, 1978, 1982, 1983; Peterson et al. 1984; Luken and Billings 1985; Moore and Knowles 1989; Grulke et al. 1990). Temperatures in the Arctic are expected to sharply increase with climate warming, raising

the possibility of increased decomposition leading to a positive feedback for global warming. Climate-induced alterations in the water table of tundra peatlands may be of equal or greater importance than temperature for carbon balance (Moore and Knowles 1989; Gorham 1991). Cottongrass tussock tundra communities in the foothills of the Brooks Range may have already become a source of CO_2 as a result of a combination of these factors (Oechel and Billings 1992).

Although belowground conditions of riparian tundra are similar to those of coastal wet tundra, riparian areas in the Foothill Province of the North Slope of Alaska have received relatively little attention from the perspective of carbon losses and storage. Soils in riparian areas are among the deepest and have the greatest quantities of stored carbon among the vegetation communities of the foothill region (Walker et al. 1989), so they are of particular importance from the perspective of carbon balance. The objectives of this study were: (1) to assess the potential rates of CO_2 efflux from riparian tundra throughout the growing season, and (2) to determine those environmental factors that most strongly affect potential CO_2 efflux. CO_2 efflux occurs simultaneously with photosynthetic fixation, and because a continuous photoperiod persists throughout the growing season in tundra systems, a direct measure of actual CO_2 efflux is not feasible. Consequently, to estimate CO_2 effluxes, we used a dark-chamber technique (Peterson and Billings 1975), which provides a measure of potential community CO_2 losses including respiration due to aboveground plant biomass but excluding that of vertebrates. This study was made in the context of an overall examination of carbon losses and their controls in an arctic watershed along a toposequence of plant communities from lichen-heath vegetation to tussock tundra and riparian vegetation.

Material and methods

Study site

This study was conducted at the U.S. Department of Energy R4D study site in the Imnavait Creek watershed along the Dalton highway in the northern foothills of the Philip Smith Mountains in arctic Alaska (68°38'N, 149°25'W). The topography, soils, and vegetation of the site have been described in detail by Walker et al. (1989). Measurements were conducted in riparian vegetation on the north edge of Imnavait Creek. The vegetation was dominated by the graminoids *Carex aquatilis* Whalenb., *Eriophorum scheuzeri* Hoppe and *E. angustifolium* Honck., with lesser amounts of the shrubs *Andromeda polifolia* L. and *Salix fuscescens* Anderss.

Carbon dioxide efflux measurements were made within six plots (2×10 m) that were randomly selected along a linear transect adjacent to Imnavait Creek. These plots were dominated by *Carex aquatilis* and will be referred to as *Carex* plots. Soils in the *Carex* plots were predominantly pergelic cryofibrists with organic horizons extending below the depth of thaw. Decomposing *Sphagnum* and sedge leaves and roots made up the bulk of the material. A distinct transition from aerated to anaerobic conditions occurred from 5–15 cm indicated by a shift from yellow-brown to a dark brown or black horizon. For comparison with the more prevalent streamside vegetation, two additional plots were established in pure stands of *Eriophorum angustifolium* (*Eriophorum* plots). These sites were located at the base of the slope where water tracks merge with Imnavait Creek (Walker et al. 1989). The soils were histic pergelic cryaquepts with shallow (2–5 cm), loose organic horizons comprised of decomposing sedge leaves and roots above a gray silty clay that probably resulted from deposition from downslope water flow. These soils are frequently flooded and the lower portion of the organic layer was noticeably anaerobic. Soil bulk density for the upper 5 cm of soil and live plant aboveground biomass with full vegetation development are shown in Table 1. All work was done from elevated aluminum bridges with fiberglass legs to minimize damage to the plots from trampling and physical disturbance of the substrate that might enhance the release of CO_2.

Site environments

Microclimate was monitored continuously at a single site in the creek basin during the 1990 growing season to obtain a general description of environmental conditions. Precipitation, photosynthetic photon flux density, humidity, air temperature, and soil temperatures at 1, 5, 10, and 20 cm below the moss surface were measured. Sensors were read with a Campbell 21X micrologger (Campbell Scientific, Logan, Utah) with 5-min scans and the data were stored as hourly averages.

In addition to the microclimate monitoring for the basin, quantitative measurements of soil environmental factors were made weekly for each plot. Measurements included depth to water table, soil solution pH, and soil oxygen diffusion rate. Depth to water table below the soil surface was measured at three locations per plot in wells made of perforated polyvinyl chloride (pvc) pipes. pH was measured within the wells using glass membrane electrodes and a portable pH/mv meter. Depth of thaw was measured at three marked locations per plot using a graduated stainless rod. Oxygen diffusion rate was measured polarographically at various depths with a soil oxygen diffusion ratemeter (Model D, Jensen Instruments, Tacoma Washington) and platinum electrodes (Letey and Stolzy 1964). One depth profile for oxygen diffusion rate was established per plot on a weekly basis. A point in the profile was taken to be aerated when readings were greater than a threshold value of 0.25 μA, which corresponds to a oxygen diffusion rate of 0.015 μg O_2 cm^{-2} min^{-1}.

CO_2 efflux

Efflux of CO_2 was measured using a system similar to that described by Oberbauer et al. (1991). Measurements were made weekly on six

Table 1. Mean soil bulk density (g soil dry weight cm^{-3}, 0–5 cm depth, $n=6$), soil carbon (percentage soil dry weight, 0–5 cm depth, $n=6$), seasonal average soil moisture (g H_2O g^{-1} soil dry weight, 0–5 cm depth, $n=36$ for *Carex*, $n=12$ for *Eriophorum*), and moss biomass (g m^{-2}), and aboveground vascular plant biomass (g dry weight m^{-2}, $n=12$ for *Carex*, 4 for *Eriophorum*) ± 1 SE for *Carex* and *Eriophorum* plots

Community	Bulk density	Percent carbon	Soil moisture	Moss biomass	Vascular biomass
Carex	0.078 (0.005)	29.8 (2.8)	10.91 (0.63)	216 (60)	54 (10)
Eriophorum	0.153 (0.006)	20.0 (1.5)	4.48 (0.38)	0 (0)	132 (45)

Biomass values are derived from that measured in sample tubes on 24 July

dates between 18 June and 24 July 1990, a period that covers the majority of the active plant growth period. Sampling was conducted over a 24-h period at 4-h intervals starting at 2000 hours. Carbon dioxide flux was measured as the transient rate of change of CO_2 concentration in sealed opaque white pvc tubes inserted into the soil. The edges of the tubes (8 cm inner diameter) were sharpened to aid insertion into the soil. In addition, a serrated knife was used to make a circular cut into the soil in which the tube was inserted to minimize soil compression. Because destructive sampling of biomass and soil moisture followed completion of the measurements for each sampling date, sample tubes were relocated for each sample date. Sample tubes were implanted 10–15 cm deep into the soil at least 5 days in advance of measurements in order to minimize CO_2 release by physical processes or from damaged tissues. For the *Carex* plots, two tubes were located randomly along the edge of each plot providing a total of 12 tubes per sample date in the *Carex* community. For the *Eriophorum* plots, which were on slight inclines, tubes were located sequentially from the low end of the plots to minimize effects on samples taken on later dates. A total of four sample tubes were used per sample date in the *Eriophorum* community. The typical vegetation included within a single sample tube from the *Carex* plots included a *Sphagnum* mat with several sedge tillers and occasional small dicots. In the *Eriophorum* plots, spacing of tillers was such that no more than one tiller and frequently no tillers were included within the sample tubes.

The sample tubes remained open until immediately preceding a measurement when they were sealed closed with a pvc cap. A gas-tight seal was provided by contact between the polished ends of the tubes and a ring of closed-cell foam mounted on the inside of the cap; an 800-g weight gently placed on top of the cap aided sealing. Inlet and outlet ports were located near the center of the chamber cap. The inlet port was extended within the chamber with a 12-cm piece of tubing so that air entered near the bottom of the chamber but was removed near the top. This arrangement maximized mixing of chamber air while minimizing the possibility that any water at the bottom of the chamber might enter the outlet air line. We used an unventilated chamber design because previous experience had indicated that vigorous stirring of the air and/or motor vibration releases CO_2 trapped within soil air spaces resulting in abnormally high efflux rates. A flow rate of 28 $cm^3\ s^{-1}$ was used in all cases. Chamber volumes depended on the height of the tube above the soil and ranged from 600 to 1300 cm^3 with an average of about 900 cm^3. Chamber volume was determined for each measurement based on the volume of air space above the soil (or standing water) with the assumption that soil air space was negligible relative to the total volume of the chamber. Observations were begun when complete mixing of the system volume was judged to occur as indicated by a steady rate of change in CO_2 concentration, which was usually reached in 1–3 min. The change in CO_2 concentration was monitored over a 30-s interval using a Li-Cor Li-6200 portable gas exchange system (Li-Cor, Inc, Lincoln, Nebraska). Changes in CO_2 concentration over the period averaged approximately 5 $\mu l\ l^{-1}$. Three observations were made per sample tube at each sampling interval to verify that complete mixing of the system air volume had been attained as indicated by similar readings of efflux rate for the three observation intervals. If readings from the three intervals were not stable, the procedure was repeated. Typically the last two observations were within $\pm 5\%$ of each other.

Simultaneous with the CO_2 efflux measurement, soil temperature was measured within 2–3 cm of each soil tube using copper-constantan thermocouples made of 23 gauge wire threaded through 4 mm-diameter wooden dowels and inserted to 1, 5, and 10 cm depth. Thermocouples were placed in the soil several days in advance of measurements. Temperatures were read with a Campbell 21X micrologger using the internal panel reference.

Following completion of a 24-h sampling period, the depth of thaw and depth to water table with respect to the soil surface were recorded for each sample tube. Depths to water table were measured by observing to what level water filled in the hole resulting from removal of the soil within the sample tube. In practice, however, depths to water table greater than 25 cm, such as were found on the last sample date, could not be measured by this method and were treated as equal to 25 cm. Depth of thaw was determined using a graduated stainless steel rod inserted into the soil until frozen soil was encountered. A sample of the upper 5 cm of soil was placed in soil tins for determination of percent water content on a dry weight basis. The aboveground biomass within each tube was harvested and separated into mosses and vascular plants. Both soil tins and plant biomass were oven dried at 80° C for 48 h or more before determination of dry weight. Soil moisture on a volumetric basis (g H_2O cm^{-3} soil) was calculated as the product of soil water content on a soil dry weight basis and soil bulk density (Table 1). Soil bulk densities were determined from 15×15 cm blocks of soil that were cut out, dried at 80° C, and weighed.

Rate data analysis

The average of the last two of the three observations made for each sample tube during each sample period were taken as the final flux rate. The flux rates from the two tubes per plot were treated as subsamples and averaged to calculate a mean value per plot for each sampling period. All calculations of daily and seasonal means and their standard errors are based on such averaged plot values. During some measurements (less than five per measurement date) it was apparent that the process of sampling disturbed CO_2 held in the soil and therefore resulted in abnormally high and unstable efflux rates. These instances were noted and samples were removed from the analyses. Seasonal differences were tested using the mean daily CO_2 efflux for each plot on a given sample date using a two-way analysis of variance. The correlations between soil environmental factors and CO_2 efflux at different sample dates of the season were assessed using Spearman rank correlation.

Regression modelling

The CO_2 efflux data were fitted to a model (Eq. 1) incorporating the Arrhenius function for temperature and an asymptotic function for depth to water table with the intent to develop a simple mathematical description for CO_2 efflux from riparian tundra in response to soil environmental factors. An asymptotic model was chosen based on preliminary examination of the data which suggested that at depths greater than 10 cm, depth to water table had little effect.

$$R_S = C \cdot e^{(-E/R \cdot T_k)} \cdot e^{(S_{wt})} \tag{1}$$

where C is a constant providing units of $\mu mol\ m^{-2}\ s^{-1}$, R_S is rate of CO_2 efflux ($\mu mol\ m^{-2}\ s^{-1}$), R is the gas constant (8.31 $J\ mol^{-1}\ °K^{-1}$), T_k is the soil temperature (K) at 1 cm depth, E is the apparent activation energy ($J\ mol^{-1}$), and S_{wt} is an empirical function representing the effect of soil water table. The parameter S_{wt} was determined as a function of soil water table.

$$S_{wt} = A \cdot W_t / (W_t + B) \tag{2}$$

where W_t is depth to water table below soil surface (cm) and A and B are regression coefficients. Parameters E, A, and B were estimated using nonlinear least-squares regression.

Microbial respiration

To estimate the contribution of microbes to system CO_2 efflux, we measured basal microbial respiration rate throughout the season and then scaled it for the effects of soil temperature and depth to water table. Basal respiration of soil samples from each of the plots was measured in our field laboratory at weekly intervals during the study period under standard conditions following procedures of Cheng and Virginia (1992). The method is based on a modification of the techniques developed by Anderson and Domsch (1978) and

Cheng and Coleman (1989). For these measurements, soil samples of 0–5 cm depth below the green moss layer were extracted, the live roots and rhizomes were removed by hand, and the soil homogenized. Care was taken to remove as much of the fine root material as practical, but some fine roots undoubtedly remained. Fifteen grams of soil material were placed into sealed 125 ml Erlenmeyer flasks attached to an open gas exchange system. The depth of soil in the flasks was usually less than 2 cm. Because the soils were always moist when field collected, measurements were taken using the natural hydration levels. Incubation temperature was maintained by partially submerging the flasks in a water bath maintained at 22° C. Carbon dioxide concentrations were measured with an infrared gas analyzer (Li-Cor 6251, Li-Cor, Inc, Lincoln, Nebraska) using a flow rate of 0.18 l min^{-1}. Preliminary measurements indicated that effluxes stabilized within the first 20–30 min and maintained a stable rate for 4–5 h following sealing of the flasks. To standardize the measurements, respiration readings were taken 40 min after sample placement in the gas exchange system. The short time that samples were in the flasks and low flow rates used precluded significant dehydration of the samples during measurement. Soil samples were measured within 1 week of collection. Significant seasonal changes in basal respiration rate between sampling dates were not detected.

Temperature response curves of microbial respiration were used to scale the basal microbial respiration rate to soil temperatures measured in the field. To obtain these response curves, soil samples from 0–5 cm depth were collected in mid-July, placed in sealed plastic bags, and shipped under refrigeration to the laboratory in San Diego. Samples were stored at 2–5° C for 30 days until measurements could be made. Similarity between respiration rates in the laboratory and measurements of basal respiration of fresh material in the field at comparable temperatures indicated that samples were not detrimentally affected by the storage period (mean values at 22° C were within 10% of each other). Sample preparation and measurement followed procedures described above for the basal measurements. Preliminary experiments indicated that homogenized riparian soils, similar to those found under *Carex*, are insensitive to water content between 700 and 1500% water (Cheng et al. unpublished), which spans the range of holding capacity and water contents measured under field conditions (Fig. 1). Respiration of the samples was determined at 5, 10, 15, 25, and 35° C and a regression equation was computed using linear regression of log-transformed data (r^2 was greater than or equal to 0.99 in all cases).

Estimates of microbial respiration for each field sampling date were made by adjusting the mean seasonal basal respiration rate for the effect of field soil temperatures and water table. The temperature effect was applied by adjusting the intercept of the temperature response so that the rate at 22° C corresponded to the mean seasonal basal rate measured at 22° C. The mean of soil temperatures taken at 1 and 5 cm depth during field measurements was then input into the adjusted temperature response curve to estimate a respiration rate for field soil temperatures. Microbial respiration per gram of soil was converted to a per square meter basis by multiplying by the soil bulk density and the volume of soil in 1 m^2 to a depth of 10 cm. The effect of water table (as a surrogate for soil aeration) was included by multiplying the estimated m^2 rate by the percentage reduction from the maximum predicted by Eq. 1 at depths to water table shallower than 10 cm. While this rate per square meter is based on bulk density and respiration characteristics determined only for samples taken from 0–5 cm depth, subsequent examination of the profile in these soils indicated that as respiration rate per gram dry weight of soil decreases with depth, bulk density increases and tends to offset changes on a soil volume basis.

Results

Seasonal patterns

Depth to frozen soil in the *Carex* plots increased linearly from 18 June to 24 July (Fig. 1A). In contrast, thaw depth in the *Eriophorum* plots was shallow early in the season but increased rapidly in midseason and ultimately attained a greater mean depth than the *Carex* plots. Daily mean soil temperatures recorded for 5 cm depth adjacent to the soil tubes showed an increasing trend over the season in both communities but were clearly influenced by diurnal weather factors (Fig. 1B). Soil temperatures at 5 cm depth were greater in the *Carex* plots than in the *Eriophorum* plots despite the greater thaw depth in the *Eriophorum* plots. The greater thaw depths in the *Eriophorum* plots probably resulted from greater thermal conductivity of the mineral soils and the thermal energy delivered in water which constantly flowed through these sites downslope from water tracks. The combination of moving water and melting of the underlying permafrost in these soils simultaneously buffers them against variations in surface temperature (Harley et al. 1989) and resulted in lower soil temperatures than the *Carex* plots.

Depth to water table increased over the season for both communities and was greater for the *Carex* plots than for the *Eriophorum* plots for most of the sample period (Fig. 1C). Overall, the distance of water table from the surface paralleled the seasonal increase in thaw depth. In the *Carex* plots, the depth of standing water above frozen soil was approximately 20 cm for much of the season except when the water table rose following a large rainfall on 2 July (Fig. 1C, 1D). Soil water content in the upper 5 cm showed an overall seasonal decrease in the *Carex* plots reflecting the lowering of the water table, with temporary fluctuations due to rainfall on 2 July (Fig. 1E). In contrast, soil water content in the *Eriophorum* plots was more or less constant throughout the season, with the exception of 9–10 July, when water content appeared higher than other sampling dates. This abnormally high value is an artifact of the chance selection of samples composed entirely of organic soil instead of the usual organic-mineral mixture encountered for other sample dates. As a result of these low bulk density samples, the measured water content on 9–10 July was much higher than for other sample dates. Likewise, the overall lower soil moisture values for the *Eriophorum* plots resulted from the greater bulk density of the soil in these plots compared to that of the *Carex* plots and do not necessarily reflect a difference in water availability. Changes in aerated soil depth were correlated with changes in depth to water (Fig. 1C, 1F). The methods which we utilized suggested that aeration changed only near the surface, even when water table decreased to much lower levels. Aerated soil depths were greater for the *Carex* plots than the *Eriophorum* plots. Soil solution pH was nearly constant for both vegetations and was slightly higher for the *Eriophorum* plots (Fig. 1G).

Seasonal changes in CO_2 efflux (Fig. 1H) mirrored changes in the depth to water table (Fig. 1C) and to a lesser extent, soil moisture and aerated depth (Fig. 1E, 1F). Rates were low early in the season when water tables were high, increased as water table fell, only to decrease in response to the higher water table resulting from the 14 mm rainfall on 2 July. After 2–3 July, CO_2 effluxes again increased as depth to water table fell. The seasonal patterns of CO_2 efflux for the two sites were similar though rates in the *Carex* plots tended to be greater than

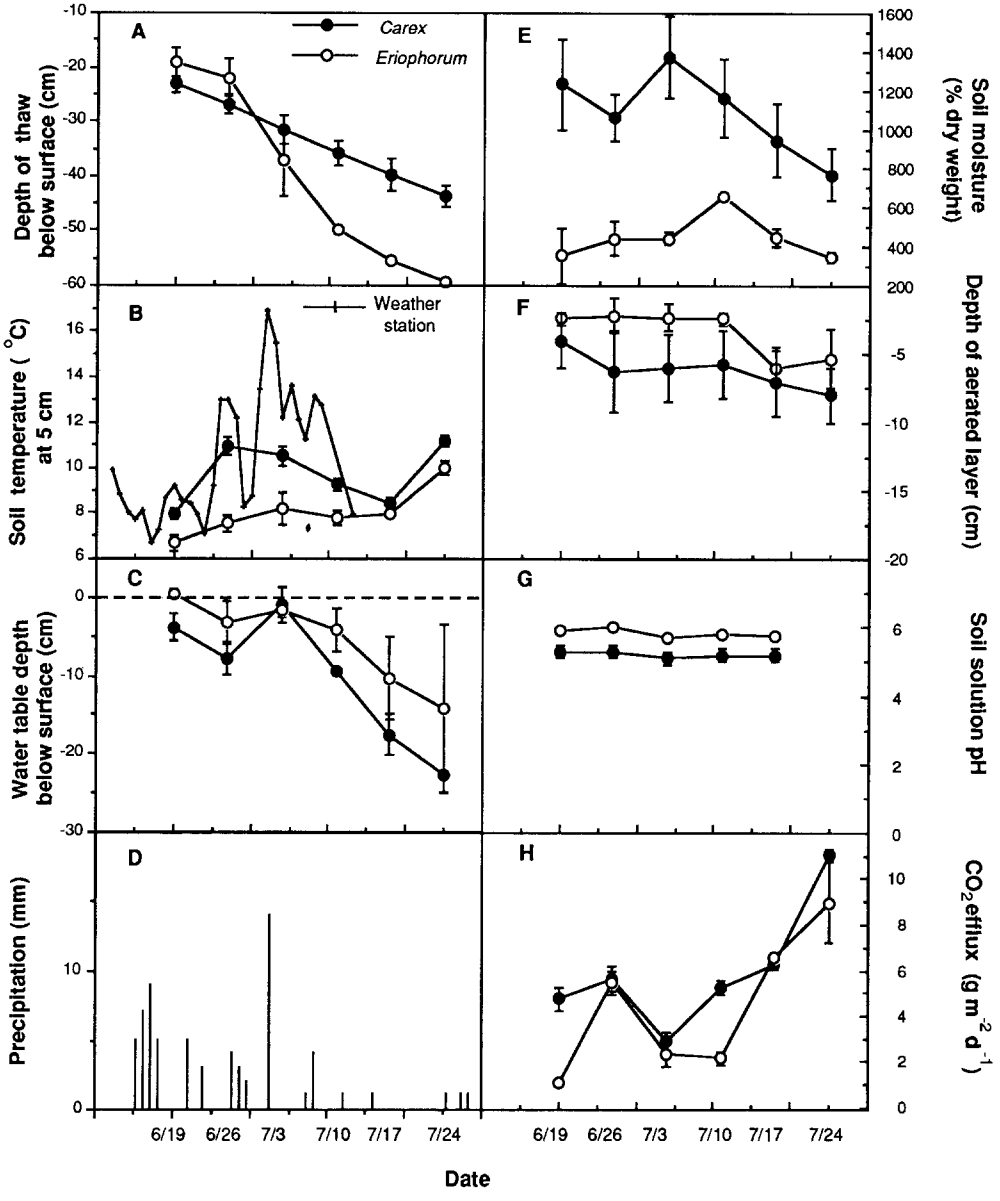

Fig. 1A–H. Seasonal patterns of **A** soil depth of thaw, **B** soil temperature at 5 cm depth, **C** soil depth to water table, **D** rainfall, **E** soil water content, **F** depth of soil aerated layer, **G** soil solution pH and **H** mean daily ecosystem CO_2 efflux based on integration of instantaneous measurements at 4-h intervals, for *Carex* and *Eriophorum* plots. Values are means ± 1 SE. $n = 6$ for *Carex* and $n = 2$ for *Eriophorum*. Symbols: —●— *Carex*; —○— *Eriophorum*, ---+--- continuous record of daily mean soil temperature at 5 cm depth for a single probe in *Carex* plot 4 recorded by the micrometeorological station

those from the *Eriophorum* plots. The efflux of the *Eriophorum* plots also remained low longer than that of the *Carex* plots following the heavy rainfall in mid-season, presumably due to continued drainage of upslope areas into the water tracks where the *Eriophorum* plots were situated. By the last sampling date, rates of CO_2 efflux from both sites were more than double early-season rates, with those from the *Carex* plots exceeding 10 g m^{-2} d^{-1}. Differences in soil CO_2 efflux from the *Carex* plots over the season were statistically significant (Table 2). Because of the small sample sizes, significant seasonal differences in *Eriophorum* plots were not detected, although the changes were of the same magnitude as those from the *Carex* plots.

The data were subjected to a correlation analysis to determine which factors covaried with CO_2 efflux both on a seasonal and a sample date basis (Table 3). In this analysis, only environmental factors that were directly monitored near the sample tubes were included. Thus, soil aeration was not considered; rather, direct measurements of depth to water table were utilized. When data for all sample tubes were taken together, thereby incorporating both seasonal and site variability, the factor in both communities most highly correlated with CO_2 efflux was depth to water table. Of the other soil characteristics, soil surface temperature, thaw depth, soil temperature at 5 cm depth and water content followed in order of decreasing correlation. Correlation coefficients for moss and vascular plant biomass were similar to those for soil temperature and thaw depth in the *Carex* plots, but were not significant for the *Eriophorum* plots.

Seasonal variation was examined without site variability effects by correlating the mean values of CO_2 efflux for a sample date with mean values for soil parameters. The strongest correlation with CO_2 efflux on a seasonal basis was with soil water content, followed by water table, thaw depth, moss and vascular plant biomass, and then soil temperature (Table 3). When data for each sampling date were considered separately (thereby examining site variability without seasonal variability), the pattern of the correlations in the *Carex* plots indicated that the relative

importance of both depth to water table and soil temperature changed with sampling date (Table 3). The importance of water table was high early in the season but generally decreased as the season progressed.

Diurnal patterns

Diurnal patterns of CO_2 efflux generally reflected changes in soil temperature, the soil parameter that changes most strongly on a hourly time scale (Fig. 2). Daily ranges of temperature and CO_2 efflux were generally greater for the *Carex* than for the *Eriophorum* plots, again probably a result of the greater heat capacity of the *Eriophorum* plot soils. With few exceptions, CO_2 efflux over the course of the day was strongly correlated with soil temperatures (Table 4). The highest correlations were found with temperature at 1 cm depth. However, carbon dioxide efflux over the day may also have been affected by changes in water table on some sample dates. For example, on 2–3 July, when a heavy rainfall immediately preceded sampling, water table in some of the sample tubes increased 3–5 cm during the following day.

Table 2. Results of analysis of variance and Tukey HSD for pairwise comparisons for seasonal differences in CO_2 efflux from *Carex* and *Eriophorum* dominated plots

Source	*df*	SS	MS	*P*
Carex				
Date	5	15.86	3.17	0.000
Plot	5	2.78	0.55	0.020
Eriophorum				
Date	5	6.42	1.28	0.237
Plot	1	1.50	1.50	0.189

Mean CO_2 efflux ($g\ m^{-2}\ day^{-1}$)

Date	*Carex*	*Eriophorum*
18–19 June	4.61 ab	1.11 a
25–26 June	5.61 ab	5.47 a
2–3 July	2.86 a	2.43 a
9–10 July	5.26 ab	2.18 a
16–17 July	6.28 b	6.57 a
23–24 July	11.06 c	8.96 a

Means in the same column followed by the same letter are not significantly different at $P<0.05$

Regression modelling

The results of correlation analyses (Table 3) suggested that depth to water table and soil temperature would be the best factors to include in a mathematical description of instantaneous CO_2 effluxes from riparian tundra. While changes in water table are assumed to affect CO_2 efflux via soil aeration, water table was chosen as an independent variable because it is more easily measured and should be predictable based on topography and hydrological budgets. The linkage between water table and soil profile aeration requires further careful study.

A model was developed that incorporated an asymptotic function for the depth to water table (cf. Eq. 1) and an Arrhenius temperature function. The data were fit to the model and regression coefficients estimated by least-squares regression (Table 5). The regression coefficients suggest a steeper response to temperature and a greater sensitivity to depth to water table for the *Eriophorum* plots

Table 3. Spearman rank correlations (r_S) for seasonal changes in integrated diurnal CO_2 efflux with soil properties

Date	T1cm	T5cm	T10cm	Thaw	Table	WC	Moss	Vasc	*n*
Carex									
ALL TUBES	0.34*	0.18	0.04	0.35*	0.76*	−0.30*	0.46*	0.40*	72
ALL DATES	0.43	0.43	−0.03	0.71	0.88*	−1.00*	0.54	0.49	6
18–19 June	0.36	0.12	0.24	−0.27	0.77*	0.36	0.73*	0.15	12
25–26 June	−0.39	0.01	−0.22	−0.14	0.92*	−0.18	0.52	0.52	12
2–3 July	0.34	−0.16	−0.50	−0.14	−0.04	0.14	0.34	0.43	12
9–10 July	0.34	0.28	0.15	−0.09	0.34	−0.57*	0.17	0.74*	12
16–17 July	0.40	0.40	0.31	0.33	0.32	0.07	−0.10	−0.03	12
23–24 July	0.04	0.02	−0.15	0.17	0.33	−0.37	−0.03	0.50	12
Eriophorum									
ALL TUBES	0.56*	0.47*	0.38	0.36	0.71*	−0.01	–	0.17	24
ALL DATES	0.83	0.71	0.71	0.77	0.82	−0.02	–	0.20	6
18–19 June	1.00*	0.63	0.60	0.40	−0.77	−0.02	–	0.40	4
25–26 June	0.40	0.40	0.40	0.40	0.80	0.40	–	−0.80	4
2–3 July	0.00	0.40	0.40	−0.40	1.00*	−0.40	–	−0.40	4
9–10 July	0.00	−0.20	0.40	0.11	0.40	0.80	–	1.00*	4
16–17 July	−0.80	−0.40	0.40	−0.80	0.00	−0.80	–	−0.80	4
23–24 July	0.40	0.40	0.40	0.80	0.95*	−0.40	–	0.80	4

Column headings: T1cm, T5cm, and T10cm = mean soil temperatures at 1, 5, and 10 cm depth, respectively; Thaw = depth to frozen soil; Table = depth to water table; WC = percent soil moisture by weight; Moss = moss biomass; Vasc = vascular plant biomass; n = sample size.
* indicates correlation is significantly different from zero at $P<0.05$. ALL TUBES includes all dates and all sample tubes. ALL DATES correlates mean values of all tubes for each sample date. Individual dates correlate mean daily values for each tube

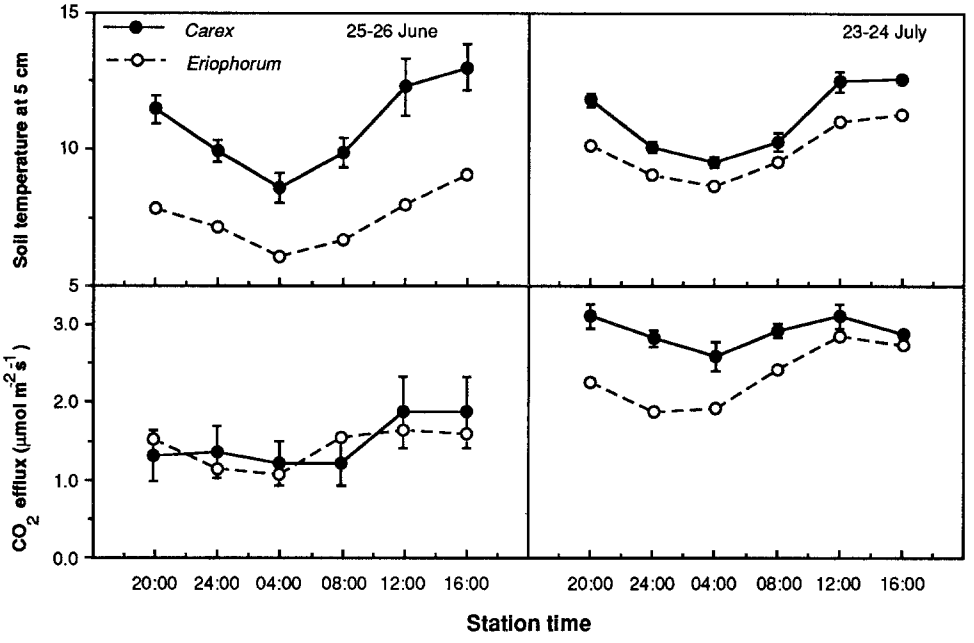

Fig. 2. Diurnal pattern of mean ±1 SE for soil temperature at 5 cm depth and ecosystem CO_2 efflux for 25–26 June (*left panels*) and 23–24 July 1990 (*right panels*). *Solid dot and line, Carex; open dot and dashed line, Eriophorum*

Table 4. Spearman rank correlations (r_S) for mean CO_2 efflux and mean soil temperature for the six sample periods on a sampling date

Date	1 cm	5 cm	10 cm
Carex			
18–19 June	−0.31	−0.37	−0.13
25–26 June	0.77	0.89*	0.43
2–3 July	1.00*	0.94*	0.54
9–10 July	1.00*	0.94*	0.37
16–17 July	0.94*	0.60	−0.37
23–24 July	0.54	0.60	0.31
Eriophorum			
18–19 June	0.71	0.83*	0.49
25–26 June	0.88*	0.77	0.20
2–3 July	0.31	0.14	0.20
9–10 July	0.94*	0.94*	0.77
16–17 July	0.60	0.14	−0.32
23–24 July	1.00*	0.83*	0.32

* indicates correlation is significantly different from zero at $P<0.05$

Table 5. Parameters E, A, and B estimated for model represented by Eq. 1 and Spearman rank correlation (r_S) between measured values and values calculated using Eq. 1

	E	A	B	r_S	n
Carex	29,144	13.319	0.321	0.77*	398
Eriophorum	71,178	30.359	0.044	0.80*	132

n = sample size
* indicates correlation is significantly different from zero at $P<0.05$

compared to the *Carex* plots. While the small sample size for the *Eriophorum* plots precludes any definitive statements about differences between the two communities, greater sensitivity to water table change in *Eriophorum* is reflected in Fig. 1 as very small changes in surface layer aeration that lead to large changes in CO_2 efflux. The regression model described the pattern and range of measured values fairly well. Spearman rank correlations between the measured and model-generated values were 0.77 and 0.80 for the *Carex* and the *Eriophorum* plots, respectively. The only data range from the *Carex* plots that was not adequately covered by the model corresponded to effluxes less than 1 μmol m^{-2} s^{-1} at depths to water table between 5 and 10 cm.

Microbial respiration

To determine the potential contribution of microbial respiration to measured CO_2 effluxes, the basal microbial respiration rate was scaled to field temperatures using temperature responses of microbial respiration and scaled to field water tables levels using Eq. 1. The patterns of estimated microbial respiration showed strong correspondence to daily mean CO_2 efflux as calculated from the integration of diurnal field measurements (Fig. 3). The correspondence between measured and actual rates was particularly close late in the season when depth to water table had minimal effect on the estimated microbial respiration. Spearman correlations (r_S) between estimated and measured daily mean CO_2 efflux were 0.93 for both *Carex* and *Eriophorum* plots.

Discussion

The results of this study indicate that CO_2 efflux from riparian tundra communities varies primarily in response to changes in the depth to water table and/or soil moisture and changes in soil temperature. Of the two *Eriophorum* plots, the lowest mean efflux was found for the plot with the highest water table, and among the *Carex* plots, the lowest mean rates of efflux were found for the plots with

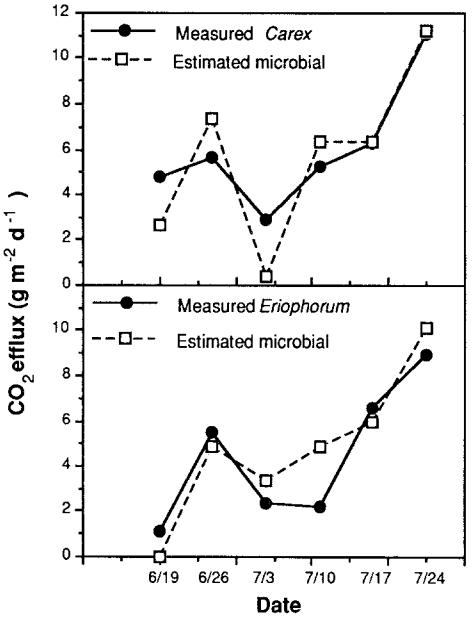

Fig. 3. Seasonal patterns of measured mean daily ecosystem CO_2 efflux (based on integration of instantaneous measurements at 4-h intervals) and estimated daily microbial respiration based on observed temperature and depth to water table for *Carex* and *Eriophorum* plots in the field. *Solid dot and line*; measured CO_2 efflux; *open square and dashed line*, estimated microbial respiration

the highest mean water table ($r_S = 0.94$). Presumably the mechanism controlling CO_2 loss in response to depth to water table is related to oxygen diffusion limitation. Our measurements of oxygen diffusion rate were not apparently of sufficient resolution to indicate all changes in aeration that occurred with seasonal changes in water table and CO_2 efflux. However, even with the present method it was apparent that rates of CO_2 efflux were low until the depth of aeration increased during late season and that seasonal trends in depth to water table and depth of aeration were similar. Our use of water table as an indicator of aeration is further supported by Whalen et al. (1993) who, based on micro-oxygen electrode measurements, suggest that moist tundra soils remain oxygenated to the water table with a rapid depletion of oxygen at or within 1 cm of the water table.

Soil moisture has often been identified as an important control on arctic ecosystem CO_2 effluxes (Billings et al. 1982, 1983; Luken and Billings 1985; Oberbauer et al. 1991). In this study, correlations between soil moisture and CO_2 efflux were very high from a seasonal perspective, but explained less of the site variability in CO_2 effluxes than depth to water table. We attempted to fit the CO_2 efflux data to a model incorporating a parabolic function for soil moisture content and an Arrhenius temperature function (Siegwolf 1987; Oberbauer et al. 1991). The correspondence between measured and calculated values was considerably lower for this model ($r_S = 0.47$ for *Carex* plots) than for the model using depth to water table ($r_S = 0.77$). This result is probably a consequence of the very high soil moistures observed throughout the study; soils were usually above field capacity and probably at no time during the season was respiration limited by low soil water contents. As described in Methods, preliminary laboratory studies suggest that microbial respiration from riparian soils is insensitive to soil moisture across a large range of soil water contents.

Soil temperature is a factor which modifies the respiration rates permitted by prevailing water table or thaw depth. The results of the correlation analysis and the microbial respiration estimates suggest that early season rates were limited by low soil temperatures, particularly in the *Eriophorum* plots. Late in the season, as water tables fell, soil temperature appeared to contribute to the high observed CO_2 efflux rates. Nevertheless, seasonal increases in mean soil temperature were small and the primary effect of temperature is seen in diurnal changes in CO_2 efflux. Temperature at 1 cm depth rather than a measurement at greater depth was most strongly correlated with diurnal changes in CO_2 efflux. Temperatures near the soil surface can change rapidly depending on radiation and wind conditions and therefore a deeper soil temperature, more indicative of average soil conditions, might be expected to provide a better correlation. Oberbauer et al. (1991) found that temperature at 5 cm rather than 2 cm depth provided a better overall correlation with CO_2 efflux in drier tussock and water track tundra. The difference in results of the two studies may be related to the very high soil water contents found in this study. High soil water contents would tend to buffer rapid changes in surface temperatures. The smaller diurnal variation in temperature and CO_2 efflux for the *Eriophorum* plots, which had greater bulk densities and higher water levels, tend to support this idea.

The estimates of microbial respiration presented would suggest that microbial respiration accounts for a major portion of measured CO_2 efflux. These rates, however, are based on the assumptions that (1) soil temperature predominantly determines diurnal rate changes, (2) that microbial respiration CO_2 flux originates equally from all points within the upper 10 cm of the soil profile when the layers are above the water table, and (3) that respiration characteristics throughout 0–10 cm depth are similar to those we measured for the upper 5 cm. The regression model analysis indicates that CO_2 exchanged at the surface is affected by decreasing water table until depth to water table is at least 10 cm (10 cm is a compromise depth that might be loosely accepted for both stands). Nevertheless, CO_2 released as the water table lowers might actually originate closer to the surface as suggested by measurements of aerated depth (Fig. 1F). If this is true, then respiration characteristics and bulk density used in the estimate are correct but estimates will be high, since greater respiring volume was used. If respiratory CO_2 fluxes do originate as deep as 10 cm, better estimates must consider depth profiles in both respiration characteristics and bulk density. Furthermore, homogenized soil, such as that used for the basal respiration measurements, may have higher rates of respiration than undisturbed soil. All of these factors suggest that our estimates of microbial respiration, particularly for the late season dates when water table had fallen below 5 cm, may be high in comparison to the field situation.

The measured field effluxes clearly include a component from aboveground and root biomass as well as that from

microbial biomass. However, because the response of root biomass to water table and plant biomass in general to temperature are likely to be similar to the responses of microbial biomass, it is not possible to separate the efflux of microbial biomass from that of plant biomass. The strength of the control of efflux by water table and the close correspondence between the seasonal patterns of measured efflux and estimated microbial respiration suggest that belowground biomass (plant + microbes) is primarily responsible for the observed seasonal patterns of CO_2 efflux. Such a result is not surprising for wet graminoid tundra; Billings et al. (1978) point out that 85–98% of the living plant biomass in wet tundra is below ground with the biomass of dead roots and rhizomes exceeding that of the living biomass.

We measured aboveground biomass in the sample tubes on each measurement date to assess the extent to which site and seasonal differences in CO_2 efflux rates could be attributed to differences in plant biomass. An analysis of covariance indicated that total aboveground biomass was a significant covariate with CO_2 efflux over the season for both the *Carex* and *Eriophorum* plots ($P < 0.01$). The late-season increase in effluxes seen in both communities corresponds to and probably results from greater aboveground biomass as well as the increase in soil temperature and depth to water table. However, as the work of Billings et al. (1978) suggests, the aboveground biomass was only a small fraction of the living biomass in these communities. We extracted live root and rhizome biomass from the sample tubes on one date (2–3 July). For those samples, aboveground biomass contributed only 12 and 5% to the total living biomass for the *Carex* and *Eriophorum* plots, respectively. The finding of significant covariance for aboveground biomass and significant correlations between biomass and efflux could have resulted from a correlation between above and belowground biomass as well as from the actual contribution of aboveground biomass to efflux. The root biomass values obtained for 2–3 July were also used to examine the relation between root biomass and rates of CO_2 efflux. The correlation between root biomass and CO_2 efflux was negative ($r_S = -0.49$), probably because water tables were very high on that date overwhelming any effect of root biomass that might have been present.

The results of this study provide field data in support of the microcosm studies of Billings et al. (1982, 1983), that suggested that depth to water table was an extremely important control for net carbon exchange of coastal wet tundra. Moore (1989) and Moore and Knowles (1989) have also shown large differences in CO_2 efflux for fen sites and peatland sites with different water tables. The implications of these findings were clearly raised by Billings et al. (1982); any climate change that raises or lowers the water table will have profound effects on carbon storage or loss from wet tundra systems, particularly in combination with increased soil temperature. Rates of CO_2 efflux measured in this study are comparable to rates found for other tundra and subarctic sites (Peterson and Billings 1975; Poole and Miller 1982; Billings et al. 1982, 1983; Luken and Billings 1985; Moore 1986, 1989; Giblin et al. 1991). In a study in the same general region as our study site, Giblin et al. (1991) measured effluxes from a wet sedge site three times over the season in 1986 and found a seasonal average efflux of 0.4 g C $m^{-2} day^{-1}$. Although they did not report on the depth to water table, they indicated that soils in the wet sedge remain saturated suggesting that the low effluxes may have been due to high water table. Depending on the water table, community respiration from our sites ranged from 0.3 to 3 g carbon $m^{-2} day^{-1}$ (1–10 g CO_2 m^{-2} day^{-1}), although for much of the season, rates were 1.6 g C m^{-2} day^{-1} or less. Seasonal averages were 1.6 and 1.2 g C m^{-2} day^{-1} for *Carex* and *Eriophorum* plots, respectively.

Although these values are measures of potential carbon losses because they include respiratory losses of darkened photosynthetic tissue, they suggest that carbon losses from these communities are a substantial fraction of primary productivity. Shaver and Chapin (1991) estimated annual production of similar wet sedge tundra communities at a site slightly south of our study site to be approximately 200 g biomass m^{-2} $year^{-1}$, or 100 g C m^{-2} $year^{-1}$ assuming biomass is composed of 50% carbon. If we conservatively estimate that only 36% of the measured effluxes are due to aboveground biomass (Peterson and Billings 1975), then the annual productivity of the *Carex* plots would be lost in roughly 98 days. Although it is unlikely that effluxes early in the season before our measurements were begun contribute much to the seasonal total, our study terminated when carbon losses were at their maximum. These high effluxes probably persisted into August before soils cooled and water table rose. Consequently, it is clearly possible that an amount of carbon greater than or equal to the annual productivity could have been lost over the growing season. This conclusion is plausible considering that Oechel and Billings (1992) suggest that nearby tussock tundra may be losing carbon at a rate of 180–360 g m^{-2} $year^{-1}$ as a result of global climate change.

Carbon dioxide effluxes are also interesting as an indicator of decomposition from the standpoint of nutrient release. For most tundra communities, decomposition is the primary means by which nutrients become available. Nadelhoffer et al. (1991) used laboratory cultures to examine the temperature response of mineralization of carbon, nitrogen, and phosphorus for soils of six tundra communities, including a riparian community. They found no response to temperature between 3 and 9° C, but a very large increase between 9 and 15° C. They suggest that mineralization rates are insensitive to temperature between 3 and 9° C because soil temperatures in the field are usually below 9° C. At our study sites, however, temperature frequently exceeds 9° C to depths at least as great as 5 cm. Furthermore, diurnal patterns of ecosystem CO_2 efflux and laboratory temperature responses suggest that temperature should affect mineralization over the entire range of temperatures measured including 3–9° C (Figs. 1B, 2). One reason for the difference in findings may be that laboratory cultures of Nadelhoffer et al. (1991) were maintained at constant temperatures for 13 weeks, long enough for changes to occur in the microbial communities in response to the treatments. In contrast, we measured short-term changes probably related to temperature responses of metabolism and not changes associated with changes in microbial biomass. Our studies indicate that for

riparian communities, water table/soil aeration and temperature are the primary controls on microbial activity and that if information on these environmental factors is available, CO_2 efflux rate is predictable based on relatively simple regression equations. Despite the inherent difficulties remaining, the model presented may be quite useful in predicting and examining spatial patterns in CO_2 efflux from tundra communities.

Acknowledgements. This research was supported by the United States Department of Energy OHER/ERD as part of the R4D program (Grant No. DE-FG03-84ER60250). Logistical support by the Institute of Arctic Biology of the University of Alaska, Fairbanks is greatly appreciated. Scott Urquhart, James F. Reynolds, and Ross Virginia aided in the sampling design and layout of the plots. Joseph Lumianski assisted with the descriptive plot measurements of pH and thaw depth. Field assistance by Lisa Balduman, Margaret Zalejko, Marcy Benzel, and Bo Ostendorf are gratefully acknowledged. Laura Knott assisted in the laboratory measurements of the temperature response of microbial respiration.

References

Anderson JPE, Domsch KH (1978) A physiological method for the quantitative measurement of microbial biomass in soil. Soil Biol Biochem 10: 215–221

Billings WD, Peterson KM, Shaver GR, Trent AW (1977) Root growth, respiration, and carbon dioxide evolution in an arctic tundra soil. Arct Alp Res 9: 129–137

Billings WD, Peterson KM, Shaver GR (1978) Growth, turnover, and respiration rates of roots and tillers in tundra communities. In: Tieszen LL (ed) Vegetation and Production Ecology of an Alaskan Arctic Tundra. Springer, New York, pp 415–434

Billings WD, Luken JO, Mortenson DA, Peterson KM (1982) Arctic tundra: a source or sink for atmospheric carbon dioxide in a changing environment. Oecologia 53: 7–11

Billings WD, Luken JO, Mortenson DA, Peterson KM (1983) Increasing atmospheric carbon dioxide: possible effects on arctic tundra. Oecologia 58: 286–289

Chapin FS III, Fetcher N, Kielland K, Everett K, Linkins AE (1988) Productivity and nutrient cycling of Alaskan tundra: enhancement by flowing soil water. Ecology 69: 693–702

Cheng W, Coleman DC (1989) A simple method for measuring CO_2 in a continuous air-flow system: modifications to the substrate-induced respiration technique. Soil Biol Biochem 21: 385–388

Cheng W, Virginia RA (1992) Measurement of microbial biomass in arctic tundra soils using fumigation-extraction and substrate-induced respiration procedures. Soil Biol Biochem (in press)

Giblin AE, Nadelhoffer KJ, Shaver GR, Laundre JA, McKerrow AJ (1991) Biogeochemical diversity along a riverside toposequence in arctic Alaska. Ecol Monogr 61: 415–435

Gorham E (1991) Northern peatlands: role in the carbon cycle and probably responses to climatic warming. Ecol Appl 1: 182–195

Grulke NE, Riechers GH, Oechel WC, Hjelm U, Jaegar C (1990) Carbon balance in tussock tundra under ambient and elevated atmospheric CO_2. Oecologia 83: 485–494

Harley PC, Tenhunen JD, Murray KJ, Beyers J (1989) Irradiance and temperature effects on photosynthesis of tussock tundra *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska. Oecologia 79: 251–259

Kummerow J, Mills JN, Ellis BA, Hastings SJ, Kummerow A (1987) Downslope fertilizer movement in arctic tussock tundra. Holarct Ecol 10: 312–319

Letey J, Stolzy LH (1964) Measurement of oxygen diffusion rates with the platinum microelectrode I. Theory and equipment. Hilgardia 35: 545–554

Luken JO, Billings WD (1985) The influence of microtopographic heterogeneity on carbon dioxide efflux from a subarctic bog. Holarct Ecol 8: 306–312

Moore TR (1986) Carbon dioxide evolution from subarctic peatlands in Eastern Canada. Arct Alp Res 18: 189–193

Moore TR (1989) Plant production, decomposition, and carbon efflux in a subarctic patterned fen. Arct Alp Res 21: 156–162

Moore TR, Knowles R (1989) The influence of water table levels on methane and carbon dioxide emissions from peatland soils. Can J Soil Sci 69: 33–38

Nadelhoffer KJ, Giblin AE, Shaver GR, Laundre JA (1991) Effects of temperature and substrate quality on element mineralization in six arctic soils. Ecology 72: 242–253

Oberbauer SF, Tenhunen JD, Reynolds JF (1991) Environmental effects on CO_2 efflux from water track and tussock tundra in Arctic Alaska, USA. Arct Alp Res 23: 162–169

Oechel WC, Billings WD (1992) Effects of global change on the carbon balance of arctic plants and ecosystems. In: Chapin FS III, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J (eds) Arctic ecosystems in a changing climate. Academic Press, San Diego, pp 139–168

Peterson KM, Billings WD (1975) Carbon dioxide flux from tundra soils and vegetation as related to temperature at Barrow Alaska. Am Midl Nat 94: 88–98

Peterson KM, Billings WD, Reynolds DN (1984) Influence of water table and atmospheric CO_2 concentration on the carbon balance of arctic tundra. Arct Alp Res 16: 331–335

Poole DK, Miller PC (1982) Carbon dioxide flux from three arctic tundra types in north-Central Alaska, USA. Arct Alp Res 14: 27–32

Siegwolf R (1987) CO_2-Gaswechel von *Rhododendron ferrugineum* L. im Jahresgang an der alpinen Waldgrenze. Ph.D. dissertation, Universitat Innsbruck

Shaver GR, Chapin FS IIIW (1991) Production:biomass relationships and element cycling in contrasting arctic vegetation types. Ecol Monogr 61: 1–32

Walker DA, Binnian E, Evans BM, Lederer ND, Nordstrand E, Webber PJ (1989) Terrain, vegetation, and landscape evolution of the R4D research Site, Brooks Range foothills, Alaska. Holarct Ecol 12: 238–261

Whalen SC, Reeburgh WS, Reimers CE (1993) Control of tundra methane emission by microbial oxidation. In: Reynolds JF, Tenhunen JD (eds) Landscape function: implications for ecosystem response to disturbance, a case study in arctic tundra (Ecological Studies). Springer, Berlin Heidelberg New York (in press)