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Abstract

Tundra ecosystems constitute large stocks of carbon and might therefore, if climate warming releases CO_2, induce positive feedback and amplify temperature increase. We studied the effect of a 2.5°C temperature increment, induced by controlled infrared irradiation, on various components of the carbon balance of a High Arctic tundra ecosystem at Zackenberg in Northeast Greenland (74°N, 21°W) over the 1999 growing season. Gross photosynthesis (P_{gross}), belowground respiration (R_{soil}), and canopy respiration (R_{canopy}) were regularly determined with closed dynamic CO_2 exchange systems, and the whole-growing season C-balance was reconstructed by relating these components to potentially controlling factors (green cover, soil moisture, radiation, soil and canopy temperature, and thawing depth). Thawing depth and green cover increased in heated plots, while soil moisture was not significantly affected. P_{gross} increased 24.2%, owing to both a green cover and a physiological influence of warming. Belowground respiration was enhanced 33.3%, mainly through direct warming impact and in spite of lower Q_{10} in the heated plots; the factors controlling R_{soil} were day of the year and soil moisture. R_{canopy} did not differ significantly between treatments, although green cover was higher in the heated plots. This tundra ecosystem acted as a relatively small net sink both under current (0.86 mol CO_2 m^{-2}) and heated (1.24 mol CO_2 m^{-2}) conditions. Nevertheless, turnover increased, which was best explained by a combination of direct and indirect temperature effects, and delayed senescence.

Introduction

In the Arctic, we can expect to observe global warming at its most powerful (Maxwell, 1992). Scenarios of temperature increase for 2080 in arctic regions, vary between 0.5 and 7.5°C in summer and between 2.5 and 16°C in winter (McCarthy et al., 2001). Already in previous decades, a warming trend was observed in the Alaskan Arctic (Lachenbruch and Marshall, 1986). Future warming could alter soil moisture, active layer depth, decomposition rates, and permafrost distribution, and lead to an oxidation of soil C (Mitchell et al., 1990). About 80% of the organic carbon in the world's terrestrial ecosystems is in soil, and of this, about 11 to 14% is stored in tundra (Schlesinger, 1984; Wookey, 2002). As a result, this biome has the potential for releasing large stocks of C. Increasing temperatures can change a net carbon sink into a net carbon source and vice versa (Billings et al., 1982), because plant and ecosystem responses can feed back to climate change both positively and negatively (Oechel et al., 1998). A negative feedback can arise from decreased albedo in response to higher vegetation cover (Bonan et al., 1992), and a positive feedback from increases in net loss of CO_2 to the atmosphere if respiration is stimulated more (or reduced less) than photosynthesis (Oechel et al., 1993). An accelerated net loss of carbon to the atmosphere is feasible and has been suggested by laboratory experiments in the early 1980s (Billings et al., 1982) and by more recent field experiments during the snow-free season on dry heath and moist tussock tundra (Jones et al., 1998). However, at the same site as Jones et al. (1998) but in a different year, Hobbie and Chapin (1998) found no effect of a 4°C temperature elevation on net summer CO_2 balance of upland tussock tundra, although carbon turnover was stimulated. Research by Christensen et al. (1997) on *Cassiope tetragona* subarctic heath in Abisko, Sweden, revealed no significant warming effect on ecosystem dark efflux. In addition, in the study of Johnson et al. (2000), wet sedge tundra ecosystems exhibited only subtle effects of warming on both photosynthesis and ecosystem respiration. To make climate predictions, it is essential to estimate the right scope of warming influences. Most previous studies on arctic carbon balance have been conducted in the Low Arctic, and as there are variances in climatic parameters with the High Arctic, trends can be different. Furthermore, terrestrial ecosystems seem to respond differently to climate change on several time scales. Therefore, to include all effects, both short-term (or fine-scale studies) and long-term studies are important and useful for predicting and modeling these responses (Le Dizès et al., 2003).

In the current study we determined the carbon balance over the snow-free season in tundra vegetation in the High Arctic of Northeast Greenland. Warming was simulated with the Free Air Temperature Increase (FATI) technique; a constant difference in surface temperature of 2.5°C was generated between treated and untreated plots. The first objective was to assess if a warmer climate would shift the tundra-ecosystem towards a (larger) source. Second, because previous studies in Low Arctic and Subarctic were inconclusive, we disentangled influences of warming on three main components of the C-balance: (i) uptake of CO_2 by photosynthesis, (ii) loss of CO_2 by belowground respiration, and (iii) loss of CO_2 by canopy respiration. Finally, to generalize from our research, we investigated possible factors (green cover, soil moisture, thawing depth, senescence) that govern each component.

Materials and Methods

PLOT SELECTION AND SITE DESCRIPTION

Experimental warming was conducted in 1999 at the Zackenberg research station in Northeast Greenland (74°28′N, 20°34′W, 25-m

1523-0430/04 $7.00

elevation) on tundra vegetation classified as "wet," although the summers are usually dry. In the lower part of the Zackenberg area, species richness of vascular plants is very high (150) for a region above 74°N in Greenland and vegetation cover is almost uniform (Meltofte and Thing, 1997). The site has a well-developed Podzol soil and is in the zone of continuous permafrost with an active layer 20 to 80 cm thick (Meltofte and Thing, 1997). The growing season lasts approximately 2 mo, mean annual air temperature is −10.4°C, and annual precipitation 215 mm (means for 1961–90, Danish Meteorological Institute). The experimental site was a lower grassland plateau where we selected six similar tundra plots (40 × 50 cm), dominated by *Salix artica* Pall. and *Arctagrostis latifolia* Griseb., with *Carex bigelowii* Torr. ex Schwein, *Polygonum viviparum* L., *Juncus castaneus* Sm., and *Dryas* spp. as subdominants. Living plant cover was estimated with pin-frames placed on the plots, which recorded the species with a vertical needle at each point of a 500-point matrix (40 × 50 cm). Plots were allocated to two temperature groups to have approximately equal cover and species composition before heating began (MANOVA of cover by species, $P > 0.05$, $F_{1,4}$ between 0.007 and 3.766). From 2 July to 26 August, three plots were continuously warmed with infrared radiation (0.8–3 μm); three others served as controls.

TEMPERATURE INCREASE METHOD AND ENVIRONMENTAL MEASUREMENTS

The Free Air Temperature Increase (FATI) system was designed to homogeneously heat limited areas of short (less than 30 cm) vegetation (Nijs et al., 1996, 2000). Individual FATI-units consisted of two 1500-W infrared irradiation sources in a waterproof housing and were placed on a tripod north of the plots to minimize blockage of incoming solar radiation. Control plots had "dummy" FATI-units without lamps. Radiation from the FATI-lamps below 0.8 μm was filtered out to avoid photomorphogenetic effects and prevent nighttime illumination by the FATI unit. The FATI-optimizer (Nijs et al., 2000), a home-made electronic device, was used to harmonize the FATI-units to produce highly similar surface temperature increments (target +2.5°C) in each of the heated communities. Noncontact semiconductor sensors with a 10° field of view ("infracouple," type OS39-MVC-6, Omega Engineering, Stamford, Connecticut, US) monitored surface temperature of the vegetation. Soil temperature at 2.5, 7.5, 15, and 30 cm depth and air temperature at a height of 5 cm were measured with NTC-thermistors (EC95, Thermometrics, New Jersey, US). Photosynthetically active radiation (*PAR*) was measured with a gallium-arsenide sensor (JYP-1000, SDEC, France) fixed in an open place near the FATI-site. Data loggers (16 kb, 12-bit, eight-channel; DL2E, DeltaT, Cambridge, UK) recorded all aforementioned parameters once every 30 min from 2 July 1999 1200 h until 29 August 1999 1730 h Local Day Time (LDT). Thawing depth was sampled nine times during the season in the center of each plot with a fiberglass rod of 5 mm diameter. Simultaneously, soil volumetric water content was measured with time domain reflectometry (Trime-FM, Eijkelkamp Agrisearch Equipment, The Netherlands) over the upper 11-cm soil horizon (one reading per quadrant per plot). Five soil cores (diameter 4.4 cm, length 35 cm) were taken in the vicinity of the plots on 5 July to determine the amount of carbon in the soil.

CO_2 EXCHANGE

In all available gas exchange systems, uncertainties can occur because of chamber pressure artifacts (Lund et al., 1999), but there is no reference technique to test a particular system (Rayment and Jarvis, 1997). We measured CO_2 exchange with a dynamic closed system, generally considered the best available enclosure technique to determine soil and whole-ecosystem trace gas fluxes (Lund et al., 1999; Janssens et al., 2000). The system consisted of an infrared gas analyzer (CIRAS, PPSystems, Hitchin, Hertfordshire, UK) and either an 8-cm-tall, 0.17-L cylindrical, one-piece, custom-made PVC chamber for belowground respiration (hence referred to as soil respiration, R_{soil}), or a 30-cm-tall, 4.5-L cylindrical polymethylpentene chamber (model CPY-2, PPSystems) for net ecosystem CO_2 exchange rate ($CER_{ecosystem}$). The chambers were placed on 7-cm-high collars, 5-cm diameter for the soil chamber (one per plot) and 13-cm diameter for the ecosystem chamber (two per plot), which were positioned into the ground at the end of the previous season to compensate for possible root death. For the soil collars we selected bare spots within the plots, free of vascular plants, although most of them contained some moss. The ecosystem chambers were placed to have nearly equal total plant cover in the two treatments before heating began. In the ecosystem chamber, a thermistor and an internal 0.4 to 0.7-μm sensor measured air temperature and *PAR*, respectively. Humidity inside and outside the gas exchange circuit was maintained equal by a water vapor equilibrator; flow rate was 0.1 L min^{-1}. We measured net ecosystem CO_2 exchange in ambient *PAR* ($CER_{ecosystem}$) and in the dark by covering the chamber ($CER_{ecosystem,dark}$). Soil respiration (R_{soil}) was measured directly on the soil. Since $CER_{ecosystem} = P_{gross} + R_{soil} + R_{canopy}$ and $CER_{ecosystem,dark} = R_{soil} + R_{canopy}$, we could determine gross photosynthesis (P_{gross}) by subtracting $CER_{ecosystem,dark}$ from $CER_{ecosystem}$, and canopy respiration (R_{canopy}) by subtracting R_{soil} from $CER_{ecosystem,dark}$. We measured in nine different periods during the season, generally from 0900 h until 2000 h LDT, to encompass the seasonal variation in canopy cover, thawing depth and water availability, all of which may influence the C-balance components (P_{gross}, R_{soil} and R_{canopy}). Each period covered two, sometimes three days, in order to include a broad range of *PAR* and temperature values. Because flux data were not collected continually, we reconstructed the carbon balance by interpolating the three components (P_{gross}, R_{soil}, and R_{canopy}) individually. To this end, P_{gross} was fitted as a function of *PAR*:

$$P_{gross} = \frac{\alpha \cdot P_{gross,max} \cdot PAR}{\alpha \cdot PAR + P_{gross,max}} \quad (1)$$

with α stand-level quantum yield and $P_{gross,max}$ asymptotic P_{gross} at infinite *PAR*.

The regression was done with the pooled measurements of each measurement period separately (hereafter represented by the first or middle day of the year (DOY) of that period), because photosynthetic capacity changes during the season. The resulting α and $P_{gross,max}$ values were fitted as a function of time (eq. 2) to reconstruct the time course of instantaneous P_{gross} from instantaneous *PAR* over the whole period. The function we used was:

$$\alpha \, or \, P_{gross,max} = a \cdot (DOY - b)^2 + c \quad (2)$$

with a, b, c constants indicating pointedness, time of peak and maximum of the parabola, respectively. Contrary to P_{gross}, R_{soil}, and R_{canopy} readings taken in different periods were pooled and fitted as a function of T_{soil} at 2.5 cm depth and T_{air} at 5 cm, respectively:

$$R_{soil} = A \cdot Q_{10}^{\frac{(T_{soil}-10)}{10}} \quad (3)$$

$$R_{canopy} = A \cdot Q_{10}^{\frac{(T_{air}-10)}{10}} \quad (4)$$

with A respiration rate at 10°C and Q_{10} temperature-sensitivity of respiration. Time courses of R_{soil} and R_{canopy} were then reconstructed from instantaneous T_{soil} and T_{air}, respectively, over the whole period.

STATISTICAL ANALYSIS

We conducted all analyses with SPSS 10.0. Tests of normality were Kolmogorov-Smirnov and Shapiro-Wilk. Univariate or

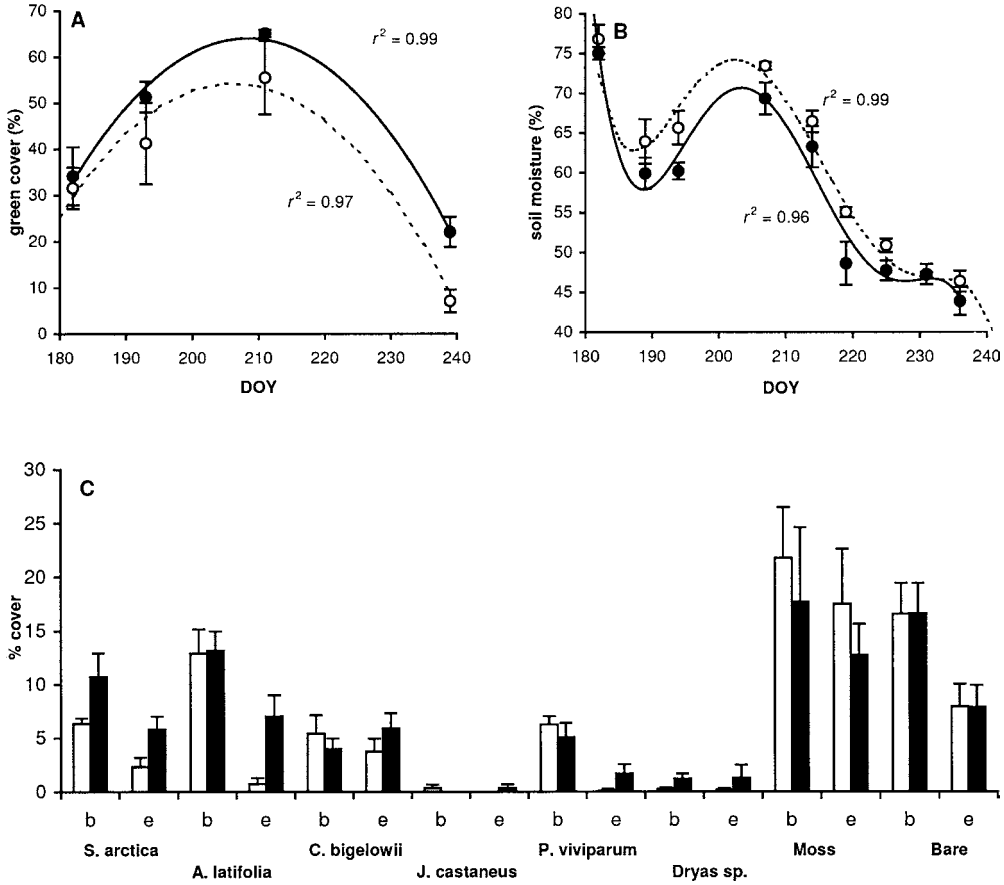

FIGURE 1. (A) Time course of green cover during the season determined from pin-frame measurements. Means ± 1 SE on different days of the year (DOY), and fitted polynomial curve (2nd order) for the unheated (○, dotted line) and heated (●, solid line) treatment. (B) Time course of soil moisture during the season. Means ± 1 SE on different DOY, and fitted polynomial curve (5th order) for the unheated (○, dotted line) and heated (●, solid line) treatment. (C) Percentage cover of living vascular plants by species, mosses and bare soil, at the beginning (b) and end (e) of the irradiation period from 2 July to 29 August 1999. Plant parts were considered completely senesced if chlorophyll could no longer be detected visually. Average ± 1 SE of three heated (filled bars) and three unheated (open bars) plots.

Multivariate analyses of variance (ANOVA, MANOVA, or ANCOVA with a covariate) were utilized to test effects of and interactions between factors. Data on seasonal dynamics, gathered on the same plots during the season, were analyzed with repeated-measures ANOVA with date of measurement as within-subject factor and treatment as between-subject factor. When sphericity (tested with Mauchly's test) was violated we used MANOVA instead, which is independent of sphericity (O'Brien and Kaiser, 1985). We applied various types of nonlinear regression to fit dependent variables to time.

Results

Over the period of warming, vegetation temperature was elevated on average with 2.50 ± SD 0.71, 2.48 ± SD 0.34, and 2.44 ± SD 0.42°C, above means of 9.26, 7.90, and 7.92°C in FATI units 1, 2, and 3, respectively. Of the instantaneous increments in surface temperature, 78% fell within ± 0.5 °C of the target increment of +2.5°C, all FATI-units combined. Soil temperature was increased on average 2.58 ± SD 1.11, 2.13 ± SD 0.77, 1.62 ± SD 0.73, and 0.86 ± SD 0.77°C at 2.5, 7.5, 15, and 30 cm depth, respectively, and air temperature at a height of 5 cm, 1.09 ± SD 0.66°C. Total cumulative incident *PAR* over the season was 2052 mol m^{-2}. From spring to autumn, mean thawing depth augmented from 29.8 ± SE 1.0 and 30.5 ± SE 1.4 cm to 65.9 ± SE 0.6 and 72.7 ± SE 0.4 cm in the control and heated treatment, respectively (significant difference, repeated-measures ANOVA, $P < 0.05$, $F_{1,22} = 22.438$), while average soil moisture was lowered from 76.8 to 46.4% (control) and from 75.1 to 44.0% (heated). Throughout the season mean soil moisture was consistently lower in the heated plots, though not significantly (Fig. 1A, repeated-measures ANOVA, $P > 0.05$, $F_{1,22} = 3.757$). Total living cover increased between early and mid season, from 31.5 to 55.5% and from 34.1 to 65.2% for unheated and heated plots, respectively (average of three replicate plots in each case). Treatment differences became significant at the end of the season (Fig. 1B, MANOVA, $P < 0.05$, $F_{1,4} = 13.538$), when green cover was reduced to 7.1% in the unheated plots and to 22.1% in the heated plots. In particular *Arctagrostis latifolia*, though not uniquely, contributed to this effect (Fig. 1C).

Treatment, *PAR* and DOY significantly influenced P_{gross} (Fig. 2A, ANCOVA with *PAR* as covariate, $P < 0.05$, with $F_{1,334} = 36.977$, $F_{1,334} = 418.296$, and $F_{8,334} = 21.338$, respectively), but no interaction occurred between DOY and treatment ($P > 0.05$, $F_{8,334} = 1.658$). We consequently fitted P_{gross} to *PAR* (eq. 1) to derive separate curves for control and heated plots for every DOY (Fig. 2B). Warming effects on photosynthesis capacity were absent at the start of the season (1 on Fig. 2B) and gradually increased as the season progressed, to become significant (2 on Fig. 2B) from DOY 226 on (repeated-measures ANOVA, $P < 0.05$, $F_{1,34} = 6.153$). Gross photosynthesis was always higher in heated plots and decreased later in the season than in the control plots. To reconstruct P_{gross} from *PAR* over the entire period, $P_{gross,max}$ and α were calculated for every measurement day per treatment and were fitted as a function of time (eq. 2; Figs. 2C, D). Parameter a being lower (–0.006 ± SE 0.002) in unheated than in

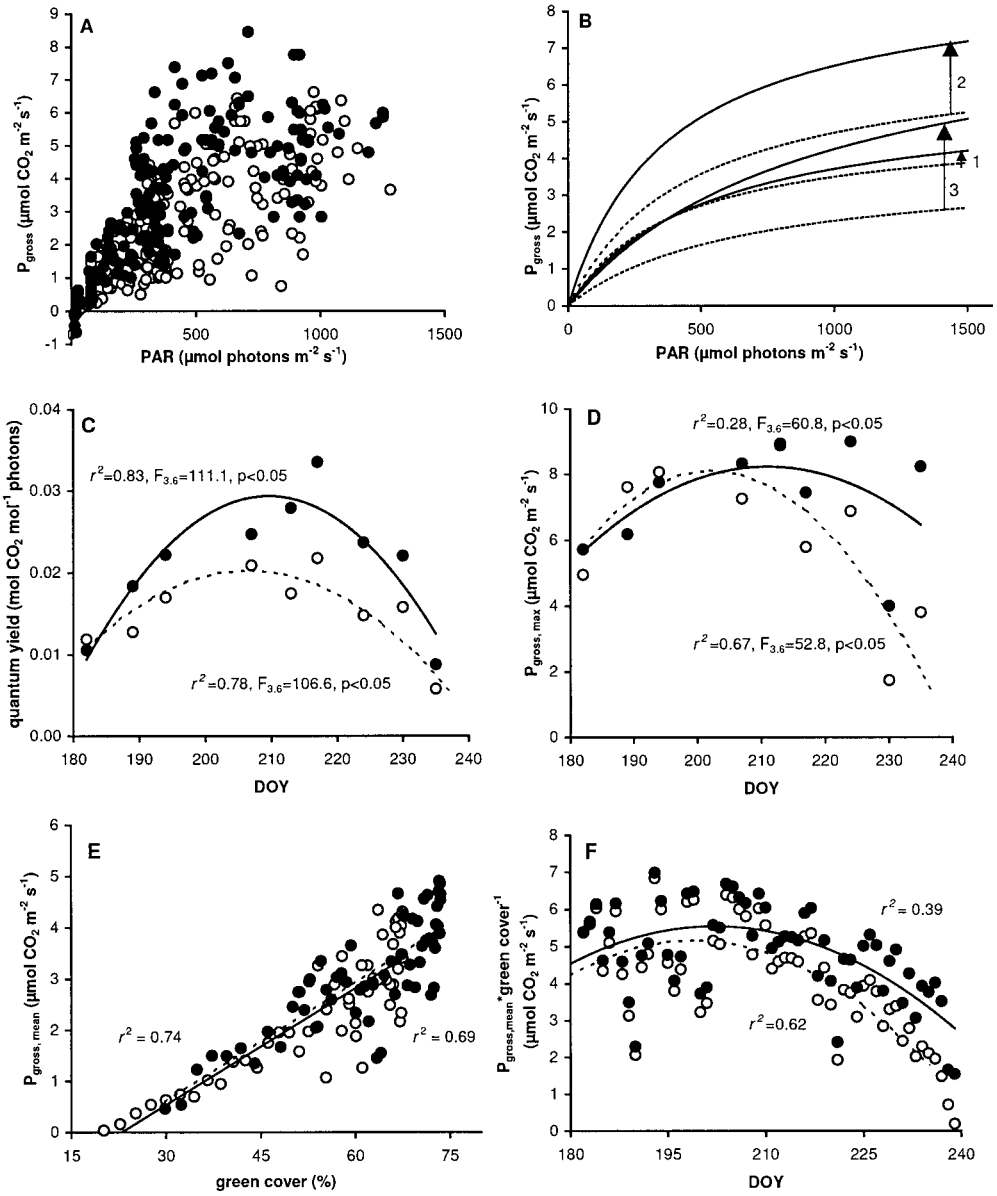

FIGURE 2. (A) Gross photosynthesis (P_{gross}) of the tundra vegetation as a function of incident photosynthetically active radiation (PAR) in ambient conditions or under simulated heating, all measurements during the entire season combined. (B) Curves fitted (eq. 1) to P_{gross}, from unheated plots and heated plots on three characteristic days during the season; 1: Day of the year (DOY) 182 (spring), 2: DOY 224 (mid season with largest treatment difference), 3: DOY 235 (autumn). (C, D) Time course of stand-level quantum yield (α in eq. 1) and maximum gross photosynthesis ($P_{gross,max}$ in eq. 1), respectively. Data by DOY and fitted polynomial curves (2nd order) for heated and unheated plots separately. (E) Daily mean gross photosynthesis plotted as a function of green cover for heated and unheated communities separately. (F) Time course of mean gross photosynthesis per unit green cover. Data by DOY and fitted polynomial curves (2nd order) for heated and unheated plots separately. Open symbols (○), dotted lines, and closed symbols (●), solid lines, for the unheated and heated treatment, respectively.

heated plots (–0.002 ± SE 0.001) (Fig. 2D), $P_{gross,max}$ decreased faster in the control plots by the end of the season. Time of seasonal peak $P_{gross,max}$ (parameter b) was 8 d earlier for the vegetation in ambient (DOY 204 ± SE 3) than in heated (DOY 212 ± SE 2) conditions. By contrast, the seasonal maximum of $P_{gross,max}$ (parameter c) was almost the same (unheated: 8.12 ± SE 0.78 µmol CO_2 m^{-2} s^{-1} vs. heated: 8.23 ± SE 0.82 µmol CO_2 m^{-2} s^{-1}). Maximum quantum yield was lower (Fig. 2C; c = 0.020 ± SE 0.001 vs. 0.029 ± SE 0.002 mol CO_2 mol^{-1} photons) and was reached earlier (b = DOY 208 ± SE 1 vs. DOY 210 ± SE 1) in the unheated relative to the heated treatment. From the time courses of α and $P_{gross,max}$ we reconstructed P_{gross} from *PAR* for the whole season. This yielded a cumulative photosynthesis of 12.21 mol CO_2 m^{-2} in ambient conditions and 15.17 mol CO_2 m^{-2} under simulated warming, an augmentation of 24.2%. Daily mean gross photosynthetic rate ($P_{gross,mean}$) was positively influenced by percentage green cover (Fig. 2E, linear regression, with $r^2 = 0.74$ and 0.69 for the heated and unheated treatment, respectively; not significantly different, ANCOVA, *GC* as covariate, $P > 0.05$, with $F_{1,113} = 1.061$). We next calculated $P_{gross,mean}$ per unit green cover and plotted the seasonal course of this variable (Fig. 2F). Since in both treatments the curve was not horizontal, also other factors than green cover affected P_{gross} (e.g., *PAR*, temperature and senescence). The difference (Fig. 2F, ANCOVA, DOY as covariate, $P < 0.05$, $F_{1,113} = 9.650$) between the curves reflects the remaining physiological influence of the warming treatment, after the structural influence (green cover) has been filtered out.

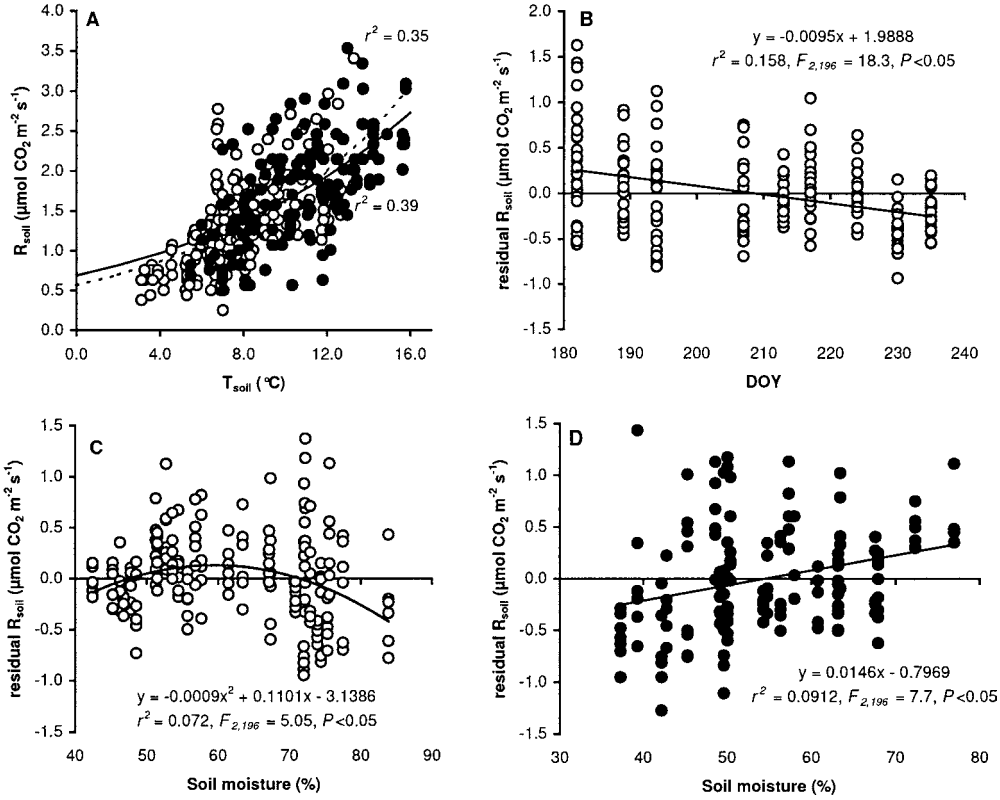

FIGURE 3. (A) Soil respiration (R_{soil}), from all measurement days, as a function of soil temperature (T_{soil}) at a depth of 2.5 cm. Separate curves are fitted (eq. 3) for control (○, dotted line) and heated (●, solid line) plots. (B, C) Residual soil respiration ($Respiration_{observed}$–$Respiration_{fitted}$) for control plots as a function of DOY and soil moisture. (D) Residual soil respiration for plots under simulated warming as a function of soil moisture.

Treatment, T_{soil} and DOY had a significant effect on R_{soil} (ANCOVA, T_{soil} as covariate, $P < 0.05$, with $F_{1,335} = 20.740$, $F_{1,335} = 21.218$ and $F_{8,335} = 12.484$, respectively); interaction between DOY and treatment was absent ($P > 0.05$, $F_{7,335} = 0.332$). We therefore created two different $R_{soil} - T_{soil}$ relationships for the control and heated plots (Fig. 3A), as a basis for reconstructing belowground efflux. This relationship does not reckon with the observed DOY-effect, but by computing residuals ($R_{observed} - R_{fitted}$), we verified whether the R_{soil} variation not explained by the model could be attributed to additional factors. This way, effects of DOY, but also of soil moisture and thawing depth, could participate in the reconstruction without adding complexity to the original formula (eq. 3). For the unheated plots, the most significant relationship was between the residuals and DOY, probably reflecting senescence (Fig. 3B, linear fit, $r^2 = 0.158$, $P < 0.05$, $F_{2,196} = 18.3$). We next recalculated the residuals, including the DOY equation, to search for other significant factors and found that also soil moisture significantly affected R_{soil} (Fig. 3C, nonlinear fit, $r^2 = 0.072$, $P < 0.05$, $F_{2,196} = 5.05$). The final equation to reconstruct R_{soil} for the unheated vegetation was then:

$$R_{soil} = a \cdot Q_{10}^{\frac{(T_{soil}-10)}{10}} + b \cdot DOY + c + d \cdot VWC^2 + e \cdot VWC + f \quad (5)$$

with VWC volumetric water content and a, b, c, d, e, f constants. For the warmed vegetation, only the effect of soil moisture was significant (Fig. 3D, linear fit, $r^2 = 0.0912$, $P < 0.05$, $F_{2,153} = 7.7$), therefore the resulting equation was:

$$R_{soil} = a \cdot Q_{10}^{\frac{(T_{soil}-10)}{10}} + b \cdot VWC + c \quad (6)$$

Both treatments reacted differently to temperature; Q_{10} was 2.86 ± SE 0.28 and 2.37 ± 0.20 SE for the unheated and heated plots, respectively. Eventually R_{soil} was reconstructed using the soil moisture record of the entire season (Fig. 1B), yielding cumulative R_{soil} values of 6.03 mol CO_2 m^{-2} for the unheated and 8.04 mol CO_2 m^{-2} for the heated plots, or a 33.3% increase.

Canopy respiration was not affected by the warming treatment when compared at the same temperature (ANCOVA, T_{air} as covariate, $P > 0.05$, $F_{1,331} = 3.289$), neither was there an interaction between DOY and treatment ($P > 0.05$, $F_{7,331} = 1.000$). The first allowed us to express R_{canopy} with a single relationship (eq. 4) applicable to the entire growing season (Fig. 4A). In a new ANCOVA with the two treatment-groups combined, R_{canopy} was influenced by T_{air} ($P < 0.05$, $F_{1,339} = 38.790$). Also here we calculated the residuals to test if DOY, green cover (GC) or soil moisture explained additional variation. Only the effect of green cover was significant (Fig. 4B, a nonlinear fit, $r^2 = 0.032$, $P < 0.05$, $F_{3,346} = 3.79$); the resulting equation was:

$$R_{canopy} = a \cdot Q_{10}^{\frac{(T_{air}-10)}{10}} + b \cdot GC^2 + c \cdot GC + d \quad (7)$$

with a, b, c, d constants. With the seasonal courses of GC for both treatments (Fig. 1A) we reconstructed R_{canopy}. This revealed a 10.8% higher cumulative value for the heated plots (5.89 mol CO_2 m^{-2}) than for the unheated plots (5.32 mol CO_2 m^{-2}).

Reconstructed daily CO_2 fluxes of the three carbon balance components are shown in Figure 5A. Canopy respiration peaked halfway the season, but treatment differences were small. For R_{soil} the differences were more substantial, especially in the middle of the season. The R_{soil} curve for the unheated plots decreased gradually from the start, while it stayed at around the same level until the middle of the season in the heated plots. In spring, a relatively low P_{gross} combined with a relatively high R_{soil} was responsible for a positive C-balance (Fig. 5A). In the middle of the season, a slightly increased total respiration ($R_{soil} + R_{canopy}$) was overcompensated by a more strongly

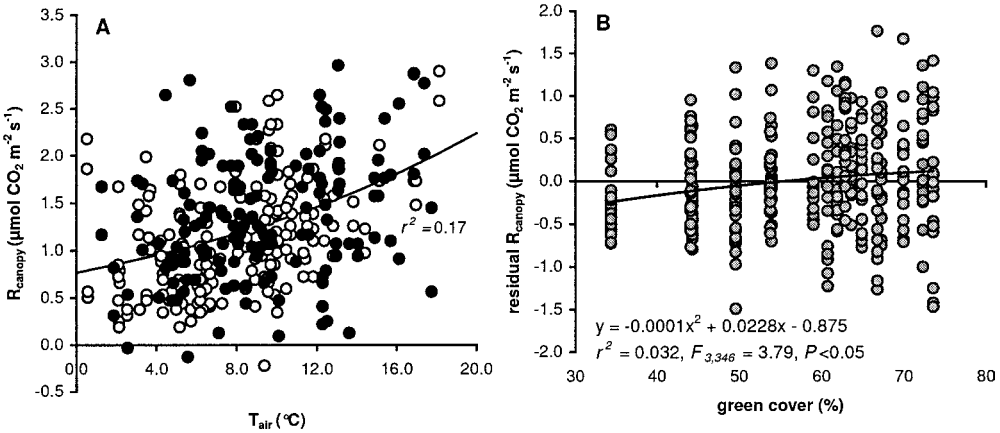

FIGURE 4. (A) Canopy respiration (R_{canopy}) *as a function of air temperature* (T_{air}) *at 5 cm height. Measurements pooled over all measurement days of the year (DOY), and fitted curve (eq. 3) for control (○) and heated (●) plots combined. (B) Residual canopy respiration for control plots as a function of green cover* ($Respiration_{observed}$–$Respiration_{fitted}$).

increased photosynthesis, which made the balance negative (Fig. 5B). At the end of summer, carbon was lost due to a much stronger decline of P_{gross} relative to ecosystem respiration. Figure 5C summarizes the reconstructed carbon balance over the entire period. Gross photosynthesis was the largest component, followed by R_{soil} and R_{canopy}. In absolute terms, P_{gross} was enhanced most by the heating, in relative terms R_{soil} was stimulated more. Overall, the experimental plots were C-sinks with a total uptake of 0.86 mol CO_2 m^{-2} in the unheated and 1.24 mol CO_2 m^{-2} in the heated plots. Total carbon in the soil outside the plots at the beginning of the season amounted to 204.26 ± SD 21.23 mol m^{-2}, so the additional sequestration was minor, mainly owing to increases in P_{gross} and $R_{canopy} + R_{soil}$ almost canceling out.

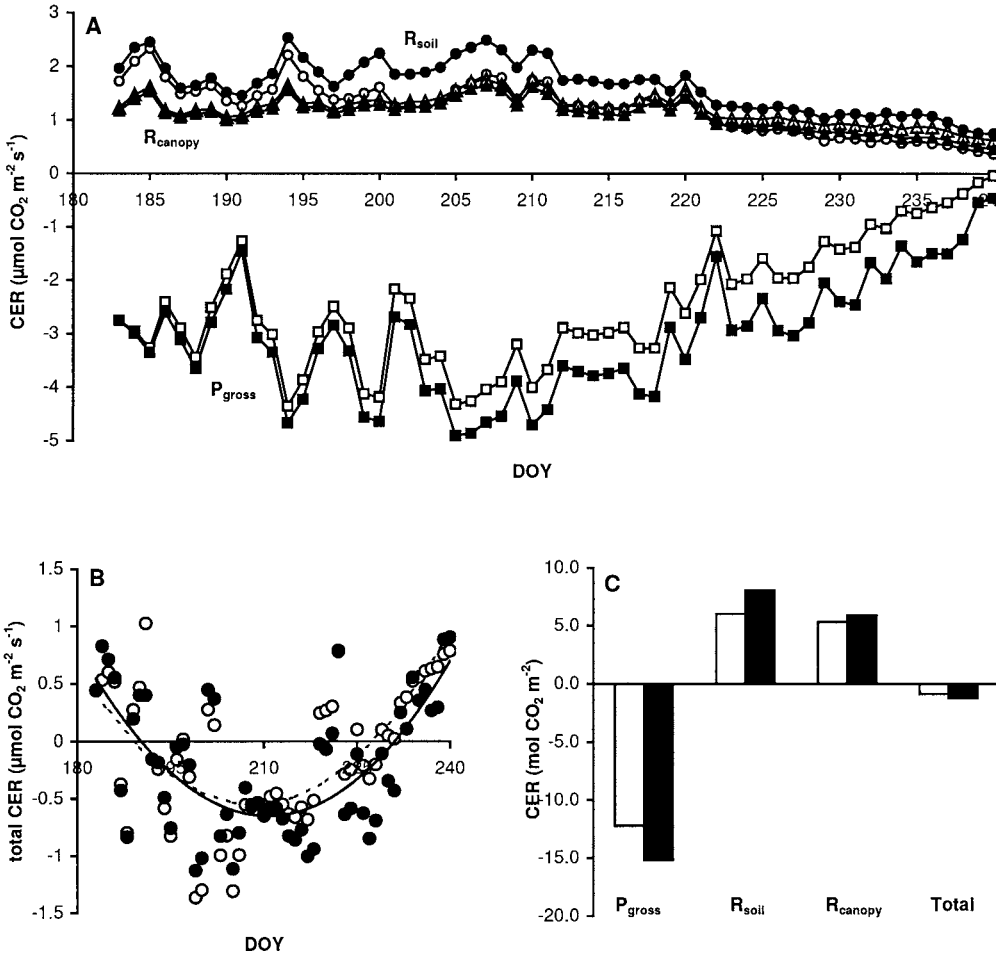

FIGURE 5. (A) Reconstructed time course of daily CO_2 exchange rate (CER) separated into the three components: photosynthesis (P_{gross}), *soil respiration* (R_{soil}) *and vegetation respiration* (R_{canopy}). *DOY: day of the year. (B) Reconstructed time course of daily total net* $CER_{ecosystem}$. *(C) Cumulated CER over the entire growing season, separated by the three components. Values in (A, B, C) are averages for the three control plots (open symbols or bars) and the three heated plots (closed symbols or bars). Positive values are CO_2 release.*

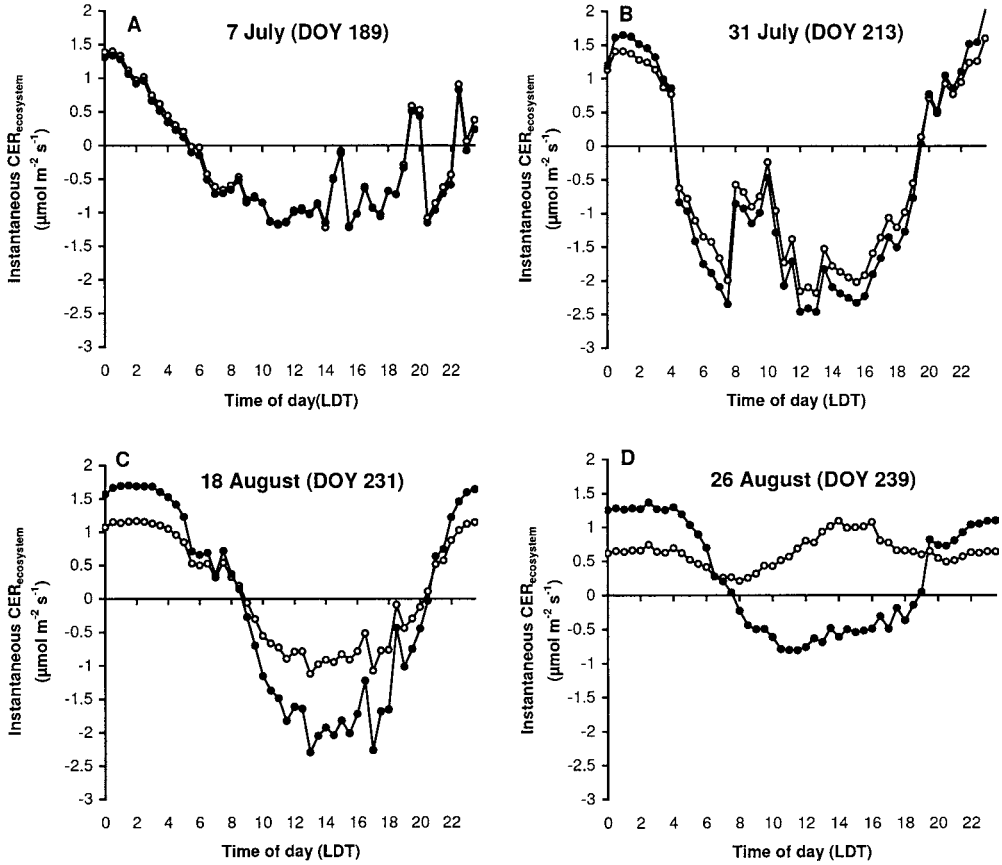

FIGURE 6. Daily course of net ecosystem CO_2 exchange rate ($CER_{ecosystem}$*) on DOY 189 (A), 213 (B), 231 (C), 239 (D), respectively (all sunny days), for the unheated (○) and heated (●) treatment. Reconstructed values based on separately modeled gross photosynthesis, soil respiration and canopy respiration. Positive values are CO_2 release.*

Different daily courses of $CER_{ecosystem}$ appeared during the season (Fig. 6). At the start (Fig. 6A), there was no difference between the heated and unheated treatment and the balance was positive at night and negative during the day. Further in the season (Fig. 6B), treatment differences increased and so did both release and uptake, as well as the duration of daily C-sequestration, clearly because of higher green cover (Fig. 4B) and thus accompanying higher photosynthesis. This trend continued after the growing season peak, although the period of sequestration became shorter and shifted to later in the day (Fig. 6C). At the end of the season (Fig. 6D) the unheated plots had almost constant CO_2 release, whereas the heated plots still had a lower level during the day, but a higher during the night. Figure 7 illustrates the accuracy of the reconstruction by regressing measured, instantaneous, $CER_{ecosystem}$ on instantaneous $CER_{ecosystem}$ predicted from separately modeled gross photosynthesis, soil respiration, and canopy respiration. The regression being linear indicates that the reconstruction is reliable, although part of the observed $CER_{ecosystem}$ could not be explained ($r^2 = 0.61$), possibly due to high variation of R_{canopy}. In spite of the uncertainty associated with predicting individual values of instantaneous $CER_{ecosystem}$, average predicted and average observed instantaneous $CER_{ecosystem}$ over the season were close (difference 0.037 µmol m^{-2} s^{-1}) relative to the range of $CER_{ecosystem}$ values (from –4 to 4 µmol m^{-2} s^{-1}), indicating that the seasonal balance was accurate.

Discussion

In this study we investigated consequences of whole-season warming for three processes that contribute to the carbon balance of a High Arctic tundra ecosystem, gross photosynthesis, belowground (heterotrophic + root) respiration, and canopy respiration. Most previous heating experiments were carried out using conventional methods such as greenhouses and open top chambers (Dormann and Woodin, 2002). These techniques can give unrealistically high temperature rise, the increment is not constant and, at night, warming

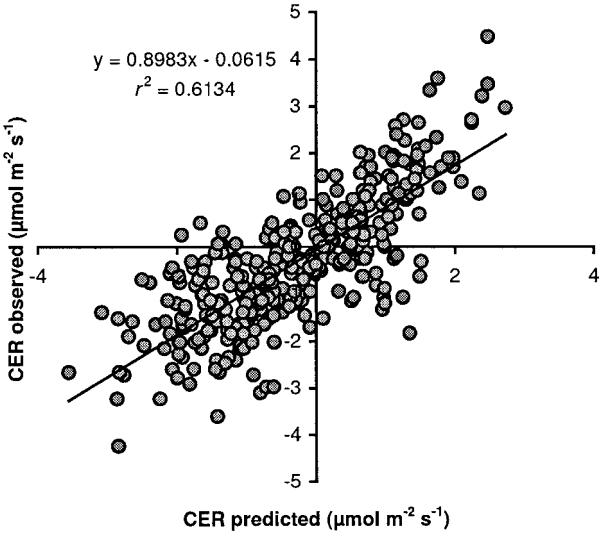

FIGURE 7. Instantaneous observed net ecosystem CO_2 exchange rate ($CER_{ecosystem}$*) as a function of instantaneous predicted* $CER_{ecosystem}$*. Pooled measurements of the whole growing season.*

can be close to zero (Kennedy, 1995; Marion et al., 1997). Earlier research may for this reason have led to biased conclusions about warming effects. By applying the FATI-technique such bias was avoided, as temperature rise is not accomplished through a greenhouse effect but with modulated infrared heating (Nijs et al., 2000). To avoid further artifacts, the FATI-systems were not turned on until the snow had totally melted and running melting water had disappeared, which took approximately one week. Soil thawing during this week was rapid, and the plots may have been a small CO_2 source which was not included in the budget.

The largest component of the carbon balance in our experiment was photosynthesis. Rising temperatures can affect photosynthesis rates in two ways: (i) by a direct influence on enzyme kinetics, and (ii) indirectly via changes in leaf area or nutrient uptake. Direct effects probably have no lasting impact on the long term, unless the growth potential also augments (Sage and Sharkey, 1987). Moreover, photosynthetic acclimatization often reduces the effect of higher temperatures (Oberbauer and Oechel, 1989). Previous research indicates that photosynthesis and growth in arctic vegetation are more limited by nutrient availability than by production of photosynthate (Tissue and Oechel, 1987). For these reasons direct effects in our plots could be small. If temperatures rise, decomposition rates increase and formerly unavailable nitrogen can become available, enhancing primary productivity (Nadelhoffer et al., 1992). Uptake of nutrients can likewise be stimulated by higher root activity in a warmer soil (Oechel and Billings, 1992). As a consequence, higher leaf area and green cover can occur (Barnes et al., 1998), increasing whole-plant photosynthesis even if photosynthetic rates per unit leaf area do not (Oechel and Billings, 1992). In our study, green cover was enhanced in the heated plots (Fig. 1A), and the positive relationship between $P_{gross,mean}$ and percentage green cover (Fig. 2E) suggests that part of the P_{gross}-stimulation can indeed be ascribed to more vigorous growth. Nevertheless, there was also a substantial fraction not related to vegetation structure (Fig. 2F). Combined, direct and indirect effects led to an increase in seasonal photosynthesis of almost 25%, which constituted the greatest change of the three C-balance components in absolute figures (2.96 mol CO_2 m^{-2}).

However, in relative terms, belowground respiration was enhanced more by the warming. Temperature was also the factor to which soil respiration was most sensitive (Fig. 3A). Contrary to the findings of Johnson et al. (2000), the unheated plots in our experiment responded more strongly to temperature change (higher Q_{10}) than the heated plots. A possible reason for this is that Q_{10} itself is temperature dependent (Schleser, 1982; Janssens and Pilegaard, 2003). Temperature sensitivity of soil respiration would be higher if temperatures were low, owing to the higher probability that temperature becomes the limiting factor. In heated plots, temperature would be less limiting because the mean soil temperature is higher. For example, at low temperature, small increases can have disproportionate effects on population size, and thus on soil respiration, of micro-organisms (Janssens and Pilegaard, 2003). Alternatively, lower Q_{10} in a warmer environment could arise from changes in microbial community structure, *in casu* dominance of species with a higher temperature optimum, which mitigates increases in respiratory CO_2 release (Rustad and Norby, 2002). Increased root density in a warmer climate through and subsequent enhanced substrate availability can stimulate heterotrophic respiration (Raich and Schlesinger, 1992), which would shift the entire $R_{soil} - T_{soil}$ curve upwards. In our experiment, R_{soil} at low temperature was increased by the long-term effect of warming, but at high temperature it was decreased (Fig. 3A), in other words, the curve was tilted. This implies that the 33.3% seasonal increase in R_{soil} was caused mainly by the direct influence of the 2.5°C warming. Soil respiration was measured directly on the soil on bare spots fully surrounded by vegetation; readings consequently represent intermediate values between the probably higher respiration at full cover and the probably lower respiration of larger bare spots which were not selected. This also may influence the canopy respiration, although not the sum of soil and canopy respiration (measured with ecosystem chambers) and therefore the total carbon balance remains unbiased.

In the summer of 1999, high precipitation in the Zackenberg region gave rise to high soil moisture (Fig. 1B), which may quench temperature changes (Campbell and Norman, 1998). Nevertheless, in our experiment there was only a delay of 2 d before the temperature difference between heated and unheated plots became stable. In other words, background temperature variation may have been leveled off by the wet soils, but treatment temperature increments were not. In a warmer environment, the upper soil layer will dry out first. This may have stimulated soil respiration in our heated plots, on top of the direct warming effect. Soil moisture had a different residual effect on soil respiration in both treatments (Figs. 3C, 3D). A linear effect occurred in the heated plots whereas in the unheated plots an optimum was reached at a water content of 60%. The latter confirms that low soil moisture induces stress through water deficit, and that wet soils limit microbial respiration by oxygen deficit and by a water film on the substrate impeding diffusion (Skopp et al., 1990). Absence of high water contents (>80%) may have caused an erroneous estimate of the (linear) relation observed in the heated treatment. Other aspects of water relationships likely to change in a warmer climate are evapotranspiration, thawing depth and active layer thickness, the increase of which improves drainage and nutrient availability (Oechel and Billings, 1992; Mooney et al., 1999). Several studies have found higher carbon efflux in northern areas that were drained (Silvola, 1986; Davidson et al., 1998; Oechel et al., 1998). Also Oechel et al., (1998) observed elevated temperature apparently interacting with drainage, exacerbating net carbon loss. However, on the long term, this effect was neutralized or even changed direction by increasing primary productivity (Oechel and Billings, 1992). Whether these effects of drainage will occur at our site in the future, is difficult to predict from our data. If soil moisture decreases till median values (60%), higher soil respiration can be expected. If the soil continues to dry, soil respiration could be limited (Fig. 3C).

End-of-season senescence is another process that controls soil respiration. As part of R_{soil} is root respiration, R_{soil} will decrease faster in senescing vegetation. Senescence is a protecting mechanism against low winter temperatures that is believed to be controlled by photoperiod in arctic regions, rather than by temperature (Barnes et al., 1998; Arft et al., 1999). However, in our heated plots the onset of senescence was delayed and the process itself was slower (color analysis of vegetation images, Marchand et al., unpublished), potentially allowing soil respiration to remain high longer through higher root activity. Postponed senescence could at the same time have detrimental effects on survival, for example, if nutrient loss through insufficient end-of-season resorption from senescing leaves prior to the first major frosts, is aggravated. The observed stronger decrease in photosynthesis late in the season in the control plots relative to the heated plots (Fig. 5A), is in agreement with delayed senescence (cf. also Fig. 6D, where the vegetation in unheated plots hardly photosynthesized anymore at the end of the season, while in the heated plots there was still photosynthesis). Recent studies suggest that respiration during winter can have important effects on the annual carbon budget of arctic ecosystems (Oechel et al., 1997; Fahnestock et al., 1998). In spite of air temperatures decreasing substantially in autumn, soil temperatures in the arctic are highest in this season (Meltofte and Thing, 1997), allowing metabolic activity of soil organisms to remain high until late in the year, thereby increasing annual carbon release and nutrient mineralization (Nadelhoffer et al., 1992; Grogan and Chapin, 1999). Warmer autumn soils in a future climate, as in our heated plots, may therefore amplify these effects.

Nevertheless, from our data we see that, although soil respiration was still higher at the end of the season in the heated plots, both the treatment difference and the absolute efflux had already been much reduced (Fig. 5A). Large shifts in the overall annual C-balance due to autumn/winter effects of warming are therefore unlikely, even if this balance could well turn out to be positive. Another possible consequence of higher mean winter temperatures is earlier thaw of the soil in spring. This could augment soil respiration at the beginning of the season, although also growth and photosynthesis can be stimulated earlier (McCarthy et al., 2001).

Also for canopy respiration, temperature was the most influencing factor (Fig. 4A). However, contrary to soil respiration, the response curve was not significantly shifted by the heating treatment, in spite of the higher green cover in the warmed plots (which one would expect to promote R_{canopy}). This suggest that either specific leaf area was increased by warming (in other words, that green cover increase did not reflect biomass increase), or, if biomass did increase, that specific respiration (per unit mass) was reduced. However, with the residual analysis (Fig. 4B) we detected that Figure 4A concealed an influence of green cover on canopy respiration, in other words, R_{canopy} values above the curve in Figure 4A originated relatively more from dates and/or plots with higher cover, and vice versa. It is therefore likely that the observed higher green cover in the heated plots (Fig. 1A) effectively enhanced canopy respiration, but not enough to be detected in the scattered data on Figure 4A. The seasonal course of canopy respiration matches the seasonal green cover evolution, exhibiting a maximum in the middle of the growing season and a decrease after the peak in green cover, although this time trend combines cover effects with effects of decreasing temperatures and possibly also the onset of senescence. Improved supply of nutrients in a warmer environment has been reported to enhance enzyme concentrations and thus leaf respiration (Barnes et al., 1998), but this seems unlikely in our experiment in view of the similarity of R_{canopy}. With a Q_{10} of 1.71, canopy respiration was less sensitive to warming than soil respiration, a trend also observed at this location in 1998 (Mertens et al., 2001). This is in agreement with findings of Rustad and Norby (2002), who observed higher temperature sensitivities in the various components of soil respiration. Overall, warming enhanced carbon efflux through canopy respiration with 10.8%, which makes it the component that was least influenced by the treatment.

During July and August 1999, simulated warming hardly affected the total carbon balance of our high arctic tundra ecosystems (both were a small sink), but turnover was increased through significant stimulation of all components. This is consistent with a meta-analysis of soil warming studies, mostly from temperate sites, which showed that soil respiratory C losses and plant growth increased at about the same rate (Rustad et al., 2001). In tundra, the trend of compensating influx and efflux is observed also in current climate. For example, using a closed gas exchange system, Oechel et al. (1998) observed net ecosystem exchange rates in wet sedge tundra ecosystems at 70°N which were comparable to those in our High Arctic grass-dominated tundra, although the values for photosynthesis and ecosystem respiration were only half as large. Similar observations, also chamber measurements, are available from Nordstroem et al. (2001) for a High Arctic fen ecosystem in the Zackenberg area itself: while ecosystem respiration fluxes were on average lower (6.27 g CO_2 m^{-2} d^{-1}) than in our unheated and heated plots (8.87 and 10.88 g CO_2 m^{-2} d^{-1}, respectively), average net ecosystem CO_2 exchange rate was similar. Also in the Zackenberg area, tundra dominated by *Salix arctica* and grassland tundra dominated by *Arctagrostis latifolia*, *Carex saxatilis* and *Eriophorum triste*, had respiration and photosynthesis rates which were themselves close to those in the current study (Christensen et al., 2000). However, even if vegetation type and climate warming would not have large impact on ecosystem C-balance, net exchange may shift when atmospheric CO_2-concentration is increased at the same time (Rastetter et al., 1997). Although complex to manage in remote locations, estimates of future changes in atmospheric CO_2 and climate would benefit from research on interaction between CO_2 and temperature impact on tundra ecosystems.

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