Biogeosciences Discussions

Seasonality in a boreal forest ecosystem affects the use of soil temperature and moisture as predictors of soil CO$_2$ efflux

S. M. Niinistö[1,*], S. Kellomäki[1], and J. Silvola[2]

[1]School of Forest Sciences, University of Eastern Finland, P.O. Box 111, 80101 Joensuu, Finland
[2]Department of Biology, University of Eastern Finland, P.O. Box 111, 80101 Joensuu, Finland
[*]currently at: Finnish Forest Research Institute, Vantaa Unit, P.O. Box 18, 01301 Vantaa, Finland

Correspondence to: S. M. Niinistö (sini.niinisto@iki.fi)

Discussion Paper | Discussion Paper | Discussion Paper | Discussion Paper

BGD

8, 2811–2849, 2011

Seasonality of soil CO$_2$ efflux in a boreal forest

S. M. Niinistö et al.

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◄◄ | ►►

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Abstract

Our objectives were to identify factors related to temporal variation of soil CO$_2$ efflux in a boreal pine forest and to evaluate simple predictive models of temporal variation of soil CO$_2$ efflux. Soil CO$_2$ efflux was measured with a portable chamber in a Finnish

5 Scots pine forest for three years, with a fourth year for model evaluation. Plot averages for soil CO$_2$ efflux ranged from 0.04 to 0.90 g CO$_2$ m^{-2} h^{-1} during the snow-free period, i.e. May–October, and from 0.04 to 0.13 g CO$_2$ m^{-2} h^{-1} in winter. Soil temperature was a good predictor of soil CO$_2$ efflux. A quadratic model of ln-transformed efflux explained 76–82% of the variation over the snow-free period.

10 The results revealed strong seasonality: at a given soil temperature, soil CO$_2$ efflux was higher later in the snow-free period than in spring and early summer. Regression coefficients for temperature (approximations of a Q_{10} value) of month-specific models decreased with increasing average soil temperatures. Efflux in July, the month of peak photosynthesis, showed no clear response to temperature or moisture. Inclusion of a

15 seasonality index, degree days, improved the accuracy of temperature response models to predict efflux for the fourth year of measurements, which was not used in building of regression models. Underestimation during peak efflux (mid-July to late-August) remained uncorrected. The strong influence of the flux of photosynthates belowground and the importance of root respiration could explain the relative temperature insensitiv-

20 ity observed in July and together with seasonality of growth of root and root-associated mycorrhizal fungi could explain partial failure of models to predict magnitude of efflux in the peak season from mid-July to August.

The effect of moisture early in the season was confounded by simultaneous advancement of the growing season and increase in temperature. In a dry year, however, the

25 effect of drought was evident as soil CO$_2$ efflux was some 30% smaller in September than in the previous wet year. Although soil temperature was a good overall predictor of soil CO$_2$ efflux, possibly partly due to its proxy-like quality for covarying processes, strong seasonality of the temperature response observed in this boreal forest

corroborates recent findings concerning the importance of seasonal changes in carbon inputs to processes producing CO_2 in soil.

1 Introduction

Soil CO_2 efflux, also called soil respiration, constitutes most of the total respiration in forest ecosystems (e.g. Janssens et al., 2001). It originates from root and rhizosphere respiration as well as from respiration by soil microbes and fauna associated with decomposition of organic matter. It has been reported to be regulated directly or indirectly by two major environmental factors, temperature and moisture, with soil temperature usually having an overriding influence in forest ecosystems (e.g. Witkamp, 1966; Schlesinger, 1977). As soil temperature and moisture often covary in field conditions, it has been difficult to separate their effects (Schlesinger, 1977; Davidson et al., 1998), especially as in many cases the influence of soil moisture in forest ecosystems has been small or undiscernible (e.g. Russell and Voroney, 1998).

Other factors affecting soil CO_2 efflux are vegetation and substrate quality, ecosystem productivity, relative allocation of primary production above- and belowground, dynamics of the above- and belowground flora, fauna and microorganisms and land-use and disturbance regimes (Rustad et al., 2000). Substrate availability, in particular, has recently emerged as an important factor behind temporal variation in soil CO_2 efflux (Högberg et al., 2001; Davidson et al., 2006).

Seasonality, especially seasonality of the temperature response, is an aspect of temporal variation of soil CO_2 efflux that has received less attention. Seasonality affecting soil CO_2 efflux can be seen as a combination of the seasonal variation in environmental variables, in substrate availability and quality to different CO_2 producing processes, and their interactions.

Boreal forest ecosystems are characterized by distinct seasons: long snow-covered winters and relatively short snow-free seasons comprised of spring, summer and autumn. In a boreal pine forest, 95% of the annual carbon gain can be obtained during

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

the six warmest months (Linder and Lohammer, 1981). Intensity of the growing season can be seen in the rapid increase in photosynthesis early in the season in pines growing in cold climates, compared to a slower change in pines growing in warm climates, which photosynthesize all year (Teskey et al., 1994). Recently, soil CO$_2$ efflux has been observed to be strongly influenced by the flux of recent photosynthates to the roots (Högberg et al., 2001; Keel et al., 2006). Root production of woody plants and grasses as well as mycelial production of ectomycorrhizal fungi have been found to have a seasonal pattern (Wallander et al., 1997, 2001; Steinaker et al., 2010), which most likely influences temporal variation of forest soil CO$_2$ efflux through root respiration and root-associated heterotrophic respiration. Microbial populations and litter inputs also vary seasonally (Lipson et al., 1999). Thus we hypothesize that, in addition to environmental variables such as temperature and moisture, soil CO$_2$ efflux of a boreal forest is affected by other factors that vary according to season, thus resulting in seasonality of soil CO$_2$ efflux.

Here, we investigated temporal variation of soil CO$_2$ efflux and environmental characters that affect this variation in a boreal forest in Finland. Objectives of the study were to assess the level of soil CO$_2$ efflux in this pine ecosystem, to identify factors related to its temporal variation and to evaluate simple predictive models of temporal variation. The 3-yr measurement campaign enabled us to analyse the effect of season. For model evaluation, a fourth snow-free period of measurements at the same site and on a neigboring site was included.

2 Materials and methods

2.1 Site and weather description

The study site was located in Huhus (62°52′ N, 30°49′ E), some 30 km from Mekrijärvi Research Station, University of Joensuu, Finland. The mean annual temperature at the nearby meteorological station is 2.1 °C, with monthly means of 16.0 °C for July and

–10.6 °C for January. Mean annual precipitation is 667 mm, of which an average of 400 mm falls between May and October (Drebs et al., 2002). Precipitation in May–October during the experiment was 370, 545, and 265 mm in 1997, 1998, and 1999, respectively. The average air temperature of 13.4 °C at the site in June–August 1998 was 1.5–2.0 °C lower than the average for the other study years.

The site was situated in a forested area of managed Scots pine stands (*Pinus sylvestris* L.). At the beginning of the study, tree height in the area was 10–13 m for 76% of the trees. The average leaf-area index was estimated to be 2.07 m^2 m^{-2} ground area (Kellomäki and Wang, 1999). The ground was covered with mosses, such as *Pleurozium schreberi* (Brid.) Mitt., *Hylocomnium splendens*, *Dicranum* sp., *Polytrichum* sp., lichens, such as *Cladina* spp., *Cladonia* spp. and *Cetraria islandica* (L.) Ach., and dwarf shrubs, such as blueberry (*Vaccinium myrtillus*) and lingonberry (*Vaccinium vitis-idaea* L.). The pine needle litterfall was 136 g m^{-2} a^{-1} in average. When soil particles smaller than 20 mm in diameter were considered, the upper 30 cm of soil, i.e. the main tree-rooting zone, was classified as podsolized sandy till. Small stones with a diameter of 20–60 mm, however, made up about one sixth of the soil volume. The average depth of the top layer, which consisted of dead moss and litter, was 5.7 cm and that of the underlying organic layer, i.e. humus, was 2.5 cm.

2.2 Measurement of soil CO$_2$ efflux and temperature

Three plots for soil CO$_2$ efflux measurements were established in two forest stands representing two stages of forest development; Plots 1 and 2 in a stand about 65 yr old (thinned about 10 yr before, diameter at 1.3 m 18.4 and 21.5 cm on average in 1998, with 600 and 650 stems ha^{-1}, on Plots 1 and 2, respectively) and Plot 3 in a pole-stage forest about 40 yr old (with an average diameter of 11.1 cm and 2000 stems ha^{-1}, not yet thinned). Each plot was 20 m × 20 m and had 10 randomly chosen permanent measurement points in a 2 m × 2 m grid. Plot means were used as observations of soil CO$_2$ efflux.

S. M. Niinistö et al.

Steel collars with a diameter of 10 cm and height of 6 cm were inserted 2–4 cm into the surface soil so that their tops were level with the tops of the mosses or lichens. CO$_2$ efflux was measured for 120 s with an infra-red gas analyzer and a portable closed system with an opaque chamber that had a volume of 1.17 dm^3 (EGM-1 with SRC-1, PP Systems, Hitchin, UK) (Niinistö et al., 2004). The type of measurement chamber can lead to an overestimation of 10–20% on bare soil (Pumpanen et al., 2004). Values for soil CO$_2$ efflux included dark respiration of mosses and lichens in this study. Measurements were made twice per measuring day, one or two days a week throughout the snow-free period of three years, i.e. from June to October 1997 and from May to October 1998–1999, with a three-week gap in September–October 1997 and in August 1998 due to equipment failure. For purposes of model evaluation, measurements of soil CO$_2$ efflux were taken from Plot 1 in Huhus and from a plot with an identical set-up in a young Scots pine stand at nearby Mekrijärvi Research Station in 2000.

Soil was covered with snow from November to late April or early May each year. Winter measurements were made once a month at 4–6 locations in February–April 1999 and March–April 2000. Large closed chambers (54–115 dm^3) were used on 60 cm × 60 cm measurement locations cleared of snow, and air in the headspace was sampled every 15 min during each 60-min measurement (Crill, 1991; Larmola et al., 2004). The CO$_2$ concentration of samples was analyzed on the same day with an infrared gas analyzer (Uras 3E, Hartman & Braun AG, Frankfurt a. M., Germany). The flux was calculated based on a linear rise in CO$_2$ concentration in the headspace during the measurement. In connection with chamber measurements, air of undisturbed snow packs was sampled with a metal straw and its CO$_2$ concentration analyzed. Snow was sampled and weighed, and its porosity was calculated using the density of pure ice (0.9168 g cm^{-3}), which resulted in porosities of 55% to 79%.

During the snow-free period, soil temperature was measured adjacent to each collar at the time of the CO$_2$ efflux measurement. It was recorded at a depth of about 1–2 cm in the organic layer, i.e. about 6 cm measured from the top of the mosses and lichens with a portable temperature probe (STP-1, PP Systems, Hitchin, UK). Later,

soil temperatures at equivalent depth and within 100 m of the plots, measured by the Vaisala Weather Station (MILOS 500, Vaisala Oy, Helsinki, Finland), were used in the modelling analyses.

2.3 Soil moisture measurements

Soil moisture was monitored with three different methods: tensiometers, water-content reflectometers and gravimetric sampling (Table 1). Soil water potential was measured with tensiometers starting from the second year (1998) on days for measuring soil CO_2 efflux, with the exceptions being freezing conditions early or late in the season or on some very dry days in 1999. No soil moisture measurements were made yet in 1997. Starting in 1999, water-content reflectometers monitored soil water content continuously. In addition, the gravimetric water content of upper soil layers, i.e. moss, litter, and the organic layer was determined on days for measuring soil efflux (Table 1).

Tensiometer plots were situated on gentle slopes and small depressions next to Plot 1 and on flat terrain next to Plot 3; 2 to 3 tensiometers were placed at depths of 5, 10, 20 and 30 cm of mineral soil, i.e. to the depth of the main rooting zone. To convert tensiometer readings to values for soil water content, the water retention curve was determined in the laboratory in desorption for depths of 5–30 cm with a tension chamber and a pressure plate apparatus (Klute, 1986). Soil water retention ranged, on average, from 0.55 m^3 m^{-3} at saturation (−0.1 kPa) to 0.25 m^3 m^{-3} at −10 kPa and 0.07 m^3 m^{-3} at the wilting point (−1554 kPa). Water-content reflectometers were installed close to Plot 1 and placed horizontally at mineral soil depths of 5, 15, and 25 cm. There was also a sensor in the surface layer, which consisted of both the organic layer and the topmost mineral soil. Velocity of the electromagnetic waves along the 30-cm sensor rods was converted to volumetric water content using equations based on soil-specific calibration (Appendix A).

Differences in water content between measurement depths in mineral soil were small, but at all times of measurement the surface layer was wetter than the mineral soil layers (Table 1). Water-content reflectometers were found to give about 0.10 m^3 m^{-3}

lower values than the comparable values calculated from tensiometer readings with the help of a cubic model of water retention. This was probably due to small stones, which were too big to be included in core samples for water retention analysis but were abundant in the soil. Still, the seasonal patterns were similar, which resulted in a good correlation between the two methods (Spearman rank correlation coefficient, $r_s = 0.89$–0.97 for different depths, $P < 0.001$).

2.4 Modelling and statistical analyses

Different models of soil temperature and moisture response were fitted to the data and data subsets (Table 2). Because soil temperature recorded at the weather station was found to be as good a predictor as temperature measured adjacent to each collar, it was therefore used in model analyses. For analyses containing observations from 1997, however, temperature readings next to the collars were used because of the discontinuity in weather station measurements in 1997. In the efflux data for late summer of 1997, sudden extreme values of 4 to $6\,\mathrm{g\,CO_2\,m^{-2}\,h^{-1}}$ from a measurement point (caused most likely by a rapid increase in fungal activity as found in Savage and Davidson, 2003) were excluded from the plot averages to allow assessment of the effect of temperature on soil CO$_2$ efflux. The complete 6-month data from the two later years, 1998 and 1999, were used for further multivariable analysis, because the data of 1997 lacked soil moisture measurements.

The temperature response of CO$_2$ efflux was modelled as an exponential function (as in Anderson, 1973; Davidson et al., 1998, Niinistö et al., 2004). Logarithmic transformation of CO$_2$ efflux was used because it linearized the temperature response and corrected heteroscedasticity for both the linear and quadratic models tested. In multivariable analysis, different factors were tested as predictors of logarithmic transformation of soil CO$_2$ efflux (Table 2). Degree days or temperature sum was calculated according to the guidelines of the Finnish Meteorological Institute by cumulatively totalling those parts of the daily air temperature that exceeded a threshold of 5 °C. Summing up started when daily air temperatures had continuously exceeded 5 °C for five days in

spring and ended when daily temperatures had been below the threshold temperature for five consecutive days in autumn.

Regression and correlation analyses were carried out with SPSS 16.0 software (SPSS Inc, Chicago, USA). Differences in regression coefficients and intercepts between linear regressions were tested with Student's t-test. To correct the bias caused by the logarithmic transformation, half of the total residual variance was added to the logarithmic prediction for model evaluation. Root Mean Squared Errors and Akaike's Information Criterion were used for comparing models and tolerance was used to assess multicollinearity.

3 Results

3.1 Temporal pattern and range of soil CO_2 efflux

Soil CO_2 efflux peaked in July–August, in general, following changes in soil temperature (Fig. 1a, b). However, a drop in July 1999 appeared to be related to a steep decline in soil water content at the same time (Fig. 1b, d). In general, plot averages ranged from 0.04 to 0.90 g CO_2 m^{-2} h^{-1} during the snow-free period in 1997, 1998 and 1999. The minimum for individual point observations was 0.02 g CO_2 m^{-2} h^{-1} in the freezing conditions of May 1999, and the maximum was 2.25 g CO_2 m^{-2} h^{-1}, which was measured after thunderstorms in July 1997.

Sudden extreme values of 4 to 6 g CO_2 m^{-2} h^{-1} from a measurement point were found in August–September 1997 that were most likely caused by a rapid increase in fungal respiration. In the following years, similar but less extreme increases were observed in individual points in August–October that resulted in fungal fruit bodies found inside measurement collars (Fig. 2).

Winter fluxes ranged from a mean of 0.044 g CO_2 m^{-2} h^{-1} in February 1999 to 0.134 g CO_2 m^{-2} h^{-1} in March 2000, the average being 0.06 g CO_2 m^{-2} h^{-1} for 1999 and 0.12 g CO_2 m^{-2} h^{-1} for 2000. The snow layer decreased in depth from February to

April and became more compacted and layered with icier streaks, trapping CO_2 efflux from the soil more effectively. CO_2 concentration close to the soil surface varied with the characteristics of the snow pack: under well-aerated snow cover, in February 1999 it was 400–700 ppm, whereas under the deep and layered snow of March 2000 it was, on average, 1050 ppm (Fig. 3).

3.2 Response to temperature and seasonality of the temperature response

According to a linear regression model for the combined data for the snow-free periods of years 1997, 1998 and 1999, variation in soil temperature (T_{soil}) next to the collars explained 67% of the variation in the natural logarithm of soil CO_2 efflux (Ln-Flux) (Fig. 4). A quadratic LnFlux model captured low efflux rates at the lowest soil temperatures better than the linear LnFlux model and did not overestimate efflux at the highest temperatures as the linear model did (Fig. 4). This resulted in a significantly smaller root mean square error (RMSE, by about 20%) and greater coefficient of variation ($R^2 = 0.76$ for 1997–1999 in Fig. 4, 0.82 for 1998–1999 in Table 2) than the linear model. The further developed version of the Arrhenius function, the so-called Lloyd & Taylor model (Lloyd and Taylor, 1994), also performed well and with a satisfactory residual pattern ($R^2 = 0.64$, Fig. 4).

According to analyses of one-, two- or three-year data, at a given temperature, soil CO_2 efflux was higher later in the snow-free period than in spring and early summer. Observations grouped by month indicated a difference between early and late season (Fig. 5a). Based on month-specific temperature response models for pooled 1997–1999 data, regression coefficients for temperature, and thus approximations for Q_{10} values, decreased with increasing average soil temperature (Fig. 5b, c). The month of May had the lowest predicted CO_2 efflux at 10 °C and August the highest.

Efflux observations in July showed no clear response to soil temperature at the time of measurement: no response to temperature in pooled three-year data or in 1998 and 1999 separately, but a weak positive response to temperature in July 1997 ($R^2 = 0.15$, $p = 0.013$, $n = 41$). Correspondingly, for 12 of the 15 collars that remained the same for

the three-year period, analyses of the efflux of individual measurement collars revealed no temperature response in July and a weak response for 3 collars (only with soil temperature $\leq 20\,^\circ$C). The 24-h and 48-h averages for soil or air temperature failed to explain the variation in soil CO_2 efflux in July 1999.

3.3 Response to soil moisture

A decrease in soil moisture was correlated with an increase in soil CO_2 efflux during the the first three months of the snow-free period in both years (Spearman's rho (ρ) between LnFlux and soil water content was -0.68 in May–July 1998 and -0.80 in May–July 1999 compared to -0.51 and -0.73 between soil temperature and soil water content in May–July 1998 and in May–July 1999, respectively, $p < 0.001$). There was a strong negative correlation between soil water content and time in May–July. Soil water content decreased with time after the maximum water content in May, after the snow-melt (ρ between soil water content and Julian Day was -0.80 in 1998 and -0.94 in 1999, $P < 0.001$). A similar strong, but positive correlation was found between soil CO_2 efflux and time (ρ between LnFlux and Julian Day was $+0.81$ in May–July 1998 and $+0.87$ in May–July 1999, $P < 0.001$). There was no clear correlation between soil CO_2 efflux and soil moisture during the latter part of the snow-free period, August–October, in either year.

When observations for which the soil matric potential was smaller than -10 kPa were selected, soil CO_2 efflux increased linearly with increasing soil moisture. The negative effect of dry conditions was notable in 1999. For instance, soil CO_2 efflux at $10\,^\circ$C was one third smaller in September 1999 ($\theta_{\text{mean}} = 0.08 \pm 0.018$ (s.d.) $m^3\,m^{-3}$) than in September 1998 ($\theta_{\text{mean}} = 0.19 \pm 0.016$ (s.d.) $m^3\,m^{-3}$, estimated from matric potential measurements) although mean soil temperature during the measurements was the same and the range of temperatures was similar (Fig. 1c, d).

Accordingly, for observations for which soil moisture was below $0.10\,m^3\,m^{-3}$ in 1999, mainly in August and September, variation in water content of mineral soil alone

explained 64% of the variation in LnFlux ($P < 0.001$, $n = 89$); and addition of soil temperature added only some 8% more to the explained variation. Correspondingly, the month-specific temperature models based on 3-yr data overestimated efflux in the driest conditions, i.e. when soil water content was below $0.8\,\mathrm{m^3\,m^{-3}}$ in August and September 1999.

However, residuals calculated by subtracting efflux predicted by the month-specific temperature models from observed efflux did not, in general, show any trend with soil water content for the entire range of soil moisture for 1998 and 1999. Variation in mineral soil moisture did not explain the variation in CO_2 efflux in July 1998 or July 1999 ($n = 38$, 1998 and 47, 1999), but there was some positive correlation between LnFlux and gravimetric water content of moss and the organic layer measured at the time of flux measurements in July of the dry year 1999 (Spearman's rho 0.70 and 0.45, $p < 0.001$ and <0.02, $n = 29$).

3.4 Multiple regression models, their evaluation and estimates of annual efflux

In multiple regression models for the entire snow-free period, soil temperature was the dominant predictor of ln-transformed soil CO_2 efflux (LnFlux). Addition of the square of soil temperature markedly improved the model (Table 2). Multiple regression models were based on pooled data for the years 1998 and 1999 because the data for 1997 lacked observations on soil water content.

Degree days, i.e. cumulative sum of daily air temperatures exceeding $5\,^\circ\mathrm{C}$ or its alternatives Julian Day and degree days divided or multiplied by Julian Day, were better auxiliary predictors of LnFlux than soil moisture was (Table 2). A multiple regression model with soil temperature, degree days as an index of seasonality and their squares as predictors was found to have a good fit for the entire snow-free period, especially due to its evenly distributed residuals with respect to measured efflux. Inclusion of the square of degree days was justified on the basis of the decrease in RMSE, but addition of soil moisture was not justified nor was inclusion of an interaction variable of

Seasonality of soil CO$_2$ efflux in a boreal forest

S. M. Niinistö et al.

soil temperature x degree days. Residuals for the model with soil temperature, degree days and their squares did not vary with soil moisture.

The performance of different regression models was compared to independent sets of soil CO$_2$ efflux data collected on two sites, Huhus and Mekrijärvi, in the year 2000.
5 The chosen LnFlux models based on pooled 1998 and 1999 data measured in Huhus, a simple linear temperature model, a quadratic temperature model, with or without soil moisture, and a combined quadratic temperature and quadratic degree days model (Table 2) were used to predict efflux on Plot 1 in Huhus. In addition, the quadratic temperature models with and without degree days were used to estimate the efflux on
10 a plot of identical design in another young pine stand in nearby Mekrijärvi.

In general, models overestimated the efflux at low temperatures, i.e. in May and October at both sites. The relatively greatest single overestimation, up to 110–140% by models without degree days as a seasonality index and approximately 60% by combined temperature and degree days model, occurred on a typical spring day in May:
15 air and surface soil temperatures were clearly above 10 °C but efflux was still relatively low, 0.21 g CO$_2$ m^{-2} h^{-1}. The greatest consistent underestimation occurred in Huhus during the peak season in August: an average of 35% by the linear temperature model, about 25–30% by the quadratic temperature model with or without soil moisture and an average of 17% by the quadratic temperature model with the degree days (Fig. 6). For
20 Mekrijärvi, the greatest underestimations with the quadratic temperature and degree days model were also made for two days of peak flux that occurred there in July.

On the whole, the quadratic temperature and degree days model performed best with a high correlation between measured and predicted flux both in Huhus ($R^2 = 0.90$, $p < 0.001$) and in Mekrijärvi ($R^2 = 0.89$, $p < 0.001$). Inclusion of degree days in the
25 temperature model resulted in a notable decrease in average difference between measured and predicted flux for both sites (Fig. 7). It especially improved predictions at low temperatures in May but also, in general, in June to September, although not in October (Fig. 6).

For Huhus, the difference between measured and predicted was, on average, 14% of the average (0.45 g CO_2 m^{-2} h^{-1}) for the measured flux using the quadratic temperature model with degree days. There was a small bias connected with observations from the three days of peak flux, 18 July and 1 and 15 August. In comparison, the linear and quadratic temperature models gave unbiased estimates; i.e. regression intercepts were not significantly ($p < 0.001$) different from 0 nor did the regression coefficients differ significantly from 1 (1:1 line), but the correlation between measured and predicted efflux was notably smaller ($R^2 = 0.56$ and 0.61, $p < 0.001$). Predictions made by the quadratic soil temperature model with moisture differed slightly from the 1:1 line of predicted versus measured efflux, indicating small bias.

Despite a small bias, a quadratic temperature and degree days also gave good predictions for the nearby Scots pine site in Mekrijärvi; the difference between measured and predicted was, on average, 12% of the average (0.47 g CO_2 m^{-2} h^{-1}) for the measured flux. Exclusion of a measuring point with a burst of efflux related to fungal growth starting in August, at maximum four-fold compared to the plot mean, improved the fit.

3.5 Annual estimates

Different models of LnFlux (Table 2) resulted in small differences in cumulative estimates of soil CO_2 efflux. For the six snow-free months in 1998, the estimate predicted with the quadratic temperature and degree days model and continuous weather data was 3% greater than the estimate of 1509 g CO_2 m^{-2} by the quadratic temperature model. For the six snow-free months of 1999, estimates with the quadratic temperature and degree days model and the quadratic temperature and soil moisture model were within 1% of the estimate of 1533 g CO_2 m^{-2} by the quadratic temperature model. The difference in the estimated sum of soil CO_2 efflux between the snow-free periods of 1998 and 1999 was small, 1–1.5%. The period from June to August represented 50–60% of the annual estimate.

Accumulated efflux during winter was calculated using the average of the winter measurements in February–April 1999 for 1998 and the average of the measurements in

March–April 2000 for 1999. The six winter months thus represented, on average, 14% of the annual soil CO_2 efflux for the snow-free period of 1998 combined with the winter 1998–1999 and 25% for the snow-free period of 1999 combined with the winter 1999–2000. The greater efflux in winter 1999–2000 compared to the winter before resulted in a 15% greater annual sum for the latter 12 month period (i.e. 2050 g CO_2 m^{-2} a^{-1}). Although the models underestimated the efflux during the period of peak efflux (see Sect. 3.4), the greater efflux in the latter winter had a greater effect on the annual estimates than a correction of +15% for the efflux in July–August would have had.

4 Discussion

4.1 Range of soil CO_2 efflux and annual sum

The soil CO_2 efflux measured here was within the range reported for boreal Scots pine forests (e.g. Högberg et al, 2001; Pumpanen et al., 2003a). Our annual estimates also corresponded to those obtained for some forest ecosystems in the boreal zone (e.g. Kurganova et al., 2003; Wang et al., 2003) but were smaller than others (Russell and Voroney, 1998; Rayment and Jarvis, 2000; Domisch et al., 2006). Overestimation of soil surface efflux for the site covered mainly with a feathermoss, *Pleurozium schreberi*, can be estimated to be some 10% for including moss dark respiration in conditions with an average efflux of 0.42 g CO_2 m^{-2} h^{-1}, average water content in moss of 250% and average air temperature at the time of measurements 15 °C in 1999 (see Silvola, 1985, 1992).

The range of soil CO_2 efflux measured in winter in this study in a pine forest was smaller than that measured in a Finnish spruce stand (Domisch et al., 2006) but similar to the range of efflux in other boreal forests (Winston et al., 1997; Kurganova et al., 2003; Pumpanen et al., 2003a). The contribution of the snow-covered period to the annual estimate of soil CO_2 emissions in 1999 corresponded to the previously reported estimates, 5 to 22%, for boreal forests with an equally long snow-covered period

(Kurganova et al., 2003; Wang et al., 2003; Domisch et al., 2006). The greater efflux in winter 1999–2000 compared to winter 1998–1999 could be explained by higher soil temperatures in January–April 2000, when temperatures remained around 0 °C, as winter flux has been suggested to be sensitive to interannual variation in temperature (Winston et al., 1997). Differences in substrate availability and in snowpack structure could also have been contributing factors. The more layered snowpack early in 2000 probably caused CO_2 to accumulate in soil more than it had under better-aerated snowpack in 1999. Melt-freeze crusts in snow appeared to restrict transportation of CO_2 for at least a month or two in late winter, contrary to earlier observations (Winston et al., 1997); but the extent of the restriction appeared to be dependent on the weather pattern in this climate.

4.2 Seasonality of temperature response

At a given temperature, soil CO_2 efflux was observed to be higher later in the snow-free period than in spring and early summer, which is similar to findings in a Douglas-fir forest (Drewitt et al., 2002) and is supported by the month-specific models and results for model validation in this study. Variation in soil moisture did not explain the seasonality of the temperature response. Monthly averages and models agreed with earlier findings of greater efflux in autumn compared to spring at comparable temperatures in a temperate forest (Crill, 1991). Our monthly models resulted in a pattern of predicted soil CO_2 efflux identical to that found in a Siberian pine forest study (Shibistova et al., 2002), with the month of May having the lowest CO_2 efflux at 10 °C and August having the highest.

Our results can be partly attributed to temporal variation in root-associated respiration. In our study, peak CO_2 efflux occurred in July–August, and the highest soil CO_2 efflux at a given temperature was found in August. Although root growth was not monitored at our site, maximum root production usually lags by several weeks behind the aboveground growth of trees (e.g. Steinaker et al., 2010). At our site diameter growth typically started by the third week of June (S. Kellomäki, unpublished data). The annual

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

increment in diameter of pines was small, about 1 mm a^{-1} at a height of 1.3 m, which made day-to-day monitoring of growth difficult despite continuously recording bands around tree trunks. In our region, however, the fine root biomass and root growth in Scots pine forests have been observed to peak late in the summer or early autumn, in
5 July, August or September, differing in different stands and from year to year (Makkonen and Helmisaari, 2001; Helmisaari et al., 2009).

Correspondingly, the peak root and mycorrhizal respiration in a Swedish tree-girdling experiment was observed in August, following a pattern similar to ours for maximum solar irradiance at the end of June and a period of high air- and soil temperatures in
10 July (Högberg et al., 2001; Bhupinderpal-Singh et al., 2003). Results from this boreal pine-girdling experiment suggest a correlation between soil CO$_2$ efflux and biomass of the external mycelium of ectomycorrhizal fungi, which can contribute 30–40% of the soil microbial biomass in our type of Scots pine stands (Högberg and Högberg, 2002). In addition to the fact that flux of photosynthates supports a considerable portion of soil
15 microbial biomass consisting of ectomycorrhizal fungi, dissolved organic carbon from mycorrhizal fungi is also a potentially important source of carbon for other soil microbes (Högberg and Högberg, 2002).

The seasonal pattern of root growth and rapid growth of external mycelium of ectomycorrhizal fungi in coniferous boreal forests later in the season, from July to September or October, compared to the earlier part of the snow-free period (Wallander et al.,
20 1997, 2001), could partly explain differences in CO$_2$ efflux level between early- and late-season month-specific temperature models as well as underestimation of CO$_2$ efflux in mid-July–August by the soil temperature and degree days model. Similarly, underestimation of CO$_2$ efflux with a temperature response model covering the entire snow-free period was observed by Kolari et al. (2009) for July–August in another
25 Finnish Scots pine forest.

The influence of fast flux of photosynthates on soil CO$_2$ efflux, through the roots and root-associated respiration, has been suggested to be proportionally largest in the middle of the growing period; consequently, soil temperature may not exert major

control on root respiration at that time, but recent aboveground weather conditions affecting photosynthesis may have an effect (Russell and Voroney, 1998; Ekblad et al., 2005). In the girdling experiment, sensitivity of root respiration to soil temperature was correspondingly found to be lower than that of heterotrophic respiration in mid-July and early August (Bhupinderpal-Singh et al., 2003). A greater proportion of soil CO_2 originating from roots and root-associated respiration and greatly influenced by flux of photosynthates could help to explain the relative temperature insensitivity of soil CO_2 efflux in our study in July compared to other parts of the snow-free period, especially as the highest monthly mean photosynthesis at our site has been measured for July (Zha et al., 2007). Others have also found a weak or no correlation between CO_2 efflux from forest soil and soil temperature during the peak period of soil CO_2 efflux and temperature in summer (Russell and Voroney, 1998; Kelliher et al.,1999; Curiel Yuste et al., 2004) or between efflux and soil temperature and moisture (Schlentner and VanCleve, 1985). In our study, variation in soil moisture did not clearly explain the variation in CO_2 efflux in July, contrary to the results of a study in a Siberian pine forest (Kelliher et al., 1999).

The differences in the level of soil CO_2 efflux at low temperatures between spring and autumn could be partly due to differences in temperatures within the soil column during warming and cooling (see Reichstein et al., 2005) and to differences in size of the unfrozen volume of soil (Rayment and Jarvis, 2000). The greatest overestimations with temperature models were thus often associated with cool conditions in May and October with afternoon surface temperatures that were noticeably higher than the morning temperatures. Differences in substrate availability and in size and composition of the microbial population could also contribute to the higher level of soil CO_2 efflux at a given temperature in October compared to May. Microbial populations have been observed to decline in spring after snowmelt but increase during autumn (Lipson et al., 1999, 2000) with maximum mineralization of soil carbon in Finnish forests observed in October (Kähkönen et al., 2002). The supply of photosynthates to the roots has also been found to be smaller in forests in spring than in autumn (Keel et al., 2006), which

in our study could have resulted in lower root respiration and, through a priming effect, also in lower microbial respiration in spring. Growth of ectomycorrhizal fungi has correspondingly been observed to be more rapid from July until September or October than in spring or early summer (Wallander et al., 1997, 2001). Also in our study, increases in efflux that could be directly linked to fungal activity occurred from August to October as shown by the appearance of fruit bodies inside individual collars.

In addition, fresh carbon inputs in the form of needle litter during the latter part of the snow-free period may have had a positive effect on level of soil CO$_2$ efflux. Needle litterfall collected monthly or bi-monthly at the site peaked in late summer and early autumn, similarly to a study on a the temporal pattern of needle litterfall in Finnish pine forests (Ukonmaanaho, 2007). Together the needle litterfall in August and September formed half of the annual needle litterfall at our site (S. M. Niinistö, unpublished data). Although the amount of litter from dwarf shrubs of the understorey can be small compared to tree litter in this kind of pine forests (Hilli et al., 2008), the senescence of dwarf shrubs, especially *V. myrtillus* at our site, could have provided a fresh input of carbon to CO$_2$ producing soil microbes in the autumn.

4.3 Response of CO$_2$ efflux to moisture

The overall response of soil CO$_2$ efflux to moisture at our site in the dry year 1999 resembled the response measured in a temperate forest where dry conditions decreased soil CO$_2$ efflux in August and September, whereas with increasing moisture there was a decreasing trend early and late in the year (Davidson et al., 1998). Negative effects of dry conditions on soil CO$_2$ efflux previously found in temperate and boreal forests (Savage and Davidson, 2001; Subke et al., 2003; Kolari et al., 2009) were evident in our forest also when shorter periods of time were compared. Efflux was 30% lower in September of the dry year 1999 (precipitation in the snow-free period 50% of that in 1998) compared to the previous September, with a similar mean soil temperature and temperature range. A corresponding decrease in microbial respiration was observed in Finnish forest soils during a dry August (Vanhala, 2002).

There was a decline in measured soil CO$_2$ efflux with an increase in soil moisture at the high end of the range. It is unlikely that even at the high levels of soil moisture at our site, the requirements of sufficient aeration would not have been met in the coarse and well-drained sandy till in question, i.e. the production processes of CO$_2$ were probably not hindered by excess moisture. According to calculations based on 45% porosity with stoniness accounted for, the soil air space in our experiment ranged from 0.21 to 0.29 m^3 m^{-3} (1998) and to 0.40 m^3 m^{-3} (1999). Moreover, the approximated optimum water content in the B horizon for soil CO$_2$ efflux, 0.25–0.30 m^3 m^{-3} for our soil (based on the model by Skopp et al., 1990 and adapted for a Finnish till by Pumpanen et al., 2003b), was not exceeded even in the wet year of 1998. Similarly, no decrease in microbial CO$_2$ production, and consequently CO$_2$ evolution, was detected for a type of mineral soil similar to ours nor for a similar type of organic layer, i.e. boreal mor in conditions close to saturation, at water contents exceeding ours (Ilstedt et al., 2000; Schjønning et al., 2003).

The negative relationship between soil CO$_2$ efflux and soil moisture at high soil moisture observed in our study could thus have been an artifact, reflecting not the influence of soil moisture per se but rather some other covarying factor – such as temperature (Carlyle and Than, 1988; Davidson et al., 1998). On the other hand, the negative relation between CO$_2$ efflux on the soil surface and soil moisture could be partly due to high moisture slowing the transportation of CO$_2$. In our case, there was a strong correlation between time and soil moisture during the first half of the snow-free period, which suggests that in our multivariable regression models soil moisture, with its negative regression coefficient, could have been a surrogate for time, i.e. progress of the growing season and associated processes when soil moisture decreased steadily after snow melt in early May. The same temporal pattern of soil moisture and the similar negative correlation between soil moisture and coniferous root growth have been observed during a snow-free period in Canada (Steinaker et al., 2010). In our month-specific analyses there was also no evidence of a decline associated with high soil moisture. As noted before (e.g. Kane et al., 2003), our data, i.e. soil CO$_2$ efflux observations

together with simultaneous measurements of natural variation of soil moisture, do not, however, enable us to properly distinguish between the effects of soil moisture and time, i.e. seasonality or temperature.

Inclusion of the moisture of moss, litter or the organic layer did not improve models that already included moisture of mineral soil as a variable. The intensity of soil CO$_2$ efflux measurements or gravimetric sampling may not have been great enough to capture short-term efflux fluctuations from these layers nor to capture the effect of smaller rain events, which has been found to be transient, but possibly significant (Kelliher et al., 1999; Savage and Davidson, 2003).

4.4 Multivariable approach

Temperature probably functioned as such a good predictor because many environmental factors and ecosystem processes, such as solar irradiation, carbon uptake and plant growth, varied in concert with its variation in this boreal ecosystem over a typical "arch" of the snow-free period (e.g. Euskirchen et al., 2003). Temperature may also have acted as a proxy for other environmental variables, conditions and processes, thus calling temperature models "temperature-associated response models" may be justified.

Different processes producing soil CO$_2$ efflux respond to changes in environmental conditions with different time lags; thus averages of environmental factors, such as the 24-h average of soil temperature in this study, make reasonable predictors of soil CO$_2$ efflux. Transport of substrates to CO$_2$-producing processes and transport of produced CO$_2$ are also influenced by prevailing conditions, which further complicates assessment of response times. For instance, flux between photosynthesis of tree canopy and soil CO$_2$ efflux has been found to be relatively rapid, 1–6 days through root and rhizosphere respiration, i.e. autotrophic respiration together with mycorrhizal and free microbial respiration (Ekblad and Högberg, 2001; Ekblad et al., 2005), but seasonally variable in magnitude (Keel et al., 2006). The link between canopy photosynthesis and soil CO$_2$ efflux will not, however, render the concept of temperature response of soil

S. M. Niinistö et al.

CO$_2$ efflux useless in boreal forests, partly due to the proxy-like quality of temperature and partly because of the controlling effect of temperature on heterotrophic respiration, the proportion of which may be greater in boreal coniferous forests than in temperate forests (Subke et al., 2006).

5   There is a need for more process-based models that take into account the question of substrate supply and distinguish between the direct effects of temperature and moisture and their effects on substrate diffusion and availability (Davidson et al., 2006). The phenology of the ecosystem regulates the substrate supply to the soil CO$_2$ efflux and to ecosystem respiration in general. It can explain some of the variation not ac-
10 counted for by temperature-associated variation (Goulden et al., 1997). Accordingly, the basal rate of soil respiration has been found to vary seasonally with photosynthesis in temperate forest stands (Sampson et al., 2007). Addition of an index of seasonality, such as the degree days, improved the accuracy of models in this study, as has been reported previously for respiration and soil CO$_2$ efflux in boreal forests (Goulden
15 et al.,1997; Lavigne et al., 1997; Richardson et al., 2006). This addition was supported by a model-evaluation exercise, although the consistent underestimation of flux during the peak season from mid-July to late-August was not corrected for. Differences between annual estimates produced with different models were yet small. Our results from the peak flux period in July and August, however, lent support to previous con-
20 clusions concerning the importance of inclusion of canopy processes (e.g. Irvine et al., 2005; Sampson et al., 2007), for upper-storey trees as well as understorey dwarf shrubs. Model predictions could also be improved by inclusion of the dynamics of root and mycorrhizal fungi production, which can be significant covarying processes of soil CO$_2$ efflux in boreal forests (Högberg and Högberg, 2002). Extremely high, but
25 sporadic, values of efflux related most likely to fungal activity appeared to be difficult to predict, but precipitation patterns could help to explain sudden drops in efflux from these individual measurement points during bursts of respiration. Our observations on the timing of these maximum values related to fungal activity stress the need for predictions of fungal respiration to be linked with the phase of the growing season.

Models of season-specific temperature and moisture response could be a step forward and provide less biased estimates by accounting for driving variables that are not explicitly included in the model (e.g. DeForest et al., 2006). In conditions of pronounced seasonal variation of boreal forests, shorter-term models that take into account the phase of the season would help distinguish between the effects of temperature, moisture and above- and belowground phenological development. In addition, watering experiments could give valuable insight into the role of soil moisture even in humid boreal forest ecosystems.

Appendix A

Soil-specific calibration on Campbell's CS615 water content reflectometers

Soil-specific calibration was carried out separately for the topmost 30 cm of mineral soil (density $0.98\,\mathrm{g\,cm^{-3}}$) and for the undisturbed sheet of the organic layer, which also contained some of the topmost mineral soil (density of $0.31\,\mathrm{g\,cm^{-3}}$). Samples in large buckets (diameter 28 cm, $n = 3$) were saturated with water; eight measurements were made for each water content, and samples were weighed during drying at room temperature. Finally, to determine the dry mass, mineral soil samples were dried at $105\,^\circ\mathrm{C}$ and the organic/surface soil layer at $70\,^\circ\mathrm{C}$. During calibration, water content was 0.14–$0.43\,\mathrm{m^3\,m^{-3}}$ for the surface layer and 0.06–$0.51\,\mathrm{m^3\,m^{-3}}$ for the mineral soil; the sensor output was 0.88–1.30 ms for the surface layer and 0.80–1.25 ms for mineral soil, which corresponded to the range in the field during May–October. Linear regressions were run with an output period (τ) in milliseconds at $20\,^\circ\mathrm{C}$ as the independent variable and the volumetric soil water content (θ) in $\mathrm{m^3\,m^{-3}}$ as the dependent variable for mineral and surface soil separately. Regression models were the following:

$$\theta = -0.679 + 0.923 \cdot \tau, \quad \text{with} \quad r^2 = 0.98 \quad \text{(mineral soil)}, \text{ and}$$

$$\theta = -0.374 + 0.616 \cdot \tau, \quad \text{with} \quad r^2 = 0.96 \quad \text{(organic layer/surface soil)}.$$

Seasonality of soil CO$_2$ efflux in a boreal forest

S. M. Niinistö et al.

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

|◄ | ►|

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

BGD

8, 2811–2849, 2011

Seasonality of soil CO$_2$ efflux in a boreal forest

S. M. Niinistö et al.

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◀ | ▶

◀ | ▶

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

The equation for mineral soil was similar to a previous calibration made for sandy soils with the same sensor (Kim and Benson, 2002). Compared to the soil-specific calibration, the manufacturer's standard calibration underestimated some 3 to 20–30% or 0–0.07 m^3 m^{-3} for mineral soil within the output range in the field in 1999. This was considerably less than, for instance, in a case of tropical clay soils (Veldkamp and O'Brien, 2000). The manufacturer's standard calibration equation applied here was for conditions in which electrical conductivity was equal to or smaller than 1 dS m^{-1} (Campbell Scientific Inc., 1999).

References

Anderson, J. M.: Carbon dioxide evolution from two temperate, deciduous woodland soils, J. Appl. Ecol., 10, 361–378, 1973.

Bhupinderpal-Singh, Nordgren, A., Ottosson Löfvenius, M., Högberg, M. N., Mellander, P.-E., and Högberg, P.: Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year, Plant Cell Environ., 26, 1287–1296, 2003.

Campbell Scientific Inc.: CS615 Water content reflectometer: User guide, Campbell Scientific Inc., 17 pp., 1999.

Carlyle, J. C. and Than, U. B.: Abiotic controls of soil respiration beneath an eighteen-year-old Pinus radiata stand in south-eastern Australia, J. Ecol., 76, 654–662, 1988.

Crill, P. M.: Seasonal patterns of methane uptake and carbon dioxide release by a temperate woodland soil, Global Biogeochem. Cy., 5(4), 319–334, 1991.

Curiel Yuste, J., Janssens, I. A., Carrara, A., and Ceulemans, R.: Annual Q_{10} of soil respiration reflects plant phenological patterns as well as temperature sensitivity, Glob. Change Biol., 10, 161–169, 2004.

Davidson, E. A., Belk, E., and Boone, R. D.: Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest, Glob. Change Biol., 4, 217–227, 1998.

Davidson, E. A., Janssens, I. A., and Luo, Y.: On the variability of respiration in terrestrial ecosystems: moving beyond Q_{10}, Glob. Change Biol., 12, 154–164, 2006.

DeForest, J. L., Noormets, A., McNulty, S. G., Sun, G., Tenney, G., and Chen, J.: Phenophases alter the soil respiration-temperature relationship in an oak-dominated forest, Int. J. Biometeorol., 51, 135–144, 2006.

Domisch, T., Finér, L., Ohashi, M., Risch, A. C., Sundström, L., Niemelä, P., and Jurgensen, M. F.: Contribution of red wood ant mounds to forest floor CO_2 efflux in boreal coniferous forests, Soil Biol. Biochem., 38, 2425–2433, 2006.

Drebs, A., Nordlund, A., Karlsson, P., Helminen, J., and Rissanen, P.: Climatological statistics of Finland 1971–2000, Climatic Statistics of Finland, 1, 1–99, 2002.

Drewitt, G. B., Black, T. A., Nesic, Z., Humphreys, E. R., Jork, E. M., Swanson, R., Ethier, G. J., Griffis, T., and Morgenstern, K.: Measuring forest floor CO_2 fluxes in a Douglas-fir forest, Agr. Forest Meteorol., 110, 299–317, 2002.

Ekblad, A. and Högberg, P.: Natural abundance of ^{13}C in CO_2 respired from forest soils reveals speed of link between tree photosynthesis and root respiration, Oecologia, 127, 305–308, 2001.

Ekblad, A., Boström, B., Holm, A., and Comstedt, D.: Forest soil respiration rate and δ^{13}C is regulated by recent above ground weather conditions, Oecologia, 143, 136–142, 2005.

Euskirchen, E. S., Chen, J., Gustafson, E. J., and Ma, S.: Soil respiration at dominant patch types within a managed northern Wisconsin landscape, Ecosystems, 6, 595–607, 2003.

Goulden, M. L., Daube, B. C, Fan, S.-M., Sutton, D. J., Bazzaz, A., Munger, J. W., and Wofsy, S. C.: Physiological responses of a black spruce forest to weather, J. Geophys. Res., 102(D24), 28987–28996, 1997.

Helmisaari, H.-S., Ostonen, I., Lõhmus, K., Derome, J., Lindroos, A.-J., Merilä, P., and Nöjd, P.: Ectomycorrhizal root tips in relation to site and stand characteristics in Norway spruce and

Scots pine stands in boreal forests, Tree Physiol., 29, 445–456, 2009.

Hilli, S., Stark, S., and Derome, J.: Water-extractable organic compounds in different components of the litter layer of boreal conferous forest soils along a climatic gradient, Boreal Environ. Res., 13 (Suppl. B), 92–106, 2008.

Högberg, M. N. and Högberg, P.: Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil, New Phytol., 154, 791–795, 2002.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Högberg, M. N., Nyberg, G., Ottosson-Löfvenius, M., and Read, D. J.: Large-scale forest girdling shows that current photosynthesis drives soil respiration, Nature, 411, 789–792, 2001.

Ilstedt, U., Nordgren, A., and Malmer, A.: Optimum soil water for soil respiration before and after amendment with glucose in humid tropical acrisols and a boreal mor layer, Soil Biol. Biochem., 32, 1591–1599, 2000.

Irvine, J., Law, B. E., and Kurpius, M. R.: Coupling of canopy exchange with root and rhizosphere respiration in a semi-arid forest, Biogeochemistry, 73, 271–282, 2005.

Janssens, I. A., Lankreijer, H., Matteucci, G., Kowalski, A. S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E. J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Guðmundsson, Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N. O., Vesala, T., Granier, A., Schulze, E.-D., Lindroth, A., Dolman, A. J., Jarvis, P. G., Ceulemans, R., and Valentini, R. V.: Productivity overshadows temperature in determining soil and ecosystem respiration across European forest, Glob. Change Biol., 7, 269–278, 2001.

Kähkönen, M. A., Wittmann, C., Ilvesniemi, H., Westman, C. J., and Salkinoja-Salonen, M. S.: Mineralization of detritus and oxidation of methane in acid boreal coniferous forest soils: seasonal and vertical distribution and effects of clear-cut, Soil Biol. Biochem., 34, 1191–1200, 2002.

Kane, E. S., Pregitzer, K. S., and Burton, A. J.: Soil respiration along environmental gradients in Olympic National Park, Ecosystems, 6, 326–335, 2003.

Keel, S. G., Siegwolf, R. T. W., and Körner, C.: Canopy CO_2 enrichment permits tracing the fate of recently assimilated carbon in a mature deciduous forest, New Phytol., 172, 319–329, 2006.

Kelliher, F. M., Lloyd, J., Arneth, A., Lühker, B., Byers, J. N., McSeveny, T. M., Milukova, I., Grigoriev, S., Panfyorov, M., Sogatchev, A., Varlagin, A., Ziegler, W., Bauer, G., Wong, S.-C.,

Seasonality of soil CO_2 efflux in a boreal forest

S. M. Niinistö et al.

and Schulze, E.-D.: Carbon dioxide efflux density from the forest floor of a central Siberian pine forest, Agr. Forest Meteorol., 94, 217–232, 1999.

Kellomäki, S. and Wang, K.-Y.: Short-term environmental controls on heat and water fluxes above a boreal coniferous forest: model computations compared with measurements by eddy correlation, Ecol. Model., 124(2–3), 145–173, 1999.

Kim, K. C. and Benson, C. H.: Water content reflectometer calibrations for final cover soils, Geo Engineering Report, No. 02–12. Geo Engineering Program, University of Wisconsin-Madison, Madison, Wisconsin, USA, 110 pp., 2002.

Klute, A.: Water retention: Laboratory methods, in: Methods of Soil Analysis, Part 1. Physical and Mineralogical Methods, 2nd edn., edited by: Klute, A., Agronomy Monograph No. 9, American Society of Agronomy and Soil Science Society of America, Madison, WI, USA, 635–662, 1986.

Kolari, P., Kulmala, L., Pumpanen, J., Launiainen, S., Ilvesniemi, H., Hari, P., and Nikinmaa, E.: CO_2 exchange and component CO_2 fluxes of a boreal Scots pine forest, Boreal Environ. Res., 14, 761–783, 2009.

Kurganova, I., Lopes de Gerenyu, V., Rozanova, L., Sapronov, D., Myakshina, T., and Kudeyarov, V.: Annual and seasonal CO_2 fluxes from Russian southern taiga soils, Tellus, 55B, 338–344, 2003.

Larmola, T., Alm, J., Juutinen, S., Huttunen, J. T., Martikainen, P. J., and Silvola, J.: Contribution of vegetated littoral zone to winter fluxes of carbon dioxide and methane from boreal lakes, J. Geophys. Res., 109, d19102, doi:10.1029/2004JD004875, 2004.

Lavigne, M. B., Ryan, M. G., Anderson, D. E., Baldocchi, D. D., Crill, P. M., Fitzjarrald, D. R., Goulden, M. L., Gower, S. T., Massheder, J. M., McCaughey, J. H., Rayment, M., and Striegl, R. G.: Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements at six coniferous boreal sites, J. Geophys. Res., 102(D24), 28977–28985, 1997.

Linder, S. and Lohammer, T.: Amount and quality of information on CO_2-exchange required for estimating annual carbon balance of coniferous trees, in: Understanding and predicting tree growth. Studia Forestalia Suecica, edited by: Linder, S., 160, 73–87, 1981.

Lipson, D. A., Schmidt, S. K., and Monson, R. K.: Links between microbial population dynamics and nitrogen availability in an alpine ecosystem, Ecology, 80(5), 1623–1631, 1999.

Lipson, D. A., Schmidt, S. K., and Monson, R. K.: Carbon availability and temperature control the post-snowmelt decline in alpine soil microbial biomass, Soil Biol. Biochem., 32, 441–448,

Seasonality of soil CO_2 efflux in a boreal forest

S. M. Niinistö et al.

Title Page

Abstract	Introduction
Conclusions	References
Tables	Figures

|◄ | ►|

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

2000.

Lloyd, J. and Taylor, J. A.: On the temperature dependence of soil respiration, Funct. Ecol., 8, 315–323, 1994.

Makkonen, K. and Helmisaari, H.-S.: Fine root biomass and production in Scots pine stands in relation to stand age, Tree Physiol., 21, 193–198, 2001.

Niinistö, S. M., Silvola, J., and Kellomäki, S.: Soil CO_2 efflux in a boreal pine forest under atmospheric CO_2 enrichment and air warming, Glob. Change Biol., 10, 1363–1376, 2004.

Pumpanen, J., Ilvesniemi, H., Perämäki, M., and Hari, P.: Seasonal patterns of soil CO_2 efflux and soil air CO_2 concentration in a Scots pine forest: comparison of two chamber techniques, Glob. Change Biol., 9, 371–382, 2003a.

Pumpanen, J., Ilvesniemi, H., and Hari, P.: A process-based model for predicting soil carbon dioxide efflux and concentration, Soil Sci. Soc. Am. J., 67, 402–413, 2003b.

Pumpanen, J., Kolari, P., Ilvesniemi, H., Minkkinen, K., Vesala, T., Niinistö, S., Lohila, A., Larmola, T., Morero, M., Pihlatie, M., Janssens, I., Curiel Yuste, J., Grünzweig, J. M., Reth, S., Subke, J.-A., Savage, K., Kutsch, W., Østreng, G., Ziegler, W., Anthoni, P., Lindroth, A., and Hari, P.: Comparison of different chamber techniques for measuring soil CO_2 efflux, Agr. Forest Meteorol., 123, 159–176, 2004.

Rayment, M. B. and Jarvis, P. G.: Temporal and spatial variation of soil CO_2 efflux in a Canadian boreal forest, Soil Biol. Biochem., 32, 35–45, 2000.

Reichstein, M., Subke, J.-A., Angeli, A. C., and Tenhunen, J. D.: Does the temperature sensitivity of decomposition of soil organic matter depend upon water content, soil horizon, or incubation time?, Glob. Change Biol., 11, 1754–1767, 2005.

Richardson, A. D., Braswell, B. H., Hollinger, D. Y., Burman, P., Davidson, E. A., Evans, R. S., Flanagan, L. B., Munger, J. W., Savage, K., Urbanski, S. P., and Wofsy, S. C.: Comparing simple respiration models for eddy flux and dynamic chamber data, Agr. Forest Meteorol., 141, 219–234, 2006.

Russell, C. A. and Voroney, R. P.: Carbon dioxide efflux from the floor of a boreal aspen forest. I. Relationship to environmental variables and estimates of C respired, Can. J. Soil Sci., 78, 301–310, 1998.

Rustad, L. E., Huntington, T. G., and Boone, R. D.: Controls on soil respiration: Implications for climate change, Biogeochemistry, 48, 1–6, 2000.

Sampson, D. A., Janssens, I. A., Curiel Yuste, J., and Ceulemans, R.: Basal rates of soil respiration are correlated with photosynthesis in a mixed temperate forest, Glob. Change

Biol., 13, 2008–2017, 2007.

Savage, K. E. and Davidson, E. A.: Interannual variation of soil respiration in two New England forests, Global Biogeochem. Cy., 15(2), 337–350, 2001.

Savage, K. E. and Davidson, E. A.: A comparison of manual and automated systems for soil CO_2 measurements: trade-off between spatial and temporal resolution, J. Exp. Bot., 54, 891–899, 2003.

Schjønning, P., Thomsen, I. K., Moldrup, P., and Christensen, B. T.: Linking soil microbial activity to water- and air-phase contents and diffusivities, Soil Sci. Soc. Am. J., 67, 156–165. 2003.

Schlentner, R. E. and Van Cleve, K.: Relationships between CO_2 evolution from soil, substrate temperature, and substrate moisture in four mature forest types in interior Alaska, Can. J. Forest Res., 15, 97–106, 1985.

Schlesinger, W. H.: Carbon balance in terrestrial detritus, Annu. Rev. Ecol. Syst., 8, 51–81, 1977.

Shibistova, O., Lloyd, J., Zrazhevskaya, G., Arneth, A., Kolle, O., Knohl, A., Astrakhantceva, N., Shijneva, I., and Schmerler, J.: Annual ecosystem respiration budget for a Pinus sylvestris stand in central Siberia, Tellus, 54B, 568–589, 2002.

Silvola, J.: CO_2 dependence of photosynthesis in certain boreal forest and peat mosses and simulated photosynthesis at various actual and hypothetical CO_2 concentrations, Lindbergia, 11, 86–93, 1985.

Silvola, J.: Moisture dependence of CO_2 exchange and its recovery after drying in certain boreal forest and peat mosses, Lindbergia, 17, 5–10, 1992.

Skopp. J., Jawson, M. D., and Doran, J. W.: Steady-state areobic microbial activity as a function of soil water content, Soil Sci. Soc. Am. J., 54, 1619–1625, 1990.

Steinaker, D.-F., Wilson, S. D., and Peltzer, D. A.: Asynchronicity in root and shoot phenology in grasses and woody plants, Glob. Change Biol., 16, 2241–2251, 2010.

Subke, J.-A., Reichstein, M., and Tenhunen, J. D.: Explaining temporal variation in soil CO_2 efflux in a mature spruce forest in Southern Germany, Soil Biol. Biochem., 35, 1467–1483, 2003.

Subke, J.-A., Inglima, I., and Cotrufo, M. F.: Trends and methodological impacts in soil CO_2 efflux partitioning: A metaanalytical review, Glob. Change Biol., 12, 921–943, 2006.

Teskey, R. O., Whitehead, D., and Linder, S.: Photosynthesis and carbon gain by pines, Ecol. Bull., 43, 35–49, 1994.

Seasonality of soil CO_2 efflux in a boreal forest

S. M. Niinistö et al.

Title Page

Abstract	Introduction
Conclusions	References
Tables	Figures

◄◄ ►►

◄ ►

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Ukonmaanaho, L.: Litterfall production on 14 Level II plots during 1996–2003, Working Papers of the Finnish Forest Research Institute, 45, 63–68, 2007.

Vanhala, P.: Seasonal variation in the soil respiration rate in coniferous forest soils, Soil Biol. Biochem., 34, 1375–1379, 2002.

5   Veldkamp, E. and O'Brien, J. J.: Calibration of a frequency reflectometry sensor for humid tropical soils of volcanic origin, Soil Sci. Soc. Am. J., 64, 1549–1553, 2000.

Wallander, H., Massicotte, H. B., and Nylund, J.-E.: Seasonal variation in protein, ergosterol and chitin in five morphotypes of Pinus sylvestris L. ectomycorrhizae in a mature Swedish forest, Soil Biol. Biochem., 29(1), 45–53, 1997.

10   Wallander, H., Nilsson, L. O., Hagerberg, D., and Bååth, E.: Estimation of the biomass and seasonal growth of external mycelium of ecotomycorrhizal fungi in the field, New Phytol., 151, 753–760, 2001.

Wang, C., Bond-Lamberty, B., and Gower, S. T.: Soil surface CO_2 flux in a boreal black fire chronosequence, J. Geophys. Res., 108(D3), 8224, doi:10.1029/2001JD000861, 2003.

15   Winston, G. C., Sundquist, E. T., Stephens, B. B., and Trumbore, S. E.: Winter CO_2 fluxes in a boreal forest, J. Geophys. Res., 102(D24), 28795–28804, 1997.

Witkamp, M.: Rates of carbon dioxide evolution from the forest floor, Ecology, 47(3), 492–494, 1966.

Zha, T., Niinistö, S., Xing, Z., Wang, K.-Y., Kellomäki, S., and Barr, A. G.: Total and component
20   carbon fluxes of a Scots pine ecosystem from chamber measurements and eddy covariance, Ann. Bot.-London, 99, 345–353, 2007.

Seasonality of soil CO_2 efflux in a boreal forest

S. M. Niinistö et al.

Title Page

Abstract	Introduction
Conclusions	References
Tables	Figures

|◄ | ►|

| ◄ | ► |

| Back | Close |

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

S. M. Niinistö et al.

Table 1. Measurements of water potential and water content of soil on days when soil CO$_2$ efflux was measured.

Variable and Method	Make and Manufacturer/Method	Unit	Frequency	Time period	Min	Mean	Max	Soil layer
					Range of area mean		
Soil water potential								
Tensiometers	Pressure transducer Tensimeter, Soil Moisture Inc., AZ, USA	kPa	Once/ twice a day	15 May–29 Sep 1998	−11	−7	−4	5–30 cm
				25 May–12 Oct 1999	−52	−24	−4	5–30 cm
Soil water content								
Reflectometers	CS615 sensors CR10X datalogger, Campbell Scientific, Shepshed, LE, UK	m^3 m^{-3}	Every 15 min	26 Apr–19 Oct 1999	0.18	0.25	0.37	Surface
					0.07	0.15	0.28	2–28 cm
Gravimetric	Dry mass determined after in oven at 105 °C for 24 h	%	Once a day	15 May–22 Oct 1998	181	451	946	Litter
					147	260	456	Organic
					29	38	53	0–10 cm
				1 Jun–19 Oct 1999	61	287	756	Moss
					68	228	758	Litter
					35	99	241	Organic
					9	23	46	0–10 cm

Seasonality of soil CO$_2$ efflux in a boreal forest

S. M. Niinistö et al.

Table 2. Comparison of multiple regression models for the pooled 1998 and 1999 data. Independent variables: soil temperature at 5 cm depth (T_{soil}), water content of the upper 30 cm of mineral soil (swc), degree days i.e. cumulative sum of daily temperatures exceeding 5 °C (T-Sum).

Dependent variable	Model	Independent variables x_i	Estimates for											
			F_{model}	df_{model}	df_{error}	SS	RMSE	R^2	AIC	β_0	β_1	β_2	β_3	β_4
Ln(Flux in mg CO$_2$ m^{-2} h^{-1})		LnFlux= $\beta_0 + \beta_1 x_1 + \beta_2 \cdot x_2 + ... + \beta_i \cdot x_i$												
		Temperature and Water content Models												
	1	T_{soil}	980.68*	1	392	103.94	0.326	0.71	−882	4.7796	0.0980			
	2	T_{soil}, T_{soil}^2	901.06*	2	391	119.54	0.258	0.82	−1066	4.3462	0.2210	−6.081 × 10^{-3}		
	3	T_{soil}, swc	592.62*	2	391	103.39	0.304	0.75	−935	5.2101	0.0899	−1.1880		
	4	T_{soil}, swc, swc^2	441.25*	3	390	112.37	0.291	0.77	−968	4.7559	0.0852	5.515	−22.563	
	5	T_{soil}, T_{soil}^2, swc	665.40*	3	390	121.70	0.247	0.84	−1098	4.6512	0.2050	−5.548 × 10^{-3}	−1.215	
	6	T_{soil}, T_{soil}^2, swc, swc^2	601.10*	4	389	125.22	0.228	0.86	−1159	4.1447	0.2025	−5.673 × 10^{-3}	6.841	−24.535
		Models with Seasonality Index												
	7	T_{soil}, T_{soil}^2, T-Sum	779.00*	3	390	124.68	0.231	0.86	−1151	4.2078	0.2031	−5.088 × 10^{-3}	2.890 × 10^{-4}	
	8	T_{soil}, T_{soil}^2, T-Sum, T-Sum^2	912.38*	4	389	131.47	0.199	0.90	−1304	4.1330	0.1814	−4.787 × 10^{-3}	1.732 × 10^{-3}	1.137 × 10^{-6}

Variables also tested included mineral soil matric potential, water content of moss, litter or organic layer, plot, time of measurements, Julian Day, month, interaction variables such as $T_{soil} \cdot$ swc and T-Sum/Jday (models not shown). RMSE = a square root of mean squared error, AIC = Akaike's Information Criterion. * denotes statistical significance at the 0.001 risk level.
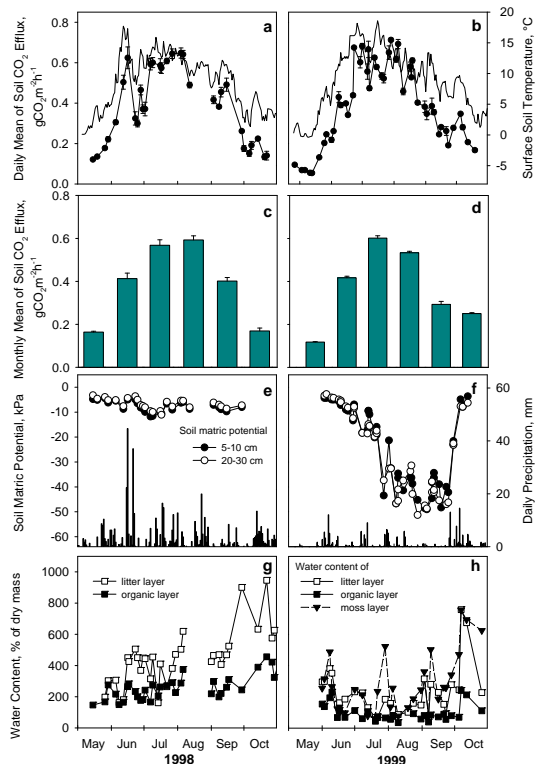
Fig. 1. (a, b) Daily means of soil CO$_2$ efflux in May–October 1998 **(a)** and 1999 **(b)** shown with black circles, standard error bars presenting variation between three plots. Each plot represents an average of 10 measurement points. Soil temperature at 5 cm depth is depicted with solid black line. **(c, d)** Monthly means of soil CO$_2$ efflux in May–October 1998 and 1999, standard error bars presenting variation between three plots. **(e, f)** Average soil matric potential at 5–10 cm depth (open circles) and at 20–30 cm depth (black circles) and daily precipitation depicted with black bars in 1998 **(e)** and 1999 **(f)**. **(g, h)** Gravimetric water content of litter (open squares), organic (black squares) and moss layer (triangles) in 1998 **(e)** and 1999 **(f)**.

Full Screen / Esc

Printer-friendly Version

Interactive Discussion
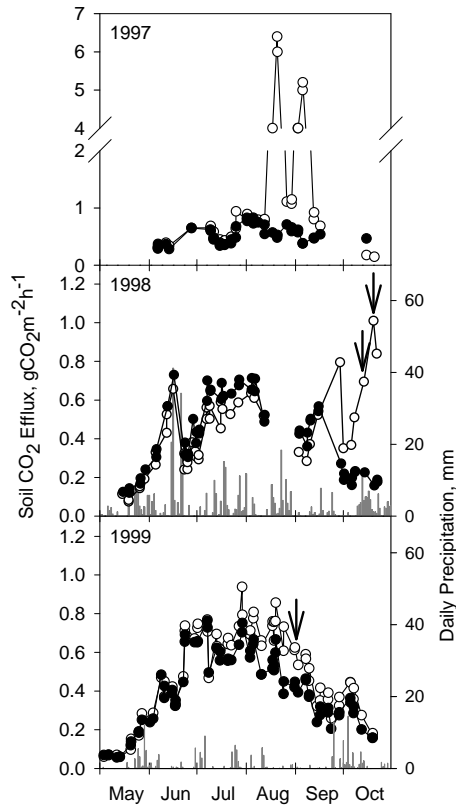
Fig. 2. Three examples of how fungal respiration increased soil CO$_2$ efflux from a point. Plot averages of 9–10 points are represented by black circles and efflux from an individual point by open circles, one or two measurements per measuring day. Daily precipitation is depicted with grey bars. Arrows point at occasions when a fungal fruit body was found in a collar and removed.
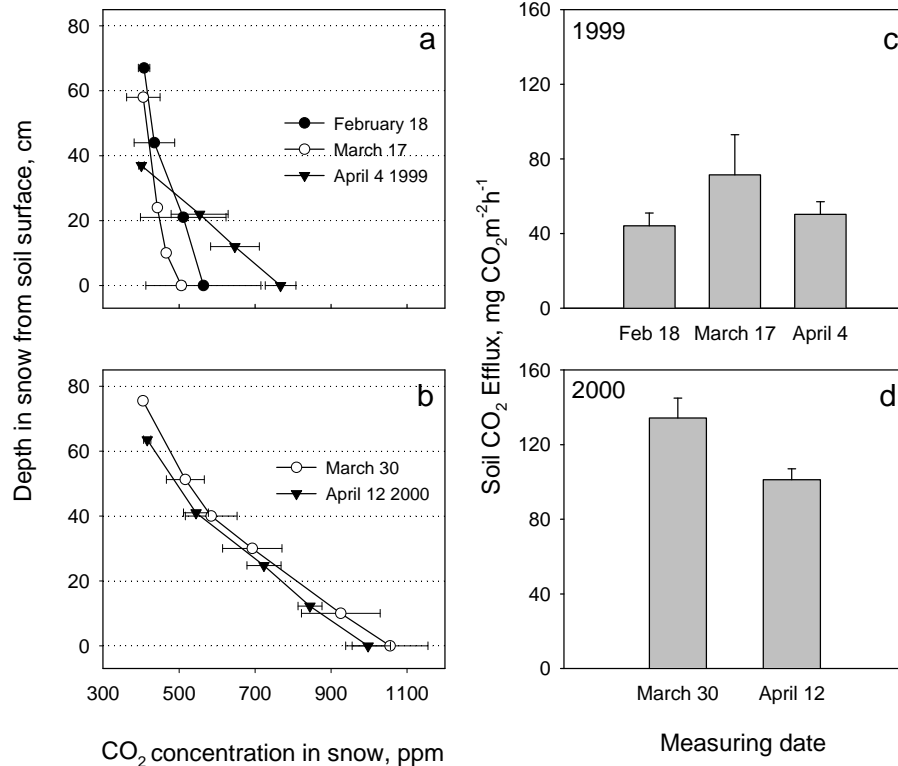
Fig. 3. (a, b) Concentration of CO_2 in snow (s.e. as error bars, $n = 2$–4). The top-most symbols represent average concentration in the top 2 cm of snow. **(c, d)** Soil CO_2 efflux in winter in 1999 **(c)** and 2000 **(d)**, standard error bars presenting variation between two plots measured, $n = 3$ per plot.
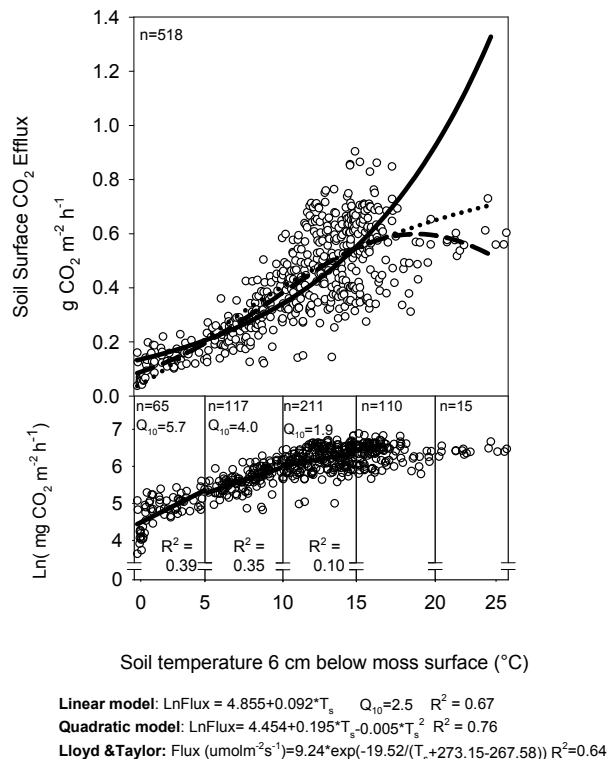
Fig. 4. Temperature response of pooled three-year data on soil CO$_2$ efflux (1997–1999). Solid lines illustrate linear regression, a dashed line indicates quadratic regression and a dotted line indicates the Lloyd and Taylor (1994) version of the Arrhenius function. Soil temperature (T_s) was measured next to collars with hand-held probe. Q_{10} of the linear regressions was calculated as $Q_{10} = e^{10 \cdot b_1}$, b_1 from the temperature response model formulated as Ln-Flux $= b_0 + b_1 \cdot T_{soil}$. All relations for which R^2 is given were statistically significant, as were regression coefficients and constants ($p < 0.001$).
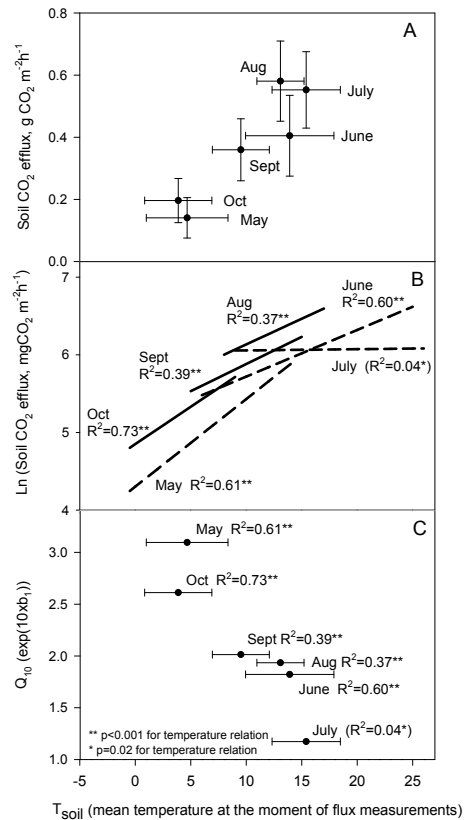
Fig. 5. (A) Means for soil CO_2 efflux and soil temperature for monthly subsets of three-year data (1997–1999). Error bars represent standard deviation. Number of observations varied from 50 (May) to 126 (July). **(B)** Month-specific temperature-response models based on three-year data (1997–1999). Models formulated as $LnFlux = b_0 + b_1 \cdot T_{soil}$. **(C)** Q_{10} calculated as $Q_{10} = e^{10 \cdot b_1}$, b_1 from the temperature-response model formulated as $LnFlux = b_0 + b_1 \cdot T_{soil}$. Constants, b_0's were 4.302 (May), 5.121 (Jun), 6.042 (Jul), 5.475 (Aug), 5.182 (Sep), and 4.851 (Oct). Regression coefficients, b_1's, did not differ statistically significantly between May and October, but the constants did ($p < 0.001$). The same was true for comparisons between June, August and September.
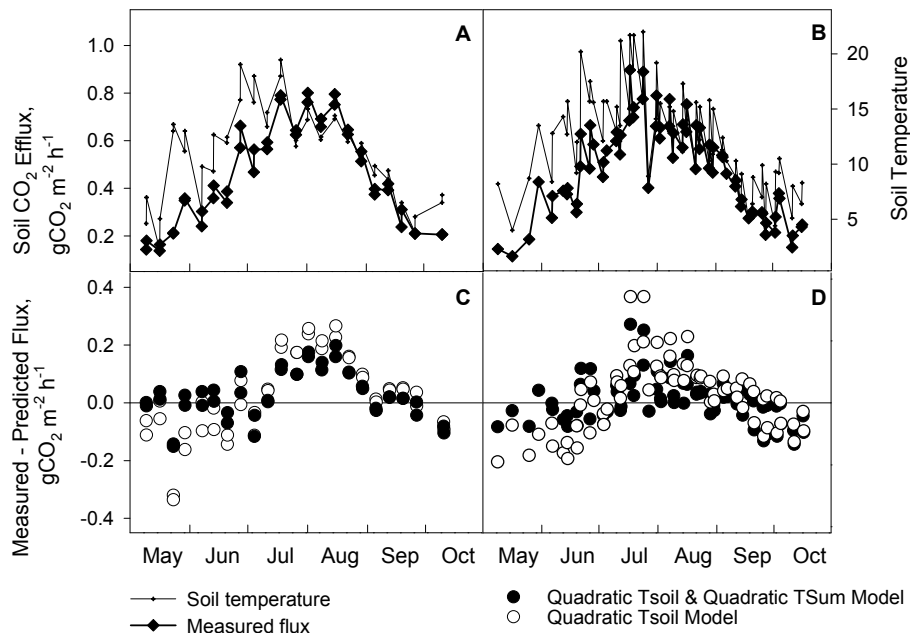
Fig. 6. Model evaluation: Soil CO$_2$ efflux and soil temperature at the time of measurements in 2000 **(A)** in Huhus and **(B)** in Mekrijärvi and difference between measured and predicted efflux **(C)** in Huhus and **(D)** in Mekrijärvi. Models formulated as LnEfflux $= b_0 + b_1 \cdot T_{soil} + b_2 \cdot T_{soil}^2$ and LnEfflux $= b_0 + b_1 \cdot T_{soil} + b_2 \cdot T_{soil}^2 + b_3 \cdot T\text{-Sum} + b_4 \cdot T\text{-Sum}^2$. Note: T-Sum = degree days. See Table 2 for values of regression coefficients.
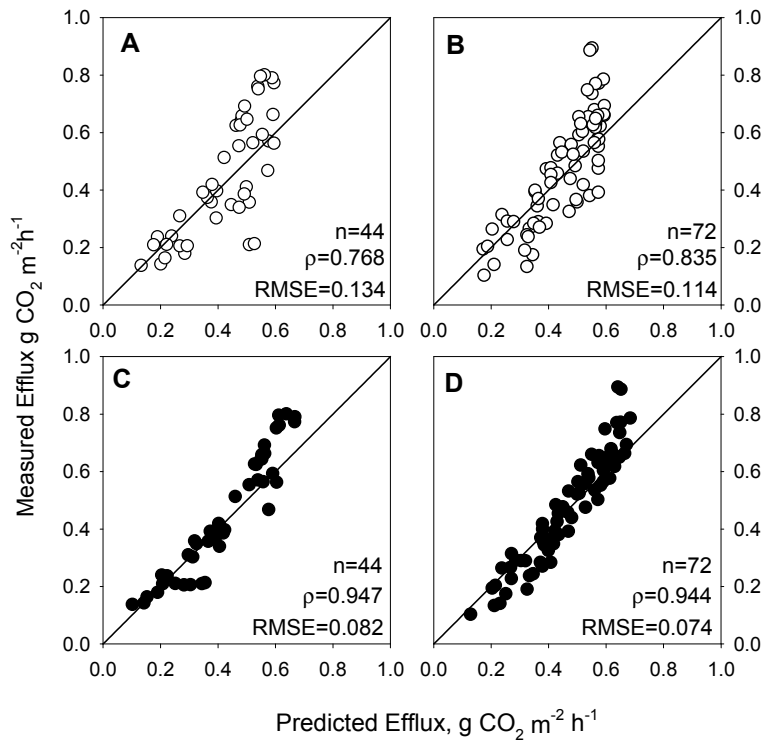
Fig. 7. Predicted versus measured efflux in evaluation data in 2000. **(A)** Predicted efflux in Huhus in 2000 with the quadratic soil temperature model. **(B)** Predicted efflux in Mekrijärvi in 2000 with the quadratic soil temperature model. **(C)** Predicted efflux in Huhus in 2000 with the quadratic soil temperature and degree days model. **(D)** Predicted efflux in Mekrijärvi in 2000 with the quadratic soil temperature and degree days model.