

Wintertime CO₂ evolution from a boreal forest ecosystem

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We investigated wintertime ecosystem activity and CO₂ efflux over three winters (1 November–28 February 1997–2000) in a boreal Scots pine stand in Finland. During the three winters the cumulative wintertime CO₂ efflux measured with continuously operating soil chambers directly from the soil surface was between 103 and 144 g m⁻², and between 240 and 330 g m⁻² when measured by an eddy covariance method or estimated from the soil sample endogenous CO₂ production. The flux measured directly from the soil surface is probably an underestimation due to the ice formation within the chamber. Photosynthesis was found to be active also during winter and metabolic activity was found to show extrapolated zero at –5 °C to –10 °C.

Introduction

Wintertime production of CO₂ is believed to be critical for the annual carbon budget of boreal forests. It has been suggested to contribute 17% or more of the annual amount evolved from the soil in alpine, arctic and temperate ecosystems (Winston *et al.* 1997, Fahnstock *et al.* 1999). The relationship between production and decomposition determines whether a system is a sink or source of atmospheric CO₂. In old forests these two fluxes are of similar magnitude and changes in climate and the length of growing season can shift a forest from being a sink to be a source of carbon (Valentini *et al.* 2000).

CO₂ is produced within the soil by heterotrophic microbial respiration and by autotrophic root respiration. Soil microorganisms release CO₂

by oxidizing organic debris and return the carbon assimilated by plants back to the atmosphere. In boreal forests and in the arctic, decomposition is often slow due to unfavorable climate: low temperature and high humidity. The soil temperature remains between 0–5 °C most of the year.

The effect of global climate warming has been predicted to be strongest at high latitudes, but the actual temperature increase is still under debate. Current climate scenarios predict arctic surface air temperature increase varying from 2 to 7 °C at the latitudes between 60°N and 90°N by the year 2080, depending on whether the impact of cloud feedbacks have been included in the predictions (Jylhä *et al.* 2004, Vavrus 2004). The highest temperature increases are expected to occur in winter.

Because the biological activity in the soil is strongly temperature dependent (Davidson *et*

al. 1998, Kirschbaum 2000), an increase in the temperature would have a substantial effect on the carbon balance of boreal forest soils. Changes in the decomposition rate of soil organic matter could possibly lead to a feedback effect and acceleration of global warming (Cox *et al.* 2000).

Despite the importance of winter in the ecosystem carbon balance, only a few studies exist where soil CO₂ effluxes (Zimov *et al.* 1993, Winston *et al.* 1997, Billings *et al.* 1998, Mast *et al.* 1998, Fahnestock *et al.* 1999, Pumpanen *et al.* 2003) let alone other ecosystem CO₂ fluxes have been monitored continuously throughout the winter. Most of the studies on soil CO₂ efflux in boreal forests (Winston *et al.* 1997, Billings *et al.* 1998, Goulden *et al.* 1998, Lytle and Cronan 1998, Gullledge and Schimel 2000, Morén and Lindroth 2000) and in arctic tundra (Billings *et al.* 1982, 1984, Fahnestock *et al.* 1998) have been conducted on a weekly or monthly basis during the growing season. Thus, the winter period, covering one third of the year at high latitudes, is relatively poorly known in terms of ecosystem CO₂ fluxes and underlying processes.

We measured wintertime carbon dioxide fluxes from soil, canopy and ecosystem using chamber and eddy covariance techniques in the field and endogenous CO₂ production in the laboratory. Our aim was to analyse the amount of wintertime fluxes and the factors affecting the efflux rate of a managed coniferous forest with shallow or no frost in soil.

Material and methods

The Scots pine stand used in this study was sown in 1962 on a burned, mechanically prepared soil. Site preparation is a common process on almost all forest soils in Finland. In burning a proportion of the logging residue, the ground vegetation and recalcitrant humic compounds are burnt, and an increase in soil pH follows. However, almost 40 years after the burning a new litter layer has been established, so that the effect on pH has decreased and the site represents in many features such sites that have not been burnt. The soil is a podzol on glacial till, with the soil pH (H₂O) increasing from 4.4 in the humus to 5.3 in the ground soil. There were downward

decreasing gradients for total soil organic carbon from 300 mg of C g⁻¹ in humus layer to 4 mg of C g⁻¹ at the depth of 20 cm (ground soil), and of nitrogen from 10 mg of N g⁻¹ to 0.3 mg of N g⁻¹ (Ilvesniemi and Pumpanen 1997). The C and N analyses were done using Leco CSN-1000 analyser (Leco corporation, St. Joseph, MI, USA).

We measured CO₂ efflux continuously and simultaneously with chambers directly from the surface of the soil, from the canopy using shoot chambers, and above the canopy using an eddy covariance method. In addition, the endogenous CO₂ evolution was measured in the laboratory.

The CO₂ flux from soil was measured *in situ* using two online soil chambers (Haataja and Vesala 1997, Hari *et al.* 1999, Pumpanen *et al.* 2001). In chamber measurements the atmospheric CO₂ concentration is measured by an infrared gas analyzer (URAS 4, Hartman Braun). The open dynamic chambers are made of acrylic, with slightly different geometry for shoot and soil measurements. The top of the chamber is opened pneumatically between measurements. The measurement interval was 15, 24 and 57 minutes during the years 1997, 1998 and 1999, respectively, and the chamber was closed for 70 s. The flow rate of the air stream through the chamber was set by Brooks mass Flow controller (Model 5850 E). The photosynthetically active radiation (PAR) was measured within the shoot chambers with Li-Cor 190 SP PAR sensors.

The soil endogenous CO₂ production at 7 °C was measured in the laboratory (5 g of fresh soil in a 120-ml glass bottle sealed with a rubber stopper) from freshly cored soil monoliths collected on 9 October 1997, 4 December 1997, 15 January 1998, 14 October 1998 and 17 February 1999 at natural moisture conditions. Three to five cores were taken on each sampling occasion. Each core was divided into a humus layer, eluvial layer, illuvial layer (divided in two halves) and ground soil samples. Separated layers of the cores were pooled for analysis. The head-space CO₂ concentration was measured after incubation by a gas chromatograph. The Q_{10} values (the relative change in the respiration rate over a 10 °C increase in the temperature) of the samples were determined according to Kähkönen *et al.* (2001).

The half-hour average canopy level CO₂ flux densities were observed by the eddy covariance

technique. The method was applied by using commercially available instrumentation and standard calculation techniques (Moncrieff *et al.* 1997, Aubinet *et al.* 2000, Markkanen *et al.* 2001, Suni *et al.* 2003). Between 1 November and 28 February during the winters 1997, 1998 and 1999, the experimental data covered 34%, 38% and 57% of the period, respectively. Some observations were not considered reliable due to technical reasons or low turbulence conditions (friction velocity < 0.2 m s⁻¹). A regression between the observed reliable CO₂ flux densities F (in units $\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and air temperature T (in °C) under the conditions when no photosynthesis occurred was generated. The obtained relationship, $F = 29.1e^{(0.0638 \times T)}$, was applied on a half-hourly basis to replace the missing and unreliable data, and the occasions when photosynthesis was observed. The final CO₂ flux time series, being representative for the Scots pine stand respiration, contained 4840 original measurements.

Results and discussion

The study spanned from November to February over three winters (1997–2000, Julian days from 305 to 59) when average air temperatures were -4.0, -6.5 and -2.9 °C and the daily average temperatures ranged from -30 °C to 4 °C. The snow cover was permanent at the site from the end of November onwards, and the depth of snow varied between 30 and 50 cm by 28 February. The soil temperatures showed the typical wintertime inverse temperature gradient with the highest soil temperatures deepest in the soil (Fig 1). The soil temperature never dropped below the freezing point under the humus layer (thickness 4 cm). This shallow frost is different from that described for Siberian (Zimov *et al.* 1993) or Canadian (Winston *et al.* 1997) situations, where the frost was deep for long periods.

The CO₂ flux from the soil decreased from 150–350 mg m⁻² h⁻¹ in early November to values < 20 mg m⁻² h⁻¹ in January and February. The inter-annual variation in the evolution of the CO₂ flux was large and appeared to be connected with the average soil temperature. The cause of spatial variation between chambers (Fig. 2) can be

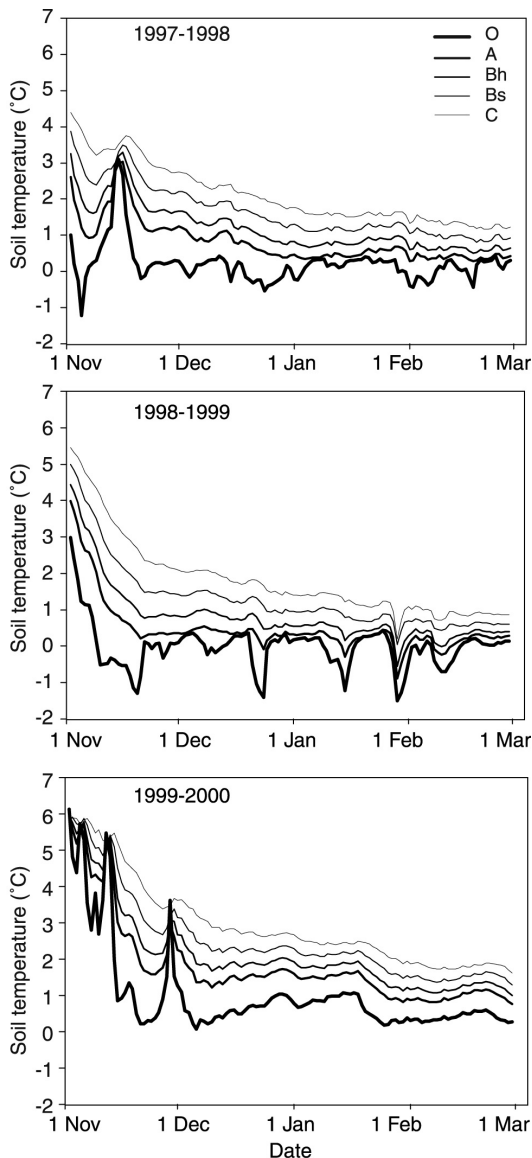


Fig. 1. Temperature of successive horizons of podzolic forest soil at Hyytiälä forestry field station, southern Finland (61°48'N, 24°19'E, 181 m a.s.l.).

assumed to follow the distribution of roots and easily decomposable litter.

The cumulative efflux of CO₂ from 1 November to 31 December in the years 1997, 1998 and 1999 measured with two soil chambers averaged 103, 86 and 144 g m⁻², respectively (Fig. 2). In January and February the fluxes were < 20 mg of CO₂ m⁻² h⁻¹ and on many days they were < 10 mg of CO₂ m⁻² h⁻¹, having only a small influence

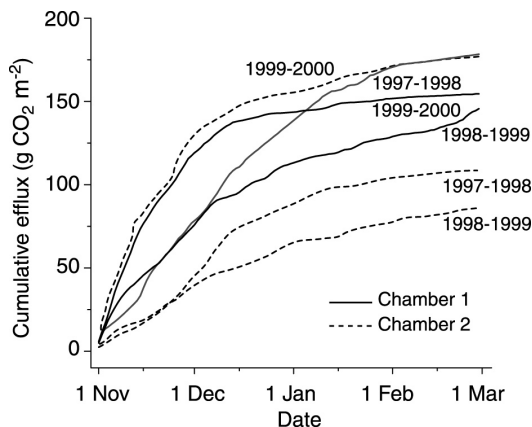


Fig. 2. The spatial and inter-annual variation in the carbon dioxide efflux from the soil surface measured by *in situ* chambers in the Hyytiälä Scots pine stand. The measurements of chamber one are shown by solid lines, and those of chamber two by dotted lines.

on the cumulative wintertime efflux. The annual-average soil CO_2 flux measured from the same site (1998–1999) was $2500 \text{ g of CO}_2 \text{ m}^{-2}$ (recalculated from Pumpanen *et al.* 2003).

The average winter fluxes of CO_2 in sub-alpine soils in Rocky Mountain national park were 78, 57 and $27 \text{ g of CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in dry, moist and saturated soils, respectively, which accounted for 8%–23% of the annual CO_2 fluxes of these soils (Mast *et al.* 1998). In the study of Fahnestock *et al.* (1999), non-growing season wintertime carbon fluxes ranged from 2 g of CO_2 per season in moist dwarf shrub communities to 97 g of CO_2 in natural snow drift communities, with an average of wintertime CO_2 efflux of $45 \text{ g of CO}_2 \text{ m}^{-2}$ for all low arctic tundra communities. This was 17% of the annual flux. Winter and early spring CO_2 efflux from tundra communities of North Alaska was $48\text{--}400 \text{ g of CO}_2 \text{ m}^{-2}$ (Fahnestock *et al.* 1998). For old black spruce and young jack pine forests in Manitoba, Canada, Winston *et al.* (1997) reported the highest wintertime fluxes of $< 100 \text{ mg of CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in November, decreasing to $10 \text{ mg of CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in February. Epron *et al.* (1999) reported a similar, very low CO_2 efflux from acid (pH 4.9) gleyic luvisol in the period November–February in Hesse forest, eastern France ($48^\circ 40' \text{N}$, $7^\circ 05' \text{E}$, elevation 305 m), with an average soil temperature of 2.1°C at -10 cm , similar to that in Hyytiälä soils of $3 \pm 1^\circ \text{C}$ at the same depth.

In October (first sampling of soil for laboratory analysis) when the average humus temperature was 2.9°C and 4.8°C in 1997 and 1998, respectively, the endogenous CO_2 production had a steep descending gradient from the top of the soil (Fig. 3). When the humus temperature in December reached an average of 0°C , it retained only 20% of its October activity, whereas the deeper soil horizons retained up to 50% of the activities, showing a change in the relative importance of different soil layers as a source of CO_2 .

In the laboratory the CO_2 evolution was measured from soil samples with an incubation method at 7°C . In order to estimate the cumulative CO_2 emissions of the Hyytiälä forest soil the values were corrected for the actual soil temperatures of the different horizons (Fig. 1) using measured Q_{10} values of 2.8 for November and December and 2.3 for January and February (Kähkönen *et al.* 2001). A cumulative calculated efflux of about 274, 267 and $301 \text{ g of CO}_2 \text{ m}^{-2}$ was obtained for the three successive years 1997, 1998 and 1999 respectively (Fig. 4). The calculated efflux for the winter 1999–2000 is based on the average of the measured activity of the two preceding years and actual temperatures of that winter.

The cumulative wintertime CO_2 fluxes from the same Scots pine stand at Hyytiälä measured by eddy covariance method are shown in Fig. 4. The obtained cumulative CO_2 evolution over the winter periods 1997–1998, 1998–1999 and 1999–2000 (a total of 4840 measured hours) was 238, 270 and 330 g m^{-2} , respectively. The fluxes from 1 November to 31 December (Fig. 4) were on average around $100 \text{ mg of CO}_2 \text{ m}^{-2} \text{ h}^{-1}$, i.e. practically identical to those emitted by the soil (Fig. 2), but later in the winter the eddy covariance effluxes differed from the soil surface flux measurements. The annual total ecosystem respiration measured by the eddy covariance method at the same site in years 2000 and 2001 were 2900 and $3300 \text{ g of CO}_2 \text{ m}^{-2} \text{ a}^{-1}$, respectively (Kolari *et al.* 2004).

To keep the chamber attached to the soil surface operating during the deep-snow period (January–February), a part of the snow around and within the chamber had to be removed. This removal of insulation may have reduced the soil temperature underneath the chamber, explaining partly the low efflux rates measured with soil chambers in late winter.

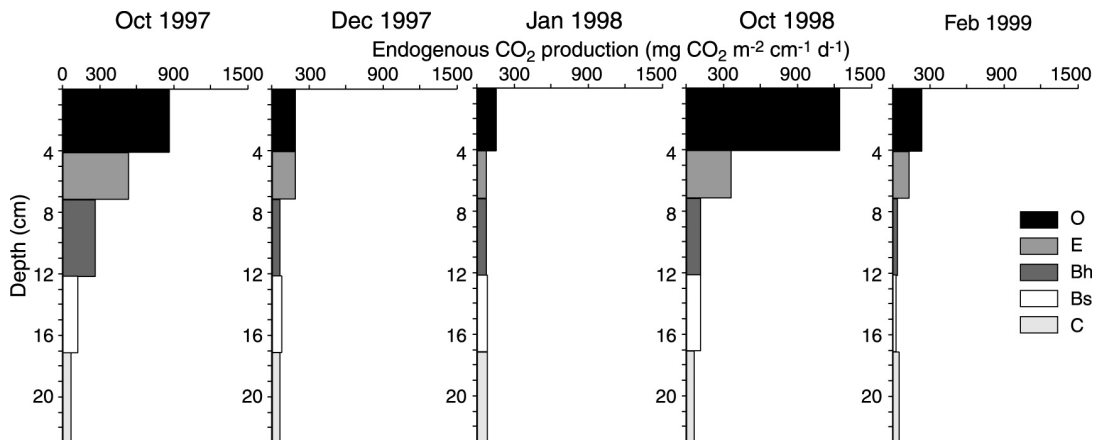


Fig. 3. Soil endogenous CO₂ production at 7 °C as measured in the laboratory from freshly cored soil cores. The soil cores were separated into successive horizons.

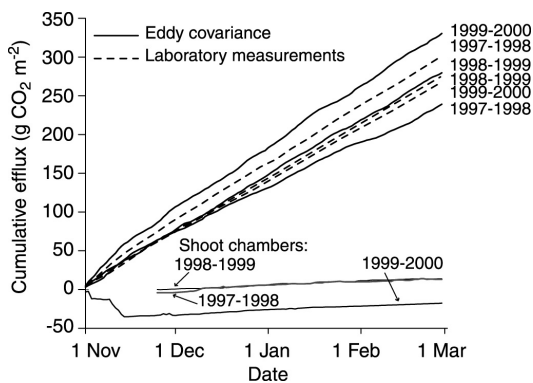


Fig. 4. The cumulative net efflux of CO₂ (NEE) from the forest over the winter period (1 November to 28 February). An eddy covariance method was used to measure the above canopy fluxes (continuously increasing solid lines) and continuously operated shoot chambers for the canopy flux (lines going almost asymptotically with x-axis, showing also net photosynthesis). The dotted lines show the estimated cumulative CO₂ emission based on the laboratory measurements, corrected for the measured actual soil temperature (Fig. 1) and the measured values of Q_{10} , 2.8 in December and 2.3 in January and February.

The contribution of the Hyttiälä Scots pine canopy to the CO₂ efflux was measured using the shoot chambers *in situ*. The shoot response was transformed to the values expressed as g of CO₂ m⁻² soil surface by applying the needle biomass (g m⁻²) of the stand (Ilvesniemi and Liu 2001). The cumulative wintertime CO₂ efflux (between 1 November and 28 February) of the shoots was

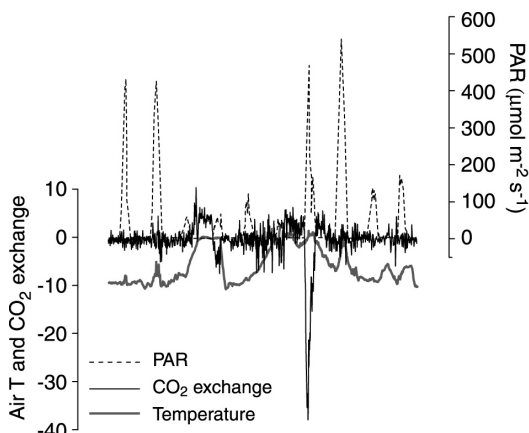


Fig. 5. The effect of temperature and radiation on shoot carbon exchange in spring 1998 (5–14 February). The dashed line denotes PAR, thin solid line CO₂ exchange (mg m⁻² h⁻¹) and thick line air temperature, (°C) at 4.2 m height.

around 15 g of CO₂ m⁻² over the two first winters studied (Fig. 4). The rate of photosynthesis was so high in the early winter 1999 that the cumulative CO₂ showed net carbon accumulation.

Figure 5 shows the coupling of the shoot CO₂ efflux with air temperature and solar radiation over a selected period. The shoots were photosynthetically active also during winter, when the air temperature was near 0 °C over more than one successive day, and when the global radiation exceeded 20 mmol m⁻² s⁻¹. On 5 and 6 February when PAR was high and air temperature was around -10 °C,

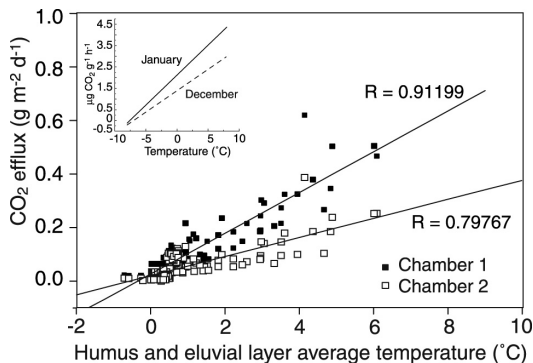


Fig. 6. CO₂ efflux from the soil measured with *in situ* chambers.

a negligible carbon exchange was found. On 8 February the air temperature increased to near zero, but because a very low amount of PAR was available, shoot respiration instead of photosynthesis could be observed. On 11 February when the average air temperature was near 0 °C for two successive days and the sky was cloudless, a significant uptake of CO₂ was detected, reflecting closely the diurnal changes of PAR. On 12 February the amount of PAR was comparable to that on 11 February, but no uptake of CO₂ could be detected due to the preceding cold night.

The conclusion from the results shown in Figs. 2–5 is that during the winter, the Scots pine forest emitted around 250 g of CO₂ m⁻², the main source (> 90%) being the forest soil. The reason for larger wintertime emissions from the Hyttiälä soil as compared with that measured in France (Epron *et al.* 1999) can lie in the shallow soil frost and simultaneous high soil moisture content in Hyttiälä (Davidson *et al.* 1998), as the wintertime soil temperatures were quite similar at both sites. The snow cover not only effectively insulates the soil against the cold air (Fig. 1) but also protects it against evaporation of water.

The endogenous respiration in the Hyttiälä soil, measured from freshly sampled soil cores incubated in the laboratory, showed extrapolated zero activity at –5 °C to –10 °C (average –7 °C). The zero CO₂ efflux for the soil chambers was extrapolated to humus and eluvial layer average temperature of 0 °C (Fig. 6). Respiration (CO₂ efflux) and photosynthesis (CO₂ influx) of the Scots pine were observed when the air temperature (at 4.2 m height) was higher than –5 °C

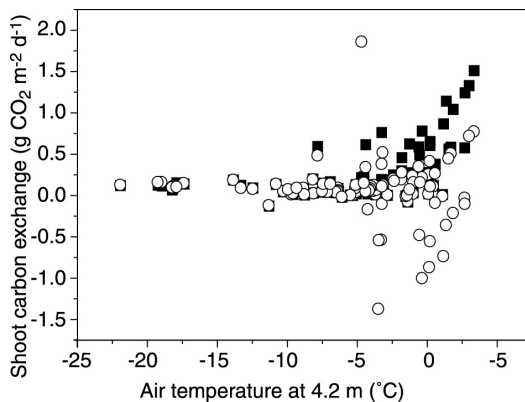


Fig. 7. The shoot CO₂ exchange response on air temperature. Solid symbols indicate night-time measurements (respiration only) and open symbols indicate 24-hour net flux.

(Fig. 7). The data obtained with laboratory measurements showed that the temperature dependence of forest soil carbon dioxide metabolism was approximately the same as for that measured for the Scots pine shoots, averaging at –7 °C. This is also similar to the zero point measured for organic litter decomposition in Harvard Forest in Massachusetts (Goulden *et al.* 1998).

The temperature responses obtained in this study (Q_{10} of 1.8–3.0) are similar to the data shown for Harvard forest and for Siberian tundra humus (Boone *et al.* 1998, Christensen *et al.* 1999), but lower than the values of Q_{10} between 4.5 and 8 presented by Kirschbaum (1995) for various types of soil and geographic regions. Considering the already high carbon dioxide emissions from the soil, and the relatively low temperature response, the 10% loss of soil organic carbon as a response to 1 °C increase of temperature proposed by Kirschbaum (1995) does not seem to apply for this type of boreal forest soils.

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References

Aubinet M., Grelle A., Ibrom A., Rannik Ü., Moncrieff J., Foken T., Kowalski A.S., Martin P.H., Berbigier

- P., Bernhofer Ch., Clement R., Elbers J., Granier A., Grünwald T., Morgenstern K., Pilegaard K., Rebmann C., Snijders W., Valentini R. & Vesala T. 2000. Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. *Adv. Ecol. Res.* 30: 113–175.
- Billings W.D., Luken J.O., Mortensen D.A. & Peterson K.M. 1982. Arctic tundra: a source or sink for atmospheric carbon dioxide in a changing environment? *Oecologia* 53: 7–11.
- Billings W.D., Peterson K.M., Luken J.O. & Mortensen D.A. 1984. Interaction of increasing atmospheric carbon dioxide and soil nitrogen on the carbon balance of tundra microcosms. *Oecologia* 65: 26–29.
- Boone R.R., Nadelhoffer K.J., Canary J.D. & Kayer J.P. 1998. Roots exert a strong influence on sensitivity of soil respiration. *Nature* 393: 570–572.
- Cox P.M., Betts R.A., Jones C.D., Spall S.A. & Totterdell I.J. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408: 184–187.
- Davidson E.A., Belk E. & Boone R.D. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biology* 4: 217–227.
- Epron D., Farque E., Lucot E. & Badot P.-M. 1999. Soil CO₂ efflux in a beech forest: dependence on soil temperature and soil water content. *Ann. For. Sci.* 56: 221–226.
- Fahnestock J.T., Jones M.H. & Welker J.M. 1999. Wintertime CO₂ efflux from arctic soils: implications for annual carbon budgets. *Global Biogeochemical Cycles* 13: 775–779.
- Fahnestock J.T., Jones M.H., Brooks P.D., Walker D.A. & Welker J.M. 1998. Winter and early spring CO₂ efflux from tundra communities of northern Alaska. *J. Geophys. Res.* 103: 29023–29027.
- Goulden M.L., Wofsy S.C., Harden J.W., Trumbore S.E., Crill P.M., Gower S.T., Fries T., Daube B.C., Fan S.-M., Sutton D.J., Bazzaz A. & Munger J.W. 1998. Sensitivity of boreal forest carbon balance to soil thaw. *Science* 279: 214–216.
- Gulledge J. & Schimel J.P. 2000. Controls on soil carbon dioxide and methane fluxes in a variety of taiga forest stands in interior Alaska. *Ecosystems* 3: 269–282.
- Haataja J. & Vesala T. (eds.) 1997. Smear II, Station for Measuring Forest Ecosystem–Atmosphere Relation. *University of Helsinki Department of Forest Ecology publications* 17: 30–37.
- Hari P., Keronen P., Bäck J., Altimir N., Linkosalo T., Pohja T., Kulmala M. & Vesala T. 1999. An improvement of the method for calibrating measurements of photosynthetic CO₂ flux. *Plant, Cell and Environment* 22: 1297–1301.
- Ilvesniemi H. & Liu C. 2001. Biomass distribution in a young Scots pine stand. *Boreal Env. Res.* 6: 3–8.
- Ilvesniemi H. & Pumpanen J. 1997. Appendix 6. In: Haataja J. & Vesala T. (eds.), Smear II, Station for Measuring Forest Ecosystem–Atmosphere Relation. *University of Helsinki Department of Forest Ecology publications* 17: 92–96.
- Jylhä K., Tuomenvirta H. & Ruosteenoja K. 2004. Climate change projections for Finland during the 21st century. *Boreal Env. Res.* 9: 127–152.
- Kähkönen M., Wittman C., Kurola J., Ilvesniemi H. & Salokinoja-Salonen, M. 2001. Microbial activity of boreal forest soil in cold climate. *Boreal Env. Res.* 6: 19–28.
- Kirschbaum M.U.F. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biol. Biochem.* 27: 753–760.
- Kirschbaum M.U.F. 2000. Will changes in soil organic carbon act as a positive or negative feedback on global warming? *Biogeochemistry* 48: 21–51.
- Kolari P., Pumpanen J., Rannik Ü., Ilvesniemi H., Hari P. & Berninger F. 2004. Carbon balance of different aged Scots pine forests in southern Finland. *Global Change Biology* 10: 1106–1119.
- Lytle D.E. & Cronan C.S. 1998. Comparative soil CO₂ evolution, litter decay, and root dynamics in clear-cut and uncut spruce–fir forest. *Forest Ecology and Management* 103: 121–128.
- Markkanen T., Rannik Ü., Keronen P., Suni T. & Vesala T. 2001. Eddy covariance fluxes over a boreal Scots pine forest. *Boreal Env. Res.* 6: 65–78.
- Mast M.A., Wickland K.P., Striegl R.T. & Clow D.W. 1998. Winter fluxes of CO₂ and CH₄ from subalpine soils in Rocky Mountain National Park, Colorado. *Global Biogeochemical Cycles* 12: 607–620.
- Moncrieff J.B., Massheder J.M., de Bruin H., Elbers J., Friberg B., Heutsunkveld B., Kabat P., Scott S., Soegaard H. & Verhoef A. 1997. A system to measure surface fluxes of energy, momentum and carbon dioxide. *J. Hydrology* 188–189: 589–611.
- Morén A.-S. & Lindroth A. 2000. CO₂ exchange at the forest floor of a boreal forest. *Agricultural and Forest Meteorology* 101: 1–14.
- Pumpanen J., Ilvesniemi H., Perämäki M. & Hari P. 2003. Seasonal patterns of soil CO₂ efflux and soil air CO₂ concentration in a Scots pine forest: comparison of two chamber techniques. *Global Change Biology* 9: 371–382.
- Pumpanen J., Ilvesniemi H., Keronen P., Nissinen A., Pohja T., Vesala T. & Hari P. 2001. An open chamber system for measuring soil surface CO₂ efflux; Analysis of error sources related to the chamber system. *J. Geophys. Res.* 106: 7985–7992.
- Suni T., Rinne J., Reissel A., Altimir N., Keronen P., Rannik Ü., Dal Maso M., Kulmala M. & Vesala T. 2003. Long-term measurements of surface fluxes above a Scots pine forest in Hyytiälä, southern Finland, 1996–2001. *Boreal Env. Res.* 4: 287–301.
- Valentini R., Matteucci G., Dolman A.J., Schulze E.-D., Rebmann C., Moors E.J., Granier A., Gross P., Jensen N.O., Pilegaard K., Lindroth A., Grelle A., Bernhofer C., Grünwald T., Aubinet M., Ceulemans R., Kowalski A.S., Vesala T., Rannik Ü., Berbigier P., Loustau D., Gudmundsson J., Thorgeirsson H., Ibrom A., Morgenstern K., Clement R., Moncrieff J., Montagnani L., Minerbi S. & Jarvis P.G. 2000. Respiration as the main determinant of carbon balance in European forests. *Nature* 404: 861–865.
- Vavrus S. 2004. The impact of cloud feedbacks on arctic cli-

- mate under greenhouse forcing. *J. Climate* 17: 603–614.
- Winston G.C. & Sundquist E.T. 1997. Winter CO₂ fluxes in a boreal forest. *J. Geophys. Res.* 102: 28795–28804.
- Zimov S.A., Zimova G.M., Daviodov S.P., Daviodova A.I., Voropaev Y.V., Voropaeva Z.V., Prosiannikov S.F. & Prosiannikova O.V. 1993. Winter biotic activity and production of CO₂ in Siberian soils: a factor in the greenhouse effect. *J. Geophys. Res.* 98: 5017–5023.

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