

Heterotrophic soil respiration in forestry-drained peatlands

Kari Minkkinen¹), Jukka Laine²), Narasinha J. Shurpali³), Päivi Mäkiranta⁴),
Jukka Alm⁵) and Timo Penttilä⁶)

¹) Department of Forest Ecology, P.O. Box 27, FI-00014 University of Helsinki, Finland (e-mail: kari.minkkinen@helsinki.fi)

²) Finnish Forest Research Institute, Parkano Research Unit, FI-39700 Parkano, Finland

³) University of Kuopio, Department of Environmental Sciences, FI-70211 Kuopio, Finland

⁴) Finnish Forest Research Institute, Kannus Research Unit, FI-69101 Kannus, Finland

⁵) Finnish Forest Research Institute, Joensuu Research Unit, FI-80101 Joensuu, Finland

⁶) Finnish Forest Research Institute, Vantaa Research Unit, FI-01301 Vantaa, Finland

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Heterotrophic soil respiration (CO₂ efflux from the decomposition of peat and root litter) in three forestry-drained peatlands with different site types and with a large climatic gradient from the hemi-boreal (central Estonia) to south (southern Finland) and north boreal (northern Finland) conditions was studied. Instantaneous fluxes varied between 0 and 1.3 g CO₂-C m⁻² h⁻¹, and annual fluxes between 248 and 515 g CO₂-C m⁻² a⁻¹. Variation in the annual fluxes among site types was studied only in the south-boreal site where we found a clear increase from nutrient-poor to nutrient-rich site types. More than half of the within-site variation was temporal and explained by soil surface (–5 cm) temperature (T₅). The response of soil respiration to T₅ varied between the sites; the most northerly site had the highest response to T₅ and the most southerly the lowest. This trend further resulted in increased annual fluxes towards north. This unexpected result is hypothesised to be related to differences in site factors like substrate quality, nutrient status and hydrology but also to temperature acclimation, i.e., adaptation of decomposer populations to different climates.

Introduction

Finland is obliged by the Kyoto protocol (UNFCCC 1997) to report annually its anthropogenic greenhouse gas (GHG) emissions to the UN Framework Convention on Climate Change (UNFCCC), including GHG emissions from land use, land use change and forestry (LULUCF). Land use changes, such as afforestation of croplands or drainage of natural peatlands for the purpose of production forestry may significantly affect GHG emissions from the site. In Finland a substantial land use change has taken place in

peatlands: approximately 60% of the original peatland area (10 million ha) has been drained and managed, and nowadays ca. 4.9 million ha of the forest land in Finland is classified as drained peatland forest (Finnish Forest Research Institute 2004), while 4 million ha have remained undisturbed.

Peatlands are carbon (C) accumulating ecosystems sustained by a humid climate and a high water table. In such conditions, the organic matter (OM) produced is decomposed only partially in the aerobic soil surface and accumulated as peat. In water-saturated conditions, decom-

position is much slower because of low oxygen content as well as phenol toxicity (Freeman *et al.* 2001) and lower temperatures in the deeper layers (Minkkinen *et al.* 1999). After drainage, some of this peat bulk becomes aerated and is thus susceptible again to faster aerobic decomposition. In addition, the growing forest inputs new types of fresh litters to the system, thus providing additional substrates for decomposition at the soil surface or in the peat. As fresh litter is rich in soluble carbohydrates and cellulose, its decomposition rate is faster than that of “old” peat, which is enriched with lignin-like and other recalcitrant compounds (Berg *et al.* 1982, Udegraff *et al.* 1995, Belyea 1996, Haraguchi *et al.* 2002).

The decomposition rate of OM can be estimated by measuring soil respiration (SR) *in situ*, as has been done in drained peatlands (Glenn *et al.* 1993, Silvola *et al.* 1996a, 1996b, Alm *et al.* 1999, von Arnold *et al.* 2005a, 2005b). SR is, however, derived not only from decay, i.e. heterotrophic respiration (animals, microbes), but also from the respiration of autotrophs (plants). In earlier studies, litter decomposition and often root respiration have also been included in the reported estimates of SR rates. Drainage enhances SR compared to natural peatlands because of faster oxidation of OM in aerobic conditions and because of higher root respiration attributed to increased root biomass. Root respiration has been estimated to contribute 10%–40% of SR in drained peatland forests (Silvola *et al.* 1996b) which is in line with the reported values from forests in mineral soils (Bowden *et al.* 1993, Nakane *et al.* 1996, Lytle and Cronan 1998, Hanson *et al.* 2000, Högberg *et al.* 2001, Widén and Majdi 2001, Bond-Lamberty *et al.* 2004). In addition to aeration, SR is driven by temperature (Lloyd and Taylor 1994, Davidson and Janssens 2006), and is thus strongly dependent on prevailing climatic conditions.

Statistical models derived from *in situ* measurements have been used to explain and to predict seasonal/annual greenhouse gas emissions from drained peatlands (Silvola *et al.* 1996a, von Arnold *et al.* 2005a, 2005b). For soil CO₂ effluxes the most important explanatory variables have been soil temperature, water table

level (WT) and site type, describing the nutrient status of the site. However, if CO₂ emissions are to be estimated at national level, e.g., for national greenhouse gas inventories, the models need to be based on input variables that are extensively available across the whole country. In Finland such routinely measured variables are e.g., tree stand characteristics and site type distributions from the National Forest Inventories performed by the Finnish Forest Research Institute, and weather data (air temperatures, precipitation, etc.) monitored by the Finnish Meteorological Institute. Although WT is an important variable as describing the state of anoxia in peatlands, it is not routinely measured and cannot be reliably predicted from the data available. Site type, however, reflects the post-drainage development of vegetation, and approximates WT in drained peatlands, WT being deeper in the more nutrient-rich sites on average. Moreover, the temporal dynamics of WT and soil temperature are intercorrelated and thus the dynamics in soil temperature also contains information of water table dynamics.

In this study we aimed to quantify the rate of heterotrophic decomposition of old OM, i.e. the decomposition rate of peat and previously deposited (> 1-year-old) litter, later referred to as soil respiration (SR), in three forestry-drained peatlands in different site types and climatic conditions. Additionally, we aimed to model the response of SR to soil temperature and use the models with long-term weather data, in order to estimate weather-driven long-term variation in annual CO₂ efflux from peat in forestry-drained peatlands. These data and models provide a tool for estimating GHG emission factors for forestry-drained peatlands in Finland (Alm *et al.* 2007).

Material and methods

The sites

SR was measured in forestry-drained peatlands at two sites in Finland and one in Estonia (Table 1). The most southerly site, representing the hemiboreal vegetation zone, is situated at Väätsa, central Estonia. The site was originally a rich fen

and was drained for forestry purposes in 1959, using 150 m ditch spacing and a 1.4 m ditch depth. The site was ploughed and planted with 2-year-old Scots pine (*Pinus sylvestris*) seedlings in 1961. The resultant tree stand consists mostly of Scots pine with an understorey of Norway spruce (*Picea abies*) and pubescent birch (*Betula pubescens*), and no thinning or wood removal has occurred. The site is very fertile, the ground vegetation is rich with herbs and it is classified as herb-rich type (Rhtkg, Table 1) according to Laine (1989). Peat depth varies from 235 to 300 cm.

The second site is situated at the Vesijako Research Forest of Finnish Forest Research Institute, south-boreal part of Finland. The site was originally a treed mire with an ombrotrophic centre and minerotrophic lagg. The mire was drained for the first time in 1915 and reditched in 1933 and 1954. The tree stand evolved after the first drainage was regenerated through seed-tree cutting in 1945–1950, and the second-generation post-drainage Scots pine stand has been managed with two commercial thinnings before starting the SR monitoring presented here. The current tree stand consists mostly of pine (83%), the rest being spruce and birch. Site types (Laine 1989) in the area vary from dwarf shrub type (Vatkg) to herb-rich type (Rhtkg). The peat depth varies from 100 to over 300 cm.

The most northerly site is situated at the Kivalo Research Forest of the Finnish Forest Research Institute, north-boreal part of Finland. The site was originally a treed minerotrophic fen. It was drained for the first time in 1933 and is now classified as *Vaccinium myrtillus* type (Mtkg; Laine 1989). The peat layer is thin, 30–90 cm. Larger, over-storey trees were harvested in the 1950s and the remaining understorey

was managed with a pre-commercial thinning to develop to the present stand. A light commercial thinning followed by complementary ditching to the present ditch spacing of 30–35 meters was accomplished in 1985–1986. The tree stand is dominated by pine, with some spruce and birch in the understorey.

In Vesijako and Kivalo the sites were subdivided to fairly large (ca. 0.5 ha) felling treatment subsites, including a clear-fell treatment in winter 2001–2002 on both sites and a thinning treatment in Vesijako. In this paper, plots from all treatments were included equally, as no differences in the SR rates of old peat were detected among the treatments (K. Minkkinen unpubl. data).

The climatic conditions varied greatly between the sites, as well as between years (Table 2). The temperature sum (d.d. > 5 °C) at the northernmost site was 865 d.d. (average for 1961–1990) while at the southernmost site it averaged 1421 d.d. (average for 1991–2005, Türi weather station, 20 km south of the site). The temperatures measured at the site, under a closed tree stand canopy were, however, clearly lower than those at the weather station in Türi (Table 2). In Finland the measurement years 2002–2003 were much warmer than 1961–1990 (Table 2), especially at Kivalo. During the snow-free season (May–October) differences in temperatures between sites were relatively small, but winters were colder, the more northerly the site (Table 2). Precipitation increases ca. 100 mm a⁻¹ per site towards the south. The differences in weather conditions resulted in different soil temperatures at the sites, mean soil temperatures at 5 cm increasing ca. 1 °C per site from north to south (Table 2) and the effective time for decomposition (d.d. > 0 °C) being clearly longer in the south.

Table 1. General description of the study sites.

Site	Coordinates	Elevation (m a.s.l)	Site type ¹⁾	Number of plots	Stand volume (m ³ ha ⁻¹)	Drainage year
Väätsa	58°59'N, 25°27'E	78	Rhtkg	20	148–179	1959
Vesijako	61°22'N, 25°07'E	115	Vatkg–Rhtkg	48	164–185	1915, 1933, 1954
Kivalo	66°21'N, 26°37'E	180	Mtkg	28	136	1933, 1950, 1985

¹⁾ Rhtkg = herb-rich type; Mtkg = *Vaccinium myrtillus* type; Ptkg = *Vaccinium vitis-idaea* type; Vatkg = dwarf shrub type; Jätkg = *Cladina* type (Laine 1989).

Plot preparation

SR was measured from 20–48 evenly distributed plots ($d = 31.5$ cm) per site. To eliminate autotrophic respiration, ground vegetation was removed and the plot was kept free of any vegetation by regular cutting. For the same reason, roots were cut with 30 cm deep metal cylinders (collars). Newly deposited litter was removed and the plots were kept free of litter by means of mosquito nets placed on the plots.

At the Väätsa site 20 plots were prepared in 2002. Since the site had been ploughed, ten plots were placed on the furrow and 10 on the ridge. Measurements were conducted in 2002 and 2003. Here we report the results from 2003, when a year had passed since root-cutting. At Vesijako and Kivalo sites measurement plots were prepared and roots cut in 2001. Here we report the results from 2002–2004.

Measurements

SR was measured using a portable IR-analyser equipped with a closed-chamber system (EGM-3 and EGM-4 + SRC-1, PP-systems, UK; for closer method description *see* Alm *et al.* 2007). The litter net was removed prior to measurement. The chamber was placed on the collar for a measurement period of 81 seconds in the summer season (May–October) and up to 144 seconds in the winter when fluxes were low. In

winter fluxes were measured on top of the snow with the help of a snowboard, keeping the chamber from sinking into the snow.

Air and soil temperatures (5 cm) and water table depth (cm below the peat surface) were measured simultaneously with every CO₂ efflux measurement (except during winter). The depth of 5 cm was chosen for measuring the soil temperature since it was observed to be the best single depth for predicting soil CO₂ efflux and it was not possible to measure temperature from several depths, although these could have provided even better explanatory power. Because of possible peat subsidence inside the collar, the distance from the collar edge to the peat surface was measured every summer to estimate the real height and volume of the chamber headspace. Continuous weather data (air and soil temperatures, precipitation, PAR) were also collected with a weather station on the site. Miniature temperature data-loggers (i-button, Dallas Semiconductor Corp.) were used to obtain plotwise soil temperature data.

Calculations

Fluxes were calculated (automatically by the EGM program) from the linear change in CO₂ concentration in the chamber headspace over time. All measurements were checked afterwards and corrected if nonlinearity (leakage) or other anomalies were observed. Fluxes were corrected

Table 2. Weather conditions at the sites during the measurement years and in 1961–1990 (1991–2005 in Väätsa). T_{air} is air temperature (°C) 2 m above ground and T5 soil temperature (°C) 5 cm below ground.

Site	Years	T _{air} mean annual	T _{air} mean summer	T _{air} sum (d.d. > 5°C)	Precipitation (year/winter) (mm)	T5 mean annual	T5 mean summer ¹⁾	T5 sum (d.d. > 0 °C)
Väätsa	2003	5.0	11.5	1293	725/271	6.2	11.1	2277
	1991–2005	4.8	12.1	1421				
Vesijako	2002	3.8	10.8	1336	601/228	5.3	10.2	1875
	2003	3.8	11.2	1254				
	2004	4.0	11.7	1300				
	1961–1990	3.4	11.2	1239				
Kivalo	2002	0.4	9.4	1150	538/199	4.5	8.9	1710
	2003	1.4	9.6	1043				
	2004	1.5	9.3	976				
	1961–1990	−0.2	8.5	865				

¹⁾ May–October

for the actual chamber headspace (= chamber + collar) volume and temperature (estimated from the air temperature).

SR in peat soils is closely dependent on soil temperature, water-table level (WT) and the site type (e.g. Silvola *et al.* 1996a). WT is not a routinely measured variable in forest inventories, which limits its usability for upscaling purposes. Soil temperature, however, can be derived from air temperature, which is generally available from weather stations across the country. Site types are routinely determined in the National Forest Inventory. Consequently, we used hourly soil temperature (T5) as the driving variable to build up site-type-specific regression models of an exponential form ($y = a \times e^{b \times T5}$) to explain the variation in SR and to calculate seasonal CO₂ effluxes in every site type (Table 3). Average effluxes for winter (November–April) were integrated from the measurements. Annual effluxes were calculated by summing up the summer and winter fluxes.

A simulation approach was taken to the annual variability in SR. For every site a 30-year soil temperature data set was simulated using a weather simulation model (Kellomäki *et al.* 1993), which is based on actual air temperature data (1961–1990) from the Finnish Meteorological Institute weather stations. The COUP model (Jansson and Moon 2001) was used to estimate soil temperature from the air temperature after calibration to each site, and seasonal fluxes were calculated with the site-type specific equations using the estimated soil temperature at 5 cm depth as the input variable (Table 3).

Results

Variation in instantaneous fluxes

There was a large temporal variation in SR at all sites, closely following the variation in soil temperature at 5 cm (T5) (Fig. 1). Fluxes were close to zero at all sites when the soil surface was frozen, and the highest instantaneous fluxes (up to 1.29 g CO₂ m⁻² h⁻¹) were measured at the Vesijako site in summer 2003, when soil temperatures were at their highest. Instantaneous fluxes showed large variation during the summer seasons (May–October), ranging from 0 to 1.29 g CO₂ m⁻² h⁻¹ (Fig. 1). During the winter months, instantaneous values ranged from –0.01 to 0.27 g CO₂ m⁻² h⁻¹.

There also was large spatial variability in summertime fluxes between and within the sites (Fig. 1). The highest average fluxes were measured at the northernmost site, Kivalo, where the summertime efflux was on average 0.35 g CO₂ m⁻² h⁻¹; the corresponding values at Vesijako and Väätsa were 0.27 and 0.29 g CO₂ m⁻² h⁻¹, respectively. This result was unexpected, since soil temperatures were lowest at Kivalo and highest at Väätsa (Table 2). The relatively low variability in fluxes at the southernmost site, Väätsa, was also unexpected; the fluxes only incidentally rose above 0.6 g CO₂ m⁻² h⁻¹, although soil temperature varied almost as much as at the other sites (Fig. 1). Within-site variability in the fluxes was highest at Vesijako, where the site types also varied most. Fluxes increased from nutrient-poor to nutrient-rich site types;

Table 3. Regression models for soil respiration ($SR = a \times e^{b \times T5}$, g CO₂ m⁻² h⁻¹), and the hourly-modeled seasonal CO₂-C effluxes (g CO₂-C m⁻² season⁻¹). SE_a and SE_b are the standard errors of the coefficients. Winter efflux was interpolated from the wintertime measurements. Annual efflux is the sum of seasonal and winter efflux.

Site	Site type	<i>a</i>	<i>b</i>	SE_a	SE_b	<i>r</i> ²	<i>n</i>	Seasonal, efflux modeled	Winter efflux interpolated	Annual efflux
Väätsa ¹⁾	Rhtkg	0.1015	0.0739	0.0078	0.0055	0.53	269	298	78	376
Vesijako ²⁾	Vatkg	0.0507	0.1135	0.0039	0.0049	0.70	353	218	30	248
	Ptkg	0.0628	0.104	0.0024	0.0025	0.74	891	241	33	274
	Mtkg	0.0784	0.1046	0.0029	0.0024	0.63	1639	303	49	352
Kivalo ²⁾	Rhtkg	0.1187	0.0977	0.0104	0.0058	0.55	363	423	58	481
	Mtkg	0.1359	0.0969	0.0055	0.0032	0.56	977	410	105	515

¹⁾ 2003, ²⁾ 2002–2004

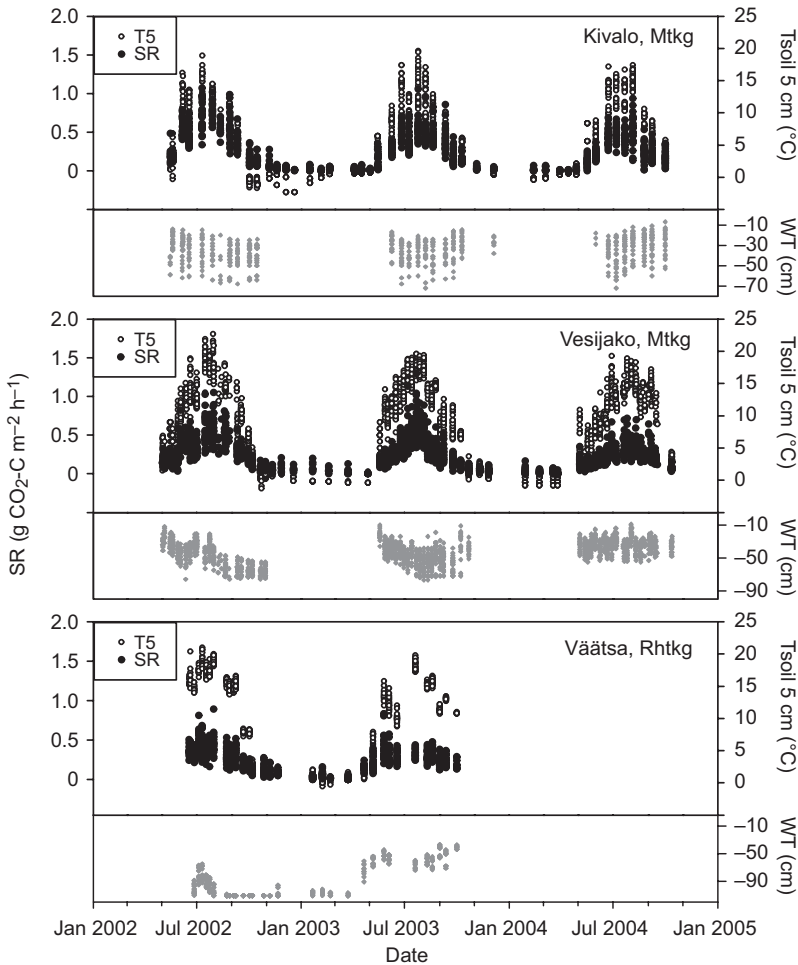


Fig. 1. Temporal variation in instantaneous soil respiration (SR), soil temperature at 5 cm (T5) and water table level (WT) at three study sites. For Väätsä, only 2003 data was used in modeling since there the roots were cut in 2002.

average summertime fluxes were 0.20, 0.22, 0.28 and 0.39 g CO₂ m⁻² h⁻¹ in Vatkg, Ptkg, Mtkg and Rhtkg site types, respectively.

Soil temperature at 5 cm explained 53–74% of the total variation within sites/site types when an exponential model was fitted to the data ($SR = a \times e^{b \times T5}$; Table 3, Fig. 2). Parameter *a*, which describes the ‘basal respiration rate’ clearly increased from nutrient-poor to nutrient rich site types within Vesijako site, and between the sites from the south to the north. Parameter *b*, describing ‘temperature sensitivity’ of SR, was quite similar at all other sites except Väätsä, where it was markedly lower. However, since these parameters are interdependent (SR is the product of *a* and *b*), both parameters influence the SR response to temperature, i.e. the absolute increase in SR vs. increase in temperature. This

response was highest at Kivalo, the northernmost site and lowest at Väätsä, the southernmost (Fig. 2), at the temperature range of 0–20 °C. The regressions usually overestimated fluxes at low temperatures, but since the models were used for predicting summer fluxes only, and winter was interpolated from the measurements, the bias in seasonal and annual estimates is not significant.

Seasonal fluxes

Measurement periods

Variation in the seasonal/annual fluxes was much smaller between the years than between the sites (Table 3). The trends were the same as with the instantaneous fluxes, seasonal and annual

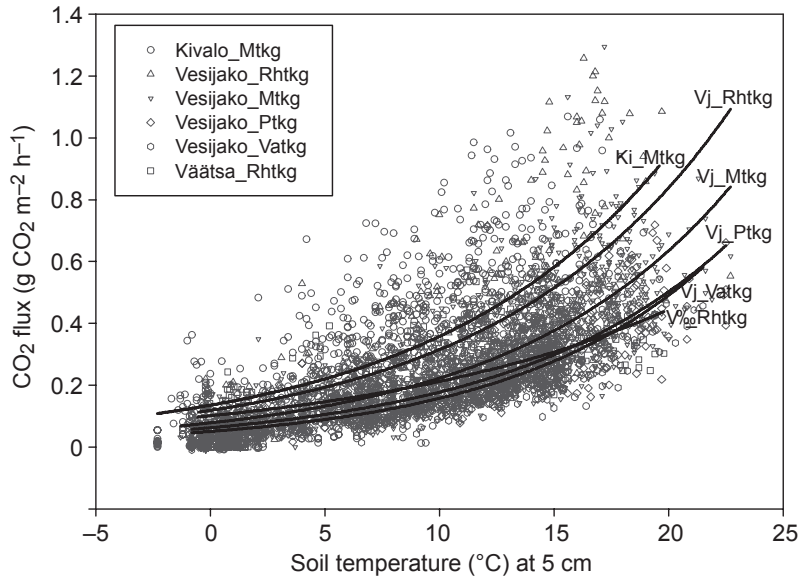


Fig. 2. The relationships between soil respiration and soil temperature (-5 cm) at all study sites and site types. Regression lines are of the form $SR = a \times e^{b \times T^5}$. See Table 3 for the parameter values.

fluxes increasing from nutrient poor to nutrient-rich site types and from the south to the north. The highest fluxes during summer season were emitted from the most nutrient-rich site at Vesijako ($423 \text{ g CO}_2\text{-C m}^{-2} \text{ a}^{-1}$), and the lowest from the poorest site type at the same site ($218 \text{ g CO}_2\text{-C m}^{-2} \text{ a}^{-1}$). Thus the full range of variation in summer season fluxes was found within one peatland. Average effluxes in winter were clearly highest at Kivalo ($105 \text{ g CO}_2\text{-C m}^{-2} \text{ a}^{-1}$), somewhat lower at Väätsa ($78 \text{ g CO}_2\text{-C m}^{-2} \text{ a}^{-1}$), and lowest at Vesijako ($30\text{--}58 \text{ g CO}_2\text{-C m}^{-2} \text{ a}^{-1}$). Consequently, when summer and winter fluxes were summed up, the highest average annual efflux was found for the most northerly site at Kivalo ($515 \text{ g CO}_2\text{-C m}^{-2} \text{ a}^{-1}$), much lower for the climatically warmest site at Väätsa ($376 \text{ g CO}_2\text{-C m}^{-2} \text{ a}^{-1}$) and the lowest ($248 \text{ g CO}_2\text{-C m}^{-2} \text{ a}^{-1}$) for Vatkg site type at Vesijako. During the study period, ground frost was almost non-existing at Kivalo due to long, warm autumns and subsequent snowfalls covering the ground before it had frozen deep. Consequently, the thick insulating snowpack kept the peat surface almost unfrozen throughout most of the winter, while at Vesijako the soil was frozen every year till the end of April. At Väätsa the soil stayed a bit warmer throughout the winter due to a generally warmer climate.

Long-term variation

The simulated weather data showed more pronounced differences between the sites than the data from the measurement period, the long-term mean soil temperature (based on data from 1961–1990) being clearly lower than that in 2002–2004 at Kivalo especially. The simulated seasonal effluxes varied between 166 and $463 \text{ g CO}_2\text{-C m}^{-2} \text{ a}^{-1}$, and again, the whole range was found within the Vesijako site (Fig. 3 and Table 4). When the seasonal means and the interpolated winter fluxes (Table 3) were summed up, average annual fluxes for the 30-year period varied between 243 and $477 \text{ g CO}_2\text{-C m}^{-2} \text{ a}^{-1}$, being highest at Kivalo (Table 4).

The relationships between the simulated annual mean soil temperatures and SR values were linear, and the interannual variation in SR within sites was largely explained by soil temperature (Fig. 3). The levels of SR (regression constants) however varied largely between the sites and site types. Mtkg site type at Kivalo (see Table 1 for site type names) produced similar fluxes as the most fertile, Rhtkg site type at Vesijako, but with much lower mean temperatures. Rhtkg site type at Väätsa was at the same level with Mtkg at Vesijako, but with higher temperatures. Thus it appears that within similar site types and soil temperatures, the heterotrophic SR

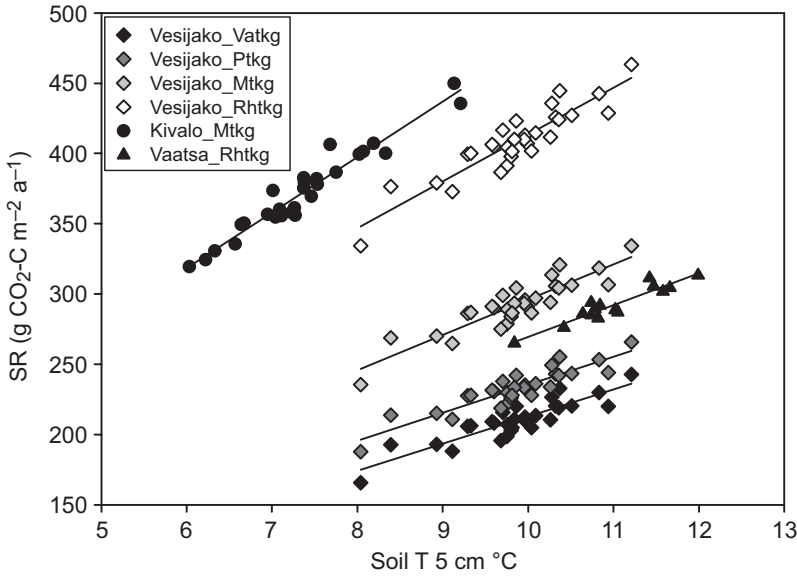


Fig. 3. The linear relationships between the simulated seasonal (May–October) long-term temperatures and soil respiration across the sites and site types. The simulation period for Väätsa was 15 years (1991–2005), but 30 years for Vesijako and Kivalo (based on 1961–1990 data).

increases towards colder climates, and therefore this interaction has to be accounted for when predicting annual CO₂ effluxes.

Discussion

Our aim was to measure heterotrophic soil respiration (SR) originating from old organic matter, i.e., peat and old litter. This separation was done by cutting the roots with metallic cylinders and by removing the above-ground vegetation and newly deposited litter from the plots. The impact of root-cutting was discernible quite early at Vesijako —

fluxes from cut-plots were significantly lowered the very next day after cuttings (K. Minkkinen unpubl. data). At the same time, however, the cut roots form a new litter pool that starts to decompose within the peat matrix. The impact of root decomposition on the fluxes decreased slowly during the following years, when no new roots could grow inside the cylinders. Thus, the efflux values measured during the years following the cutting do not include the respiration of living roots, but do partly include the decomposition of the 1–3 year old below-ground root litter. The amount of CO₂ derived from decomposing roots cannot, however, be quantified with our method.

Table 4. Simulated seasonal (May–October) long-term air and soil (5 cm) temperatures (°C) and soil respiration (SR, g C m⁻² a⁻¹) across the sites and site types. Average annual effluxes (i.e. seasonal + winter efflux, see Table 2) are shown in brackets after the seasonal mean efflux. The simulation period for Väätsa was 15 years (1991–2005), but 30 years for Vesijako and Kivalo (based on the 1961–1990 data).

	T _{air}	T ₅	SR_Vatkg	SR_Ptkg	SR_Mtkg	SR_Rhtkg
Väätsa						
mean	12.5	11.0	–	–	–	292 (370)
min	11.1	9.8	–	–	–	265
max	13.5	12.0	–	–	–	313
Vesijako						
mean	11.0	9.9	210 (240)	233 (266)	292 (341)	409 (467)
min	9.1	8.0	166	188	236	334
max	12.4	11.2	243	266	334	463
Kivalo						
mean	8.4	7.4	–	–	372 (477)	–
min	7.1	6.0	–	–	319	–
max	10.6	9.2	–	–	450	–

Plants and new above-ground litter were repeatedly removed from the plots to eliminate their impact on soil respiration. Since the removal of moss and litter layer undoubtedly affects the thermal conductivity of the soil it is probable that the temperature in the peat surface in the measurement plots (collars) was higher and variability was probably more extreme than natural. Manipulation of the moss and litter layer most probably altered also the moisture and oxygen conditions. In undisturbed conditions, the decomposing litter layer consumes oxygen and limits its diffusion down to the peat, probably keeping it less aerobic than in the treated plots. In the absence of transpiring vegetation, the peat surface may remain moister during summer; the drying of peat surface during warm summer months has been shown to decrease decomposition rates of needle and root litter in forestry-drained peatlands compared to undrained ones (Laiho *et al.* 2004). Because of all these parallel disturbance impacts of treatment, our method probably overestimates the heterotrophic respiration of peat soil.

For comparison, the work of Silvola *et al.* (1996a) is the only previous study reporting annual CO₂ effluxes from different kinds of forestry-drained peatlands in Finland (except for Martikainen *et al.* (1995) who used mainly the same CO₂ data). Temperatures in their measurement years, 1991–1992, were very close to the long-term average in Finland, and thus their study offers a good case for comparison with our results. The methods in Silvola *et al.* (1996a) were, however, somewhat different from ours in that they used open dynamic chambers, and the respiration of roots and litter was included in the fluxes. In another paper (Silvola *et al.* 1996b) they reported that the root respiration accounts for 10%–40% of the total SR. The average annual fluxes from similar site types (Vatkg-Mtkg; 347–584 g CO₂-C m⁻² a⁻¹) were higher than the average long-term estimates reported here (243–344 g CO₂-C m⁻² a⁻¹). However, if CO₂ derived from root respiration (10%–40%) is removed from their values, the annual estimates from these two studies become quite similar. No north–south comparisons can be made since their sites do not show such geographic variation.

Mäkiranta *et al.* (2007) reported soil CO₂

effluxes from afforested organic soil croplands, i.e., peatland sites that have an agricultural history (including repeated fertilization and tilling), but are now managed to grow the same tree-species as the forestry-drained ones. The annual fluxes in their data (207 to 539 g CO₂-C m⁻² a⁻¹) include the whole efflux-range in our data (248–515 g CO₂-C m⁻² a⁻¹). Their mean values from long-term (30-year) simulations (227–489 g CO₂-C m⁻² a⁻¹) are also very similar to our values (240–477 g CO₂-C m⁻² a⁻¹), suggesting that despite the very different land-use histories there are no significant differences in SR rates between these land-use forms.

Temporal variation was very closely related to changes in soil surface (5 cm) temperature. Approximately 90% of temporal variation in individual measurement plots was explained by changes in soil temperature alone (K. Minkkinen unpubl. data), whereas a lot of spatial variation within and between sites remained unexplained by temperature. One factor behind spatial variation is the availability of nutrients and the “quality” of substrates for decomposition, which are reflected in the site type. In Vesijako, the fluxes clearly increased from nutrient-poor to nutrient-rich site types (Fig. 3). A similar relationship was also reported by Silvola *et al.* (1996a).

One factor that regulates heterotrophic respiration is the thickness of aerobic peat, which is not easy to measure directly, but can be estimated by measuring the water-table level (WT) in the peat soil. Silvola *et al.* (1996a) found a close connection with average WT and SR between different site types. We found a similar but weaker relationship (results not shown), which is probably caused by smaller variation in WT; their data covered a wider range of site types with various water table levels, whereas our sites were all well-drained.

An inspection of the fluxes from peatlands in different geographical locations has led us to rather unexpected observations: a high efflux level and the highest response to temperature was seen at the northernmost site whereas the lowest response to temperature and relatively low efflux levels were recorded at the southernmost site. A similar climatic trend has also been observed in upland forest soils in Europe (Medlyn *et al.* 2005). The low fluxes in Väätsa

could partly be explained by low potassium (K) and phosphorus (P) availability. The Väätsa site before drainage was a eutrophic fen, where peat is generally characterized by a high concentration of total N, relatively high pH due to the high concentration of Ca, and very low concentration of K (Heikurainen 1953, Økland *et al.* 2001). P is known to limit litter decomposition if the N/P ratio is high (Güsewell and Freeman 2005), i.e., if P availability is low. Further, in these kind of peat soils a relatively high proportion of peat P may be Ca-bound which, under conditions of relatively high pH, may be the most insoluble and least bio-available form of P (Nieminen and Penttilä 2004). Low K and P availability are generally known to limit tree growth after forestry drainage, especially on deep-peated, initially very wet sites (Finér 1989, Moilanen *et al.* 2005, Pietiläinen *et al.* 2005) and PK fertilization has also been shown to increase total soil respiration on such sites (Silvola *et al.* 1985). In contrast, N (Olsson *et al.* 2005) and also PK fertilization (Franklin *et al.* 2003) have been found to reduce decomposition and soil respiration rates in upland forests, and N deposition has been suggested to have the same effect (Franklin *et al.* 2003). Thus the increasing N deposition from the north (ca. 1 kg N ha⁻¹ a⁻¹) to the south (ca. 4 kg N ha⁻¹ a⁻¹) could be related to the parallel trend in decomposition rates.

Decomposition in drained peatlands can be limited by dryness of the litter on the peat surface (Martikainen *et al.* 1995, Laiho *et al.* 2004). It is, however, unlikely that dryness would have limited decomposition at Väätsa during summer 2003, when water tables were on average -57 cm, only slightly deeper than at Vesijako Rhtkg plots (-51 cm). No clear limitation of SR by dryness was observed in Väätsa even in the extremely dry year 2002, when the water table dropped below 110 cm in August–October.

The different management histories among the sites may provide a partial explanation to the lowest fluxes at the southernmost site. The sites of Vesijako and Kivalo both had a history of previous commercial harvestings of the stands during some decades before the SR monitoring periods. The coarse roots of the trees harvested in these fellings were left belowground *in situ* and it is possible or even probable that much of

the woody debris of this origin, obviously of a very slow initial decomposition rate, is still contributing to the SR in these sites. In Väätsa this pool of belowground woody debris is lacking as no tree stand existed before the present one and it has not been subjected to cuttings. The litter pool of coarse roots does not, however, explain the larger SR flux at Kivalo as compared with that at Vesijako, as the harvested stockings and retained pools of coarse root debris at Vesijako were much larger.

Another hypothesis that could explain the unexpected variation among the locations is 'temperature acclimation', i.e., the adaptation of heterotrophic decomposer populations to prevailing temperature. It is possible that in northern conditions microbes become adapted to cold conditions, functioning efficiently at low temperatures and responding rapidly to increasing temperature, as indicated by the results of Domisch *et al.* (2006). When the warm season is short, as in the north generally, decomposers may function more efficiently, which was emphasized during the exceptionally warm summer of 2003 in the north.

It is known that soil C sequestration and C stores increase from the north to the south in Finland, especially in peat soils (Lappalainen 1996, Minkkinen and Laine 1998, Turunen *et al.* 2002) but also in mineral soils (Liski and Westman 1997). Higher primary production (NPP) in the south has been suggested as the primary reason for this trend, since decomposition has been assumed to increase to the south as well. However, our results indicate that it is not necessarily so, although the material is too small to prove this hypothesis.

Long-term simulations were done using simulated weather data, which showed more pronounced differences between sites than the data from the measurement years. The long-term mean soil temperature at Kivalo in particular was clearly lower than in 2002–2004. Air temperatures were transformed to soil temperatures using the COUP model (Jansson and Moon 2001). This model, however, gave biased estimates, consistently overestimating the nighttime soil temperatures compared to the measured data, introducing an average overestimation of 10% in SR values. In addition, the mean tem-

peratures for Väätsa were calculated using data from a later period, 1991–2005, which was ca. 0.5 °C warmer than 1961–1990, used for other areas. Correcting this would decrease the average long-term SR estimate for Väätsa by ca. 10 g C m⁻² a⁻¹.

The relationships between seasonal mean soil temperature and the simulated SR seem to be linear within the sites (Fig. 3), although the actual relationships (at the instantaneous measurement-level) were clearly non-linear. Thus mean soil temperature could prove to be a good and practical predictor of seasonal CO₂ fluxes, together with other factors describing spatial variability, such as site type and region. This hypothesis should, however, be tested using an independent data set with a sufficient number of independent replicates.

The temperature response of SR is a well-known fact, and this relation is evident also in the results of this study. It has therefore been suggested (Bellamy *et al.* 2005, Knorr *et al.* 2005) that the predicted climatic warming would also increase heterotrophic respiration of soil organic matter and thus the efflux of C from soils to the atmosphere, causing a positive feedback effect. Moreover, Domisch *et al.* (2006) suggested that this positive feedback could increase to the north. Our results support their hypothesis in that the response of SR to temperature was strongest in the north. It is also interesting to discover that despite the longer growing seasons in the south, the annual CO₂ effluxes through heterotrophic soil respiration in similar peat soils do not seem to increase towards warmer climates, rather the opposite. This trend or the factors behind it cannot be statistically tested using our incomplete data. It can, however, be hypothesised that the predicted climatic warming could have stronger impacts on OM decomposition and CO₂ evolution from peatland soils in the north than in the south.

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