Forest Ecology and Management 325 (2014) 60–73

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Soil CO_2 balance and its uncertainty in forestry-drained peatlands in Finland

Paavo Ojanen [a,*], Aleksi Lehtonen [b], Juha Heikkinen [b], Timo Penttilä [b], Kari Minkkinen [a]

[a] University of Helsinki, Department of Forest Sciences, P.O. Box 27, FI-00014 Helsinki, Finland
[b] Finnish Forest Research Institute, Southern Finland Regional Unit, P.O. Box 18, FI-01301 Vantaa, Finland

ARTICLE INFO

Article history:
Received 17 January 2014
Received in revised form 26 March 2014
Accepted 27 March 2014
Available online 23 April 2014

Keywords:
Boreal peatland
CO_2 exchange
Forestry drainage
Uncertainty
Upscaling
Forest inventory

ABSTRACT

To understand the global carbon cycle and the impact of human activity on climate, it is necessary to quantify the net CO_2 exchange of ecosystems in different land uses on a large scale. Methods to estimate soil net CO_2 exchange ($NE_{CO2soil}$) for drained peatland forests have been largely based on chamber measurements and statistical models. The uncertainty in these methods has not been assessed. Yet, disturbed organic soils are a globally important, potential CO_2 source due to their vast carbon storage and its sensitivity to changes in soil moisture.

In this study, we estimated the countrywide $NE_{CO2soil}$ for the 4.76 million ha of forestry-drained peat soils in Finland. We gathered available litter production and CO_2 efflux data and constructed models to be used for the upscaling of $NE_{CO2soil}$ from forest inventory data. The contribution of each model and the inventory sampling to the precision of the countrywide estimate was calculated. Also, the sensitivity to possible bias in selected model components was estimated.

Compared to the estimated mean $NE_{CO2soil}$, ranging from a source of +20 g m^{-2} year^{-1} of C to a sink of −40 g m^{-2} year^{-1} of C, the uncertainty was high. The precision of the estimate (±1 standard deviation) was ±20 g m^{-2} year^{-1} of C. Due to possible bias in the estimated belowground litter input, the overall uncertainty was much higher, around ±60 g m^{-2} year^{-1} of C.

The main reason for the high relative uncertainty was $NE_{CO2soil}$ being on average close to zero in these boreal forestry-drained peatlands. Forest inventory sample size was large enough and the data for the models were mainly sufficient. To reduce the uncertainty, better understanding of belowground carbon fluxes in order to accurately determine the C input to soil, is crucial.

1. Introduction

To understand the global carbon cycle and the impact of human activity on climate, it is necessary to quantify the net CO_2 exchange (NEE, net ecosystem exchange) of ecosystems in different land uses on a large scale. NEE is the measure of the direct CO_2 source or sink strength of an ecosystem. This information is also needed for earth system models (Heavens et al., 2013) and national greenhouse gas (GHG) reporting. As empirical studies are typically conducted on a site or plot scale, a countrywide estimate of GHG balance is essentially a generalization.

In forests, photosynthesis by trees and ground vegetation creates the input of CO_2-derived carbon (C) into the ecosystem. Plants then respire part of that C back into the atmosphere. The remaining organic C forms the net primary production (NPP) that can be divided into three pools: (1) change in plant biomass (Δ_{biom}), (2) harvested biomass (H_{biom}) and (3) litter (L). Decomposers in soil use litter as their energy and C supply, and gradually release CO_2 back into the atmosphere (D). NEE can, accordingly, be expressed as (negative sign indicating sink):

$$NEE = -\Delta_{biom} - H_{biom} - L + D. \quad (1)$$

Abbreviations: D, decomposition; H_{biom}, harvested biomass; HT, high fine root turnover, 0.85 year^{-1}; L, litter production; L_{ds}, dwarf shrub litter production; L_{fol}, tree stand foliage litter production; L_{gv}, ground vegetation litter production; L_h, herbaceous vascular plant litter production; L_m, moss litter production; L_{other}, tree stand aboveground non-foliage litter production; LT, low fine root turnover, 0.5 year^{-1}; M_{ds}, dwarf shrub biomass; M_{fol}, tree stand foliage biomass; M_{fr}, arboreal fine root biomass; M_h, herbaceous vascular plant biomass; $NE_{CO2soil}$, soil net CO_2 exchange; NFI10, 10th Finnish National Forest Inventory; NIR, Finnish National Inventory Report; PC_{ds}, the projection coverage of dwarf shrubs; PC_m, moss projection coverage; r,t, sampling region (r)–site type (t) combination; T_{season}, mean May–October air temperature; Δ_{biom}, change in plant biomass.

* Corresponding author. Tel.: +358 9 191 58139.
E-mail addresses: paavo.ojanen@helsinki.fi (P. Ojanen), aleksi.lehtonen@metla.fi (A. Lehtonen), juha.heikkinen@metla.fi (J. Heikkinen), timo.penttila@metla.fi (T. Penttilä), kari.minkkinen@helsinki.fi (K. Minkkinen).

http://dx.doi.org/10.1016/j.foreco.2014.03.049
0378-1127/

In large-scale estimations, i.e., on a regional level or countrywide, Δ_{biom} can be routinely quantified with, for example, repeated tree stand measurements and tree biomass models (e.g., Greenhouse gas emissions..., 2013, National Inventory Report..., 2013a) and H_{biom} estimated from harvest statistics (e.g., Christiansen, 2013; Ylitalo, 2012). The other two components comprise the much more argued and poorly known soil net CO_2 exchange ($NE_{CO2soil}$):

$$NE_{CO2soil} = -L + D. \quad (2)$$

L can be quantified by applying biomass turnover ratios if forest inventory data on tree stand and ground vegetation are available (e.g., Liski et al., 2006; Ortiz et al., 2013). D can be estimated using, e.g., simple one-layer mechanistic litter decomposition models (Chertov et al., 2001; Tuomi et al., 2009) if decomposition dynamics are well known and can be generalized by readily available weather data. This approach has been applied to mineral soils in forests and fields (Karhu et al., 2011, 2012; Ortiz et al., 2013).

In the case of disturbed organic soils, such as drained peatlands, mechanistic modelling of decomposition is more complicated. Information on drainage intensity and water retention in peat is needed to describe the variation of aerobic and anaerobic conditions in the soil profile (e.g., Sarkkola et al., 2010; Silvola et al., 1996a). In addition, organic matter properties of different layers in the soil profile need to be described for quantifying the CO_2 efflux from decomposition. Detailed ecosystem models describing both heat and water dynamics and C cycle do exist (e.g., Jansson and Karlberg, 2004), but verification of such models even on the site level is still largely missing. For large-scale estimations, the input data required is far beyond what typical forest inventories and weather statistics can provide. Yet, disturbed organic soils are a globally important source of greenhouse gases (Drösler et al., 2008; Hooijer et al., 2010), and estimates of their emissions are urgently needed.

Instead of mechanistic modelling, the estimation of CO_2 efflux from decomposition can be based on chamber measurements on plots where living plants have been excluded by, e.g., trenching (Subke et al., 2006). Such measurements are a relatively inexpensive and straightforward tool for acquiring extensive datasets for upscaling (Ojanen et al., 2010; von Arnold et al., 2005), although trenching is known to change soil conditions and is thus a source of error (Kuzyakov et al., 2000; Ngao et al., 2007; Subke et al., 2006). Because of its apparent simplicity, this "D–L method" has been applied to forestry-drained peatlands in GHG reporting both in Finland and Sweden as well as in estimating the latest Tier 1 emission factors for drained inland organic soils by the IPCC Wetlands Supplement (Drösler et al., 2014; Greenhouse gas emissions..., 2013; National Inventory Report..., 2013a).

With any method, knowledge on precision and accuracy is needed for the interpretation of the results. However, although the D–L method has already been used in countrywide calculations for forestry-drained peatland soils, there are no published results on its uncertainty in large-scale estimations. As most of the litter input is in any case decomposed, D and L will often be of the same magnitude, $NE_{CO2soil}$ as their remainder being an order of magnitude smaller. Thus, $NE_{CO2soil}$ may have poor relative accuracy and precision, even if L and D per se can be reliably estimated (Ojanen et al., 2012). Uncertainty analyses for mechanistic modelling and C stock change measurements in boreal mineral forest soils have resulted in uncertainties of the same order of magnitude as the estimated C balance (Ortiz et al., 2013; Peltoniemi et al., 2006).

The aim of this work was to estimate the countrywide $NE_{CO2soil}$ for forestry-drained peatland soils in Finland using the D–L method, and to assess its precision and accuracy. Since Finland has very detailed forest and peatland inventories (Korhonen et al., 2013; Tomppo et al., 2011), such a method should be applicable in Finland, if anywhere. Also, forestry drainage is an extensive form of land use in Finland (Ylitalo, 2012) and Sweden (Christiansen, 2013) with potentially high specific CO_2 emissions (Ojanen et al., 2013; Simola et al., 2012).

We gathered available litter production and decomposition data and constructed models to be used for upscaling from forest inventory data. The contribution of each model and the inventory sampling to the precision of the countrywide estimate was calculated. Also, the sensitivity to possible bias in selected model components was estimated. Based on these results, we discuss the usefulness of this method and the importance of forestry-drained boreal peatland soils as CO_2 sources.

2. Materials and methods

2.1. Framework

The estimated annual $NE_{CO2soil}$ was the combined net CO_2 exchange of soil and litter layer, similarly to Ojanen et al. (2012, 2013). Litter production (L) included that of living trees and ground vegetation (Fig. 1). Decomposition (D) included decomposition of litter and soil organic matter. Functions based on drained peatland data were used when available; otherwise, the procedure in the Finnish National Inventory Report (NIR, Greenhouse gas emissions..., 2013) was applied.

$NE_{CO2soil}$ was estimated for each 10th Finnish National Forest Inventory (NFI10, Korhonen et al., 2013) sample plot situated on forestry-drained peatland by subtracting L from D (Eq. (2)). When defined this way, positive $NE_{CO2soil}$ equals a source (emission) and negative a sink. Means $\overline{NE}_{r,t}$ for each NFI10 sampling region (r)–site type (t) combination were then calculated and finally multiplied by the respective NFI10 area estimates $A_{r,t}$, and totalled to estimate the countrywide $NE_{CO2soil}$. All calculations were done and figures drawn with the R software (R Development..., 2011).

Dead organic matter (DOM) from natural mortality and logging was not included in either the CO_2 efflux measurements (Ojanen et al., 2010) or litter input. The C storage dynamics of this DOM could be dealt with in litter and wood decomposition models (Chertov et al., 2001; Tuomi et al., 2011) at need. Although current decomposition models may not be able to handle peat soils, DOM in well-aerated conditions on drained peatlands could be assumed to decompose at a similar rate as on mineral soils (Straková et al., 2011; Vávřová et al., 2009). Furthermore, C input in precipitation including canopy throughfall and output through leaching as well as net CH_4 exchange need to be considered if the C balance of soil and DOM is desired instead of $NE_{CO2soil}$.

2.2. Data for upscaling

For the upscaling, we used the data from NFI10 (Korhonen et al., 2013) collected by systematic clustered sampling in 2004–2008. NFI10 builds on the NFI9 that has been reported in detail by Tomppo et al. (2011). All the temporary and permanent sample plots classified as forestry-drained peatland, i.e., peatland drained by ditching for forestry, were included in the data, altogether 10,800 plots. Plots were classified according to the vegetation classification of Laine (1989; see Vasander and Laine, 2008). Site types from the most fertile to the nutrient poorest were: *Herb-rich* (Rhtkg), *Vaccinium myrtillus I & II* (Mtkg I & II), *Vaccinium vitis-idaea I & II* (Ptkg I & II), *Dwarf shrub* (Vatkg) and *Lichen* (Jätkg) type. This division, although aimed primarily at describing wood production potential, also groups the sites into distinct groups based on ground vegetation, thus being potentially useful also for upscaling L of ground vegetation.

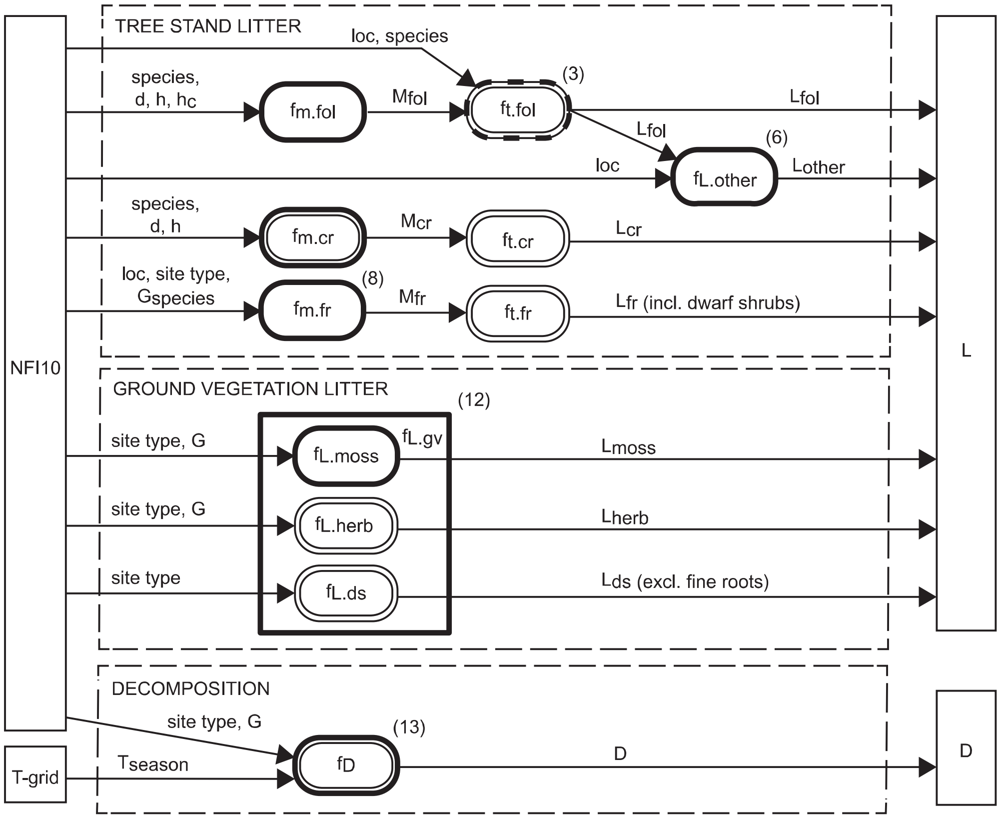

Fig. 1. The functions for plot-level estimation of litter production of living tree stand and ground vegetation (L) and decomposition of litter and soil organic matter (D) from National Forest Inventory data (NFI10) and weather statistics (T-grid). The numbers in parentheses refer to equations in body text. Uppercase letters refer to stand and lowercase letters to tree variables. fol = foliage, cr = coarse roots, fr = fine roots, M = mass, loc = location (South/North Finland), G = basal area, d = diameter, h = height, h_c = crown base height, species = species group (Scots pine, Norway spruce, deciduous trees), ds = dwarf shrub, T_{season} = mean May–October air temperature, t = turnover. Bold = included in model error estimation, inner circle = included in sensitivity analysis.

The total area of forestry-drained peatlands, 4.76 million ha, was rather evenly distributed to South and North Finland and among different site types, except for the poorest site type Jätkg, covering only 2.0% of area in the South and 1.4% in the North. The division between South and North Finland is that of NIR, the border roughly following the border between south and middle boreal vegetation zones.

Measured tree (lower case) and stand (upper case) variables, namely diameter (d), height (h), crown base height (h_c), species group (Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), deciduous trees (mainly *Betula pubescens*)), basal area (G), location and site type, were used for the estimation of L (Fig. 1). For the trees that did not have h and h_c measurements available, model estimates by Eerikäinen (2009) were used.

Mean May–October air temperature (T_{season}) for the same years 2004–2008 for each NFI10 plot was extracted from the 10 × 10 km gridded daily weather dataset of the Finnish Meteorological Institute (Venäläinen et al., 2005). T_{season}, in addition to G and site type, was used for the estimation of D (Eq. (13)). One mean value for the years 2004–2008 was used instead of annual ones for two reasons: The litter production models cannot account for inter-annual variability, and the decomposition data is cross-sectional (Ojanen et al., 2010) – and thus inadequate to describe within site year-to-year variation.

2.3. Data for model construction

For the building of the models to estimate litter production and decomposition, the following datasets on Finnish forestry-drained peatlands were used.

Available published and unpublished tree stand litter production data were gathered for the quantification of tree stand aboveground litter production. In the data (Table 1), we included sites with at least one whole year of litter trap data separated into foliage (L_{fol}) and non-foliage aboveground (L_{other}) litter. L_{other} included all collected litter except needles and leaves: twigs, cones, seeds, bark, etc. We found 16 sites with altogether 43 years of litter data. To build models for the estimation of L_{fol} from foliage biomass, we estimated species-wise foliage biomasses for each site with single tree foliage models for pine, spruce and birch (Repola 2008, 2009). Sites with L_{fol} separated according to tree species and tree stand measurements including h_c available were included in the L_{fol} modelling (Table 1).

For belowground L, belowground biomasses were needed. For the estimation of fine root biomass, arboreal fine root (d < 2 mm) data from 31 "CMON" sites (Ojanen et al., 2013) were used. For each site, the mean of 5 samples, each 15 × 15 cm in area and reaching to 20 cm depth, were used. We also included values with the same method from the Kalevansuo site (Vatkg, mean of 32 samples, Ojanen et al., 2012) and Lettosuo site (Mtkg II, mean of 49 samples), both located in South Finland (Table 1). Thus, altogether 33 sites with fine root biomass, tree stand measurements and ground vegetation projection coverage data were available. These cover South and North Finland and represent a fertility gradient from Rhtkg to Vatkg.

For the estimation of aboveground biomass and projection coverage of dwarf shrubs, herbaceous vascular plants and mosses, we constructed a ground vegetation dataset including the ground vegetation measurements of 98 forestry-drained peatland sites of the BioSoil project (Ilvesniemi et al., 2006, 2008; Ojanen et al.,

Table 1
Description of sites with annual tree stand aboveground litter production data used for the estimation of foliage turnover (Eqs. (3) and (4)) and non-foliage aboveground litter production (Eqs. (6) and (7)). Species% = share of Scots pine/Norway spruce/downy birch in the modelled foliage biomass.

Site name	Site type	Years	Location	South/North	Species%	Source
Kalevansuo	Vatkg	2006–2009	60.6°N 24.4°E	South[p]	97/0/3	Ojanen et al. (2012)
Lettosuo	Mtkg II	2010–2012	60.6°N 24.0°E	South[p,s,b]	37/48/15	T. Penttilä et al. (unpublished data)
Vesijako ctrl 1[a]	Mktg–Ptkg	2003	61.4°N 25.1°E	South[p,s]	81/14/5	Mäkiranta et al. (2010)
Vesijako ctrl 2[a]	Rhtkg–Vatkg	2003	61.4°N 25.1°E	South[p,s]	71/28/1	Mäkiranta et al. (2010)
Laiho 4	Ptkg II	1993–1997	61.6°N 24.1°E	South[p,b]	64/5/32	Laiho et al. (2003)
Laiho 5	Ptkg II	1993–1997	61.8°N 24.3°E	South[p]	81/9/11	Laiho et al. (2003)
Laiho 6	Ptkg II	1993–1994	61.9°N 24.4°E	South[b]	70/15/16	Laiho et al. (2003)
Lakkasuo	Mtkg II	2005–2007	61.8°N 24.3°E	South	90/3/8	Straková et al. (2010)
Lakkasuo	Ptkg II	2005–2007	61.8°N 24.3°E	South	97/1/2	Straková et al. (2010)
Lakkasuo	Vatkg	2005–2007	61.8°N 24.3°E	South	100/0/0	Straková et al. (2010)
Vihanti 1[a]	Mtkg II	1994–1995	64.5°N 25.0°E	North	80/0/20	M. Moilanen (unpublished data)
Vihanti 2[a]	Mtkg II	1994–1995	64.5°N 25.0°E	North	82/0/18	M. Moilanen (unpublished data)
Vihanti 3[a]	Mtkg II	1994–1995	64.5°N 25.0°E	North	84/0/16	M. Moilanen (unpublished data)
Vihanti 4[a]	Mtkg II	1994–1995	64.5°N 25.0°E	North	82/0/18	M. Moilanen (unpublished data)
Vihanti 5[a]	Mtkg II	1994–1995	64.5°N 25.0°E	North	85/0/15	M. Moilanen (unpublished data)
Kivalo	Mtkg	2002–2004	66.4°N 26.6°E	North	65/30/6	T. Penttilä (unpublished data)

[a] Replicates considered as one site in the mixed models (Eqs. (4) and (7)).
[p/s/b] Sites with pine/spruce needles/birch leaves separated and h_c data available used for fitting the model for foliage turnover (Eqs. (3) and (4)).

2013). Ninety-four of these sites were located in South Finland. Sites were rather evenly distributed between site types, except for Jätkg with only one site. Another Jätkg site with similar measurements available ("KeRoj" in Vasander, 1982) was added to the data.

For the upscaling of D, we used the annual decomposition values of 68 CMON sites (Ojanen et al., 2013). These values are based on measurements of CO_2 efflux from soil in 2007–2008, conducted with manual chambers on plots, where incoming roots had been cut with 30-cm deep metal cylinders and aboveground parts of ground vegetation and loose litter layer removed (Ojanen et al., 2010). To estimate the total decomposition-originated CO_2 production, decomposition of the loose litter layer was modelled and added to the measured CO_2 efflux (see Ojanen et al., 2013 for closer description). As no Jätkg sites were included in CMON, we incorporated three Jätkg sites with similar measurements ("L5", "I7" and "L9" in Silvola et al., 1996a,b).

2.4. Tree stand aboveground litter production models

First, single tree foliage biomass models for Scots pine, Norway spruce and birch (applied for all deciduous tree species) (function $f_{m.fol}$ in Fig. 1, Repola, 2008, 2009) were used to estimate the plot-level foliage mass of each species group (M_{fol}) from single tree d–h–h_c data. Then, foliage litter production (L_{fol}) was estimated by applying species group-wise turnover ratios β_1 of M_{fol} ($f_{t.fol}$):

$$L_{fol} = \beta_1 M_{fol}. \tag{3}$$

For birch countrywide and pine and spruce in South Finland, β_1 was estimated from the peatland litter production data (Table 1) through mixed linear regressions (Fig. 2, Table A.1):

$$\frac{L_{fol}}{M_{fol}} = \beta_1 + \gamma_{site}, \tag{4}$$

where L_{fol} is the annual foliage litterfall from the traps and M_{fol} is the site-wise modelled foliage mass. γ_{site} is the random effect of each site, necessary to give equal weight to each site despite the different number of years for different sites (Table 1).

As the number of needle cohorts in pine and spruce differs between South and North Finland (Muukkonen, 2005; Muukkonen and Lehtonen, 2004), consequently their foliage turnover rates also differ. Our L_f data did not cover North Finland, so we assumed the ratio of β_1 between South ($\beta_{1,south}$) and North ($\beta_{1,north}$) to equal that of NIR (Table 2), $\beta_{1,north}$ thus being:

$$\beta_{1,noth} = \beta_{1,south} \frac{\beta_{1,north,NIR}}{\beta_{1,south,NIR}}. \tag{5}$$

Then, non-foliage aboveground litter production from tree stand (L_{other}) was estimated as a ratio β_1 of L_{fol} ($f_{L.other}$):

$$L_{other} = \beta_1 L_{fol}. \tag{6}$$

β_1 was fitted separately for North and South Finland (Fig. 2, Table A.1) on the peatland litter production data (Table 1):

$$\frac{L_{other}}{L_{fol}} = \beta_1 + \gamma_{site}, \tag{7}$$

where γ_{site} is again the random effect of each site.

2.5. Tree stand belowground litter production models

First, single tree coarse root (d > 1 cm) biomass models for pine, spruce and birch ($f_{m.cr}$, Repola, 2008, 2009) were used to estimate the plot-level coarse root mass (M_{cr}) of each species group from single tree d (d–h for birch) data. Then, coarse root litter (L_{cr}) was estimated by applying species group-wise NIR turnover ratios ($f_{t.cr}$, Table 2) similarly to L_{fol} (Eq. (3)). The smallest coarse roots (2 mm < d < 1 cm) were not included in the models, but this should not a have remarkable effect on the total litter production, as the share of coarse roots is usually negligible (Ojanen et al. 2013) due to their low turnover ratio (Table 2).

To estimate the plot-level arboreal fine root biomass (d < 2 mm, trees + dwarf shrubs, M_{fr}), a linear model was fitted to the fine root biomass data (Fig. 3, $f_{m.fr,}$ Table A.2):

$$M_{fr} = \beta_1 G_{pine} + \beta_2 G_{spruce} + \beta_3 G_{birch} + \beta_4 PC_{ds} + \beta_{location}, \tag{8}$$

where G_{pine}, G_{spruce} and G_{birch} are the basal areas of each species group and PC_{ds} is the projection coverage of dwarf shrubs. As the model first significantly (ANOVA for residuals) overestimated M_{fr} in North Finland while underestimating it in South Finland, a dummy variable for location in South/North Finland ($\beta_{location}$) was added. This difference seemed to be connected to deeper water table in South Finland, but as it was explained by the South/North division, and no further water table data for upscaling was available, a dummy variable was considered an adequate approach. One site was discarded from the data because it was an extreme outlier. In the upscaling, mean PC_{ds} values for each site type in the ground vegetation data were applied (Table A.3).

As the fine root samples only reached to 20 cm depth, values were corrected according to Laiho and Finér (1996): 4.3% of

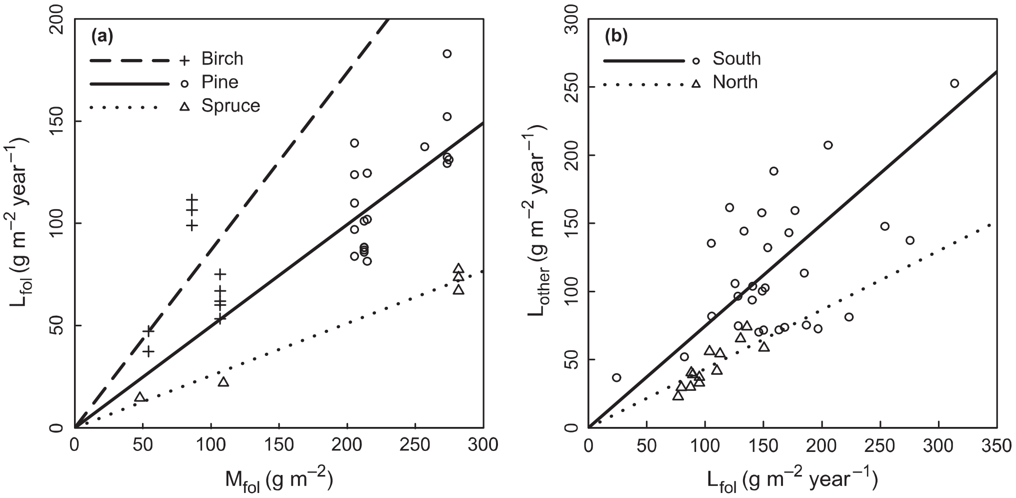

Fig. 2. (a) Species-specific foliage litter production (L_{fol}, dry mass) as a function of corresponding leaf dry mass (M_{fol}). Slopes of the lines describe the turnover ratio of foliage fitted to these data (parameter β_1 in Eq. (3)). (b) Tree stand aboveground non-foliage litter production (L_{other}, dry mass) as a function of total L_f. Regressions (Eq. (6)) are fitted separately for South and North Finland data.

Table 2
Turnover ratios (year^{-1}) adopted from the Finnish National Inventory Report (NIR, original source in parentheses) and other sources.

Name	Value	Source
Pine needle South[a]	0.245	NIR (Muukkonen, 2005)
Pine needle North[a]	0.154	NIR (Muukkonen, 2005)
Pine coarse root	0.0184	NIR (Lehtonen et al., 2004, assuming coarse root turnover equals branch turnover)
Spruce needle South[a]	0.1	NIR (Muukkonen and Lehtonen, 2004)
Spruce needle North[a]	0.05	NIR (Muukkonen and Lehtonen, 2004)
Spruce coarse root	0.0125	NIR (Muukkonen and Lehtonen, 2004, assuming coarse root turnover equals branch turnover)
Birch coarse root	0.0135	NIR (unpublished forest inventory data)
Fine root higher	0.85	NIR (Majdi, 2001; Helmisaari et al., 2002)
Fine root lower	0.50	Hansson et al. (2013), Leppälammi-Kujansuu et al. (2014)
Dwarf shrub aboveground	0.15	Ojanen et al. (2013)
Dwarf shrub rhizome	0.08	Finér and Laine (1998)
Herbaceous aboveground	1	Renews annually
Herbaceous root	1.25	Laiho et al. (2003)

[a] Used only in Eq. (5).

arboreal fine root biomass was assumed to be located in deeper soil layers. Fine root litter production (L_{fr}) was then estimated by applying published turnover ratios ($f_{t,fr}$, Table 2), as follows.

The fine root turnover of 0.85 year^{-1} applied in NIR is in accordance with the latest reviews (Brunner et al., 2013; Finér et al., 2011a). These results are mainly based on the widely used sequential coring method. Recent results of minirhizotron (Hansson et al., 2013; Leppälammi-Kujansuu et al., 2014) and isotope (Strand et al., 2008) studies indicate that this value may, however, be an overestimate: Fine root mean longevity was estimated to be 2 years and the persistence of the root carbon even higher. Owing to lacking general consensus (Finér et al., 2011b; Sah et al., 2010) and the pronounced sensitivity of the estimation of $NE_{CO2soil}$ to fine root turnover rate (Ojanen et al., 2012), we used two alternative values: 0.85 year^{-1} (HT) as in NIR, and 0.5 year^{-1} (LT) based on the root longevity of 2 years (Table 2).

Another related question of methodological accuracy is the major pathway of C from plants to soil through microbes in the rhizosphere and mycorrhiza (Clemmensen et al., 2013; Heinemeyer et al., 2007; Godbold et al., 2006). Here, we simply assume that this organic C is very short-lived in soil: We consider that it had already decomposed during the 6-month period between the trenching of the incoming roots and the start of the CO_2 efflux measurements (Ojanen et al., 2010). Thus, this source of decomposition is not included in output and consequentially is excluded from the input as well. This convenient assumption does not necessarily hold, as discussed by Ojanen et al. (2013). But, as including an extra belowground litter input is essentially the same test as the varying fine root turnover, it will pass for the purpose as well.

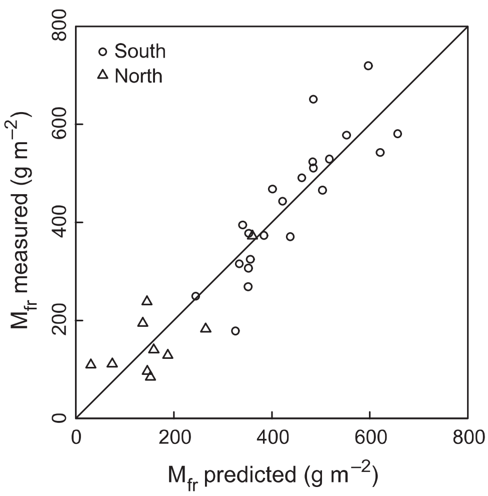

Fig. 3. Measured versus predicted arboreal fine root dry mass (M_{fr}, Eq. (7)).

2.6. Ground vegetation litter production models

Litter production was first estimated for each ground vegetation data site, separately for dwarf shrubs (L_{ds}), herbaceous vascular plants (L_h) and mosses (L_m):

$$L_{ds} = M_{ds,above} t_{ds,above} \left(1 + \frac{L_{ds,below}}{L_{ds,above}}\right) \quad (9)$$

$$L_h = M_{h,above} t_{h,above} \left(1 + \frac{L_{h,below}}{L_{h,above}}\right) \quad (10)$$

$$L_m = PC_m \frac{L_{m100\%}}{100\%} \tag{11}$$

Aboveground biomasses ($M_{ds,above}$, $M_{h,above}$) and moss projection coverage (PC_m) were from the ground vegetation data and turnover values t_{ds} and t_h from literature (Table 2). The ratios of below- and aboveground litter production $L_{ds,below}/L_{ds,above}$ and $L_{h,below}/L_{h,above}$ were mean values from the 68 CMON sites (Ojanen et al., 2013), where both above- and belowground litter production were estimated and the same ground vegetation turnover ratios applied as in this study. $L_{ds,below}$ only included litter from rhizomes, for dwarf shrub fine root mass was included in M_{fr} (Eq. (8)). Moss biomass production with 100% projection coverage ($L_{m100\%}$) was 160 ± 30 g m^{-2} year^{-1} for Rhtkg to Vatkg sites (Ojanen et al., 2013) and 71 g m^{-2} year^{-1} for Jätkg sites (Vasander, 1982).

First, the relationships of L_{ds}, L_h and L_m with G and site type were studied separately. All correlated with site type; L_h and L_m also negatively with G. Residuals did not show correlation with the north coordinate, indicating that these models can be applied also in the North. These linear models were used in the estimation of $NE_{CO2soil}$ ($f_{L.moss}$, $f_{L.herb}$, $f_{L.ds}$, Table A.4). Then, L_{ds}, L_h and L_m were summed to represent ground vegetation litter production (L_{gv}) of each site. Finally, the following model was fitted ($f_{L.gv}$, Fig. 4, Table A.4):

$$L_{gv} = \beta_1 G + \beta_{site\ type}, \tag{12}$$

where β_1 is the parameter for G and $\beta_{site\ type}$ represents the effect of each site type. This model was used in parameter uncertainty estimation instead of the separate models to adequately account for the possible correlations between L_{ds}, L_h and L_m. To estimate parameter uncertainty of $L_{m100\%}$, the separate model for L_m was used. Separate models were also applied to estimate the sensitivity of $NE_{CO2soil}$ to turnover ratios of dwarf shrubs and herbaceous vascular plants.

2.7. Decomposition model

To estimate decomposition (D), a linear model with G, site type and T_{season} as independent variables was fitted to the decomposition data (Fig. 5, Table A.5, f_D):

$$D = \beta_1 G + \beta_2 T_{season} + \beta_{site\ type}. \tag{13}$$

We utilized the results of Ojanen et al. (2010) on the modelling of annual soil respiration for choosing the best combination of variables available in NFI10 and weather statistics. G was used instead

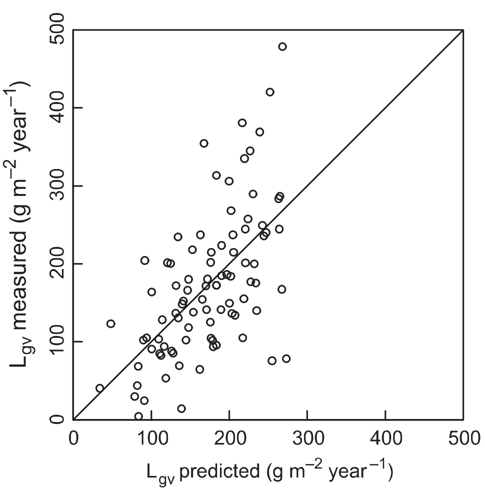

Fig. 4. Measured versus predicted ground vegetation litter production (L_{gv}, dry mass, Eq. (12)).

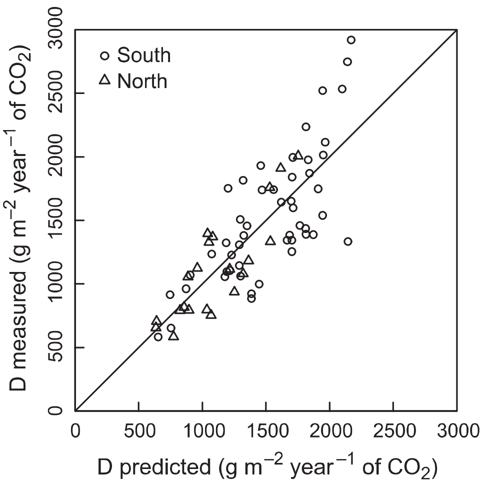

Fig. 5. Measured versus predicted decomposition of litter and soil organic matter (D, Eq. (13)).

of stem volume applied by Ojanen et al. (2010) since it was directly measured by NFI10 and the model performed as well as with stem volume.

2.8. Uncertainty analysis

The precision of the countrywide $NE_{CO2soil}$ was assessed through its variance var($NE_{CO2soil}$). The estimated variance included model error and NFI10 sampling variance. Model error due to parameter uncertainty in each linear model (Tables A.1–A.5) was estimated as follows. First, the variance–covariance matrix **vcov**(model) of the parameter estimates was multiplied from both sides by the matrix $\mathbf{X_{0r,t}}$, containing mean predictors of each region r and site type t, in order to estimate the variance–covariance matrix $\mathbf{vcov}(\overline{\mathbf{estimate}}_{\mathbf{r,t}})$ for the vector of predictions of the mean values of model estimates for each r and t:

$$\mathbf{vcov}(\overline{\mathbf{estimate}}_{\mathbf{r,t}}) = \mathbf{X_{0r,t}} \cdot \mathbf{vcov}(\mathbf{model}) \cdot \mathbf{X_{0r,t}^T} \tag{14}$$

Then, applying further steps of modelling when applicable (Fig. 1) and area estimates $A_{r,t}$ by applying the basic calculus of variance and covariance, the variance–covariance matrix of component estimates (**vcov**(component$_{r,t}$)) was calculated and its elements totalled to estimate the variance of the countrywide $NE_{CO2soil}$ var_{model} caused by each model:

$$var_{model} = \sum \mathbf{vcov}(\text{component}_{r,t}) \tag{15}$$

In the case of the nonlinear leaf and coarse root biomass models (Repola 2008, 2009, Tables A.6 and A.7), the approach was otherwise identical but instead of mean predictors, $\mathbf{X_{0r,t}}$ consisted of mean values of the first order partial derivatives of the model function (Gregoire et al., 2011; Ståhl et al., 2014).

NFI10 sampling variance of $\overline{NE}_{r,t}$ was estimated from cluster-level residuals $res_c = NE_{c,r,t} - \overline{NE}_{r,t}$, where $NE_{c,r,t}$ is the estimate based on data only from sample plot cluster c:

$$var(\overline{NE}_{r,t}) = \frac{\sum_{c=1}^{n} res_c^2}{(n-1)n} \tag{16}$$

From $A_{r,t}$, its variance var($A_{r,t}$) and corresponding $\overline{NE}_{r,t}$ and its variance var($\overline{NE}_{r,t}$), sampling variances of $NE_{CO2soil}$ due to uncertainty in the NFI area estimate (var_{area}) and mean $NE_{CO2soil}$ (var_{mean}) were then calculated as:

$$var_{area} = \sum \left[var(A_{r,t}) \cdot (\overline{NE}_{r,t})^2 \right] \tag{17}$$

$$\mathrm{var}_{\mathrm{mean}} = \sum \left[\mathrm{var}(\overline{\mathrm{NE}}_{r,t}) \cdot (A_{r,t})^2 \right] \tag{18}$$

Finally, all the variances were totalled to represent var($NE_{CO2soil}$). As model error could not be estimated for all the models (Fig. 1), var($NE_{CO2soil}$) is a minimum estimate.

For the components with model parameter errors unavailable (Fig. 1) and all those components where the possibility of bias was considered substantial, a simple sensitivity analysis was performed. For that, the effect of a 20% change in each component on $NE_{CO2soil}$ was calculated. Measured soil CO_2 efflux may be biased for two reasons: The chamber measurement per se is prone to measurement bias (Lai et al., 2012; Pumpanen et al., 2004). Also, treatment bias is likely: Cutting roots will cause an extra C input to soil and possibly change the moisture and temperature conditions, and may cause priming effects (Kuzyakov et al., 2000; Ngao et al., 2007; Subke et al., 2006).

3. Results

The selection of fine root turnover rate had a drastic effect on the estimated net CO_2 exchange of the Finnish forestry-drained peat soils: With the lower turnover of 0.5 year^{-1} (LT), a source (±1 sd) of +3.2 ± 3.3 Tg year^{-1} of CO_2 (+20 ± 20 g m^{-2} year^{-1} of C) was estimated, whereas applying the higher turnover rate of 0.85 year^{-1} (HT) resulted in a sink of −7.0 ± 3.5 Tg year^{-1} of CO_2 (−40 ± 20 g m^{-2} year^{-1} of C). The change from LT to HT increased *L* by a moderate 19%, from 55.0 to 65.2 Tg year^{-1} of CO_2. But as *D* remained at the same level, 58.2 Tg year^{-1} of CO_2, $NE_{CO2soil}$ changed by as much as 300%.

With LT, most site types were estimated to be CO_2 sources (Fig. 6). Only the relatively nutrient-poor types Ptkg II and Vatkg were sinks. With HT, all types were estimated to be sinks, except for the most fertile ones and the poorest type Jätkg in the North. Site type-specific mean emissions were higher in the North for all site types and for both LT and HT (Fig. 6). Below, results for both LT and HT are presented when markedly different. Otherwise, only results for LT are shown.

Both *L* and *D* decreased from fertile to poor types and from South to North (Fig. 7). The increase in emissions from South to North (Fig. 6) was due to the bigger decrease in *L*. The decreasing trend in emissions from the most fertile Rhtkg type to the second poorest Vatkg type was due to the bigger decrease in *D*; the poorest site type Jätkg was a source on account of the considerable drop in *L*.

Litter production consisted mainly of tree stand litter on the most fertile site types (Fig. 7). In the South, the maximum share of the tree stand was over 80% in the Rhtkg and Mtkg types. The share of ground vegetation increased from South to North,

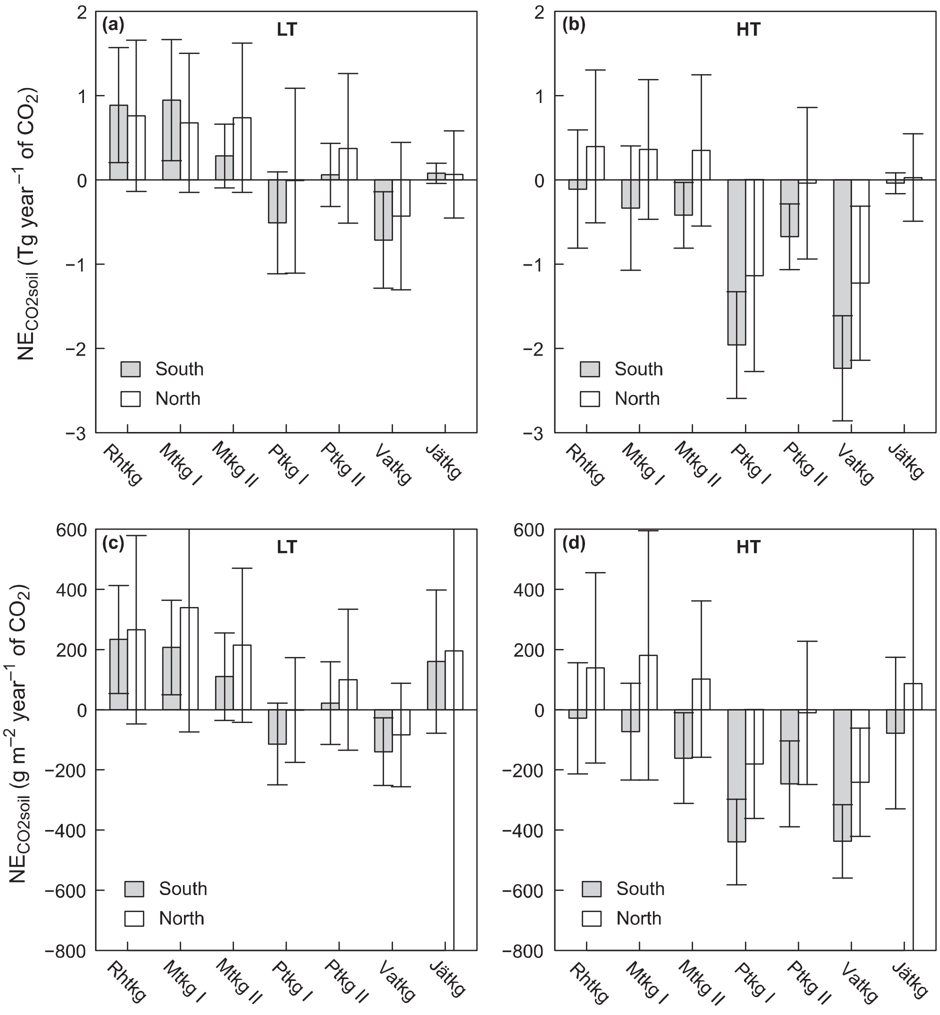

Fig. 6. Country-level (a and b) and mean (c and d) soil net CO_2 exchange ($NE_{CO2soil}$) according to site type for South and North Finland estimated using (a and c) lower (**LT**, 0.5 year^{-1}) and (b and d) higher (**HT**, 0.85 year^{-1}) fine root turnover. Error bars indicate model + sampling error (±1 sd). Positive values indicate source and negative values sink.

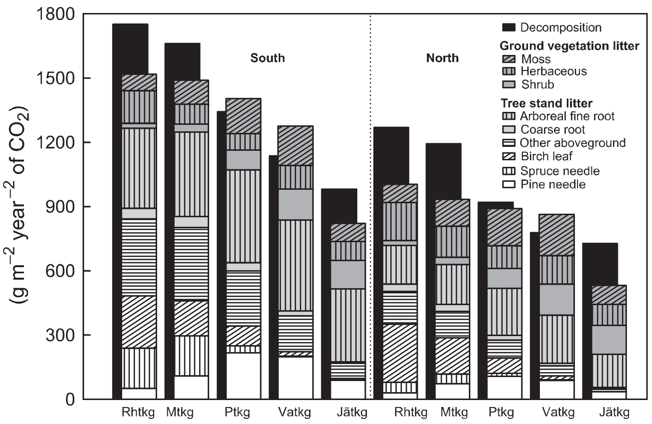

Fig. 7. The composition of mean litter production and decomposition in different site types in South and North Finland with the low fine root turnover (0.5 year^{-1}).

and gradually towards nutrient poorer types. It was over 50% in the two poorest site types in the North.

The higher estimated emissions in the North were due to two factors: (1) Although emissions clearly increased linearly by increasing T_{season} (Fig. 8), reflecting the linear effect of temperature on D (Eq. (13)), there was a clear offset between South and North, which resulted in lower emissions from a site with mean T_{season} in the South than North. This was due to the level difference in the foliage turnover and other aboveground tree stand litter functions between South and North. (2) Increasing G led to a decline in the emissions (Fig. 9). This co-variation was not simply linear, as G affected several components of $NE_{CO2soil}$ (Fig. 1). As a result of the steeper decline in the South, emissions were lower than in the North at mean G, even though they were higher or at the same level on treeless plots.

Clearly the biggest component in model error was the D model (Fig. 10), alone resulting in an sd of 2.2 Tg year^{-1} of CO_2. All the components of L caused smaller error, yet together generating an sd of the same magnitude: 2.4 (2.7 HT) Tg year^{-1} of CO_2. Of the foliage biomass models, the birch model contained a magnitude higher uncertainty (1.3 Tg year^{-1} of CO_2) than pine (0.1 Tg year^{-1} of CO_2) or spruce (0.2 Tg year^{-1} of CO_2) models. This was due to

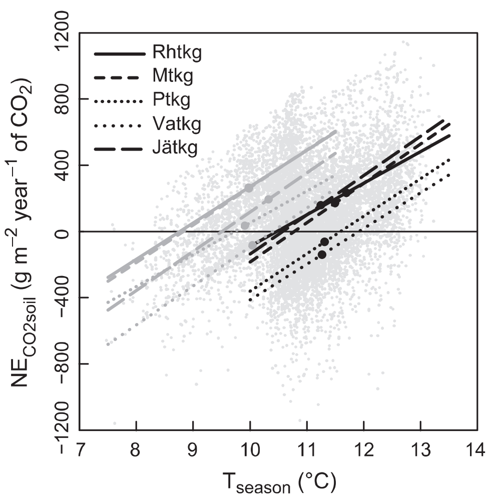

Fig. 8. Soil net CO_2 exchange ($NE_{CO2soil}$) versus May–October mean air temperature (T_{season}) of each site with the low fine root turnover (0.5 year^{-1}). Lines are linear regressions for each site type in South (black lines, T_{season} range 10–13.5 °C) and North (grey lines, T_{season} range 7.5–11.5 °C) Finland. Large dots on the lines indicate mean $T_{seasons}$ and the corresponding $NE_{CO2soil}$s according to site type. Positive values are sources.

the smaller sample size in the birch model fitting data (Repola, 2008). The error due to coarse root models was negligible (0.04 Tg year^{-1} of CO_2 for each tree species) due to the very small share of coarse root litter in L (Fig. 7). All the models performed well: Coefficients of variation ranged from as low as 1% to a moderate 17% (Fig. 10).

Compared to the $NE_{CO2soil}$ and model error components, both NFI10 area estimates and sampling produced a negligible error (Fig. 10), together accounting for an sd of only 0.2 Tg year^{-1} of CO_2. This was simply a consequence of the high number of NFI10 sample plots.

Even though the coefficients of variation were only 4% for both D and L (Fig. 10), that of $NE_{CO2soil}$ was 50% for HT and even 100% for LT. As the variances are totalled but $NE_{CO2soil} = -L + D$ and D and L were close to each other, a small relative uncertainty in D and L resulted in a large relative uncertainty in $NE_{CO2soil}$.

The sensitivity of $NE_{CO2soil}$ to parameters with unknown random error (Fig. 11) clearly divided components into different groups: The effect of coarse root turnover ratios was again negligible due to the very minor share of coarse roots in litter input (Fig. 7). The foliage turnovers in the North and ground vegetation turnovers and masses constituted a potentially considerable source of error, reflecting their greater share in L. Fine root turnover was clearly a bigger error source, as fine roots were the largest single component of L. Naturally, D was in its own order of magnitude of error, as it comprises half of the whole model.

4. Discussion

Based on this study, the current level of knowledge does not allow us to judge whether the forestry-drained peatland soils in Finland are a sink or source of CO_2, even though the NFI10 sample size was definitely large enough. With the estimated uncertainties in belowground litter production and model parameters, we can only state that $NE_{CO2soil}$ is likely to be within ±10 Tg year^{-1} of CO_2 (±60 g m^{-2} year^{-1} of C). It then depends on our perspective, whether or not we consider this level of knowledge satisfactory.

When considering the reported GHG sink of the total forestry land in Finland, −36 Tg year^{-1} of CO_2 eq. (2011, NIR), the aforementioned ±10 Tg year^{-1} of CO_2 comprises a major uncertainty. The CO_2 sink in tree biomass increment on peatlands is estimated at −16.4 Tg year^{-1} of CO_2 (2011, NIR), but the high uncertainty in soil $NE_{CO2soil}$ hinders the evaluation of the importance of drained peatland forests as CO_2 sinks. The uncertainty is large also compared to Finland's total GHG emissions (2011, NIR excluding LULUCF sector), 67 Tg year^{-1} of CO_2 eq. Thus, for national level purposes, a more precise estimate would be necessary.

On a larger scale, the extensive forestry-drained peatland area in Finland is contributing relatively little to the global emissions from peatland drainage. For example, in Continental Europe, 16 million ha of drained peatland soils are estimated to emit 88 ± 44 Tg year^{-1} of CO_2 (Schulze et al., 2009). The Finnish forestry-drained peatlands make up 30% of this area but, based on this study, at most 10% of the emissions. The reason for this is that the specific CO_2 emissions from agricultural peat soils are an order of magnitude higher than those from forestry-drained soils (Drösler et al., 2008; Lohila et al., 2004; Maljanen et al., 2001, 2004). Thus, forestry on boreal peatlands is not the most urgent target for actions to mitigate CO_2 emissions. It should be noted, though, that emissions from forested peat soils are low *on average* and that cases with high emissions do exist. These include some of the most fertile forestry-drained sites (Ojanen et al., 2013; Minkkinen and Laine, 1998) and afforested sites with an agricultural history (Meyer et al., 2013; Lohila et al., 2007).

The estimated mean $NE_{CO2soil}$ was of the same order of magnitude, ±10–100 g m^{-2} year^{-1} of C, as the soil C balance according

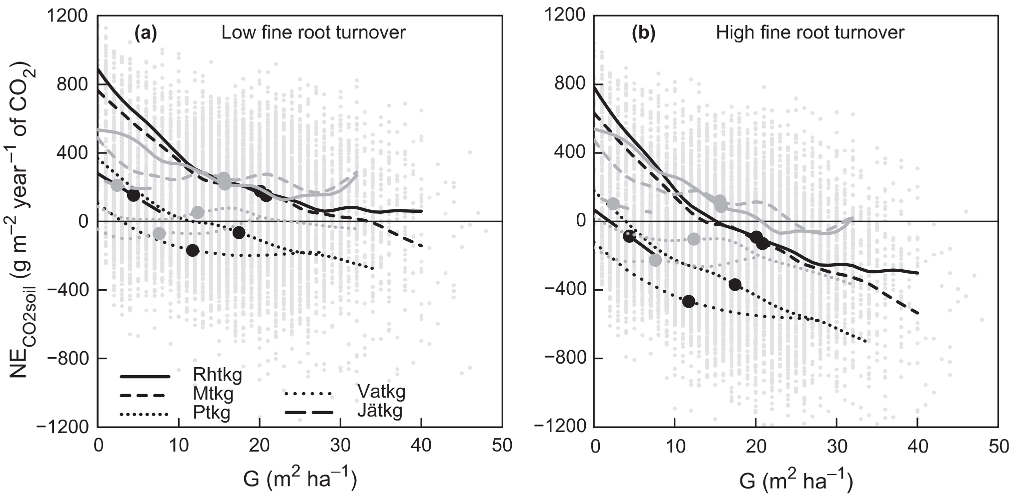

Fig. 9. Soil net CO_2 exchange ($NE_{CO2soil}$) versus basal area (G) of each site, estimated using (a) low (0.5 year^{-1}) and (b) high (0.85 year^{-1}) fine root turnover. Lines are spline interpolations (span = 0.5) for each site type in South (black) and North (grey) Finland. The highest 1 m^2 ha^{-1} G classes containing less than 5 observations are omitted from the interpolations. Large dots on the lines indicate mean Gs and the corresponding $NE_{CO2soil}$s according to site type. Positive values are sources.

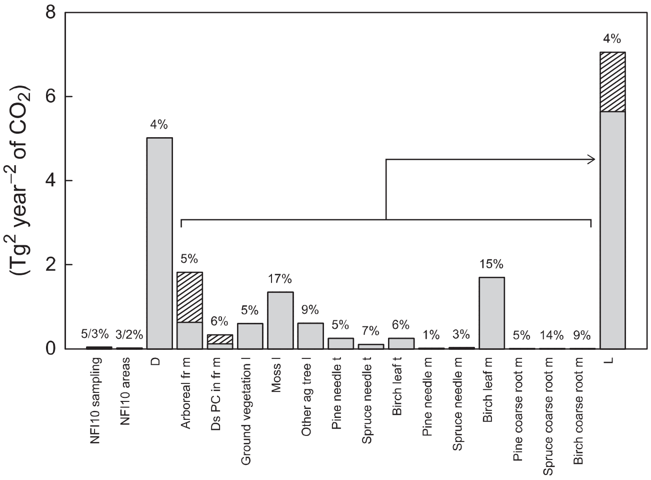

Fig. 10. Variances in the countrywide soil net CO_2 exchange due to NFI10 sampling and area estimation, and model parameter uncertainties. Shaded bars denote the higher variances with the higher fine root turnover rates in affected components. Percentages above the bars are coefficients of variation (=var$^{1/2}$/|estimated component| × 100%). The two alternative numbers above the NFI10 sampling and areas bars are due to lower/higher fine root turnover. m = mass, l = litter production, Ds = dwarf shrub, PC = projection coverage, fr = fine root, ag = aboveground.

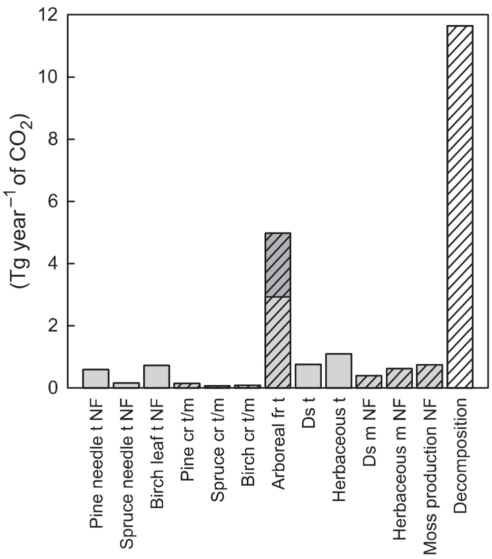

Fig. 11. Sensitivity of the country-level soil CO_2 net exchange to 20% alteration in parameters with unknown parameter error (grey bars) and to components with considerable risk to bias (shaded bars). The dark grey bar indicates the higher sensitivity when the higher arboreal fine root turnover is applied. NF = North Finland, t = turnover, cr = coarse root, m = mass, fr = fine root, Ds = dwarf shrub.

to repeated samplings and modelling studies on mineral forest soils in Sweden (Ortiz et al. 2013) and Finland (Rantakari et al., 2012), and long-term peat accumulation rates in pristine boreal peatlands (Turunen et al., 2002). Indeed, empirical studies on forestry-drained peatlands applying soil sampling methods (Minkkinen and Laine, 1998; Simola et al., 2012), eddy covariance method (Lohila et al., 2011) and soil CO_2 efflux measurements (Ojanen et al., 2013) have shown that both sinks and sources occur, suppressing the mean emissions close to zero. Thus, the importance of forestry-drained peat soils in the national level GHG reporting does not result from high specific emissions but from the extensive peatland areas (Christiansen, 2013; Ylitalo, 2012). Unfortunately, when scaling up small, relatively uncertain figures to large areas, the high uncertainty will likewise undergo upscaling. Other methods applied to boreal forest soils have yielded similar results: uncertainty of the same order of magnitude as the estimated balance (Ortiz et al., 2013; Rantakari et al., 2012).

The observed trends, increasing emissions from South to North (Fig. 8) and decreasing emissions by increasing tree stocking (Fig. 9), suggest that climate warming could even decrease emissions. Emissions could also be actively reduced by keeping forest stands highly stocked. One should, anyhow, be careful not to over-interpret the results: Trends are as sensitive to bias as are the country-level estimates. Extensive empirical studies on boreal forestry-drained peatlands in Finland (Minkkinen and Laine, 1998; Ojanen et al., 2013; Simola et al., 2012) are indecisive regarding these trends.

Our finding of poor site types serving as sinks and fertile ones as sources on average, on the other hand, is supported by most of the extensive (Minkkinen and Laine, 1998; Ojanen et al., 2013) and intensive (Lohila et al., 2011; Minkkinen et al., 1999) studies. Interestingly, however, in our study the poorest, *Lichen* type sites were estimated to be CO_2 sources: While decomposition was low, production was even lower. Sites of this low fertility have been studied

Table A.1
Mixed linear model for: (1) foliage turnover ($f_{t.fol}$, year^{-1}) of pine and spruce in South Finland and birch countrywide, and (2) the ratio of non-foliage aboveground litter production ($f_{L.other}$, L_{other}/L_{fol}) in South and North Finland. β_1 is the fixed effect and γ_{site} is the random effect of each site.

	(1) $f_{t.fol}$			(2) $f_{L.other}$	
Tree species	Pine	Spruce	Birch	South	North
β_1	0.497	0.256	0.869	0.747	0.433
var(β_1)	7.35×10^{-4}	3.00×10^{-4}	3.56×10^{-2}	7.45×10^{-3}	1.32×10^{-3}
var(γ_{site})	1.98×10^{-3}	1.44×10^{-12}	0.104	5.35×10^{-2}	1.58×10^{-3}
var(residual)	6.05×10^{-3}	1.50×10^{-3}	7.24×10^{-3}	4.17×10^{-2}	5.61×10^{-3}
N of observations	19	5	10	30	13
N of sites	5	2	3	9	2

Table A.2
Linear model for arboreal fine root biomass ($f_{m.fr}$, g m^{-2}) and the variance–covariance matrix of its parameters. Independent variables are basal areas (m^2 ha^{-1}) of pine (β_1), spruce (β_2) and deciduous trees (β_3), projection coverage of dwarf shrubs (%, β_4), and location of the site in South or North Finland ($\beta_{location}$).

β_1	8.80
β_2	6.61
β_3	17.3
β_4	4.81
β_{South}	120
β_{North}	−53.2
var(residual)	5476
N of observations	32

	β_1	β_2	β_3	β_4	β_{South}	β_{North}
β_1	5.321					
β_2	2.056	5.070				
β_3	2.162	0.285	6.011			
β_4	0.202	0.664	1.023	1.154		
β_{South}	−85.607	−59.533	−80.610	−31.601	2523.821	
β_{North}	−48.226	−40.488	−53.993	−25.838	1505.831	1582.462

Table A.3
Mean projection coverage of dwarf shrubs (%) in the ground vegetation data according to site type.

Site type	Mean	Variance	N of observations
Rhtkg	7	21	11
Mtkg I	17	12	19
Mtkg II	13	21	11
Ptkg I	38	11	22
Ptkg II	23	18	13
Vatkg	45	11	21
Jätkg	40	116	2

only by Simola et al. (2012), who not find any correlation between C balance and site fertility. As these sites are generally underproductive for forestry, rewetting could be a feasible land use option.

Our results imply three ways to reduce uncertainty. First, for the accuracy of $NE_{CO2soil}$, better understanding of belowground processes to determine the C input to soil is crucial. As demonstrated by the different outcomes when comparing different mechanistic models (Palosuo et al., 2012), analogously the *D*–*L* method is sensitive to assumptions on included components. In addition to our results, this is well demonstrated by comparing the results of GHG reporting on forestry-drained peatland soils in two neighboring countries. The estimated source is very different: 220 g m^{-2} year^{-1} of C for Sweden (National Inventory Report..., 2013a) and 50 g m^{-2} year^{-1} of C for Finland (NIR). Yet, the decomposition values applied are very close to each other despite different sources (Minkkinen et al., 2007; von Arnold et al., 2005). The difference in emissions is due to the definition that total belowground litter production is considered as input in Finland (NIR) and only 40% of total belowground litter production in Sweden (National Inventory Report..., 2013b). Thus, the difference in emissions does not result from differences in peatlands but from different methodological assumptions. This uncertainty is not limited to boreal peatlands and the *D*–*L* method, rather it is common to any land ecosystem and method relying on litter production as C input to soil.

Second, most of the models applied in this study were based on data that is not necessarily representative of the target population. CO_2 efflux and fine root biomass measurements span the geographical and most of the site type variation in Finland (Ojanen et al., 2010, 2013), for the sampling was planned in the first place to cover the variation found in the country's forestry-drained peatlands. Also, the BioSoil data on ground vegetation biomass and projection coverage is based on systematic sampling (Ilvesniemi et al., 2006, 2008), yet only representative for South Finland. Aboveground tree stand and moss litter production data are a collection of case studies clearly biased towards South Finland. The tree biomass models (Repola, 2008, 2009) are based solely on data from mineral soil forests. The poorest site type Jätkg is inadequately represented in most of the datasets. The majority of the datasets is also based on relatively short-term studies, typically covering a few years only. The magnitude of the error due to poor representativeness is difficult to quantify, but can be reduced by applying adequate random or systematic sampling when planning data collection.

Third, the precision of $NE_{CO2soil}$ could be increased simply by acquiring more and better data for model building. The obvious target for more data would be the CO_2 efflux measurements behind the *D* model that alone produced half of the uncertainty. However, to markedly reduce uncertainty, the number of study sites should be increased multifold from the current 68 (Ojanen et al., 2010), and this would be very expensive and thereby unfeasible. A more cost-efficient way could be to acquire more tree stand litter production data. Especially the data on foliage turnover is very sparse. Also, the rates of dwarf shrub biomass turnover and moss litter production are based on very few measurements compared to their considerable share in litter production. Introducing a variable describing water table depth or drainage intensity into forest inventory could enable the building of more powerful models, as soil moisture largely controls the peatland C cycle (Vasander and Kettunen, 2006).

The fundamental reason for the great relative uncertainty seemed to be due to the $NE_{CO2soil}$ of the Finnish forestry-drained peatlands being close to zero on average. Thus, the *D*–*L* method could provide results with considerably lower relative uncertainty on peatland forests with high soil CO_2 emissions, i.e., on areas where *D* is much larger than *L*, such as afforested agricultural soils (Lohila et al., 2007; Meyer et al., 2013) or tropical plantations (Hooijer et al., 2012; Jauhiainen et al., 2012). When CO_2 emissions range from hundreds to thousands of g m^{-2} year^{-1} of C, an uncertainty of a few tens of g m^{-2} year^{-1} of C would be relatively low.

Table A.4
Linear models for the litter production (g m^{-2} year^{-1}) of dwarf shrubs ($f_{L.ds}$), herbaceous vascular plants ($f_{L.herb}$) and mosses ($f_{L.moss}$) and for total ground vegetation ($f_{L.gv}$) and the variances/variance–covariance matrices of their parameters. Independent variables are site type ($\beta_{site\ type}$) and for $f_{L.herb}$, $f_{L.moss}$ and $f_{L.gv}$ also tree stand basal area (m^2 ha^{-1}, β_1).

	$f_{L.ds}$	$f_{L.herb}$	$f_{L.moss}$	$f_{L.gv}$
β_{Rhtkg}	12.4	146[a]	62.4	227
$\beta_{Mtkg\ I}$	23.0	96.5[b]	78.8	206
$\beta_{Mtkg\ II}$	16.1	146[a]	87.3	261
β_{Ptkg} I	59.7	96.5[b]	108	271
$\beta_{Ptkg\ II}$	33.8	96.5[b]	107	233
β_{Vatkg}	79.1	96.5[b]	113	298
$\beta_{Jätkg}$	72.8	61.4	51.0	187
β_1	–	−3.19	−1.00	−4.52
var(residual)	916	3372	1732	6048
N of observations	99	90	90	90

$f_{L.ds}$	Variance
β_{Rhtkg}	83.289
$\beta_{Mtkg\ I}$	48.220
$\beta_{Mtkg\ II}$	83.289
$\beta_{Ptkg\ I}$	41.644
$\beta_{Ptkg\ II}$	70.475
β_{Vatkg}	43.627
$\beta_{Jätkg}$	458.089

$f_{L.herb}$	β_1	$\beta_{Jätkg}$	$\beta_{other\ type}$	$\beta_{Rhtkg/Mtkg\ II}$
β_1	0.540			
$\beta_{Jätkg}$	−2.986	1702.372		
$\beta_{other\ type}$	−9.641	53.267	220.870	
$\beta_{Rhtkg/Mtkg\ II}$	−10.252	56.641	182.900	371.945

$f_{L.moss}$	β_1	β_{Rhtkg}	$\beta_{Mtkg\ I}$	$\beta_{Mtkg\ II}$	$\beta_{Ptkg\ I}$	$\beta_{Ptkg\ II}$	β_{Vatkg}	$\beta_{Jätkg}$
β_1	0.332							
β_{Rhtkg}	−5.089	251.301						
$\beta_{Mtkg\ I}$	−7.583	116.286	288.760					
$\beta_{Mtkg\ II}$	−7.636	117.104	174.477	368.209				
$\beta_{Ptkg\ I}$	−5.793	88.843	132.370	133.302	179.884			
$\beta_{Ptkg\ II}$	−6.284	96.374	143.590	144.601	109.704	252.274		
β_{Vatkg}	−4.507	69.121	102.985	103.710	78.682	85.351	152.401	
$\beta_{Jätkg}$	−1.834	28.118	41.894	42.189	32.008	34.720	24.902	876.398

$f_{L.gv}$	β_1	β_{Rhtkg}	$\beta_{Mtkg\ I}$	$\beta_{Mtkg\ II}$	$\beta_{Ptkg\ I}$	$\beta_{Ptkg\ II}$	β_{Vatkg}	$\beta_{Jätkg}$
β_1	1.159							
β_{Rhtkg}	−17.767	877.327						
$\beta_{Mtkg\ I}$	−26.472	405.969	1008.100					
$\beta_{Mtkg\ II}$	−26.658	408.827	609.123	1285.469				
$\beta_{Ptkg\ I}$	−20.225	310.165	462.123	465.376	627.999			
$\beta_{Ptkg\ II}$	−21.939	336.453	501.291	504.820	382.992	880.724		
β_{Vatkg}	−15.735	241.311	359.536	362.067	274.689	297.971	532.054	
$\beta_{Jätkg}$	−6.401	98.165	146.258	147.288	111.743	121.214	86.937	3059.625

[a]/[b] Site types combined for the final model due to the similarity of coefficients.

Table A.5
Linear model for decomposition (f_D, g m^{-2} year^{-1} of CO_2) and the variance–covariance matrix of its parameters. Independent variables are basal area (m^2 ha^{-1}, β_1), mean May–October air temperature (°C, β_2), and site type (β_{site} type).

β_1	14.74
β_2	242.8
β_{Rhtkg}	−1383
$\beta_{Mtkg\ I}$	−1410
$\beta_{Mtkg\ II}$	−1487
$\beta_{Ptkg\ I}$	−1654
$\beta_{Ptkg\ II}$	−1674
β_{Vatkg}	−1771
$\beta_{Jätkg}$	−1814
var(residual)	107,060
N of observations	71

	β_1	β_2	β_{Rhtkg}	$\beta_{Mtkg\ I}$	$\beta_{Mtkg\ II}$
β_1	31.763				
β_2	−156.919	2987.018			
β_{Rhtkg}	1009.484	−30191.511	330003.711		
$\beta_{Mtkg\ I}$	880.027	−29918.342	319358.831	330713.541	
$\beta_{Mtkg\ II}$	1095.593	−29687.432	311442.916	310998.760	311348.887
$\beta_{Ptkg\ I}$	1106.388	−29272.400	306448.796	305883.058	299443.763
$\beta_{Ptkg\ II}$	1158.290	−30705.400	321506.081	320923.708	314147.305
β_{Vatkg}	1394.019	−31328.913	322832.399	321199.653	316340.034
$\beta_{Jätkg}$	1504.165	−30065.011	305729.444	303348.278	300295.487

	$\beta_{Ptkg\ I}$	$\beta_{Ptkg\ II}$	β_{Vatkg}	$\beta_{Jätkg}$
$\beta_{Ptkg\ I}$	305484.219			
$\beta_{Ptkg\ II}$	309250.611	335138.991		
β_{Vatkg}	311638.026	326918.137	339519.810	
$\beta_{Jätkg}$	296013.782	310512.061	316138.347	338537.417

Table A.6
Parameter variance–covariance matrices of the single tree foliage biomass models ($f_{m.fol}$) for Scots pine (A4 in Repola 2009), Norway spruce (A10 in Repola 2009) and birch (A6 in Repola 2008). Further description of the models can be found in the original articles.

Pine	b_0	b_1	b_2	b_3
b_0	0.22658			
b_1	0.03324	0.18576		
b_2	−0.30801	−0.17824	0.52273	
b_3	0.01555	−0.01272	−0.01309	0.00384

Spruce	b_0	b_1	b_2	b_3
b_0	0.32490			
b_1	0.08541	0.56701		
b_2	−0.48605	−0.53303	1.04040	
b_3	0.02344	−0.03010	−0.01217	0.00578

Birch	b_0	b_1	b_2
b_0	16.116		
b_1	−18.516	21.418	
b_2	1.868	−2.387	0.632

Table A.7
Parameter variance–covariance matrices of the single tree coarse root biomass models ($f_{m.cr}$) for Scots pine (11 in Repola 2009), Norway spruce (19 in Repola 2009) and birch (14 in Repola 2008). Further description of the models can be found in the original articles.

Pine	b_0	b_1
b_0	0.03168	
b_1	−0.05400	0.09923

Spruce	b_0	b_1
b_0	0.11290	
b_1	−0.23358	0.56852

Birch	b_0	b_1	b_2
b_0	0.22240		
b_1	0.14550	0.72730	
b_2	−0.10840	−0.18510	0.07426

Acknowledgements

We thank the following researchers, teams and institutions (in alphabetical order) for their contribution: Tiina Badorek, Kalle Eerikäinen, Soili Kojola, Raija Laiho, Mikko Moilanen, Meeri Pearson, Jaakko Repola, BioSoil team, National Forest Inventory team, Finnish Meteorological Institute.

This study was funded by the Environmental Research Pool of the Finnish Energy Industries (Energiateollisuuden ympäristöpooli) and the Graduate School in Forest Sciences (GSForest).

Appendix A

See Tables A.1–A.7.

References

Brunner, I., Bakker, M.R., Björk, R.G., Hirano, Y., Lukac, M., Aranda, X., Børja, I., Eldhuset, T.D., Helmisaari, H.S., Jourdan, C., Konôpka, B., López, B.C., Miguel Pérez, C., Persson, H., Ostonen, I., 2013. Fine-root turnover rates of European forests revisited: an analysis of data from sequential coring and ingrowth cores. Plant Soil 362, 357–372.

Chertov, O.G., Komarov, A.S., Nadporozhskaya, M.A., Bykhovets, S.S., Zudin, S.L., 2001. ROMUL – a model of forest soil organic matter dynamic as a sustainable tool for forest ecosystem modeling. Ecol. Modell. 138, 289–308.

Christiansen, L. (Ed.) 2013. Swedish Statistical Yearbook of Forestry. <http://www.skogsstyrelsen.se/en/AUTHORITY/Statistics/Statistical-Yearbook-/Statistical-Yearbooks-of-Forestry/> Swedish Forest Agency.

Clemmensen, K., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R.D., Wardle, D.A., Lindahl, B.D., 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science 339, 1615–1618.

Drösler, M., Freibauer, A., Christensen, T.R., Friborg, T., 2008. Observations and status of peatland greenhouse gas emissions in Europe. Ecol. Stud. 203, 237–256.

Drösler, M., Verchot, L., Freibauer, A., Pan, G., et al. 2014. Chapter 2: drained inland organic soils. In: Hiraishi, T., Krug, T., Tanabe, K., Srivastava, N., Jamsranjav, B., Fukuda, M., Troxler, T. (Eds.), 2013 Supplement to the 2006 IPCC Guidelines for National.

Eerikäinen, K., 2009. A multivariate linear mixed-effects model for the generalization of sample tree heights and crown ratios in the Finnish National Forest Inventory. For. Sci. 55, 480–493.

Finér, L., Laine, J., 1998. Root dynamics at drained peatland sites of different fertility in southern Finland. Plant Soil 201, 27–36.

Finér, L., Ohashi, M., Noguchi, K., Hirano, Y., 2011a. Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. For. Ecol. Manage. 262, 2008–2023.

Finér, L., Ohashi, M., Noguchi, K., Hirano, Y., 2011b. Factors causing variation in fine root biomass in forest ecosystems. For. Ecol. Manage. 261, 265–277.

Godbold, D., Hoosbeek, M., Lukac, M., Cotrufo, M., Janssens, I., Geulemans, R., Polle, A., Velthorst, E., Scarascia-Mugnozza, G., De Angelis, P., Miglietta, F., Peressotti, A., 2006. Mycorrhizal hyphal turnover as a dominant process for carbon input into soil organic matter. Plant Soil 281, 15–24.

Greenhouse gas emissions in Finland 1990–2011. National Inventory Report under the UNFCCC and the Kyoto Protocol. 2013. Statistics Finland.

Gregoire, T.G., Ståhl, G., Holm, S., Gobakken, T., Naesset, E., Nelson, R., 2011. Model-based inference for biomass estimation in a LiDAR sample survey in Hedmark County, Norway. Can. J. For. Res. 41, 96–107.

Hansson, K., Helmisaari, H.-S., Sah, S.P., Lange, H., 2013. Fine root production and turnover of tree and understorey vegetation in Scots pine, silver birch and Norway spruce stands in SW Sweden. For. Ecol. Manage. 309, 58–65.

Heavens, N.G., Ward, D.S., Natalie, M.M., 2013. Studying and Projecting Climate Change with Earth System Models. Nature Education Knowledge 4, 4. <http://www.nature.com/scitable/knowledge/library/studying-and-projecting-climate-change-with-earth-103087065> (Cited 25 Mar 2014).

Heinemeyer, A., Hartley, I., Evans, S., Carreira de la Fuente, J., Ineson, P., 2007. Forest soil CO_2 flux: uncovering the contribution and environmental responses of ectomycorrhizas. Global Change Biol. 13, 1786–1797.

Helmisaari, H.-S., Makkonen, K., Kellomäki, S., Valtonen, E., Mälkönen, E., 2002. Below- and above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. For. Ecol. Manage. 165, 317–326.

Hooijer, A., Page, S., Canadell, J.G., Silvius, M., Kwadijk, J., Wösten, H., Jauhiainen, J., 2010. Current and future CO_2 emissions from drained peatlands in Southeast Asia. Biogeosci. 7, 1505–1514.
Hooijer, A., Page, S., Jauhiainen, J., Lee, W.A., Lu, X.X., Idris, A., Anshari, G., 2012. Subsidence and carbon loss in drained tropical peatlands. Biogeosci. 9, 1053–1071.
Ilvesniemi, H., Korpela, L., Tamminen, P., Tonteri, T., 2006. BioSoil-aineiston avulla tutkitaan maaperän hiili- ja ravinnevarastojen muutoksia sekä aluskasvillisuutta. Pro Terra 29, 99–100.
Ilvesniemi, H., Tamminen, P., Tonteri, T., Korpela, L., 2008. BioSoil in Finland. Working Papers of the Finn. For. Res. Inst. 74, 31–32.
Jansson, P.-E., Karlberg, L., 2004. Coupled Heat and Mass Transfer Model for Soil–Plant–Atmosphere Systems. Royal Institute of Technology, Dept of Civil and Environmental Engineering, Stockholm.
Jauhiainen, J., Hooijer, A., Page, S., 2012. Carbon dioxide emissions from an Acacia plantation on peatland in Sumatra, Indonesia. Biogeosci. 9, 617–630.
Karhu, K., Wall, A., Vanhala, P., Liski, J., Esala, M., Regina, K., 2011. Effects of afforestation and deforestation on boreal soil carbon stocks – comparison of measured C stocks with Yasso07 model results. Geoderma 164, 33–45.
Karhu, K., Gärdenäs, A., Heikkinen, J., Vanhala, P., Tuomi, M., Liski, J., 2012. Impacts of organic amendments on carbon stocks of an agricultural soil – comparison of model-simulations to measurements. Geoderma 189–190, 606–616.
Korhonen, K., Ihalainen, A., Viiri, H., Heikkinen, J., Henttonen, H.M., Hotanen, J-P., Mäkelä, H., Nevalainen, S., Pitkänen, J., 2013. Suomen metsät 2004–2008 ja niiden kehitys 1921–2008. Metsätieteen aikakauskirja 3/2013, 269–333.
Kuzyakov, Y., Friedel, J.K., Stahr, K., 2000. Review of mechanisms and quantification of priming effects. Soil Biol. Biochem. 32, 1485–1498.
Lai, D., Roulet, N., Humphreys, E., Moore, T., Dalva, N., 2012. The effect of atmospheric turbulence and chamber deployment period on autochamber CO_2 and CH_4 flux measurements in an ombrotrophic peatland. Biogeosci. 9, 3305–3322.
Laiho, R., Finér, L., 1996. Changes in root biomass after water-level drawdown on pine mires in southern Finland, Scand. J. For. Res. 11, 251–260.
Laiho, R., Vasander, H., Penttilä, T., Laine, J., 2003. Dynamics of plant-mediated organic matter and nutrient cycling following water-level drawdown in boreal peatlands. Global Biogeochem. Cycles 17, 1053.
Laine, J., 1989. Metsäojitettujen soiden luokittelu (Summary: Classification of peatlands drained for forestry). Suo 40, 37–51.
Lehtonen, A., Sievänen, R., Mäkelä, A., Mäkipää, R., Korhonen, K.T., Hokkanen, T., 2004. Potential litterfall of Scots pine branches in southern Finland. Ecol. Modell. 180, 305–315.
Leppälammi-Kujansuu, J., Salemaa, M., Berggren Kleja, D., Linder, S., Helmisaari, H.-S., 2014. Fine root turnover and litter production of Norway spruce in a long-term temperature and nutrient manipulation experiment. Plant Soil 374, 73–88.
Liski, J., Lehtonen, A., Palosuo, T., Peltoniemi, M., Eggers, T., Muukkonen, P., Mäkipää, R., 2006. Carbon accumulation in Finland's forests 1922–2004 – an estimate obtained by combination of forest inventory data with modeling of biomass, litter and soil. Ann. For. Sci. 63, 687–697.
Lohila, A., Aurela, M., Tuovinen, J.-P., Laurila, T., 2004. Annual CO_2 exchange of a peat field growing spring barley or perennial forage grass. J. Geophys. Res. 109, D18116.
Lohila, A., Laurila, T., Aro, L., Aurela, M., Tuovinen, J.-P., Laine, J., Kolari, P., Minkkinen, K., 2007. Carbon dioxide exchange above a 30-year-old Scots pine plantation established on organic-soil cropland. Boreal Environ. Res. 12, 141–157.
Lohila, A., Minkkinen, K., Aurela, M., Tuovinen, J.-P., Penttilä, T., Ojanen, P., Laurila, T., 2011. Greenhouse gas measurements in a forestry-drained peatland indicate a large carbon sink. Biogeosci. 8, 3203–3218.
Majdi, H., 2001. Changes in fine root production and longevity in relation to water and nutrient availability in a Norway spruce stand in northern Sweden. Tree Phys. 21, 1057–1061.
Mäkiranta, P., Riutta, T., Penttilä, T., Minkkinen, K., 2010. Dynamics of net ecosystem CO_2 exchange and heterotrophic soil respiration following clearfelling in a drained peatland forest. Agric. For. Meteorol. 150, 1585–1596.
Maljanen, M., Martikainen, P., Walden, J., Silvola, J., 2001. CO_2 exchange in an organic field growing barley or grass in eastern Finland. Global Change Biol. 7, 679–692.
Maljanen, M., Komulainen, V.-M., Hytönen, J., Martikainen, P., Laine, J., 2004. Carbon dioxide, nitrous oxide and methane dynamics in boreal organic agricultural soils with different soil characteristics. Soil Biol. Biochem. 36, 1801–1808.
Meyer, A., Tarvainen, L., Nousratpour, A., Björk, R., Ernfors, M., Grelle, A., Kasimir Klemedtsson, Å., Lindroth, A., Räntfor, S.M., Rütting, T., Wallin, G., Weslien, P., Klemedtsson, L., 2013. A fertile peatland forest does not constitute a major greenhouse gas sink. Biogeosci. 10, 7739–7758.
Minkkinen, K., Laine, J., 1998. Long-term effect of forest drainage on the peat carbon stores of pine mires in Finland. Can. J. For. Res. 28, 1267–1275.
Minkkinen, K., Laine, J., Shurpali, N.J., Mäkiranta, P., Alm, J., Penttilä, T., 2007. Potential litterfall of Scots pine branches in southern Finland. Boreal Environ. Res. 12, 115–126.
Minkkinen, K., Vasander, H., Jauhiainen, S., Karsisto, M., Laine, J., 1999. Post-drainage changes in vegetation composition and carbon balance in Lakkasuo mire, Central Finland. Plant Soil 207, 107–120.
Muukkonen, P., 2005. Needle biomass turnover rates of Scots pine (*Pinus sylvestris* L.) derived from the needle-shed dynamics. Trees 19, 273–279.
Muukkonen, P., Lehtonen, A., 2004. Needle and branch biomass turnover rates of Norway spruce (*Picea abies*). Can. J. For. Res. 34, 2517–2527.
National Inventory Report Sweden 2013. 2013a. Swedish Environmental Protection Agency.
National Inventory Report Sweden 2013. Annexes. 2013b. Swedish Environmental Protection Agency.
Ngao, J., Longdoz, B., Granier, A., Epron, D., 2007. Estimation of autotrophic and heterotrophic components of soil respiration by trenching is sensitive to corrections for root decomposition and changes in soil water content. Plant 301, 99–110.
Ojanen, P., Minkkinen, K., Alm, J., Penttilä, T., 2010. Soil–atmosphere CO_2, CH_4 and N_2O fluxes in boreal forestry-drained peatlands. For. Ecol. Manage. 260, 411–421.
Ojanen, P., Minkkinen, K., Lohila, A., Badorek, T., Penttilä, T., 2012. Chamber measured soil respiration: a useful tool for estimating the carbon balance of peatland forest soils? For. Ecol. Manage. 277, 132–140.
Ojanen, P., Minkkinen, K., Penttilä, T., 2013. The current greenhouse gas impact of forestry-drained boreal peatlands. For. Ecol. Manage. 289, 201–208.
Ortiz, C., Liski, J., Gärdenäs, A., Lehtonen, A., Lundblad, M., Stendahl, J., Ågren, G., Karltun, E., 2013. Soil organic carbon stock changes in Swedish forest soils – a comparison of uncertainties and their sources through a national inventory and two simulation models. Ecol. Modell. 251, 221–231.
Palosuo, T., Foereid, B., Svensson, M., 2012. A multi-model comparison of soil carbon assessment of a coniferous forest stand. Environ. Modell. Softw. 35, 38–49.
Peltoniemi, M., Palosuo, T., Monni, S., Mäkipää, R., 2006. Factors affecting the uncertainty of sinks and stocks of carbon in Finnish forests soils and vegetation. For. Ecol. Manage. 232, 75–85.
Pumpanen, J., Kolari, P., Ilvesniemi, H., 2004. Comparison of different chamber techniques for measuring soil CO_2 efflux. Agric. For. Meteorol. 123, 159–176.
R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, <http://www.R-project.org/>.
Rantakari, M., Lehtonen, A., Linkosalo, T., Tuomi, M., Tamminen, P., Heikkinen, J., Liski, J., Mäkipää, R., Ilvesniemi, H., Sievänen, R., 2012. The Yasso07 soil carbon model – testing against repeated soil carbon inventory. For. Ecol. Manage. 286, 137–147.
Repola, J., 2008. Biomass equations for birch in Finland. Silva Fenn. 42, 605–624.
Repola, J., 2009. Biomass equations for Scots pine and Norway spruce in Finland. Silva Fenn. 43, 625–647.
Sah, S.P., Jungner, H., Oinonen, M., Kukkola, M., Helmisaari, H.-S., 2010. Does the age of fine root carbon indicate the age of fine roots in boreal forests? Biogeochem. 104, 91–102.
Sarkkola, S., Hökkä, H., Koivusalo, H., Nieminen, M., Ahti, E., Päivänen, J., Laine, J., 2010. Role of tree stand evapotranspiration in maintaining satisfactory drainage conditions in drained peatlands. Can. J. For. Res. 40, 1485–1496.
Schulze, E., Ciais, P., Luyssaert, S., et al., 2009. Importance of methane and nitrous oxide for Europe's terrestrial greenhouse-gas balance. Nat. Geosci. 2, 842–850.
Silvola, J., Alm, J., Ahlholm, U., Nykänen, H., Martikainen, P., 1996a. CO_2 fluxes from peat in boreal mires under varying temperature and moisture conditions. J. Ecol. 84, 219–228.
Silvola, J., Alm, J., Ahlholm, U., Nykänen, H., Martikainen, P., 1996b. The contribution of plant roots to CO_2 fluxes from organic soils. Biol. Fertil. Soils 23, 126–131.
Simola, H., Pitkänen, A., Turunen, J., 2012. Carbon loss in drained forestry peatlands in Finland, estimated by re-sampling peatlands surveyed in the 1980s. Eur. J. Soil Sci. 63, 798–807.
Ståhl, G., Heikkinen, J., Petersson, H., Repola, J., Holm, S., 2014. Sample-based estimation of greenhouse gas emissions from forests – a new approach to account for both sampling and model errors. For. Sci. 60, 3–13.
Straková, P., Anttila, J., Spetz, P., Kitunen, V., Tapanila, T., Laiho, R., 2010. Litter quality and its response to water level drawdown in boreal peatlands at plant species and community level. Plant Soil 335, 501–520.
Straková, P., Niemi, R., Freeman, C., Peltoniemi, K., Toberman, H., Heiskanen, I., Fritze, H., Laiho, R., 2011. Litter type affects the activity of aerobic decomposers in a boreal peatland more than site nutrient and water table regimes. Biogeosci. 8, 2741–2755. http://dx.doi.org/10.5194/bg-8-2741-2011.
Strand, A., Pritchard, S., McCormack, M., Davis, M., Oren, R., 2008. Irreconcilable differences: fine-root life spans and soil carbon persistence. Science 319, 456–458.
Subke, J., Inglima, I., Cotrufo, M., 2006. Trends and methodological impacts in soil CO_2 efflux partitioning: a meta-analytical review. Global Change Biol. 12, 921–943.
Tomppo, E., Heikkinen, J., Henttonen, H.M. 2011. Designing and Conducting a Forest Inventory – Case: 9th National Forest Inventory of Finland. Springer, Managing Forest Ecosystems 21.
Tuomi, M., Thum, T., Järvinen, H., Fronzek, S., Berg, B., Harmon, M., Trofymow, J.A., Sevanto, S., Liski, J., 2009. Leaf litter decomposition – estimates of global variability based on Yasso07 model. Ecol. Modell. 220, 3362–3371.
Tuomi, M., Laiho, R., Repo, A., Liski, J., 2011. Wood decomposition model for boreal forests. Ecol. Modell. 222, 709–718.

Turunen, J., Tomppo, E., Tolonen, K., Reinikainen, A., 2002. Estimating carbon accumulation rates of undrained mires in Finland – application to boreal and subarctic regions. Holocene 12, 69–80.
Vasander, H., 1982. Plant biomass and production in virgin, drained and fertilized sites in a raised bog in southern Finland. Ann. Bot. Fenn. 19, 103–125.
Vasander, H., Kettunen, A., 2006. Carbon in Boreal Peatlands. In: Wieder, R., Vitt, D. (Eds.), Boreal Peatland Ecosystems. Ecological Studies 188. Springer-Verlag, pp. 165–194.
Vasander, H., Laine, J., 2008. Site type classification on drained peatlands. In: Korhonen, R., Korpela, L., Sarkkola, S. (Eds.), Finland–Fenland: Research and Sustainable Utilisation of Mires and Peat. Finnish Peatland Society, Maahenki Ltd., Helsinki, pp. 146–151.
Vávřová, P., Penttilä, T., Laiho, R., 2009. Decomposition of Scots pine fine woody debris in boreal conditions: Implications for estimating carbon pools and fluxes. For. Ecol. Manage. 257, 401–412.
Venäläinen, A., Tuomenvirta, H., Pirinen, P., Drebs, A., 2005. A basic Finnish climate data set 1961–2000 – description and illustrations. Finn. Met. Inst. Reports 2005 (5), 1–27.
Von Arnold, K., Hånell, B., Stendahl, J., Klemedtsson, K., 2005. Greenhouse gas fluxes from drained organic forestland in Sweden, Scand. J. For. Res. 20, 400–411.
Ylitalo, E. (Ed.), 2012. Finnish Statistical Yearbook of Forestry, Finnish Forest Research Institute <http://www.metla.fi/julkaisut/metsatilastollinenvsk/index-en.htm>.