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ORIGINAL PAPER

Pools and fluxes of carbon in three Norway spruce ecosystems along a climatic gradient in Sweden

Dan Berggren Kleja · Magnus Svensson · Hooshang Majdi · Per-Erik Jansson · Ola Langvall · Bo Bergkvist · Maj-Britt Johansson · Per Weslien · Laimi Truusb · Anders Lindroth · Göran I. Ågren

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Abstract This paper presents an integrated analysis of organic carbon (C) pools in soils and vegetation, within-ecosystem fluxes and net ecosystem exchange (NEE) in three 40-year old Norway spruce stands along a north-south climatic gradient in Sweden, measured 2001–2004. A process-orientated ecosystem model (CoupModel), previously parameterised on a regional dataset, was used for the analysis. Pools of soil organic carbon (SOC) and tree growth rates were highest at the southernmost site (1.6 and 2.0-fold, respectively). Tree litter production (litterfall and root litter) was also highest in the south, with about half coming from fine roots (<1 mm) at all sites. However, when the litter input from the forest floor vegetation was included, the difference in total litter input rate between the sites almost disappeared (190–233 g C m^{-2} $year^{-1}$). We propose that a higher N deposition and N availability in the south result in a slower turnover of soil organic matter than in the north. This effect seems to overshadow the effect of temperature. At the southern site, 19% of the total litter input to the O horizon was leached to the mineral soil as dissolved organic carbon, while at the two northern sites the corresponding figure was approx. 9%. The CoupModel accurately described general C cycling behaviour in these ecosystems, reproducing the

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D. B. Kleja (✉)
Department of Soil Sciences, Swedish University of Agricultural Sciences, 7014, SE 750 07 Uppsala, Sweden
e-mail: Dan.Berggren@mv.slu.se

M. Svensson · P.-E. Jansson
Department of Land and Water Resources Engineering, Royal Institute of Technology, Stockholm, Sweden

H. Majdi · G. I. Ågren
Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

O. Langvall
Asa Experimental Forest and Research Station, Swedish University of Agricultural Sciences, Lammhult, Sweden

B. Bergkvist
Department of Ecology, University of Lund, Ecology Building, Lund, Sweden

M.-B. Johansson
Department of Forest Soils, Swedish University of Agricultural Sciences, Uppsala, Sweden

P. Weslien
Department of Plant and Environmental Sciences, Göteborg University, Goteborg, Sweden

L. Truusb
Institute of Ecology, Tallin University, Tallin, Estonia

A. Lindroth
Department of Physical Geography and Ecosystem Analysis, Lund University, Lund, Sweden

differences between north and south. The simulated changes in SOC pools during the measurement period were small, ranging from -8 g C m^{-2} year^{-1} in the north to +9 g C m^{-2} year^{-1} in the south. In contrast, NEE and tree growth measurements at the northernmost site suggest that the soil lost about 90 g C m^{-2} year^{-1}.

Keywords Soil carbon · Boreal ecosystems · Climatic gradient · CoupModel · Root litter · Dissolved organic carbon

Introduction

Forest soils of northern latitudes cover extensive areas and contain significant amounts of carbon. Temperate forest ecosystems account for about 25% of global terrestrial ecosystem carbon, of which about half is stored in soil organic matter (King et al. 1997). Thus, a small change in carbon balances of the soils in these ecosystems, for example as a result of climate change or nitrogen deposition, would have a significant effect on atmospheric CO_2 content.

Net changes in SOC are the result of differences between input rates of litter and soil organic carbon (SOC) decomposition rates. The litter input rate is largely related to net primary production (NPP) of forest ecosystems, which in turn strongly depends on climatic factors such as temperature and precipitation, as well as nutrient supply rates (King et al. 1997; Bergh et al. 1999). In temperate and boreal forests of the Nordic countries, an increase in temperature and atmospheric CO_2 concentration would probably result in increased NPP, at least on a short time-scale (Bergh et al. 2003). Long-term effects on NPP are more difficult to predict, since they may involve climatic effects on nutrient cycling between soil and vegetation. Another factor that needs to be considered is the response of forest floor vegetation to climate change. A growing number of studies indicate that forest floor vegetation contributes significantly (10–30%) to NPP in boreal forests (Mälkönen 1974; O'Connell et al. 2003). However, the longevity of above- and below-ground components of major forest floor species is poorly known, making estimates of their contribution to litter production uncertain. The effect of a possible increase in litter input following global warming might well be balanced by increased SOC decomposition rate. Laboratory incubation experiments generally show an increased C mineralisation rate with temperature (Fang et al. 2005). In the field, however, the effect of increased soil temperature on SOC decomposition can be more complex. For example, recent *in situ* soil-warming experiments show that the initial stimulation of soil respiration declines with time, a result that has been interpreted as a gradual depletion of the labile SOC pool (Knorr et al. 2005; Eliasson et al. 2005). Thus, the labile fraction of SOC seems to respond rapidly to temperature changes. However, stabile organic matter with long turnover times (decades to centuries) makes up the majority of organic C in most soils. Accordingly, it is the temperature sensitivity of this pool that is of major concern in a global warming perspective. Unfortunately, the decomposition rate of stable SOC is difficult to measure because of its slowness, and is currently a matter of scientific debate. Some researchers claim that the decomposition rate of stable SOC is even more sensitive to temperature than that of labile SOC (Ågren 2000; Knorr et al. 2005), whereas others claim that it is fairly insensitive to temperature (Giardina and Ryan 2000; Fang et al. 2005).

When predicting future effects of climate change on SOC pools in boreal forest ecosystems, it is important to consider the depth-distribution of SOC. According to a recent inventory of organic carbon pools in boreal forest soils in Scandinavia, 70–80% of the organic carbon in the upper 100 cm is normally found in the mineral soil (Callesen et al. 2003). Root litter and dissolved organic carbon (DOC) constitute the main sources of C to the mineral soil in these profiles. The fluxes of root litter and DOC have been estimated separately in quite a number of studies, but there are few where they have been studied simultaneously at the same site. Furthermore, the flux of C via fine roots in these studies has been estimated based on traditional root study methods, without taking into account the life span of intact individual roots (cf. Majdi 1996). According to Zech and Guggenberger (1996), DOC constituted about 75% of the total C input to mineral soil in a Norway spruce ecosystem at Fichtelgebirge, Germany, with some reservations regarding the value of root litter input. However, it is not only net fluxes of C into the mineral soil of these constituents that are needed for assessing their relative importance to C sequestration in mineral soils, but also their decomposition rates.

Differences in quality and in the ability of dissolved organic matter to interact with dissolved ions (Al and Fe(III)) and Fe and Al (hydr)oxide surfaces (Kaiser and Guggenberger 2003; Schwesig et al. 2003) may result in different decomposition rates for these substrates.

One approach to study the impact of temperature on SOC pool size and turnover is the use of natural climatic gradients (Simmons et al. 1996; Liski and Westman 1997; Giardina and Ryan 2000). Simmons et al. (1996) investigated forest floor C pools in a climatic gradient in Maine, USA, and found that C pools were larger at the coolest sites, despite no significant differences in (above-ground) litter inputs, indicating a significant temperature sensitivity of both labile and stable SOC. In contrast, Liski and Westman (1997) and Giardina and Ryan (2000) came to the conclusion that decomposition rate of stable SOC is insensitive to temperature.

In the present study, which forms part of the integrated research programme LUSTRA (Land Use Strategies for Reducing Greenhouse Gas Emissions), we measured C pools in soils and vegetation, within-ecosystem C fluxes and net ecosystem exchange of CO_2 at three sites with 40-year-old Norway spruce forest. The annual mean temperature at the locations ranged from 1.2°C to 5.5°C from north to south. The objectives of the present work were to: (i) Present an integrated picture of measured C pools and fluxes at the three LUSTRA sites (Fig. 1); (ii) investigate the ability of the ecosystem model CoupModel—previously parameterised on a region-based dataset—to describe within-ecosystem C fluxes and net ecosystem exchange of CO_2 at these sites; and (iii) establish possible links between climatic factors and C pools and fluxes at these sites.

Fig. 1 Location of the LUSTRA field sites and their nearest official meteorological stations

Materials and methods

Brief description of LUSTRA field sites

Field measurements were conducted at three sites along a south–north transect in Sweden: Asa (57°08′ N), Knottåsen (61°00′ N) and Flakaliden (64°07′ N). The sites were chosen with the intention of establishing a climatic gradient whilst maintaining other environmental parameters as constant as possible. Properties of the sites are summarised in Table 1. The ranges in mean annual temperature was 1.2–5.5°C and in mean annual precipitation 523–688 mm. Norway spruce (*Picea abies* (L.) Karst.) is the dominant tree species at all sites and the stands are about 40 years old. Base saturation and pH of the soils are given in Table 2. All sites are situated on acidic bedrock and the soils are Haplic Podsols (FAO 1990) developed on sandy loamy tills with low clay contents (<8%). At each site, three plots (30 × 30 m^2) per moisture class—dry, mesic and moist—were selected. The denomination of the moisture classes

Table 1 Brief description of the LUSTRA field sites

	Asa	Knottåsen	Flakaliden
Latitude	57°08′ N	61°00′ N	64°07′ N
Longitude	14°45′ E	16°13′ E	19°27′ E
Altitude (m a. s. l.)	190–200	315–320	310–320
Mean annual air temperature (°C)[a]	5.5	3.4	1.2
Mean length of growing season (days)[b]	190	160	120
Mean annual precipitation (mm)[a]	688	613	523
Nitrogen deposition (kg ha^{-1} $year^{1}$)[c]	8.8	4.4	2.6
Sulphur deposition (kg ha^{-1} $year^{1}$)[c]	4.9	2.6	1.8
Major tree species	Picea abies	Picea abies	Picea abies
Stand age in 2001 (years)	38 (41)[d]	37	42
Basal area (m^2 ha^{-1})[e]	26 ± 1.7	18 ± 2.8	20 ± 1.5
Soil type according to FAO (1990)	Podsols	Podsols	Podsols
Vegetation zone	Boreo-nemoral	Boreal	Boreal

[a] Long-term averages (1961–1990) from nearest meteorological station (Asa: Berg, Knottåsen: Åmotsbruk, Flakaliden: Kulbäcksliden)

[b] Days with average temperature >5°C

[c] Data from nearby sites for 2001 (Asa: Aneboda; Knottåsen:Jädraås; Flakaliden: Gammtratten)

[d] Figure within brackets is for plot 5

[e] Mean ± standard error of the mean ($n = 6$)

Table 2 Base saturation (BS) and pH(H_2O) in the soil profiles at Asa, Knottåsen and Flakaliden

Site	Horizon	pH (H_2O)	BS%
Asa	O	3.55	66
	Mineral soil (5–25 cm)	4.33	5.9
Knottåsen	O	4.15	83
	B (0–20 cm)	4.78	28
Flakaliden	O	4.18	80
	B (0–20 cm)	5.01	42

Sampling was based on horizon at Knottåsen and Flakaliden and on depth in mineral soil at Asa due to a lack of well-defined A and E horizons in the latter. Data from Berggren et al. (2004)

follows that used by the Swedish National Survey of Forest Soils and Vegetation and is based on average depth to the groundwater level during the vegetation period; dry >2 m, mesic 1–2 m and moist <1 m. This paper reports measurements made at the 6 dry and mesic plots, which were similar with respect to C pools in soils and trees, litter fall and DOC fluxes. At Flakaliden the plots were situated within a slope that was equal to the fetch of an eddy-flux tower, which was used for estimating the net C exchange of the ecosystem (Lindroth et al. 2007). For detailed site descriptions, see Berggren et al. (2004).

Brief land-use history of sites

The sites were clear-cut in 1963 (Flakaliden and Knottåsen) or 1966 (Asa). Present stands were planted in 1963 (Flakaliden), 1968 (Knottåsen) or 1967 (Asa) with 4-year-old Norway spruce seedlings. The former forest generation at the Asa site was a mixed spruce-pine stand of ages varying between 80 years and 120 years and at the other sites a Norway spruce stand of an age of >100 years.

Measurements of soil C and N pools

Soil samples were taken systematically at 20 positions in all plots (30 × 30 m^2) using a grid system. Sampling was by horizon in the O and E horizons and by fixed depth in the B horizon except at Asa, where sampling of the mineral soil was by fixed depth due to the absence of a well-developed E horizon. For the O horizon sampling, a soil corer with an inner diameter of 100 mm was used, while for mineral soil sampling (down to a depth of 25 cm in the mineral soil or the B horizon) a soil corer with a diameter of 44 mm was used. Prior to analysis, all sub-samples (20) were pooled to generate one composite sample for each layer per plot. Mineral soil layers below 25 cm were sampled from each wall of one $1 \times 1 \times 1$ m^3 pit dug just outside the plot. Prior to analysis, all sub-samples (4) were pooled to generate one composite sample for each 10 cm layer. Soil bulk density was determined on separate samples taken from each pit wall (2 samples per wall) at 50 cm depth using a soil corer (3 cm, diameter 44 mm). Carbon and nitrogen contents of composite samples were analysed using an elemental analyser (LECO CNS-1000).

Stone and boulder frequency was accounted for in all calculations of C and N pools in mineral soil layers. The content of stones and boulders was estimated by the so-called rod penetration method (Viro 1952) in which an iron rod with a diameter of 0.010 m was thrust into the soil at 36 points systematically distributed over the plot area and the penetration depth was determined. Using the empirical relationship proposed by Viro (1952) and modified by Tamminen and Starr (1994), the mean penetration depth (p) was transformed to the volumetric content of stones and boulders (S&B) using the regression equation: $\text{S\&B} = 83-(2.75 \cdot p)$. Stone and boulder volumes determined at plot level are reported in Berggren et al. (2004).

Measurements of tree growth

Standing biomass and growth on the plots were estimated for the period 2001–2004. Diameter was measured on all trees, and height was measured on sample trees every year from 2001 in the plots at Asa and Knottåsen, and only in 2004 at Flakaliden. Height was assessed on all tallied trees by secondary functions. To estimate diameter and height for the years before the measuring programme started, height growth and annual ring width (measured on bore cores) were measured on the sample trees and height and diameter were assessed on all trees every year by secondary functions for height growth and diameter growth. Dry weight biomass for different fractions of the trees was estimated using biomass functions by Marklund (1988) and the carbon content was assumed to be 50% of the biomass in all fractions. Mean C sequestration per year was estimated by the mean difference in the estimated C content in living biomass between two consecutive years in the period 2001–2004.

Measurements of litter production

Above-ground litter production

Annual litterfall from trees was measured using circular litter traps with a nominal sampling area of 0.32 m^2. Five traps were randomly distributed per plot. Each litter trap consisted of a terylene net with a mesh size of 0.1 mm and closed at its lower end by a string. The traps were placed 0.9 m above ground. The litter traps were emptied twice a year and the litter from each trap was sorted into two fractions: needles/leaves and a composite fraction (other material) consisting of all the other components collected (e.g., seeds, twigs ≤ 5 mm, bark and cones). The fractions were dried at 85°C for 48 h and weighed individually. The C flux was obtained by assuming a litterfall C content of 50%.

Above-ground litter production of field and bottom layer vegetation was estimated from measured biomass (Berggren et al. 2004). Nine quadratic plots (0.25 m^2) were evenly spread along one diagonal line of each 30×30 m^2 plot. All above-ground plant material was sampled and sorted into the groups: shrubs, grasses and bottom layer (lichens and mosses); dried at 70 °C, and weighed. A carbon content of 50% was assumed. Above-ground litter production of field layer vegetation (shrubs and grasses) was obtained by assuming a turnover rate of 0.18 year^{-1} (Tyler et al. 1973). The corresponding value for mosses was set to 0.2 year^{-1} (Rühling and Tyler 1970).

Below-ground litter production

Below-ground litter production of tree and field layer vegetation (fine roots <1 mm in diameter) in O horizon and mineral soil was calculated by combining root biomass (g m^{-2}) obtained from soil cores and turnover (year^{-1}) as the inverse of longevity (Majdi 1996) obtained by minirhizotron technique; i.e., the same technique was used for both types of roots at all three sites.

Root biomass of both tree and ground vegetation was determined using soil coring, with stone and boulder volumes in mineral soil layers accounted for. At Flakaliden experimental site, adjacent to the LUSTRA site in the same Norway spruce stand, four cores (7.2 cm in diameter) of the forest floor and eight (5 cm in diameter) of the mineral soil layer (0–30 cm) were taken randomly in control plots (n = 3) corresponding to mesic plots at the LUSTRA site (Majdi and Andersson 2005). The Similar numbers of cores were taken from the forest floor and mineral soil layer (0–50 cm) at the Asa and Knottåsen sites (dry and mesic plots; n = 6). Sampling was in 2000, 2002 and 2004 at Asa and in 2000, 2002 and 2003 at Knottåsen. When calculating plot-wise average values, data for all three years were used. Handling and treatment of samples followed the procedure described by Majdi and Andersson (2005). Spruce roots were separated from understorey vegetation roots and rhizomes, and then sorted into diameter sizes (0–1 mm and 1–2 mm). Fine roots from all species of understorey vegetation were pooled for each permutation of plot and soil horizon. Dry weights were converted to C pools by assuming a C content of 50%.

Two acrylic minirhizotron tubes (100 cm long, 5 cm inner diameter and 6 cm outer diameter) were installed horizontally in the forest floor and vertically in the mineral soil (0–50 cm) at each of the three mesic plots at Knottåsen (Majdi et al. 2007) and Asa in 1999 and in control plots at Flakaliden experimental site in 1997 (Majdi and Andersson 2005). In order to allow for recolonisation of fine roots, no mini-rhizotron observations were made until two years after their installation. Recordings started in June 2001 and continued from June to October 2003 in Asa and Knottåsen. At Flakaliden site the recording started in June 1997 and ended in August 1998 (Majdi and Andersson 2005). On each filming occasion, a PAL colour S-VHS video camera (Circon, Santa Barbara, California) was lowered into each mini-rhizotron tube by a square indexing aluminium handle, with recording holes at intervals of 1.35 cm. The image size was 1.8 × 1.35 cm^2. Fine roots (<1 mm) of spruce and field layer vegetation were observed separately and the separated by visual criteria.

Image files were digitized using the interactive software RooTracker (Craine and Tremmel 1995) and each root was assigned a unique identification number. Using RooTracker, tracings and identification numbers from previously digitized images were recalled and laid over subsequent images. Roots that were observed in a frame for the first time and were white were considered "new". These "new" roots were included in longevity estimations. If they remained white or brown in colour on subsequent occasions, they were classified as living and taken into account for production measurements. Roots were defined as *dead* when they turned black and produced no new roots on subsequent occasions. We traced dead roots on all subsequent occasions until they disappeared completely from the images. Roots were classified as missing when they decayed or disappeared. Fine root turnover (year^{-1}) for the two categories was calculated as the inverse of median root longevity, i.e., the time by which roots accounting for 50% of roots were dead. See Majdi and Andersson (2005) and Majdi et al. (2007) for data on fine root dynamics and a detailed description of measurements and calculations at Flakaliden and Knottåsen.

DOC measurements

Fluxes of dissolved organic carbon (DOC) were determined below the O and B horizons. The O horizon leachate was sampled using zero tension lysimeters (30 cm^2), made of plexiglass and polyethylene (PE) netting. Soil solution from the lower part of the B horizon (40–50 cm soil depth) was continuously sampled using tension lysimeters (Teflon/quartz, Prenart super quartz, vacuum 50 kPa). In each of the three dry and three mesic plots per site, three lysimeters were installed below the O horizon and two below the B horizon, i.e., 18 lysimeters below the O horizon and 12 below the B horizon were used per site. Sampling was bi-weekly during 2001, and once every fourth week during 2003 and 2004. Dissolved organic C was measured using a Shimadzu TOC-5000 A analyser, usually within one week of sampling. See Fröberg et al. (2006) for data on DOC fluxes and dynamics during the period 2000–2001, and a detailed description of lysimeter installations and handling of samples.

Average vertical soil water fluxes in the six plots were calculated using the CoupModel (see below). Dissolved organic C fluxes in soils were calculated by multiplying simulated water fluxes and average DOC concentrations (18 or 12 lysimeters) per sampling period.

Simulations using the CoupModel

Brief description of the model

CoupModel (Jansson and Karlberg 2004), formerly known as the SOIL or SOILN model (Jansson and Halldin 1979; Johnsson et al. 1987; Eckersten et al. 1998) is a process-orientated ecosystem model accounting for the major abiotic and biotic components in the soil-plant-atmosphere system. The basic structure of the model is a depth profile of the soil, and calculations of water and heat flows are based on common soil properties, e.g., the water retention curve, functions for unsaturated and saturated hydraulic conductivity, the heat capacity including the latent heat at thawing/melting and functions for the thermal conductivity. Carbon and N balances and the dynamics of plant development are also simulated, as are the interactions between plant and physical driving forces. The only dynamic input data necessary are precipitation, air temperature, wind speed, air humidity and radiation.

Below, model assumptions and setting of relevance for the present paper are briefly described. More details are given in Svensson et al. (2007). Soil organic matter in CoupModel was represented by two pools: litter (fast turnover rate) and humus (slow turnover rate). Microbes were implicitly represented in the substrate. The decomposition rates of the litter and humus pools were described as first order rate process. The products of litter decomposition are CO_2 (respiration), humus and, conceptually, microbial biomass and metabolites, whereas CO_2 is the only product of humus decomposition. The fraction of C and N being transformed from the litter to the humus pool was determined by a humification factor, set to 0.2 in all simulations. The humification factor could conceptually be compared to the limit-value concept (e.g., Berg et al. 1996) and the used value is similar to the values for pine and spruce presented in Berg (2000). In addition to the processes described above, C (and N) can also be transformed to DOC (and DON) from the humus and litter pools, as regulated by first order rate coefficients. The DOC (and DON) may also be transformed back to humus, as controlled by immobilisation rate parameters. Dissolved organic compounds may also be transported and redistributed in the soil profile as a convective flux governed by water flow. Temperature and moisture effects on the turnover of soil organic matter were accounted for using standard functions suggested by Ratkowsky et al. (1982) and Johnsson et al. (1987), respectively.

Plant N uptake is driven by N demand, which is related to the C assimilation rate and assumed CN ratios of different plant components. Mineral N is taken up from nitrate and ammonium pools in proportion to the relative sizes of these pools. In cases of N deficiency, i.e., when estimated uptake was less than the estimated demand, N is allowed to be extracted in organic form (Näsholm et al. 1998). The organic N uptake rate is assumed to be proportional to the pool size of N in the humus pool. Both mineral and organic N uptake is related to the root distribution in the soil profile. The fluxes of inorganic N from the litter and humus pools are driven by C turnover, and are related to the CN ratio of the decomposed product and the substrates. Thus, there is a strong link between C and N mineralisation rates in the model.

Modelling approach and parameterisation

In this work, the intention was to simulate within-ecosystem C fluxes and net ecosystem exchange of CO_2 at the three LUSTRA sites, using model parameter values obtained from the regional study by Svensson et al. (2007), thus validating the model at another scale. The development of the present stands, including their field layer vegetation, from plantation to 2004 was simulated using a combination of climatic data (precipitation, air temperature, wind speed, air humidity and radiation) from nearby official meteorological stations (1961–1996) and LUSTRA data (1997–2004). A description of the climatic measurements performed at the LUSTRA sites can be found in Berggren et al. (2004). Site-specific soil physical properties were used in the simulations. The level and timing of simulated forest management practices were based on historical data for each site and assumptions made in Svensson et al. (2007). At both Flakaliden and Asa, the stands were thinned in 1971, whereby 60% of the tree biomass was cut down and left as litter. At Knottåsen a thinning was performed in 1986, whereby 30% of the tree biomass was cut down and left as litter.

In the simulation approach applied on the LUSTRA sites, we allowed both the rate constant for humus decomposition (k_h) and the uptake rate of organic N uptake by plants (O_H) to vary on a regional basis (Table 3), as found in the calibrations in Svensson et al. (2007).

Results and discussion

Carbon pools in soils

The SOC pool at the Asa site was about 1.5 times larger than that at the two northern sites (Table 4). Thus, SOC pools at the LUSTRA field sites follow the general national trend, with increasing pool size when moving from north to south (Callesen et al. 2003; Olsson et al. 2007). Also soil N pools increased from north to south, as indicated by the CN ratios given in Table 4, and followed the national gradient in N deposition (Table 1). The differences in soil C pools between sites could be related to different factors such as climate, historical land-use and N deposition. According to the evaluation made by Olsson et al. (2007), the N deposition showed the strongest correlation to C stocks in dry and mesic Swedish forest soils. A major fraction (77–88%) of SOC was found in the mineral soil, which is in accordance with findings by Callesen et al. (2003). The amount of SOC at depth >50 cm was small at Asa (12%) and Knottåsen (11%), but significant at Flakaliden (27%). In general, little is known about pool sizes of SOC in deep soil layers (>50 cm) in Scandinavian forest soils on glacial till, partly due to practical problems with sampling. However, results of an inventory reported by Karltun (1995) confirm that Flakaliden is not a unique case. It is likely that SOC at these depths is strongly associated with inorganic precipitates (Fe (hydr)oxides and imogolite type materials) having reactive surfaces (Eusterhues et al. 2003).

Table 3 Rate constants for decomposition of the humus pool (k_h) and organic N uptake by vegetation (O_H) used in the CoupModel simulations made on the LUSTRA sites

Site	k_h (day^{-1})	O_H (day^{-1})
Asa	$1.9 \cdot 10^{-4}$	2.2×10^{-5}
Knottåsen	$2.8 \cdot 10^{-4}$	4.0×10^{-5}
Flakaliden	$3.7 \cdot 10^{-4}$	6.5×10^{-5}

Rate constants for Asa, Knottåsen and Flakaliden corresponded to Nässjö, Mora and Lycksele, respectively, in the regional simulations (Svensson et al. 2007). The rate constants given are normalised to optimal temperature (25°C) and moisture

Table 4 Pools of C and C/N ratio in soil layers at the LUSTRA field sites

Horizon /depth	Site	C pool (kg m^{-2})	C/N (g g^{-1})
O-horizon	Asa	2.34 ± 0.30 a	31.8 ± 0.79 b
	Knottåsen	1.27 ± 0.12 b	34.5 ± 1.59 b
	Flakaliden	0.87 ± 0.09 b	40.4 ± 0.82 a
0–50 cm	Asa	8.82 ± 0.58 a	27.2 ± 0.88 b
	Knottåsen	5.23 ± 0.28 b	29.0 ± 1.12 ab
	Flakaliden	5.26 ± 0.26 b	31.5 ± 1.13 a
0–100 cm	Asa	10.00 ± 0.65 a	27.0 ± 1.05 b
	Knottåsen	5.86 ± 0.32 b	28.7 ± 1.10 ab
	Flakaliden	7.22 ± 0.68 b	33.5 ± 2.37 a

Values represent mean ± standard error of the mean ($n = 6$). Different letters indicate statistically significant differences between sites ($P < 0.05$)

Carbon pools in vegetation

The tree biomass at Asa was about twice that at the two northern sites, which is in accordance with the growth rates measured during 2001/2002–2004 (Table 5). The tree growth at the LUSTRA plots followed the national pattern, with higher growth rates in the south (Skogsdata 2003; Bergh et al. 2005). The observed national pattern is probably best explained by a combination of a higher N supply rate and a longer growing season in the south (Tamm 1991; Bergh et al. 2005).

Pools of organic C in other living components—tree fine roots, field and bottom layer vegetation—are shown in Table 6. The fine root (<2 mm) biomass of trees varied between 196 g C m^{-2} and 111 g C m^{-2}, being highest at Asa. These values agree well with those reported by Helmisaari et al. (2007) for eight Norway spruce stands in Finland (92–185 g C m^{-2}), a country with similar climatic conditions as Sweden. The field layer vegetation made up a significant contribution (37–44%) of the total fine root biomass at the two northernmost LUSTRA sites, whereas the contribution was small at Asa (11%). As a result the total fine root biomass was highest at Knottåsen (272 g C m^{-2}) and similar in size at Asa and Flakaliden (221 g C m^{-2} and 197 g C m^{-2}, respectively). The same observation was made by

Table 5 Pools of C in trees (2004) and annual net C accumulation in trees at the LUSTRA field sites

Site	C pool tree (kg m^{-2})	C accumulation (g m^{-2} year^{-1})				
		Stem + stump	Living branches	Dead branches	Coarse roots	Total
Asa	7.95 ± 0.63 a	233 ± 19	96 ± 12	4.8 ± 0.5	71 ± 6	405 ± 29 a
Knottåsen	4.60 ± 0.89 b	98 ± 13	62 ± 10	1.9 ± 0.2	37 ± 6	199 ± 29 b
Flakaliden	4.63 ± 0.39 b	137 ± 13	41 ± 3	3.8 ± 0.3	37 ± 3	219 ± 19 b

The latter values are for the period 2001–2004 (Asa and Flakaliden) or 2002–2004 (Knottåsen). Values represent mean ± standard error of the mean ($n = 6$). Different letters indicate statistically significant differences between sites ($P < 0.05$)

Table 6 Biomass (g C m^{-2}) of tree roots, field and bottom layer vegetation at the LUSTRA field sites

	Asa		Knottåsen		Flakaliden	
	O horizon	Mineral soil	O horizon	Mineral soil	O horizon	Mineral soil
Tree						
Roots <1 mm	27 ± 4	77 ± 4	42 ± 9	49 ± 5	17 ± 2	48 ± 16
Roots 1—2 mm	33 ± 2	59 ± 5	36 ± 5	45 ± 2	20 ± 4	26 ± 0
Field layer						
Roots <1 mm	6 ± 4	15 ± 3	23 ± 2[a]	26 ± 1[a]	10 ± 3[a]	27 ± 7[a]
Roots 1—2 mm	3 ± 1	1 ± 1	49 ± 8[a]	2 ± 1[a]	40 ± 26[a]	9 ± 4[a]
Above ground	6 ± 1		66 ± 15		55 ± 8	
Bottom layer	78 ± 8		107 ± 17		108 ± 12	

Values represent mean ± standard error of the mean ($n = 6$). Root biomasses given for Flakaliden represent the control plots in the Flakaliden experimental area (Majdi and Andresson 2005)

[a] $n = 3$

Helmisaari et al. (2007), who found a high contribution (40%) of fine root from the field layer vegetation at their northern sites. The above ground biomasses of the field layer vegetation at the LUSTRA sites followed the same pattern as the fine root biomasses. The higher biomasses of the field layer at the two northern sites is probably related to lower stand density and naturally narrower tree crowns in the north compared to the south allowing more light to penetrate to the forest floor in the north. Also composition of the field layer vegetation differed between the sites. The dwarf shrubs *Vaccinium myrtillus* and *Vaccinium vitis-idaea* dominated strongly at the two northern sites (80–90%), but were less frequent at Asa, where grasses (mainly *Deschampsia flexuosa*) constituted a significant fraction (50%) of the field layer biomass (Berggren et al. 2004). According to the Swedish National Forest Inventory, there is a clear national pattern in Norway spruce forest ecosystems, with field layer vegetation dominated by dwarf shrubs in central and northern parts of Sweden, whereas grass species dominate in the south or field layer vegetation is lacking (Johansson et al. 2007).

Input of carbon to soil as litter

The amount of litter input is a key parameter in determining C and nutrient dynamics of soils. The place where litter is deposited—on the surface as litterfall or in the soil profile as root litter—is also of importance (Rasse et al. 2005). Litterfall from trees was highest in the south (Table 7), in accordance with the observation of tree biomasses (Table 5). Furthermore, the relationship between needle litter fall and basal are at the three LUSTRA sites seems to follow the general national trend (Figs. 2 and 3).

Fine root turnover data in the present study ranged from 0.5 year^{-1} to 1.1 year^{-1}, with no apparent north-south trend (Table 8), are basis for estimation of root litter production. Our estimates are close to those obtained in other studies in similar spruce

Table 7 Estimates of above- and below-ground litter production (g C m^{-2} $year^{-1}$) at the LUSTRA field sites

	Asa	Knottåsen	Flakaliden
Above ground			
Tree	101 ± 5	68 ± 15	60 ± 7
Field layer	1 ± 0	12 ± 3	10 ± 1
Bottom layer	16 ± 2	21 ± 4	22 ± 2
Sum above	118	101	92
Below ground			
Tree			
O horizon	22	38	9
Mineral soil (0–50 cm)[a]	62	44	48
Field layer			
O horizon	5	21	11
Mineral soil (0–50 cm)[a]	12	29	30
Sum below	101	132	98
Total ecosystem	219	233	190

Values represent mean ± standard error of the mean ($n = 6$). The below ground litter production is based on fine root biomasses (<1 mm) given in Table 6 and turnover values given in Table 8

[a] Flakaliden 0–30 cm

forests (Ostonen et al. 2005). King et al. (2002) reported a turnover of 0.94 $year^{-1}$ for loblolly pine fine roots (<1 mm). There was no consistent difference in fine root turnover between Noway spruce roots and the field layer vegetation. To our knowledge no attempts have been made earlier to estimate turnover of field layer vegetation, beside the study of Majdi and Andersson (2005) made at Flakaliden.

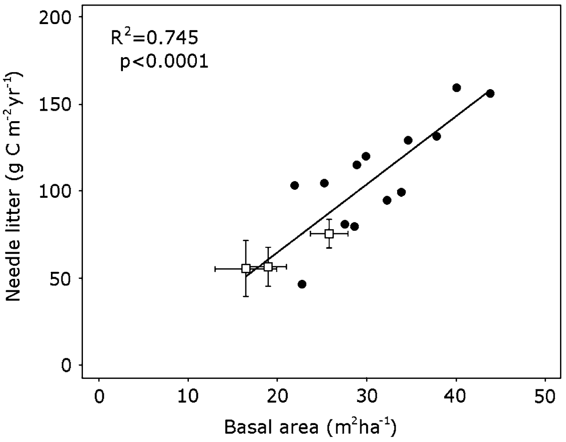

Fig. 2 Linear relation for needle litterfall in Norway spruce stands as compared to basal area. LUSTRA sites (□) (±standard error) and 50–70-year-old stands situated in south-central Sweden (Berg et al. 1999; Johansson and Gränlls 1989) (●)

The strength of our estimation of root turnover is the direct observation of roots from birth until they disappear. However, minirhizotrons are only able to estimate most dynamic roots (<1 mm) and not roots with larger diameter (>1 mm) for which isotope techniques as ^{14}C and ^{13}C may be more suitable (Majdi et al. 2005). Longevity estimates by minirhizotron method may overestimate turnover if the median longevity underestimates the mean due to a positively skewed fine root age distribution (Tierney and Fahey 2002). In C isotope studies, the mean residence time (MRT) of C is used to define root age or time needed for a group of fine roots to turn over once, and its inverse is used to calculate turnover (Matamala et al. 2003; Majdi et al. 2005). However, the MRT approach is likely to overestimate the average life span of fine roots. Using ^{14}C method, Gaudinski et al. 2001 estimated longevity of fine roots (<2 mm) to 3–18 years, which is longer than our estimates of 1–2 years (Table 8). The discrepancy between the minirhizotron and isotope methods could also be due to dilution of isotope signals by nonstructural carbohydrates reserves (Luo 2003).

For the reasons given above, only fine roots (<1 mm) were used in the calculation of root litter using the biomass values given in Table 6. Since the estimates of root turnover is strongly dependent on the technique used, a strength of our study is that we have used the same technique at all three sites, and both for tree and field layer roots, facilitating direct comparisons between sites and vegetation types. For trees the amount of litter from fine roots was about equal (0.8–1.2 times) to above-ground litter input, resulting a gradient in total litter production from trees, being highest in the south (Table 7). However, when litter input from the field and bottom layer vegetation was included, the gradient disappeared (219 g C m^{-2} $year^{-1}$ at Asa, compared to 233 g C m^{-2} $year^{-1}$ and 190 g C m^{-2} $year^{-1}$ at Knottåsen and Flakaliden, respectively), mainly because of the large input of litter from the field layer vegetation at the two northern sites. The contribution of litter from the bottom layer vegetation (mosses and lichens) was rather similar at all three

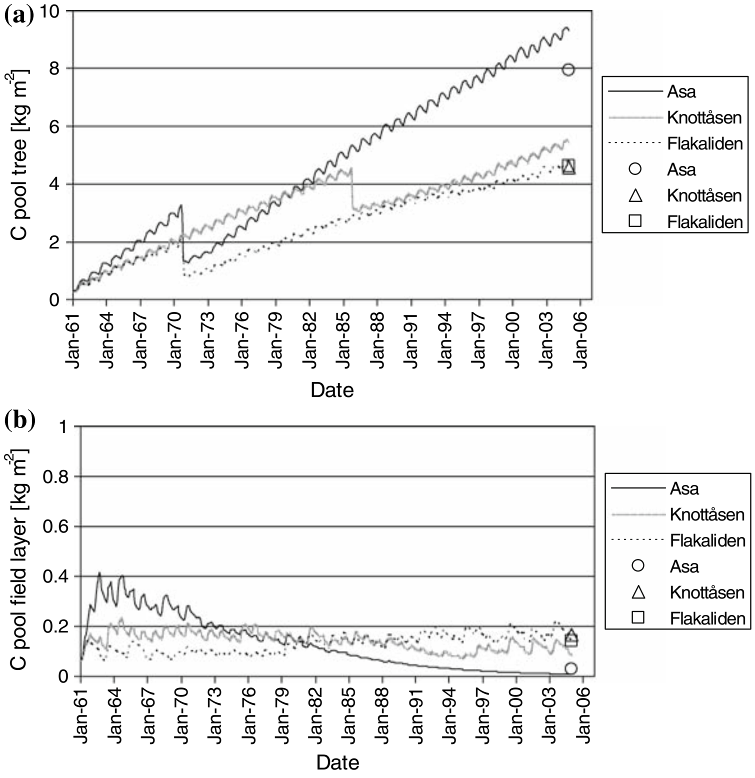

Fig. 3 Measured (symbols) and modelled (lines) changes in C pools in (**a**) trees and (**b**) field layer vegetation. Measured tree and field layer biomass values are from Tables 5 and 6, respectively. Note that the total field layer biomass value represents the sum of above-ground and fine roots (<2 mm), i.e., is an underestimate of the actual total biomass

Table 8 Fine root (<1 mm in diameter) turnover (year^{-1}) in O horizon and mineral soil layers of Norway spruce roots and field layer vegetation

	Asa	Knottåsen	Flakaliden
O horizon			
Field layer vegetation	0.8	0.9	1.1
Spruce	–[b]	0.9	0.5
Mineral soil (0–50 cm)[a]			
Field layer vegetation	0.8	1.1	1.1
Spruce	0.8	0.9	1.0

Data for Asa and Knottåsen are average values for the mesic plots, and Flakaliden data are for the control plots at the Flakaliden experimental area. All Flakaliden data are from Majdi and Andersson (2005), and the turnover data for spruce roots at Knottåsen are from Majdi et al. (2007)

[a] Flakaliden 0–30 cm

[b] not determined

sites (about 20 g C m^{-2} year^{-1}). Accordingly, our measurements suggest that litter production from field and bottom layer vegetation could make a significant contribution to soil C input in boreal coniferous forest ecosystems. Existing data on litter production by field layer (dwarf shrubs and perennial grasses) and bottom layer vegetation in boreal forests is sparse. However, recent estimates of gross primary production (GPP) and net primary production (NPP) support the view that it might be of significant importance. For example, Kolari et al. (2006) estimated GPP of the forest floor vegetation in a boreal Scots pine forest in southern Finland to be 130 g C m^{-2} year^{-1}, which amounted to 13% of total ecosystem GPP, while O'Connell et al. (2003) estimated that the forest floor NPP in a black spruce forest in Canada constituted 14% of total ecosystem NPP. In an earlier study, Mälkönen (1974) estimated that the contribution of forest floor NPP could be as much as 21–29% of total NPP in Finnish boreal Scots pine forests. The corresponding figures for the LUSTRA sites were 14%, 12% and 3% for Knottåsen, Flakaliden and Asa, respectively. To arrive at these figures we used data on tree growth (Table 5) and litter production (Table 7), and assumed that the field and bottom layer biomass was in steady state.

Turnover rates of C in O horizons

At the age of 40 years, we expect that litter production and litter decomposition are more or less in equilibrium with each other in the type forest represented by the LUSTRA sites (cf. Ågren et al. 2007). The rates of litter production at this stand age are also representative for the entire rotation period; using the combination of yield and allometric functions as done by Ågren and Hyvönen (2003) and Ågren et al. (2007) the needle plus branch litter production at e.g., Knottåsen is estimated to 53 g C m^{-2} year^{-1} at age 40 years and 90 g C m^{-2} year^{-1} as an average for the entire rotation period. However, of the litter production 26 g C m^{-2} year^{-1} comes from residues produced at harvests and do not appear in the litter measurements made at the LUSTRA sites. The measured 68 g C m^{-2} year^{-1} (Table 7) is therefore consistent with model estimates. Turnover times of C can be estimated from litter production (above-ground plus below-ground O horizon, Table 7) and soil C pools (Table 4) giving for the O horizon at Asa (16 year), Knottåsen (8 year), and Flakaliden (11 year), respectively. The longer turnover time in the south (Asa) than in the north (Knottåsen and Flakaliden) is opposite the one expected from the climatic gradient, see e.g., Ågren et al. (2007). Since litter inputs are approximately equal at the three sites, the differences in soil C pools are the major cause of the variability in turnover times. In contrast, Simmons et al. (1996) investigated forest floor C pools in a climatic gradient (mean annual temperature range 2.0°C to 6.2°C) in Maine, USA and found, as expected, that C pools were larger at the coolest sites, despite no significant differences in measured litter inputs. One possible explanation for the different results out study and that of Simmons et al. (1996) could be that they only measured tree litterfall, ignoring the contribution from roots and forest floor vegetation. Another is that in our transect, a warmer climate coincides with increased N status, as is evident from N deposition (Table 1) and CN ratio of the soil organic matter (Table 4), whereas the opposite was true in the study by Simmons et al. (1996). There is a substantial body of evidence showing that decomposition of recalcitrant soil organic matter proceeds at a slower rate in N-rich environments (e.g., Berg 2000; Neff et al. 2002; Waldrop et al. 2004). The most likely mechanism by which N deposition leads to a suppression of organic matter decomposition is through the action on phenol oxidase activity. Elevated concentrations of inorganic N has been shown to suppress the activity of lignin-degrading phenol oxidase released by microorganism (Carriero et al. 2000; Waldrop et al. 2004). Thus, the effect of N availability in the Swedish gradient seems to overshadow the effect of temperature.

Fluxes of DOC and root litter into mineral soil and their implications

The major fraction of SOC in boreal forests is found in mineral soil layers, e.g., 77–88% at the LUSTRA sites (Table 4). Carbon enters mineral soil layers either as root litter or as DOC leached from the O horizon. The LUSTRA dataset is unique, because both these fluxes were quantified at all three sites. Fluxes of DOC from the O horizon ranged between 9.3 g C m^{-2} year^{-1} and 28 g C m^{-2} year^{-1}, with the highest flux at Asa (Table 9). Our values were in the central to lower range of those reported by Michalzik et al. (2001), who compiled data from 42 ecosystem studies performed mainly in Europe and USA. At the LUSTRA sites, on average 12% (6–19%) of the total litter input to the O horizon was lost as DOC

Table 9 Annual fluxes of DOC and root litter in soils at the LUSTRA field sites

	Asa (g C m^{-2} year^{-1})	Knottåsen (g C m^{-2} year^{-1})	Flakaliden (g C m^{-2} year^{-1})
DOC			
Below O horizon	28 ± 4.8	9.3 ± 1.0	14 ± 2.0
Below B horizon	1.8 ± 0.5	0.2 ± 0.0	0.6 ± 0.2
Net retention in B horizon	26 ± 4.2	9.1 ± 1.0	13 ± 1.9
Roots			
Litter input (mineral soil 0—50 cm)	74	73	78[a]
Total input to mineral soil	100	82	91
%DOC of total	26	11	14

The DOC fluxes are mean values for 2001, 2003 and 2004 ±standard error of the mean (inter-annual variation; $n = 3$). Root litter data are from Table 7

[a] Flakaliden: mineral soil 0-30 cm

(Tables 7 and 9). Furthermore, almost all DOC (95%) leached from the O horizon was captured in the top 50 cm of the mineral soil (Table 9). This sorption was high compared to soils in many other temperate forests (Michalzik et al. 2001). Soils at the LUSTRA sites are poorly aggregated, resulting in a low degree of preferential flow paths and thus good contact between soil particle surfaces and the percolating solution. Furthermore, the B horizons of Swedish Podzols are generally rich in inorganic iron (goethite and ferrihydrite) and aluminium (imogolite-type minerals) precipitates (Karltun et al. 2000), which have reactive surfaces. The total amount of carbon sorbed in the B horizon was between 9 g m^{-2} $year^{-1}$ and 26 g m^{-2} $year^{-1}$, which corresponds to 0.2–0.4% of the carbon stocks in the mineral soil down to 50 cm depth for dry and mesic plots (Table 4).

Compared to the input of root litter, the flux of DOC to the mineral soil was small, ranging between 11 and 26% of the total C input (Table 9). However, in order to assess the role of DOC and root litter in SOC build-up in mineral soil layers, both the fluxes and the quality of the two substrates must be considered. As shown by Kalbitz et al. (2003), dissolved organic matter leached from podsol O horizons consists to a large fraction of recalcitrant, humified organic matter. Root litter, on the other hand, needs to be decomposed before entering the pool of humified organic matter. One way to obtain an estimate of the relative contribution of DOC and root litter in SOC build-up in mineral soil layers is to use the assumptions made in CoupModel regarding DOC and root litter dynamics, namely: (i) DOC captured in the mineral soil becomes part of the humus pool; (ii) a humification factor of 0.2, as for needle litter (Berg 2000), can be applied to root litter decomposition, i.e., 20% of the root litter entering the mineral soil becomes part of the humus pool; and (iii) when becoming part of the humus pool, DOC and root litter decompose at the same rate. Taking this approach, we arrived at DOC values of 64%, 38% and 45% for Asa, Knottåsen and Flakaliden, respectively, using the data in Table 9, i.e., DOC and root litter seem to be of approximately equal importance for the build-up of organic C in the upper 50 cm of the mineral soil at the LUSTRA sites. There are only a few attempts reported in the literature where the relative contribution of DOC and root litter to the pool of organic C in the mineral soil has been examined. Michalzik et al. (2003) modelled the dynamics of DOC in two Norway spruce ecosystems in Germany and Norway and found that DOC accounted for 73–89% of the C build-up in the mineral soil. Neff and Asner (2001) arrived at a considerably lower value, 25%, in their modelling exercise. This great discrepancy between estimates indicates that this question warrants more research, particularly regarding the decomposition rates and pathways of root litter.

Modelling of C fluxes using CoupModel

In the simulations, CoupModel reconstructed the present ecosystems, represented by trees and field layer vegetation, using information on current soil C and N pools and site-specific soil texture and climatic driving variables. As shown in Fig. 3, the simulated C pools in tree and field layer vegetation in 2004 agreed rather well with the measured data, with the difference between Asa and the two northern sites being reproduced. The model predicted the highest field layer biomass during the initial phase of stand development at Asa, whereas the field layer biomass was more stable at the two northern sites throughout stand development. Simulations showed that field layer biomass in the 40-year-old stands was inversely related to tree leaf area index, which was about 6 at Asa and 3 at the two northern sites.

An integrated picture of all modelled and measured fluxes of C in the three ecosystems is presented in Fig. 4. Despite good agreement between measured and modelled tree biomass, the model underestimated tree growth during the measurement period (2001/2002–2004) at all three sites, in that the modelled values ranged between 44 and 70% of the measured. This was a direct consequence of the calibration approach used in the regional study (Svensson et al. 2007) where primarily the level of steady state tree biomass in closed forest ecosystems was used as a means to put focus on the main regulating factors for tree growth (climate and N). Thus, the regional model did not describe the dynamics of tree growth in young stands accurately, which could be seen on the local scale at the LUSTRA sites. Still, as the simulated standing biomass was in good agreement, the above ground tree litter production was described reasonably well (±25%) by the model at all three sites.

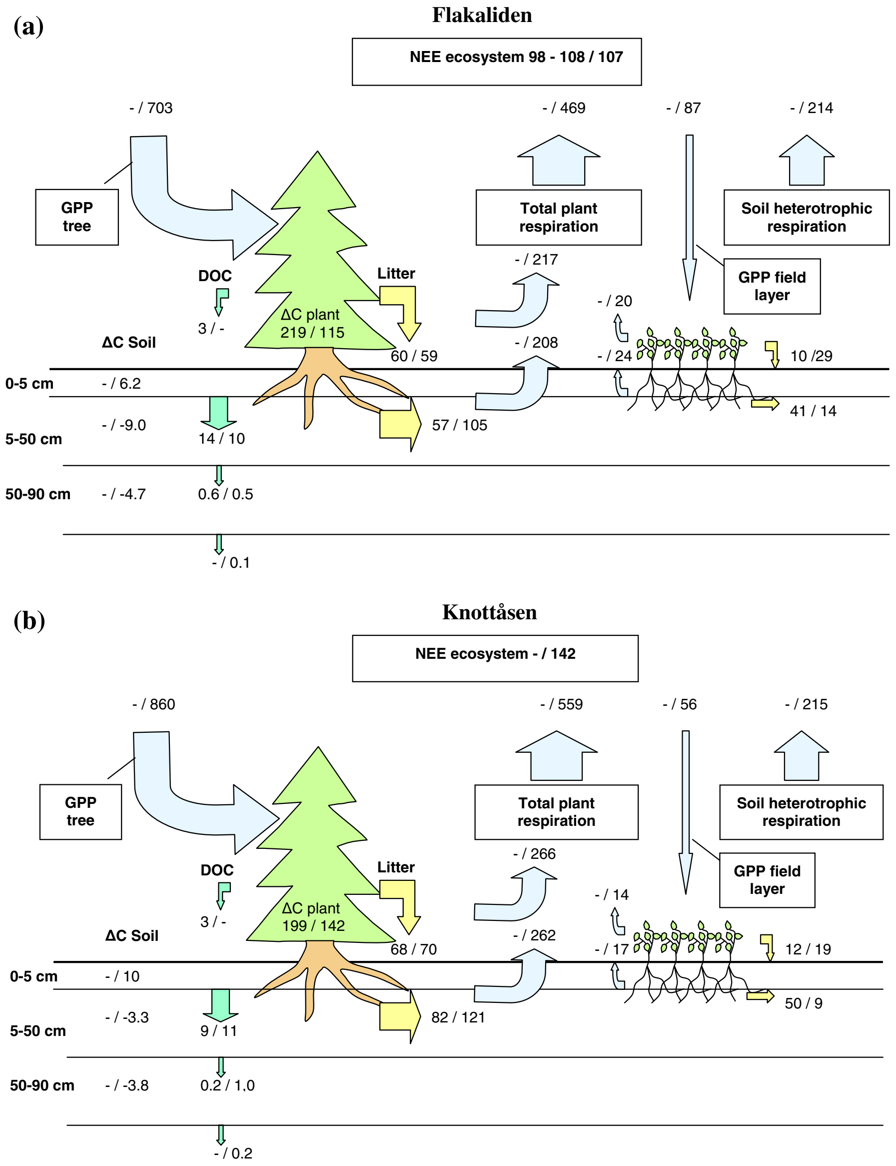

Fig. 4 Average C fluxes and rate of storage change (g C m^{-2} year^{-1}) for the dry and mesic plots (n = 6) at the LUSTRA field sites (**a**) Flakaliden, (**b**) Knottåsen, and (**c**) Asa. The fluxes shown are based on measurements made during all or part of the period 2001–2004 or simulated using CoupModel (measured/simulated). Data on net ecosystem exchange (NEE) at Flakaliden are taken from Lindroth et al. (2007). Bottom layer vegetation is not considered in the figure

The simulated below ground litter production from tree fine roots was overestimated according to the measurements (Fig. 4), from +50% in Knottåsen to 230% in Asa. One apparent reason for this is that only measured fine roots (<1 mm) are included in Fig. 4. However, as discussed above, also methodological difficulties regarding determination of root turnover exist, making field estimates of root litter production uncertain. It is therefore of interest to compare the allocation pattern of photosynthetic assimilates to roots obtained in the simulations with the CoupModel with recent field estimates for a boreal Scots pine forest in Sweden (Högberg et al. 2002). The CoupModel generates roots by allocating a pre-specified fraction of assimilates to root growth, of which the major part is being transformed to root litter, and root

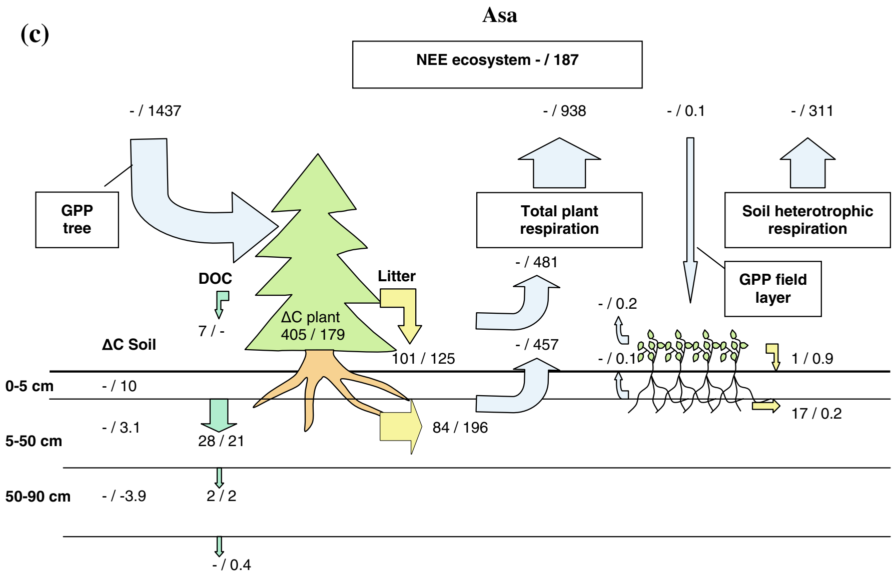

Fig. 4 continued

respiration. In the simulations we allocated 40% of GPP to roots, corresponding to of 52–54% of the net photosynthetic production at the three sites (Fig. 4). The latter values correspond reasonably well with the value of 65% reported by Högberg et al. (2002). The simulated respiratory losses from the roots varied between 66 and 70%, compared to 75% reported by Högberg et al. (2002). Thus, in our simulations the fraction of assimilated C allocated to roots, and of that fraction, the fraction allocated to roots growth agrees with general principles for allocation. This suggests that tree root litter production rates are underestimated in Table 7, which, at least partly, can be explained by only fine root litter (<1 mm) being included.

Regarding litter production by field layer vegetation, the model captured the general national trend, with a significant contribution to total litter production in the north and a minor contribution in the south. However, the large input of root litter from field layer vegetation, as indicated by the measurements, was not reflected in the simulations, whereas the above ground litter production was overestimated. Apparently, by using a common radiation use efficiency for both trees and field layer vegetation, and reasonable leaf area indexes for field layer, it was not possible to explain the high field estimated root litter inputs. In order to describe the measured litter fluxes of the field layer vegetation a more efficient photosynthesis would have been necessary, together with a largely enhanced allocation to the fine roots. Since only the <1 mm fraction was considered, it is reasonable to assume that the root litter estimates of the field layer vegetation represent underestimates, rather than overestimates, in line with the discussion above for tree roots.

As discussed above, the flux of DOC from the O horizon makes a significant contribution to the C build-up in the mineral soil. The model were able to describe the measured DOC fluxes at the three sites, within 70–120% (Fig. 4), using the same set of parameter values. In the present version of CoupModel, the production of DOC in each soil layer is proportional to the SOM pool in that layer (Svensson et al. 2007), hence the major explanation for the higher DOC flux from the O horizon at Asa was the larger SOM pool at this site. In addition the difference in within year dynamics with an extended period of soil water flows in the south of Sweden during especially autumn, and occasionally winter, was a contributing factor.

At Flakaliden, the net ecosystem exchange of C (NEE) was determined during 2001 and 2002 using the eddy covariance method (Lindroth et al. 2007), and the average for that period is given in Fig. 4a. All three dry plots and one mesic plot were situated within the fetch area of the tower, and a systematic investigation of tree growth rates within the fetch area showed values in accordance with the dry and mesic LUSTRA plots (Lindroth et al. 2007). As shown in Fig. 4a, the modelled annual average value of the net ecosystem exchange (107 g C m^{-2} year^{-1}) was in accordance with the measured (98–108 g C m^{-2} year^{-1}). However, the within year dynamics in Fig. 5 showed differences between the simulated and the measured NEE, especially during the summer period where a large simulated influx of C was not seen in the measurements. The reason for this discrepancy was not resolved within this study, but it is reasonable to assume that the difference was related to a largely underestimated soil heterotrophic respiration in the simulations since tree growth was underestimated, as discussed above.

Simulated average changes in soil C pools during the period 2001–2004 were small, ranging from – -8 g C m^{-2} year^{-1} in Flakaliden to +9 g C m^{-2} year^{-1} in Asa (Fig. 4), i.e., soils seemed to be close to steady state, reflecting the regional estimates and patterns in Svensson et al. (2007) based on 100-year simulations. In contrast, budget calculations for the soil at Flakaliden, using figures on NEE and C accumulation in trees, suggested that the soil system lost a significant portion of C, i.e., 79–105 and 64–93 g C m^{-2} year^{-1} during 2001 and 2002 respectively (Lindroth et al. 2007). However, the flux measurement takes into account all sources and sinks in the ecosystem. One source of C not taken into account in the modelling was the decomposition of coarse debris and stumps remaining from the clear-cut in 1963, which probably could explain at least part of the discrepancy between the measured and modelled soil C balance.

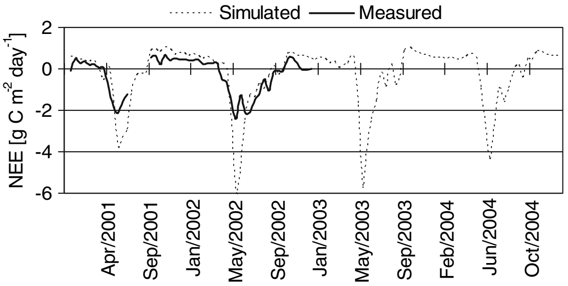

Fig. 5 Measured and modelled net ecosystem exchange (NEE) at Flakaliden (14-days averages). Note that negative values represent a net C influx to the ecosystem

Considering site history and stand age, the simulated average changes in soil C pools during the period 2001–2004 seem to be realistic. At all sites there had been spruce-dominated forests for >150 years, at the two remote northern sites probably much longer (Berggren et al. 2004). Previous studies have shown that disturbances caused by harvesting and site preparation may cause initial losses of soil C, usually followed by a slow increase as the new stand develops. The stands at the LUSTRA sites were all about 40 years during the measurement period (Table 1). In a recent study, Peltoniemi et al. (2004) investigated soil C pools in 64 Norway spruce and Scots pine stands of different ages in southern Finland and found that there was a slight increase in organic C pools in the O horizon with increasing stand age, on average 5 g C m^{-2} year^{-1}, with no detectable change in the mineral soil. Thus, the simulated changes in the O horizon (0–5 cm) of 6–10 g C m^{-2} year^{-1} at the LUSTRA sites seem to be realistic in this respect (Fig. 4).

Conclusions

The Norway spruce forest ecosystems at the three LUSTRA sites appeared to be representative of their respective region in terms of soil C pools, tree growth rates and composition and density of forest floor vegetation.

The major fraction of SOC was found in mineral soil layers (77–88%). The major flux (74–89%) of C into the mineral soil (0–50 cm) was as root litter, the rest being DOC leached from the O horizon. However, due to the recalcitrant nature of DOC, we estimated that its relative contribution to SOC build-up was considerably higher, ranging between 38 and 64%, emphasizing the need to consider both these fluxes when modelling the C dynamics in boreal forest soils (podsolic soils).

Our measurements illustrate the important role of forest floor vegetation, in particular field layer vegetation, in C cycling in northern boreal forest ecosystems. At the two northern sites the field layer vegetation constituted about 30% of the total litter input, whereas this figure at the southernmost site was 8%.

We found no support for the idea that the higher C stock at the southern site was caused by a much higher input rate of litter. Instead, we propose that a higher N deposition and N availability in the south result in a slower turnover of soil organic matter than in the north. This effect seems to overshadow the effect of temperature.

CoupModel predicted changes in SOC pools to be small during the measurement period, ranging from -8 g C m^{-2} year^{-1} at the northernmost site to +9 g C m^{-2} year^{-1} at the southernmost. In contrast, measurements of NEE and tree growth at the northernmost site suggest that the soil lost significant amounts of C during the period 2001–2002, about 90 g C m^{-2} year^{-1} (Lindroth et al. 2007). At least part of the discrepancy between measured and modelled soil C balance at the northernmost site could probably be explained by the CO_2 release from decomposition of coarse debris and stumps remaining from the clear-cut in 1963, not being accounted for in the simulations.

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