Biogeochemistry (2008) 89:95–119
DOI 10.1007/s10533-007-9134-y

ORIGINAL PAPER

Modelling soil C sequestration in spruce forest ecosystems along a Swedish transect based on current conditions

Magnus Svensson · Per-Erik Jansson · Dan Berggren Kleja

Received: 3 September 2006 / Accepted: 13 May 2007 / Published online: 31 July 2007

Abstract The change of current pools of soil C in Norway spruce ecosystems in Sweden were studied using a process-based model (CoupModel). Simulations were conducted for four sites representing different regions covering most of the forested area in Sweden and representing annual mean temperatures from 0.7°C to 7.1°C. The development of both tree layer and field layer (understory) was simulated during a 100-year period using data on standing stock volumes from the Swedish Forest Inventory to calibrate tree growth using different assumptions regarding N supply to the plants. The model successfully described the general patterns of forest stand dynamics along the Swedish climatic transect, with decreasing tree growth rates and increasing field layer biomass from south to north. However, the current tree growth pattern for the northern parts of Sweden could not be explained without organic N uptake and/or enhanced mineralisation rates compared to the southern parts. Depending on the assumption made regarding N supply to the tree, different soil C sequestration rates were obtained. The approach to supply trees with both mineralised N and organic N, keeping the soil C:N ratio constant during the simulation period was found to be the most realistic alternative. With this approach the soils in the northern region of Sweden lost 5 g C m^{-2} $year^{-1}$, the soils in the central region lost 2 g C m^{-2} $year^{-1}$, and the soils in the two southern regions sequestered 9 and 23 g C m^{-2} $year^{-1}$, respectively. In addition to climatic effects, the feedback between C and N turnover plays an important role that needs to be more clearly understood to improve estimates of C sequestration in boreal forest ecosystems.

Keywords Boreal · Carbon · CoupModel · Climate · Nitrogen · Organic nitrogen uptake

Introduction

Forest ecosystems have attracted increased attention in efforts to describe the global carbon (C) budget. Forests of the northern hemisphere in particular play an important role, as these soils contain around 40% of the total amount of C in world forest biomes (Dixon et al. 1994), and as a significant increase in air temperature is expected here (IPCC 2001). The increased temperature could affect the C balance and, given the large pools, even a slight change could have large consequences on

---

M. Svensson (✉) · P.-E. Jansson · D. Berggren Kleja
Department of Land and Water Resources Engineering, Royal Institute of Technology (KTH), Brinellvägen 28, 100 44 Stockholm, Sweden
e-mail: svensson@kth.se

D. Berggren Kleja
Department of Soil Sciences, Swedish University of Agricultural Sciences, Box 7014, 75007 Uppsala, Sweden

atmospheric CO_2 levels (Wang and Polglase 1995; Mahli et al. 1999; Ciais et al. 2005), hence the importance of studying the soil C dynamics of these forest ecosystems.

The major processes for the soil C balance are accumulation through litter production from plants and losses through soil respiration from decomposition of soil organic matter. The net change in C content in forest soils is a fine balance between these two large fluxes and a small change in either of the fluxes can obviously have a significant effect on the soil C balance. Both fluxes are correlated with climate (Raich and Schlesinger 1992; Bergh et al. 1998) but the extent of this correlation is under debate. Some findings indicate that soil respiration is more sensitive to climate variability than net primary production and thus the input of litter to the soil (Kirchbaum 2000; Valentini et al. 2000), others that the difference is less (Liski et al. 1999; Giardina and Ryan 2000). Nitrogen (N) availability, which affects net primary production (Tamm 1991; Iivonen et al. 2006; Newman et al. 2006), is affected by decomposition rates (Melillo et al. 1993) and is thus another important regulating factor to consider. Nitrogen has been shown to be the major regulating factor for tree growth in Sweden (Tamm et al. 1999) and in a recent study by de Vries et al. (2006), the importance of N deposition for soil C sequestration in European forests was demonstrated. In a similar way to climate, N affects the inflow of C to the soil. Since the present ecosystems are normally far from N saturation, increased amounts of N lead to increased tree growth and hence increased litter production. However, unlike climate, where increased temperature may lead to increased output of C from the soil through increased decomposition, several studies have shown that increased N can hamper decomposition and the related outflow of C from the soil (Berg 2000; Fleischer 2003; Zak et al. 2006). Carbon stocks in Swedish forest soils decrease from south to north (Callesen et al. 2003; Berggren Kleja et al. 2007; Olsson et al. 2007), which is somewhat contradictory to the situation in other countries, where the largest pools of soil C are found at higher latitudes (cf. Kane et al. 2005). The reason for this difference is unclear, but larger soil C pools in southern Sweden might partly be explained by higher N deposition (Olsson et al. 2007).

To interpret current soil C pools in forest ecosystems and future trends, it is important to understand these major regulating processes—both in terms of contribution to the net C soil changes and possible interactions between the processes. Studies of plant-soil interactions in such a complex system as a forest ecosystem often rely on the use of various process-orientated models and thus it is essential that the models describe the difference between above- and below-ground climate. This was clearly indicated in some recent studies by Euskirchen et al. (2006) and Monson et al. (2006), which showed the interactions between changes in growing season length, soil thermal dynamics and C dynamics. To enable the influence of the current climate on both C assimilation and C release to be simulated, an approach including feedback between abiotic processes and the turnover of C and N in the entire soil-plant system is needed. Without this aspect, the use of the model would be restricted to systems where the physical characteristics are known or independent of the N and C processes.

The approach reported here is based on a coupled ecosystem model for heat and mass transport in the soil-plant-atmosphere system (CoupModel). The model simulates the response to climate of above-ground biomass, litter formation and decomposition of organic matter. Simulations were conducted for four sites representing four different regions in Sweden, covering annual average temperatures from 0.7°C to 7.1°C, and were run for a 100-year period. The simulated systems were thus allowed to develop from young newly established forests to mature closed forests and to demonstrate the long-term link between the N uptake and N storage in the soil. Both tree- and field (understory) layers were considered where information on standing tree biomass in different age classes was used to calibrate the model.

The main objectives of this study were (i) to estimate trends in soil C storage in Swedish Norway spruce ecosystems based on available regional data on tree growth and C pools; (ii) to identify key factors determining long-term ecosystem C dynamics; and (iii) to present a newly developed version of CoupModel including new assumptions for forest ecosystem applications in the boreal region.

Materials and methods

Site description and measurements/data

Climate

Simulations were run for four different regions in Sweden with climatic data taken from four representative sites, Lycksele in the north, Mora and Nässjö in central Sweden and Ljungbyhed in the south (Fig. 1). For these sites meteorological data, with daily mean values from 1961 to 1986, were available from the Swedish Meteorological and Hydrological Institute (SMHI) (Table 1). The datasets were of high quality and completeness with respect to all driving variables (air temperature, air humidity, wind speed, cloudiness and precipitation). The 25-year climatic data set was duplicated to cover a 100-year period. Nitrogen deposition was based on official data from the Swedish Environmental Research Institute (IVL 2006). The deposition data for each site were taken from a regionally representative measuring point or if several points were available, a mean value was calculated (Table 1). The N deposition values for each region were assumed to remain constant during the whole simulation.

Table 1 General description of climate variables and N deposition

	Lycksele	Mora	Nässjö	Ljungbyhed
Location	64°59′ N 18°66′ E	61°00′ N 14°59′ E	57°64′ N 14°69′ E	56°08′ N 13°23′ E
Altitude (m a.s.l.)	223	161	305	76
Mean annual air temperature (°C)	0.7	3.3	5.2	7.1
Mean annual precipitation (mm)	613	630	712	838
Annual N deposition[a] (kg/ha)	1.5^{b}	3.5^{c}	7.5^{d}	12.5^{e}

[a] Open field deposition of both NH_4 and NO_3

[b] IVL site: AC02A

[c] IVL sites: S23A; W90, 92A; Z04A; X05A

[d] IVL site: F12A

[e] IVL sites: M10A; L07A; L1 (IVL 2006)

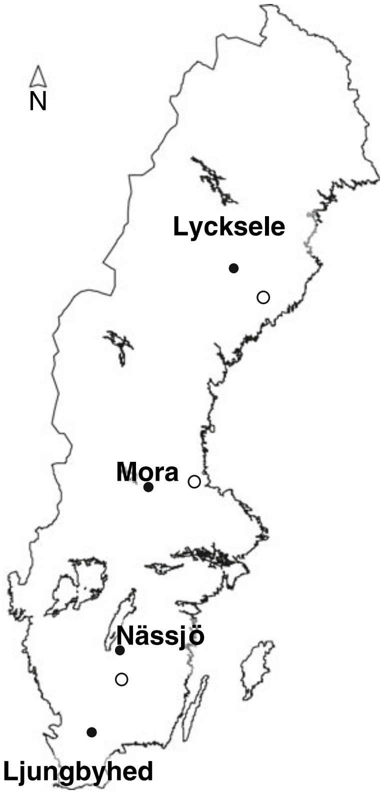


Fig. 1 Swedish gradient. Filled circles = representative sites for each simulated region; open circles = corresponding LUSTRA common field sites (Flakaliden, Knottåsen and Asa)

Plant

Measured tree biomass values for the regions were based on standing stock volume data (Table 2) taken from the Swedish Forest Inventory (NFI) (Skogsdata 2003). The mean values of standing stocks for age classes 81–101 years and 101–121 years were assumed to be representative for a forest stand at the age of 100 years. The standing stock volumes were recalculated to dry weight biomass using expansion factors presented in the Swedish National Inventory Report (SNV 2005), which in turn were developed from the functions proposed by Näslund (1947) and Marklund (1988) (Table 3). These singletree regression functions for Scots pine, Norway spruce and birch are assumed to be representative for Swedish conditions. Fine root biomass is not included in these functions, but was approximated to 2% of the standing stock biomass, which is

Table 2 Standing stock volumes (m^3 ha^{-1}), distribution of pine/spruce/broadleaved trees/dead trees (%) for different age classes and different regions (Skogsdata 2003)

Region	Age class (year) Age (year)	3–11 7	11–21 16	21–31 26	31–41 36	41–61 51	61–81 71	81–101 91	101–121 111
Västerbotten	Volume	8	13	28	59	102	139	137	153
	Tree distribution[a,b]	45/37/16/2							
	Tot. biomass[c]	296	482	1037	2185	3778	5149	5075	5667
Dala upr	Volume	11	20	57	103	172	195	215	212
	Tree distribution[a,b]	49/40/9/2							
	Tot. biomass[c]	403	732	2087	3770	6296	7138	7870	7761
Jkpg	Volume	19	30	96	158	213	269	272	281
	Tree distribution[a,b]	31/54/13/1							
	Tot. biomass[c]	718	1133	3626	5967	8045	10160	10273	10613
Skåne	Volume	17	55	131	218	236	282	286	296
	Tree distribution[a,b]	12/46/41/1							
	Tot. biomass[c]	672	2174	5178	8616	9328	11146	11304	11699

Total biomass (g C m−2) calculated with expansion factors according to Table 3

[a] Pine/spruce/broadleaved/dead trees

[b] Same tree distribution for all age classes

[c] Includes stem, branch, stump and fine roots

Table 3 Expansion factors for recalculation of standing stock volumes (m^3 ha^{-1}) to dry weight (kg dw m^{-2}) from SNV (2005)

	Dry weight biomass[a]
Scots pine	660
Norway spruce	770
Broadleaved trees	815
Dead trees	736

[a] Includes stem, branch and stump

in accordance with measurements (Helmisaari et al. 2002; Berggren Kleja et al. 2007). In the recalculations to dry weight biomass, the regional distribution of different tree species (Skogsdata 2003) was considered. The total dry weight for each age class was calculated as the sum of the contribution from the different fractions of pine/spruce/broadleaved trees/dead trees, according to the distribution in Table 3 and the expansion factors for each fraction in Table 2. The same distribution was considered for all age classes, as this was the only available information. C content was assumed to be equal to 0.5 of the dry weight biomass.

Model description

The CoupModel (Coupled Model), originating from the SOIL and SOILN-models (Jansson and Halldin 1979; Johnsson et al. 1987; Eckersten and Jansson 1991), is a coupled ecosystem model based on a balance between abiotic and biotic processes in the soil-plant-atmosphere system. The most relevant parts of the model are described below, with a list of equations in Appendix 1. A detailed description is given by Jansson and Karlberg (2004) and a review of the software has been presented by Jansson and Moon (2001). In Eckersten et al. (1995) the growth model routine in SOILN was presented for forest ecosystems in simulations of flows of water, heat, carbon and nitrogen in a spruce stand in Germany. Reasonable estimates were simulated for water and heat, but given too few detailed measurements the carbon and nitrogen model could not be fully evaluated especially regarding plant N uptake and N leaching. A review of the SOIL and SOILN models and how they have been used to simulate water, heat and N conditions for arable land and forest in the Nordic countries was made by Jansson et al. (1999a). Eckersten and Beier (1998) presented a simulation on N dynamics in spruce stands from Denmark and SW Sweden, implementing organic N uptake. In a study by Gärdenäs et al. (2003) long-term effects on N balances of coniferous forest stands in Sweden due to N fertilisation and N deposition using the SOIL and SOILN models were simulated. In order to simulate observed tree growth, the simulations pointed towards the importance of considering plant organic N uptake. In a recent study by Karlberg et al. (2006), estimates of carbon fluxes and turnover times for five different terrestrial ecosystems using the CoupModel were showed.

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. C and N balances and the dynamics of plant development are simulated, as are the interactions between plants and physical driving forces, e.g., how the plant cover influences both aerodynamic conditions in the atmosphere and the radiation balance at the soil surface. The only dynamic input data necessary are precipitation, air temperature, wind speed, air humidity and radiation. As two (or more) plant layers are simulated, the equations (Appendix 1) are calculated for each plant layer. Competition is enabled between different plant layers with respect to the interception of light, uptake of water and N. In the current study, two plant layers were simulated, where the field layer represented an understory layer of dwarf shrubs.

Plant growth

In the present application (see Appendix 1 for equations and Table 4 for a list of parameter values), input of C to the system was simulated by an empirical function (Eq. 1) based on the light use efficiency (Monteith 1977), where rate of photosynthesis is assumed to be proportional to the global radiation absorbed by the canopy but limited by unfavourable temperature and water conditions and N availability—expressed as response functions ranging between zero and unity (Eqs. 2–4). Assimilated C was allocated according to pre-specified fractions to the different components of the vegetation (leaf, stem, coarse root and fine roots) (Eq. 5). Both growth respiration and maintenance respiration were accounted for (Eq. 6), with a Q10 temperature response function for the maintenance respiration (Eq. 7). Litterfall from leaf, stem, coarse roots and fine roots was calculated as fractions of standing biomass (Eq. 8). Leaf and stem litter was added to the uppermost litter compartment of the soil, whereas root litter was added to all soil litter compartments in proportion to the distribution of roots.

The plant N uptake (Eq. 9) was driven by the C assimilation rate and minimum C:N ratios for the different components of the plant, as proposed by Ingestad and Agren (1988), i.e., a calculated plant N demand. Soil N available for plant uptake was allocated to tree and field layers in relation to their respective N demands. A specified fraction of the mineral N in the soil was assumed to be easily available for plant uptake per day (Eq. 10). Mineral N was taken up from the nitrate and ammonium pools in proportion to the relative sizes of the pools. In the event of N deficiency, i.e., when estimated uptake was less than the estimated demand, a supplementary mechanism was assumed by allowing N to be extracted in organic form (Eckersten and Beier 1998). The organic uptake was assumed to be proportional to the actual storage of N in humus (Eq. 11) (B. Lindahl, unpubl. data). Both mineral N and organic N uptake were functions of root distribution in the soil profile. Consequently the N uptake rate was dependent on both the mineral N content of the soil and the amount of organic N storage in the soil. Allocation of N to plant parts followed in principle C allocation, but was implemented with the highest priority for the roots, followed by the stem and finally the leaves (Eq. 12). Litterfall was calculated as first order rate processes from all plant components with an enhanced leaf litter fall rate assumed at high LAI values. The amount of N in litterfall was calculated analogously to C in litterfall (Eq. 13). Simultaneously with litterfall simulation, specified fractions of both C and N were retained in the plant in a mobile pool (Eqs. 14–15) that was used in the spring to start the development of new leaves (Eqs. 16–17).

Soil

To account for differences in substrate, the soil organic material was represented by two pools: *Litter* with a high turnover rate and *Humus* with a low turnover rate. The decomposition rates of the litter and humus pools were calculated as first order rate processes (Eq. 18). The products of litter decomposition were CO_2

Table 4 List of parameter values

Property	Value[a]	Unit	Comment
Plant biotic processes			
Radiation use efficiency[b]: ε_L	8	g Dw MJ^{-1}	Charles-Edwards et al. 1986
Leaf temp. response photosynthesis:			
p_{mn}	−4	°C	Larcher (2003)
p_{o1}	10	°C	Larcher (2003)
p_{o2}	25	°C	Larcher (2003)
p_{mx}	40	°C	Larcher (2003)
Leaf C:N ratio response: $p_{CN,Opt}$	25	–	Wikström and Ericsson (1995)
$p_{CN,Th}$	75/100	–	Wikström and Ericsson (1995)/Assumed
C allocation: f_{root}	0.4	–	Assumed
f_{leaf}	0.2/0.4	–	Assumed
f_{cr}	0.2	–	Assumed
Plant growth and maintenance resp:			
k_{gresp}	0.21	day^{-1}	Linder & Troeng (1981)
$k_{mrespleaf}$	$1.5 \cdot 10^{-3}$	day^{-1}	Adjusted to LAI in Lycksele
$k_{mrespstem}$	$1.5 \cdot 10^{-4}$	day^{-1}	Linder and Troeng (1981); Bossel (1996)
$k_{mresproot}$	$5.0 \cdot 10^{-3}$	day^{-1}	Linder and Troeng (1981); Bossel (1996)
$k_{mrespcroot}$	$1.5 \cdot 10^{-4}$	day^{-1}	Assumed similar as stem
Air temp response for respiration:			
t_{Q10}	2	–	Penning de Vries and van Laar (1982)
t_{Q10bas}	25	°C	Penning de Vries & van Laar (1982)
Litter rate: (leaf) l_{Lc}	$4 \cdot 10^{-4}/0.055$	day^{-1}	Based on assumed lifetime
(stem) l_{Sc}	$2.74 \cdot 10^{-5}/$ $2.74 \cdot 10^{-4}$	day^{-1}	Based on assumed lifetime
(croot) l_{CRc}	$2.74 \cdot 10^{-5}/$ $2.74 \cdot 10^{-4}$	day^{-1}	Based on assumed lifetime
(root) l_{Rc}	$2.74 \cdot 10^{-3}$	day^{-1}	Majdi and Andersson (2005)
Leaf litter rate enhanced coeff.: k_{LAI}	0.08	–	Based on assumed max LAI
Plant N: $cn_{MinRoot}$	40	–	Persson and Nilsson (2001)
$cn_{MinCRoot}$	400/80	–	Assumed similar as stem
$cn_{MinStem}$	400/80	–	Assumed
$cn_{MinLeaf}$	22	–	Nilsson et al. (2001)
Fraction of soil mineral N available for plant uptake: f_{Nupt}	0.12	–	Johnsson et al. (1987)
Plant uptake of organic nitrogen:			
O_L	0	day^{-1}	B. Lindahl pers. comm.
O_H	$2.2 \cdot 10^{-5}$– $9.0 \cdot 10^{-5}$	day^{-1}	Adjusted (Table 8)
Carbon retention at leaf litterfall: m_{retain}	0.2	–	Assumed
Reallocation of C and N at leafing: m_{shoot}	0.1	–	Assumed
Soil nitrogen and carbon processes			
Decomposition rate litter: k_l	0.0136	day^{-1}	Developed from Berg et al. (1991)
Decomposition rate humus: k_h	$1.1 \cdot 10^{-4}$– $7.0 \cdot 10^{-4}$	day^{-1}	Adjusted (Table 8)
Decomposition efficiency litter: $f_{e,l}$	0.5	–	Johnsson et al. (1987)
Decomposition efficiency humus: $f_{e,h}$	0.5	–	Assumed same as litter

Table 4 continued

Property	Value[a]	Unit	Comment
Humification fraction litter: $f_{h,l}$	0.2	–	Johnsson et al. (1987)
C:N ratio microbes: cn_m	20	–	Assumed
DO rate coefficient litter: d_{DOL}	$5 \cdot 10^{-4}$	day^{-1}	Based on data from Berggren Kleja et al. (2007)
DO rate coefficient humus: d_{DOH}	$1 \cdot 10^{-4}$	day^{-1}	Based on data from Berggren Kleja et al. (2007)
Fixation rate of DOC: d_{DOD}	0.5	day^{-1}	Based on data from Berggren Kleja et al. (2007)
Temperature max value Ratkowsky function: t_{max}	25	°C	Seyferth (1998)
Temperature min value Ratkowsky function: t_{min}	−8	°C	Seyferth (1998)
Saturation activity: $p_{\theta satact}$	0.6	–	Johnsson et al. (1987)
Optimum soil moisture content lower value coefficient: $p_{\theta Low}$	13	vol %	Johnsson et al. (1987)
Optimum soil moisture content upper value coefficient: $p_{\theta Upp}$	8	vol %	Johnsson et al. (1987)
Plant abiotic processes			
Specific leaf mass: $p_{l,sp}$	100/35	$g\ C\ m^{-2}$	Bossel (1996)/ Foster and Brooks (2005)
Extinction coefficient: k_{rn}	0.5	–	Model default
Surface canopy cover: p_{cmax}	1	$m^2\ m^{-2}$	Assumed
p_{ck}	0.5/10	–	Assumed
Plant albedo: a_{pl}	10/20	%	Assumed
Stomatal conductance: g_{ris}	11.23	$MJ\ m^{-2}\ day^{-1}$	Jansson et al. (1999b)
g_{max}	0.01	$m\ s^{-1}$	Based on Alavi and Jansson (1995)
g_{vpd}	359	Pa	Jansson et al. (1999b)
Root flexibility degree for water uptake: f_{umov}	0.6	–	Model default
Max plant height: p_{hmax}	30/0.3	m	Assumed
Max root depth: p_{zroot}	−0.7/−0.2	m	Assumed
Max leaf lifetime: l_{life}	7/2	year	Assumed

[a] When two values are given, the first corresponds to the tree layer and the second to the field layer

[b] The CoupModel uses absorbed incident solar radiation. All units of quantum efficiency have been transferred to this unit according to Sinclair and Muchow (1999) Bonhomme (2000)

(respiration), humus and conceptually, since the microbes were implicitly included in the litter pool, microbial biomass and metabolites (Eq. 19) (Fig. 2), which thus constituted internal cycling. The only flow from the humus pool was the respiratory losses (Eq. 20). The associated flux of N when C was decomposed from litter to humus was calculated from a C:N ratio representing the microbes (Eq. 21), with the mineralisation/immobilisation of N dependent on the C:N ratio in the source pool (Eq. 22).

Organic matter in the soil organic pools described above was considered to be vertically immobile, but dissolved organic matter (DOM) was generated from the immobile pools. The flux from the litter pool to the DOM pool was determined by a rate parameter and common response functions for temperature and soil moisture (Eq. 23). The flux between the DOM pool and the humus pool was calculated slightly differently, as DOM could be both released and fixed to the humus pool (Eq. 24). The organic solutes were transported vertically by convection through the vertical water flow (Eq. 25) and also as flows associated with the calculated water drainage flow out of the soil profile. The same equations used for dissolved organic C were used analogously for the corresponding N fluxes.

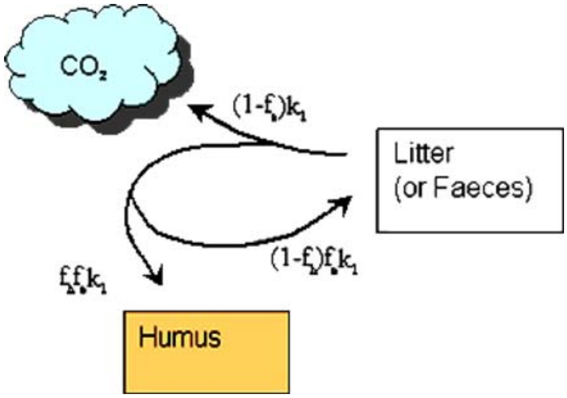


Fig. 2 The conceptual partitioning of internal turnover, losses to atmosphere and humification of C during decomposition in the CoupModel

Common response functions

Two response functions were used in multiple processes. The response function to account for soil temperature (Eq. 26) was based on a function by Ratkowsky et al. (1982). The soil moisture response function was a simple function related to three different regions of the soil moisture retention curve. Microbial activity is reduced, on either side of an optimal level, by both too low and too high water contents. The minimum water content for process activity is determined by the wilting point whereas a fixed degree of activity is specified when saturation is reached (Eq. 27).

Physical processes and feedback

The simulations of soil temperature, soil moisture conditions and the soil water flows were based on the basic Darcy and Fourier laws. The most important interaction between the C turnover and the physical conditions was governed by the leaf area index (LAI) and the ratio between actual and potential transpiration. Both in turn influenced the input of C to the system and both were strongly correlated with the temperature and the moisture. Leaf area index was estimated directly in proportion to the simulated amount of biomass of the leaf compartment (Eq. 28). The LAI in turn determined both the amount of radiation that was adsorbed for possible C assimilation (Eq. 29), the potential canopy resistance (Eqs. 30–31) and the amount of net radiation that was available for estimating the potential transpiration. To estimate the partitioning of intercepted radiation between the two plant layers, canopy surface cover was calculated (Eq. 32).

Potential transpiration was calculated from Penman's combination equation (1953) in the form given by Monteith (1965) (Eq. 33). Actual transpiration was calculated as the integrated result of possible stresses, given as response functions for soil water potential and soil temperature, at each soil depth (Eq. 34). These functions were used according to previously defined default values for the model. A compensatory uptake of water by roots in layers with no water stress and in accordance with the relative fraction of the roots in these layers was also considered (Eq. 35).

Modelling approach and parameterisation

The development of a managed Norway spruce ecosystem with both tree and field layers was simulated. The simulations were run during a 100-year period, enabling the simulated system to develop from a young newly established forest to a mature closed forest. The trends of current soil C pools were simulated based on available data of the current conditions (management, tree growth, soil C and N pools). Some selected unknown parameters were estimated by forcing values so that the simulated tree growth (closed forest) agreed with observations. A focus on the main regulating factors for tree growth (climate and N) and thus the inflow of C to the soil was hence taken. An important principle followed was to use the same parameterisation for all regions, i.e., with a minimum of site-specific data, in order to evaluate the general applicability of the model. By this approach the difficulty of how to describe e.g., management and N dynamics at a historical scale (>1000 years), was circumvented.

Patterns of field layer vegetation dynamics in managed spruce forest ecosystems are poorly described in the literature. Therefore, to simulate a reasonable development of the field layer, and dynamics in relation to the tree layer, some assumptions were made: (i) competition for radiation results in a lesser field layer in southern regions of Sweden, where the forest canopy is more closed; and (ii) the different light regimes in respective plant layers result in different allocation patterns. Otherwise, the field layer was only allowed to differ from the tree layer with respect to obvious differences in shape-related parameters (e.g., height). The field layer biomass values presented in Berggren Kleja et al. (2007) were used as guideline values in the model calibration. Minimum C:N ratios for stem ($cn_{MinStem}$) and coarse roots ($cn_{MinCRoot}$) were assumed to be similar and at a level that resulted in reasonable simulated C:N ratios. It was further assumed that the C:N ratio for these plant parts in the field layer was significantly lower than that for the corresponding plant parts in the tree layer. Maintenance respiration for stem and coarse roots was also assumed to be similar and based on literature values (Table 4). Leaf maintenance respiration was correlated with LAI so that the simulated LAI in Lycksele roughly corresponded to the LAI at the LUSTRA site Flakaliden, as measured in 2003 (M. Svensson, unpubl. data). The same parameter value was then used for all regions.

General guidelines from the Swedish Forest Agency (2005) regarding forest management were used in the simulations, i.e., one cleaning after 10 years, followed by the first thinning after 40 years and the second and last thinning after 80 years. These management practices were only applied to the tree layer. On the cleaning occasion, a relatively large proportion of the standing tree biomass (60%) was cut down and left as Litter. This approach was based on the assumption that the cleaning not only represented a removal of the managed tree species (Norway spruce) but also of other (broadleaved) trees and bushes that are commonly known to appear in managed forests during early stages after a clear-cut. On both thinning occasions, 20% of the stem biomass was assumed to be removed from the system and 5% turned into Litter. For the other parts of the tree (coarse roots, roots and leaves) nothing was removed and hence 25% was turned into Litter.

Fine root litter rates were based on a study by Majdi and Andersson (2005) and stem, coarse roots and leaf litter rates on assumed lifetimes where stem and coarse roots were assumed to be similar. The field layer was assumed to shed leaves in autumn and the tree layer all year around. The LAI Enhance parameter was chosen to give an approximate maximum LAI of 6 for the tree layer at the site in the south (Ljungbyhed). The same parameter value was then used for all regions. The different calculated canopy cover values for respective plant layers were based on the assumptions that the field layer covered the soil surface relatively quickly (i.e., at low LAI) but that canopy closure for the tree layer occurred at higher LAI.

Final values of the simulated tree biomass (i.e., at 100 years) were adjusted in order to agree with measured standing stock volumes at the respective sites using three different approaches (I–III), all with the main focus of supplying the growing trees with sufficient N. Two model parameters were varied to achieve this—the humus decomposition rate (k_h) and the rate of plant organic N uptake (O_H):

I. A fixed k_h at all sites and a variable O_H;
II. A variable k_h and no organic N uptake (O_H equal to zero) and
III. A variable k_h and variable O_H. In this approach we assumed soil C:N ratio to be in steady-state during the 100-year simulations.

Approach I, which was successfully used in a recent study by Gärdenäs et al. (2003) for simulating tree growth and N leaching for Swedish conditions, was hypothesized as the most reasonable approach of N supply. To our knowledge, no studies have used variable decomposition rate coefficients, and empirical findings supports mycorrhizae mediated organic N uptake in boreal forest ecosystems (Näsholm et al. 1998; Wallenda et al. 2000). Mycorrhizae play an important role in nutrient uptake by plants. In addition to increasing the adsorptive area of plants roots, and thus increasing nutrient uptake, the mycorrhizae hyphae also have the ability to exudate proteases which release amino acids from SOM and make them available for uptake (Smith and Read 1997). It has further been shown that the main part of tree root tips in boreal forests is associated with ectomycorrhizae (Taylor et al. 2000). Approach II was chosen as a classical model (cf Schimel and Bennet 2004), leaving out organic N uptake. Approach III was later added as a compromise between the two other approaches when the results from these simulations regarding the soil C:N ratio dynamics was analysed (see below).

In approach I, the value of k_h found in the simulations for the most southern region (Ljungbyhed) was used in the further simulations in the other regions as this value represented the lowest value along the transect. To establish the decomposition rate for Litter (k_{Litter}), a separate calibration exercise was performed. Norway spruce needle litter decomposition data (Berg et al. 1991) from three sites on a north–south transect through Sweden (Norrliden, Jädraås, and Målilla) were used in this exercise. Since no differences were found for k_{Litter}, the mean value (0.0136 day^{-1}) was used in the regional simulations (Table 5). Rate coefficients for DOC were adjusted against measurements of DOC concentrations at the three LUSTRA sites (Berggren Kleja et al. 2007).

Initial soil C stocks were based on preliminary evaluation of the Swedish National Forest Soil Inventory database, giving the following relationship between soil C stock (0–50 cm) and latitude (M. Olsson, pers. comm.):

$$y = -0.3879x + 31.372$$

where x denotes latitude and y is soil organic content (kg C m^{-2}). This equation differs slightly, but not significantly, from that given by Olsson et al. (2007). Since the dataset only included soil C pools to a depth of 50 cm, extra C had to be added for the 50–100 cm soil layers. Based on data presented in Berggren Kleja et al. (2007), we assumed that this amount constituted 10.9% of the total soil C pool (Table 6). Initial soil N was calculated based on initial soil C and C:N ratios at the LUSTRA sites (Berggren Kleja et al. 2007) and at Skånes Värsjö (M. Olsson, pers. comm.). Initial soil C and N pools were assumed to be equally partitioned between Humus (95%) and Litter (5%) at the respective site, and distributed in the soil profile so as to decrease exponentially with depth. The C:N ratio of the internally represented microbes (cn_m) in the model, conceptually viewed as a well humified material, was set to 20 corresponding to the mean value (n = 1591) of the C:N ratio in the B horizon for Swedish forest podzols (E. Karltun, pers. comm.).

An 11.3 m deep soil profile of 20 layers, with increasing thickness from 5 cm in the uppermost layer to 100 cm in the bottom layer, was simulated. The rather deep soil profile was chosen based on prior experience of simulations of soil temperature dynamics with frost conditions, in order to generate reasonable lower boundary conditions. The soil physical properties used in the simulations were based on mean values from measurements of soil texture in 37 soil profiles from different forest sites located in northern, central and southern Sweden (CoupModel database 2006). The same soil physical properties were used in all simulations and dry and mesic conditions were simulated through a drainage level of 1.5 m. Parameter values describing hydrology, radiation and snow were taken from previous simulations made in similar environments, i.e., a Norway spruce forest on sandy silty till (Alavi and Jansson 1995; Gustafsson et al. 2004).

Table 5 Summary of separate calibration of parameter k_{Litter} using datasets from Norrliden, Jädraås and Målilla from Berg et al. (1991)

Site	n*	k_{Litter} (day^{-1})	
		Average	Stdev
Norrliden	6	0.0155	0.0022
Jädraås	4	0.0114	0.0021
Målilla	5	0.0132	0.0031
All	15	**0.0136**	0.0029

Value in bold (0.0136) was used in all simulations for forest stand development over 100 years

* Number of datasets

Table 6 Initial values of soil C (Olsson et al. 2007), C:N ratio (Berggren Klejal et al. 2007) and calculated N

Site	C Soil[a] (g C m^{-2})	C Humus[b] (g C m^{-2})	C Litter[c] (g C m^{-2})	N Soil (g N m^{-2})	N Humus[b] (g N m^{-2})	N Litter[c] (g N m^{-2})	C:N ratio
Lycksele	7006	6655	350	223	212	11	31.5
Mora	8567	8139	428	295	280	15	29.1
Nässjö	9995	9495	500	367	349	18	27.2
Ljungbyhed	10666	10133	533	539	512	27	19.8

[a] 10.9% C added for 50–100 cm soil layers

[b] assumed to 95% of total pool

[c] assumed to 5% of total pool

Results

Plant dynamics and climate

For all the N supply approaches used, simulated tree biomass dynamics during 100 years generally agreed well with measured standing stocks, exemplified by approach I in Fig. 3. A noteworthy discrepancy between model and measurement was an overestimated growth in the young stand (~15–30 years) in the north (Lycksele) and for about the same period an underestimated growth in the south (Ljungbyhed). The LAI for the tree layer had equal dynamics for all sites (Fig. 4), with a levelling off at around 30 years, but with an average value of around 3 in the north and 6 in the south. Simulated field layer biomass showed different development in the north compared with the south (Fig. 4). In the south, the field layer built up a large biomass in the first years of the simulation, followed by an almost exponential decrease, leaving only a minor field layer at later stages. The field layer in the north did not show a major build up phase in the beginning, but instead had a more stable development with roughly the same biomass during the whole simulation period. The contribution from the field layer to totally adsorbed global radiation in the simulated ecosystem also varied along the north–south transect (Table 7). In the north the field layer was responsible for 17% of adsorbed radiation, whereas in the south the corresponding figure was only 5%.

Mean annual gross primary production (GPP) varied along the transect from 626 g C m^{-2} $year^{-1}$ in the north to 1275 g C m^{-2} $year^{-1}$ in the south, with the central sites Mora (892 g C m^{-2} $year^{-1}$) and Nässjö (1139 g C m^{-2} $year^{-1}$) intermediate (Table 7). Net primary productivity (NPP), defined as GPP minus respiratory losses, showed related differences with the highest value in the south (463 g C m^{-2} $year^{-1}$) and the lowest in the north (265 g C m^{-2} $year^{-1}$). The NPP:GPP ratio was 0.42 in Lycksele, 0.40 in Mora, 0.38 in Nässjö and 0.36 in Ljungbyhed (Table 7), which demonstrated larger respiratory losses in the south because of higher mean biomass pools during the long common turnover time of the simulated trees.

Total mean annual plant litter production ranged from 200 g C m^{-2} $year^{-1}$ in the north to 326 g C m^{-2} $year^{-1}$ in the south (Table 7), with somewhat more than 50% coming from root litter. The contribution from the field layer to litter production varied from 28% in the north to 14% in the south for aboveground plant litter, while the corresponding figures for root litter were 12% and 5%.

The mean annual air temperature was reflected in the growth air temperature sum (based on daily mean air temperature above 5°C) with the highest values in the south (1525°C day) and the lowest in the north (901°C day) (Table 7). A comparison of annual mean soil temperatures at a depth of 10 cm in the simulated profile revealed differences that were markedly less pronounced than the corresponding air temperature

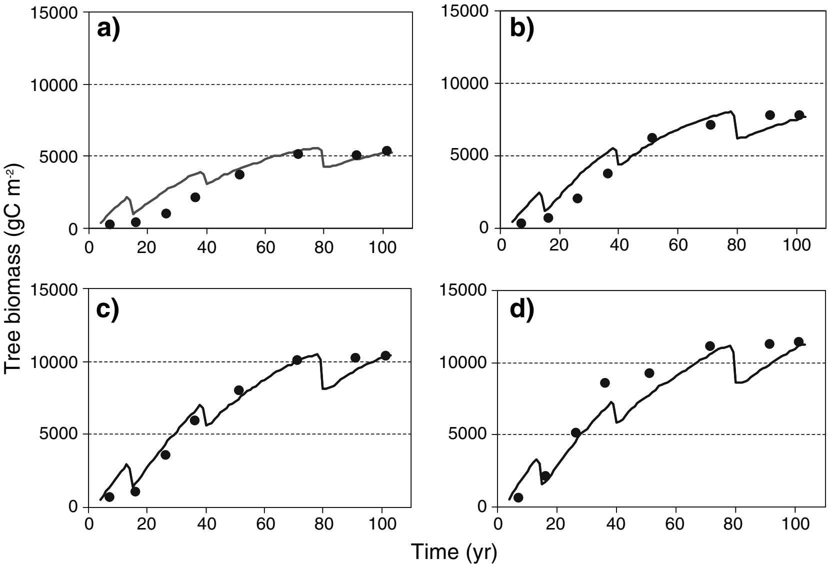
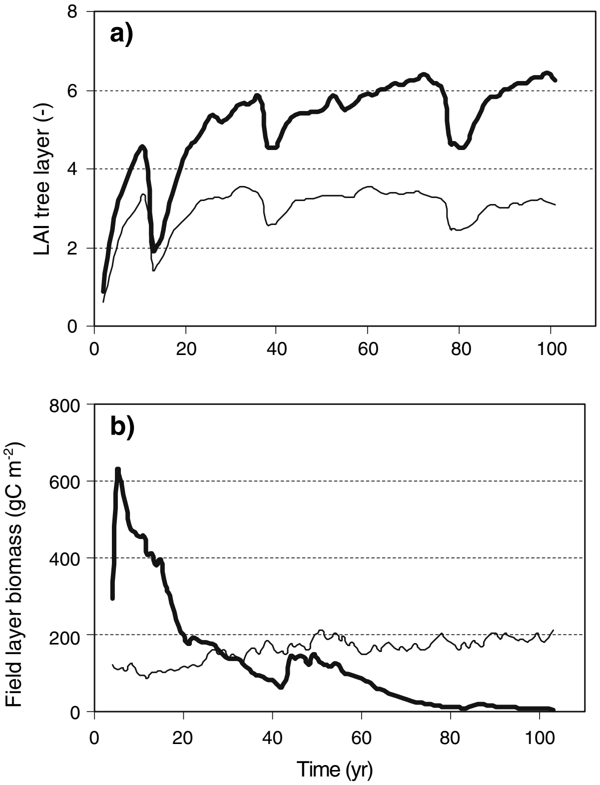


Fig. 3 Simulated tree biomass (solid line) with modelling approach I, and measured standing stock volumes (filled circles) from NFI (Skogsdata 2003): (**a**) Lycksele, (**b**) Mora, (**c**) Nässjö and (**d**) Ljungbyhed

Fig. 4 (**a**) Simulated tree layer leaf area index (LAI) and (**b**) field layer biomass (g C m^{-2}) during 100 years in Lycksele (thin line) and Ljungbyhed (thick line)



differences. The mean annual soil temperature at 10 cm depth in the simulated soil profile at the northern site was 3.0°C compared to a mean annual air temperature of 0.7°C. Corresponding figures for the southern site were 6.5°C in the soil and 7.1°C in the air. Differences in soil climate were apparent in the combined response to soil temperature and soil moisture of SOC decomposition, exemplified by the 10 cm depth in the soil profile. The mean value during the simulation period was 0.12, 0.15, 0.17 and 0.21 in Lycksele, Mora, Nässjö and Ljungbyhed, respectively (Table 7), i.e., the mean annual decomposition rate increased from 12% to 21% of the optimal conditions for the respective sites. Decomposition rates were mainly limited by temperature, the retarding effect of soil moisture being 0.84 in Lycksele, 0.88 in Mora, 0.96 in Nässjö and 0.97 in Ljungbyhed.

Soil C and N

Decomposition rate coefficients (k_h) for SOC and corresponding rates for organic N plant uptake (O_H) varied widely along the transect as a consequence of the different N supply assumptions (Table 8). Approach I, with the same relatively low value ($1.1 \cdot 10^{-4}$ day^{-1}) for k_h, resulted in organic uptake rates with increasing values from south to north, i.e., from Nässjö to Lycksele (Table 8). Organic N plant uptake in Ljungbyhed was not considered, as a k_h of $1.1 \cdot 10^{-4}$ day^{-1} was adequate to meet measured tree biomass, hence only approach I was simulated at this site. The different values of O_H in this approach resulted in an increased degree of organic N uptake from south to north, ranging from 39% in Nässjö to 62% in Lycksele. In approach II, with variable k_h and no organic N plant uptake, k_h in the north had to be 6.4 times higher than that in the south (Table 8) in order to explain measured standing stocks at 100 years (Table 2). Approach III, with a soil C:N ratio in steady-state, gave intermediate values of k_h and O_H compared to the other two approaches (Table 8).

The different N supply assumptions resulted in substantial differences regarding soil C:N ratios (Fig. 5, Table 2). With the variable organic N uptake and fixed k_h, the C:N ratio in Lycksele increased from the initial value of 31.4 to a final value of 44.5 after 100 years, as a weighted average for the whole soil

Table 7 Summary of plant- and climate-related variables of simulated ecosystem

	Unit	Lycksele I	Mora I	Nässjö I	Ljungbyhed I
Plant					
GPP	g C m^{-2} year^{-1}	626	892	1139	1275
NPP	g C m^{-2} year^{-1}	265	356	435	463
NPP/GPP	–	0.42	0.40	0.38	0.36
Change in tree layer	g C m^{-2} year^{-1}	53	77	104	113
Change in field layer	g C m^{-2} year^{-1}	2	1	0	0
Harvest	g C m^{-2} year^{-1}	14	20	26	27
Tot Plant Litter production	g C m^{-2} year^{-1}	200	261	308	326
Litter prod. (tot above)	g C m^{-2} year^{-1}	92	116	131	143
Litter prod. (tot below)	g C m^{-2} year^{-1}	108	146	177	184
Litter prod. (% field above)	%	28	22	11	14
Litter prod. (% field below)	%	12	9	4	5
Climate					
Growth Air Temp Sum	°C day	901	1162	1302	1525
LAI Tot	–	3.9	4.9	5.5	5.9
LAI field layer	–	0.9	0.9	0.5	0.7
Adsorbed Rad Total	MJ m^{-2} day^{-1}	5.6	6.7	7.5	7.7
Adsorbed Rad Field (of Tot)	%	17	11	5	6
Air Temp	°C	0.7	3.3	5.2	7.1
Mean Soil Temp 10 cm	°C	3.0	4.1	5.0	6.5
Temp Theta Response 10 cm[a]	–	0.12	0.15	0.17	0.21

The different variables are represented by average annual values for the 100-year simulation period. For the different calibration approaches the plant- and climate-related variables were similar and for simplicity the relationships found in approach I are presented

[a] Scaling factor for soil climate effect on decomposition rate for SOM

profile. The increase was less pronounced in the south. A variable k_h and no organic N uptake resulted in the opposite trend, with decreasing C:N ratio with time in Lycksele from 31.4 to 22.9, in Mora from 29.0 to 22.7 and in Nässjö from 27.2 to 22.8.

The different approaches also gave considerably different results regarding soil C dynamics (Fig. 6; Table 8). With a low k_h and variable organic N uptake, large amounts of C were sequestered in all soils along the transect, ranging between 23 g C m^{-2} year^{-1} and 29 g C m^{-2} year^{-1}. A variable k_h and no organic N uptake gave the opposite picture, with losses of soil C, especially in the northern part of the transect (Fig. 6; Table 8). Finally, the C:N ratio steady-state approach resulted in soil C changes where the northern ecosystems were almost in a steady-state situation regarding SOC and the southern systems were sequestering C in the soil: Lycksele −5 g C m^{-2} year^{-1}; Mora −2 g C m^{-2} year^{-1}, Nässjö +9 g C m^{-2} year^{-1} and Ljungbyhed +23 g C m^{-2} year^{-1}.

Respiratory losses from the soil in the simulated ecosystems varied both in relation to the transect and in relation to the different N supply assumptions (Table 8). Mean annual soil respiration for Lycksele varied between 352 g C m^{-2} year^{-1} and 397 g C m^{-2} year^{-1}, with the higher values for approach I and the lower for approach II. Similar changes occurred for the other regions. The ratio between soil respiration and total ecosystem respiration showed relatively similar values along the transect, with the highest value in Lycksele (0.69) for approach II and the lowest value in Ljungbyhed (0.63) for approach I. The heterotrophic part of soil respiration resembled the results regarding total soil respiration, though the difference between north and south was more pronounced. The highest ratio between heterotrophic soil respiration and total soil respiration was again in Lycksele with approach II using a variable k_h and no organic N uptake (0.56) and the lowest in Ljungbyhed (0.43).

Table 8 Summary of soil carbon and nitrogen variables of simulated ecosystem for three different modelling approaches are presented: I = fixed k_h and variable organic N uptake; II = variable k_h, and no organic N uptake and III = soil C:N ratio in steady-state

	Unit	Lycksele I	Lycksele II	Lycksele III	Mora I	Mora II	Mora III	Nässjö I	Nässjö II	Nässjö III	Ljungbyhed I
Soil C											
Change in soil	$g\ C\ m^{-2}\ year^{-1}$	23	−25	−5	28	−22	−2	29	−10	9	23
Decomposition Rate (k_h)	day^{-1}	1.1E-04	7.0E-04	3.7E-04	1.1E-04	4.5E-04	2.8E-04	1.1E-04	3.0E-04	1.9E-04	1.1E-04
Total Soil Respiration	$g\ C\ m^{-2}\ year^{-1}$	352	397	383	495	523	521	624	653	635	704
Tot Soil Resp/Tot Resp	–	0.66	0.69	0.68	0.64	0.67	0.66	0.64	0.65	0.64	0.63
Soil Heterotrophic Resp.	$g\ C\ m^{-2}\ year^{-1}$	174	222	205	232	271	260	278	316	294	302
Soil Het Resp/Tot Soil Resp	–	0.49	0.56	0.53	0.47	0.52	0.5	0.45	0.48	0.46	0.43
Soil N											
Leaching	$g\ N\ m^{-2}\ year^{-1}$	0.12	0.20	0.14	0.13	0.21	0.15	0.09	0.17	0.11	0.23
Mineral plant uptake	$g\ N\ m^{-2}\ year^{-1}$	1.17	3.08	1.75	1.84	3.83	2.63	2.87	4.68	3.54	4.8
Total plant uptake	$g\ N\ m^{-2}\ year^{-1}$	3.09	3.08	3.13	4.04	3.83	3.97	4.71	4.68	4.63	4.8
Organic uptake (of total)	%	62		44	54		34	39		24	
Organic uptake rate (O_H)	day^{-1}	9.0E-05		6.5E-05	6.5E-05		4.0E-05	3.7E-05		2.2E-05	
Change in soil	$g\ N\ m^{-2}\ year^{-1}$	−0.13	−0.26	−0.17	−0.02	−0.14	−0.06	0.37	0.26	0.34	0.71
Soil C:N ratio (initial)	–	31.4	31.4	31.4	29	29	29	27.2	27.2	27.2	19.8
Soil C:N ratio (final)	–	44.5	22.9	31.6	38.7	22.7	29	31.9	22.8	27.1	21.2

The different variables are represented with average annual values for the 100-year simulation period

Discussion

General and specific patterns of forest ecosystem dynamics

Simulated GPP along the transect was consistent with values reported from other studies in similar systems (e.g., Williams et al. 1997), but on average 74% lower than values reported from the LUSTRA sites (Lindroth et al. 2007, Table 4). This difference could be due to the simulation representing a mean value from 100 years, whereas LUSTRA represented measurements in a 40-year-old forest, which is likely to be in a productive phase. The simulated NPP/GPP ratio of between 0.36 and 0.42 (Table 7) was the same as the values reported from the two most northern LUSTRA sites (Lindroth et al. 2007, Table 4), whereas the southern LUSTRA site Asa showed a higher value (0.46) compared to the corresponding site Nässjö (0.38). The reason for this difference was not clarified. The simulated ratios were lower than the values reported by Waring et al. (1998), but lower ratios have been reported from boreal forests (Ryan et al. 1997).

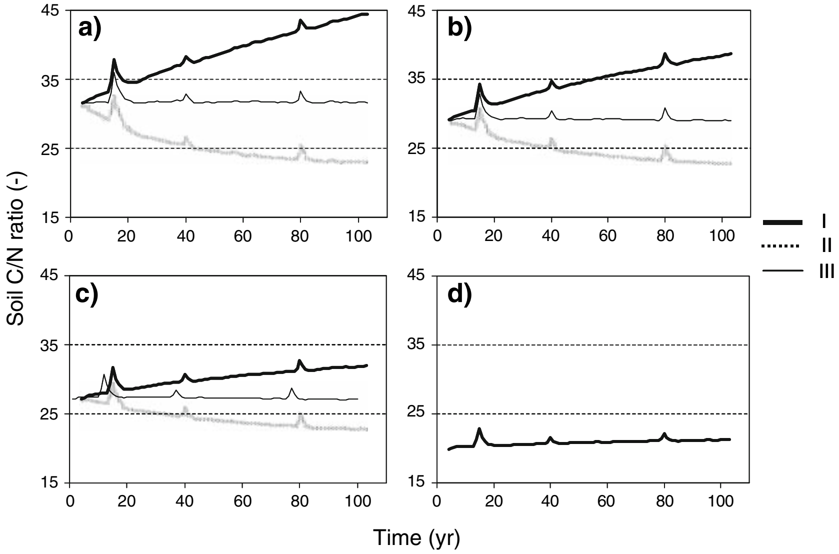


Fig. 5 Soil C:N ratio dynamics during 100 years simulation for (**a**) Lycksele, (**b**) Mora, (**c**) Nässjö and (**d**) Ljungbyhed. Three different modelling approaches are presented: I (thick line) = fixed k_h and variable organic N uptake; II (dotted line) = variable k_h, and no organic N uptake and III (thin line) = soil C:N ratio in steady-state

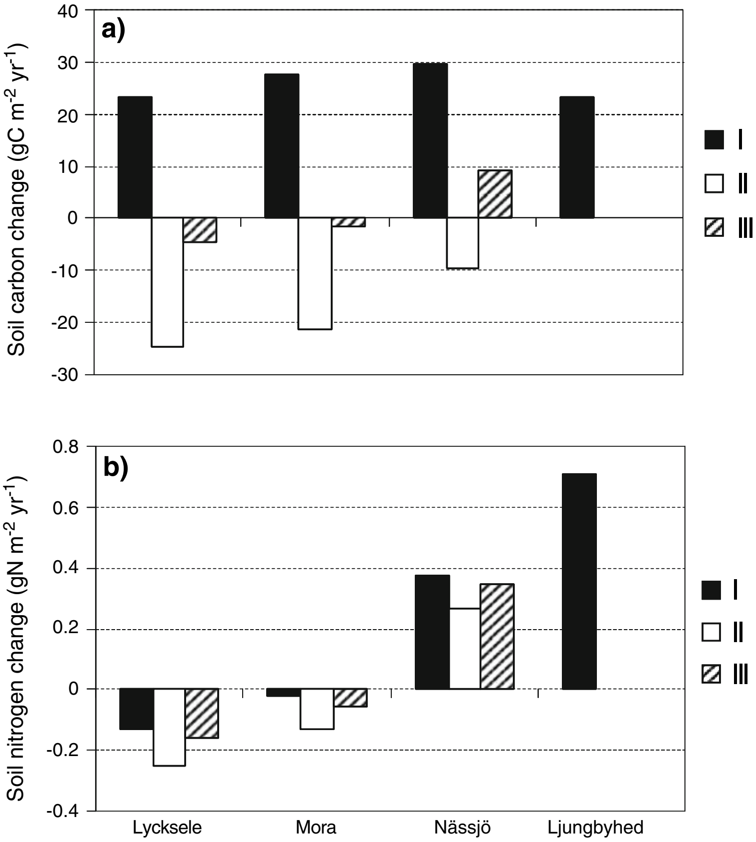


Fig. 6 Average annual change of (**a**) soil C and (**b**) soil N pools during 100-year simulation for Lycksele, Mora, Nässjö and Ljungbyhed. Three different modelling approaches are presented: I = fixed k_h and variable organic N uptake; II = variable k_h, and no organic N uptake and III = soil C:N ratio in steady-state

Measured standing stock in a 100-year-old forest in the respective region (Table 2) was the only information that was used to adjust simulated tree biomass. Apart from this, the simulated tree growth was the result of independently chosen parameters regarding plant properties (Table 4) and forest management strategies. The agreement between model and measurement was good, but tree growth was overestimated in the early stages in the north, while it was underestimated in the south. Several possible aspects could explain this discrepancy. One contributing factor could be that the simulations performed in the study covered a transition from boreal coniferous forest ecosystems in the northern part of Sweden to forests in the temperate southern part of the country. Hence, some model parameters regarding plant characteristics, e.g., allocation patterns, should perhaps have been more site-specific or preferably region-specific. Another aspect that was not considered was the timing and intensity of forest management practices, which are performed at a later stage in the north and less biomass is removed during e.g., thinning compared with the south (Swedish Forest Agency 2005). In the simulations, an average timing and average level of intensity were assumed. Competition between the field layer and tree seedlings in the early phases, damage to growing trees as a consequence of cold weather, parasites or grazing animals are other factors that probably vary along the gradient. However, the difference in dynamics between simulated biomass and measured standing stocks during the rotation period was not of a magnitude to significantly affect the forest C balance during the simulation period. The size of the biomass pools, and thus the amounts of litter produced (Table 7), was considered to be more important than the timing of the litter production. The simulated mean annual litter production and the relative contribution from above- and below-ground plant parts were similar to findings reported in other studies (Berg and Meentemyer 2001; Berggren Kleja et al. 2007) and were hence considered reasonable.

The relationship between tree layer and field layer in terms of competition for radiation was clearly demonstrated (Fig. 4). As the tree LAI in the ecosystem in the south of Sweden increased and levelled off at around 6, the field layer showed a simultaneous decrease. This development was not the case in the north, where the field layer was stable through the entire simulation period, and the tree LAI had a maximum of around 3. The different field layer dynamics described for north and south were also reflected in the LAI of the field layer and hence the amount of adsorbed radiation, since the field layer in the north adsorbed 17% of total adsorbed global radiation in the ecosystem compared to only 6% in the south (Table 7). This could be compared to the NPP of 21–29% estimated by Mälkönen (1974) in the field layer of Scots pine stands in Finland and also to the results in a recent study by Kolari et al. (2006), who demonstrated the importance of forest floor vegetation for photosynthetic production in boreal forests. The importance of the field layer for the C balance was indicated by its contribution to the total litter production of the ecosystem, which amounted to 19% in the north compared to 9% in the south (Table 7).

The differences in mean air temperatures along the transect with an equal gradient in air temperature sums reflected the differences in growing season. This difference in aboveground climate, which affects plant growth, was not equally pronounced in the belowground climate, which affects SOC decomposition (Table 7). In the north, the difference between mean soil temperature at 10 cm depth and mean air temperature was +2.3°C, while the corresponding figure for the south was −0.6°C. Hence, in the northern ecosystem the model had accounted for a major insulating factor in the plant-soil system that was not apparent in the southern ecosystem. The main explanation for this insulation was the effect of snow, but the denser field layer in the north could also have a contributing effect. The modelled difference of +2.3°C is in accordance with values found by Beskow (1935). The site in the southern part of Sweden showed the opposite effect, with the mean soil temperature being less than the mean air temperature. A reasonable explanation for this temperature difference, apart from generally snow-free conditions during wintertime, was the denser tree canopy (Fig. 4) insulating the below-canopy environment from radiation.

Trends in soil C storage

The described differences in soil climate were evident in the differing response of SOC decomposition rate, with less effect in the south compared to the harsher soil climate in the north (Table 7). The contribution from total soil respiration (autotrophic plus heterotrophic) to total ecosystem respiration (63–69%) and the contribution from heterotrophic soil respiration to total soil respiration (43–56%) did not differ from what has been reported in the literature (Högberg et al. 2001; Schuur and Trumbore 2006). Hence, none of the simulated soil respiratory losses could be used to assess the different calibration approaches. For example in Lycksele, where k_h varied by a factor of 6.4, the difference in total soil respiration only varied by a factor of 1.1, indicating the difficulty of using soil respiration measurements to estimate k_h. The main explanation for this behaviour was that the major proportion of soil heterotrophic respiration ($\sim$80%) originated from the litter fraction. On the other hand, varying k_h greatly influenced soil C pool changes during the 100-year simulations.

Approach I, with a low k_h and variable O_H, resulted in substantial sequestration of C in the soil (Table 8), with roughly equal amounts along the Swedish transect. The increase in the SOC pool in both Lycksele (+33%) and Ljungbyhed (+21%) over only a 100-year period could not be considered reasonable. 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. This should be compared with the simulated average rates of 28 g C m^{-2} year^{-1} and 23 g C m^{-2} year^{-1} for the Mora and Lycksele regions, which are located at the same latitudes as the sites in the Finnish study. The organic N uptake along the gradient, from 62% of total plant N uptake in Lycksele to 39% in Nässjö, was not unreasonable (T. Näsholm pers. comm.) and the increasing reliance on organic N uptake at increasing latitudes was also in correspondence to newly presented theory (Schimel and Bennet 2004). However, the high organic N uptake caused the soil C:N ratio to change from 31.4 to 44.5 in Lycksele, with similar but less pronounced patterns in the other regions (Fig. 5; Table 8). This development over only 100 years was considered to be unlikely. Few measurements of C:N ratio dynamics in soils over longer time periods are available, but Dodd et al. (1994) reported a relatively constant C:N ratio in a study covering more than 100 years. Furthermore, the concept of constant soil C:N ratio was used by de Vries et al. (2006) when estimating C sequestration in European forests and forest soils.

Approach II, with variable k_h and no organic N uptake, gave completely different results, i.e., the soils lost large amounts of C except in the south. In the north, 35% of the current SOC pool was lost during 100 years. At the same time the soil C:N ratio changed from the initial 31.4 to 22.9. Both these trends were considered to be equally unlikely, based on the findings in Peltoniemi et al. (2004) and the discussion on the C:N ratio above. Furthermore, there is experimental evidence showing that organic N uptake by plants does occur in boreal forest ecosystems (Näsholm et al. 1998).

Approach III, with an assumption of soil C:N ratio being stable during the simulation period, resulted in small losses of C from the soils in Lycksele and Mora (-5 g C m^{-2} year^{-1} and -2 g C m^{-2} year^{-1}) whereas the sites in the south of Sweden at the same time sequestered 9 g C m^{-2} year^{-1} and 23 g C m^{-2} year^{-1}. The simulated soil C losses in the north could be related to the N balance, which showed that Lycksele lost 0.17 and Mora 0.06 g N m^{-2} year^{-1}. DeLuca et al. (2002) reported that boreal forests of northern Scandinavia take up 0.15 g N m^{-2} year^{-1} to 0.2 g N m^{-2} year^{-1} through fixation by mosses. An N uptake of that magnitude in Lycksele and Mora would help close the N balance and thus put less demand on N mineralisation to meet measured regional tree growth in the simulations. This would result in less soil C losses and hence the simulated losses of C from northern soils could be an overestimation and the SOC pools could be even closer to steady-state.

Even though the calibration approach III, with variable k_h and organic N uptake, seems to give the most reliable and consistent pattern regarding soil C and N dynamics, the extent to which the different approaches would apply to the different regions is still an open question. For example, the boreal forest ecosystems in Sweden could have a relatively high organic plant N uptake and related increases in C:N ratio compared to the temperate coniferous forests in the south, where the organic plant N uptake could be less or not apparent at all, and where the soil C:N ratio might be balanced or even decreasing. Earlier simulations using the SOIL-N model demonstrated the difficulty of using data on decomposition rates from laboratory incubations in order to parameterise the model to meet measurements of tree growth and N leaching (Eckersten and Beier 1998). As a consequence, the possibility of a supplementary organic N uptake was implemented. The current study supports the conclusion of earlier studies with the SOIL-N model that the simulated forest ecosystems need a supplementary mechanism, in addition to what can be supplied from N mineralisation, in order to agree with measured standing stocks.

Long term ecosystem C dynamics—key factors

To analyse the factors affecting current soil C pools, a ratio between variables for the most southern region in the transect (Ljungbyhed) and the corresponding region in the northern part of the transect (Lycksele) was constructed (Table 9).

The ratio of plant growth was 2.05, which was significantly larger than the production of litter (1.63). Two main factors could explain this - the contribution of the field layer to the total litter production in the north, where a relatively small part of the total biomass (~5%) contributed to 19% of the total litter production (Table 7); and the lower NPP/GPP ratio of the southern ecosystem, which indicated larger plant respiratory losses here compared to in the north, leaving less biomass to be transferred into litter.

As indicated in Table 9, the current soil C pool in the Ljungbyhed region was 1.52 larger than in the northern (Lycksele) region. This figure is similar to the relationship between total litter production (1.63), so if decomposition rates had been the same in the north and south, the different litter input rates would have explained the current difference in soil C pools. However, the simulated climatic effect on the SOC decomposition rate was 1.78. As discussed above, this effect was largely related to the lower soil temperatures in the north. In other words, these results indicated that had long-term simulations been performed using the same values of k_h for all regions, as in approach I, the simulated soil C pools in the northern regions would have been larger than the soil C pools in the southern regions, which is the opposite pattern of the observed data.

Table 9 The ratio Ljungbyhed:Lycksele for plant and climate variables based on values in Table 7 and soil C from Table 6

Variable	Ratio
Plant and climate	
Air temperature	10.14
Growth air temperature sum	1.69
Plant growth	2.05
Total litter production	1.63
Soil temperature 10cm	2.16
Climate effect on SOC decomposition rate	1.78
Soil C	
Soil carbon pool (current value)	1.52

In the calibration approach III, where both k_h and O_H were allowed to vary along the climatic transect, both parameters increased from south to north (Table 8). The k_h parameter needed to be set 3.36 times higher in the north (Lycksele) than in the south (Ljungbyhed) in order to match tree growth, keeping the C:N ratio at a constant value and changes in soil C pools at reasonable rates (cf. Peltoniemi et al. 2004). The reason for the suggested lower decomposition rate coefficient in the south compared to the north is not clear. One possible explanation could be high levels of available N through deposition hampering decomposition, since there is experimental evidence to indicate that decomposition of SOC proceeds at a slower rate in N-rich environments. In a recent field experiment performed at Flakaliden, Olsson et al. (2005) found that heterotrophic respiration was significantly lower in N-fertilised plots than in untreated plots. Furthermore Schimel and Bennet (2004), suggested a new model where N mineralisation is conceptualised as gross mineralisation combined with a competition between microbes and plants over mineralised N. Given a system limited by N the competition could force the microbes to enhance the decomposition. Still, it is unclear to what degree this could explain the higher decomposition rate coefficients in the north compared to the south. Another possible explanation could be a different temperature sensitivity for SOC decomposition than that used in the simulations. SOC decomposition in the north was reduced by a factor of 1.78 compared with in the south, mainly due to lower soil temperatures. However, at the same time the decomposition rate coefficient (k_h) was 3.36 times higher in the north, indicating that even if no response function for soil temperature had been considered at all, which has been proposed (e.g., Giardina and Ryan 2000), the decomposition rate of the humus pool in the north would still have been higher.

The 1.69 ratio for the growing season (air temperature sums) clearly showed the importance of climate in explaining the larger tree growth in the south compared to the north. However, this ratio was significantly lower than the corresponding ratio for plant growth (2.05), indicating yet another regulating factor. The explanation for this enhanced growth over and above the contribution from the prolonged growing season was most likely the larger N availability in the southern ecosystem (Table 1; Table 6), which highlights the importance of considering N supply when simulating spruce forest ecosystems and/or making predictions of climate change on soil C dynamics.

Conclusions

The modelling approach with feedback between abiotic processes and turnover of C and N in the soil-plant system was successful in describing general patterns in managed forest stands during a period long enough to be relevant for C sequestration issues. We believe this is a viable approach for the necessary differentiation between the combined effects of climate and N on C pool dynamics in forest ecosystems.

The tree growth pattern observed along a transect covering the main forested areas in Sweden could not be explained without organic N uptake and/or enhanced mineralisation rates for the northern regions of the country, compared to the southern regions.

The difficulty of using measurements for estimating decomposition rates for SOC with a low turnover rate (k_h) was clearly indicated. A modelling approach where both k_h and organic N uptake were allowed to vary along the climatic transect while soil C:N ratio was assumed to be in steady-state produced the most consistent results in terms of long-term trends (100 years) in soil C and N pools. Applying this approach, forest soils in the south of Sweden were sequestering C (10–20 g C m^{-2} year^{-1}), whereas forest soils in the centre and north of the country were close to steady-state.

Acknowledgements The authors express their gratitude to Dr. David Gustafsson and Dr. Louise Karlberg for technical advice on the modelling, as well as comments on the manuscript. The work formed part of the LUSTRA research programme, supported by the Foundation for Strategic Environmental Research, Mistra.

Appendix 1 List of equations

Equation	Definition	No.
Plant biotic processes		
$C_{Atm\to a} = \varepsilon_L f(T_l) f(CN_l) f(E_{ta}/E_{tp}) R_{s,pl}$ where ε_L is a parameter representing the radiation use efficiency.	Rate of photosynthesis (g C m^{-2} day^{-1})	(1)
$f(T_l) = \begin{cases} 0 & T_l < p_{mn} \\ (T_l - p_{mn})/(p_{o1} - p_{mn}) & p_{mn} \le T_l \le p_{o1} \\ 1 & p_{o1} < T_l < p_{o2} \\ 1 - (T_l - p_{o2})/(p_{mx} - p_{o2}) & p_{o2} \le T_l \le p_{mx} \\ 0 & T_l > p_{mx} \end{cases}$ where p_{mn}, p_{o1}, p_{o2} and p_{mx} are parameters.	Response function for leaf temperature (–)	(2)
$f(CN_l) = \begin{cases} 1 & CN_{leaf} < p_{CN,Opt} \\ 1 + \frac{CN_{leaf} - p_{CN,Opt}}{p_{CN,Opt} - p_{CN,Th}} & p_{CN,Opt} \le CN_{leaf} \le p_{CN,Th} \\ 0 & CN_{leaf} > p_{CN,Th} \end{cases}$ where $p_{CN,Opt}$ and $p_{CN,Th}$ are parameters and CN_{leaf} is the C:N ratio in the leaf.	Response function for leaf C:N ratio (–)	(3)
$f(E_{ta}/E_{tp}) = \frac{E_{ta}}{E_{tp}}$	Response function for soil moisture (–)	(4)
$C_{a\to Root} = f_{root} \cdot C_{Atm\to a}$ $C_{a\to Leaf} = f_{leaf} \cdot C_{Atm\to a}$ $C_{a\to Stem} = \left((1 - f_{root} - f_{leaf}) \cdot C_{Atm\to a}\right) \cdot (1 - f_{cr})$ $C_{a\to CRoot} = \left((1 - f_{root} - f_{leaf}) \cdot C_{Atm\to a}\right) \cdot f_{cr}$ where f_{root}, f_{leaf} and f_{cr} are parameters.	Carbon allocation to root, leaf, stem and coarse root respectively (g C m^{-2} day^{-1})	(5)

Appendix 1 continued

Equation	Definition	No.
$C_{Leaf\rightarrow Resp} = k_{mrespleaf} \cdot f(T_a) \cdot C_{leaf} + k_{gresp} \cdot C_{a\rightarrow Leaf}$ where $k_{mrespleaf}$ is the maintenance respiration coefficient for leaves, k_{gresp} is the growth respiration coefficient, and $f(T_a)$ is the temperature response. The equation calculates respiration from stem, roots and coarse roots by exchanging $k_{mrespleaf}$ to $k_{mrespstem}$, $k_{mresproot}$, $k_{mrespcroot}$, and using the corresponding storage pools.	Plant growth and maintenance respiration from leaves (g C m^{-2} day^{-1})	(6)
$f(T_a) = t_{Q10}^{(T_a - t_{Q10bas})/10}$ where t_{Q10} and t_{Q10bas} are parameters.	Air temperature response function for respiration (–)	(7)
$C_{Leaf\rightarrow Litter} = l_{Lc} \cdot C_{Leaf} \cdot e^{(A_l \cdot k_{LAI})}$ where l_{Lc} is a rate parameter, A_l the LAI and k_{LAI} the LAI Enhanced Coefficient parameter. Stem, coarse roots and fine roots are calculated analogously using l_{Sc}, l_{CRc} and l_{Rc} , except for the exponential function for enhanced leaf litterfall.	Leaf litter rate carbon (day^{-1})	(8)
$N_{Demand} = \left(\frac{C_{a\rightarrow Root}}{cn_{MinRoot}} + \frac{C_{a\rightarrow CRoot}}{cn_{MinCRoot}} + \frac{C_{a\rightarrow Stem}}{cn_{MinStem}} + \frac{C_{a\rightarrow Leaf}}{cn_{MinLeaf}}\right) - N_{MobileReallo\rightarrow Leaf}$ where $cn_{MinRoot}$, $cn_{MinCRoot}$, $cn_{MinStem}$ and $cn_{MinLeaf}$ are parameters and $N_{MobileReallo}$ is equal to the nitrogen content in the mobile nitrogen pool at that time-step.	Plant nitrogen demand (g N m^{-2} day^{-1})	(9)
$N_{Mineral\rightarrow Plant} = f_{NUpt} \cdot (N_{NO_3} + N_{NH_4})$ where f_{NUpt} is a parameter.	Plant uptake of mineral nitrogen (g N m^{-2} day^{-1})	(10)
$N_{Organic\rightarrow Plant} = N_{Litter} o_L \cdot \frac{N_{Litter} o_L}{(N_{Litter} o_L + N_{Humus} o_H)} + N_{Humus} o_H \cdot \frac{N_{Humus} o_H}{(N_{Litter} o_L + N_{Humus} o_H)}$ where o_L and o_H are parameters for maximum uptake rates.	Plant uptake of organic nitrogen (g N m^{-2} day^{-1})	(11)
$N_{a\rightarrow Root} = \min(N_a, \frac{C_{a\rightarrow Root}}{cn_{MinRoot}})$ $N_{a\rightarrow CRoot} = \min(N_a - N_{a\rightarrow Root}, \frac{C_{a\rightarrow CRoot}}{cn_{MinCRoot}})$ $N_{a\rightarrow Stem} = \min(N_a - N_{a\rightarrow Root} - N_{a\rightarrow CRoot}, \frac{C_{a\rightarrow Stem}}{cn_{MinStem}})$ $N_{a\rightarrow Leaf} = \min(N_a - N_{a\rightarrow Root} - N_{a\rightarrow CRoot} - N_{a\rightarrow Stem}, \frac{C_{a\rightarrow Leaf}}{cn_{MinLeaf}})$ where $cn_{MinRoot}$; $cn_{MinCRoot}$, $cn_{MinStem}$ and $cn_{MinLeaf}$ are parameters.	Nitrogen allocation to root, coarse root, stem and leaf respectively (g N m^{-2} day^{-1})	(12)
$N_{Leaf\rightarrow Litter} = l_{Lc} \cdot N_{Leaf} \cdot e^{(A_l \cdot k_{LAI})}$	Leaf litter rate nitrogen (day^{-1})	(13)
$C_{Leaf\rightarrow Mobile} = C_{Leaf\rightarrow LitterSurface} \cdot m_{retain}$ where m_{retain} is a parameter.	Carbon retention at leaf litterfall (g C m^{-2} day^{-1})	(14)
$N_{Leaf\rightarrow Mobile} = C_{Leaf\rightarrow Mobile} / cn_{MinLeaf}$ where $cn_{MinLeaf}$ is a parameter.	Nitrogen retention at leaf litterfall (g N m^{-2} day^{-1})	(15)
$C_{Mobile\rightarrow Leaf} = C_{Mobile} \cdot m_{shoot}$ where m_{shoot} is a parameter.	Reallocation of carbon from mobile pool to leaves at leafing (g C m^{-2} day^{-1})	(16)
$N_{Mobile\rightarrow Leaf} = N_{Mobile} \cdot m_{shoot}$	Reallocation of nitrogen from mobile pool to leaves at leafing (g N m^{-2} day^{-1}).	(17)
Soil nitrogen and carbon processes		
$C_{DecompL} = k_l f(T) f(\theta) C_{Litter}$ where k_l is a parameter. Decomposition of the humus pool is calculated analogously using the parameter k_h.	Decomposition of litter, carbon (g C m^{-2} day^{-1})	(18)
$C_{Litter\rightarrow CO_2} = (1 - f_{e,l}) \cdot C_{DecompL}$ $C_{Litter\rightarrow Humus} = f_{e,l} f_{h,l} C_{DecompL}$ $C_{Litter\rightarrow Litter} = f_{e,l}(1 - f_{h,l}) \cdot C_{Decomp}$ where $f_{e,l}$ and $f_{h,l}$ are parameters.	Decomposition products from litter (g C m^{-2} day^{-1})	(19)

Appendix 1 continued

Equation	Definition	No.
$C_{Humus \to CO_2} = (1 - f_{eh}) \cdot C_{DecompH}$ where $f_{e,h}$ parameter is a parameter.	Decomposition products from humus (g C m^{-2} day^{-1})	(20)
$N_{Litter \to Humus} = C_{Litter \to Humus} / cn_m$ where cn_m is a parameter representing the C:N ratio of the microbes.	Decomposition of litter, nitrogen (g N m^{-2} day^{-1})	(21)
$N_{Litter \to NH_4} = C_{DecompL} \left(\frac{1}{CN_{Litter}} - \frac{f_{e,l}}{cn_m} \right)$ Mineralisation / immobilisation of nitrogen from humus is calculated analogously. A negative value of the flux means that a net immobilisation takes place.	Mineralisation/immobilisation of nitrogen (g N m^{-2} day^{-1})	(22)
$C_{Litter1 \to DO} = d_{DOL1} f(T) f(\theta) C_{Litter1}$ where d_{DOL} is a rate parameter and $f(T)$ and $f(\theta)$ are the common response functions for temperature and soil moisture. The equation is used analogously to calculate the flux of nitrogen from litter to the dissolved organic nitrogen pool.	Flux from litter to dissolved organic carbon (g C m^{-2} day^{-1})	(23)
$C_{Humus \to DO} = f(T) f(\theta) \cdot (d_{DOH} C_{Humus} - d_{DOD}(z) C_{DO})$ where d_{DOH} is the rate parameter for formation of dissolved organic C, d_{DOD} is the rate parameter for the fixation of dissolved organic C, $f(T)$ and $f(\theta)$ are the common response functions for temperature and soil moisture, $\theta(z)$ is the soil moisture content and Δz is the depth of the soil horizon. The equation is used analogously to calculate the flux of nitrogen from humus to the dissolved organic nitrogen pool.	Flux from humus to dissolved organic carbon (g C m^{-2} day^{-1})	(24)
$q_{DOC} = \frac{C_{DO}(z)}{\theta(z)\Delta z} \cdot q_w$ where q_w is the vertical water flow. The equation is used analogously to calculate the flux of dissolved organic nitrogen.	Vertical redistribution of dissolved organic carbon (gC m^{-2} day^{-1})	(25)
$f(T) = 1 \qquad T > t_{max}$ $f(T) = \left(\frac{T - t_{\min}}{t_{\max} - t_{\min}} \right)^2 \qquad t_{min} < T < t_{max}$ $f(T) = 0 \qquad T < t_{min}$ where t_{min} and t_{max} are parameters.	Response function for soil temperature (Ratkowsky function) (-)	(26)
$f(\theta(z)) = p_{\theta satact} \qquad \theta(z) = \theta_s$ $f(\theta(z)) = \min \left(\left(\frac{\theta_s - \theta(z)}{p_{\theta Upp}} \right)^{p_{\theta p}} (1 - p_{\theta satact}) + p_{\theta satact}, \left(\frac{\theta(z) - \theta_{wilt}}{p_{\theta Low}} \right)^{p_{\theta p}} \right) \qquad \theta_{wilt} < \theta(z) < \theta_s$ $f(\theta) = 0 \qquad \theta(z) < \theta_{wilt}$ where $p_{\theta satact}$, $p_{\theta Upp}$, $p_{\theta Low}$ and $p_{\theta p}$ are parameters and the variables, θ_s,θ_{wilt} and θ are the soil moisture content at saturation, at wilting point and at the actual soil moisture content respectively.	Response function for soil moisture (-)	(27)
Plant abiotic processes		
$A_l = C_{Leaf} \cdot p_{l,sp}$ where $p_{l,sp}$ is a parameter for the specific leaf mass.	Leaf area index (m^2 m^{-2})	(28)
$R_{s,pl} = \left(1 - e^{-k_{rn} \frac{A_l}{f_{cc}}} \right) \cdot f_{cc} (1 - a_{pl}) R_{is}$ where k_{rn} is the light use extinction coefficient given as a single parameter common for all plants, f_{cc} the surface canopy cover and a_{pl} the plant albedo.	Plant interception of global radiation (MJ m^{-2} day^{-1})	(29)
$r_s = \frac{1}{\max(A_l\, g_l, 0.001)}$ where g_l is the stomatal conductance.	Stomatal resistance (s m^{-1})	(30)
$g_l = \frac{R_{is}}{R_{is} + g_{ris}} \frac{g_{\max}}{1 + \frac{(e_s - e_a)}{g_{vpd}}}$ where g_{ris}, g_{max} and g_{vpd} are parameter.	Stomatal conductance per leaf area (m s^{-1})	(31)

Appendix 1 continued

Equation	Definition	No.
$f_{cc} = p_{c\max}(1 - e^{-p_{ck}A_l})$ where p_{cmax} and p_{ck} are parameters .	Surface canopy cover ($m^2\ m^{-2}$)	(32)
$L_v E_{tp} = \frac{\Delta R_n + \rho_a c_p \frac{(e_s - e)}{r_a}}{\Delta + \gamma\left(1 + \frac{r_s}{r_a}\right)}$ where R_n is net radiation available for transpiration, e_s is the vapour pressure at saturation, e is the actual vapour pressure, ρ_a is air density, c_p is the specific heat of air at constant pressure, L_v is the latent heat of vaporisation, Δ is the slope of saturated vapour pressure versus temperature curve, γ is the psychrometric "constant", r_s is an "effective" surface resistance and r_a is the aerodynamic resistance.	Potential transpiration (mm day^{-1})	(33)
$E^*_{ta} = E^*_{tp} \int_{z_r}^{0} f_\psi(z) f_T(z) r(z)$ where $r(z)$ is the relative root density distribution, z_r is root depth and f_ψ, and f_T are response functions for soil water potential and soil temperature.	Actual transpiration before compensatory uptake (mm day^{-1})	(34)
$E_{ta} = E^*_{ta} + f_{umov} \cdot (E^*_{tp} - E^*_{ta})$ where f_{umov} is the degree of compensation, E^*_{ta} is the uptake without any account of compensatory uptake and E^*_{tp} is the potential transpiration with eventual reduction due to interception evaporation.	Actual transpiration (mm day^{-1})	(35)

References

Alavi G, Jansson P-E (1995) Transpiration and soil moisture dynamics for spruce stands of different canopy densities and water availability. In: Nilsson L-O, Hüttl RF, Johansson UT, Mathy P (eds) Nutrient uptake and cycling in forest ecosystem, vol 21. Ecosystem Research Report pp 41–51. Luxembourg, ISBN 92-826-9416-X

Berg B, Booltink H, Breymeyer A, Ewertsson A, Gallardo A, Holm B, Johansson M-B, Koivuoja S, Meentemeyer V, Nyman P, Olofsson J, Pettersson A-S, Staaf H, Staaf I, Uba L (1991) Data on needle litter decomposition and soil climate as well as site characteristics for some coniferous forest sites 2nd edn. Section 2. Data on needle litter decomposition. Swedish University of Agricultural Sciences, Department of Ecology and Environmental Research, Report No 42

Berg B (2000) Litter decomposition and organic matter turnover in northern forest soils. For Ecol Manage 133:13–22

Berg B, Meentemeyer V (2001) Litter fall in some European coniferous forests as dependent on climate: A synthesis. Can J For Res 31:292–301

Bergh J, McMurtrie RE, Linder S (1998) Climatic factors controlling the productivity of Norway spruce: a model-based analysis. For Ecol Manage 110:127–139

Berggren Kleja D, Svensson M, Majdi H, Langvall O, Jansson P-E, Lindroth A, Weslien P, Bergkvist B, Johansson M-B (2007) Pools and fluxes of carbon in three Norway spruce ecosystems along a climatic gradient in Sweden. Manuscript (this volume)

Beskow G (1935) Soil freezing and frost heaving with special application to roads and railroads. SGU Serie C No 375 Årsbok 26(3) 242 pp [In Swedish]

Bonhomme R (2000) Beware of comparing RUE values calculated from PAR vs. solar radiation or absorbed vs. intercepted radiation. Field Crop Res 68:247–252

Bossel H (1996) TREEDYN3 forest simulation model. Ecol Model 90:187–227

Callesen I, Liski J, Raulund-Rasmussen K, Olsson MT, Tau-Strand L, Vesterdal L, Westman CJ (2003) Soil carbon stores in Nordic well-drained forest soils—relationship with climate and texture class. Global Change Biol 9:358–370

Charles-Edwards DA, Doley D, Rimmington GM (1986) Modelling plant growth and development. Academic Press, Australia, 235 pp

Ciais PH, Reichstein M, Viovy N, Granier A, Ogée J, Allard V, Aubinet M, Buchmann N, Bernhofer CHR, Carrara A, Chevallier F, De Noblet N, Friend AD, Friedlingstein P, Grünwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert G, Soussana JF, Sanz MJ, Schulze ED, Vesala T, Valentini R (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529–533

CoupModel database (2006) Available at: http://www.lwr.kth.se/Vara%20Datorprogram/CoupModel/index.htm

DeLuca TH, Zackrisson O, Nilsson MC, Sellstedt A (2002) Quantifying nitrogen-fixation in feather moss carpets of boreal forests. Nature 419:917–920

de Vries W, Reinds GJ, Gundersen P, Sterba H (2006) The impact of nitrogen deposition on carbon sequestration in European forests and forest soils. Global Change Biol 12:1151–1173

Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J (1994) C pools and flux of global forest ecosystems. Science 263:185–190

Dodd ME, Silvertown J, Mcconway K, Potts J, Crawley M (1994) Stability in the plant communities of the Park Grass Experiment: The relationships between species richness, soil pH and biomass variability. Philos Trans Roy Soc London Ser B – Biol Sci 346:185–193

Eckersten H, Jansson P-E (1991) Modelling water flow, nitrogen uptake and production for wheat. Fertilizer Res 27:313–329

Eckersten H, Gärdenäs A, Jansson P-E (1995) Modelling seasonal nitrogen, carbon, water and heat dynamics of the Solling spruce stand. Ecol Model 83:119–129

Eckersten H, Beier C (1998) Comparison of N and C dynamics in two Norway spruce stands using a process oriented simulation model. Environ Pollut 102:395–401

Euskirchen ES, McGuire AD, Kicklighter DW, Zuang Q, Clein JS, Dargaville RJ, Dye DG, Kimball JS, McDonald KC, Melillo JM, Romanovsky VE, Smith NV (2006) Importance of recent shifts in soil thermal dynamics on growing season length, productivity, and carbon sequestration in terrestrial high-latitude ecosystems. Global Change Biol 12:731–750

Foster TE, Brooks JR (2005) Functional groups based on leaf physiology: are they spatially and temporally robust? Oecologia 144:337–352

Fleischer S (2003) CO_2 Deficit in temperate forest soils receiving high atmospheric N-deposition. Ambio 32: 2–5

Gärdenäs A, Eckersten H, Lillemägi M (2003) Modeling long-term effects of N fertilization and N deposition on the N balance of forest stands in Sweden. 30 pp. Emergo 2003:3 ISNN 1651-7210

Giardina CP, Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. Nature 404:858–861

Gustafsson D, Lewan L, Jansson P-E (2004) Modeling water and heat balance of the boreal landscape - comparison of forest and arable land in Scandinavia. J Applied Met 43(11):1750–1767

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 165:17–326

Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Högberg MN, Nyberg G, Ottosson-Löfvenius M, Read DJ (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411:789–792

Iivonen S, Kaakinen S, Jolkkonen A, Vapaavuori E, Linder S (2006) Influence of long-term nutrient optimization on biomass, carbon, and nitrogen acquisition and allocation in Norway spruce. Can J For Res 36(6):1563–1571

Ingestad T, Agren GI (1988) Nutrient uptake and allocation at steady-state nutrition. Physiol Plant 72:450–459

IPCC (2001) In: Houghton HJ (ed) Climate change 2001: the scientific basis. Contribution of Working group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK

IVL (2006) Luftföroreningar i skogliga provytor – Resultat till och med september 2005 Report B1682 Swedish Environmental Research Institute Stockholm Sweden 52 pp [In Swedish with English summary.] Available at: http://www.ivl.se/rapporter/pdf/B1682.pdf

Jansson P-E, Halldin S (1979) Model for the annual water and heat flow in a layered soil. In: Halldin S (ed) Comparison of forest and energy exchange models. Int Soc For Ecol Model, Copenhagen, pp 145–163

Jansson P-E, Persson T, Kätterer T (1999a) N Processes in Arable and Forest Soils in the Nordic Countries – Field-scale modelling and experiments. TemaNord 1999:560. Nordic Council of Ministers, Copenhagen, 203 pp

Jansson P-E, Cienciala E, Grelle A, Kellner E, Lindahl A, Lundblad M (1999b) Simulated evapotranspiration from the Norunda forest stand during the growing season of a dry year. Agric For Meteorol 98–99:621–628

Jansson P-E, Moon D (2001) A Coupled model of water, heat and mass transfer using object orientation to improve flexibility and functionality. Environ Model Software 16(1):37–46

Jansson P-E, Karlberg L (2004) Coupled heat and mass transfer model for soil-plant-atmosphere systems. Royal Institute of Technology, Department of Civil and Environmental Engineering., Stockholm, Sweden, 435 pp (ftp://www.lwr.kth.se/CoupModel/ CoupModel.pdf)

Johnsson H, Bergström L, Jansson P-E, Paustian K (1987) Simulated N dynamics and losses in a layered agricultural soil. Agric Ecosys Environ 18:333–356

Kane ES, Valentine DW, Schuur EAG, Dutta K (2005) Soil carbon stabilization along climate and stand productivity gradients in black spruce forests of interior Alaska. Canadian J For Res 35:2118–2129

Karlberg L, Gustafsson D, Jansson P-E (2006) Modelling carbon turnover in five terrestrial ecosystems in the boreal zone using multiple criteria of acceptance. Ambio 35(8):448–458

Kirchbaum MUF (2000) Will changes in soil organic carbon act as a positive or negative feedback on global warming? Biogeochemistry 48:21–51

Kolari P, Pumpanen J, Kulmala L, Ilvesniemi H, Nikinmaa E, Grönholm T, Hari P (2006) Forest floor vegetation plays an important role in photosynthetic production of boreal forests. For Ecol Manage 221:241–248

Larcher W (2003) Physiological plant ecology: ecophysiology and stress physiology of functional groups, 4th edn. Springer-Verlag, Berlin, 523 pp

Linder S, Troeng E (1981) The seasonal variation in stem and coarse root respiration in a 20-year old Scots pine (*Pinus sylvestris* L.). Mitteilungender Forstlichen Bundes-Versuchsanstalt (Wein) 142:125–139

Lindroth A, Klemedtsson L, Grelle A, Weslien P, Langvall O (2007) Measurement of net ecosystem exchange, productivity and respiration in three spruce forests in Sweden shows unexpectedly large soil carbon losses. Biogeochemistry (this volume)

Liski J, Ilvesniemi H, Mäkelä A, Westman CJ (1999) CO_2 emissions from soil in response to climatic warming are overestimated—The decomposition of old organic matter is tolerant to temperature. Ambio 28:171–174

Mahli Y, Baldocchi DD, Jarvis PG (1999) The C balance of tropical, temperate and boreal forests. Plant, Cell and Environment 22:715–740

Majdi H, Andersson P (2005) Fine root production and turnover in a Norway spruce stand in northern Sweden: Effects of N and water manipulation. Ecosystems 8:191–199

Mälkönen E (1974) Annual primary production and nutrient cycle in some Scots pine stands. Commun Inst For Fenn 84:1–87

Marklund LG (1988) Biomass functions for pine, spruce and birch in Sweden. Swed Univ Agri Sci Dept For Survey. Report 45, 73 pp [In Swedish with English summary.]

Melillo JM, McGuire AD, Kicklighter DW, Moore III B, Vorosmarty CJ, Schloss AL (1993) Global climate change and terrestrial net primary production. Nature 363:234–240

Monson RK, Lipson DL, Burns SP, Turnipseed AA, Delany AC, Williams MW, Schmidt SK (2006) Winter forest soil respiration controlled by climate and microbial community composition. Nature 439:711–714

Monteith JL (1965) Evaporation and environment. In: Fogg GE (ed) The state and movement of water in living organisms, 19th Symp Soc Exp Biol. The Company of Biologists, Cambridge, pp 205–234

Monteith JL (1977) Climate and the efficiency of crop production in Britain. Phil Trans Royal Soc (London), Series B:281:277–294

Näsholm T, Ekblad A, Nordin A, Giesler R, Högberg M, Högberg P (1998) Boreal forest plants take up organic nitrogen. Nature 392:914–916

Näslund M (1947) Funktioner och tabeller för kubering av stående träd. Tall, gran och björk i södra Sverige samt i hela landet. Meddelande från Statens Skogsförsöksanstalt 36:3 [In Swedish]

Newman GS, Arthur MA, Muller RN (2006) Above- and below-ground net primary production in a temperate mixed deciduous forest. Ecosystems 9:317–329

Nilsson L-O, Östergren M, Wiklund K (2001) Hur påverkas träden ovan mark? In: Persson T, Nilsson L-O (eds) Skogabyförsöket – effekter av långvarig kväve- och svaveltillförsel till ett skogsekosystem. Naturvårdsverket, Rapport 5173, Stockholm, 51–74 [In Swedish with English summary.]

Olsson M, Erlandsson M, Nilsson T, Nilsson Å, Stendahl J (2007) Organic carbon in Swedish podsols and their relation to site factors. Biogeochemistry (this volume)

Olsson P, Linder S, Giesler R, Högberg P (2005) Fertilization of boreal forest reduces both autotrophic and heterotrophic respiration. Global Change Biol 11:1745–1753

Peltoniemi M, Mäkipää R, Liski J, Tamminen P (2004) Changes in soil carbon with stand age—an evaluation of a modeling method with empirical data. Global Change Biol 10:2078–2091

Penman HL (1953) The physical basis of irrigation control. In: Synge PM (ed) Report of the 13th Intern Hortic Congr, 1952, Roy Horticultural Soc, London, vol II, 913–924

Penning de Vries FWT, van Laar HH (1982) Simulation of Plant Growth and Crop Production. Simulation Monographs, Wageningen, The Netherlands, 307 pp

Persson T, Nilsson L-O (2001) Skogabyförsöket – effekter av långvarig kväve- och svaveltillförsel till ett skogsekosystem. Naturvårdsverket, Rapport 5173, Stockholm. 220 pp [In Swedish with English summary]

Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B:81–99

Ratkowsky DA, Olley J, McMeekin TA, Ball A (1982) Relationship between temperature and growth rate of bacterial cultures. J Bacteriol 149:1–5

Ryan MG, Lavigne MB, Gower ST (1997) Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. J Geophys Res Atmos 102(D24):28871–28883

Schimel JP, Bennett J (2004) Nitrogen mineralisation: challenges of a changing paradigm. Ecology 85:591–602

Schuur EAG, Trumbore SE (2006) Heterotrophic contribution to soil respiration from boreal black spruce forest: using isotopes to partition sources to soil carbon dioxide flux. Global Change Biol 12:165–176

Seyferth U (1998) Effects of soil temperature and moisture on carbon and nitrogen mineralisation in coniferous forests. Licentitate thesis, Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, Uppsala

Sinclair TR, Muchow RC (1999) Radiation use efficiency. Adv Agron 65:215–265

Skogsdata (2003) Aktuella uppgifter om de svenska skogarna från Riksskogstaxeringen. SLU, Inst för skoglig resurshushållning och geomatik 114 pp [In Swedish]

Smith SE, Read DJ (1997) Mycorrhizal symbiosis, 2nd edn. Academic Press, London, UK

SNV (2005) Sweden's National Inventory Report 2005 - Submitted under the United Nations Framework Convention on Climate Change. Report 5451, Swedish Environmental Protection Agency, Stockholm, Sweden, pp 216 Available at: http://www.naturvardsverket.se/bokhandeln

Swedish Forest Agency (2005) Grundbok för skogsbrukare. Skogsstyrelsens förlag, Jönköping, Sweden. p 190 [In Swedish]

Tamm CO (1991) Nitrogen in terrestrial ecosystems, questions of productivity, vegetational changes, and ecosystem stability. Ecol Stud 81, Springer-Verlag, Berlin, Germany, 115 pp

Tamm CO, Aronsson A, Popovic B, Flower-Ellis J (1999) Optimum nutrition and nitrogen saturation in Scots pine stands. Studia Forestalia Suecia 206:1–126

Taylor AFS, Martin F, Read DJ (2000) Fungal diversity in ectomycorrhizal communities of Norway spruce (*Picea abies* (L.) Karst.) and beech (*Fagus sylvatica* L.) along northsouth transects in Europe. In: Schulze E-D (ed) Carbon and nitrogen cycling in European forest ecosystems ecological studies. Springer-Verlag, Berlin, Germany, pp 343–365

Valentini R, Matteucci G, Dolman AJ, Schulze E-D, Rebmann C, Moors EJ, Granier A, Gross P, Jensen NO, Pilegaard K, Lindroth A, Grelle A, Bernhofer C, Grünwald T, Aubinet M, Ceulemanns R, Kowalski AS, Vesala T, Rannik Ü, Berbigier P, Loustau D, Mundson J, Thorgeirsson H, Ibrom A, Morgenstern K, Clement R, Moncreiff J, Montagnani L, Minerbi S, Jarvis PG (2000) Respiration as the main determinant of C balance in European forests. Nature 404:861–865

Wallenda T, Stober C, Högbom L, Schinkel H, George E, Högberg P, Read DJ (2000) Nitrogen uptake processes in roots and mycorrhizas. Ecological Studies 142. Springer, Berlin Heidelberg New York, pp 122–143

Wang YP, Polglase PJ (1995) Carbon balance in the tundra, boreal forest and humid tropical forest during climate change: Scaling up from leaf physiology and soil carbon dynamics. Plant Cell Env 18:1226–1244

Waring RH, Landsberg JJ, Williams M (1998) Net primary production of forests: a constant fraction of gross primary production? Tree Physiol 18:129–134

Wikström F, Ericsson T (1995) Allocation of mass in trees subject to nitrogen and magnesium limitation. Tree Physiol 15:339–344

Williams M, Rastetter EB, Fernandes DN, Goulden ML, Shaver GR, Johnson LC (1997) Predicting gross primary productivity in terrestrial ecosystems. Ecol Appl 7:882–894

Zak DR, Holmes WE, Tomlinson MJ, Pregitzerand KS, Burton AJ (2006) Microbial cycling of C and N in northern hardwood forests receiving chronic atmospheric NO. Ecosystems 9:242–253