CARBON DYNAMICS IN SPRUCE FOREST ECOSYSTEMS - MODELLING POOLS AND TRENDS FOR SWEDISH CONDITIONS

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Preface and Acknowledgements

In 1999 the research programme LUSTRA (Land use strategies to reduce greenhouse gas emissions) started. The focus has been on forest soils and its role as a possible sink, one aim being to produce scientific support for those who are negotiating, on Sweden’s behalf, within the framework of the Framework Convention on Climate Change. Three common field sites were established and measurements initiated, and as one part of LUSTRA different modelling tools were used together with the measurements. It was within one of these sub projects I came to take part and which eventually led up to this thesis.

During the years I have been privileged to be supported, and surrounded, by several persons: Per-Erik, my main supervisor – with your positive attitude, helpfulness and knowledge, I have learnt a lot during these years; Dan, my co supervisor – you helped me keeping the main track within site among all the interesting sidetracks; David – the seemingly difficult suddenly becomes obvious when explained by you; Louise – our long a fruitful discussions over the years have also been a great source of support. All you other great personalities at LWR – the list can be made very long, and so can the list of peoples working within LUSTRA – Leif, Per, Josefine, Bosse, Ola and the personnel at the Asa forest research station, Mats, Hooshang, Stefan, Tryggve, Anders, Achim.

A good research idea, supervisors and colleagues are all good prerequisites to conduct a PhD, but without funding the result stands the risk of being meagre. This work has been funded by the Foundation for Strategic Environmental Research (Mistra) through their programme LUSTRA, and by The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (Formas).

Last but as it is usually stated, not least; my family, Lale, Selma, Ellen and my mother Maj– I would not have made it, especially during the final intense phase, without your support and love. Love you back.

Magnus Svensson
Stockholm, November 2006
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**List of Papers**

This thesis is based on the following papers, which are referred to by their Roman numerals:


ABSTRACT
Carbon (C) pools and fluxes in northern hemisphere forest ecosystems are attracting increasing attention concerning predicted climate change. This thesis studied C fluxes, particularly soil C dynamics, in spruce forest ecosystems in relation to interactions between physical/biological processes using a process-based ecosystem model (CoupModel) with data for Swedish conditions. The model successfully described general patterns of C and N dynamics in managed spruce forest ecosystems with both tree and field layers. Using regional soil and plant data, the change in current soil C pools was $-3 \text{ g C m}^{-2} \text{ yr}^{-1}$ in northern Sweden and $+24 \text{ g C m}^{-2} \text{ yr}^{-1}$ in southern Sweden. Simulated climate change scenarios resulted in increased inflows of 16-38 g C m$^{-2}$ yr$^{-1}$ to forest ecosystems throughout Sweden, with the highest increase in the south and the lowest in the north. Along a north-south transect, this increased C sequestration mainly related to increased tree growth, as there were only minor decreases in soil C pools. Measurements at one northern site during 2001-2002 indicated large soil C losses $(96 \text{ g C m}^{-2} \text{ yr}^{-1})$, which the model successfully described. However, the discrepancy between these large losses and substantially smaller losses obtained in regional simulations was not explained. A simulation based on Bayesian calibration successfully reproduced measured C, water and energy fluxes, with estimated uncertainties for major components of the simulated C budget. Site-specific measurements indicated a large contribution from field layer fine roots to total litter production, particularly in northern Sweden. Mean annual tree litter production was 66% higher at the most southerly site (240 g C m$^{-2}$ yr$^{-1}$ compared with 145 g C m$^{-2}$ yr$^{-1}$ in the north), but when field and bottom layers were included the difference decreased to 16% (total litter production 276 g C m$^{-2}$ yr$^{-1}$ and 239 g C m$^{-2}$ yr$^{-1}$ respectively). Regional simulations showed that decomposition rate for the stable soil C fraction was three times higher in northern regions compared with southern, providing a possible explanation why soil C pools in southern Sweden are roughly twice as large as those in the north.

Keywords: boreal; climate; CoupModel; net ecosystem production; nitrogen; process-based model; soil carbon;

INTRODUCTION
Increased anthropogenic emissions of CO$_2$ and their predicted effects on global climate (IPCC, 2001) and world ecosystems have placed the focus on global carbon (C) cycles and related fluxes. Forest ecosystems have attracted increased attention in efforts to describe the global C budget and the forests of the northern hemisphere in particular play an important role, as these forest soils contain around 40% of the total amount of C in world forest biomes (Dixon et al., 1994). Moreover, these ecosystems are situated where a significant increase in air temperature is expected (IPCC, 2000). The increased temperature could affect the C balance and, given the large pools, even a slight change could have large consequences on atmospheric CO$_2$ levels (Wang & Polglase, 1995; Mahli et al., 1999; Ciais et al., 2005), hence the importance of studying the C dynamics of these forest ecosystems and of understanding the regulating processes and of further relating these processes to climate. The Kyoto Protocol (IPCC, 2003), which is currently the global community’s answer to address the global climate change problem, has acknowledged the enhanced focus on these ecosystems from the scientific community. One rather debated part of the Protocol states that when countries that have ratified the treaty draw up a budget of greenhouse gases, it should be based on sinks/sources directly related to changes in land use and to forestry and furthermore that these sinks/sources must be verified through measured changes in trees and soil. However, the net changes in both these main parts of the forest ecosystem are relatively small compared with two large fluxes of C. For the tree, the
inflow through gross primary productivity (GPP) is counterbalanced by outflows from respiratory losses, resulting in the net primary productivity (NPP). Both these measures of productivity are strongly dependent on climatic factors such as temperature and precipitation, as well as nutrient supply rates (King et al., 1997; Bergh et al., 1999), and an increased temperature due to climate change is likely to result in increased productivity in boreal forest ecosystems (e.g. Mäkipää et al., 1999; Bergh et al., 2003).

Litter production from the tree, which is strongly related to NPP, constitutes the inflow of C to the soil, and thus if forest productivity increases due to climate change, the inflow of C to the soil will also increase. Much like the net change in the tree, the inflow of C to the soil is counterbalanced by losses through soil respiration from decomposition of soil organic matter. There seems to be consensus as regards the effects of climate change on NPP, and some findings indicate that soil respiration is more sensitive to climate variability than NPP (Kirchbaum, 2000; Valentini et al., 2000). However, the effect on soil organic matter decomposition is under debate regarding the temperature sensitivity of the fraction with a long turnover time, which makes up the major proportion of soil C. Some studies indicate a relatively high sensitivity (Ågren, 2000; Knorr et al., 2005), others that it is rather insensitive to temperature (Liski et al., 1999; Giardina & Ryan, 2000).

Nitrogen (N) availability, which affects net primary production (Tamm, 1991; Ivonen et al., 2006; Newman et al., 2006), is affected by decomposition rate (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. Since current ecosystems are normally far from N saturation, increased amounts of N lead to increased tree growth and hence increased litterfall. This was clearly indicated in a study by Strömgren and Linder (2002) who, in a heating experiment conducted in a boreal Norway spruce forest ecosystem in Sweden, reported increased GPP as a consequence of increased N supply in the heated plots. 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).

In order to interpret current C pools, fluxes and future trends in forest ecosystems, it is important to understand the major abiotic and biotic regulating processes. Furthermore, it is essential to consider how these plant and soil regulating processes are related to above- and below-ground climate and the difference between these positions in the system, as changes in atmospheric conditions are not directly linked to changes in soil climate conditions (Gärdenäs and Jansson, 1995). In order to identify and quantify the regulating factors, given these important considerations, an approach where they are coupled with feedbacks seems necessary.

It is also important to relate the C budget to different scales, where measurements from the system can be available at one scale but reveal important effects in another. Changes in soil C are a good example of this, since they are small compared with the pools and thus difficult to measure unless performed over an extended period and with many replicates. Another aspect to consider is differences in turnover times. The major proportion of the soil C has a long turnover time and hence could be referred to as relatively stable. The pool of C in trees, on the other hand, given the more dynamic environment for which anthropogenic influence is an important factor, could be considered more unstable or uncertain in long time scales, although it is easier to measure.

The complexity of the processes regulating the forest system as outlined above necessitates the use of a modelling tool.
Plant-soil interactions and climatic influences on these interactions indicate the importance of a flexible modelling approach to describe the differences between above- and below-ground climates. A modelling approach without a dynamic interaction between abiotic and biotic sub-models, i.e. a static approach, restricts the use of the model to systems where the physical characteristics are known or independent of the C and N processes. 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 of great interest. Such an approach is also likely to generate sound predictions of effects within the forest system due to climatic change scenarios, where the major uncertainties can be identified. Thus a number of different ecosystem models have been presented during recent years. One simplified approach to study climatic effects on C budgets is by using natural climatic gradients, an approach adopted in the debate on soil C temperature sensitivity as discussed above (e.g. Giardina and Ryan, 2000), and also in a recent study by Meyer et al. (2006). However, measurements from a climatic gradient can also be used to validate existing models, i.e. to determine the ability of the models to describe the main components of energy, water, C and N fluxes in a forest ecosystem under different climate regimes.

Models as described above are usually referred to as process-based models (PBMs), and are commonly used in forest research ( cf Landsberg, 2003; Van Oijen et al., 2004) as flexible and general tools with potentially high predictive capacity. However, one problem with PBMs is that they tend to develop a complexity, reflecting the complexity of the system the models are set up to describe, and hence the need for data to calibrate the model is large. This demand can rarely be fully supplied by measurements and hence can be viewed as an uncertainty, or incomplete knowledge about the system, when calibrating the model. One method to address this problem is to adopt a Bayesian calibration procedure as proposed by e.g. Van Oijen et al. (2005). This method focuses on minimising the uncertainty of the calibrated parameters, instead of maximising the goodness of fit between measurements and model output. The main advantage with this methodology is that it quantifies the uncertainty in both the input and the simulated outputs using a probabilistic approach. The method makes a bridge between measurements and observations since it accounts for the uncertainty in the measurements and it demonstrates the extent to which the uncertainty in predictions can be reduced by adding new data or new alternative models.

**Objectives**

In the present work, a process-based ecosystem model (CoupModel) was used to simulate forest C and N dynamics in relation to energy and water. The simulations were performed at different scales using data and measurements for Swedish conditions, covering mean air temperatures from 0.7°C to 7.1 °C and gradients of N pools and decomposition. The simulated soils were considered to be dry and mesic, constituting the main proportion of Swedish forest soils, and thus moist and wet soils were not included.

The main objective of the work was to study C fluxes in spruce forest ecosystems with the emphasis on soil C dynamics in relation to interactions between physical and biological processes.

Specific objectives were to:

- Estimate trends in soil C storage in managed Swedish Norway spruce ecosystems during a 100-year period, based on available regional data on tree growth and C pools and using different assumptions for N supply (Paper I);

- Present an integrated picture of C pools and fluxes at three different Norway spruce forest sites in Sweden along a climatic gradient measured during 4 years, and compare a regionally representative model based on the parameterisation in Paper I.
with the site-specific measurements obtained (Paper II);
Identify how a change in climate affects abiotic factors of importance for the ecosystem C dynamics presented in Paper I, determine the processes governing the inflows and outflows of C from the ecosystem and quantify the extent to which limiting factors for key ecosystem processes are expected to change (Paper III);
Quantify the major fluxes of C, heat and water in a boreal Norway spruce forest stand during a 4-year period, including uncertainty estimates, and estimate parameter values including internal model structure correlations in relation to measurements and to the major components in the simulated C budget (Paper IV).

BACKGROUND
A brief theoretical background and overview of the main interactions between abiotic and biotic processes in the forest ecosystem (Fig. 1), which form the focus of this thesis, are presented below.

Energy and water
Global radiation is the main energy source for the system. A small fraction is taken up by photosynthesis of plants but the major partitioning of the energy is between the atmosphere and the soil system. The plant layer(s) and the related physical characteristics govern the partitioning and thus also the environmental conditions for plant and soil development. Leaf area index (LAI), defined as one single side of the total green leaf area per unit ground surface area, is often used for characterising plant canopies in process-based models (Running and Coughlan, 1988; Bonan, 1993). The net radiation at the soil surface is the result of incoming long-wave and short-wave radiation penetrating through the canopy and is thus affected by e.g. canopy albedo (which is relatively low for forests), LAI and canopy surface coverage.

Excluding the energy used in photosynthesis, the energy balance of the system is usually given as:

\[ R_n = LE + H + G \]  

where \( R_n \) is the net radiation, \( LE \) is the latent heat flow, \( H \) the sensible heat flow and \( G \) the heat flux into the ground.

The related water balance is usually given as:

\[ P = E + R + \Delta S \]  

where precipitation (\( P \)) is the main input of water to the system. This input is balanced by the losses to atmosphere through the evapotranspiration (\( E \)) driven by available energy and air humidity, thus linking the two large abiotic balances. Runoff (\( R \)), usually as a lateral flow in forests, and change in soil water storage (\( \Delta S \)) are the two other components in the balance. Transpiration is the major part of (\( E \)) and can account for over 50% of these losses. A crucial plant feature for the amount of transpiration is the stomatal conductance (Monteith, 1965), which in turn is closely linked to the leaf area of the tree. As with radiation, the plant layer intercepts precipitation and the evaporative losses from intercepted water can be in the range of 10-35% of precipitation (Kittredge, 1948; Zinke, 1967). This partitioning of the precipitation and the related losses included in (\( E \)) can have a large effect on the amount of water available at the soil surface and, through the infiltration process, the soil moisture content.

Snow is an important factor to consider in boreal forest energy and water balances. Snow has a much higher albedo than bare soil or plants, indicating a lowered net radia-
tion for conditions with a snow layer. However, this effect is not so pronounced in a forest, where plants are of considerable height compared with a field or a clear-cut. According to Harding and Pomeroy (1996), interception of snow in a forest canopy can reduce the depth of the snow layer on the ground by up to 30%. Through the low thermal properties of snow and the related insulating effect, an altered snow layer thickness in turn has an impact on the forest soil heat flux. Beskow (1935) reported differences between air and soil temperature of up to 2°C as a consequence of the snow insulating effect.

Through the interception of radiation and water, LAI affects both the energy and water balance, reflected as an altered soil climate. In addition, LAI has a direct connection to transpiration by the interception of net radiation and further to photosynthesis by the interception of photosynthetically active radiation (PAR). The apparent interaction between plant and soil and the related linkage between abiotic and biotic processes can thus be conceptualised through LAI (Fig. 1).

**Plant and soil carbon**

Gross primary production (GPP), i.e. the photosynthetic process in which CO₂ is reduced to carbohydrates through captured light, is the main process for carbon uptake in forests. Photosynthetically active radiation and air temperature are the main limiting environmental factors for GPP, availability of soil nutrients and water being the other main limiting factors for uptake of CO₂ and growth. Among the nutrients, N is of major importance and has been shown to be the major regulating factor for tree growth in Sweden (Tamm et al., 1999), where the main source of N is from decomposition of soil organic matter (see below). Other important sources are organic N uptake as demonstrated by Näsholm et al. (1998) or through N-fixing bacteria in symbiosis with feather mosses, which in a recent study by DeLuca et al. (2002) were shown to contribute significantly to N inflow in boreal forest ecosystems.

Of the fixed C, roughly half is lost due to respiratory losses in the form of growth and maintenance respiration. The growth respiration is a relatively stable fraction of the C consumption whereas the maintenance respiration is closely, and positively, correlated to temperature. The remaining C, after respiratory losses, is referred to as net primary production (NPP). The ratio NPP/GPP was shown to be a rather conservative value (0.42-0.53) by Waring et al. (1998), but significantly lower values (~0.25) have been reported from boreal forest ecosystems (Ryan et al., 1997). The NPP is allocated to the major components of the tree, i.e. stem, leaf (needles) and root. This allocation is affected by different environmental factors, but the specific regulating processes are complex (e.g. Cannell and Dewar, 1994). One example is decreased radiation or an environment with low irradiance, e.g. the understory, which can enhance allocation to the leaves, another that decreased nutrient availability and soil moisture can affect the allocation patterns to the roots. A more empirical allocation description is to allocate specific fractions to respective plant parts, based on different correlation functions (e.g. Marklund, 1988). These functions are in turn often based on easily available data such as stem diameter at breast height, and are the result of extended empirical analyses.

The different tree parts are the source of the litterfall, which is the major input of C and nutrients to the soil. An important factor to consider is the different life lengths of the two major components of the litterfall, where needles may live for approximately 5 years and fine roots around 1 year (Majdi et al., 2006). The decomposition of the litter by micro-organisms releases CO₂ and, together with plant respiration from the roots, this represents a major carbon loss from the system, i.e. the soil respiration. Through decomposition of litter a minor proportion of the soil organic matter is transformed into more recalcitrant organic matter (humus). As a consequence of litterfall, litter is predominant in the topsoil and humus in the deeper mineral soil layers. This differentiation is
Table 1. Brief description of sites included in Papers I-IV, and standing biomass and measured litter production (g C m\(^{-2}\) yr\(^{-1}\)) at the sites compared to simulations in Papers II and IV.

<table>
<thead>
<tr>
<th>Site description</th>
<th>Lycksele</th>
<th>Flakaliden</th>
<th>Mora</th>
<th>Knottåsen</th>
<th>Nässjö</th>
<th>Asa</th>
<th>Ljungbyhed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude</td>
<td>64°35'N</td>
<td>64°07'N</td>
<td>60°58'N</td>
<td>61°00'N</td>
<td>57°38'N</td>
<td>57°08'N</td>
<td>56°05'N</td>
</tr>
<tr>
<td>Longitude</td>
<td>18°40'E</td>
<td>19°27'E</td>
<td>14°35'E</td>
<td>16°13'E</td>
<td>14°41'E</td>
<td>14°45'E</td>
<td>13°04'E</td>
</tr>
<tr>
<td>Altitude (m a.s.l.)</td>
<td>223</td>
<td>310-320</td>
<td>161</td>
<td>315-320</td>
<td>305</td>
<td>190-200</td>
<td>76</td>
</tr>
<tr>
<td>Mean annual air temperature (°C)</td>
<td>0.7/3.3</td>
<td>1.2</td>
<td>3.3/5.8</td>
<td>3.4</td>
<td>5.2/8.4</td>
<td>5.5</td>
<td>7.1/10.1</td>
</tr>
<tr>
<td>Mean annual precipitation (mm)</td>
<td>613/704</td>
<td>523</td>
<td>629/701</td>
<td>613</td>
<td>711/717</td>
<td>688</td>
<td>838/890</td>
</tr>
<tr>
<td>N deposition (g N m(^{-2}) yr(^{-1}))</td>
<td>1.5</td>
<td>2.6</td>
<td>3.5</td>
<td>4.4</td>
<td>7.5</td>
<td>8.8</td>
<td>12.5</td>
</tr>
<tr>
<td>Soil C (g C m(^{-2}))</td>
<td>7006</td>
<td>7220</td>
<td>8567</td>
<td>5860</td>
<td>9995</td>
<td>10000</td>
<td>10666</td>
</tr>
<tr>
<td>Soil N (g N m(^{-2}))</td>
<td>223</td>
<td>216</td>
<td>295</td>
<td>204</td>
<td>367</td>
<td>370</td>
<td>539</td>
</tr>
<tr>
<td>Soil C/N ratio (-)</td>
<td>31.5</td>
<td>33.5</td>
<td>29.1</td>
<td>28.7</td>
<td>27.2</td>
<td>27</td>
<td>19.8</td>
</tr>
</tbody>
</table>

Biomass and litter production

<table>
<thead>
<tr>
<th>Unit</th>
<th>Measured</th>
<th>Simulated (^1)</th>
<th>Measured</th>
<th>Simulated</th>
<th>Measured</th>
<th>Simulated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biomass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>tree layer g C m(^{-2}) yr(^{-1})</td>
<td>4630/4211</td>
<td>4697/3635</td>
<td>4600</td>
<td>5424</td>
<td>7950</td>
<td>9292</td>
</tr>
<tr>
<td>field layer g C m(^{-2}) yr(^{-1})</td>
<td>142</td>
<td>170/190</td>
<td>167</td>
<td>110</td>
<td>30</td>
<td>10</td>
</tr>
<tr>
<td>Litter production tree above g C m(^{-2}) yr(^{-1})</td>
<td>60</td>
<td>59/51</td>
<td>68</td>
<td>70</td>
<td>101</td>
<td>125</td>
</tr>
<tr>
<td>below g C m(^{-2}) yr(^{-1})</td>
<td>85</td>
<td>105/67</td>
<td>134</td>
<td>121</td>
<td>139</td>
<td>196</td>
</tr>
<tr>
<td>Litter production field above g C m(^{-2}) yr(^{-1})</td>
<td>10</td>
<td>29/-</td>
<td>12</td>
<td>19</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>below g C m(^{-2}) yr(^{-1})</td>
<td>62</td>
<td>14/7</td>
<td>79</td>
<td>9</td>
<td>19</td>
<td>0</td>
</tr>
</tbody>
</table>

\(^1\)Current climate/SWECLIM A2 \(^2\)Mean value dry and mesic plots/mean footprint area \(^3\)PaperII/PaperIV

also a result of redistribution of dissolved organic carbon (DOC) from topsoil to mineral soil. These processes result in large pools of organic matter in the mineral soil, 70-80% of SOM to a depth of 1 m in Scandinavian boreal forest soils (Callesen et al., 2003), with in very general terms a turnover time from 100 years to several centuries, compared with from 10 years to several decades for organic matter in more shallow layers, where the pools are smaller. These processes are further strongly linked to soil temperature and soil moisture, which e.g. explains the large carbon pools in wet forest soils where decomposition has been hampered through poor aeration or anoxic conditions in the soil compared with upland soils.

Mechanistic understanding of the processes of decomposition of soil organic matter, mineralisation of nutrients and formation of humus is incomplete, to say the least, and hence different models exist. In brief, a process-based decomposition model needs to address three aspects: (i) the external environment, usually soil temperature and soil moisture; (ii) substrate quality, where one or several fractions of the substrate can be used or a continuous quality decrease; and (iii) decomposer organisms.

The within-year dynamics of all the biological processes described, both above- and below-ground, closely follow the dynamics of regulating abiotic factors such as radiation and, particularly for boreal ecosystems, air temperature. One example is decreased air temperature leading to decreased soil temperature, which in turn generates soil conditions that restrict water uptake by trees (Jansson & Halldin, 1979; Mellander et al., 2006).
MATERIALS AND METHODS

Site descriptions and data

Papers I and III

Four different regions in Sweden were studied using climatic data taken from four representative sites, Lycksele (64°35'N), Mora (60°58'N), Nässjö (57°38'N) and Ljungbyhed (56°05'N) (Table 1, Fig. 2). Daily mean values of meteorological data (air temperature, air humidity, wind speed, cloudiness and precipitation) from 1961-1986 from Swedish Meteorological and Hydrological Institute (SMHI) were duplicated to cover a 100-year period. Nitrogen deposition for the respective sites was based on official data from IVL (2006), and the N deposition values for each region were assumed to remain constant during the whole simulation period.

Measured tree biomass values for the regions were based on standing stock volume data taken from the Swedish Forest Inventory (NFI) (Skogsdata, 2003), and pools of soil C and N were based on an evaluation of the Swedish National Forest Soil Inventory database given by Olsson et al. (2006) and C/N ratios as shown in Paper II (Table 1). The soil physical properties used in the simulations were based on mean values of soil texture measurements for 37 soil profiles from different forest sites located in northern, central and southern Sweden.

The two climate scenarios in Paper III were obtained from the SWECLIM project, using the Hadley Centre simulations of scenario A2 and B2 according to IPCC. Both scenarios correspond to increased emissions of greenhouse gases during the next 100 years leading to increased mean annual air temperatures and increased total annual precipitation, compared with the current climate, for all sites included in the study (Table 1).

Papers II and IV

Data and measurements for a 4-year period (2001-2004) were taken from the three common field sites used within the research programme LUSTRA (Land Use Strategies for Reducing Greenhouse Gas Emissions): Asa in southern Sweden (57°08'N), Knottåsen in the centre (61°00'N) and Flakaliden in the north (64°07'N) (Table 1, Fig. 2). At all sites the forest stands are dominated by managed middle-aged Norway spruce (Picea abies [L] Karst). In Paper IV, only data from Flakaliden were considered.

At each site, mean hourly data were recorded for climatic variables (global radiation, air temperature, relative humidity, precipitation and wind speed), fluxes of CO₂, heat and water (using eddy covariance method) and soil temperature. Pools of C in trees and field layers and litter production
both as litterfall and as fine root litter (determined using a mini-rhizotron technique) were measured, as were soil C and N pools, fluxes of DOC and soil physical properties. The measurements were conducted at both dry and mesic plots within a hydrological transect.

Model description
The model used in the simulations in Papers I-IV, the CoupModel (Jansson & Karlberg, 2004), formerly known as the SOIL or SOILN-model (Jansson & Halldin, 1979; Eckersten et al., 1998), is a coupled ecosystem model based on a balance between abiotic and biotic processes in the soil-plant-atmosphere system (Figure 3). 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. Carbon 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 used are calculated for each respective plant layer. Competition is enabled between different plant layers with respect to the interception of light, uptake of water and N. A detailed description of the most relevant parts of the model for the simulations presented in this thesis can be found in Paper I. In addition, a detailed review of the model and how it has been used to simulate water, heat and N conditions for arable land and forest in the Nordic countries has been made by Jansson et al. (1999).

Figures 3. Schematic picture of the CoupModel, with water and energy flows to the left and carbon and nitrogen to the right.

Modelling approach and parameterisation
Regional scale approach
The development of a managed Norway spruce ecosystem with both tree and field layers was simulated (Papers I and III). 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 approach chosen 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.

General guidelines from the Swedish Forest Agency (2005) regarding forest management were used in the simulations, i.e. one cleaning after 10 yrs, followed by the first thinning after 40 yrs and the second and last thinning after 80 yrs. The same management regime was assumed for all regions along the transect.

In Paper I, three different approaches for N supply to the plants were used. Measured tree biomass was used to calibrate different levels of decomposition rate and organic N uptake and in a third approach the calibra-
tion was performed under the assumption of a stable soil C/N ratio during the simulation period. Only N, identified as the main limiting nutrient for tree growth in the system studied (Tamm *et al.*, 1999), was considered in the simulations.

**Climate change application of regional approach**

The third approach in Paper I was considered the most reasonable and these simulations were consequently used as the reference (current) simulation in Paper III.

**Downscaling of regional approach to site-specific scale**

Based on the simulations from the third approach in Paper I, as described above, the development of the managed Norway spruce ecosystems at the three LUSTRA sites, with both tree and field layers, was simulated from plantation to the measurements performed in 2001-2004 (Paper II). For each LUSTRA site, the parameter set from the corresponding regional site was used (Fig. 2). Forest management was based on site-specific information.

**Site-specific calibration**

In Paper IV, Bayesian methodology was used to calibrate 33 parameters of relevance for the C budget as the plant and soil dynamics during 4 years in a boreal Norway spruce forest stand were simulated. Based on the findings in Paper II, an extra soil fraction representing coarse debris and stumps was added.

**RESULTS AND DISCUSSION**

**Energy and water interactions**

**Model predictions of abiotic conditions based on climate change scenarios (Papers I and III)**

The influence of above-ground climate on below-ground climate was clearly shown in Paper I as differences between mean annual soil temperature at 10 cm depth and mean air temperature. In the north the difference was +2 °C and thus the model successfully accounted for the major insulation factor in the plant-soil system. The main insulation effect was presumably from snow, although the field layer could also have had an effect. The modelled difference of +2 °C is in accordance with values reported by Beskow (1935). In the southern ecosystem the soil temperature was slightly colder than the air temperature, and thus there was no insulation effect in this region. A reasonable explanation for the different behaviour in the south, apart from the generally snow-free conditions during wintertime, was the denser tree canopy insulating the below-canopy environment from radiation. The various relationships between air and soil temperature along the north-south transect were altered in the climate change scenarios (Paper III), where the northern site did not experience the same increase in mean annual soil temperature as the southern site. This was because the reduced snow depth and snow cover period counteracted the increased air temperature at the northern sites, resulting in hardly any change in soil temperature during winter and relatively small overall increases in mean annual soil temperature (Fig. 4). Consequently, the mean annual maximum frost depth was not affected significantly at the two northern positions along the transect. Obviously, the combination of the remaining relatively deep soil frost and the increased soil temperature during the vegetation period will be very important for the functioning of the northern ecosystem. On the other hand, in the south the soil temperatures increased both during summer and winter (Fig. 4) and soil temperature remaining above 0 °C during winter will be important for the functioning of the southern ecosystem, since it is likely to have an impact on soil carbon dynamics.

**Model performance compared with measured abiotic conditions (Paper IV)**

Simulated soil temperature in general showed good agreement with measured data, but with a tendency to overestimate the amplitude, i.e. too warm in summer and too cold in winter (Fig. 5). The overestimation during summer was larger than the underestimation during winter, resulting in a mean error (ME) of around 1 °C for dry plots and
close to 0 °C for mesic plots (i.e. the dry plots were colder than the mesic plots). This was unexpected and opposed to the patterns found in soil temperature measurements at the other LUSTRA sites (measurements not presented) where the mesic plots showed systematically lower soil temperatures. The colder dry soils at Flakaliden were probably caused by differences in winter temperatures or in snow cover, but need further analysis to be clarified.

In general the model showed reasonable agreement with net radiation (RNT), latent heat flux (LE) and sensible heat flux (H), although systematic differences for LE in particular were obvious (Fig. 5). Simulated RNT dynamics were underestimated during late winter 2001 and also, though not equally apparent, during the same period 2002. Latent heat flux was largely overestimated during May to September for both 2001 and 2002, whereas H showed opposing patterns so that when LE showed good agreement H did not, particularly during the winter 2001/2002. The ME for both LE and H confirmed the overestimation, though at a higher degree for LE. Underestimated evaporation in the measurements, especially evaporation from intercepted precipitation, is one likely explanation for the underestimated LE in the simulations (Gustafsson et al., 2004). Another explanation is the compromise in the calibration process, where LE and H were correlated to the same parameter but with different signs.

Plant carbon dynamics

Data on plant carbon pools and litter production (Papers I, II and IV)
The C pools in trees at the LUSTRA sites (Papers II and IV) were in accordance with the national pattern (Skogsdata, 2003) described in Paper I (Table 1, Fig. 7). Litter input from trees followed the expected gradient in tree growth, with the highest values in the south and the lowest in the north (Table 3). Field layer composition at
the respective sites also followed the general national Swedish pattern, and the measurements showed that these parts of the ecosystem only made up a small fraction of the C pool of living biomass, between 4-10% compared with the C pool in tree biomass (Table 1). However, one striking result in Paper II was the high input of litter, mainly as fine root litter, from the field layer vegetation at the two northern sites Knottäsen and Flakaliden. When the litter input from the field and bottom layer vegetation was included, the difference in total litter production between the sites almost disappeared (276 g C m$^{-2}$ yr$^{-1}$ at the southern site Asa, this is compared with 314 C m$^{-2}$ yr$^{-1}$ at Knottäsen and 249 g C m$^{-2}$ yr$^{-1}$ at Flakaliden) (Table 1). The measurements presented in Paper II thus suggest that litter production from field and bottom layer vegetation makes a significant contribution to soil C input in boreal coniferous forest ecosystems. Existing data on litter production by field layer (dwarf shrubs and perennial grasses) and bottom layer vegetation in such forests is sparse. Estimates of gross primary production (GPP) and net primary production (NPP) from Scots pine forests in Finland (Mälkönen, 1974; Kolari et al., 2006) and from a black spruce forest in Canada (O’Connell et al., 2003) support the view that litter from field layers might be of significance. These authors reported values between 13-29%, compared with 5-21% at the LUSTRA sites in the present study where the higher values were obtained at the most northern site and a field and bottom layer biomass in steady state was assumed for a 4-year period.
the growing tree with N were simulated, and it was concluded that the simulated forest ecosystems needed a supplementary mechanism, in addition to what could be supplied from N mineralisation, in order to agree with measured standing stocks. The study in Paper I thus supported the conclusion of earlier studies using the SOIL-N model by Beier et al. (2001). Näsholm et al. (1998) has presented experimental evidence showing that organic N uptake by plants can occur in boreal forest ecosystems, while DeLuca et al. (2002) reported that boreal forests of northern Scandinavia take up 0.15 to 0.2 g N m\(^{-2}\) yr\(^{-1}\) through N-fixing bacteria in symbiosis with feather mosses. However, the extent to which the different model approaches for supplying N to growing trees would apply in different geographical regions is still an open question.

Simulated tree growth was overestimated in the early stages of stand establishment in the north, while it was underestimated in the south (Fig. 7). Several factors could explain this discrepancy. One contributing factor could be that the simulations performed in Paper I 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 or competition between the field layer and tree seedlings in...
the early phases, should perhaps have been more site-specific or preferably region-specific. Here, the same parameters were used in all simulations. This discrepancy was considered to be the main explanation for the underestimated tree growth in Paper II, where the regional patterns did not coincide with site-specific measurements in that the modelled values ranged between 44-70% of the measured values. However, as the simulated standing biomass was in relatively good agreement with measurements, so too were the litter production from trees and the relative contribution from above- and below-ground plant parts (Table 1).

The simulated field layers in Paper I showed different dynamics from north and south, as a consequence of different LAI values in the tree layer, which were also reflected in the amount of absorbed radiation. The field layer in the north absorbed 19% of total absorbed global radiation in the ecosystem compared with only 6% in the south, i.e. values close to those discussed above. This relationship, and thus the importance of the field layer for the C balance, was also seen in the contribution to the total litterfall of the ecosystem, which amounted to 22% in the north compared with 9% in the south (Table 1). The model captured the general national trend, with a significant contribution to total litter production in the north and a minor contribution in the south. However, the large input of root litter from the field layer vegetation, as indicated by the measurements, was not reflected in the simulations. This was also found in Paper IV, where a thorough calibration process based on site-specific information was conducted and where the simulations were successful in describing a C budget for the simulated forest ecosystem (Table 2). However, the fine root litter production from the field layer was largely underestimated, and only around 10% of the measured litter production was accounted for in the simulations (Table 1). For the field layer, which has a much higher turnover rate of the total biomass, the litter production could only have been increased by a sub-

Table 2. Carbon budget from Flakaliden (Papers II and IV) and from Lycksele and Ljungbyhed (Papers I and III) with responses for GPP and soil decomposition. The C budget components are average values for the respective simulation period (g C m\(^{-2}\) yr\(^{-1}\)).

<table>
<thead>
<tr>
<th>C budget component</th>
<th>Measurement</th>
<th>Simulation II</th>
<th>Simulation IV</th>
<th>Simulation I/III(^{a})</th>
<th>Simulation I/III(^{a})</th>
</tr>
</thead>
<tbody>
<tr>
<td>GPP</td>
<td>790</td>
<td>641±74</td>
<td>627/199</td>
<td>1275/544</td>
<td></td>
</tr>
<tr>
<td>Total ecosystem resp.</td>
<td>683</td>
<td>570±55</td>
<td>562/183</td>
<td>1115/506</td>
<td></td>
</tr>
<tr>
<td>NPP</td>
<td>321</td>
<td>277</td>
<td>267/60</td>
<td>463/120</td>
<td></td>
</tr>
<tr>
<td>NPP/GPP</td>
<td>0.41</td>
<td>0.43</td>
<td>0.43-0.03</td>
<td>0.36/0.04</td>
<td></td>
</tr>
<tr>
<td>Soil heterotr. respiration</td>
<td>214</td>
<td>207±31</td>
<td>202/44</td>
<td>303/82</td>
<td></td>
</tr>
<tr>
<td>NEP (total)</td>
<td>96 (^{1})</td>
<td>107</td>
<td>71±37</td>
<td>65/16</td>
<td>160/38</td>
</tr>
<tr>
<td>NEP (night-time)</td>
<td>-336 (^{1})</td>
<td>-526 (^{1})</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NEP (daytime)</td>
<td>347 (^{1})</td>
<td></td>
<td>339 (^{1})</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Change of plant biomass</td>
<td>201</td>
<td>115</td>
<td>138±37</td>
<td>54</td>
<td>115</td>
</tr>
<tr>
<td>Total litter production</td>
<td>217</td>
<td>207</td>
<td>141(^ {4})</td>
<td>201/42</td>
<td>327/80</td>
</tr>
<tr>
<td>Change of soil C</td>
<td>-105</td>
<td>-8</td>
<td>-69/18</td>
<td>-3/-1</td>
<td>24/-2</td>
</tr>
</tbody>
</table>

\(^{1}\)Mean value 2001-2002 \(^{2}\)Current climate/change with SWECLIM A2

\(^{3}\)Current climate\% change with SWECLIM A2 \(^{4}\)from mean parameter simulation (MeanP).
stantial increase in GPP. Obviously the estimated light interception by the field layer in the model was not sufficient to explain such a high GPP of the field layer and simultaneously keep the LAI of the tree layer to the observed mean value of 3.5. So, either there were errors in the measurements and/or the estimation of the error in the calibration was incorrect, or the model used was incorrect or based on the wrong assumptions. Obviously, measurements need to be re-evaluated or some major assumptions in the model simulations have to be changed.

Model predictions of GPP and NPP based on climate change scenarios (Paper III)

Substantial increases in GPP on an annual basis were obtained for both climate scenarios at all sites, ranging from 24-32% in the north to 32-43% in the south (Table 2). The difference between north and south was less pronounced for NPP, as an effect of increased maintenance respiration especially in the south. This indicates the importance of considering plant respiratory losses in order to describe effects and changes in plant biomass and thus effects on litter production. Air temperature effects were relatively similar at all latitudes, whereas the effects of changed water and nitrogen stress showed large differences between the sites (Table 2).

For the most northerly site, the enhanced soil temperature decreased the water shortage in May, corresponding to a shift of 2-3 weeks, whereas the major influence on the most southerly site, besides improved conditions in the spring, was an enhanced water stress during the summer counteracting the improved nitrogen conditions (Fig. 6). The main explanation for this effect in the south was the reduced summertime precipitation rates, but also the longer growing season, increased LAI values and increased evaporative demand from the atmosphere. The N limitation on GPP shifted so that the southern sites became less N limited due to increased mineralisation of the soil N pools, especially during late winter and spring (Fig. 6). On average, the mean N limitation on GPP decreased at all sites, but only by about 5% in the north, whereas it decreased by more than 30% in the south (Table 2). A possible explanation is that the higher soil C/N ratio in the north did not respond with the same rate of N supply to the trees as was the case in the south, with its lower soil C/N ratio. The strong N limitation at the northern site persisted, whereas the southern site could benefit more efficiently from the enhanced soil respiration. Hence, the simulations demonstrated that GPP was governed to a large extent by indirect effects of climate factors on nitrogen availability, and to a lesser extent by the direct effects of temperature and water conditions. These results are supported by soil heating experi-

![Figure 7. Simulated tree biomass (solid line) and standing stock volumes (filled circles) from NFI (Skogsdata, 2003): a) Lycksele and b) Ljungbyhed.](image-url)
ments conducted in a northern Norway spruce forest in Sweden, which suggested that the increased GPP was related to an increased soil N supply rate (Strömgren & Linder, 2002). The overall simulation results of increased GPP are also similar to what has previously been reported by Kellomäki & Väisänen (1997) for similar forests in Finland. However, these authors explained their increase mainly as a result of CO$_2$ increase in the atmosphere and not as increased nitrogen availability.

Soil carbon dynamics

**Measurements of soil carbon pools and DOC (Paper II)**

The pools of SOC at the LUSTRA field sites followed the general national trend, with increasing pool size from north to south (Olsson et al., 2006) and with the pool at the southern site about 1.5 times larger than that at the northern site (Table 1). A major fraction (77-88%) of SOC was found in the mineral soil, which is in accordance with findings by Callesen et al. (2003). The soil N also showed increased pools from north to south and consequently the C/N ratio of the soils had a trend with the highest values in the north. Nitrogen pools followed the national gradient in N deposition, though it is most likely that this gradient is also related to other factors, such as climate and historical land use.

The results regarding DOC in Paper II showed that on average the equivalent of 10% of the total litter input to the O horizon was leached downwards in the profile and on average 95% of this was captured in the top 50 cm of the mineral soil. Compared with the input of root litter, the flux of DOC to the mineral soil ranged between 9-19% of the total C input. However, when the quality of the two different substrates was considered, the DOC and root litter seemed to be of approximately equal importance for the build-up of organic C in

![Figure 8. Simulated GPP (upper panels), NPP (upper middle) soil heterotrophic respiration (middle lower), and NEP (lower) as a function of mean monthly values during 100 years according to current climate and scenarios B2 and A2, representing two positions in a transect from north (left panels) to south (right panels) through Sweden.](image-url)
the upper 50 cm of the mineral soil at the LUSTRA sites. This apparently important contribution to the build-up of recalcitrant soil C and the assumptions behind these estimations need more research but the finding is considered to be a reasonable first estimate.

**Model estimates of soil carbon dynamics (Papers I, II and IV)**

In Paper I, 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%) were similar to values reported in the literature (Högberg et al., 2001; Schuur & Trumbore, 2006). The peak in annual heterotrophic soil respiration in simulations occurred in July for all the sites and the annual pattern largely followed the soil temperature pattern (Fig. 8). The fact that soil temperature was more important than soil moisture in these results may be a consequence of the study being restricted to well-drained soils, and it is likely that results would be different if a wider moisture regime were considered.

In Paper I, three different approaches to supply the growing tree with N were simulated. With the first and second of these approaches the soil C/N ratio deviated greatly from the current value and there were massive changes in the soil C pool, most pronounced at the most northerly site (Fig. 9). An approach where the soil C/N ratio was kept stable during the simulation period was thus considered to give more reliable and consistent patterns regarding soil C and N dynamics. One consequence of this approach was that the parameter deciding the decomposition rate for the soil C fraction with long turnover rate in the CoupModel ($k_h$) had to be set higher at higher latitudes. This conclusion was also drawn from ratios constructed between the most southerly site and the most northerly site regarding the major components of the C budget. The simulated litter production was 1.61 times higher in the south than in north but at the same time the simulated climatic effect on the SOC decomposition rate was 1.75 times higher, which was largely related to the higher soil temperatures in the south. This suggested that, given a long-term perspective, there should be no difference between the soil C pools in the north and those in the south. However, the ratio for the current soil C pool was 1.52, indicating a differentiation of decomposition rates along the transect. Although the simulations in Paper IV were conducted at only one site, the calibrated parameter value for $k_h$ was in accordance with the value found in Paper I for the corresponding northern site. The measurements at the LUSTRA sites in Paper II, with relatively similar litter production along the transect (Table 1), indicated an even more pronounced differentiation of the decomposition rates, given the same climatic effect on decomposition as above. One
possible explanation for the different rates could be that in Sweden, the warmer climate coincides with increased N status, as indicated by the soil C/N ratio, and there is experimental evidence indicating that decomposition of SOC proceeds at a slower rate in N-rich environments (e.g. Neff et al., 2002; Olsson et al., 2005). Another possible explanation could be that the temperature sensitivity of SOC decomposition differed from that used in the simulations. However, even if no response function for soil temperature had been considered at all, which has been proposed (e.g. Giardina & Ryan, 2000), the decomposition rate of the humus pool in the north would still have been higher, in order to meet measured tree growth.

Given the assumption of a stable soil C/N ratio, relatively small losses of C were simulated from the soils at the two more northern sites (-3 g C m$^{-2}$ yr$^{-1}$ and -2 g C m$^{-2}$ yr$^{-1}$) (Table 2), whereas the sites in the south of Sweden at the same time sequestered 9 g C m$^{-2}$ yr$^{-1}$ and 24 g C m$^{-2}$ yr$^{-1}$, figures that can be compared with those from a recent study by Peltoniemi et al. (2004). Those authors 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 (average 5 g C m$^{-2}$ yr$^{-1}$) in organic C pools in the O horizon with increasing stand age, with no detectable change in the mineral soil. Unsurprisingly, the results in Paper II showed similar figures for soil C change during the period 2001-2004, ranging from -8 g C m$^{-2}$ yr$^{-1}$ in the north to +9 g C m$^{-2}$ yr$^{-1}$ at the southern LUSTRA site (Table 2). In contrast, budget calculations for the soil at the northern site (Flakaliden), using figures on NEP and C accumulation in trees, suggest that the soil lost a significant amount of C, namely 100 and 86 g C m$^{-2}$ yr$^{-1}$ during 2001 and 2002 respectively (Lindroth et al., 2006). One source of C not considered in the simulations was the decomposition of coarse debris and stumps remaining from the clear-cut in 1963. However, according to a simulation performed using the Q-model (Ågren and Bosatta, 1998), these components might only account for approx. 20 g C m$^{-2}$ yr$^{-1}$ (G. Ågren, pers. comm.). So, even when losses from stumps and coarse debris and uncertainties in measurements were taken into account, the C budget strongly suggested that the soil at Flakaliden was a net source of C during 2001-2002.

In the simulations in Paper IV, an extra pool of soil C (Litter 2) was added in order to mimic the coarse debris and stumps. Total losses of soil C (Table 2) were in agreement with the calculated changes reported in Lindroth et al. (2006), with the major proportion coming from the Litter 2 fraction. This loss was more than twice that estimated by the Q-model. However, if the Litter 2 fraction not had been included in the simulations, the losses from the other fractions would have been higher. Other possible explanations for the great losses of soil C are: (i) some fundamental change in the regulating factors; (ii) unknown systematic errors in the eddy correlation measurements; (iii) large between-year variations which were not captured by the regionally based model. The latter refers to the site-specific measurements, which were based on only two years (with gaps), and thus possible large between-year variations could have been missed given this short period. Obviously, further research is needed to resolve this question.

**Model predictions of soil carbon dynamics based on climate change scenarios (Paper III)**

Soil carbon dynamics (Fig. 8) and the related change in the soil C pool (Table 2, Fig. 10) showed minor changes as a consequence of the climate change scenarios, as opposed to the increased tree growth. One main explanation for this is the inert behaviour of the ecosystem, where the change in soil C was shown as the result of two counterbalancing fluxes so that the increased litter production due to increased tree growth was mirrored in increased soil heterotrophic respiration, resulting in only small changes in soil C as a consequence of climate change (Table 2). One difference in seasonal patterns was that the most northerly site did not have altered respiration in the winter, whereas the most
southerly site increased respiration losses substantially during the winter period. This was a direct effect of the asymmetry in the relationship between air temperature and soil temperature, caused by the influence of snow depth and soil frost as discussed above (Fig. 4). Relative changes because of climate change during the summer, when the highest respiration losses take place, were more uniform for all the different sites.

**Net ecosystem production**

**Model performance compared with measured NEP (Papers II and IV)**

In Paper II, the regional representation of annual average NEP value (Table 2) for the Flakaliden site (107 g C m\(^{-2}\) yr\(^{-1}\)) was in accordance with the measured NEP (95 g C m\(^{-2}\) yr\(^{-1}\)). However, as discussed above, both simulated tree growth and simulated changes in soil C showed differences compared with measured data. The NEP in Paper IV was the result of the site-specific Bayesian calibration procedure. The simulated dynamics of NEP, as aggregated values (Fig. 11a), showed good agreement during winter periods but the results during the summer period were less clear, especially during 2001, where several negative peaks in measured NEP were not represented in the simulated values. The mean annual NEP was underestimated compared with measurements, but was still positive and showed relatively large variation (Table 2). However, it should be emphasised that the measurements were the mean annual values for 2001-2002 and the simulated NEP was a mean value for 2001-2004. Furthermore, the summer of 2001 was the period with the largest gaps in measurements, which is likely to have affected the simulation results, especially as they coincided with the most

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*Figure 10. Simulated mean annual values of net ecosystem exchange with their corresponding partitioning into change in soil storage, export of dissolved organics, change in tree biomass and export of stem in conjunction with thinning for four positions in the transect according to current climate (C), scenario B2 and scenario A2 (left to right bare respectively).*
dynamic period during the yearly cycle, compared with 2002 where the gaps were not only less but also more evenly spread in time.

The NEP was separated into night-time values (global radiation <0.5 MJ m\(^{-2}\) day\(^{-1}\)), which consists of periods without photosynthesis, and daytime values (global radiation >0.5 MJ m\(^{-2}\) day\(^{-1}\)) where both photosynthetic uptake and respiratory losses are included (Fig. 11b-c). The simulated values during night-time indicated that respiratory losses were overestimated, especially during summer. The most likely explanation for this overestimation was the different representation of eddy flux measurements of \(\text{CO}_2\) flux above the canopy and the model assumptions of steady state respiration from soil and vegetation without considering \(\text{CO}_2\) storage within the canopy. This effect is most evident on calm nights with low turbulence. The overestimation in night-time respiratory losses was also seen in the annual mean value (Table 2), and was the main explanation for the underestimated annual mean total NEE, as the daytime values were in agreement with measurements. The daytime values were underestimated during spring and autumn, overestimated during summer and in agreement with measured data during the winter. The reason for this systematic difference between model and measurements was not addressed within the scope of the study.

**Model estimates and predictions of NEP based on climate change scenarios (Papers I and III)**

The major influx of C occurred in May-June for the current climate conditions and slight losses could be seen for autumn and winter (Fig. 8). The NEP consisted mainly of a change in tree biomass and in export of stem biomass at thinning, whereas the change in soil C was a small fraction (Fig. 10). The climate change simulations showed increased positive values, especially during March-June, with the same general tendency remaining for the different components of the net ecosystem flux before and after the climate change.

**Uncertainties and different scales**

In Paper IV, coupled C, water and heat fluxes were described together with estimated uncertainties for all the major components of the simulated C budget. The uncertainties, which tend to represent a weakness in goodness of fit calibrations, were relatively low and were the result of 33 calibrated parameters according to the Bayesian methodology used. All calibrated parameters showed correlations to other parameters (>0.3 or < -0.3), on average to 12 other parameters, which illustrate the high degree of coupling between the different sub-models and processes included in the model. It also emphasises the importance of considering parameters in a process-based model (PBM), not as a singularity but in...
relation to other parameters, or preferably like a cluster of parameters related to specific measurements or affecting a certain model output. Hence, the simulations demonstrated that uncertainty in our estimates could successfully be reduced and that the dependence between different parameters could be clarified. Many parameters were correlated to either measurements or model output or both, and some of the parameter correlations to model output lacked corresponding measurements of that specific entity, e.g. soil respiration. Given this, there seems to be scope for further analysis of the C budget, with decreases in uncertainties possible.

The simulations in Papers I-III lacked estimates of uncertainties. It can thus only be concluded that the simulated C budget was considered reasonable compared with other different sources and also compared with the C budget presented in Paper IV (Table 2) apart from soil C changes as discussed above. Furthermore, the calibrated parameter set in Paper IV showed general agreement with the parameter set used in Papers I-III which, apart from decomposition rates and rates for organic N uptake, was the same along the Swedish transect. The simulations with the mean parameter set in Paper IV generated a C budget in accordance with the C budget from the Bayesian calibration, but the parameter set was not independently tested, e.g. by using it in simulations at a southern site.

The CoupModel was successful in describing general patterns of C and N dynamics in a managed spruce forest ecosystem with both tree and field layers, along a Swedish climatic gradient. This was true for the simulations in Paper I, which were based on regional data and run over 100 years, as well as when these simulations were compared with site-specific measurements corresponding to a 4-year sub-period during the 100-year period (Paper II). This demonstrates the ability of the model to handle different scales in time and space under varying regulating factors, and hence strengthens the credibility of the climate change scenarios presented. As stated above, reasonable results using site-specific data measured during a 4-year period were presented in Paper IV. However, the extent to which these parameter values would be able to describe a C budget during 100 years according to regional data was not demonstrated, although it was obvious that the large losses of soil C in Paper IV were not in accordance with regional patterns estimated in Paper I. Regardless of the reason behind this discrepancy, it shows that we have to be careful when transferring information from one scale to another. The issue of how extensive measurements must be to capture variations within days, between days or between years and to be suitable for long-term predictions is still unclear. A two-year period seems too short, at least if the model is expected to use the data as a basis for long-term simulations. Furthermore, this short-term scale of measurement is unsuitable not only for between-year variations, but also for ecosystem dynamics on a larger scale, e.g. as indicated in Paper I, where tree growth deviated from regional patterns (Fig. 7).

**Conclusions**

Reasonable estimates of annual changes in forest soil C pools for different regions along the Swedish climatic gradient were presented, and could thus be used for upscaling to national level. Predictions of the effects of climate change scenarios on the C budget in these ecosystems were also presented and considered reasonable. These estimates and predictions were based on data from regional statistics of soil and plant pools and a process-based model that successfully described general patterns of C and N dynamics in a managed spruce forest ecosystem with both tree and field layers.

Several factors important for the C budget were identified and quantified and could thus be important to consider for modellers and managers. These included the need for another source of N in addition to mineralised N in order to meet measured standing stocks in the simulated tree growth; different decomposition rates for the soil C fraction with long turnover rate along the Swedish
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transect; and the importance of DOC as a contributor to the build-up of recalcitrant soil C. In addition to these factors affecting current forest C dynamics, two important limiting factors for tree growth, water and N, showed differing effects along the Swedish transect as a consequence of climate change.

Using a Bayesian calibration procedure the fluxes of C, water and heat for one boreal Norway spruce forest stand were successfully described, in accordance with site-specific measurements and with quantified uncertainties for all major components in the C budget. However, the simulated soil C change, which was in agreement with measurements, differed greatly from the simulation estimates based on regional data, where the soil C losses were much less. The reason behind this discrepancy when the model was based on data from different scales was not clarified.

Measurements of litter production along the Swedish transect showed basically no difference in litter production between the northern and southern forest ecosystems, mainly due to large inputs of litter from field layer fine roots. Regardless of scale, the model was not able to describe this large C flux.

**Future research**

Carbon budgets of forest ecosystems must be based on reliable methods and data, where both measurements and models are likely to be included and where uncertainties must be addressed. The uncertainty and validity of data originating from different temporal and spatial scales are still not clear. This thesis, which used a model (CoupModel) as a tool to understand basic spruce forest C budgets, identified large differences regarding soil C change between using measurements from a regional long-term scale and site-specific data from a short-term scale. This discrepancy needs further research to be resolved.

Another factor with a major bearing on the C budget in forest ecosystems and where the model and measurements deviated was the importance of litter production from the field layer. To get agreement, the empirical data would need to be re-evaluated or some major assumptions in the model simulations would have to be changed.

Finally, the Bayesian method is likely to give good results in calibration of process-based models on a long-term scale, in order to study allocation patterns and the competition between tree and field layers. Both these factors are likely to have significant effects on the understanding of C dynamics and management of forest ecosystems in the northern hemisphere.
REFERENCES


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]


