

## How Forest Management and Climate Change Affect the Carbon Sequestration of a Norway Spruce Stand?

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### ABSTRACT

Mitigation of climate change by forest carbon sequestration is one of the ecosystem services that will be taken into account in future forest planning. The potential capacity of forests to sequester carbon is determined by edaphic and climatic factors, but the actual carbon accumulation is highly controlled by management. The effects of the management practices on stand development are successfully analyzed with traditional stand simulators that rely on empirical data. One of the current challenges is to understand how ecosystem services, such as carbon sequestration and timber production, can be managed in the changing climate, i.e. under conditions of which there are no observations. The objective of this study was to investigate the responses of forest soil and vegetation to a climate change under different management scenarios ranging from intensive thinning to unmanaged stands. The responses of tree growth and forest carbon sequestration to changes in temperature and precipitation (+3 °C and +10%, respectively) under different management scenarios were investigated with a process-based forest model (PipeQual) which was combined to a soil decomposition model (ROMUL) and a soil water balance model. According to our simulations, the growth response of Norway spruce to increased temperature was positive. Carbon stocks of both vegetation and soil were increased with the changing climate in all the simulated management scenarios. In the changing climate decomposition of soil organic matter was accelerated, however, increased litter input resulting from enhanced growth of vegetation compensated this decrease. Intensively harvested stands had a decreased carbon stock in the vegetation, which resulted in low litter production and decline in soil carbon stock after thinnings. The simulations with the process-based forest growth and soil model can guide management by determining a sustainable level of biomass harvest.

*Keywords:* carbon sequestration, climate change, forest management, growth modeling, soil decomposition model

### INTRODUCTION

Forest carbon sinks have a significant role in global carbon balance, and the mitigation of climate change by forest carbon sequestration is one of the ecosystem services that will be taken into account in future forest planning. Forest carbon sinks and sources resulting from forest management and land-use changes were already included in the Kyoto protocol

(UNFCCC, 1997) and, most likely, forests are increasingly considered in the future commitments under the Climate Convention. Thus, evaluation of the management systems in terms of their influence on carbon balance is needed for future planning of effective measures to mitigate climate change. The effects of climate change on coniferous forest ecosystems have been widely studied by model simulations (e.g. GE *et al.*, 2010; KELLOMÄKI and KOLSTRÖM, 1993; KELLOMÄKI and KOLSTRÖM, 1994; KELLOMÄKI *et al.*, 2008; LASCH *et al.*, 2005; MÄKIPÄÄ *et al.*, 1999;

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WANG *et al.*, 1996). The potential of forest management practices to influence the forest-atmosphere carbon balance in the changing climate can also be analyzed with process-based models (see however BRICEÑO-ELIZONDO *et al.*, 2006; LASCH *et al.*, 2005; MIKHAILOV *et al.*, 2004). Such analysis, including extreme management options ranging from non-managed forests to intensive harvests, could guide the forest policy that is aiming to mitigate climate change with modified management practices.

At a landscape scale, variation in the forest carbon sequestration results from age-class distribution and the amount of harvests, as well as from year-to-year variation of the climatic parameters (LISKI *et al.*, 2006). At a stand scale, the potential capacity of forests to sequester carbon is determined by edaphic and climatic factors, but the actual carbon accumulation is highly controlled by management, i.e., the timing and intensity of the harvests (thinning and final cutting) and the proportion of the removed biomass (LASCH *et al.*, 2005; MÄKIPÄÄ *et al.*, 1999; NABUURS *et al.*, 2008; PALOSUO *et al.*, 2008; PUSSINEN *et al.*, 2002). The effects of management on forest carbon stocks are typically evaluated with stand simulators that rely on empirical data (e.g. HYNYNEN *et al.*, 2005; PALOSUO *et al.*, 2008), but their applicability to new stand structures and changing climatic conditions cannot be validated. One of the current challenges is to understand how ecosystem services (e.g. carbon sequestration, timber production, ecosystem functions maintained by diversity of species) can be managed in the changing environment, i.e., under conditions of which there are no observations.

Changes in the climate will affect both the primary production and the decomposition of organic matter. Understanding tree growth and its interaction with soil processes is required for projections of forest carbon sequestration potential in different management and climate change scenarios. Both at large scale and at a stand scale, the carbon stocks of vegetation and soil may change in either direction, which underlines the importance of including all relevant carbon pools into the analysis (LISKI *et al.*, 2006; MÄKIPÄÄ *et al.*, 1999). KARJALAINEN *et al.* (2003) predicted that, under changing climatic conditions, the carbon sinks of both trees and soil will be larger than under the current climatic conditions. In Finland, average growth was predicted to increase by 30% resulting in a 30% increase in biomass C stock and a 7% increase in soil C stock (KELLOMÄKI *et al.*, 2008). In southern Finland, the growth response of Norway spruce to climate change was predicted to be marginal or even negative (KELLOMÄKI *et al.*, 2008). On the other hand, JANSSON *et al.* (2008) predicted that light use efficiency and water use efficiency will be improved in the future climate, resulting in increased productivity of Norway spruce stands. Based on simulations of various management alternatives with a process-based model, LASCH *et al.* (2005) concluded that the average values of carbon stocks showed hardly any net effect of climate change in the temperate mixed pine-broadleaved forests. Thus, the overall sensitivity of carbon sequestration of the boreal spruce stands to climate change remains unknown.

Several studies have indicated a considerable potential for carbon sequestration with alternative management practices (e.g. KELLOMÄKI *et al.*, 2008; e.g. LASCH *et al.*, 2005; PUSSINEN *et al.*, 2002). In general, long rotations and low intensity of thinnings have been shown to be favorable for forest carbon sequestration (LASCH *et al.*, 2005; LISKI *et al.*, 2001; PUSSINEN *et al.*, 2002). Furthermore, climate change has been predicted to enhance carbon sequestration in managed forests (e.g. HYVÖNEN *et al.*, 2007; KELLOMÄKI *et al.*, 2008). Currently, carbon sequestration is not a major objective of forest management. Rather, forests are managed for sustainable timber yield and economical profitability. The influence of more intensive harvests proposed by economical optimization of forest management (HYYTÄINEN *et al.*, 2004) on forest carbon balance has not been analyzed.

With a process-based growth model (KANTOLA *et al.*, 2007; MÄKELÄ and MÄKINEN, 2003) combined to a similar model of decomposition of soil organic matter and a soil water model (CHERTOV *et al.*, 2001), the responses of photosynthesis and respiration as well as the allocation of photosynthetates and dynamics of organic matter in the soil can be analyzed. We believe that analysis on growth response of Norway spruce with a process-based model will yield improved understanding of the effects of management practices on forest growth and carbon sequestration in the changing conditions. Coupling of the dynamic stand and the soil models makes it easy to determine the whole dynamics of carbon within the forest ecosystem, including both the stand and C sequestration into the soil. With the designed set of growth and soil models, one can analyze differences of the proposed management scenarios in terms of timber production and carbon stock changes of forest vegetation and soil. The relative sensitivity of carbon sequestration in the different management scenarios to the changing climate will be assessed in order to understand the potential risks and sensitivity of forest carbon to management and climatic conditions.

The objective of this study was to investigate the responses of tree growth and forest carbon sequestration in Norway spruce stands to changes in temperature and precipitation under different management scenarios. The management scenarios were: (i) thinnings from below and final harvest according to the current recommendations, (ii) a management plan based on economic optimization (delayed thinnings from above with higher removals and early harvest), (iii) natural development without management.

## METHODS

### Modelling

The model troika used in this study consists of three process-based models: the PipeQual stand growth model (KANTOLA *et al.*, 2007; MÄKELÄ and MÄKINEN, 2003; MÄKELÄ *et al.*, 2008), the Romul decomposition model for litter and soil

organic matter (CHERTOV *et al.*, 2001) and a simple model for the soil water content and temperature (Fig 1). The stand growth model simulates the development of the stand depending on environmental conditions and management and produces, among other things, output of the produced litter, which is then used as an input for the decomposition model. The soil climate model uses daily weather data (air temperature, irradiance, water vapor pressure deficit and precipitation) to simulate soil conditions which are then used as an input for the decomposition model. The decomposition model simulates the dynamics of the organic matter in the forest floor and soil.

The process-based growth model PipeQual (KANTOLA *et al.*, 2007; MÄKELÄ, 1997; MÄKELÄ and MÄKINEN, 2003) was used as the stand growth simulator (Fig. 2). The model represents trees in terms of biomass and form in a hierarchical structure comprising tree, whorl, and branch levels. At the tree level, the biomass components include foliage, fine roots, stem, branches, and transport roots biomass, and the tree form is described by tree height, diameter, crown ratio, crown width, and root system extension. At the whorl level, the whorl module describes the vertical structure of stem and branches. At the branch level, the branch module provides the annual dynamics of individual branches and their properties in each whorl. The stand consists of several tree size classes each represented by a mean tree of the size class, and the distribution of trees is assumed random.

Tree growth is calculated on the basis of photosynthesis and the growth and the maintenance respiration of live biomass components. Tree photosynthesis is based on the canopy GPP and its allocation between trees on the basis of their size and position with respect to shading. Total growth is allocated to the biomass components on the basis of structural constraints, including the pipe model (SHINOZAKI *et al.*, 1964) and the theory of crown allometry (MÄKELÄ and SIEVÄNEN, 1992). These also determine the extension growth of the dimensional variables. Mortality is calculated using a semi-empirical model and is mainly related to competition for light.

The impacts of weather have been included in the present (preliminary) model version through effective temperature sum (ETS), which in Finland has been found to be a good proxy for the climate-related variation of GPP (HÄRKÖNEN *et al.*, 2010). The effective temperature sum (ETS) was defined as the sum of those daily mean temperatures that exceeded the threshold temperature (+5 °C). ETS has an impact on the stand level GPP (HÄRKÖNEN *et al.*, 2010), the specific maintenance respiration rates, and the allocation of growth between foliage and wood (PALMROTH *et al.*, 1999).

The Romul decomposition model was presented by CHERTOV *et al.* (2001), and is a further development of the earlier SOMM model (CHERTOV and KOMAROV, 1996; CHERTOV and KOMAROV, 1997). Our application utilizes a new set of functions defining the decomposition rates of soil ash and nitrogen content, temperature, and soil water (CHERTOV *et al.*, 2007) (Appendix 1). The Romul model handles the litter as separate cohorts based on the

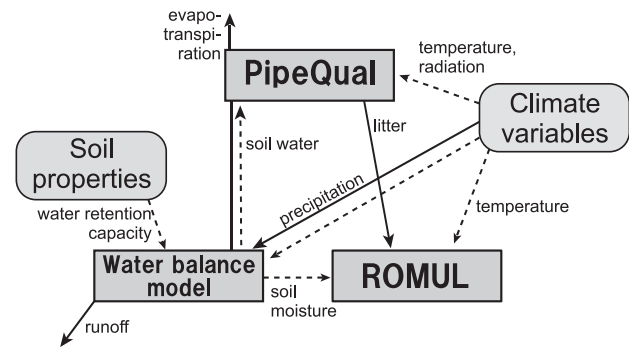


Fig.1 The applied process-based forest model (PipeQual) was combined with a soil water balance model and a soil decomposition model (ROMUL). Solid lines, flow of material (litter or water); dotted lines, influence.

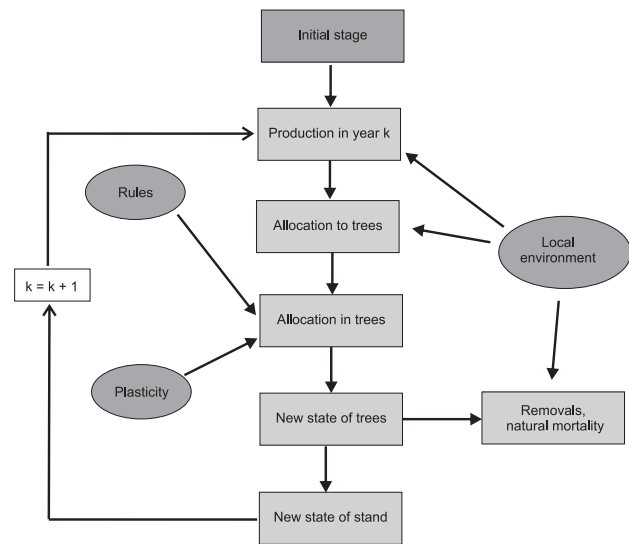
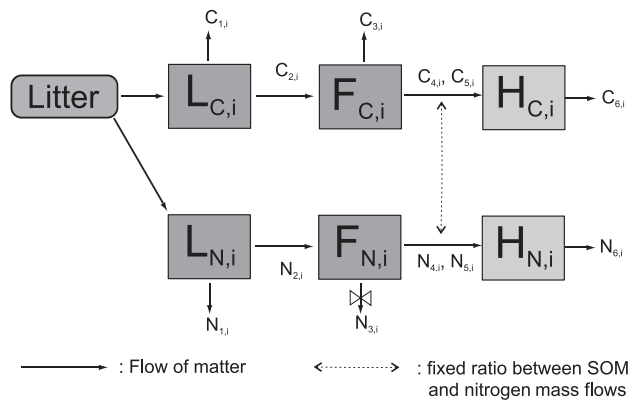


Fig.2 The structure of the stand growth model (PipeQual)

origin (litter from needles, shoots, fine roots, coarse roots and stems), which makes coupling with a stand model most straightforward. The model has two parallel mass flows, one for the soil organic matter (SOM) and the other for the corresponding nitrogen. These are presented as separate mass flows, but the nitrogen content of the organic matter in the decomposing soil affects the decomposition rate in many phases (Fig. 3).

The fresh litter enters the model in storages for undecomposed litter (" $L_{Ci}$ " for SOM and (" $L_{Ni}$ " for corresponding N, in Fig. 3), where " $i$ " refers to the separate cohorts for litter from different origins. Part of this litter is metabolized by the decomposing organisms, and the corresponding carbon is released as gaseous  $CO_2$  (flows  $C_{li}$  in Fig. 3). Majority of the organic matter ends up in a more slowly decomposing complex of



index  $i$  refers to *needle, shoot, fine root, coarse root or stem*

#### SOM / carbon fluxes

$$C_{1,i} = k_{1,i}(L_{N,i}/L_{C,i}, L_i \text{ ash content, soil T, soil REW}) \cdot L_{C,i}$$

$$C_{2,i} = k_{2,i}(L_{N,i}/L_{C,i}, L_i \text{ ash content, soil T, soil REW}) \cdot L_{C,i}$$

$$C_{3,i} = k_{3,i}(F_{N,i}/F_{C,i}, L_i \text{ ash content, soil T, soil REW}) \cdot F_{C,i}$$

$C_{4,i}$ ,  $C_{5,i}$  depend on corresponding nitrogen fluxes  $N_{4,i}$ ,  $N_{5,i}$  with a specific C/N -ratio of 24.0 for *Bacteria* and *Aithropoda*, and 12.8 for *Lumbricidae*

$$C_6 = k_6(H_N/H_C, H \text{ ash content, soil T, soil REW}) \cdot H_C$$

#### Nitrogen fluxes

$$N_{1,i} = k_{1,i}(L_{N,i}/L_{C,i}, L_i \text{ ash content, soil T, soil REW}) \cdot L_{N,i}$$

$$N_{2,i} = k_{2,i}(L_{N,i}/L_{C,i}, L_i \text{ ash content, soil T, soil REW}) \cdot L_{N,i}$$

$$N_{3,i} = k_{3,i}(F_{N,i}/F_{C,i}, F_i \text{ ash content, soil T, soil REW}) \cdot F_{N,i}$$

$$N_{4,i} = k_{4,i}(F_{N,i}/F_{C,i}, F_i \text{ ash content, soil T, soil REW}) \cdot F_{N,i}$$

$$N_{5,i} = k_{5,i}(F_{N,i}/F_{C,i}, F_i \text{ ash content, soil T, soil REW}) \cdot F_{N,i}$$

$$N_6 = k_6(H_N/H_C, H \text{ ash content, soil T, soil REW}) \cdot H_N$$

Fig. 3 A flow-chart and mass-flow functions of the ROMUL model

partly decomposed organic matter and humus (flows  $C_{2i}$  and storages " $F_{C,i}$ " in Fig. 3). Some of the material in the " $F_{C,i}$ " storages is also metabolized by the decomposing organisms, releasing a further amount of gaseous  $\text{CO}_2$  (flows  $C_{3i}$  in Fig. 3).

Parallel to the flux of soil organic matter, nitrogen in the litter is stored in the storage  $L_{N,i}$ , and it flows, as a result of decomposition, into the storage  $F_{N,i}$ . The nitrogen flux out of the system ( $N_{1i}$  and  $N_{3i}$ ), corresponding to the release as gaseous  $\text{CO}_2$  from the decomposition of SOM, is considered mineralized nitrogen, thus in a form available to plants.

The contents of the storages  $F_{C,i}$  eventually ends up in the storage of immobilized humus (" $H_C$ " in Fig. 3). There is only one common storage " $H_C$ " for immobilized humus, unlike the previous phases, where the organic matter was divided into cohorts based on the litter origins. The first three decomposition coefficients ( $k_1$ ,  $k_2$ ,  $k_3$ ) are obtained by statistical methods from laboratory experiments with different litter cohorts. The coefficients of decomposition,  $k_{i,j}$ , ( $j=1..3$ ) depend on the nitrogen and ash content of the originating cohort, as well as

the soil temperature and water content. The  $k_6$  coefficient for soil decomposition is constant, hence the decomposition of H fraction is modified only by temperature and soil moisture. The corresponding coefficient for nitrogen mineralization from the H fraction has an additional component slowing down the process when C/N ratio in the humus compartment is low (CHERTOV *et al.*, 2001).

The transformation of organic matter into the compartment  $H_C$ , i.e. mass flows  $C_{4,i}$  and  $C_{5,i}$ , is based on the assumption that all the matter in the compartment "H" is mostly produced by the metabolism of the decomposing organisms (*Bacteria*, *Arthropoda* and *Lumbricidae*), and we use a C/N ratio for these groups obtained from soil biology experiments. Therefore, nitrogen has a special role in this phase: first, the rate of nitrogen moving from compartments  $F_{N,i}$  into the compartment  $H_N$  is calculated using some modifiers in the main scheme of SOM decomposition, because carbon and nitrogen dynamics have different rates of transformation, and thereafter, a corresponding amount of organic matter, typical for the type of decomposers and depending on the C/N ratio of produced humus (24.0 for *Bacteria* and *Arthropoda* and 12.8 for *Lumbricidae*), is moved from the compartments  $F_{C,i}$  to the compartment  $H_C$ .

The immobilized humus pool is also decomposing, at a rather slow rate, modified by the soil temperature and moisture conditions. The decomposition flux, C, has a range of a minimum 1–2% annually up to 15% annually, depending on the soil texture and the clay content. Maximal rate of H decomposition may be observed for arable soils. On the other hand, as roughly half of the soil organic matter in the boreal zone is in the compartment H, the value of the rate factor  $k_6$  has a significant effect on the total storage of organic matter in the soil.

The temperature and soil moisture modifiers of the fluxes take a variety of forms, given as step-wise defined functions. Typically, all these show an optimal range of values, where the decomposition takes place at a full rate and tapers off outside the optimal conditions (Appendix 1). The optimal conditions for different fluxes are, however, somewhat different.

The soil water model is a simple application of an "open bucket" type model. In other words, it considers the soil a vessel, or a bucket, holding the water within. The bucket is filled with precipitation. The "depth" of the bucket translates into the soil water holding capacity, or the difference between saturation, at which the soil can no more hold the water, and a wilting point, at which plants cannot extract any more water remaining in the pores of the soil. Once the saturation point is exceeded, any additional water flows out of the system. Evapotranspiration (ET) drains the bucket. ET depends on stand characteristics, but most of all, environmental conditions. Here we used a simple relationship obtained as a statistical fit to evapotranspiration data from eddy covariance measurements in Hyttälä, Southern Finland (ILVESNIEMI *et al.*, 2010). Although the model is preliminary, there is already an indication that it does work for a wide variety of vegetation types and

weather conditions, even with the same parameterization (unpublished work). Therefore, the ET model was used independently of the stand model.

The ET model is as follows:

$$E_t = [E_0 \cdot f(PAR) \cdot f(T) \cdot f(VPD) + a_1 \cdot PAR + a_2] \cdot f(\theta), \quad (1)$$

where  $E_0$  is maximum rate of evapotranspiration,  $1.74 \cdot 10^2$  (mm/day), constants  $a_1 = 0.0007$  and  $a_2 = 0.0836$ ,  $f(PAR)$  is a modifier function depending on PAR,  $f(T)$  is a modifier function depending on delayed temperature average with a time constant of 14 days, and  $f(VPD)$  is a modifier function depending on the water vapour pressure deficit VPD.

Function  $f(\theta)$  is a drought modifier (DUURSMA *et al.*, 2008) based on the relative soil water content  $\theta$ :

$$f(\theta) = \begin{cases} 0, & \theta \leq 0.1 \\ \frac{\theta - 0.1}{0.05}, & 0.1 < \theta < 0.15 \\ 1, & \theta \geq 0.15 \end{cases} \quad (2)$$

The soil temperature model is a simple delayed average driven by the air temperature, with a low limiter:

$$\Delta T_{Soil} = (T_{Air}^* - T_{Soil}) / \tau, \quad (3)$$

and

$$T_{Air}^* = \max(T_{Air}, T_{min}). \quad (4)$$

where  $T_{min} = -0.45^\circ\text{C}$  = minimum soil temperature,  $T_{Soil}$  = actual soil temperature,  $T_{Air}$  = air temperature, and  $\tau$  = time constant (8.3 days).

We represented the current climate using a mean of daily temperature and the precipitation data from the period 1961-2007, supplied by the Finnish Meteorological Institute (Appendix 1). For PipeQual simulations, this was further used for computing the respective ETS. The geographic location for the calculations was Southern Finland.

A simple method of uniform temperature and precipitation increases were used to simulate the climate change. The current predictions for the A2 climate change scenario (IPCC, 2001) suggest an increase of about 10% in precipitation and +3 °C of the average temperature in the summer months for Southern Finland, which is why the changed climate conditions were simply to simulated by adding 3°C for each temperature value in the "average year" data and the corresponding rainfall figures were multiplied by a value of 1.1. The addition of 3 Celsius degrees underestimates the warming of the winter months somewhat, but this is not considered to have much of an effect on the decomposition in the soil.

For the PipeQual model, it was estimated that the temperature sum of 1,720 degree days corresponds to a temperature rise of 3 degrees, compared to the calculated temperature sum of 1,200 degree days for current conditions. These values were used as the simulation inputs for the model.

## Management Options

All the simulations were started as if the stand had been previously managed according the current recommendations and had been growing in the current climatic conditions. In other words, the initial state of soil carbon and nitrogen stocks, similar for all simulations, was derived from the end state of such a simulation. The initial litter input to the system was the final state of such a simulated stand, short of the stem wood, therefore simulating a harvest where the entire harvest residue was left to decompose in the stand.

We simulated the stand development and soil conditions under 3 management options (Table 1). The first option is based on the recommendations of the national authority for good practice guidance and the recommendations for forest management (Tapio Forest Center). This conventional scenario has the primary aim of timber production. According to this option, the stand is thinned twice, based on reaching a target basal area which also depends on the dominant height. The thinnings are from below, leaving the dominant trees to grow until final harvest.

The second option aims in optimizing the monetary outcome from the stand. This economical optimum has been calculated with a model that incorporates PipeQual, economics and optimization (HYTYIÄINEN *et al.*, 2004). The parameters are fixed throughout the optimization period, for example prices are constant and the interest rate is 3%. In the applied version of the model (NIINIMÄKI *et al.*, manuscript), the roadside prices we choose (51.17 € per m<sup>3</sup> for sawtimber and 25.00 € per m<sup>3</sup> for pulpwood) were in line with 2009 levels and reflect the fact that Finnish forest sector is in transition and that timber demand and prices are predicted to be at somewhat lower levels compared to their history (HETEMÄKI and HÄNNINEN, 2009; HÄNNINEN and SEVOLA, 2009). The harvesting costs are calculated using cost models for mechanized cutting and hauling similar to KUITTO *et al.* (1994). The optimization problem uses the classical formula by FAUSTMANN (1849) as the objective function. It calculates the net present value of the stand over an infinite horizon also known as the bare land value (BLV). The optimization was conducted using the generalized pattern search (GPS) algorithm. The optimized variables include, the initial stand density, the number, type and intensity of thinnings, and the rotation period. The maximization of bare land value leads to a rather different management scheme, i.e., the first thinning is delayed compared to the previous conventional management scheme, but the thinning is then more intense, as is the second thinning, and also the overall rotation time is shorter. The use of interest rate shortens the economically optimal rotation period (HYTYIÄINEN *et al.*, 2004; NIINIMÄKI *et al.*, manuscript). The actual structure of the scheme depends, of course, quite heavily on economical parameters, such as the overall interest rate (3%), and the relative prices of pulp and saw timber (HYTYIÄINEN *et al.*, 2004; NIINIMÄKI *et al.*, manuscript).

The third option was a "no-management" one. In other

words, the stand was left to grow without any operations. The reduction of the number of stems is solely due to natural mortality.

## RESULTS

### Stand Succession and Carbon Stock Changes

The simulated stands were a carbon source for the first two decades after a stand replacing harvest (clear-cutting) in all different scenarios (Fig. 4). The vegetation was remarkable carbon sink for the most of the years after stand establishment (Fig. 5A-5C). The carbon sink of vegetation was highest in the middle-aged stands, but the size of the vegetation carbon sink strongly depended on timing of the thinnings (Fig. 5A, Table 1). At the time of the thinnings, carbon stock of trees decreased remarkably (drop to negative values not shown in Fig. 5A and 5B, but change reported in Table 1). The carbon sink of vegetation was larger for a few years after thinnings in comparison to years before a treatment (Fig. 5A and 5B), but the total carbon sink of vegetation and soil was decreased because soil was carbon source after thinnings (Fig. 6A-6B and Fig. 7A-7B). The carbon removals from a stand at the time of the first and second thinning was 8 Mg/ha and 15.7 Mg/ha, respectively, when the current management regime was applied (Fig. 4A, Table 1).

At the start of the simulation, after a clear-cutting, carbon

stock of litter and soil increased as the harvest residues were left on the site (Fig. 4). Thereafter, the soil carbon stock decreased for some 20 years, because the tree biomass was low and consecutively litter fall from the living trees was lower than the amount of carbon released due to decomposition (Fig. 4). After being a carbon source during early succession, the soil tended to turn into a carbon sink; however, the increased amounts of litter following the thinnings increased the decomposition rate and tended to turn the soil into a carbon source, at least for a few years after the treatment (Fig. 6A-6B).

### The Effect of Climate Change on Carbon Sequestration of Forest Vegetation and Soil

In the changing climate, both biomass and soil carbon stocks were higher than in the current climate (Fig. 4). In the unmanaged stands of intermediate age, the average carbon sink of vegetation varied from 1.5 to 2.5 Mg/ha/year, being about 1 Mg/ha/year higher in the changed climate (Fig. 5C). When the stands grew older, the difference between the climate options reduced, but finally at the age of 100 years vegetation carbon sink in the changed climate was strongly reduced due to high natural mortality.

In the changing climate, the rate of decomposition increased with temperature and precipitation, but the increase in the biomass stock and litter production was even larger. Thus, in the changing climate the rate of soil carbon sequestration and

Table 1 Harvests in different scenarios under current and changing (A2) climate

Management scenario	Climate	1st thinning				2nd thinning				3rd thinning				Final harvest			
		Year	Harvested stem volume	Carbon in harvested stemwood	Carbon in the other harvested biomass compartments	Year	Harvested stem volume	Carbon in harvested stemwood	Carbon in the other harvested biomass compartments	Year	Harvested stem volume	Carbon in harvested stemwood	Carbon in the other harvested biomass compartments	Year	Harvested stem volume	Carbon in harvested stemwood	Carbon in the other harvested biomass compartments
		a	m <sup>3</sup> /ha	Mg/ha	Mg/ha	a	m <sup>3</sup> /ha	Mg/ha	Mg/ha	a	m <sup>3</sup> /ha	Mg/ha	Mg/ha	a	m <sup>3</sup> /ha	Mg/ha	Mg/ha
Current recommendations	Current climate	36	43.6	8.0	7.3	62	85.4	15.7	10.4	-	-	-	-	84	357	65.4	36.4
	A2	30	45.2	8.3	7.6	56	84.3	15.5	9.2	-	-	-	-	75	481	88.5	46.6
Economical optimum	Current climate	48	34.7	6.4	4.4	62	40.2	7.4	4.7	-	-	-	-	80	386	71.2	35.6
	A2	25	22.5	3.8	5.3	43	33.5	5.7	4.3	49	12.1	2.1	1.7	54	326	55.5	33.5
No thinning	Current climate	-	-	-	-	-	-	-	-	-	-	-	-	150*	750*	142.4*	46.2*
	A2	-	-	-	-	-	-	-	-	-	-	-	-	150*	829*	186.6*	58.8*

\* not harvested, but simulated status of the living trees at the age of 150 years.

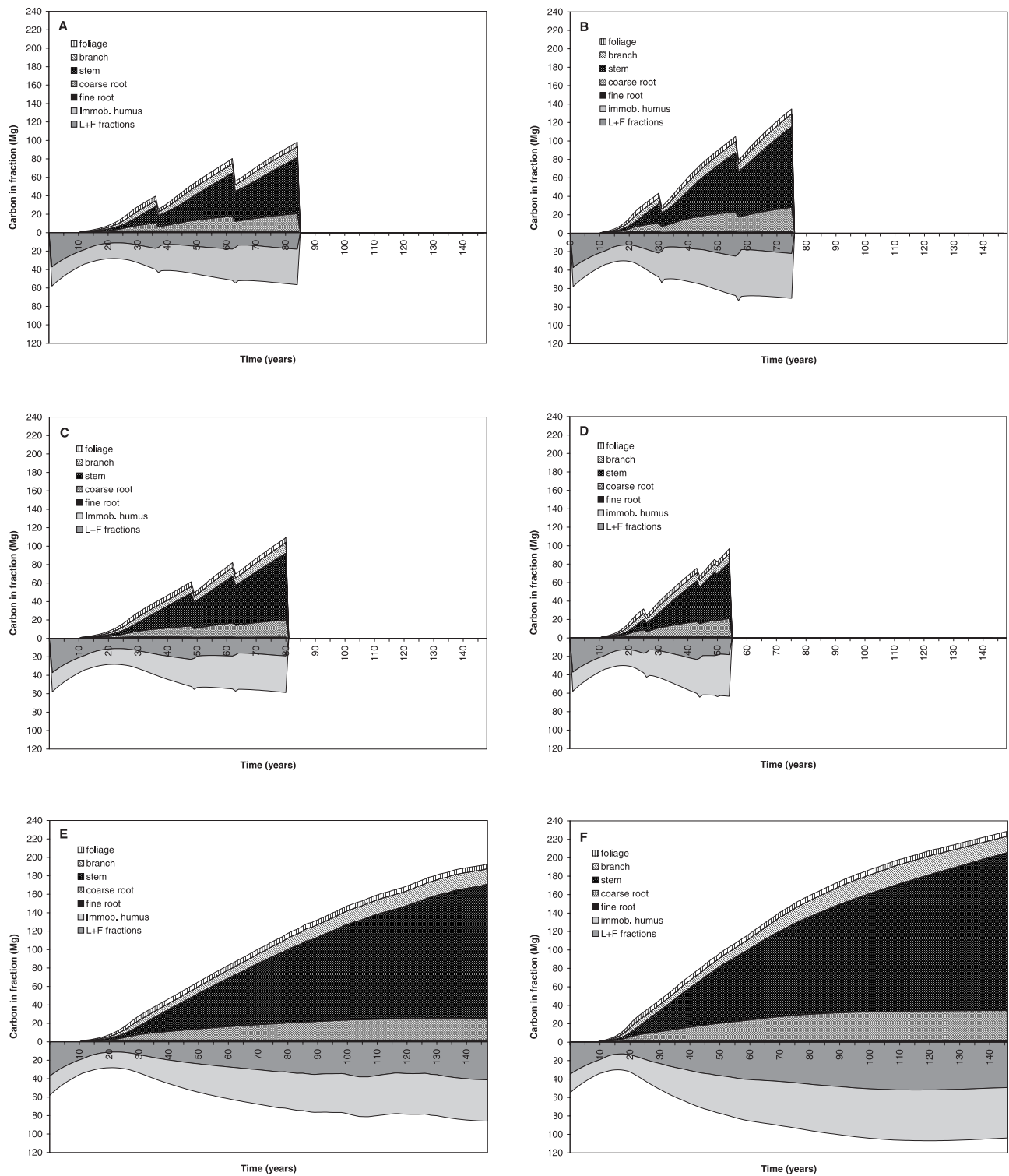


Fig. 4 The carbon stocks of biomass compartments and soil fractions with different management scenarios in the current (A, C, and E) and the changing climate (B, D, and F). The simulated management scenarios were (i) thinnings and final harvesting according to the current recommendations (Tapio) (A and B), (ii) management practices based on economic optimization (C and D), and (iii) no management (E and F).

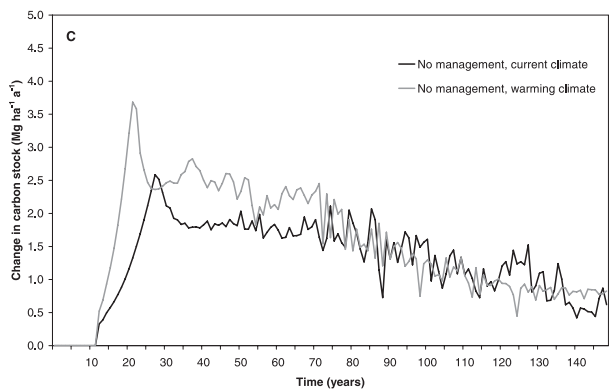
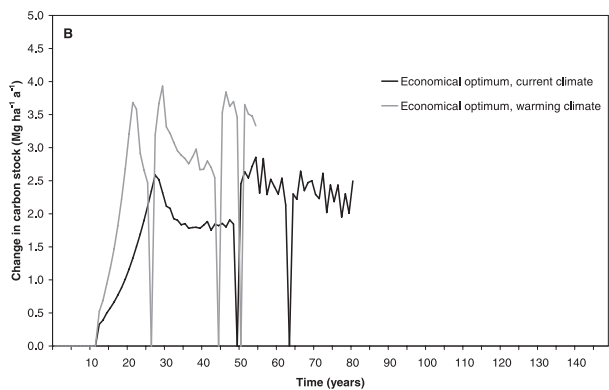
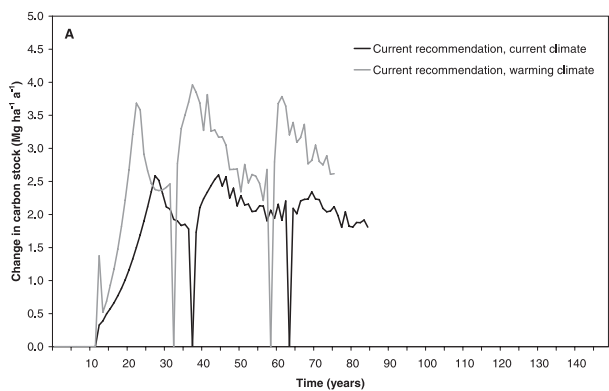


Fig.5 The change in the biomass carbon stock under current and changing climate conditions with current management practices (A), management based on economic optimization (B), and no management (C)

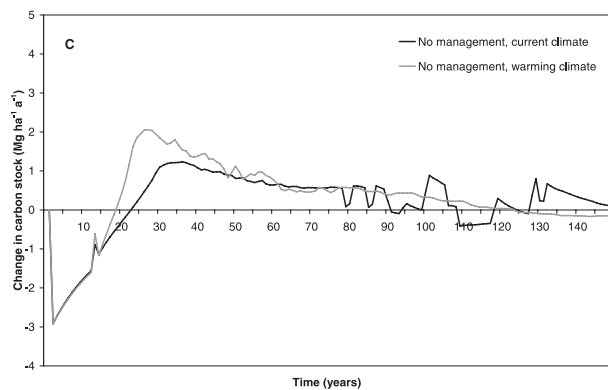
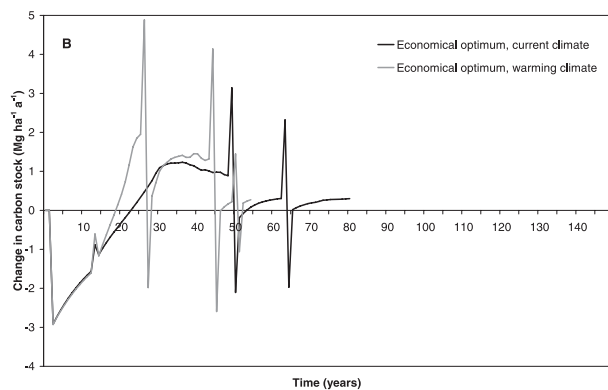
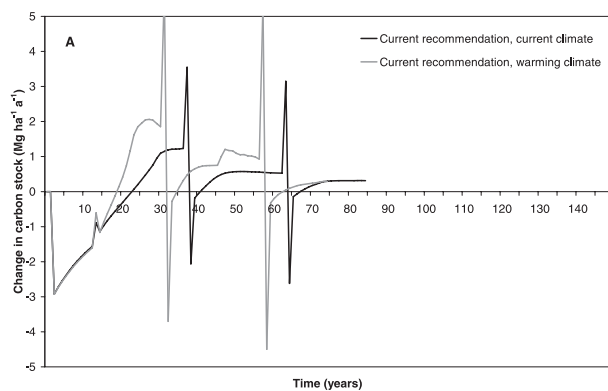


Fig.6 The change in the soil carbon stock with different management scenarios under current and changing climate conditions Management scenarios (A, B, and C) as in Fig.5.

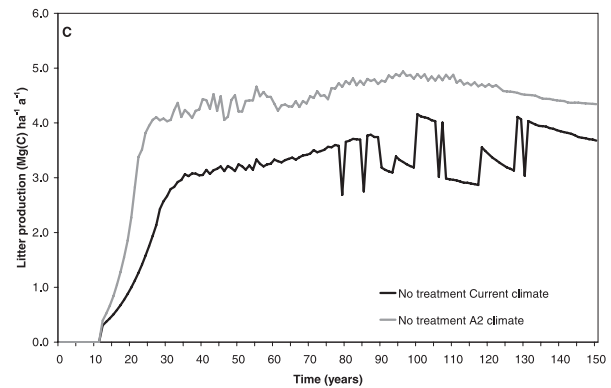
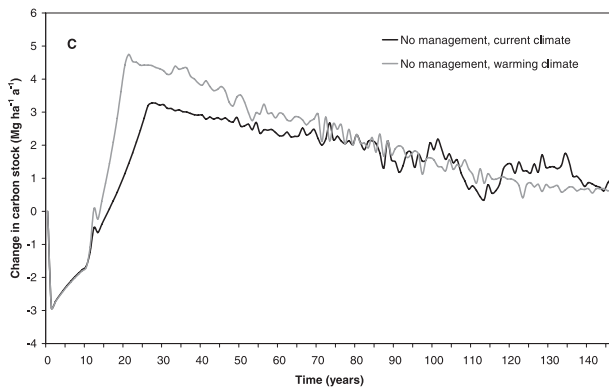
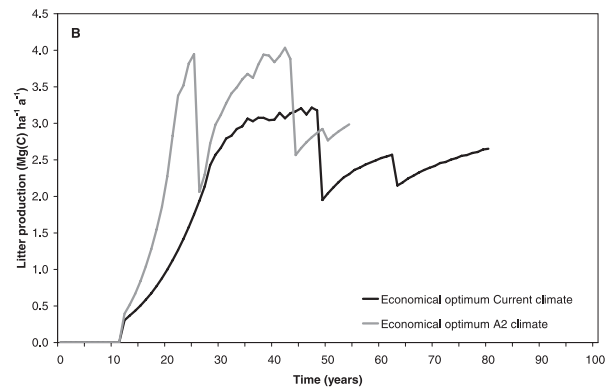
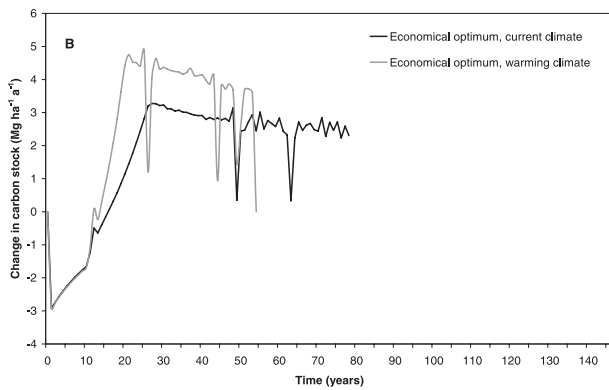
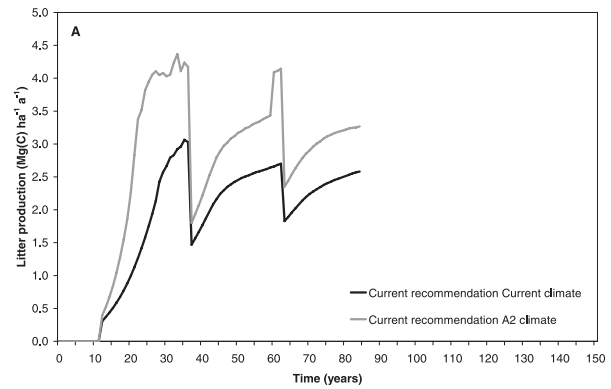
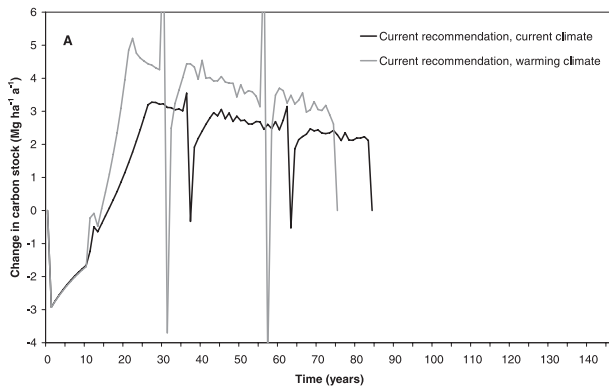


Fig. 7 The net change in the stand carbon stock (including both tree stand and soil) with different management scenarios under current and changing climate conditions Management scenarios (A, B, and C) as in Fig 5.

Fig. 8 The litter production with different management scenarios under current and changing climate conditions Management scenarios (A, B, and C) as in Fig 5.

soil carbon stock tends to be higher than in the current climate (Fig. 6A-6C and Fig. 4).

#### Carbon Sequestration Affected by Management

In addition to the tendency of tree biomass accumulating with the stand age, the vegetation carbon stock was driven by the timing and the intensity of timber harvests. After commercial thinnings after the stand age of 40 years, the biomass carbon stocks with current management were 13 Mg/ha lower in comparison to the unmanaged stand (Fig. 4). Mature stands of both current and economically optimal management regime had lower biomass carbon stock than unmanaged forests at the same age (Fig. 4). Mature unmanaged forest was a carbon sink for entire simulation period of 150 years (Fig. 7C). The amount of carbon removed from the managed stands with harvested stem wood is lower than difference seen in the standing carbon stock between managed and unmanaged stands (Fig. 4, Table 1).

The economic optimization of thinnings resulted in a higher biomass of the carbon stock in the stands younger than 50 years and to a lower biomass in the older stands in comparison to the current management recommendations (Fig. 4). Length of the rotation period was shorter with the economically optimal management scenario, which resulted in lower average carbon stock of biomass over a rotation period. At the age of 70 years in the current climatic conditions, the biomass carbon stock was largest in the unmanaged stands (Fig. 4). Economically optimal thinnings resulted in a lower standing tree biomass and, a lower proportion of the biomass was allocated to the stem wood (Fig. 4).

The economically optimal thinning regime in the current climate resulted in relatively fast soil carbon sequestration until the first thinnings, but thereafter the soil carbon sink was very small (Fig. 4), because the flux of carbon from vegetation to soil (i.e., the amount of litter) was greatly reduced after removals (Fig. 8B, Table 1). The amount of produced litter tends to be low for a few years after thinnings with decreased amount of living trees, since the litter production is directly dependent on the standing biomass (Fig. 4, Fig. 8A-8C).

### DISCUSSION

Our estimates of the average net primary production (NPP) (i.e., the rate of carbon bound in plant structures together with annual litter production) as well as the predicted amount of carbon in the vegetation and soil were consistent with earlier studies in boreal coniferous stands (FINÉR *et al.*, 2003; LISKI *et al.*, 2001; MÄKIPÄÄ *et al.*, 1999). In this study, a simulation was made for a spruce stand at a mesic site type, which is the most common site type (fertility class) in Southern Finland. Norway spruce is one of the dominant tree species in Northern Europe (SYKES and PRENTICE, 1995), and in Finland the majority of the mesic sites are spruce dominated (REINIKAINEN *et al.*, 2000).

Thus, our simulations of Norway spruce stands reflect the potential climate responses of a large proportion of forests in Southern Finland.

In our simulations, Norway spruce had a positive growth response to the changing climate in an unmanaged stand as well as in a forest stand managed according to the current recommendations. A considerable increase in the net primary production (NPP) and in the net ecosystem exchange (NEE) of Norway spruce stands was also predicted by BERGH *et al.* (2005) and JANSSON *et al.* (2008). In a review on forest growth in a changing climate, KIRSCHBAUM (2000) concluded that growth has a positive response to increasing temperature, provided that adequate water is available, since photosynthesis is positively affected by a temperature increase. Additionally, the ratio of respiration to photosynthesis is not significantly altered with an increase in temperature. BRICEÑO-ELIZONDO *et al.* (2006) simulated increased growth of Norway spruce with elevated temperature, but in Southern Finland this positive growth response was sensitive to concurrent reduction of precipitation. Earlier studies with a gap type ecosystem model have predicted an opposite (declining) trend in the growth of Norway spruce in a changing climate (e.g. KARJALAINEN, 1996; KELLOMÄKI *et al.*, 2008), but the responses of tree species to temperature were based on a simple approximation of a multiplicative model from the biogeographical range of species distribution, which introduces large uncertainties into the model predictions (see AUSTIN, 1992). The simulated positive growth response to an increase in temperature is consistent with analyses of increment chronologies, which have shown that the growth of Norway spruce is positively related to temperature in a wide range of temperatures (e.g. MIINA, 2000; MÄKINEN *et al.*, 2000). Some negative relationship is seen only with Norway spruce growth and the temperatures of previous July and August (MIINA, 2000), which results from enhanced flowering of Norway spruce that decreases growth in the following year (PUKKALA, 1987).

According to our simulations, the carbon accumulation in the forest soil was increased in the changing climate. The increase in the soil carbon stock as a result of increased temperature and precipitation was also reported by CAO and WOODWARD (1998) and KARJALAINEN *et al.* (2003). However, some studies with a gap type ecosystem model (MÄKIPÄÄ *et al.*, 1999) and with a dynamic soil carbon model combined to a forest scenario model (KARJALAINEN *et al.*, 2002) have also reported an opposite trend. JANSSON *et al.* (2008) simulated ecosystem responses to a climate change with a coupled ecosystem model that included feedbacks of nitrogen cycling, and they found only small changes in soil carbon of Norway spruce stands in Sweden. In our simulations, a positive response of soil carbon to a climate change was mainly due to the increased biomass production and the resulting increase in the litter input to the forest soil. Our stand growth model may underestimate natural mortality, which would lead to a slightly overestimated biomass production and an underestimated input of dead wood into the soil. On the other hand, our current implementation of

the ROMUL model does not consider the effect of log dimensions to the rate of decomposition, and therefore in the current results, the decomposition rate of tree stems is overestimated. The slower rate of stem wood decomposition may well overcome the effect of underestimated mortality.

In the simulations of the changing climate, the rate of decomposition was increased, but the increase in the litter production was even larger. Thus, our results suggest that boreal forest soils may act as carbon sinks also in the changing climate, provided that the balance between the litter produced by standing biomass and the rate of decomposition remains sustainable. A positive feedback between nitrogen availability and enhanced growth of trees followed by increased litter production may further increase the carbon sink potential of the stand biomass and soil carbon stocks of boreal conifer stands in the changing climate (see also JANSSON *et al.*, 2008). The potential enhancement of growth due to the increased availability of nitrogen will be introduced to our model in the next development phases.

In the simulation of the managed forests, vegetation acted as a carbon sink excluding the times of harvest, but the carbon sink in managed forests was smaller than that in the unmanaged stands. Decline in soil carbon stock for the first two decades after a clear-cutting was followed by a continuous soil carbon sequestration in the unmanaged stand, but in the managed stands soil was a carbon source for some years after the thinnings. Heavy thinnings can turn forest soil to a net carbon source for some years after treatments. The decreasing trend of soil carbon stock can be strengthened, if heavy thinnings are continued over several rotation periods. Short rotation periods may also decrease site productivity (SEELY *et al.*, 2002). According to our simulations, the forest carbon stock was at its largest in the unmanaged forests and unmanaged stands were net carbon sinks also in the end of the simulation at the age of 150 years. The result is consistent with a number of previous reports; e.g., COOPER (1983), THORNLEY and CANNELL (2000), MIKHAILOV *et al.* (2004), SCHMID *et al.* (2006) and ERIKSSON (2006) have reported that unmanaged forests store more carbon than their managed counterparts. In addition, GARCIA-GONZALO *et al.* (2007) have shown that shifting to thinning regimes that allowed a higher stocking density of trees resulted in an increase in carbon sequestration. Based on simulations with a process-based model, LASCH *et al.* (2005) have concluded that long rotation combined with a low thinning intensity is the best management scenario, if the objective is to maximize carbon sequestration in temperate pine-broadleaved forests.

Climate change will greatly affect forest ecosystems and their carbon sequestration potential, but in managed forests carbon accumulation is also strongly driven by management decisions. Sustainability of alternative management regimes has to be considered from both ecological and economical aspects before science based recommendations for management in changing environment can be launched. The conflict between carbon management, and management to optimize the econom-

ic values of forestry was already demonstrated by ERIKSSON (2006), who concluded that a strategy with no thinning, which would maximize the carbon pool, would not be ideal from an economic perspective. A future challenge is to link biodiversity measures and economical optimization routines to the model. We conclude that simulations with the process-based forest growth model together with a soil model can be of help in developing ecologically and economically sustainable management practices.

#### ACKNOWLEDGEMENTS

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#### LITERATURE CITED

- AUSTIN, M. P., (1992): Modelling the environmental niche of plants: implications for plant community response to elevated CO<sub>2</sub> levels. *Aust. J. Bot.* **40**: 615-630
- BERGH, J., LINDER, S. and BERGSTRÖM, J., (2005): Potential production of Norway spruce in Sweden. *For. Ecol. Manage.* **204**: 1-10
- BRICEÑO-ELIZONDO, E., GARCIA-GONZALO, J., PELTOLA, H. and KELLOMÄKI, S., (2006): Carbon stocks and timber yield in two boreal forest ecosystems under current and changing climatic conditions subjected to varying management regimes. *Env. Sci. Policy* **9**: 237-252
- CAO, M. and WOODWARD, F. I., (1998): Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. *Nature* **393**: 249-252
- CHERTOV, O. G., BYKHOVETS, S. S., NADPOROZHKAYA, M. A., KOMAROV, A. S. and LARIONOVA, A. A., (2007): Evaluation of the rates of transformation of soil organic matter in the ROMUL model. In: KUDEYAROV V. N. (ed) Modelling of organic matter dynamics in forest ecosystems. Moscow Hayka, Moscow: 83-99 (in Russian)
- CHERTOV, O. G. and KOMAROV, A. S., (1996): Model of soil organic matter and nitrogen dynamics in natural ecosystems. In: POWLSON D. S., SMITH, P. and SMITH, J. U. (eds) Evaluation of soil organic matter models using existing long-term datasets, NATO ASI, vol. I 38. Springer-Verlag, Heidelberg: 231-236
- CHERTOV, O. G. and KOMAROV, A. S., (1997): SOMM: A model of soil organic matter dynamics. *Ecol. Model.* **94**: 177-189
- CHERTOV, O. G., KOMAROV, A. S., NADPOROZHSKAYA, M., BYKHOVETS, S. S. and ZUDIN, S. L., (2001): ROMUL - a model of forest soil organic matter dynamics as a substantial tool for forest ecosystem modeling. *Ecol. Model.* **138**: 289-308
- COOPER, F. C., (1983): Carbon storage in managed forests. *Can.*

- J. For. Res. **13**: 155-166
- DUURSMA, R. A., KOLARI, P., PERAMAKI, M., NIKINMAA, E., HARI, P., DELZON, S., LOUSTAU, D., ILVESNIEMI, H., PUMPPANEN, J. and MAKELA, A., (2008): Predicting the decline in daily maximum transpiration rate of two pine stands during drought based on constant minimum leaf water potential and plant hydraulic conductance. *Tree Physiol.* **28**: 265-276
- ERIKSSON, E., (2006): Thinning operations and their impact on biomass production in stands of Norway spruce and Scots pine. *Biomass and Bioenergy* **30**: 848-854
- FAUSTMANN, M., (1849): Berechnung des Werthes, welchen Waldboden, sowie noch nicht haubare Holzbestände für die Waldwirthschaft besitzen [Calculation of the value which forest land and immature stands possess for forestry]. *Allgemeine Forst- und Jagd-Zeitung* **25**: 441-455 (in German)
- FINÉR, L., MANNERKOSKI, H., PIIRAINEN, S. and STARR, M., (2003): Carbon and nitrogen pools in a old-growth, Norway spruce mixed forest in eastern Finland and changes associated with clear-cutting. *For. Ecol. Manage.* **174**: 51-63
- GARCIA-GONZALO, J., PELTOLA, H., BRICENO-ELIZONDO, E. and KELLOMÄKI, S., (2007): Changed thinning regimes may increase carbon stock under climate change: A case study from a Finnish boreal forest. *Climatic Change* **81**: 431-454
- GE, Z.-M., ZHOU, X., KELLOMÄKI, S., WANG, K.-Y., PELTOLA, H., VÄISÄNEN, H. and STRANDMAN, H., (2010): Effects of changing climate on water and nitrogen availability with implication on the productivity of Norway spruce stands in Southern Finland. *Ecol. Model.* **221**: 1731-1743
- HETEMÄKI, L. and HÄNNINEN, R., (2009): Arvio Suomen puunjalostuksen tuotannosta ja puunkäytöstä vuosina 2015 ja 2020 (Summary: Outlook for Finland's forest industry production and wood consumption for 2015 and 2020). Working Papers of the Finnish Forest Research Institute **122**: 1-63 (In Finnish)
- HYNYNEN, J., AHTIKOSKI, A., SIITONEN, J., SIEVÄNEN, R. and LISKI, J., (2005): Applying the MOTTI simulator to analyse the effects of alternative management schedules on timber and non-timber production. *For. Ecol. Manage.* **207**: 5-18
- HYVÖNEN, R., ÅGREN, G. I., LINDER, S., PERSSON, T., COTRUFO, M. F., EKBLAD, A., FREEMAN, M., GRELE, A., JANSSENS, I. A., JARVIS, P. G., KELLOMÄKI, S., LINDROTH, A., LOUSTAU, D., LUNDMARK, T., NORBY, R. J., OREN, R., PILEGAARD, K., RYAN, M. G., SIGURDSSON, B. D., STRÖMGREN, M., VAN OIJEN, M. and WALLIN, G., (2007): The likely impact of elevated [CO<sub>2</sub>], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. *New Phytol.* **173**: 463-480
- HYYTÄINEN, K., HARI, P., KOKKILA, T., MÄKELÄ, A., TAHVONEN, O. and TAIPALE, J., (2004): Conneting a process-based forest growth model to stand-level economic optimization. *Can. J. For. Res.* **34**: 2060-2073
- HÄNNINEN, R. and SEVOLA, Y., (2009): Finnish forest sector economic outlook 2009-2010. Finnish Forest Research Institute. [www.metla.fi/julkaisut/suhdanekatsaus/index-en.htm](http://www.metla.fi/julkaisut/suhdanekatsaus/index-en.htm). (Accessed on Oct. 18, 2010)
- HÄRKÖNEN, S., PULKKINEN, M., DUURSMA, R. A. and MÄKELÄ, A., (2010): Estimating annual GPP, NPP and stem growth in Finland using summary models. *For. Ecol. Manage.* **259**: 524-533
- ILVESNIEMI, H., PUMPPANEN, J., DUURSMA, R., HARI, P., KERONEN, P., KOLARI, P., KULMALA, M., MAMMARELLA, I., NIKINMAA, E., RANNIK, U., SIIVOLA, E., POHJA, T. and VESALA, T., (2010): Water balance of a boreal Scots pine forest. *Boreal Env. Res.* **15**: 375-396
- IPCC, (2001): 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 & New York, 881pp
- JANSSON, P.-E., SVENSSON, M., KLEJA, D. B. and GUSTAFSSON, D., (2008): Simulated climate change impacts on fluxes of carbon in Norway spruce ecosystems along a climatic transect in Sweden. *Biogeochemistry* **89**: 81-94
- KANTOLA, A., MÄKINEN, H. and MÄKELÄ, A., (2007): Stem form and branchiness of Norway spruce as a sawn timber - Predicted by a process based model. *For. Ecol. Manage.* **241**: 209-222
- KARJALAINEN, T., (1996): The carbon sequestration potential of unmanaged forest stands in Finland under changing climatic conditions. *Biomass and Bioenergy* **10**: 313-329
- KARJALAINEN, T., PUSSINEN, A., LISKI, J., NABUURS, G.-J., EGGERS, T., LAPVETELÄINEN, T. and KAIPAINEN, T., (2003): Scenario analysis of the impacts of forests management and climate change on the European forest sector carbon budget. *For. Pol. Econ.* **5**: 141-155
- KARJALAINEN, T., PUSSINEN, A., LISKI, J., NABUURS, G.-J., ERHARD, M., EGGERS, T., SONNTAG, M. and MOHREN, G. M. J., (2002): An approach towards an estimate of the impact of forests management and climate change on the European forest sector carbon budget: Germany as a case study. *For. Ecol. Manage.* **162**: 87-103
- KELLOMÄKI, S. and KOLSTRÖM, M., (1993): Computations on the yield of timber by Scots pine when subjected to varying levels of thinning under a changing climate in southern Finland. *For. Ecol. Manage.* **59**: 237-255
- KELLOMÄKI, S. and KOLSTRÖM, M., (1994): The influence of climate change on the productivity of Scots pine, Norway spruce, Pendula birch and Pubescent birch in southern and northern Finland. *For. Ecol. Manage.* **65**: 201-217
- KELLOMÄKI, S., PELTOLA, H., NUUTINEN, T., KORHONEN, K. T. and STRANDMAN, H., (2008): Sensitivity of managed boreal forests in Finland to climate change, with implications for adaptive management. *Philos. Trans. R. Soc. Lond. Ser. B* **363**: 2341-2351
- KIRSCHBAUM, M. U. F., (2000): Forest growth and species distribution in a changing climate. *Tree Physiol.* **20**: 309-322
- KUITTO, J., KESKINEN, S., LINDROOS, J., OIJALA, T., RAJAMÄKI, J., RÄSÄNEN, T. and TERÄVÄ, J., (1994): Puutavaran koneellinen hakkuu ja metsäkuljetus [Mechanized cutting and forest haulage]. *Metsäteho Report* **410**: 1-30 + appendix. (In Finnish)

- LASCH, P., BADECK, F.-W., SUCKOW, F., LINDNER, M. and MOHR, P., (2005): Model-based analysis of management alternatives at stand and regional level in Brandenburg (Germany). *For. Ecol. Manage.* **207**: 59-74
- LISKI, J., LEHTONEN, A., PALOSUO, T., PELTONIEMI, M., EGGERS, T., MUUKKONEN, P. and MÄKIPÄÄ, R., (2006): Carbon accumulation in Finland's forests 1922-2004 - an estimate obtained by combination of forest inventory data with modelling of biomass, litter and soil. *Ann. For. Sci.* **63**: 687-697
- LISKI, J., PUSSINEN, A., PINGOUD, K., MÄKIPÄÄ, R. and KARJALAINEN, T., (2001): Which rotation length is favourable to mitigation of climate change? *Can. J. For. Res.* **31**: 2004-2013
- MIINA, J., (2000): Dependence of tree-ring, earlywood and latewood indices of Scots pine and Norway spruce on climatic factors in eastern Finland. *Ecol. Model.* **132**: 259-273
- MIKHAILOV, A. V., KOMAROV, A. S. and CHERTOV, O. G., (2004): Simulation of the carbon budget for different scenarios of forest management. *Eurasian Soil Science* **37** (SUPPL. 1): S93-S96
- MÄKELÄ, A., (1997): A carbon balance model of growth and self-pruning in trees based on structural relationships. *For. Sci.* **43**: 7-24
- MÄKELÄ, A. and MÄKINEN, H., (2003): Generating 3D sawlogs with a process-based growth model. *For. Ecol. Manage.* **184**: 337-354
- MÄKELÄ, A., PULKKINEN, M., KOLARI, P., LAGERGREN, F., BERBIGIER, B., LINDROTH, A., LOUSTAU, D., NIKINMAA, E., VESALA, T. and HARI, P., (2008): Developing an empirical model of stand GPP with the LUE approach: analysis of eddy covariance data at five contrasting conifer sites in Europe. *Global Change Biology* **14**: 98-108
- MÄKELÄ, A. and SIEVÄNEN, R., (1992): Height growth strategies in open-grown trees. *J. Theor. Biol.* **159**: 443-467
- MÄKINEN, H., NÖJD, P. and MIELIKÄINEN, K., (2000): Climatic signal in annual growth variation of Norway spruce (*Picea abies*) along a transect from central Finland to the Arctic timberline. *Can. J. For. Res.* **30**: 769-777
- MÄKIPÄÄ, R., KARJALAINEN, T., PUSSINEN, A. and KELLOMÄKI, S., (1999): Effects of climate change and nitrogen deposition on the carbon sequestration of a forest ecosystem in the boreal zone. *Can. J. For. Res.* **29**: 1490-1501
- NABUURS, G. J., THÜRIG, E., HEIDEMA, N., ARMOLAITIS, K., BIBER, P., CIENCIALA, E., KAUFMANN, E., MÄKIPÄÄ, R., NILSEN, P., PETRITSCH, R., PRISTOVA, T., ROCK, J., SCHELHAAS, M. J., SIEVANEN, R., SOMOGYI, Z. and VALLET, P., (2008): Hotspots of the European forests carbon cycle. *For. Ecol. Manage.* **256**: 194-200
- PALMROTH, S., BERNINGER, F., NIKINMAA, E., LLOYD, J., PULKKINEN, P. and HARI, P., (1999): Structural adaptation rather than water conservation was observed in Scots pine over a range of wet to dry climates. *Oecol.* **121**: 302-309
- PALOSUO, T., PELTONIEMI, M., MIKHAILOV, A., KOMAROV, A., FAUBERT, P., THÜRIG, E. and LINDNER, M., (2008): Projecting effects of intensified biomass extraction with alternative modelling approaches. *For. Ecol. Manage.* **255**: 1423-1433
- PUKKALA, T., (1987): Siementuotannon vaikutus kuusen ja männyn vuotuisen sädekasvuun. *Silva Fenn.* **21**: 145-158 (In Finnish)
- PUSSINEN, A., KARJALAINEN, T., MÄKIPÄÄ, R., VALSTA, L. and KELLOMÄKI, S., (2002): Forest carbon sequestration and harvests in Scots pine stand under different climate and nitrogen scenarios. *For. Ecol. Manage.* **158**: 103-115
- REINKAINEN, A., MÄKIPÄÄ, R., VANHA-MAJAMAA, I. and HOTANEN, J.-P., (2000). Kasvit muuttuvassa metsäluonnossa, Tammi, Jyväskylä, 384pp (In Finnish)
- SCHMID, S., THÜRIG, E., KAUFMANN, E., LISCHKE, H. and BUGMANN, H., (2006): Effect of forest management on future carbon pools and fluxes: a model comparison. *For. Ecol. Manage.* **237**: 65-82
- SEELY, B., WELHAM, C. and KIMMINS, H., (2002): Carbon sequestration in a boreal forest ecosystem: results from the ecosystem simulation model, FORECAST. *For. Ecol. Manage.* **169**: 123-135
- SHINOZAKI, K., YODA, K., HOZUMI, K. and KIRA, T., (1964): A quantitative analysis of plant form - the pipe model theory. I. Basic analysis. *Jpn. J. Ecol.* **14**: 97-105
- SYKES, M. T. and PRENTICE, I. C., (1995): Boreal forest futures: modelling the controls on tree species range limits and transient responses to climate change. *Water Air Soil Poll.* **82**: 415-428
- THORNLEY, J. H. M. and CANNELL, M. G. R., (2000): Managing forests for wood yield and carbon storage: a theoretical study. *Tree Physiol.* **20**: 477-484
- UNFCCC, (1997): Kyoto Protocol. <http://unfccc.int/resource/docs/convkp/kpeng.pdf>.
- WANG, K.-Y., KELLOMÄKI, S. and LAITINEN, K., (1996): Acclimation of photosynthesis parameters in Scots pine after three years exposure to elevated temperature and CO<sub>2</sub>. *Agr. For. Meteorol.* **82**: 195-217

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**Appendix 1** Equations of the ROMUL decomposition model as reported by CHERTOV *et al.* (2007) and daily variation of temperature and soil moisture

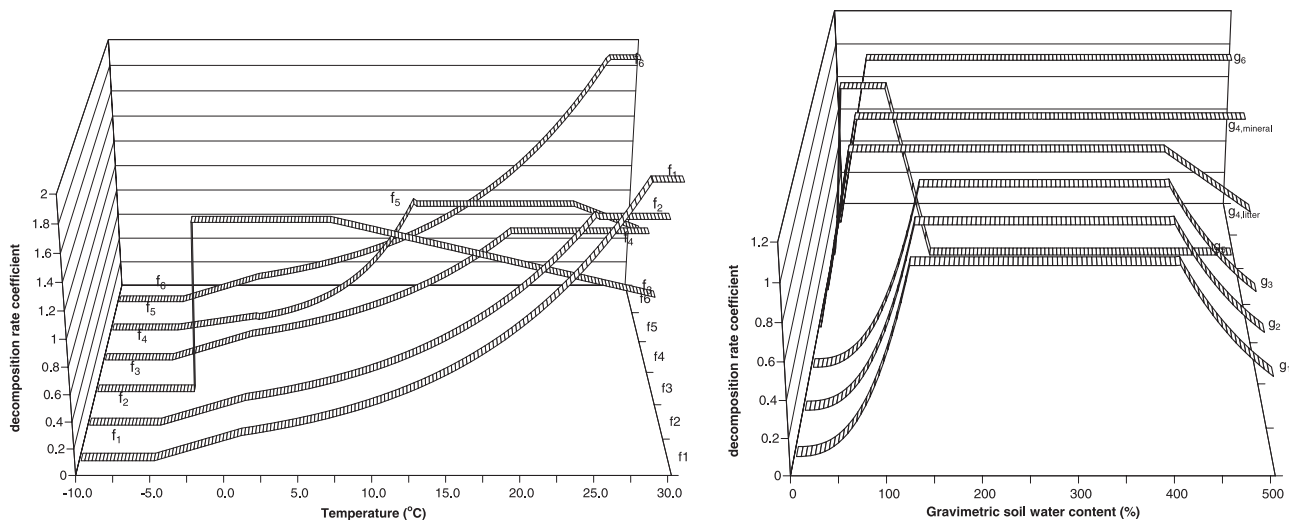


Fig.A1 Temperature and moisture dependencies of the soil fluxes

The sub-indices of the functions refer to the corresponding  $k$ -factors, i.e. the coefficient  $k_s$  of mass flow (from  $Lx,i$  fraction to  $Fx,i$  fraction) is adjusted with the temperature coefficient  $f_s$  and the soil moisture coefficient  $g_s$ .

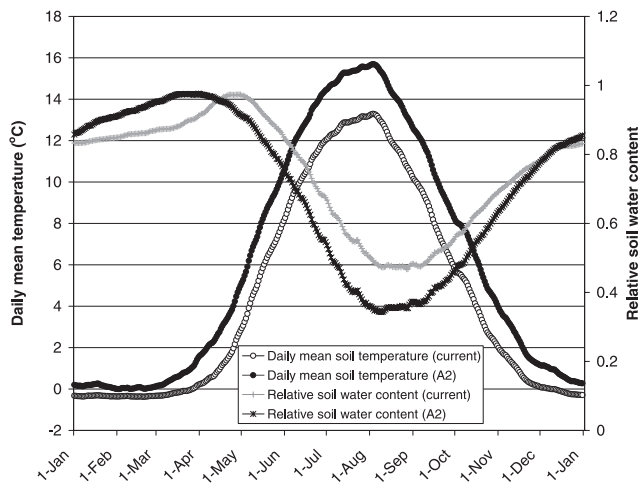


Fig.A2 Variation of the daily temperature and relative soil moisture content in the current and changing climate