

Changed thinning regimes may increase carbon stock under climate change: A case study from a Finnish boreal forest

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Abstract A physiological growth and yield model was applied for assessing the effects of forest management and climate change on the carbon (C) stocks in a forest management unit located in Finland. The aim was to outline an appropriate management strategy with regard to C stock in the ecosystem (C in trees and C in soil) and C in harvested timber. Simulations covered 100 years using three climate scenarios (current climate, ECHAM4 and HadCM2), five thinning regimes (based on current forest management recommendations for Finland) and one unthinned. Simulations were undertaken with ground true stand inventory data (1451 hectares) representing Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and silver birch (*Betula pendula*) stands. Regardless of the climate scenario, it was found that shifting from current practices to thinning regimes that allowed higher stocking of trees resulted in an increase of up to 11% in C in the forest ecosystem. It also increased the C in the timber yield by up to 14%. Compared to current climatic conditions, the mean increase over the thinning regimes in the total C stock in the forest ecosystem due to the climate change was a maximum of 1%; but the mean increase in total C in timber yield over thinning regimes was a maximum of 12%.

Keywords Adaptation · Forest management · Carbon stock · Forest ecosystem · Carbon in timber yield · Boreal forests · Climate change · Modelling

1 Introduction

The rapid increase of greenhouse gases in the atmosphere, especially carbon dioxide (CO₂), may change the global climate substantially in the foreseeable future (Parry 2000; IPCC 2001; Carter et al. 2002). Global warming is expected to have a major effect on carbon (C) stocks of boreal forests, since the productivity of these ecosystems is known to be limited by temperature, short growing season and limited availability of nitrogen (Linder 1987;

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Kellomäki et al. 1997a; Mäkipää et al. 1998a, b). In northern Europe, an increase of 2–7 °C in mean annual temperature (T) and an increase of 6–37% in mean annual precipitation with a concurrent increase in CO₂ is forecast by 2100 (Carter et al. 2002). This means an elongation of the growing season and enhancement of the decomposition of soil organic matter in the long run, thereby increasing the supply of nitrogen (Raich and Schlesinger 1992; Melillo et al. 1993; Kirschbaum 1994; Lloyd and Taylor 1994). This may further enhance forest growth and the accumulation of C in the biomass in northern Europe, where water is not currently a limiting factor (Kellomäki et al. 1997b).

In recent years, there has been an increasing tendency to consider forest ecosystems as possible CO₂ sinks (Díaz-Balteiro et al. 2003). This is because, for example, in northern Europe during the last few decades, both the growing stock and the amount of C in living biomass have increased, primarily as a result of changes in forest management (Cannell and Dewar 1995; Kauppi et al. 1995). Thus, human activities have several direct and indirect influences on forest ecosystems and their carbon sequestration potential (Karjalainen 1996a, b; Nabuurs and Schelhaas 2002).

In the above context, forests switch between being a sink (when growing biomass) or a source of C (when losing biomass), depending on the stage of succession, specific disturbance or management regime and activities (Masera et al. 2003). Net change in the C stocks (trees, soil, wood products) shows whether these are C sinks (accumulating C) or C sources (losing C). However, it should be noted that the state of these stocks varies over time. Therefore, it is important to look at the long-term dynamics of C stocks, not only at particular years (Karjalainen et al. 1999; Nabuurs and Schelhaas 2002). The adoption of the Kyoto Protocol, with its acknowledgement that forests can affect the atmospheric CO₂ concentration, has resulted in many studies about the possibilities of enhancing and maintaining carbon sequestration of the forests. Long-term simulation studies based on current management recommendations (business-as-usual) have indicated that the total ecosystem C stocks in unmanaged boreal forests are larger than those in managed forests (Bengtsson and Wikström 1993; Karjalainen 1996b; Thornley and Cannell 2000; Finér et al. 2003).

On the other hand, as forest management affects the amount of C stocks in the forest ecosystem, forest management decisions can still be a cost-effective means of reducing net emissions and enhancing carbon sequestration of forests (Kauppi et al. 2001; Pussinen et al. 2002). The measures of enhancing carbon sequestration along with producing timber may include changes in management, e.g. changing rotation length, improving harvesting and regeneration techniques, selecting more productive species or provenances, improving silviculture (including fertilisation) and also increasing the percentage of protected forests without management (Dewar and Cannell 1992; Nabuurs and Mohren 1995; Cannell and Dewar 1995; Karjalainen 1996a; Schlamadinger and Marland 1996; Marland and Schlamadinger 1999; Liski et al. 2001; Seely et al. 2002). In this context, forest modelling can be used as a dynamic tool for decision-makers in order to predict the effect of climate change on C stocks in the forest ecosystem and to plan the most appropriate management under climate change.

Some previous model-based studies have predicted an increase in growth in boreal conditions under a changing climate when business-as-usual management was applied (Kellomäki and Kolström 1993; Karjalainen 1996b; Kellomäki et al. 1997a; Talkkari 1998; Pussinen et al. 2002). However, there may be a need to adapt the management practices to the altered dynamics of the forest ecosystem to avoid increasing self-thinning and to optimally utilise the increasing growth and yield. This implies, for example, earlier and/or heavier thinnings and a shorter rotation length (Kellomäki et al. 1997a). Thus, the climate change may greatly influence the economic profitability of forestry.

Simulation of forest growth and yield can be based on empirical or process-based models. Empirical models are widely used to support decision-making in forestry, especially when site-specific predictions on growth and timber yield based on existing inventory data are required. However, empirical models are based on the assumption that future environmental conditions will be similar to those of the past. Therefore, these calculations exclude the impacts of any environmental changes on tree growth. This is opposite to process-based models, which are based on physiological processes controlled by climatic and edaphic factors. But until now, the use of process-based models for assessment of regional or management unit level impact has been limited. Typically, the structure of process-based models is complex; and to initiate calculations a detailed description of the properties of sites and trees is needed. This substantially limits the use of process-based models in day-to-day management. Recently, increased awareness of the influence of changing environmental conditions on forest growth has, however, led to an increased interest in applying process-based models to forest management in order to understand how forests grow and develop under changing environment and management (Landsberg and Waring 1997; Mäkelä 1997; Battaglia and Sands 1998; Lindner 2000; Mäkelä et al. 2000a,b; Sands et al. 2000).

In the future, it will be required to develop adaptive management strategies to cope with the effects of climate change on forests in order to ensure the sustainable use of forest resources (Lindner 2000). Since there are still great uncertainties about the regional characteristics of the future climate, as well as about the response of our forests to changes in the atmospheric and climatic conditions, the development of adaptive management strategies should be based on sensitivity and risk analyses. For this purpose, a regional assessment that takes into account the consequences of both management and climate change on the productivity of forests and C stocks in the forest ecosystem appears to be useful as a first step towards making recommendations for forest planning under climate change.

In the above context, this study is one of the first attempts to evaluate the current management guidelines in the light of changing climatic conditions with regard to C stock in the boreal forest ecosystem. We applied a physiological growth and yield model to assess how management and climate change are likely to affect C stock in a forest management unit, with forests dominated by Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and silver birch (*Betula pendula*) stands. More specifically, we focused on the assessment of management and climate change effects on forest C stock in terms of C in the forest ecosystem (C in above and below ground tree biomass and C in soil) and C in timber yield. Model-based analysis was used to identify proper management regimes for managing these forests in a sustainable way by modifying the current management recommendations for Finnish conditions.

2 Material and methods

2.1 Outline of the model used in the study

This study utilised a process-based model (FINNFOR) (Kellomäki and Väisänen 1997), which was designed to simulate the impacts of climate change on the photosynthetic production with the consequent effects on growth and timber yield in boreal forests for Scots pine, Norway spruce and silver birch dominated stands. The model has been explained more in detail in previous publications (Kellomäki and Väisänen 1997; Matala et al. 2003; Garcia-Gonzalo et al. 2006) but here we present some details.

Calculation of photosynthetic production. The physiological core of the FINNFOR model is the biochemical sub-model of photosynthesis developed by Farquhar et al. (1980) and von Caemmerer and Farquhar (1981). The rate of photosynthetic production is linked to climatic variables through biochemical processes (e.g. photosynthesis, respiration) and to soil through stomatal conductance, which is controlled by soil moisture and temperature (hydrological and nitrogen cycles). Respiration losses include day, maintenance and growth respiration. The remaining amount of photosynthesis (net photosynthesis) is converted to the growth of foliage, branches, coarse roots, fine roots and stem.

Growth and properties of trees. The initial tree population is divided into cohorts representing trees with the same properties. Each cohort is defined by the tree species, the number of trees per hectare, diameter (cm), height (m) and age (year). These variables are used as the inputs of the initial stand data for the simulations and they are updated annually during the simulation. First, the annual total net photosynthesis of the representative trees in each cohort is calculated based on the hourly rate of net photosynthesis. This rate of net photosynthesis refers to the rate of photosynthesis after all respiration losses are removed from the gross photosynthesis. Second, the annual total net photosynthesis is converted to dry matter and allocated to the biomass growth of different tree organs following the allometric growth among organs (Matala et al. 2003). Thereafter, the diameter at breast height (DBH) (cm) of the stem (1.3 m above ground level) and the tree height are calculated with the help of an empirical equation developed by Marklund (1988). Stocking controls the dynamics of the ecosystem through mortality and management by modifying the structure of the tree population, with resulting changes in canopy processes and availability of resources for physiological processes and consequent growth.

Mortality. The rate of mortality of trees is updated every five-years based on the model developed by Hynynen (1993), who applied the model of Reineke (1933) in modelling the mortality of Scots pine, Norway spruce and silver birch. At the beginning of each simulation step for mortality, the probability of survival for trees in each cohort is calculated with regard to the stocking in the stand, the position of the trees in the stand (dominant, co-dominant, intermediate and suppressed) and the life span of the trees. At the end of each simulation step, the stocking of stem wood in the whole tree population is compared with the self-thinning threshold which determines the maximum allowable stocking per unit area. If the threshold has been reached, mortality is triggered, and the number of trees it is reduced in each tree cohort.

Decomposition of soil organic matter and mineralisation of nitrogen. For the decomposition of litter (dead organic material from any compartment of trees) and humus (soil organic matter) the model utilises the algorithm developed by Chertov and Komarov (1997). Decomposition rates of different types of litter and soil organic matter are determined by soil temperature and the moisture, nitrogen and ash content of the litter. Litter moisture is a linear function of that of the mineral topsoil. Nitrogen is released through the decomposition of litter and soil organic matter. The immobilisation of nitrogen in the mineral topsoil is a function of the carbon/nitrogen ratio in the humus. The atmospheric deposition of nitrogen is included in the soil model.

The air temperature affects the soil temperature and moisture as detailed by Kellomäki and Väisänen (1996 1997). Furthermore, the temperature and moisture gradients between the soil surface and lower soil layers are influenced by the thickness of organic soil layer and snow cover; they drive the transfer of water and heat into the soil utilising an hourly time step. The soil surface temperature is further used in computing the downward flow of heat which is the sum of heat conduction and convection. The water on the soil surface represents direct precipitation, precipitation through the canopy and water from melting snow.

Soil moisture and temperatures are interlinked in such a way that the volumetric water content depends on the soil temperature and evaporation of water from the soil; both are affected by air temperature (Kellomäki and Väisänen 1996). Similarly, the water in the soil influences soil temperature through its heat content and heat capacity as related to the physical properties of the soil. Snow accumulating on soil surface affects soil frost and the soil temperature. In spring time the snow melt will substantially recharge the water content of the soil. The soil moisture conditions are given layer by layer in terms of volumetric water content and water tension.

Thinning and timber assortments. Thinning reduces the basal area in the tree population. This reduction is converted to the number of trees to be removed from each cohort. For this, the following have to be taken into account: the mean diameter (weighted by the basal area) for trees in the stand before thinning, the diameter in the cohort and the pattern of the thinning (from above or from below). In thinnings from above, mainly dominant and co-dominant trees representing the upper quartile of the diameter distribution are removed; if thinning from below is applied, suppressed and intermediate trees representing the lower quartile of the diameter distribution are removed. Those trees removed in thinnings and final cutting are converted to sawlogs and pulpwood. The term sawlog refers to the butt part of the stem with a minimum diameter of 15 cm at the top of the log, while pulpwood refers to the other parts of the stem, with a minimum diameter of 6 cm. The remainder of the stem represents logging residue as well as branches and needles.

Meteorological data. For its simulations the model can use synthetic meteorological data based on real weather statistics, following the algorithm detailed by Strandman et al. (1993). Optionally, measured values for the climatic variables or values based on future weather simulations can be used. In this study the latter option was used. The CO₂ concentration in the air is calculated separately, and can be determined for the given climate change scenarios in terms of either stepwise increases or a gradual rise. The hourly computations can run for one or several years and represent both the active and dormant seasons.

2.2 Validation and performance of the model

The validation and performance of the model has been studied and presented in detail in several papers: (i) model validation against growth and yield tables (Kellomäki and Väisänen 1997), (ii) eddy covariance measurements (Kramer et al. 2002) and (iii) measurements of the growth history of trees in thinning experiments (Matala et al. 2003). Furthermore, parallel simulations have been recently carried out with the help of a conventional growth and yield model (Motti) (Matala et al. 2003). Motti has been developed as a decision-support tool for the use in stand-level analyses in forest management planning based on parameters obtained from both extensive permanent sample plots and forest inventory data for Finnish conditions (Hynynen et al. 2002). In this model comparison, Matala et al. (2003) found that in general the outputs of the models agreed well in terms of relative growth rates regardless of tree species, they concluded that both models predict competition within a stand and the effect of position on tree growth in a similar way. As expected, the statistical model (Motti) was less sensitive to initial stand conditions and management than the FINNFOR model. In general, the two models matched well in their dynamics and predictions both in unmanaged and in managed stands of Scots pine, Norway spruce and silver birch (growing on medium fertility sites in central Finland). Thus, we believe that the FINNFOR model can be expected to provide realistic predictions for timber production and C stocks in forest ecosystem under current climate conditions.

Table 1 Description of the representative stands and the management unit. The tree species are the dominant species in the stand

Soil fertility types and tree species	Representative stands		Study area represented	
	Area (ha)	Number of stands	Area (ha)	Number of stands
1. <i>Oxalis myrtillos</i> type (OMT)				
Norway spruce (<i>Picea abies</i>)	14	9	300	227
2. <i>Myrtillos</i> type (MT)				
Scots pine (<i>Pinus sylvestris</i>)	9	8	137	96
Norway spruce (<i>Picea abies</i>)	10	9	633	423
Silver birch (<i>Betula pendula</i>)	7	7	106	102
3. <i>Vaccinium</i> type (VT)				
Scots pine (<i>Pinus sylvestris</i>)	10	9	275	170
Total	50	42	1451	1018

Since FINNFOR predictions are valid for current climate and provided that the growth dynamics will be similar under changing climate, we expect that the model predictions will be realistic also under climate change because they are based on physiological processes. Parameters of the physiological processes are based on data from long-term forest ecosystem and climate change experiments representing the range of climate change forecasted for Finland (Wang et al. 1996; Medlyn et al. 2001, 2002).

2.3 Description of the study area

The management unit used in this study was located in eastern Finland, near Kuopio (63°01'N 27°48'E, average altitude 94 m above sea level). It consisted of 1451 hectares of forests inventoried in 2001, which corresponded to 1018 stands (Table 1). The study area was dominated by Norway spruce, i.e., 933 ha, 64% of the total area. Scots pine dominated stands covered 28% (412 ha) and silver birch dominated stands covered 7% (106 ha). The sites were of *Oxalis Myrtillos* (OMT), *Myrtillos* (MT) and *Vaccinium* (VT) types (Cajander 1949). Most of the stands were located on sites of medium fertility (MT 621 stands, 876 ha). A total of 170 stands were on the poor sites (VT, 275 ha) and 227 stands on the most fertile sites (OMT, 300 ha). The dominant tree species on the OMT sites was Norway spruce, whilst Scots pine was in the majority on the VT sites. The stands on the MT sites were mostly dominated by Norway spruce, but stands dominated by silver birch and Scots pine were also present (often the stands were a mixture of these three species).

The representative stands for each species, age classes and soil fertility types for the simulations were selected based on available information in each stand. This information included dominant tree species, average stand age, height and diameter at breast height (both weighted by basal area), stand density (trees ha⁻¹) and soil fertility type. The age class distribution of the tree species in the management unit is presented in Table 2.

2.4 Simulations

2.4.1 Layout for the simulations

In order to reduce the number of simulations, representative stands were selected from the management unit. All 1018 stands were classified into groups with the same dominant tree

Table 2 Age class distribution showing the percentage of area occupied by each species area in the management unit (age class 1 means 0–10 age; 2 means 11–20 etc.)

Age class	Scots pine (%)	Norway spruce (%)	Silver birch (%)	Management unit on average (%)
1	25	33	50	32
2	21	9	14	13
3	27	7	17	14
4	9	6	5	7
5	6	3	5	4
6	2	5	4	4
7	4	7	0	6
8	4	11	5	9
9	1	18	0	12
Total (%)	100	100	100	100

Table 3 Management regimes (five thinning regimes and one unthinned)

Management	Description of thinning regimes
BT(0,0)	Basic thinning (business-as-usual) with upper limit before thinning and lower limit of basal area after thinning equal to current recommendations (Yrjölä 2002).
BT(15,0)	Upper limit of basal area increased by 15%, but lower limit as in BT(0,0)
BT(15,15)	Upper and lower limits of basal area increased by 15%
BT(30,0)	Upper limit of basal area increased by 30% and lower limit as in BT(0,0)
BT(30,30)	Upper and lower limits of basal area increased by 30%
UT(0,0)	No thinning performed, only final clear cutting.

species (Scots pine, Norway spruce or silver birch), age class (10 year intervals; 0–100 years) and soil fertility type (OMT, MT, VT). A typical stand representing the normal growing situation was selected from each group. A total of 42 representative stands were chosen for simulations. The number of trees in each representative stand was then divided equally into three cohorts. In the first cohort, the values of DBH and height of trees were those obtained in the inventory. In the second cohort, the values of DBH and height were 15% larger than those in the inventory data. In the third cohort, the values of DBH and height were reduced by 15%. In each representative stand an initial dry weight of organic matter in the soil of 70 Mg ha⁻¹ was used. The site fertility determined tree species-specific needle/leaf nitrogen content for simulations (see Matala et al. 2005). Stands were simulated over 100 years using various management and climate scenarios. The total C stock in trees (C in the above and below ground biomass), C stock in soil and C in timber yield in the 42 representative stands were then extrapolated to the whole management unit (1451 hectares) based on the area represented by each of those 42 stands (Table 1).

2.4.2 Management

The management recommendations currently applied in practical forestry (Yrjölä 2002) were used to define the business-as-usual management (Table 3). The recommendations are species-specific, using the dominant height and basal area for defining the timing and intensity of thinning (i.e. basic thinning). Whenever a given upper limit for the basal area (thinning threshold) at a given dominant height is encountered, thinning is triggered. In this

work, stands were thinned from below and sufficient trees were removed to achieve the recommended basal area for the dominant height. Thus, the timing of thinning was adjusted to the growth and development of the tree population to take place before the occurrence of mortality due to crowding. This is valid in stands with a dominant height ≥ 12 m, which is the threshold of dominant height that allows thinning. Prior to this phase, trees may die as a result of crowding. However, random mortality still works before and after the threshold value of the dominant height. In order to simplify the calculations, regardless of the site type of the representative stand, the thinning rules used in the simulations followed those currently recommended for both medium and fertile sites (MT and OMT sites). This was done because most of the sites (83%) were MT and OMT.

In our work, to achieve various thinning regimes, the basic thinning given in management recommendations (Yrjölä 2002) was varied. Because the basal area that triggers the thinning and the remaining basal area after thinning can be changed in many ways, to limit the final number of the thinning regimes to a reasonable level, a preliminary analysis was completed. After combining the changes in the basal area remaining after thinning and the thinning threshold, both with the variables 0%, $\pm 15\%$ and $\pm 30\%$, a matrix of 25 thinning regimes was constructed. Then we simulated the development of Scots pine, Norway spruce and silver birch stands (with 2500 saplings ha^{-1}) growing on MT site type over the 100 years with a fixed final clearcut at the end of the simulation period. In addition, each of the species was simulated without thinnings, with only clearcutting at the end of simulation period.

According to the analysis, only a limited number of regimes were reasonable in terms of total stem wood production; i.e. the total stem wood growth was not less than that obtainable with current recommendations (business-as-usual). Furthermore, regimes with an excessive number of thinnings and a small volume of harvested timber were excluded. In such cases, the economic profitability was expected to be very low for any forest owner and/or forest company (based on stumpage prices). The only thinnings that fulfilled these criteria were those where the upper limit that triggered thinning was increased, either alone or concurrently with the remaining basal area (compared to current recommendations). In all, six management regimes for each species (five thinning regimes and one unthinned) were used for further analyses (Table 3). The five thinning regimes for each species were; Basic Thinning BT(0, 0), two regimes based on increasing the thinning threshold by 15% and 30%, allowing further growth before thinning (BT(15, 0) and BT(30, 0)), and two other regimes, that combined the increased thinning threshold with the increase in the remaining basal area in the stand after thinning by 15% and 30%, ((BT(15,15) and BT(30, 30)) allowing higher stocking of trees in the forests over the rotation.

The simulations with the representative stands were carried out over 100 years under different forest management and climate scenarios. Regardless of tree species or site types, in all managements the stand was clearcut when it was 100 years old or earlier if the average DBH of the trees exceeded 30 cm; these criteria for final cutting were adapted from Finnish management guidelines (Yrjölä 2002). If a stand was clearcut before the end of the simulation period, the site was planted with the same species that occupied the site prior to clearcutting. Regardless of tree species and site, the initial density of these stands was 2500 saplings ha^{-1} . Once the stand was established, the simulation continued until the end of the 100 year period.

2.4.3 Climate change scenarios

For the simulations we used the current climate and two climate change scenarios developed by the Potsdam Institute for Climate Impact Research (PIK), Germany. The weather data for the period 1961–1990 represented the “current” climate used over the period 2000–2100

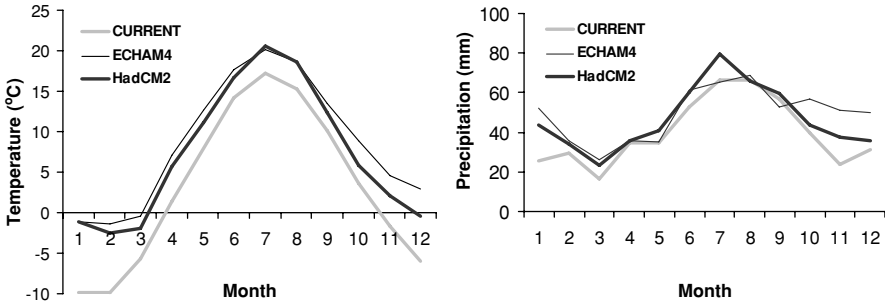


Fig. 1 Annual variation in mean monthly air temperature and precipitation for the climate scenarios over the last 30 years of simulation (2071–2100)

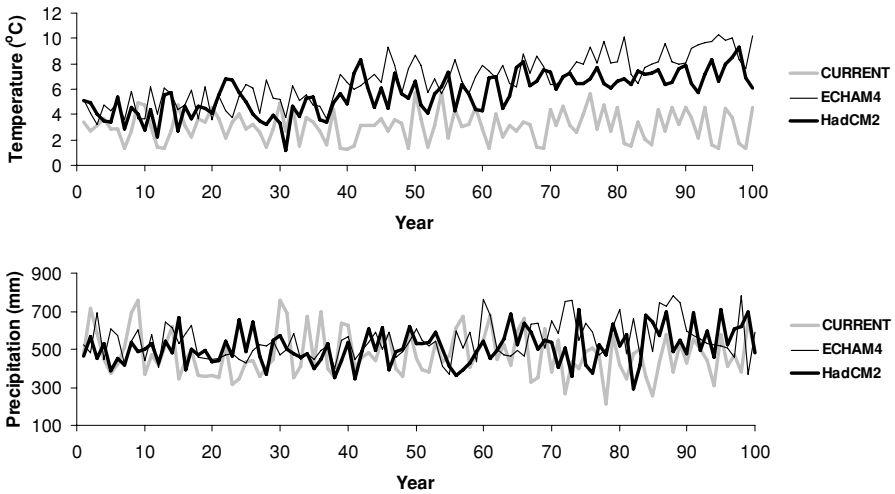


Fig. 2 Variation in mean annual air temperature and precipitation for the climate scenarios over the simulation period

by repeating this 30 year data over the whole simulation period (see Kellomäki et al. 2005). The first climate change scenario was the HadCM2 scenario which was based on the model prediction derived from the Hadley Centre Global Circulation Model (GCM) (Erhard et al. 2001; Sabaté et al. 2002). The second scenario was the ECHAM4 scenario developed by the Max Plank Institute, Hamburg, Germany (Kellomäki et al. 2005). Data for both scenarios were based on the greenhouse emission scenario IS92a (Houghton et al. 1990).

In the scenario representing the current climate, the annual mean temperature and precipitation at the end of the simulation period (2071–2100) were 3.1°C and 478 mm yr⁻¹, respectively. Under the HadCM2 scenario, for the same period these figures increased by 4.2°C and 85 mm yr⁻¹. Under the ECHAM4 scenario, the increase was higher than under the HadCM2 scenario; i.e. 5.5°C and 113 mm yr⁻¹ with different seasonal distribution than the HadCM2 scenario (Figures 1 and 2). Under the current climate, the CO₂ concentration was kept constant at a value of 350 ppm. On the other hand in both climate change scenarios

a gradual and nonlinear increase up to 653 ppm over the period 2000–2100 was used. This increment in CO₂ concentration ([CO₂]) followed the equation:

$$\text{CO}_2(t) = 350 \cdot e^{0.0063 \cdot t}, \quad (1)$$

where t is year of simulation and 350 ppm is the initial CO₂ concentration in first year of simulation ($t = 0$, year 2000). Relative humidity and radiation were not affected by the scenarios.

2.4.4 Simulation outputs and data analyses

To indicate the impacts of the forest management regimes and the climate change on C stocks at the management unit level over the 100 year simulation period, we analysed the different variables that characterise C stocks in the forest ecosystem. The C stock in trees (C in the above and below ground biomass) and the C stock in soil were calculated in terms of the mean C storage over the simulation period (Mg C ha⁻¹). In addition, the total C stock in harvested timber (Mg C ha⁻¹) was calculated and analysed.

3 Results

3.1 Effects of management and climate scenarios on carbon storage in the forest ecosystem

3.1.1 Response of the whole management unit under the current climate

Carbon in the forest ecosystem. For the unthinned regime (UT(0,0)), the carbon storage (over 100 years) in the ecosystem (C in trees and C in soil) over the management unit was, on average, 154 Mg C ha⁻¹, while the corresponding percentage of C storage in trees was 48% (73 Mg C ha⁻¹) and 52% for C in soil (81 Mg C ha⁻¹). Under the Basic Thinning BT(0,0) regime, C stock in the ecosystem was 45% lower than that under UT(0,0). However, the thinning regime had a clear effect on total C storage in the ecosystem (Table 4). The increase in the threshold triggering thinning (thinning delayed from that of the BT(0,0) regime) and remaining basal area after thinning, with the consequent increase in wood stocking throughout the rotation, increased the total C stock in the ecosystem regardless of tree species and site fertility. When the upper limit of basal area for thinning was increased by 15% in BT(15,0) and 30% in BT(30,0), C stock increased by 3% and 6% respectively compared to that under BT(0,0). If the remaining basal area after thinning was also increased, C stock in the ecosystem was further enhanced up to 11% for BT(30,30). The C stock in forest ecosystem was highest when no thinning was applied.

The management regimes were species-specific, but the effect of different management regimes on the total C storage in the ecosystem gave the same pattern for all species (Table 4). In Scots pine, the increase in the total C stock was a maximum of 14% for BT(30,30) compared to that of BT(0,0); similarly, for silver birch the maximum was 15% for BT(30,30). In Norway spruce the increase in C stock was lower, reaching a maximum of 11% for BT(30,30). Under all thinning regimes, the lowest C stock per hectare was found in silver birch and the highest in Norway spruce.

Carbon in trees and in soil. The C stock in trees followed the same pattern as total C storage in the ecosystem but the relative effect of management was larger (Table 4). An

Table 4 Total C stock in forest ecosystem (C in trees and Carbon in soil) (Mg C ha⁻¹) under current climate conditions and effect of changing management in increment (%) of total C sequestered compared to BT(0,0). See the explanation for the legends of management regimes in Table 3

Management regime	Total C in forest ecosystem (C in trees + C in soil)		Total C in trees (Above + below)		Total C above ground		Total C below ground		Total C in soil	
	Mg C ha ⁻¹	%	Mg C ha ⁻¹	%	Mg C ha ⁻¹	%	Mg C ha ⁻¹	%	Mg C ha ⁻¹	%
Scots pine										
BT(0,0)	68	–	31	–	27	–	3.5	–	37	–
BT(15,0)	70	3	32	6	28	6	3.7	5	38	2
BT(30,0)	73	7	34	12	30	12	3.9	10	39	3
BT(15,15)	73	7	34	12	30	12	3.9	10	39	3
BT(30,30)	78	14	37	22	33	23	4.3	20	41	7
UT(0,0)	95	38	45	47	40	47	5.1	44	50	31
Norway spruce										
BT(0,0)	128	–	46	–	35	–	11.4	–	82	–
BT(15,0)	131	2	48	4	36	4	11.8	4	83	1
BT(30,0)	136	6	52	12	39	13	12.5	10	84	2
BT(15,15)	135	6	51	10	39	11	12.3	8	84	3
BT(30,30)	142	11	56	20	43	21	13.2	16	86	5
UT(0,0)	188	47	90	94	69	96	21.3	87	98	20
Silver birch										
BT(0,0)	56	–	22	–	20	–	2.3	–	34	–
BT(15,0)	58	3	23	6	21	6	2.5	6	35	2
BT(30,0)	60	7	25	12	22	12	2.6	11	35	3
BT(15,15)	61	8	25	13	22	13	2.6	13	36	5
BT(30,30)	64	15	27	25	24	25	2.9	25	37	9
UT(0,0)	80	44	35	62	31	62	3.8	61	45	32
Management unit (average)										
BT(0,0)	106	–	40	–	32	–	8.5	–	66	–
BT(15,0)	109	3	42	5	33	5	8.8	4	67	1
BT(30,0)	112	6	45	12	36	13	9.3	10	68	3
BT(15,15)	112	6	44	11	35	11	9.2	9	68	3
BT(30,30)	118	11	48	21	38	22	9.9	17	70	6
UT(0,0)	154	45	73	83	58	83	15.4	81	81	23

increase in the thinning threshold increased C stock in trees, especially if the remaining basal area was also increased. The same pattern was observed in the case of C in soil but the relative change was smaller.

The increase of C in trees over the whole management unit was a maximum of 21% for BT(30,30) compared to that of BT(0,0) which gave 40 Mg C ha⁻¹. C stock in trees for UT(0,0) scenario was 83% higher than that under BT(0,0). This pattern was followed for the tree species studied and also for both components of C in trees (C above and below ground). The corresponding increase of C in soil ranged from 1% for BT(15,0) to 6% BT(30,30) compared to that of BT(0,0) which gave 66 Mg C ha⁻¹. For the UT(0,0) scenario C in soil was 23% higher than that under BT(0,0). This pattern held for the three species; in Scots pine, C in soil increase for BT(30,30) was 7% and in silver birch 9%. In Norway spruce the increase was lower, a maximum of 5% for BT(30,30). Under no thinning the increase of C in soil compared to BT(0,0) was 31% for Scots pine, 32% for silver birch and 20% for Norway spruce.

3.1.2 Response of the whole management unit under climate change

Carbon in the forest ecosystem. The effect of climate change scenarios on C stock in the forest ecosystem (C in trees plus C in soil) varied within the management regimes. Compared to current climate, C stock in the forest ecosystem over the whole management unit increased

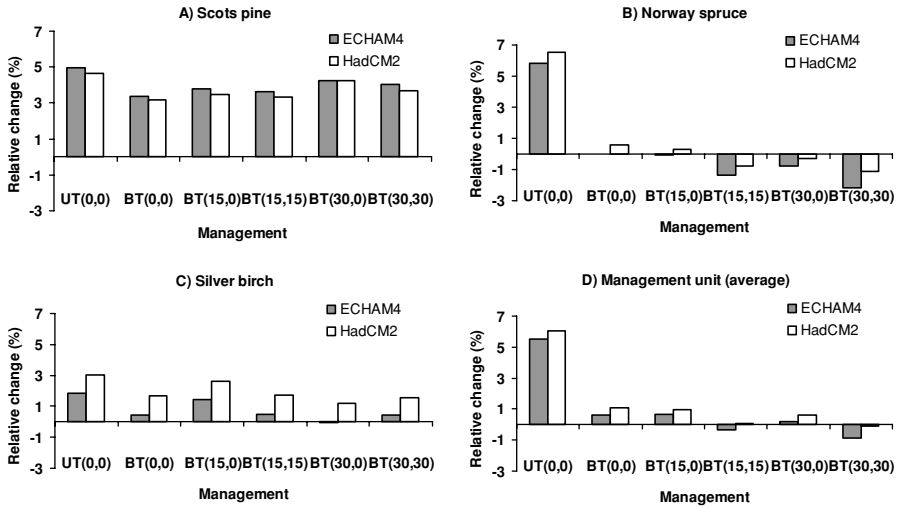


Fig. 3 Effects of climate change on total C stock in the forest ecosystem (C in trees and C in soil) of all species in the management scenarios, taking the current climate as the baseline. See key to the management scenarios in Table 3

slightly for some thinning regimes (excluding unthinned) and decreased for the remainder (Figure 3). However, for the unthinned regime UT(0,0) the increase due to the climate change was clear, being 5% and 6% for ECHAM4 and HadCM2, respectively. Moreover, the climate change scenarios showed different effects depending on the species (Figure 3). For thinned stands, Scots pine showed the strongest response to the climate change, with a mean increase of C stock in the forest ecosystem of 4% for both climate change scenarios. Following the same pattern, the increase for silver birch was similar for all thinning regimes and was, on average, 1% for the ECHAM4 and 2% for the HadCM2 climate. Unlike for Scots pine and silver birch, the climate change effect, for Norway spruce, varied within the thinning regimes; e.g. remaining constant or increasing slightly for BT(0,0) whilst decreasing for BT(30,30) for both the ECHAM4 and the HadCM2 climates. Regardless of tree species, the increase of C stock in the ecosystem due to the climate change was higher in the unthinned regime UT(0,0) than under thinned ones (Figure 3).

Under changing climate, the thinning regime affected C stock in the forest ecosystem in the same way as in the current climate for all species (Table 5). The highest values for C stock in the forest ecosystem for the whole management unit were found for UT(0,0), being 162 and 163 Mg C ha⁻¹ for the ECHAM4 and HadCM2 climates, respectively, which were 52% greater than those of BT(0,0). For thinned stands the highest C stock for all species was with BT(30,30). On average, the C stock in the forest ecosystem over the whole management unit under BT(30,30) was 117 and 118 Mg C ha⁻¹ under the ECHAM4 and HadCM2 climates respectively (10% higher than that under BT(0,0)). Regardless of species and site, the effect of management under climate change affected the different C stocks in the same way and by the same magnitude as under current climate conditions (Table 5).

Carbon in trees and in soil. Regardless of species and management regime, both climate change scenarios showed a clear increment of C stock in trees (Figure 4). Compared to the current climate, the mean increment of total C stock in trees over the whole management unit within thinning regimes (excluding unthinned) was about 8% and 6% for the ECHAM4 and

Table 5 Total C stock in forest ecosystem (including C in trees and Carbon in soil) (Mg C ha⁻¹) and effect of given management regimes on the total carbon stock expressed as a % compared to BT(0,0). Results under climate change scenarios; numbers without parentheses refer to the ECHAM4 climate and numbers between parentheses refer to the HadCM2 climate. See the explanation for the legends of management regimes in Table 3

Management regime	Total C in forest ecosystem (C in trees + C in soil)				Total C in trees (Above + Below)				Total C Above ground				Total C Below ground				Total C in soil	
	Mg C ha ⁻¹		%		Mg C ha ⁻¹		%		Mg C ha ⁻¹		%		Mg C ha ⁻¹		%		Mg C ha ⁻¹	%
	Scots pine																	
BT(0,0)	71 (70)	–	–	–	35 (34)	–	–	31 (30)	–	–	–	–	–	–	–	–	36 (37)	–
BT(15,0)	73 (73)	4 (4)	6 (6)	6 (6)	37 (36)	6 (6)	6 (6)	33 (32)	4 (4)	4 (4)	4 (4)	4 (4)	4 (4)	4 (4)	5 (5)	36 (37)	2 (2)	
BT(30,0)	76 (76)	8 (8)	13 (13)	13 (14)	39 (38)	13 (14)	13 (14)	35 (34)	13 (14)	13 (14)	13 (14)	13 (14)	13 (14)	13 (14)	10 (10)	37 (38)	4 (4)	
BT(15,15)	76 (76)	7 (7)	11 (11)	12 (11)	39 (38)	11 (11)	12 (11)	34 (33)	12 (11)	12 (11)	12 (11)	12 (11)	12 (11)	12 (11)	9 (10)	37 (38)	3 (3)	
BT(30,30)	81 (81)	15 (15)	22 (22)	23 (23)	42 (41)	22 (22)	23 (23)	38 (37)	23 (23)	23 (23)	23 (23)	23 (23)	23 (23)	23 (23)	19 (19)	38 (39)	7 (7)	
UT(0,0)	99 (99)	40 (40)	49 (48)	49 (49)	52 (50)	49 (48)	49 (49)	46 (45)	49 (49)	49 (49)	49 (49)	49 (49)	49 (49)	49 (49)	44 (44)	47 (48)	32 (32)	
	Norway spruce																	
BT(0,0)	128 (129)	–	–	–	51 (49)	–	–	38 (37)	–	–	–	–	–	–	–	–	78 (80)	–
BT(15,0)	131 (131)	2 (2)	4 (4)	4 (4)	52 (51)	4 (4)	4 (4)	39 (38)	4 (4)	4 (4)	4 (4)	4 (4)	4 (4)	4 (4)	3 (3)	79 (80)	1 (1)	
BT(30,0)	135 (135)	5 (5)	9 (10)	10 (10)	55 (54)	9 (10)	10 (10)	41 (40)	10 (10)	10 (10)	10 (10)	10 (10)	10 (10)	10 (10)	8 (8)	79 (81)	3 (2)	
BT(15,15)	133 (134)	4 (4)	7 (7)	7 (7)	54 (53)	7 (7)	7 (7)	40 (39)	7 (7)	7 (7)	7 (7)	7 (7)	7 (7)	7 (7)	5 (5)	80 (82)	3 (2)	
BT(30,30)	139 (140)	8 (9)	13 (14)	14 (15)	57 (56)	13 (14)	14 (15)	43 (42)	14 (15)	14 (15)	14 (15)	14 (15)	14 (15)	14 (15)	11 (11)	81 (84)	5 (5)	
UT(0,0)	199 (201)	56 (56)	108 (110)	114 (116)	105 (103)	108 (110)	80 (79)	80 (79)	114 (116)	114 (116)	114 (116)	114 (116)	114 (116)	114 (116)	90 (90)	94 (97)	21 (23)	
	Silver birch																	
BT(0,0)	56 (57)	–	–	–	24 (24)	–	–	22 (21)	–	–	–	–	–	–	–	–	32 (33)	–
BT(15,0)	59 (59)	4 (4)	7 (7)	8 (7)	27 (27)	7 (7)	8 (7)	24 (21)	8 (7)	8 (7)	8 (7)	8 (7)	8 (7)	8 (7)	6 (6)	33 (34)	2 (2)	
BT(30,0)	60 (60)	6 (6)	10 (10)	10 (10)	26 (26)	10 (10)	10 (10)	23 (23)	10 (10)	10 (10)	10 (10)	10 (10)	10 (10)	10 (10)	9 (10)	33 (34)	4 (4)	
BT(15,15)	61 (61)	8 (8)	12 (12)	12 (12)	27 (26)	12 (12)	12 (12)	24 (24)	12 (12)	12 (12)	12 (12)	12 (12)	12 (12)	12 (12)	12 (12)	33 (34)	5 (5)	
BT(30,30)	65 (65)	15 (15)	24 (23)	24 (23)	30 (30)	24 (23)	24 (23)	27 (26)	24 (23)	24 (23)	24 (23)	24 (23)	24 (23)	24 (23)	23 (23)	35 (36)	9 (9)	
UT(0,0)	82 (83)	46 (46)	62 (62)	62 (62)	39 (39)	62 (62)	62 (62)	35 (35)	62 (62)	62 (62)	62 (62)	62 (62)	62 (62)	62 (62)	61 (61)	43 (44)	33 (34)	

(Continued on next page)

Table 5 (Continued)

Management regime	Total C in forest ecosystem (C in trees + C in soil)		Total C in trees (Above + Below)		Total C Above ground		Total C Below ground		Total C in soil	
	Mg C ha ⁻¹	%	Mg C ha ⁻¹	%	Mg C ha ⁻¹	%	Mg C ha ⁻¹	%	Mg C ha ⁻¹	%
BT(0,0)	106 (107)	–	44 (43)	–	34 (34)	–	10 (9)	–	62 (64)	–
BT(15,0)	109 (110)	3 (3)	46 (45)	4 (4)	36 (35)	5 (5)	10 (10)	3 (3)	64 (66)	1 (1)
BT(30,0)	113 (113)	6 (6)	49 (48)	10 (10)	37 (37)	11 (11)	10 (10)	8 (8)	63 (65)	3 (2)
BT(15,15)	112 (112)	5 (5)	48 (47)	8 (8)	38 (37)	8 (9)	10 (10)	6 (6)	64 (66)	3 (3)
BT(30,30)	117 (118)	10 (10)	51 (50)	16 (16)	40 (40)	17 (18)	11 (11)	12 (13)	66 (68)	5 (6)
UT(0,0)	162 (163)	52 (52)	85 (83)	93 (94)	67 (66)	95 (97)	18 (17)	84 (84)	77 (80)	24 (25)
Management unit (average)										

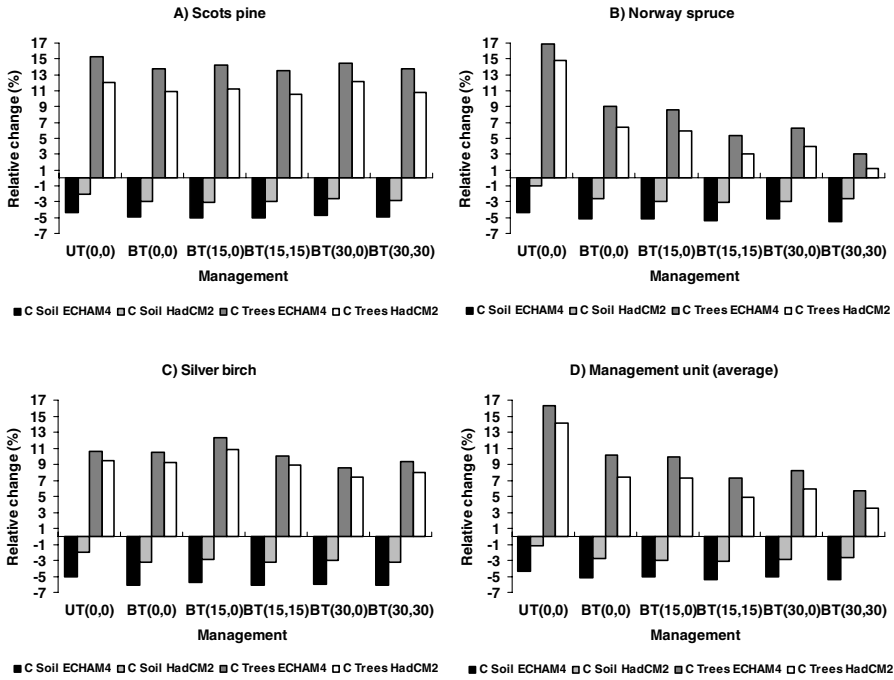


Fig. 4 Effects of climate change on C stock in soil and C stock in trees (above- and below-ground biomass) of all species in the management scenarios, taking the current climate as the baseline. See key to the management scenarios in Table 3

HadCM2 climates respectively. For unthinned stands the increment was larger, 16% and 14% for ECHAM4 and HadCM2, respectively. Scots pine showed the strongest response to the climate change in thinned stands, with a mean increase of 14% and 11% for the ECHAM4 and HadCM2 climates, respectively, without differences between regimes; for the unthinned regime UT(0,0) the increment was about the same, 15% for ECHAM4 and 12% for HadCM2. In silver birch, the increase for thinned stands was 10% for the ECHAM4 climate and 9% for the HadCM2 climate with small differences between the thinning regimes; for the unthinned stands the increases were 11% and 9% for ECHAM4 and HadCM2, respectively. Norway spruce again reacted differently; the effect of climate change varied within the thinning regimes. The increase of C stock in trees was the highest for BT(0,0), 9% for ECHAM4 and 7% for HadCM2 climate; the smallest increase was found for BT(30,30), 3% for the ECHAM4 and 1% for the HadCM2 climate. The unthinned stands showed the strongest response, increasing the C stock in trees by about 17% for the ECHAM4 and 15% for the HadCM2 climate.

Regardless of species and management regime, C in soil reacted differently to climate change than C stock in trees. Both climate change scenarios showed a clear decrease of C in soil compared to that under current climatic conditions (Figure 4). The mean decrease of C in soil over the whole management unit within thinning regimes (excluding unthinned) was about 5% and 3% for the ECHAM4 and HadCM2 climates, respectively, compared to that under the current climate. For unthinned stands the decrease was smaller, 4% and 1% for ECHAM4 and HadCM2, respectively. For conifers the same pattern and magnitude of decrease were the same, while for silver birch the decrease was slightly higher. Compared to

Table 6 Total C storage in harvested timber (Mg C ha^{-1}) under current climate and effect of changing management expressed as increment (%) compared to BT(0,0). See the explanation for the legends of management regimes in Table 3

Management regime	Management unit (average)		Scots pine stands		Norway spruce stands		Silver birch stands	
	Total C Mg C ha^{-1}	%	Total C Mg C ha^{-1}	%	Total C Mg C ha^{-1}	%	Total C Mg C ha^{-1}	%
BT(0,0)	126	–	100	–	144	–	69	–
BT(15,0)	129	3	104	4	147	2	71	3
BT(30,0)	132	5	108	8	150	4	73	5
BT(15,15)	133	6	108	8	151	5	75	6
BT(30,30)	141	12	115	15	159	11	80	12
UT(0,0)	96	–24	75	–24	109	–24	61	–11

the other species, Norway spruce showed a smaller response of C in trees to climate change, especially for thinning regimes BT(30,30), BT(15,15) and BT(30,0). This smaller response to climate change along with the decrease of C in soil resulted in a negative balance for total C in the forest ecosystem under these three thinning regimes comparing the total C in forest ecosystem under current climate with that under climate change.

3.2 Effects of management and climate scenarios on carbon in harvested timber

3.2.1 Response of the whole management unit under the current climate

Over the whole management unit, if no thinning was applied (UT(0,0)) the total C in harvested timber (sawlog and pulpwood) was 96 Mg C ha^{-1} (Table 6). This is 24% less than that under the Basic thinning (BT(0,0)), which yielded 126 Mg C ha^{-1} over the rotation. C in timber yield tended to increase when thinning was done later than that under the Basic thinning (BT(0,0)). The increment of C stock in harvested timber over the whole management unit was around 3% and 5% under BT(15,0) and BT(30,0) compared to that under BT(0,0). This tendency was further enhanced if the remaining basal area in the stand after thinning was also kept higher than in the BT(0,0) regime, with a higher stocking of trees and higher timber yield over the rotation. The BT(15,15) and BT(30,30) regimes increased the total C stock in timber yield per the unit area by 6% and 12%, respectively, of that under BT(0,0).

The tree species studied followed the same pattern as the whole management unit regarding C in timber. Under basic thinning BT(0,0), Norway spruce produced 144 Mg C ha^{-1} and Scots pine 100 Mg C ha^{-1} (24% reduction in C in timber yield for both conifers if no thinning was applied). Silver birch produced 69 Mg C ha^{-1} under basic thinning (11% reduction if UT(0,0) thinning was applied). For all species, the largest amount of C in harvested timber was found under the BT(30,30) thinning regime, the value being highest for Norway spruce (159 Mg C ha^{-1} , 11% increase) followed by Scots pine (115 Mg C ha^{-1} , 15%) and silver birch (80 Mg C ha^{-1} , 17%) (Table 6).

3.2.2 Response of the whole management unit under climate change

Regardless of species and management regimes, both climate change scenarios showed an increase of C in timber yield relative to current climate conditions, the increment being higher in the ECHAM4 climate than in the HadCM2 climate. For the total unit, the mean

Table 7 Total C storage in harvested timber (Mg C ha⁻¹) and effect of a given management regime expressed as increment (%) compared to BT(0,0). Results under climate change scenarios; the numbers without parentheses refer to the ECHAM4 climate and the numbers between parentheses refer to the HadCM2 climate. See the explanation for the legends of management regimes in Table 3

Management regime	Management Unit (average)		Scots pine stands		Norway spruce stands		Silver birch stands	
	Total C Mg C ha ⁻¹	%	Total C Mg C ha ⁻¹	%	Total C Mg C ha ⁻¹	%	Total C Mg C ha ⁻¹	%
BT(0,0)	140 (138)	–	120 (117)	–	155 (154)	–	81 (80)	–
BT(15,0)	144 (143)	3 (3)	126 (122)	5 (5)	159 (159)	2 (3)	84 (83)	4 (4)
BT(30,0)	150 (148)	7 (8)	132 (128)	10 (9)	166 (165)	7 (7)	86 (84)	6 (6)
BT(15,15)	149 (147)	6 (7)	131 (127)	9 (8)	164 (164)	6 (6)	88 (86)	9 (8)
BT(30,30)	159 (157)	13 (14)	141 (136)	17 (16)	174 (173)	12 (13)	94 (92)	16 (16)
UT(0,0)	111 (110)	–20(–20)	88 (86)	–27(–27)	127 (125)	–19(–19)	69 (68)	–15(–15)

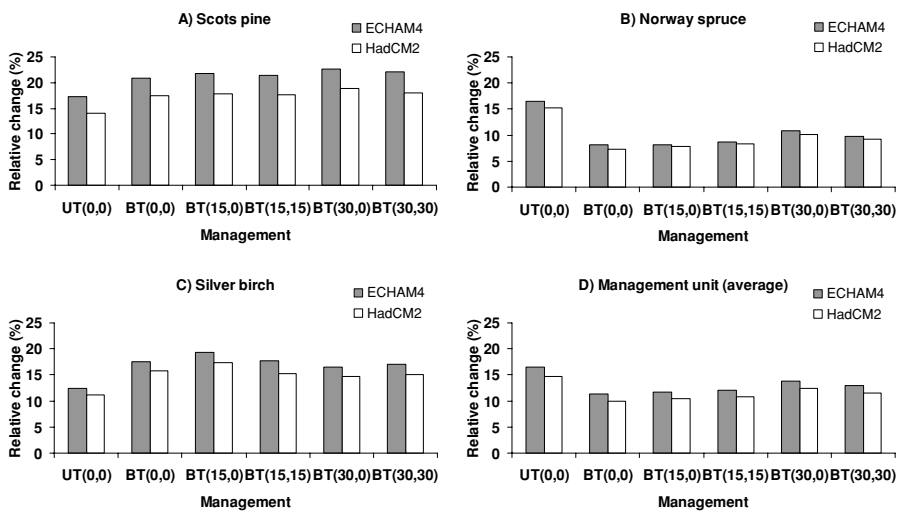


Fig. 5 Effect of climate change on C in timber yield of all species in the management scenarios, taking the current climate as the baseline. See key to the management scenarios in Table 3

increase for the thinned stands was 11% for the HadCM2 and 12% for the ECHAM4 scenario compared to the current climatic conditions (Figure 5). The mean increase of C in timber yield for Scots pine under thinning was 18% and 22% for the HadCM2 and ECHAM4 climates, respectively. For silver birch, the mean increase was 16% under the HadCM2 climate and 18% under the ECHAM4 climate. The response of Norway spruce was clearly smaller than that of Scots pine and silver birch, i.e. 9% for both climate-change scenarios. Under no thinning UT(0,0), the corresponding increase in timber yield was larger than for the thinned stands, ranging between 15% and 16% for the HadCM2 climate and ECHAM4 climate, respectively. This larger increase of timber yield when no thinning was applied (UT(0,0)) was held for Norway spruce, but not for Scots pine and silver birch, for which the increase due to the climate change under UT(0,0) was smaller than that for thinned stands (Figure 5). Under the changing climate, the thinning regime affected the C in the timber yield in the same way as in the current climate, with the highest values for BT(30,30) for all species (Table 7).

4 Discussion and conclusions

The impacts of transient climate change scenarios on currently existing forests have not been investigated in detail and the evaluations available have been based on current management practices (e.g. Lasch et al. 1999; Lindner 2000; Lexer et al. 2002). However, current management should be modified to respond properly to climate change. In the above context, this study is among the first in which a process-based growth and yield model was used to assess how both forest management and changing climatic conditions will affect total C stock in a selected forest management unit in boreal conditions over the next 100 years. More specifically, the total C stock in trees (C in the above and below ground biomass), C stock in soil and C in timber yield were analysed.

The results showed that management had a clear effect on the mean C stock in the forest ecosystem. Regardless of tree species and climate scenario, an increase in the thinning threshold increased the total C stock in the forest compared to levels of Basic Thinning regime BT(0,0), which represents the current forest management practice in Finland (Yrjölä 2002). This tendency was further enhanced if the remaining basal area was increased concurrently with the increase in the thinning threshold. Thus, the highest C stock in the forest ecosystem for thinned stands was found when BT(30,30) was applied. This management has earlier been found to give the highest timber yield (Garcia-Gonzalo et al. 2006). This result is in concordance with the findings of Thornley and Cannell (2000), who conclude that in a forest ecosystem it is possible to increase the timber yield and the C storage at the same time. However, regardless of the climate scenario, the C storage in the forest was highest when there was no thinning, UT(0,0). This result indicated that for monetary purposes the unthinned regime (with only final cutting) is not a real option; if only C stock is taken into account, the best management regime would be the UT(0,0) regime.

Earlier, long-term simulation studies have also indicated that the total C stocks in unmanaged boreal forests are larger than those in managed forests (Dewar and Cannell 1992; Bengtsson and Wikström 1993; Karjalainen 1996b; Thornley and Cannell 2000; Finér et al. 2003). This is due to the larger amount of biomass (because of high stand density) and litter production in unmanaged stands compared to managed ones. There is a large difference of increment in C stock in forest ecosystem for BT(30,30) and the unthinned regime UT(0,0) compared to BT(0,0), increments of 11% and 45%, respectively. This suggests that in order to enhance C stock without a rise in the mortality in the stands the thinning thresholds may be increased further than the 30% used in this study. However, the C stock also depends on the tree species, stand structure, age class distribution and properties of the site (Mäkipää et al. 1998b, 1999; Vucetich et al. 2000; Pussinen et al. 2002). In this study, the effect of management on C stock in trees was higher than that in soil; C in soil appeared as more stable than other C stocks as was also suggested earlier by Seely et al. (2002).

An increase in temperature and precipitation with a concurrent elevation in CO₂ enhanced total C stock in the forest ecosystem in boreal conditions by 6% for unthinned stands under both climate change scenarios. For thinned stands, the mean increment for the HadCM2 climate was 1%, while for the ECHAM4 climate the amount of C in the ecosystem decreased slightly depending on the thinning regime. This difference found between the two climates was due to the higher temperature and precipitation used in the ECHAM4 climate scenario, these higher temperatures increases the decomposition of C present in soil. A similar pattern in total C sequestration was described by Karjalainen et al. (1999), who concluded that a moderate increase in temperature seems to enhance C sequestration in forests, while a more pronounced temperature increase could make forests turn from C sinks into C sources.

Previously, Mäkipää et al. (1999) found that under changing climate the total C stock in boreal forests will decrease.

These results of C stock in the ecosystem at the management unit were very much influenced by Norway spruce, which occupies 64% of the management unit area. Whereas the mean C stock in the ecosystem increased for Scots pine and silver birch under climate change similarly for all the thinning regimes, for Norway spruce the response differed within the thinnings regimes. Regardless of the climate change scenario, C in the ecosystem, remained constant or increased slightly for BT(0,0) and BT(15,0) but decreased for the others, especially for BT(30,30). This negative effect on C in the ecosystem of the thinned Norway spruce stands was caused by a smaller increment of C in trees for Norway spruce compared to the other species; this combined with the decrease of C in soil resulted, for some managements, in a decrease in total C in the ecosystem.

Moreover, the different response to climate change of C in Norway spruce trees, depending on the thinning regime, was explained by the different climate impact on the rotation length. Norway spruce had, in relative terms, a stronger reduction of rotation length due to the climate change for BT(30,30) than for BT(0,0). This means that in BT(30,30), under climate change, the increase in growth is counteracted by the shorter time the trees are in the forest (shorter rotation); and though the mean C stock in trees (over 100 years) increases due to the climate change it is less pronounced than for the other management regimes. The reduction of rotation length for the other management regimes under climate change were less pronounced than for BT(30,30). These results might have been different if a fixed rotation length had been used instead of diameter criterion. In addition, Norway spruce has higher water retention in the crown and superficial root system. Therefore the more stocking of trees in the stand the less water from precipitation is available for the root system. Thus, even if under climate change all the thinning regimes increased growth and the stock of C in trees, this increase was less pronounced, in relative terms, in the thinning regimes that allowed more stocking of trees in the stand. The water availability also explains why the increment of C stock in trees in Norway spruce was smaller than in the other species; Scots pine and silver birch are less sensitive to the lack of water due to the deeper root system and smaller retention of water in the crown.

Furthermore, the effect on rotation length also helps to explain the smaller response of Norway spruce to climate change compared to the other species. As a consequence of the acceleration of growth, the rotation length for Scots pine and silver birch was slightly reduced when compared to that under current climate, for Norway spruce this reduction was more pronounced. This shortened rotation for Norway spruce, under climate change, affects the amount of C in trees as it is measured as an average over the whole simulation period; thus the increase in C in trees is, when compared to current climate, less pronounced than in the other species. When the unthinned regime was used, for Norway spruce, the climate change did not affect the rotation length and consequently the trees remained in the stand over the whole simulation period; therefore the increase of C in trees was similar to that for Scots pine. Again these results might have been different if a fixed rotation length had been used as a criterion for final cutting because the maximum diameter used was reached earlier under climate change thereby reducing the rotation length and thus limiting the increase of C in trees under climate change.

However, the effect on rotation length and the water availability do not completely explain the fact that C in Norway spruce trees had the smallest response to climate change. This smaller response is also explained in some degree by the heavier first thinning used in the simulations in Norway spruce compared to Scots pine. However, the thinning rules applied here were adapted for each species from the Finnish guidelines (see Yrjöola 2002). Therefore,

the Norway spruce stands remained less dense compared to the Scots pine stands. Also the thinnings were done earlier under climate change, more rapidly reducing the number of trees per hectare. As a result, the increase of average C in trees per hectare in Norway spruce due to climate change was less pronounced than that of Scots pine and silver birch. When no thinnings were applied (UT(0,0)) the impact of climate change on Norway spruce was similar to Scots pine.

The age class distribution also explains partly this smaller response. Scots pine and silver birch were highly dominated by young stands (73% and 81% respectively), and they had few stands older than 70 years (5%). Norway spruce had less proportion of young stands (49%) and had many stands older than 70 years (29%). This means that under climate change most of the Norway spruce stands are cut many years before the end of the simulation and then the mean C stock in trees is smaller than for the other species.

We found that C stock in trees under climate change for the thinned stands increases by an average of 6% and 8% for HadCM2 and ECHAM4, respectively. This is in concordance with previous results (Mäkipää et al. 1999; Karjalainen et al. 2003), which indicated that a warmer climate in the boreal region of southern Finland would increase C stock in the forest vegetation (10%). Regardless of tree species, in our results C in soil decreased compared to current climate conditions; the relative decrease was smaller for unthinned stands due to the higher mortality compared to thinned ones with resulting supply of C to the soil. The decrease of C in soil has been described by other authors, who found global warming to be likely to increase microbial decomposition of soil organic matter, causing an increased transfer of C from soil to the atmosphere, hence reducing the sink (Grace 2001; Karjalainen et al. 1999, 2003). Mäkipää et al. (1999) also found that C in soil could decrease by about 30% due to acceleration of the decomposition of soil organic matter. This result is also consistent with experimental studies where elevated temperature increased soil respiration (Peterjohn et al. 1994; Goncalves and Carlyle 1994). Other authors have suggested that C in soil may not always decrease in response to warming (Thornley and Cannell 2001). Higher increase of C stock in trees and C in harvested timber was observed for the ECHAM4 climate compared to the HadCM2 climate; this was due to the higher temperature and precipitation used in the ECHAM4 climate scenario. On the other hand, these higher temperatures increased the decomposition of C present in soil.

An increase in temperature and precipitation with a concurrent elevation in CO₂ enhanced total C stock in harvested timber for all the tree species. The increase was smaller for Norway spruce, as was the case of C in trees. This smaller response of C in timber yield is explained partly by the age class distribution of Norway spruce but also by the intensity of the thinnings recommended in Finland and used in the simulations. Those thinnings were heavy, especially in Norway spruce, and the stands remained sparser compared to the stands of Scots pine. In addition, the thinnings were done earlier under climate change resulting in a faster reduction of the number of trees per hectare. As a result, even if under climate change Norway spruce was growing faster than under current climate, the earlier and heavier reduction of number of trees limited the increase of harvested timber. Thereby the relative effect of climate change was smaller than that of Scots pine and silver birch. Moreover, when no thinnings were applied (UT(0,0)), the impact of climate change on Norway spruce was similar to that on Scots pine.

C stock in the forest ecosystem and C in the timber yield may be increased concurrently if appropriate management, with a subsequent increase in the tree stocking, is applied throughout the rotation. This study demonstrates that current thinning guidelines might not be optimal for management under changing climate nor under current climate conditions in terms of C storage in the forest ecosystem and C in timber yield as demonstrated by the

fact that management BT(30,30) always increased C sequestration compared to BT(0,0) for each climate. There is, thus, a clear need to adapt management in order to enhance carbon sequestration in-situ and also concurrently to enhance timber production.

In the simulations, the stands were thinned or clear-felled immediately when the thresholds were reached. However, at present the BT(0,0) is not necessarily the most common practice of forest owners because there is usually some delay in thinnings, especially if the aim is for higher economical profitability of thinning and clearcut. Thus, the more common management regime may currently be BT(15,0). Consequently, total C in harvested timber could be underestimated compared with the real practices of forest owners. Moreover, the same clearcut criteria were adopted in the computations regardless of tree species and sites, which differ to some degree in real practice. Furthermore, we assumed that regeneration after final cutting would always involve planting with the same species, without considering the differences between species in terms of growth and timber yield. In addition, the results obtained here are affected by age class and tree species distribution specific for this forest area; therefore, the results may not be directly extrapolated to other regions without considering these factors. However, the age class distribution of the management unit used in this study is typical of commercial forests in central and southern Finland with a dominance of young stands (Finnish Statistical Yearbook of Forestry 2001). In practice, the choice of species in regeneration and later management may be based not only on expectations for timber production, but also on carbon sequestration, species diversity and other forest uses. Thus, both under current and changing climate there are many management options, depending on the specific management objectives. In future, to cope with the various preferences in forest management objectives and to determine how forest management should be adapted to climate change, multi-criteria analysis should be applied.

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References

- Battaglia M, Sands PJ (1998) Process-based forest productivity models and their application in forest management. *Forest Ecology and Management* 102:13–32
- Bengtsson J, Wikström F (1993) Effects of whole-tree harvesting on the amount of soil carbon: model results. *NZJ. Forest Science* 23:380–389
- Cajander AK (1949) Metsätyypit ja niiden merkitys. *Acta Forestalia Fennica* 56:5–69 (in Finnish)
- Cannell MGR, Dewar RC (1995) The carbon sink provided by plantation forests and their products in Britain. *Forestry* 68:35–48
- Carter T, Bärlund I, Fronzek S, Kankaanpää S, Kaivo-oja J, Luukkanen J, Wilenius M, Tuomenvirta H, Jylhä K, Kahma K, Johansson M, Boman H, Launiainen J, Laurila T, Lindfors V, Tuovinen J-P, Aurela M, Syri S, Forsius M, Karvosenoja N (2002) The FINSKEN global change scenarios. In: Käyhkö J, Talve L (eds) *Understanding the global system, The Finnish perspective*. Painosalama, Turku, Finland p 32
- Chertov OG, Komarov AS (1997) SOMM – a model of soil organic matter dynamics. *Ecological Modelling* 94:177–189

- Dewar RC, Cannell MGR (1992) Carbon sequestration in the trees, soils and wood products of forest plantations: an analysis using UK examples. *Tree Physiology* 11:49–71
- Díaz-Balteiro L, Romero C (2003) Forest management optimisation models when carbon captured is considered: a goal programming approach. *Forest Ecology and Management* 174:447–457
- Erhard M, Lindner M, Cramer W (2001) Climate data. In: Kramer K, Mohren GMJ (eds) Long-term effects of climate change on carbon budgets of forests in Europe. ALTERRA Report 194, ALTERRA, Wageningen, The Netherlands, pp. 151–161
- Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic assimilation in leaves of C3 species. *Planta* 149:67–90
- Finér L, Mannerkoski H, Piirainen S, Starr M (2003) Carbon and nitrogen pools in an old-growth, Norway spruce mixed forest in eastern Finland and changes associated with clear-cuttings. *Forest Ecology and Management* 174:51–63
- Finnish Statistical Yearbook of Forestry (2001) *Metsätalustollinen vuosikirja*
- García-Gonzalo J, Peltola H, Briceño-Elizondo E, Kellomäki S (2006) Effects of climate change and management on growth and timber yield in boreal forests, with economic implications. (submitted to *Ecological Modelling* journal)
- Goncalves JLM, Carlyle JC (1994) Modelling the influence of moisture and temperature on net nitrogen mineralization in a forested sandy soil *Soil Biol Biochem* 26:1557–1564
- Grace J (2001) Carbon cycle. Edinburgh University Press, pp 609–629
- Houghton JT, Jenkins GJ, Ephraums JJ (eds) (1990) Climate change (1990). The IPCC scientific assessment. Intergovernmental panel on climate change (IPCC). Cambridge University Press, p 365
- Hynynen J (1993) Self-thinning models for even-aged stands of *Pinus sylvestris*, *picea abies* and *betula pendula*. *Scandinavian Journal of Forest Research* 8(3):326–336
- Hynynen J, Ojansuu R, Hökkä H, Salminen H, Siipilehto J, Haapala P (2002) Models for predicting stand development in MELA System. Finnish Forest Research Institute. Research Papers 835:p 116
- 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. (eds) Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, p 881
- Karjalainen T (1996a) Dynamics and potentials of carbon sequestration in managed stands and wood products in Finland under changing climatic conditions. *Forest Ecology and Management* 80(1–3):113–132
- Karjalainen T (1996b) Model computations on sequestration of carbon in managed forests and wood products under changing climatic conditions in Finland. *Journal of Environmental Management* 47:311–328
- Karjalainen T, Pussinen A, Kellomäki S, Määkipää R (1999) Scenarios for the carbon balance of Finnish forests and wood products. *Environmental Science and Policy* 2:165–175
- Karjalainen T, Pussinen A, Liski J, Nabuurs G-J, Eggers T, Lapveteläinen T, Kaipainen T (2003) Scenario analysis of the impacts of forest management and climate change on the European forest sector carbon budget. *Forest Policy and Economics* 5:141–155
- Kauppi PE, Tomppo E, Ferm A (1995) C and N storage in living trees within Finland since the 1950s. *Plant Soil* 168–169:633–638
- Kauppi P, Sedjo RJ, Apps M, Cerri C, Fujimori Y, Janzen H, Krankina O, Makundi W, Marland G, Masera O, Nabuurs GJ, Razali W, Ravindranath NH (2001) Options for enhancing and maintenance of Carbon sequestration Technical and economic potential of options to enhance, maintain and manage biological carbon reservoirs and Geo-Engineering. In: Metz et al.,(eds) Mitigation, IPCC Third assessment report. Cambridge University Press, Cambridge, pp 302–343
- Kellomäki S, 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. *Forest Ecology and Management* 59:237–255
- Kellomäki S, Väisänen H (1996) Model computations on the effect of rising temperature on soil moisture and water availability in forest ecosystems dominated by Scots pine in the boreal zone in Finland. *Climate Change* 32:423–445
- Kellomäki S, Väisänen H (1997) Modelling the dynamics of the forest ecosystem for climate change studies in the boreal conditions. *Ecological Modelling* 97:121–140
- Kellomäki S., Karjalainen T., Väisänen H (1997a) More timber from boreal forests under changing climate? *Forest Ecology and Management* 94:195–208
- Kellomäki S, Väisänen H, Kolström T (1997b) Model computations on the effects of elevating temperature and atmospheric CO₂ on the regeneration of Scots pine at the timber line in Finland. *Climatic Change*, 37:683–708

- Kellomäki S, Lindner M, Erhar M, Skocibusic N, Junge S, (2005) Chapter 2. Forests and climate in Europe, and climate scenarios used in the project. In: Kellomäki S, Leinonen S (eds) Management of European forests under changing climatic conditions. Research Notes 163. University of Joensuu, Forest Faculty, pp 33–44
- Kirschbaum MUF (1994) The temperature dependence of soil organic matter decomposition and the effect of global warming on soil organic C storage. *Soil Biology and Biochemistry* 27:753–760
- Kramer K, Leinonen I, Bartelink HH, Berbigier P, Borghetti M, Bernhofer C, Cienciala E, Dolman AJ, Froer O, Gracia CA, Granier A, Grünwald T, Hari P, Jans W, Kellomäki S, Loustau D, Magnani F, Matteucci G, Mohren GMJ, Moors E, Nissinen A, Peltola H, Sabaté S, Sanchez A, Sontag M, Valentini R, Vesala T (2002) Evaluation of 6 process-based forest growth models based on eddy-covariance measurements of CO₂ and H₂O fluxes at 6 forest sites in Europe. *Global Change Biology* 8:1–18
- Landsberg JJ, Waring RH (1997) A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management* 95:205–228
- Lasch P, Lindner M, Ebert B, Flechsig M, Gerstengarbe F-W, Suckow F, Werner PC (1999) Regional impact analysis of climate change on natural and managed forests in the Federal state of Brandenburg, Germany. *Environ. Modelling Assessment* 4:273–286
- Lexer MJ, Honninger K, Scheffinger H, Matulla C, Groll N, Kromp-Kolb H, Schadauer K, Starlinger F, Englisch M (2002) The sensitivity of Austrian forest to scenarios of climatic change: a large scale risk assessment based on a modified gap model and forest inventory data. *Forest Ecology and Management* 162:53–72
- Linder S (1987) Responses of water and nutrition in coniferous ecosystems. In: Schulze ED, Zwölfer H (eds.) potentials and limitations of ecosystem analysis. Springer-Verlag, Berlin, pp 180–222
- Lindner M (2000) Developing adaptive forest management strategies to cope with climate change. *Tree Physiology* 20:299–307
- Liski J, Pussinen A, Pingoud K, Mäkipää R, Karjalainen T (2001) Which rotation length is favourable to carbon sequestration? *Canadian Journal of Forest Research* 31:2004–2013
- Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. *Functional Ecology* 8:315–323
- Marland G, Schlamadinger B (1999) The Kyoto protocol could make a difference for the optimal forest-based CO₂ mitigation strategy: some results from GORCAM. *Environmental Science and Policy* 2:111–124
- Marklund LG (1988) Biomassfunktioner for tall, gran och bjork i Sverige. Summary: biomass functions for pine, spruce and birch in Sweden. Swedish University of Agricultural Sciences, Department of Forest Survey, Report 45. 73, (in Swedish, with summary in English)
- Masera OR, Garza-Caligaris JF, Kanninen M, Karjalainen K, Liski J, Nabuurs GJ, Pussinen A, De Jong BHH, Mohren GMJ (2003) Modeling carbon sequestration in afforestation, agroforestry and forest management projects: the CO2FIX V.2 approach, *Ecological Modelling* 164(2–3): 177–199
- Matala J, Hynynen J, Miina J, Ojansuu R, Peltola H, Sievänen R, Väisänen H, Kellomäki S (2003) Comparison of a physiological model and a statistical model for prediction of growth and yield in boreal forests. *Ecological Modelling* 161:95–116
- Matala J, Ojansuu R, Peltola H, Sievänen R, Kellomäki S (2005) Introducing effects of temperature and CO₂ elevation on tree growth into a statistical growth and yield model. *Ecological Modelling* (in review)
- Medlyn BE, Barton CVM, Broadmeadow MSJ, Ceulemans R, Dangeles P, Forstreuter M, Freeman M, Jackson SB, Kellomäki S, Laitat E, Rey A, Roberntz P, Sigurdsson BD, Strassemeyer J, Wang K, Curtis PS, Jarvis PG (2001) Stomatal conductance of forest species after long-term exposure to elevated CO₂ concentrations: a synthesis. *New Phytologist* 149:247–264
- Medlyn BE, Dreyer E, Ellsworth D, Forstreuter M, Harley PC, Kirschbaum MUF, Le Roux X, Montpied P, Stassenmeyer J, Walcroft A, Wang K, Loustau D (2002). Temperature response of parameters of a biochemically based model of photosynthesis. II A review of experimental data. *Plant, Cell & Environment* 25:1167–1179
- Melillo JM, McGuire AD, Kicklighter DW, Moore III B, Vorosmarty CJ, Schloss AL (1993) Global climate change and terrestrial net primary production. *Nature* 363:234–239
- Mäkelä A (1997) A carbon balance model of growth and self-pruning in trees based on structural relationships. *Forest Science* 43:7–24
- Mäkelä A, Landsberg J, Ek AR, Burk TE, Ter-Mikaelian M, Ågren GI, Oliver CD, Puttonen P (2000a) Process-based models for forest ecosystem management: current state of the art and challenges for practical implementations. *Tree Physiology* 20:289–298
- Mäkelä A, Sievänen R, Lindner M, Lasch P (2000b) Application of volume growth and survival graphs in the evaluation of four process-based forest growth models. *Tree Physiology* 20:347–355
- Mäkipää R, Karjalainen T, Pussinen A, Kukkola M (1998a) Effects of nitrogen fertilization on carbon accumulation in boreal forests: model computations compared with the results of long-term fertilization experiments. *Chemosphere* 36 (4–5):1155–1160

- Mäkipää R, Karjalainen T, Pussinen A, Kukkola M, Kellomäki S, Mälkönen E (1998b) Applicability of a forest simulation model for estimating effects of nitrogen deposition on a forest ecosystem: test of the validity of a gap-type model. *Forest Ecology and Management* 108(3):239–250
- Mäkipää R, Karjalainen T, Pussinen A, Kellomäki S (1999) Effects of climate change and nitrogen deposition on the carbon sequestration of a forest ecosystem in the boreal zone. *Canadian Journal of Forest Research* 29:1490–1501
- Nabuurs GJ, Schelhaas MJ (2002) Carbon profiles of typical forest types across Europe assessed with CO2FIX. *Ecological Indicators* 1:213–223
- Nabuurs G-J, Mohren GMJ (1995) Modelling analysis of potential carbon sequestration in selected forest types. *Canadian Journal of Forest Research* 25:1157–1172
- Parry M (ed) (2000) Assessment of potential effects and adaptations for climate change in Europe. The European acacia project. Report of a concerted action of the Environment Programme of the Research Directorate General of the Commission of the European Community. Jackson Environment Institute, School of Environmental Sciences, University of East Anglia, United Kingdom p 320
- Peterjohn WT, Melillo JM, Steudler PA, Newkirk KM, Bowles FP, Aber JD (1994) Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. *Ecol Appl* 4:617–625
- Pussinen A, Karjalainen T, Mäkipää R, Valsta L, Kellomäki S (2002) Forest carbon sequestration and harvests in Scots pine stand under different climate and nitrogen deposition scenarios. *Forest Ecology and Management* 158(1–3):103–115
- Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus B* 44:81–99
- Reineke LH (1933) Perfecting a stand-density index for even-aged forests. *Journal of Agricultural Research* 46(7):627–638
- Sabaté S, Gracia CA, Sánchez A (2002) Likely effects of climate change on growth of *Quercus ilex*, *Pinus halepensis*, *Pinus pinaster*, *Pinus sylvestris* and *Fagus sylvatica* forests in the Mediterranean region. *Forest Ecology and Management* 162(1):23–37
- Sands PJ, Battaglia M, Mummery D (2000) Application of process-based models to forest management: experience with ProMod, a simple plantation productivity model. *Tree Physiology* 20:383–392
- Schlamadinger B, Marland G (1996) Carbon implications of forest management strategies. In: Apps M, Price DT (eds) *Forest ecosystems, forest management and the global carbon cycle*. Springer, Berlin, pp 217–232
- Seely B, Welham C, Kimmins H (2002) Carbon sequestration in a boreal forest ecosystem: results from the ecosystem simulation model, FORESCAST. *Forest Ecology and Management* 169:123–135
- Strandman H, Väisänen H, Kellomäki S (1993) A procedure for generating synthetic weather records in conjunction of climatic scenario for modelling of ecological impacts of changing climate in boreal conditions. *Ecological Modelling* 70:195–220
- Talkkari A (1998) The development of forest resources and potential wood yield in Finland under changing climatic conditions. *Forest Ecology and Management* 106:97–106
- Thornley JHM, Cannell MGR (2000) Managing forests for wood yield and carbon storage: a theoretical study. *Tree Physiology* 20:477–484
- Thornley, JHM, Cannell MGR (2001) Managing soil carbon storage response to temperature: an hypothesis. *Annals of Botany* 87:591–598
- von Caemmerer S, Farquhar GD (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153:376–387
- Vucetich JA, Reed DD, Breymeyer A, Degórski M, Mroz GD, Solon J, Roo-Zielinska E, Noble R (2000) Carbon pools and ecosystem properties along a latitudinal gradient in northern Scots pine (*Pinus sylvestris*) forests. *Forest Ecology and Management* 136:135–145
- Yrjölä T (2002) Forest management guidelines and practises in Finland, Sweden and Norway. European Forest Institute. Internal Report 11:1–46
- Wang K-Y, Kellomäki S, Laitinen K (1996) Acclimation of photosynthetic parameters in Scots pine after three years exposure to elevated temperature and CO₂. *Agricultural and Forestry Meteorology* 82:195–217