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Effects of climate change and management on growth of Norway spruce in boreal conditions – an approach based on ecosystem model

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Academic dissertation

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ABSTRACT

The main aim of this work was to study the effects of climate change and management on the growth of Norway spruce (*Picea abies* (L.) Karst) in the boreal conditions based on a process-based ecosystem model (FinnFor) simulations. More specifically, it was studied: (i) how the climate change affects the growth of unmanaged Norway spruce stands in relation to the water availability from southern to northern Finland (Papers I and II); and (ii) how the climate change and varying management regimes (e.g. thinning intensity and interval) affect the net carbon uptake, total stem wood growth and timber yield in Norway spruce from southern to northern Finland, respectively (Papers III and IV). The permanent sample plots by the Finnish National Forestry Inventory (NFI) and a climate change scenario over Finland (FINADAPT for 2000–2099) by the Finnish Meteorological Institute were used in the simulations.

In southern Finland, the annual mean temperature increases by 4–6 ^{o}C compared to current climate, whereas change expected in the amount of precipitation in summertime is small. The elevated temperature increased evaporation from the canopy and ground surfaces, resulting in a higher ratio of evapotranspiration to precipitation in southern Finland. As a result, less water infiltrated into the soil profile, leading to increasing water deficit and decreasing nitrogen availability for trees (Papers I). The water deficit occurred earlier and was higher on the site with low soil water availability, resulting in lower carbon uptake and stem wood growth in Norway spruce. On average, the total stem wood growth decreased by 5–20% over most of the areas studied in southern Finland due to lower water availability under the changing climate (Paper II). On the contrary, the total stem wood growth increased by 5–38% in northern Finland under the changing climate. This increase was related to the longer growing season, and higher temperature and precipitation in summertime.

When thinning was applied in Norway spruce, the soil water deficit was mitigated due to the lower stocking and reduced water depletion, compared to no thinning (Papers III). The thinning scenarios with frequent thinnings could simultaneously increase the carbon uptake and growth rate of trees on the sites with low soil water availability. On the sites with high soil water availability, the less frequent thinnings or delayed first thinning gave the highest carbon uptake and stem wood growth, but not the highest timber yield. In general, the moderate thinning gave the highest carbon uptake, stem wood growth and timber yield in the southern regions under the changing climate (Paper IV), whereas in the north despite of thinning scenarios applied the carbon uptake and total stem wood production decreased compared to no thinning as a result of lower stocking.

Keywords: process-based ecosystem model, Norway spruce, climate change, thinning regimes, soil water availability, forest productivity

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Finally, I would like to dedicate this PhD thesis especially to my wife, Xiao Zhou, as without her love and support I could have not confidence and happiness in my life. I also would like to dedicate this thesis to my parents and relatives due to their love and support beyond borders. Last, but not the least, I would like to extend my gratitude to the Chinese Friends in Joensuu for their warm support and joyous times shared.

Zhen-Ming Ge
Joensuu

LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following papers, which are referred to in the text by the Roman numerals I–IV. Articles I and III are reproduced with the kind permission from the publishers, while the study II and IV are the author version of the submitted manuscript.

I. Ge, Z.M., Zhou, X., Kellomäki, S., Wang, K.Y., Peltola, H., Väisänen, H., Strandman, H., 2010. Effects of changing climate on water and nitrogen availability with implications on the productivity of Norway spruce stands in southern Finland. Ecological Modelling 221: 1731–1743.
doi:10.1016/j.ecolmodel.2010.03.017.

II. Ge, Z.M., Kellomäki, S., Peltola, H., Zhou, X., Wang, K.Y., Väisänen, H., Strandman, H., 2010. Impacts of climate change on the spatial patterns of forest production of Norway spruce (*Picea abies*) in relation to the water availability throughout Finland. *manuscript.*

III. Ge, Z.M., Kellomäki, S., Peltola, H., Zhou, X., Wang, K.Y., Väisänen, H., 2011. Effects of varying thinning regimes on carbon uptake, total stem wood growth, and timber production in Norway spruce (*Picea abies*) stands in southern Finland under the changing climate. Annals of Forest Science 68: 371–383.
doi: 10.1007/s13595-011-0025-y.

IV. Ge, Z.M., Kellomäki, S., Peltola, H., Zhou, X., Wang, K.Y., Väisänen, H., 2010. Regional suitability of different thinning regimes for Norway spruce from southern to northern Finland for adaption to climate change: ecosystem model based analyses on stand carbon stock, total stem wood growth and timber yield. *manuscript.*

Zhen-Ming Ge had the main responsibility for all the work done in Papers I–IV. Co-authors of separate Papers (I–IV) participated in the work mainly by commenting on the manuscripts and supporting the data analyses.

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1 INTRODUCTION

1.1 Background

Forests play an important role in the global carbon cycle. The growth of forests is also clearly influenced by the expected climate change (Dahl 1990, ACIA 2005, Parry 2007). The growth of boreal forests in northern Europe is mainly restricted by the relatively low summer temperatures and short growing season, additionally the short supply of nitrogen may also limit growth (McMurtrie et al. 1994, Tamm et al. 1995, Jarvis and Linder 2000). In these conditions, the simultaneous changes in climatic variables such as temperature, atmospheric CO_2 and precipitation and edaphic variables may profoundly affect the future growing conditions (Beerling 1999, Kirschbaum 2000, Lindner, 2000). For example, in Finland, an increase of 2–7^{o}C in the annual mean temperature with a concurrent elevation of CO_2 by the end of the 21st century is forecasted (Carter et al. 2005, Ruosteenoja et al. 2005). At the same time, the annual precipitation is expected to increase by 6–37%, mostly in wintertime, while in the summertime it may remain the same or even be slightly less than under the current climate (Carter et al. 2005, Ruosteenoja et al. 2005).

The expected warmer and longer growing seasons may, in general, increase the forest growth and productivity in the boreal conditions (Bergh et al. 1999). Additionally, higher temperatures may also enhance the decomposition of organic matter in the soil, leading to increased nitrogen availability and a consequent increase in the growth of forests (Kirschbaum 1995, Freeman et al. 2005). However, the increase in temperature will also increase water loss through evaporation and transpiration, which may have negative effects on forest growth due to an increase in drought periods. The anticipated higher temperatures will also likely lead to a substantial reduction in the snow accumulation due to the decreased fraction of precipitation as snow, because of later snowfall and earlier snowmelt (Kellomäki and Väisänen 1996). This could limit the recharging of soil water in the springtime and early summer. Therefore, it is crucial to consider possible interactions between altered water availability and the potential nutrient availability in order to understand the effects of climate change on the productivity of boreal forests (Jarvis and Linder 2000).

Norway spruce (*Picea abies* (L.) Karst) grows throughout Europe from Norway in the northwest and Poland eastward, and also in the mountains of central Europe, southwest to the western end of the Alps, and southeast in the Carpathians and Balkans to the extreme north of Greece. Norway spruce is identified as ecologically and economically one of the most important tree species in Europe, also in the Finnish conditions. However, recent studies have shown that Norway spruce is looked upon as one of the big ‘‘losers’’ of climate change in comparison with other tree species in Northern (Jyske et al. 2010) and Central Europe (Albert and Schmidt, 2010, Yousefpour et al. 2010). This is because it has proved to be particularly sensitive to increases in temperature and/or decreases in soil water availability.

However, according to Kohler et al. (2010), the harmful effects of drought periods on Norway spruce could be decreased through proper forest management. For instance, by proper control of stand density by thinning, the growth of the remaining trees can be increased as well as the soil water and nutrient availability due to decrease in competition of resources between trees (both in above and below ground). Obviously, the possible adaptation measures to the climate change is affected by the sensitivity of the forest growth and dynamics to the changes expected to occur in the climatic and edaphic properties of the forest sites (Lindner 2000, Lasch et al. 2005). The Finnish forests have been intensively managed for timber production for a long time. However, the current forest management practices may need to be adapted to the changing climate in order to decrease the harmful effects of climate change and to fully utilize its positive effects. Only few studies is available about the opportunities provided by managed forests for timber production and carbon sequestration and the adaptive response strategies (e.g. Garcia-Gonzalo et al. 2007, Kellomäki et al. 2008a).

In order to enhance the carbon sequestration along with timber production under the changing climate the following options have been suggested: (i) lengthening the rotation (Kaipainen et al. 2004), (ii) shifting from clear-cutting systems to selective harvesting (Read et al. 2001), (iii) increasing the percentage of protected forests (Read et al. 2001) and (iv) improved silvicultural techniques, including fertilization (Mäkipää et al. 1998, Olsson et al. 2005). In addition, proper thinning practices (e.g. timing, intensity and interval) are of primary importance in controlling the stocking, and carbon stock, in the forest ecosystem, and the carbon fixation rate into the forest ecosystem (Karjalainen 1996, Thornley and Cannell 2000).

Boreal forests are slow growing and long-lived ecosystems, and therefore experimental studies alone cannot answer the question of how the climate change may affect the long-term dynamics of forests and how forests respond to different management practices under the changing climate. Previous studies on the long-term growth and dynamics of boreal forests are mostly based on empirical (statistical) growth and yield models (e.g. Hynynen et al. 2002, Matala et al. 2003), which utilize, in their parameterization and validation, inventory data representing past management and climatic conditions. Thus, their predictions for the changing climate may be biased, although they could be of benefit regarding the decision-making for management under the current climate (Matala et al. 2005). Optionally, the gap models (Botkin 1993) are available to explicitly assess the impacts of temperature, water and nutrients on growth and development of trees. However, the main goal of these models is to simulate and assess vegetation patterns over time (based on the regeneration, growth and death of individual trees), interaction between different tree species and changes in the vegetation distribution under the climate change (Keane et al. 2001, Price et al. 2001). Nevertheless, the applicability of these models might be limited for impact studies, due to the lack of consideration of the physiological mechanisms linking the growth and development of trees with the climatic and edaphic factors.

In recent years, several process-based models have been developed and successfully applied to study forest growth and dynamics under the climate change (e.g. Kellomäki and Väisänen 1997, Thornley and Cannell 2000, Mäkelä et al. 2000). Process-based models were developed to model key growth processes and fundamental factors affecting productivity such as: photosynthesis and respiration, carbon allocation, tree development and mortality, nutrient cycles and climate effects. They are mathematical representations of biological systems that incorporate our understanding of physiological and ecological mechanisms into predictive algorithms. They take into account, at the physiological level, plant responses to site factors. In addition, process-based models can provide the same prediction capacity under practical management situations as empirical models (Matala et al. 2003, 2005).

For the prediction of forest growth under the changing climate, process-based models are preferable as they could predict the growth and dynamics of forests based on physiological processes driven by hydrological and nutrient cycles and climatic factors (Mäkelä et al. 2000). Moreover, process-based models may help to understand how management should be modified in order to avoid detrimental impacts as well as to utilize the opportunities probably provided by climate change (Lindner 2000). Thus, they would offer also possibility to study the effects of climate change and forest management on water and nitrogen availability of trees with implications on the productivity of different tree species under boreal conditions.

1.2 Aims of the study

The main aim of this work was to study the effects of climate change and management on the growth of Norway spruce (*Picea abies*) in boreal conditions based on a process-based ecosystem model (FinnFor) simulations. The specific study objectives of Papers I–IV were as follows:

i. To study the effects of climate change on water and nitrogen availability with implications on the growth of unmanaged Norway spruce stands on sites with varying soil water availability in southern Finland (**Paper I**);

ii. To study the effects of climate change on the spatial patterns of the growth of unmanaged Norway spruce stands in relation to the soil water availability throughout Finland (**Paper II**);

iii. To study the effects of varying thinning regimes on carbon uptake, total stem wood growth and timber production in Norway spruce stands on sites with varying soil water availability in southern Finland under the changing climate (**Paper III**); and

iv. To study the regional suitability of different thinning regimes for Norway spruce from southern to northern Finland for adaption to climate change, considering carbon stock, total stem wood growth and timber yield (**Paper IV**).

2 MATERIALS AND METHODS

2.1 General outlines

A process-based ecosystem model (FinnFor, Kellomäki and Väisänen 1997) was used in all separate studies (Papers I–IV), to study the effects of climate change and management on the growth of Norway spruce from southern to northern Finland. More specifically, it was first used to study how the climate change affects the growth of unmanaged Norway spruce stands in relation to the water availability from southern to northern Finland (Papers I and II). Thereafter, it was used to study how the climate change and varying management regimes (e.g. thinning intensity and interval) affect together the net carbon uptake, total stem wood growth and timber yield in Norway spruce from southern to northern Finland, respectively (Papers III and IV). In the above context, it was used as inputs for model simulations data of permanent sample plots available for Norway spruce by the Finnish National Forestry Inventory (NFI) and in addition to current climate also the Finnish climate change scenario (FINADAPT for 2000–2099).

In Paper, I addressed the effects of changing climate on the carbon uptake and total stem wood growth of unmanaged Norway spruce stands on three sites in relation to soil water availability (i.e. soil moisture content) in southern Finland (61^{o}N). The FINADAPT climate change scenario (see below) for the Finnish conditions over 100-year period was utilized as the climate change scenario as in all others, too. In addition, the sensitivity of the growth was analyzed in relation to short-term (15 years) variability of temperature, precipitation and nitrogen.

In Paper II, the spatial patterns of the growth of Norway spruce stands in relation to the water availability throughout Finland were simulated over a 100-year period without management. The simulations were done based on 707 sample plots available for Norway spruce (the 9th Finnish National Forestry Inventory, NFI), covering 26.3 million ha of Finnish forest land (60°–67°N).

In Paper III, nine thinning scenarios (considering thinning intensity, thinning interval, and time of first thinning) were embedded into the model simulations to study the effects of various thinning regimes on net carbon uptake, total stem wood growth and timber production. Furthermore, the availability of soil water in the Norway spruce stands under the changing climate was studied. The simulations were done for three different Norway spruce stands of NFI sites with varying soil water availability (initial moisture content) in southern Finland (61°N).

In Paper IV, simulations were done for five pure Norway spruce stands (of total of 707 NFI sites available for Norway spruce) under different climate zones from southern to northern Finland (60°–67°N) to find out how varying thinning regimes (focusing on thinning intensity) affect net carbon uptake, total growth of stem wood and timber yield, and to identify the regional suitability of different thinning regimes for Norway spruce for adaption to the climate change, In this context, also the availability of soil water under the changing climate over the 100-year study period was studied. The outlines of the work for Papers I–IV can be seen in Figure 1.

2.2 Description of the FinnFor model used in the simulations

2.2.1 Outlines of the model

The process-based model (FinnFor) utilized in this study was initially developed by Kellomäki and Väisänen (1997). The structural and functional properties of the model have been extensively presented by Briceño-Elizondo et al. (2006) and Garcia-Gonzalo et al. (2007). Recently, the model was slightly modified (Matala et al. 2003), but still the main part of its structure and functions have remained the same. The model provides predictions on the photosynthetic production, growth, carbon and water balances in the stand level in response to varying environmental conditions. The model has been parameterized for the main tree species (e.g. Norway spruce) growing in the boreal conditions in Finland. The model works on a cohort basis; i.e. each cohort is defined by the tree species, the number of trees in each cohort (trees ha^{-1}), diameter at breast height (cm), height (m) and age (years). These variables are used as the inputs of the stand data for the simulations and are updated annually during the simulation.

Photosynthesis. The physiological parameterization of the model is partly based on data from a long-term forest ecosystem and climate change experiment (Kellomäki et al. 2000). The photosynthetic rate is calculated using the biochemical model developed by Farquhar et al. (1980) and von Caemmerer and Farquhar (1981). This is affected by the climatic variables (radiation, temperature, air humidity, CO_2), stomatal conduction (through the weather and soil conditions) and the nitrogen content of the foliage (Linder and Rook 1984, Roberntz and

Stockfors 1998, Medlyn et al. 2001, 2002). The 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. The photosynthesis works on an hourly basis.

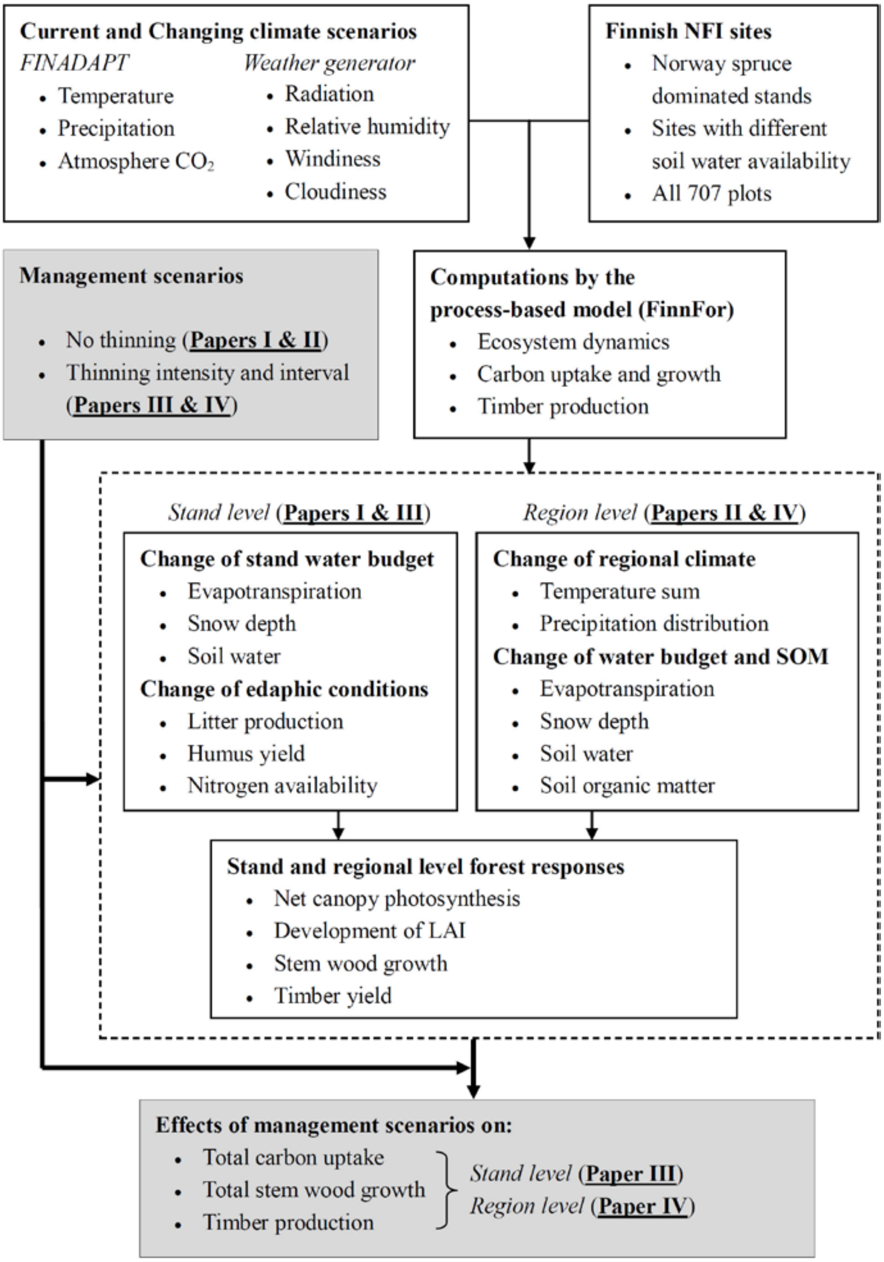

Figure 1. Outlines of the work with the links between different research tasks in Papers I–IV.

Seasonality of the physiological performance of coniferous trees is introduced in the calculations of photosynthesis through the development stage, which controls the seasonal sensitivity of photosynthesis response to environmental factors (Pelkonen and Hari 1980, Hänninen and Hari 2002). To scale up from photosynthetic biochemistry per unit leaf area to canopy photosynthesis per unit ground area, an integrated sun/shade sub-model is used to consider the daily change in the canopy net radiation, the fraction of sunlit and shaded leaves within the canopy and the stomatal conductance. The changes in biochemical parameters with increasing canopy depth are related to the decrease in leaf nitrogen (Kull and Jarvis 1995, Kellomäki and Wang 1997). The calculations of net canopy photosynthesis account separately for the contribution of sunlit and shaded leaf fractions.

$$\begin{aligned} P_{\mathrm{nc}} &= P_{\mathrm{nc.sun}} + P_{\mathrm{nc.sh}} \\ &= \int_0^L f(R_{\mathrm{nc.sun}})f(T_{\mathrm{a}})f(c_{\mathrm{a}})f(N_{\mathrm{L}})f(L_{\mathrm{sun}})f(g_{\mathrm{cs.sun}})dL + \int_0^L f(R_{\mathrm{nc.sh}})f(T_{\mathrm{a}})f(c_{\mathrm{a}})f(N_{\mathrm{L}})f(L_{\mathrm{sh}})f(g_{\mathrm{cs.sh}})dL \end{aligned} \qquad (1)$$

where P_{nc} is the net canopy photosynthesis accounting for the contribution of sunlit ($P_{\mathrm{nc.sun}}$) and shaded needle ($P_{\mathrm{nc.sh}}$) fractions, R_{nc} is the net radiation absorption of the canopy divided into sunlit ($R_{\mathrm{nc.sun}}$) and shaded ($R_{\mathrm{nc.sh}}$) fractions of needles, T_{a} is the air temperature, c_{a} is the atmosphere CO_2 concentration, N_{L} is the leaf nitrogen, L is the leaf area index divided into sunlit (L_{sun}) and shaded leaf area (L_{sh}) fractions, and g_{cs} is the canopy stomatal conductance divided into sunlit ($g_{\mathrm{cs.sun}}$) and shaded ($g_{\mathrm{cs.sh}}$) fractions of needles.

Photosynthates allocation and stemwood growth. The annual total net photosynthesis of the target trees in each cohort is calculated based on the hourly rate of net photosynthesis. The rate of net photosynthesis refers to the rate of photosynthesis after all respiration losses are removed from the gross photosynthesis. 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 (Marklund 1987, 1988, Matala et al. 2003). Thereafter, the diameter at breast height of the stem and the tree height are calculated with the help of an empirical equation developed by Marklund (1987, 1988). The stem volume is calculated as:

$$V_{\mathrm{s}} = V_{\mathrm{Initial}} + \int_0^t a\frac{P_{\mathrm{mass}}(t)}{\rho} \qquad (2)$$

where V_{s} is the total stem wood growth of the target trees, V_{Initial} is the initial volume, $P_{\mathrm{mass}}(t)$ is the annual net photosynthesis available for growth of stem wood in the year t, ρ is the wood density, and a is a parameter.

Mortality of trees. Stocking is controlled 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. The rate of mortality of trees is updated on a five-year time step based on the model developed by Hynynen et al. (2002). At the beginning of each simulation step for mortality, the probability of survival of the trees in each cohort is calculated with regard to the stocking in the stand, the position of the trees in the stand and the life span of the trees. At the end of each simulation step, the stocking of stemwood 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 is reduced in each tree cohort to the level allowed by the model developed by Reineke (1933) with the parameter values specific for Norway spruce.

Evapotranspiration. Evapotranspiration (ET) is calculated in the model as water depletion, which covers the water amount of transpiration (E_t), evaporation from canopy (E_c) and ground surface (E_g). The whole-tree transpiration is simulated using a “big leaf” model (Jarvis 1976, Kellomäki and Wang 2000a,b) considering that transpiration depends upon the cumulative effects of total leaf area, sun/shade canopy conductances and mean boundary layer conductance (McMurtrie et al. 1990, Kellomäki and Wang 1999, 2000a,b). The canopy evaporation is derived from the water pool intercepted on the foliage surface. The Penman-Monteith equation is used to compute the potential transpiration and canopy surface evaporation with net radiation interception by sunlit and shaded leaves, canopy boundary layer resistance at mean canopy height and reference height and aerodynamic resistances (Thom 1975, Monteith and Unsworth 1990). The evaporation from the ground surface is calculated using empirical and physically based approaches from an iterative solution of the energy balance (Jansson 1991a). The Penman type combination equation with the variable ground surface net radiation, aerodynamic resistances including two eddy diffusivity resistances and soil-surface resistance is employed (Monteith and Unsworth 1990). The evapotranspiration works on an hourly basis.

$$E_T = E_t + E_c + E_g \tag{3}$$

Soil profile water flow. In the model, soil water pool composed of the water storage in the soil surface, organic soil and inorganic soil, representing the layered structure of the soil profile (Kellomäki and Väisänen 1997). The calculations of the water flow in the soil profile are assumed to obey Darcy’s law. The water condition in the inorganic soil layers is adopted from Jansson (1991a,b). Inorganic soil is subdivided into a finite number of horizontally homogenous layers (11 layers in the model), and the water/heat condition of each layer is computed with the help of partial differential equations solved using Euler integration.

The water flow into the soil surface pool represents direct precipitation and precipitation through the canopy. The amount of water infiltration to the soil surface pool is calculated as a balance between the incoming and outgoing water flow including the daily water flow into the surface pool as affected by canopy interception and the ground water evaporation (Kellomäki and Väisänen 1996, 1997). The impact of the soil water on growth is introduced through the relative availability of water in the rooting zone (extractable water for tree) (Granier et al. 1999, 2000). The soil hydrological processes work on an hourly basis.

Snow dynamics. The snow conditions in a stand also affect, in addition to water storage and boundary condition for soil water flows, the soil heat boundary conditions. Precipitation is divided into rain and snow, depending on the values assigned to threshold parameters (Kellomäki and Väisänen 1996, 1997). The entire snowpack is considered to be homogeneous both horizontally and vertically. The snow dynamics is expressed as melting-freezing and snow depth variation functions. The daily amount of snowmelt is modeled as a function of temperature, which accounts for the influence of solar radiation and the soil surface heat flow (Jansson 1991a,b). The melting caused by global radiation is, to some extent, controlled by snow age. The snow dynamics work on a daily basis.

Nutrition cycle. For the decomposition of litter (dead organic material from any compartment of trees) and humus (soil organic matter), the algorithm developed by Chertov and Komarov (1997) is used. Decomposition rates of different types of litter and soil organic matter are determined by soil temperature as well as 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 immobilization 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 decomposition works on a monthly basis.

Thinning and final harvest procedures. In the FinnFor model, thinning is based on the reduction of the basal area, which is converted into the number of trees (PF(i)) to be removed from each diameter class i.

$$PF(i) = VJ \times RL(i) \times (\frac{\overline{DBH}}{DBH(i)})^{HT} \tag{4}$$

where VJ is a factor to change the basal area after thinning to that defined by the thinning rate, RL(i) is the number of trees in the diameter class i, DBH with the average symbol means the diameter for trees in the stand weighted with the basal area before thinning, and DBH(i) is the diameter in the class i. The power exponent HT defines the thinning pattern and the relative reduction in the number of trees in the diameter classes; i.e. values > 0 for the thinning from above and values < 0 for the thinning from below. The value of HT is 1, representing the thinning from below (Hynynen et al. 2002). The values of factor VJ are increased iteratively until the basal area of the stand after thinning is equal to that defined by the thinning intensity, with removal of trees from different tree cohorts. Thinning reduces the leaf area in the canopy with a linear relationship with the leaf mass in the removed trees. Recovery of leaf area is a function of the thinning regime and the growth of remaining trees.

The trees (dead trees excluded) removed in thinning and final harvest are converted into timber (sawlogs, pulp wood, and remainder of the stem, logging residues) based on stem diameter and tree height. The thinnings exclude the natural mortality between consecutive interventions, but trees could still die before the first thinning due to crowding. Throughout the rotation, a small amount of trees died randomly, even though the mortality due to crowding was excluded between different thinnings and final harvest (Hynynen et al. 2002). The timing of final harvest can be done in the model either based on mean DBH of trees or age criteria.

2.2.2 Parameterization, validation and performance of the model

The parameterization, validation and performance of the FinnFor model under the current and changing climate has been studied in detail in several previous papers, mainly as: (i) model parameterization and calibration of leaf-canopy photosynthetic rate and stomatal behavior under current and changed climates (Wang 1996, Roberntz and Stockfors 1998, Medlyn et al. 2001, 2002), (ii) model parameterization and calculation of exchange of CO_2 and H_2O between the atmosphere and the conifer stand under boreal conditions (Kellomäki and Wang 1999, 2000a,b, Kramer et al. 2002, Wang et al. 2004a,b), (iii) model simulations on the influence of interrelationship between soil water availability and forest growth in the boreal zones (Kellomäki and Väisänen 1996), (iv) model simulations on snow accumulation and soil frost in a forested landscape under climate change (Venäläinen et al. 2001, Kellomäki et al. 2010), (v) model validation against growth and yield tables, and measurements of the growth history of trees in thinning experiments (Matala et al. 2003, 2005), and (vi) sensitivity analysis of the growth of boreal conifers in regard to the changes in temperature, precipitation, atmospheric CO_2 concentration, physiological and ecological parameters (photosynthesis and respiration), and nitrogen content of leaf (Wang et al. 2004b, Briceño-Elizondo et al. 2006).

This study also investigated the performance of the model by contrasting the predicted growth against the correspondingly measured growth for the permanent sample plots of the

Finnish NFI. In these calculations, 88 plots with Norway spruce as main tree species (Figure 2a) covering the 13 Forests Centers throughout Finland (60^{o}–70^{o}N), with the growth measurements available for the period 1985–1995, were utilized. Also, the national-scale measurement values representing the NFI plots including the main coniferous (Norway spruce and Scots pine (*Pinus sylvestris*) and deciduous (birch *sp*. *Betula pendula* and *B. pubescens*) tree species in Finland were contrasted against the modeled values (Figure 2b). A clear correlation existed between the simulated and measured growth values, without systematic deviation between them. Furthermore, the growth prediction of the FinnFor model in thinned Norway spruce stand is also, in general, in line with a corresponding prediction of Motti, the statistical growth and yield model (Matala et al., 2005), under boreal conditions (Figure 2c).

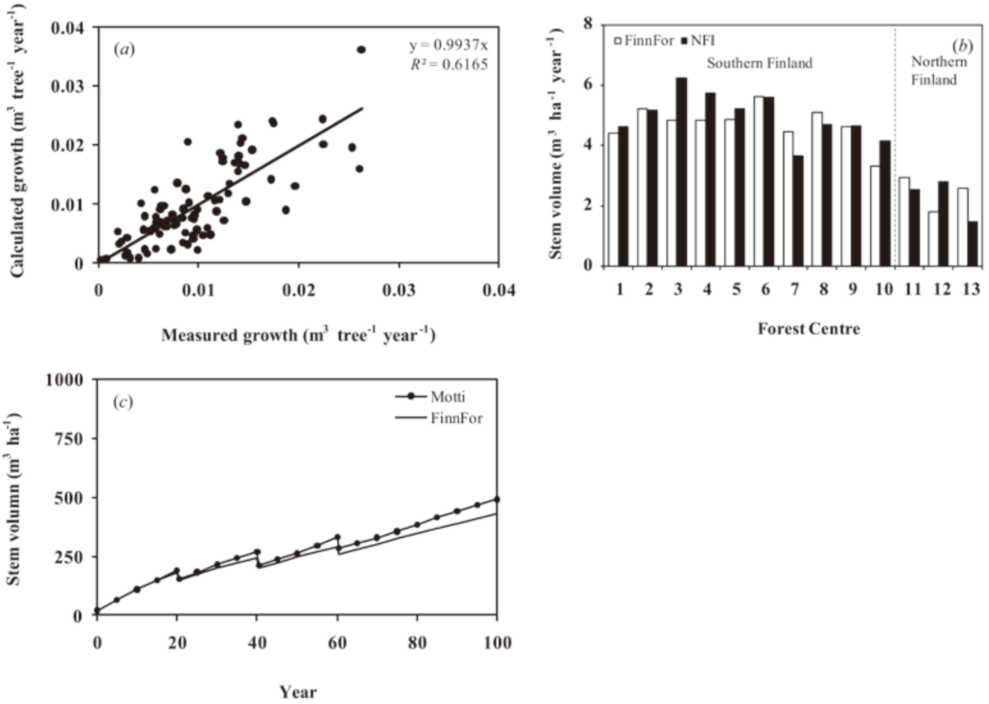

Figure 2. a: Relationship between the measured (NFI, *n* = 88 plots) and simulated (FinnFor) stem volume growth of Norway spruce for forest inventory plots throughout Finland (60^{o}–70^{o}N); b: Comparison between the measured and calculated annual growth of stem volume per hectare for different Forest Centers. The numbers 1-10 indicate the Centers in southern Finland (below N 63°), and the numbers 11–13 in northern Finland (above N 63°). The calculations represent mineral upland sites; c: Stem volume of managed Norway spruce stands (*n* = 47 plots) simulated using the Motti and FinnFor models.

2.3 Simulations and data analysis

2.3.1 Study sites (Papers I–IV)

In the work shown in Papers I and III at stand level, the simulations were done for three different forest sites representing a west-to-east (61°N) direction in southern Finland (Figure 3), and originally also occupied by young Norway spruce stands. The sites were selected from the data from the NFI in 1999–2000, based on their location, mean altitude, site fertility type and mean volumetric water content of topsoil (30 cm) (Paper I, Table 1). The sites were medium fertile (MT, *Myrtillus*) and fertile sites (OMT, *Oxalis-Myrtillus*) (Urvas and Erviö 1974). They represented different soil moisture conditions (Paper I, Table 1); i.e. site S_H represented the highest, site S_M the medium and site S_L the lowest initial soil moisture content based on Vehviläinen and Huttunen (2002).

The national-scale studies of Papers II and IV covered about 26.3 million ha of forest land as represented by the permanent sample plots of the 9th Finnish National Forestry Inventory (NFI in the years 1996–2003) (Figure 4). The NFI was based on systematic cluster sampling and it proceeded region by region over the whole country. The plots are located in blocks of four sites in the south and three in the north. The blocks form a 16 km × 16 km grid in southern and a 32 km × 32 km grid in northern Finland (Kellomäki et al. 2008a).

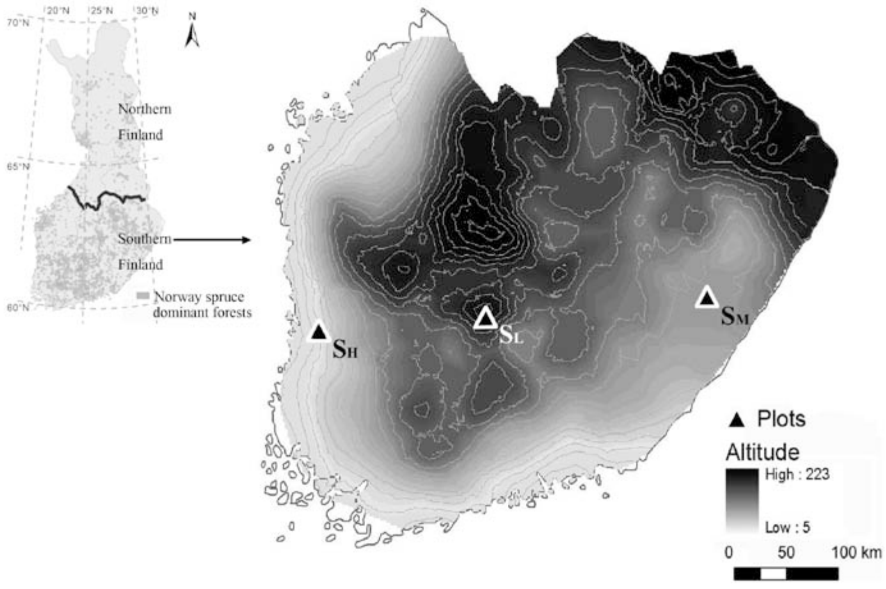

Figure 3. Location of the study sites (S_H, S_M and S_L) including the map for distribution of the Norway spruce dominated forests (upper left) and altitude gradient in southern Finland (right).

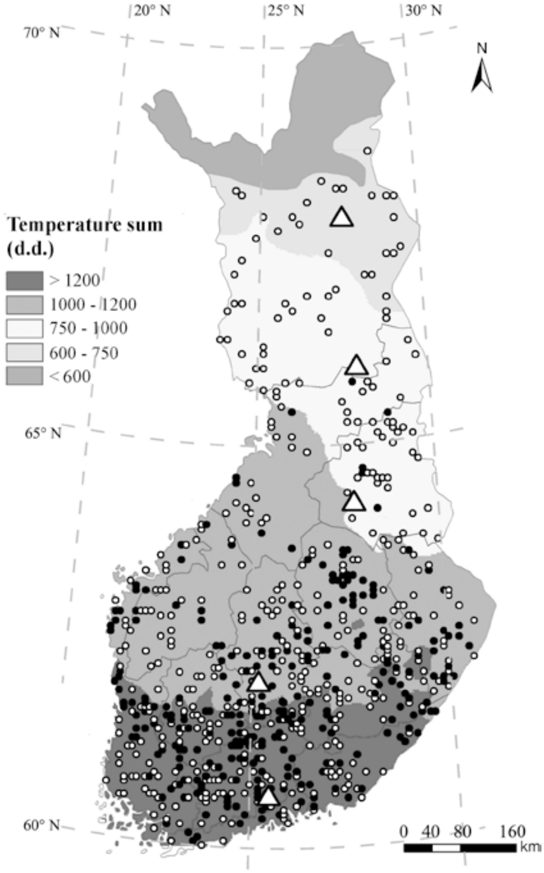

Figure 4. Location of the Norway spruce dominated plots used in the calculations. The shaded and unshaded cycles mean the site types of OMT and MT, respectively. The climatic zones were identified on the basis of the temperature sum distribution. The region with extremely low temperature sum (< 600 d.d.) was excluded in this study (not favorable for Norway spruce). The grey boundary lines divide Finland into 13 Forest Centers. Five sites with "Δ" symbol were selected for the study of management.

Of the NFI plots, 707 sample plots in Norway spruce (dominated tree species) on upland mineral soils were employed in this study (Figure 4). All of them are fertile and medium fertile sites, i.e. OMT (272 plots) and MT (435 plots) types. The amount of litter and humus (SOM) on the plots is defined on the basis of the thickness of SOM, which is regressed against the prevailing temperature sum of the plots by the site type as presented in Paper II. These values are used in initializing the simulations for a specific site type. The values are further used in calculating the amount of soil nitrogen, applying the values of the total nitrogen concentration of the humus layer by site type (Tamminen, 1991). As the regional temperature sum (Day-Degree, d.d.) affects the growth and management recommendations for Finnish forests, accordingly the whole Finland and research plots are divided for further analysis into four climatic zones on the basis of the temperature sum and site types (Figure 4).

2.3.2 Climate scenarios

The scenarios for the current and changing climate used in the simulations for the period 2000–2099 were compiled by the Finnish Environment Institute (SYKE) and Finnish Meteorological Institute (FMI) for the FINADAPT project (Carter et al. 2005, Ruosteenoja et al. 2005). The spatial resolution of the grid for the current climate was 10 km × 10 km, while for the climate change scenario the grid size was 50 km × 50 km (Carter et al. 2005, Ruosteenoja et al. 2005). In the simulations, for a given sample plot, the calculation algorithm uses the climate for the closest grid point for the climate data.

The scenario for the current climate, in terms of temperature and precipitation, represents the mean data for the period 1971–2000 repeated over the whole simulation period, with a constant CO_2 concentration of 351 ppm (the mean value for 1971–2000). The daily values of temperature and precipitation were broken down to an hourly level applying the weather generators developed by Strandman et al. (1993). The weather generator was also used to generate the hourly values of radiation, relative humidity, cloudiness and windiness by means of the weather statistics for the period 1971–2000. Air vapor pressure deficit was calculated based on air temperature and relative humidity.

The scenario for the changing climate was based on the IPCC SRES A2 emission scenario (Carter et al. 2005, Ruosteenoja et al. 2005). Over the period of 2000–2099, the mean temperatures are projected to increase by 4 ^{o}C in the summer time and more than 6 ^{o}C in the winter time under the changing climate, while the atmospheric concentration of CO_2 is 351 ppm at the start of simulation in 2000 and 840 ppm at the end of simulation in 2099. The precipitation increases by 6–37% throughout the country, with the increases in precipitation mainly occurring in the wintertime (Carter et al. 2005, Ruosteenoja et al. 2005). The weather generator was also used to calculate the hourly values of radiation, relative humidity, cloudiness, windiness and vapor pressure deficit for the changing climate scenario.

2.3.3 Thinning regimes design (Paper III, IV)

The concept of thinning scenario was used in this work to indicate the sequence of thinning interventions based on the current Finnish thinning rules (Forest Development Centre Tapio, 2006). The rules use the dominant height and basal area of trees in defining the time and intensity of thinning (Figure 5), i.e. whenever a given upper limit for the basal area (thinning threshold) at a given dominant height is encountered, thinning is triggered. Thinning scenarios were defined in relation to the “Basic Thinning” scenario BT(0, 0), where the zeros in parenthesis indicate no change in the triggering and remaining basal areas. In formulating new scenarios, the values of both parameters were changes; i.e. BT(±n, ±m) (Paper III, Table 2), where n indicates the percentage increase/decrease in the thinning threshold and m the percentage increase/decrease in remaining basal area (Figure 5). The timing of thinning was adjusted to the growth and dynamics of the tree population in such a way that thinning from below was executed whenever the triggering combination of dominant height and basal occurred. This adjustment excludes the natural mortality between consecutive interventions, but trees could still die before the first thinning due to crowding. Throughout the rotation, a small amount of trees died randomly, even though the mortality due to crowding was excluded between different thinnings and final cut (see Hynynen et al. 2002).

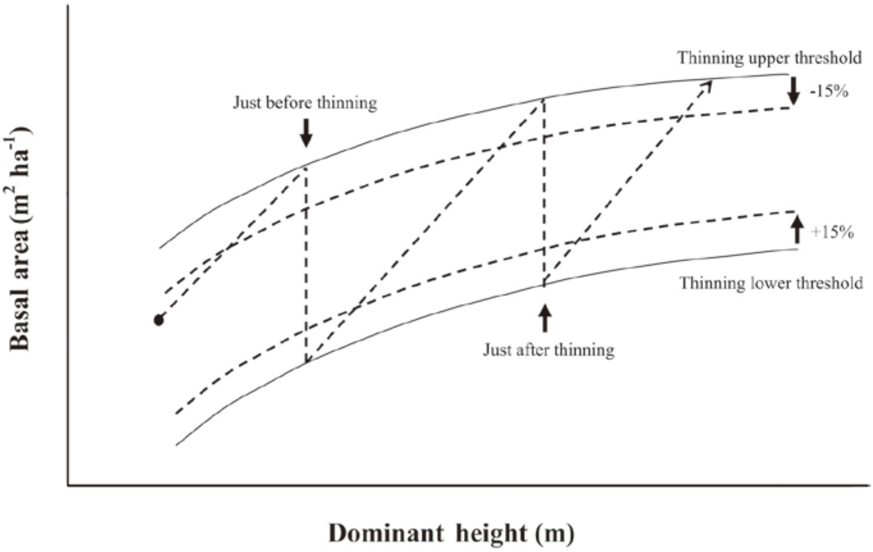

Figure 5. Principles used to define the proper thinning scenarios for final analyses with the help of the development of dominant height and basal area. The examples of -15% change of upper threshold and +15% change of lower threshold for the thinnings are expressed as dashed lines.

Based on the BT(0, 0), nine thinning scenarios (including BT(0, 0)) were created by varying the triggering and remaining basal area by 0%, ±15% and ±30% to control the thinning intensity, thinning interval and first thinning time in the work shown in Paper III. The simulations used the three Norway spruce stands with different soil water conditions in southern Finland (same as Paper I). Furthermore, a scenario with no thinning was included as a comparison.

Regarding the analyses on regional suitability of thinning regimes for Norway spruce under the changing climate in Paper IV, five sites were selected from the NFI dataset for studying management impact (Figure 4). In order to conduct the parallel comparison and avoid the structure-specific interference, the same initial stand structure (original structures were excluded) was used in the simulations regardless of site location. The initial stand density in Norway spruce stand was 2400 trees per hectare. The trees represented four cohorts, with equal distribution of age classes (600 seedlings) in each. The heights of the cohorts were 4, 8, 12 and 16 m (mean value of 10 m) and corresponding diameters at the stem butt 4, 8, 12 and 16 cm (mean value of 10 cm), respectively.

The thinning scenarios represented different thinning intensities (percentage of basal area removed), with ten fixed proportions (5, 10, 15, 20, 25, 30, 35, 40, 45 and 50%) of the basal area removed from below in each thinning. The symbols of T05, T10, T15, T20, T25, T30, T35, T40, T45 and T50 represent the thinning scenarios. Over the 100-year simulation period, three thinning and one final harvest, with the same thinning interval (25 years), were employed. This thinning interval was roughly consistent with the thinning practices conducted in the boreal forests in Finland (Hynynen et al. 2002). Furthermore, a scenario with no thinning was included as a comparison in the analysis.

3 RESULTS

3.1 Stand level effects of climate change on the carbon uptake and total growth of unmanaged stands in southern Finland related to soil water availability (Paper I)

Soil water and nitrogen availability. Regardless of site (S_H, S_M and S_L), the evaporation from canopy and ground surface was higher compared to the current climate, while canopy conductance and transpiration was lower when the changing climate was assumed (Paper I, Figures 4–5). Moreover, the increase in evaporation was larger than the decrease in transpiration under the changing climate. As a result, substantially less water infiltrated into the soil pool (Paper I, Figure 6). Regardless of site, the reduction in the amount of water in the soil profile frequently led to a water deficit, which occurred most frequently in the latter phases of the simulation period. Under the changing climate, a water deficit occurred even earlier (from 30 years onwards) on the site S_L with low soil water availability than on the sites S_H and S_M with higher soil water availability. On the sites S_H and S_M, the cumulative soil water deficit was clearly affected by the climate scenario, unlike on the site S_L.

The accumulation of soil organic matter (the gross nitrogen content) was larger under the changing climate than under the current climate, which might be due to a higher litter input (Paper I, Figure 7). However, the decomposition from litter to humus (fully humified materials) was most affected by the soil temperature and moisture. The nitrogen bound in the humus hold the most nitrogen available for the growth of trees. When the changing climate was applied, the amount of humus increased slightly during the early phase of stand development, but it was lower than that under the current climate during the later phases. Furthermore, the inflection point occurred after about 70 and 55 years of simulation on the S_H and S_M sites, respectively, and after about 30 years of simulation on the site S_L.

The carbon uptake and total growth of stem wood. Regardless of climate scenario applied, the annual canopy net photosynthesis increased rapidly during the stand development on the sites S_H and S_M (Paper I, Figure 8). On the site S_L, the increase of carbon uptake was slower due to lower soil water availability. Under the changing climate, the carbon uptake was higher than under the current climate, especially during the early phase of stand development, but it declined substantially (on average by about 35%), regardless of the site, during the latter part of the simulation period (Paper I, Table 4).

Under the changing climate, the total stem wood growth was slightly higher on the site S_H during most of the simulation period (between 2020 and 2090) compared to the current climate, but the difference disappeared from about 2095 until the end of the simulation period. On the site S_M, the corresponding difference in the stem wood growth, between the changing climate and current climate, was even higher in the middle of the simulation period. However, after the year 2075 the total stem wood growth was smaller under the changing climate than under the current climate. Whereas, on the site S_L there was no clear difference in the stem wood growth between the changing and current climate until the year 2055. But thereafter the stem wood growth was clearly lower under the changing climate. The total stem volume production over the 100-year simulation period was also clearly (and statistically significantly) lower under the changing climate on the site S_L (Paper I, Table 4).

The nitrogen uptake, canopy conductance and consequent canopy photosynthesis, clearly affected the stem volume growth over the 100-year simulation period (Paper I, Figures 5 and 8). Regardless of the site and climate scenario, the annual nitrogen uptake by trees increased during the stand development (Paper I, Figure 8). When the changing climate was assumed, the nitrogen uptake at tree level was slightly higher than under the current climate during the early stages of the simulation period (Paper I, Table 4). Under the changing climate, the nitrogen uptake by trees decreased from about 50 years onwards on the site S_H and S_M, while it decreased from about 30 years onwards on the site S_L. For all the sites, the reduction was the most evident during the latter phases of stand development.

3.2 Stand level effects of climate change and thinning scenarios on the growth of Norway spruce stands in southern Finland (Paper III)

Carbon uptake, total growth of stem wood and timber yield. The alternative thinning scenarios deviated from each other mostly in the frequency of interventions and in the timing of the first thinning (Paper III, Table 4). For example, the Basic thinning scenario (BT(0, 0)) did output two interventions during the rotation, regardless of the site, whereas the scenarios BT(-15, 0) and BT(0, +15) had three interventions. The scenarios BT(0, -15) and BT(0, -30) did output only one late intervention over the rotation as did BT(+15, 0) and BT(+15, +15).

Under the changing climate, the carbon uptake was higher for the thinning scenarios BT(+15, 0), BT(+15, +15), BT(-15, 0) and BT(0, +15) than for the Basic scenario (BT(0, 0)) on the sites S_H and S_M, and BT(+15, 0), BT(+15, +15) gave the highest values (Table 1). On the site S_L, the carbon uptake was the highest for the scenarios BT(0, +15) and BT(-15, 0) (Paper III, Figure 7).

On the sites S_H and S_M, the total stem wood growth was higher for the thinning scenarios BT(+15, 0), BT(+15, +15), BT(-15, 0) and BT(0, +15) than for BT(0, 0), and BT(+15, 0), BT(+15, +15) gave the highest values (Table 1). On the site S_L, the growth was the highest for the scenarios BT(0, +15) and BT(-15, 0) (Table 1). Regardless of the site, the scenario BT(-30, -30) had the lowest growth of stem wood and carbon uptake.

In general, management scenarios with frequent thinning, such as scenarios BT(-15, 0) and BT(0, +15), yielded more timber with higher carbon uptake and stem wood growth than scenarios with less frequent thinning (Paper III, Table 5) over the rotation, on the site with low soil water availability. On the site with high soil water availability, the scenarios with less frequent thinning gave the highest carbon uptake and stem wood growth, but not the highest timber yield (Paper III, Table 5).

Effects of thinning scenario on availability of soil water. Regardless of site, thinning increased water infiltration in the soil profile and, and thus reduced the soil water deficit compared to the situation with no thinning (Paper III, Figure 9). The thinning scenarios BT(-15,0) and BT(0,+15) with three thinnings over the rotation increased the infiltration of water into the soil the most, with consequent reduction in the soil water deficit. When applying the Basic thinning (BT(0,0)) with two interventions, the soil moisture deficit was also reduced, but less than in the previous case. Similarly, the thinning scenarios BT(+15,0) and BT(+15,+15), with one thinning over the rotation, slightly reduced the soil water deficit.

Table 1. Comparison of effects of different thinning scenarios with current basic thinning practice (BT(0, 0)) on the cumulative carbon uptake and total stem wood growth on the three sites with varying soil water availability (ranging from high (S_H) to medium (S_M) and low (S_L)), under the changing climate over the 100-year period.

Thinning scenarios	S_H		S_M		S_L	
	Carbon uptake	**Stem wood growth**	**Carbon uptake**	**Stem wood growth**	**Carbon uptake**	**Stem wood growth**
BT(0, 0)	/	/	/	/	/	/
BT(0, +15)	+	+	+	+	+	+
BT(0, -15)	–	–	–	–	–	–
BT(0, -30)	–	–	–	–	–	–
BT(+15, 0)	++	++	++	++	–	–
BT(-15, 0)	+	+	+	+	+	+
BT(+15, +15)	++	++	++	++	–	–
BT(-15, -15)	–	–	–	–	–	–
BT(-30, -30)	–	–	–	–	–	–

"+" means the values are higher and "–" lower, compared to BT(0, 0), "++" means the highest values

3.3 Regional level effects of climate change on the growth of unmanaged Norway spruce stands (Paper II)

Effects of changing climate on the regional hydrological conditions. Based on the FINADAPT climate change scenario, at the end of simulation period, the annual mean depth of the snow layer was 25–50 mm (total annual accumulation / 365 days) in the south and 50–100 mm in the north under the current climate. Under the changing climate, the snow depth was also substantially reduced due to earlier snowmelt and higher evaporation, as well as because of the decreased share of precipitation as snow (Paper II, Figure 6).

The soil water conditions were, thus, modified by the balance between the input of precipitation with snowmelt and the depletion of evaporation and water use for tree growth. The annual soil water content was on a high to medium level in most areas of southern Finland under the current climate at the end of the 100-year simulation period, and the soil moisture content was relatively lower in northern Finland due to the lower amount of precipitation. However, under the changing climate, the soil water content was much lower than that under the current climate in the southern regions, and slightly lower in the north (Paper II, Figure 6).

Effects of changing climate on the spatial patterns of forest growth. The total stem wood growth over the 100-year simulation period also makes the distinction between southern and northern Finland under the current and changing climate. The growth increases by 5–38% in most areas of the north due to changing climate, but reduces by 5–20% in the south. The total stem wood growth correlates positively with the increase in temperature sum in the north. The high temperature sum does not enhance the forest growth in the south, instead there exists a slightly negative effect because of the elevated temperature (Paper II, Figure 8).

On account of the gradually changing climate, the growth in different simulation periods separately, i.e. until years 2030, 2060 and 2099, was considered. The mean leaf area index is higher under the changing climate than that under the current climate until the year 2030 regardless of the climatic regions. But, it was from the year 2060 to 2099 in the south lower under the changing climate (Paper II, Table 2). In the northernmost regions, the leaf area index is higher over the whole 100-year simulation period compared to other regions. Slightly lower values are presented in the central-north regions at the end of the simulation period.

The average annual mean net photosynthesis is also higher under the changing climate than that under the current climate during the period 2000–2030, regardless of the climatic zone. But, it is lower from the middle of the simulation period (2030–2060) until the end of the rotation in the southern regions under the changing climate (Paper II, Table 3). In the northern regions, the annual mean net photosynthesis on most sites is higher under the changing climate over the whole simulation period.

The mean values of total stem wood growth are higher under the changing climate over the whole simulation period than under the current climate in the northern regions, especially in the northernmost part of country (by about 22%) (Paper II, Table 4). However, in the southern regions the total stem wood growth is lower under the changing climate since the middle of simulation period.

3.4 Regional level effects of climate change and varying thinning intensities on the growth of Norway spruce stands (Paper IV)

Responses of growth to thinning. In Paper IV (Figures 4–5 and Table 2), the dynamics of stand structure (leaf area index, average diameter and mortality of trees), carbon uptake and stem wood production, were compared in stands subjected to the different thinning regimes with varying thinning intensity and equal thinning intervals (25 years) and with no thinning (UT) during the 100-year simulation period under the changing climate.

On the southernmost site, the cumulative carbon uptake and the total growth of stem wood (including increased number of dead trees) were 1468 Mg C ha^{-1} and 518 m^3 ha^{-1}, respectively, without thinning. This resulted in a timber yield (in final harvest) of 424 m^3 ha^{-1}. The thinning regimes of T05, T10, T15 and T20 increased the carbon uptake and total stem wood growth by 2–4% and 1–2%, respectively. The increase in tree growth and timber yield were both 19 % higher for T10, T15 and T20, compared to that of UT. The heavy thinning regimes of T30–T50 reduced the carbon uptake and total stem wood growth, as well as the timber yield by more than 25%.

The cumulative carbon uptake and the total growth of stem wood were 1354 Mg C ha^{-1} and 485 m^3 ha^{-1} without thinning on the central southern site. On this site a timber yield of 408 m^3 ha^{-1} was obtained. The thinning regimes of T05, T10 and T15 increased the carbon uptake and total stem wood growth by 1–3%, compared to that of UT. The regimes of T10, T15 and T20 gave the highest timber yield (increase of 16%). Under the thinning regimes with > 20% thinning intensity, the carbon uptake and total stem wood growth were lower than those of UT, and the timber yield decreased with the increase of thinning intensity.

On the central site, the cumulative carbon uptake and the total growth of stem wood were 1250 Mg C ha^{-1} and 450 m^3 ha^{-1} without thinning, respectively. This resulted in a timber yield (after final harvest) of 390 m^3 ha^{-1}. Under the thinning regimes of T05 and T10, the carbon uptake and total stem wood growth were slightly higher than those of UT. The increase in timber yield was a maximum of 13% for T10, T15 and T20. The heavy thinning regimes of T20–T50 reduced the carbon uptake, total stem wood growth and timber yield. Furthermore, the timber yield was lower under the very heavy thinning intensity (50%) compared to that under UT.

The cumulative carbon uptake and the total growth of stem wood were 1012 Mg C ha^{-1} and 399 m^3 ha^{-1} without thinning on the central northern site, respectively. On this site the timber yield, after final harvest, was 364 m^3 ha^{-1}. All of the thinning regimes decreased the carbon uptake and total stem wood growth, compared to those of UT, and the reduction increased with the increase of thinning intensity. The increase in timber yield was at maximum of 6% for T5 and T10. For thinning regimes with intensity > 30%, the timber yield was lower than that of UT.

On the northernmost site, the cumulative carbon uptake and the total growth of stem wood were 672 Mg C ha^{-1} and 327 m^3 ha^{-1} without thinning, giving a timber yield (after final harvest) of 319 m^3 ha^{-1}. Regardless of the thinning regime, the carbon uptake, total stem wood growth and timber yield were lower than those of UT, and the reduction increased with the increase of thinning intensity.

Responses of water availability to thinning. Regardless of site, all of the management regimes with three thinning periods concurrently reduced the cumulative water depletion due to evapotranspiration, compared to that of UT (Paper IV, Figure 6). As a result, the water infiltration in the soil profile increased. With the increase of thinning intensity, the reduction in water depletion increased also, which in turn increased soil water availability. On the southern sites, the increase in soil water induced by the light (T05 and T10) and moderate (T15 and T20) thinning regimes enhanced the carbon uptake and the total stem wood growth (Paper IV, Figure 7), compared to UT. On the northern sites, the improved soil water availability induced by thinnings did not increase the carbon uptake and total stem wood production.

4 DISCUSSION AND CONCLUSIONS

4.1 Effects of climate change on growth of Norway spruce related to site-specific soil water availability

Boreal coniferous forests are the most widely distributed vegetation type in the world, covering 19% of the land surface of the Earth (FAO 2000). They provide various services, including timber production and carbon sequestration. The important role of forests and their management for maintaining carbon stocks and enhancing timber production is greatly emphasized (Jarvis et al. 2005). However, the growth of forests will be clearly influenced by the expected climate change (Parry 2007), particularly for Norway spruce in Europe (e.g. Bergh et al. 1999, Kellomäki et al. 2008a, Jyske et al. 2010, Yousefpour et al. 2010). The expected long-term effects of changes in climate on forest ecosystems are highly complex and can only be studied through use of comprehensive model simulations (Lindner 2000, Loustau et al. 2005, Matala et al. 2005, Kellomäki et al. 2008a).

Based on the simulations of the FinnFor ecosystem model, the aim of this study was to analyze how the changing climate in terms of elevation in temperature, atmospheric CO_2 and change of precipitation, and management, may affect the growth of Norway spruce in relation to the water availability throughout Finland over a 100-year period (2000–2099). For simulation inputs, permanent sample plots provided by the Finnish National Forestry Inventory (NFI) were used. The simulations were also based on the recent climate scenarios provided by the Finnish Meteorological Institute (FMI) and Finnish Environmental Institute (SYKE) for the FINADAPT project (Carter et al. 2005, Ruosteenoja et al. 2005).

It was found (Papers I), that the climate change would modify the physiological and physical processes of evapotranspiration and photosynthesis with the consequent effects on the leaf area and stocking (volume of growing stock). It will also affect the availability of soil water in Norway spruce, indicating decrease especially in southern Finland (Papers II). This will further affect the humus production, with impacts on the availability of nitrogen and further, the carbon uptake and forest growth. Previous simulations using the SIMA, a gap type ecosystem model (e.g. Kellomäki et al. 2008a) also indicated that the changing climate may increase the frequency of drought episodes in Finland, and thus, reduce the growth of Norway spruce especially in southern Finland.

The simulations for evapotranspiration and availability of soil water were based on classical interrelationship between the physiological response and structural changes of leaf-canopy and climatic physical variables. As a result, the leaf-canopy area expanded more under the changing climate than under the current climate when same site, initial stand conditions and management were applied in simulations (Paper I). Consequently, a larger amount of water was intercepted in the canopy and lost in evaporation than under the current climate (Paper I). However, the changing climate may create an environment with a larger physical force for evaporation (canopy and ground surface) due to a higher vapor pressure deficit and lower diffusive resistance. This could result in higher soil water deficit, especially on the stands with lower soil water availability, as found in this work. The high proportion of total precipitation lost in evapotranspiration indicated that Norway spruce may, in the future, be water-limited. This will be the case even though the total precipitation is expected to increase under the changing climate (Carter et al. 2005, Ruosteenoja et al. 2005), because precipitation is expected to increase mainly in wintertime, but little in the growing season.

In a forest ecosystem, the canopy structure affects the above- and below-canopy microclimatic conditions such as the throughfall and irradiance interception, which are crucial for carbon uptake and soil water availability (Jarvis and McNaughton 1986). In the FinnFor model, the leaf area and canopy conductance control the water budget in a stand by affecting the amount of evaporation and transpiration. The increased surface evaporation makes the soil water deficit an issue, as it influences the stomata behavior. In turn, the stressed leaf-canopy conductance will reduce the carbon uptake, transpiration and consequent tree growth (Oren et al. 1999, Ewers et al. 2000, Phillips et al. 2001).

Over the 100-year simulation period, the water availability (moisture content) of the soil organic matter layer decreased clearly under the changing climate. Despite this, the gross nitrogen content in the soil was fairly stable due to the continuous accumulation of litter and plant debris on the forest floor. However, the amount of decomposed soil organic matter (humus as available source of nitrogen) decreased during the latter phases of the simulation period regardless of site (and soil moisture context). Consequently, the simulations for the changing climate with more frequent drought episodes showed the decrease in nitrogen uptake and lower nitrogen content in the needles. The simulated canopy photosynthesis also declined during the latter stages of the simulation period with increasing water deficit on all the sites. In the FinnFor model, the soil organic matter dynamics is based on the concept of succession stages of soil organic matter decomposition utilizing different groups of soil fauna inherent to forest soils. The decomposition of litter and nitrogen retention processes directly respond to the soil moisture and temperature (Chertov and Komarov 1997, Chertov et al. 2001), which is in line with findings in studies based on laboratory and field experiments (Kirschbaum 1995, Kaste et al. 2004).

The simulations done in this work (Paper I) showed that net photosynthesis and growth increased in Norway spruce during the early stages of the simulation but declined during the latter stages. This stimulation during the earlier period occurred along with the steady elevation in air temperature and atmospheric CO_2 by the gradient climate scenario. Under the changing climate, the elevated CO_2 will increase the water use efficiency, and thus, partly compensate for the effects of water deficiency. This was previously demonstrated also, for example, by Kellomäki and Wang (1998). However, long-term CO_2 enrichment often leads to down-regulation in stomatal behavior and carboxylation efficiency (Urban 2003), and decreased leaf nitrogen (Stitt and Krapp 1999). Moreover, it is known that the amount of plant biomass, photosynthesis, and nutrient use caused by elevated temperature and CO_2 are dependent on the availability of other limiting resources (Stitt and Krapp 1999, Bergh et al. 1999, 2005). In this work, the fluctuations in water and nitrogen availability interacted with changes in temperature and CO_2 and affected the photosynthesis and, concurrently, the growth of Norway spruce (Paper I). Consequently, the changing climate increased the total stem volume growth less than one may expect purely on the basis of the elevation of temperature and atmospheric CO_2. This was evident especially for sites where the water budget most probably controls the growth and development of Norway spruce. On these sites, the total stem volume growth over the simulation period was also slightly lower under the changing climate compared to the current climate.

4.2 Effects of climate change and thinning regimes on growth of Norway spruce

In the stand level study of Paper III for southern Finland, the various thinning scenarios adopted deviated from each other mainly in terms of the number and intensity of the thinnings and the timing of the first thinning. The various thinning scenarios have an extremely important role in modification of light regimes, water cycle and nutrient balance for the remaining trees (Thornley and Cannell 2000, Kohler et al. 2010), as can be seen also based on model simulations under the changing climate during the 100-year rotation. The problems faced in forest management under the climate change are how to maintain and enhance the capacity to sequester and store carbon in the forest ecosystems, and at the same time to meet the needs of timber production.

Regardless of site, the management with frequent thinnings yielded more timber than management with less frequent or heavy thinnings. This pattern is related to the mean stocking, which was larger in the former case over the rotation. On the other hand, the thinning increased water infiltration into the soil profile and thus, reduced the soil water deficit compared to the situation with no thinning. Furthermore, the infiltration of water into the soil increased if the mean spacing was kept wider throughout the rotation with less evaporative losses from the canopy than in other cases.

An appropriate thinning scenario (timing, intensity and frequency of interventions) seems to mitigate the harmful effects which the climate change may have on the growth of Norway spruce due to evaporative losses of water. Previously, Kellomäki et al. (2008b) have also demonstrated in the Finnish conditions that the wider spacing and regular thinning may increase the water yield by 15–20% over the rotation when there is reduced evaporation from canopy surfaces.

In this work, it was found that on the sites with high soil water availability, the thinning scenarios with moderate intensive thinning (BT(-15, 0) and BT(0, +15)) and/or scenarios with delayed first thinning (BT(+15, 0/+15)) may simultaneously provide higher stem wood growth and carbon stock in stocking. This is opposite to the scenarios with earlier heavy thinnings such as BT(-30, -30), where the mean stocking is low (Paper III). Regarding the sites with low soil water availability, the thinning scenarios with moderate intensive thinning may be useful for mitigation of soil water deficit, also leading to even higher timber yield.

4.3 Regional-scale effects of climate change and management on growth of Norway spruce

Viewed from the regional scale, dynamics of the boreal forests in northern Europe is greatly controlled by the south-north gradients in climate (Paper II). Currently, the annual mean temperature drops and humidity rises towards the north, with accompanying increase in temperature limitation for growth in the northern boreal forests (Henttonen 1990). The expected climate change in turn may profoundly change water/heat gradients. On the other hand, a water limitation on growth, and thus, sensitivity to changes in precipitation can be expected in warmer conditions in the southern boreal forest (Bergh et al. 2005). In particular, the growth of Norway spruce is water-limited in many places in the southern boreal forests without management (Henttonen 1990, Bergh et al. 1999, Bradshaw et al. 2000). Despite of larger precipitation input under the changing climate, most of the precipitation is intercepted and evaporated from the dense canopy of Norway spruce. In addition, the higher evaporation from the ground surface and water use of trees, induced by the extensive elevation in temperature, could influence the soil water availability. However, in the north the negative impacts on soil water conditions are not significant due to the relatively lower depletion/input ratios. On the other hand, the snowmelt is among the key factors affecting water replenishment for the trees during spring. The reduced snowpack induced by lower snow fraction of precipitation and earlier snowmelt under the changing climate probably causes a more serious soil water deficit to decrease the growth of trees, especially in the south on soils with low water holding capacity (e.g. sandy soils).

Despite the low soil water availability in southern Finland, the decrease in the mean leaf area index and total stem wood growth do not drop to an extremely low level. This is because the elevated atmospheric CO_2 may partly compensate for the growth reduction due to increased drought episodes. Roberntz (1998) and Roberntz and Stockfors (1998) have reported previously that the elevated CO_2 alone increased net carbon uptake for Norway spruce in Sweden by 25–40% through enhanced carboxylation efficiency and photosynthesis. Wyckoff and Bowers (2010) suggested that the impacts of increasing drought on forest may be somewhat mitigated by increasing CO_2. However as in this study, the drought-induced growth decline would not be totally counteracted (e.g. Kellomäki and Wang 1998). Growth reduction was also predicted previously under the climate change by Loustau et al. (2005), who used process-based models (i.e. CASTANEA, GRAECO and ORCHIDEE) to study the impacts of climate change on gross productivity of coniferous forests in France. The expected positive effect of CO_2 elevation on growth was reduced by the increasing number of frequent and severe droughts, which resulted in an increase in water vapor deficit during the growing season (because of a pronounced shift in seasonal rainfall from summer to winter).

Based on the model simulations for five different sites, representing different climatic regions, and applying different management scenarios (Paper IV), it was found that the light and moderate thinning increased the net carbon uptake and the consequent total stem wood growth in Norway spruce, compared to unthinned treatment on the southern sites. Moreover, the moderate thinning gave the largest amount of timber yield. The results were in line with those previously reported in the long-term thinning experiments in Europe (Mäkinen and Isomäki 2004a,b, Pretzsch 2004, Pretzsch and Schütze 2009). With thinnings, the soil water deficit was mitigated due to reduced water depletion under the changing climate, coupled with the reduction in natural mortality. The effects of thinning can be explained by reduced evaporation and interception of precipitation in combination with a higher light, nutrient and water availability for trees left in the stand after thinning (e.g. Whitehead et al. 1984, Kohler et al. 2010). However, heavy thinning, in which a large proportion of the basal area is removed, will reduce the carbon uptake and total stem wood production for Norway spruce due to low stocking of remaining trees. Meanwhile, the timber yield is also decreased. This result is in agreement with the previous findings of Mäkinen and Isomäki (2004a,b) and Nilsson (2010).

According to this work, on the northern sites, the carbon uptake and total stem wood production did not increase, regardless of thinning regime compared to UT. However, in general the climate change was found advantageous to the Norway spruce in the north, because there the low-temperature is the most important limiting factor for the tree growth. The increase in temperature and precipitation, accompanied by CO_2 enrichment, clearly stimulated the growth of Norway spruce in the northern regions.

4.4 Conclusions

Norway spruce dominated forests are common in Finland, particularly in the southern parts of the country (Figures 3–4), where the drought episodes are expected to become more frequent in summer periods. Especially in southern Finland, the changing climate may create a suboptimal environment for Norway spruce. However, Norway spruce may still grow well on the fertile sites with sufficient water supply even under longer drought periods. In these conditions, Norway spruce is probably competitive with other tree species as well. But, the dominance of broad-leaved birch *sp.* may increase on less fertile sites currently occupied by Norway spruce (Kellomäki et al. 2008a). Previous studies have indicated the use of wider spacing with thinnings may reduce the occurrence of drought effects and mitigate the detrimental impacts on growth (e.g. Bréda et al. 1995, Kohler et al. 2010). Appropriate thinning regimes are needed for Norway spruce especially on sites with low water holding capacity in southern Finland to mitigate the adverse impacts of climate change in order to sustain the growth of Norway spruce dominated stands. As discussed above, the current thinning guidelines (BT(0, 0)) may need to be modified under the changing climate for Norway spruce, especially on the sites with low soil water availability.

The critical question for the Finnish forest management and forestry is how to mitigate the adverse effects and profit from the positive effects of the changing climate. On the southern sites with higher soil water deficit, the regular thinnings with moderate intensity will most probably make it possible to balance the needs for timber production and carbon storage, for example. While the less heavy thinning or even no thinning may be appropriate on the northern sites. To conclude, the appropriate choice of adaptive thinning practices under climate change is greatly dependent on the stand structure, site properties and geographical location of the site, as well as forest management objectives set by forest owner.

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