Research paper

Impacts of changing climate on the productivity of Norway spruce dominant stands with a mixture of Scots pine and birch in relation to water availability in southern and northern Finland

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A process-based ecosystem model was used to assess the impacts of changing climate on net photosynthesis and total stem wood growth in relation to water availability in two unmanaged Norway spruce (*Picea abies*) dominant stands with a mixture of Scots pine (*Pinus sylvestris*) and birch (*Betula* sp.). The mixed stands were grown over a 100-year rotation (2000–99) in southern and northern Finland with initial species shares of 50, 25 and 25% for Norway spruce, Scots pine and birch, respectively. In addition, pure Norway spruce, Scots pine and birch stands were used as a comparison to identify whether species' response is different in mixed and pure stands. Soil type and moisture conditions (moderate drought) were expected to be the same at the beginning of the simulations irrespective of site location. Regardless of tree species, both annual net canopy photosynthesis (P_{nc}) and total stem wood growth (V_s) were, on average, lower on the southern site under the changing climate compared with the current climate (difference increasing toward the end of the rotation); the opposite was the case for the northern site. Regarding the stand water budget, evapotranspiration (E_T) was higher under the changing climate regardless of site location. Transpiration and evaporation from the canopy affected water depletion the most. Norway spruce and birch accounted for most of the water depletion in mixed stands on both sites regardless of climatic condition. The annual soil water deficit (W_d) was higher on the southern site under the changing climate. On the northern site, the situation was the opposite. According to our results, the growth of pure Norway spruce stands in southern Finland could be even lower than the growth of Norway spruce in mixed stands under the changing climate. The opposite was found for pure Scots pine and birch stands due to lower water depletion. This indicates that in the future the management should be properly adapted to climate change in order to sustain the productivity of mixed stands dominated by Norway spruce.

Keywords: availability of soil water, boreal zone, climate change, ecosystem model, forest growth, mixture.

Introduction

The growth of trees depends on carbon assimilation, which requires resources such as light, water, nutrients and atmospheric CO_2 (Kirschbaum 2000). Changes in the availability of any of these resources will affect the photosynthetic rate as CO_2 enrichment will generally increase photosynthetic production and consequent growth (McMurtrie and Wang 1993). However, this effect could be counteracted and potentially overwhelmed by drought and nutrient stress (Roberntz and Stockfors 1998, Bergh et al. 1999). Additionally, the combination of elevated temperature and soil water deficit could limit forest growth even more (Bergh et al. 2005). In this respect, changes in hydrological processes through the atmosphere–canopy–soil system affect climate change impacts on temperate forests at lower latitudes (Bonan 2008). This is also likely to be the case for boreal forests at higher latitudes (Granier et al. 2007, Bonan 2008).

However, climate change impacts on the availability of soil moisture and consequent growth are still poorly understood in boreal conditions.

Boreal forests are slow-growing and long-lived ecosystems, and therefore experimental studies alone cannot answer the question of how climate change may affect the long-term dynamics of forests and how forests should be managed under climate change. In this respect, process-based growth models responsive to varying climatic conditions could be the most appropriate tools, firstly for identifying how climate change affects forest growth and, secondly, regarding how to manage forests under climate change (e.g., Mäkelä et al. 2000, van der Meer et al. 2002, Matala et al. 2003, 2006, Loustau et al. 2005). On the other hand, process-based models may provide a deeper understanding of how physiological processes, driven by hydrological and nutrient cycles and climatic factors, control tree growth and the dynamics of forest ecosystems (Loustau et al. 2005, Kint et al. 2009, Simioni et al. 2009). Moreover, process-based models allow the assessment of how the site conditions, properties of tree stands and management interact and control the growth and development of trees (Mäkelä et al. 2000, Porté and Bartelink 2002).

In boreal conditions, admixtures of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula* sp.) are common on moderately fertile and fertile sites. In Finland, for example, Norway spruce-dominant admixtures represent >33% of the total forest resources. Most forests on upland sites in Finland are growing on unsorted soils, i.e., on coarse and fine moraines, with relatively poor nitrogen content (Kellomäki 1995). The low water-holding capacity of coarse moraines may easily expose these forests to stress from soil moisture deficits (Kellomäki 1995, Kellomäki and Väisänen 1996).

In mixed forests, the responses of trees to climate change and to resource availability are more diverse than in mono-species forests (Larson 1992). The modifications in eco-physiological processes of tree growth as a result of changing climate will change the relative competitiveness of species (van der Meer et al. 2002), with consequent changes in long-term forest development. This implies that there is a need to shift forest growth modeling from the stand level toward tree cohorts in the stand or even single trees. In such models, the focus should be on the responses of tree growth to the resource availability (water, nutrients, light, etc.) as controlled by stand structure (e.g., canopy closure and tree species composition) (Bartelink 2000, Stadt and Lieffers 2000). Little is known regarding the effects of changing climate on the growth and dynamics of mixed boreal forests; in addition, only a few models for mixtures of several species have been developed (e.g., Porté and Bartelink 2002).

In this study, a process-based ecosystem model was used to study whether climate change changes the growth of Norway spruce (*P. abies*), Scots pine (*P. sylvestris*) and birch (*Betula* sp.)

growing in mixtures compared with the current climate. The growth success was indicated by total canopy photosynthesis and total stem wood growth. Management was excluded from the analyses in order to identify how the natural stand dynamics affects the availability of soil water and consequent carbon uptake and growth of trees in different stand and climatic conditions. The mixtures were grown over a 100-year rotation (2000–99) in southern (61°N) and northern (66°N) Finland with initial species shares of 50, 25 and 25% for Norway spruce, Scots pine and birch, respectively. Additionally, pure Norway spruce, Scots pine and birch stands were used in comparison to identify whether species response is different in mixed and pure stands.

Materials and methods

Outlines of the model

The process-based model (FinnFor) was developed by Kellomäki and Väisänen (1997) and further modified by Matala et al. (2003). The model has been parameterized for Scots pine, Norway spruce and birch species. The model works on a cohort basis; i.e., each cohort is defined by the tree species, the number of trees per hectare in the cohort (trees ha^{-1}), the diameter of the target tree (cm, at the height of 1.3 m if the tree height is ≥1.3 m, or at the stump height (at the height of 0.2 m) if the tree height is <1.3 m) representing the cohort, and the height (m) and age (years) of the target tree. The model is driven by hourly climatic factors (solar radiation, air temperature, precipitation, water vapor pressure, wind velocity, cloudiness and atmospheric CO_2). The details of the model were presented by Kellomäki and Väisänen (1997). Therefore, the main calculations of the model are only briefly described in this work regarding the growth and dynamics of tree stands and the main environmental factors driving them.

Main calculations on tree growth and development

Photosynthesis and growth

The hourly photosynthetic rate is calculated using the biochemical model developed by Farquhar et al. (1980) and von Caemmerer and Farquhar (1981). As demonstrated in Eqs. (1 and 2), the processes of assimilation are affected by net radiation (R_{nc}), air temperature (T_a), air humidity, atmospheric CO_2 (C_a), stomatal conductance (g_s) and nitrogen content of the foliage (N_L) (Wang et al. 1995, 1996, Kellomäki and Wang 1997, 2001, Roberntz and Stockfors 1998, Medlyn et al. 2001, 2002). Seasonality of photosynthesis of coniferous trees is introduced in the calculations through the annual stages of development, which controls the seasonal sensitivity of photosynthesis to respond to environmental factors (Pelkonen and Hari 1980, Hänninen and Hari 2002). The spring-time build-up and autumn-time senescence of birch foliage are modeled as presented by Kellomäki et al. (2001).

To scale up from photosynthetic biochemistry per unit leaf area to canopy photosynthesis per unit ground area, the model uses an integrated sunlit/shaded submodel to consider the daily change in canopy net radiation (R_{nc}), leaf area index (L, all-sided, $m^2\ m^{-2}$), and fraction of sunlit (L_{sun}) and shaded leaves (L_{sh}) within the stomatal conductance ($g_{s.sun}$ and $g_{s.sh}$). The daily dynamics of canopy conductance (g_{cs}, mmol $m^{-2}\ s^{-1}$) is obtained by summing the total stomatal conductance of all leaf classes (sunlit/shaded leaves and canopy layer) within the canopy (Kellomäki and Wang 1999, 2000). The changes in biochemical parameters with increasing canopy depth are related to the decrease in leaf nitrogen (N_L) (Kellomäki and Wang 1997). The calculations of net canopy photosynthesis (P_{nc}, Mg C) separately account for the contribution of sunlit ($P_{nc.sun}$) and shaded leaf ($P_{nc.sh}$) fractions:

$$
\begin{aligned}
P_{nc} &= P_{nc.sun} + P_{nc.sh} \\
&= \int_0^L f(R_{nc.sun})f(T_a)f(C_a)f(N_L)f(L_{sun})f(g_{s.sun})\,dL \\
&\quad + \int_0^L f(R_{nc.sh})f(T_a)f(C_a)f(N_L)f(L_{sh})f(g_{s.sh})\,dL
\end{aligned}
\tag{1}
$$

$$
g_{cs} = \frac{L_{sun}}{L}\int_0^L g_{s.sun} + \frac{L_{sh}}{L}\int_0^L g_{s.sh}
\tag{2}
$$

Stomatal conductance is assumed to be controlled by R_{nc}, T_a, vapor pressure deficit (D_a), C_a, soil moisture (θ_s) and soil temperature (T_s) (McMurtrie and Wang 1993, Kellomäki and Wang 1999, 2000), i.e.,

$$
g_s = f(R_{nc})f(T_a)f(D_a)f(C_a)f(\theta_s)f(T_s) =
\begin{cases}
g_{s.max}, & \text{if no factor is limiting} \\
g_{s.min} < g_s < g_{s.max}, & \text{if some factor is slightly limiting} \\
g_{s.min}, & \text{if some factor is completely limiting}
\end{cases}
\tag{3}
$$

where $g_{s.max}$ is the maximum and $g_{s.min}$ is the minimum value of stomatal conductance.

Dark respiration is calculated as a function of temperature over a period of 1 year as the sum of the hourly values for each tree organ. The level of the dark respiration rate was assumed to be a linear function of the nitrogen concentration of each mass component (Ryan 1995, Wang et al. 2002). The yearly values are subtracted from the net assimilation in the foliage, which is gross photosynthesis minus the respiration related to the photosynthetic processes. The remaining assimilates are available for growth of different tree organs, the consequent growth respiration being related to the biomass growth of the organ in question (Ryan 1995).

The remaining amount of photosynthesis (net photosynthesis) is converted to the mass growth of foliage, branches, coarse roots, fine roots and stem following allometric growth

between organs of the target trees representing the tree cohorts (Marklund 1987, 1988, Matala et al. 2003). Leaf mass was further converted into total leaf area (L_t, $m^2\ ha^{-1}$) by utilizing the values of the specific leaf area (SLA, area of leaf per mass unit). Photosynthates allocated to the stem are converted to the volume growth of stem wood (V_s, $m^3\ ha^{-1}$) as follows:

$$
V_s = V_{Initial} + \int_0^t a\frac{P_{mass}(t)}{\rho}
\tag{4}
$$

where $V_{Initial}$ is the initial stocking, $P_{mass}(t)$ is the annual net photosynthesis available for the growth of stem wood in the year t, ρ is the wood density and a is an empirical species-specific parameter. Additionally, stem wood growth is further calibrated based on the sample trees measured in the National Forest Inventory (NFI) plots.

Dynamics of tree populations

Tree populations are compiled based on tree cohorts. The values of the dimensions of the target trees (diameter, height, stem volume, and biomass of foliage, branches, coarse and fine roots) are updated annually. The density of tree cohorts is reduced by the mortality of the trees. It works on a 5-year time step utilizing the algorithm developed by Hynynen et al. (2002). At the beginning of each simulation step, the probability of survival of the trees in each cohort is calculated based on the stocking in the stand, the position of the trees in the stand and the lifespan of the trees. At the end of each simulation step, the stocking of stem wood of 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 cohort to the level allowed by the model developed by Reineke (1933). In the algorithm, the parameter values are specific for Scots pine, Norway spruce and birch.

Main environmental factors driving the growth and development of trees

Water depletion

Depletion of water is calculated on an hourly basis. It considers total evapotranspiration (E_T, mm), which is the sum of whole-tree transpiration (E_t, mm) and evaporation from the canopy (E_c, mm) and ground surfaces (E_g, mm) over the whole year. Whole-tree transpiration is simulated using a 'big leaf' model (Kellomäki and Wang 1999, 2000), which considers that transpiration depends upon the cumulative effects of total leaf area, sunlit/shaded canopy conductance (see Eqs. 2 and 3) and mean boundary layer conductance (Kellomäki and Wang 1999, 2000).

Evaporation from canopy surfaces is derived from the water pool intercepted on the foliage surface. The Penman–Monteith equation is used to compute evaporation on the basis of net

radiation interception in sunlit and shaded leaves, canopy boundary layer resistance at mean canopy height and reference height, and aerodynamic resistance (Monteith and Unsworth 1990). Evaporation from the ground surface is calculated using empirical and physically based approaches from an iterative solution of the energy balance (Jansson 1991a, 1991b). The Penman combination equation (Monteith and Unsworth 1990), which includes net radiation and aerodynamic resistance (including two eddy diffusivity resistances and soil surface resistance), is employed:

$$E_T = E_c + E_t + E_g \qquad (5)$$

Soil water flow

Water storage on the soil surface and in organic and inorganic soil constitute the soil water pool (Kellomäki and Väisänen 1997). The inorganic soil profile below the organic soil layer was 1 m in depth, and was subdivided into 11 horizontally homogeneous layers. The water/heat condition of each layer is computed with the help of partial differential, which is solved using Euler integration (Jansson 1991a, 1991b). The soil hydrological processes work on an hourly basis.

Water on the soil surface is presented in terms of a pool, representing direct precipitation through the canopy. The amount of water infiltration (W_{in}, mm) to the soil surface pool is calculated as a balance between the incoming and outgoing water flow, including the daily water amount in the surface pool (W_{surf}) after the interception of water in the canopy, evaporation from the surface pool (E_g) and runoff (W_{runoff}), which indicates the surface flow from the surface pool (Kellomäki and Väisänen 1996, 1997). The relative availability of water in the rooting zone (extractable water for tree) is used to calculate the potential soil water deficit (W_d, mm) (Granier et al. 1999, 2000):

$$W_{in} = W_{surf} - E_g - W_{runoff} \qquad (6)$$

$$W_d = \left[0.4 (W_x - W_w) - (W_{Soil} - W_w) \right] \qquad (7)$$

where W_x is the volumetric water content threshold used in the computations (field capacity), W_w is the volumetric water content at the wilting point and W_{Soil} is the soil volumetric water content in the rooting zone.

Available nitrogen

Nitrogen released in the decomposition of soil organic matter (SOM, litter plus humus) is determined by employing the algorithm developed by Chertov and Komarov (1997) and Chertov et al. (2001). Decomposition rates of different types of litter (foliage, twigs, stem, fine roots and coarse roots) are determined by soil temperature, soil moisture, and nitrogen and ash content of the litter. Temperature and moisture of the litter are linear functions of those in the mineral topsoil. The decomposition works on a monthly basis.

Radiation regime and shadow effect

The radiation incidental on a canopy and its layers is calculated as a sum of direct and diffuse radiation applying the model of Oker-Blom (1985, 1986). The calculations are based on (i) the probability of diffuse and direct radiation passing through the canopies of other trees and reaching trees in a particular cohort, (ii) the length of the path through tree canopies in other cohorts, (iii) the thickness of the canopy layers and (iv) the shaded area that a canopy layer produces on a particular canopy layer below it. The tree canopies are ellipsoids and the foliage area is distributed uniformly within the canopy. Trees are distributed according to the Poisson distribution within the stand, and canopy shaded area is calculated as a function of leaf area density and cross-section and diameter of canopy layers (Kellomäki and Väisänen 1997).

Parameterization, validation and performance of the model

The parameterization, validation and performance of the model have been studied in detail in several papers, mainly regarding (i) parameterization of leaf–canopy photosynthetic rate and stomatal behavior under the current and changed climate (Kellomäki and Wang 1996, 2001, Wang 1996, Roberntz and Stockfors 1998, Medlyn et al. 2001, 2002), (ii) parameterization of exchange of CO_2 and H_2O between the atmosphere and the conifer stand under boreal conditions (Kellomäki and Wang 1999, 2000, Kramer et al. 2002, Wang et al. 2004a, 2004b), (iii) parameterization of soil heat and water transfer through the soil profiles for boreal soil types (Jansson 1991a, 1991b), (iv) simulations of the influence of the interrelationship between soil moisture and forest productivity in boreal zones (Kellomäki 1995, Kellomäki and Väisänen 1996), (v) simulations on snow accumulation and soil frost in a forested landscape under climate change (Venäläinen et al. 2001), (vi) validation against growth and yield tables, and measurements of the growth history of trees in thinning experiments (Matala et al. 2003), and (vii) sensitivity analysis of the model to changes in environmental conditions (temperature, precipitation and CO_2 concentrations) (Briceño-Elizondo et al. 2006).

In addition, parallel simulations have been carried out with the help of a conventional growth and yield model (Motti, Matala et al. 2003, 2006). In this model comparison, Matala et al. (2003, 2006) found that the outputs of the models agreed well in terms of relative growth rate regardless of tree species. Furthermore, both models predicted competition within a stand and the effect of tree status in a stand (suppressed, dominant position) on tree growth in a similar way. The performance of the FinnFor model was further

investigated in our work by comparing the calculated and measured mean volume growth of 1191 sample trees over a 10-year period (1985–95) on the permanent upland sample plots of the Finnish NFI. Figure 1 shows that the calculated mean volume growth over the 10 years correlates reasonably well with the measured one regardless of tree species. Furthermore, the comparison of the calculated and measured annual mean growth of stem wood (including Scots pine, Norway spruce and birch) for different forest centers (Figure 2) showed that the performance of the model is reasonable when considering the large geographical distribution of the sample plots and their wide coverage of site types (Figure 1). There was no systematic variability observed in the measured and calculated growth values for different forest centers throughout Finland.

Study sites and climate scenarios

Site and stand descriptions

Two sites with similar initial tree species composition in mixed stands (Norway spruce ~50%, and Scots pine and birch each ~25% in regard to stand density) and stand properties (Table 1) were selected for this work based on available data of the NFI for 1999–2000 (Figure 2). The first site is located in southern Finland (NFI plot No. 37030231, close to Pori, 61°56′N, 22°01′E) and the second one in northern Finland (NFI plot No. 112013431, close to Rovaniemi, 66°37′N, 23°57′E). In both

cases, the site was of medium fertility (MT, *Myrtillus*) (Cajander 1949), with initial SOM of 70 Mg ha^{-1}. On both sites, the soil texture was sandy loam with a field capacity of 52% and a wilting point of 26% on the basis of volume (Kellomäki 1995). The initial value of soil moisture content (the mean volumetric water content at a depth of 30 cm) used in the calculations was 36% in the south and 38% in the north (both identified as moderate drought) based on Vehviläinen and Huttunen (2002). Furthermore, all management was excluded from the simulations. This was also the case for the pure Norway spruce, Scots pine and birch stands, which were used to identify whether species-specific responses were different in the mixed than in the pure stands. The initial properties of the pure stands are described in Table 1.

Climate scenarios

The scenarios for the current and changing climate used in the simulations for the period 2000–99 were compiled by the Finnish Environment Institute (SYKE) and the 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.
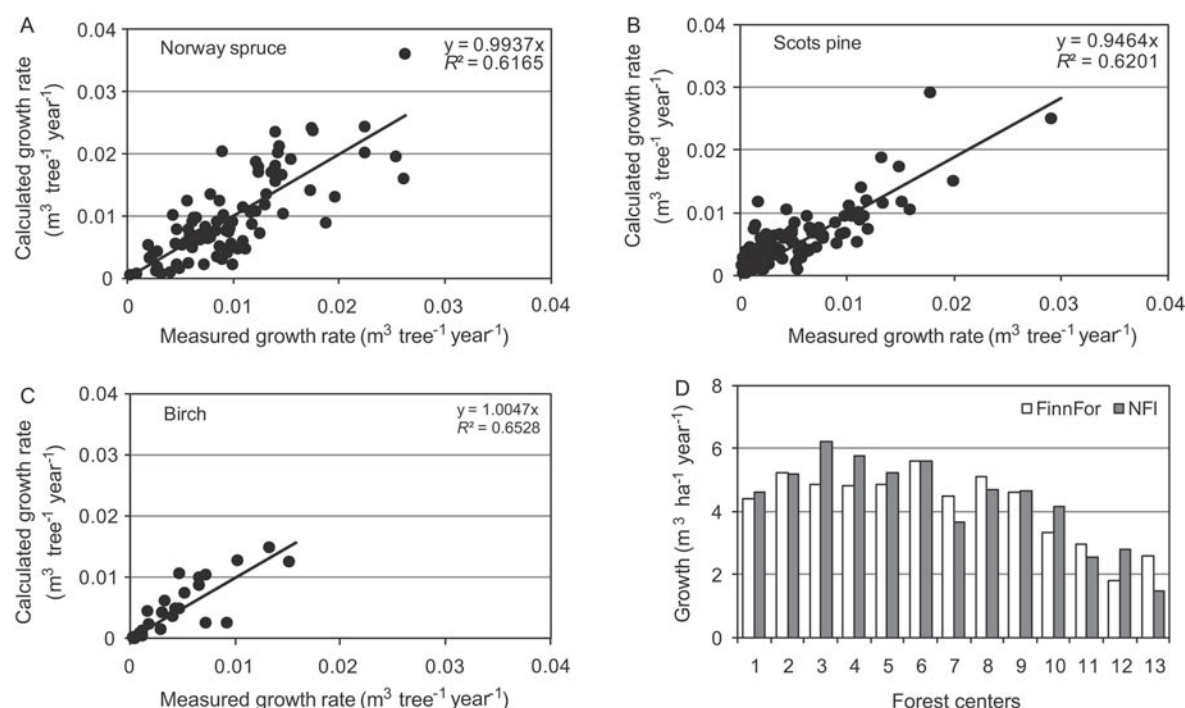
Figure 1. (a–c) Relationship between measured and simulated volume growth for different tree species, and (d) relationship between measured and calculated volume growth for different forest centers, which are indicated by the numbers on the *x*-axis. The numbers 1–10 indicate the centers representing southern Finland (below 63°N, middle and southern boreal conditions), while the numbers 11–13 indicate the centers representing northern Finland (above 63°N, northern boreal conditions).
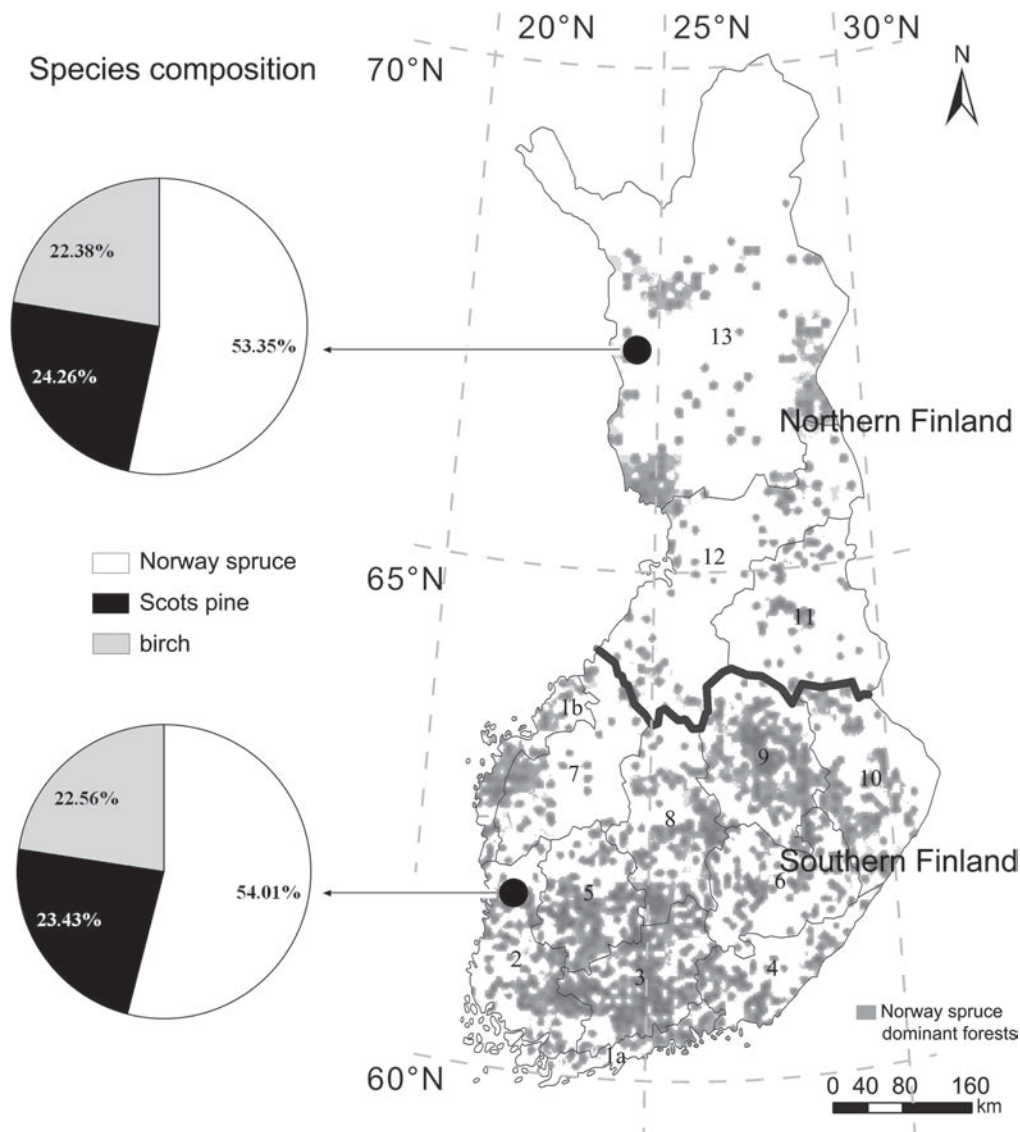
Figure 2. Location of the study sites in southern and northern Finland. The shaded area means Norway spruce dominant forests throughout Finland (referring to stem volume). The species composition of the two mixed stand sites used in this study is presented in the left figure. The numbers 1–13 indicate the forest centers.

The scenario for the current climate, in terms of temperature and precipitation, represents mean data for the period 1971–2000 repeated over the whole simulation period, with a constant CO_2 concentration of 351 ppm (the mean values for 1970–2000). The daily values of temperature and precipitation were broken down to the hourly level by applying the weather generators developed by Strandman et al. (1993). The weather generators were also used to generate hourly values of radiation, relative humidity, cloudiness and windiness by means of weather statistics for the period 1971–2000. Air vapor pressure deficit was calculated based on air temperature and relative humidity (Figure 3).

The scenario for the changing climate was predicted by means of the combined calculations of six global climate model (GCM) simulations, including CGCM2 (Canada), CSIRO Mk2 (Australia), ECHAM4/OPYC3 (Germany), GFDL R30 (USA), HadCM3 (UK) and NCAR DOE PCM (USA), based on the IPCC SRES A2 emission scenario (Carter et al. 2005, Ruosteenoja et al. 2005). Mean temperatures are projected to increase by 4–6 °C under the changing climate, while the atmospheric concentration of CO_2 is expected to rise to 840 ppm by the end of the simulation period in 2099. Figure 3 shows that the increase in annual mean temperature under the changing climate is similar on the two sites. On the northern site, the increase in annual mean precipitation is slightly higher than that on the southern site. The increases in precipitation are mainly in the wintertime (Carter et al. 2005, Ruosteenoja et al. 2005). The values of missing climatic factors (radiation, relative humidity, cloudiness and windiness) for the changing climate were assumed to be the same relative to the current climate.

Table 1. General description of the initial stand conditions with average characteristics for each species in mixed stands for the simulations.

Stand layout	Tree species mixture		
	Norway spruce	Scots pine	Birch
Southern site			
Number of cohorts	3	8	4
Density (trees ha^{-1})	1233	535	515
Leaf area index (m^2 m^{-2})	2.3	0.6	2.4
Mean diameter (cm)	12.9 ± 3.5	9.4 ± 2.4	14.7 ± 1.4
Mean height (m)	14.1 ± 3.9	10.7 ± 2.9	13.5 ± 1.0
Northern site			
Number of cohorts	2	6	2
Density (trees ha^{-1})	1392	633	584
Leaf area index (m^2 m^{-2})	1.8	0.4	1.6
Mean diameter (cm)	8.7 ± 2.0	6.4 ± 1.2	10.3 ± 0.5
Mean height (m)	10.8 ± 3.4	6.8 ± 1.7	9.6 ± 0.4

The same species-specific stand characteristics were also concurrently used for pure Norway spruce, Scots pine and birch stands in simulations.

Results

Net canopy photosynthesis and total stem wood growth of the mixed stands

Net canopy photosynthesis

On the southern site, regardless of tree species, the annual net photosynthesis (P_{nc}) tended to be lower under the changing climate than under the current climate with the exception of the early part of the simulation period (Figure 4). Over the whole simulation period, P_{nc} of Norway spruce was 15% lower than under the current climate (Table 2). This was also the case for Scots pine and birch, with P_{nc} being 13% lower under the changing climate compared with the current climate. On the northern site, the situation was different, with P_{nc} tending to be higher under the changing climate compared with the current climate throughout the simulation period. Consequently, P_{nc} over the simulation period was about 11, 21 and 10% higher for Norway spruce, Scots pine and birch, respectively, under the changing climate than under the current climate.

Total stem wood growth

On the southern site, total stem wood growth (V_s) was clearly lower when the changing climate was assumed, i.e., 9% lower for Norway spruce, 8% for Scots pine and 5% for birch compared with the current climate (Table 2), as can be expected on the basis of photosynthetic production. On the northern site, the situation was the opposite, with V_s being enhanced by 10, 20 and 8% for Norway spruce, Scots pine and birch, respectively, when the changing climate was assumed.

Leaf area and canopy conductance

Figure 5 (top panel) shows that the leaf area index (L) levels off toward the end of the rotation regardless of climate scenario and site location. Under the changing climate, the expansion of L on the southern site remained smaller than that under the current climate. This was mainly due to the reduced expansion of L for Norway spruce, whereas the expansion was nearly the same for Scots pine and birch regardless of climate scenario. On the northern site, climate change tended to increase L toward the end of the rotation, reflecting the increase of L for all the tree species. A similar development in absolute total leaf area (L_t) was also evident (Figure 5, middle panel). As the trees got older and larger, the mean canopy stomatal conductance (g_{cs}) declined regardless of climate scenario and site location (Figure 5, bottom panel). On the southern site, the values tended to be lower under the changing climate than under the current climate. On the northern site there was no clear difference in g_{cs} between the two climate scenarios.

Water depletion and soil water availability of the mixtures

Water depletion

Regardless of site location, annual evapotranspiration (E_T) under the changing climate was higher than that under the current climate (Figure 6, top panel). Over the simulations, E_T on the southern site was 84% of annual precipitation under the current climate and 90% under the changing climate. On the northern site, the share of E_T from precipitation was smaller, i.e., 76% under the current climate and 80% under the changing climate. When the components of cumulative E_T were considered separately, cumulative transpiration (E_t) and cumulative evaporation from the canopy surfaces (E_c) were the main factors affecting water depletion under the current climate (Figure 6, middle panel). When the changing climate was applied, the values of cumulative E_c and E_g (evaporation from ground surface) were higher than the values under the current climate regardless of site location.

Figure 6 (bottom panel) also shows the contribution of E_c and E_t to the depletion of water in the whole stand. Regardless of site location and climate scenario, the role of Norway spruce was much larger than that of the other tree species. This was expected based on the tree species composition representing the ratio 2:1:1 between Norway spruce, Scots pine and birch in terms of the initial stand density. The contribution rates of $E_c + E_t$ for Norway spruce, Scots pine and birch were 5.9:0.9:2.9 on the southern site and 6.0:0.8:3.1 on the northern site, respectively. Accordingly, Norway spruce and birch account for most of the water depletion due to their relatively larger leaf area (L_t).

Availability of soil water

As a result of the increasing interception of water on the canopy and evaporation from the ground surface, substantially less water infiltrated into the soil profile (W_{in}). As presented in Figure 7 (upper panel), W_{in} decreased over the simulation period regardless of site location and climate scenario. Nevertheless, the infiltration was lower on the southern site
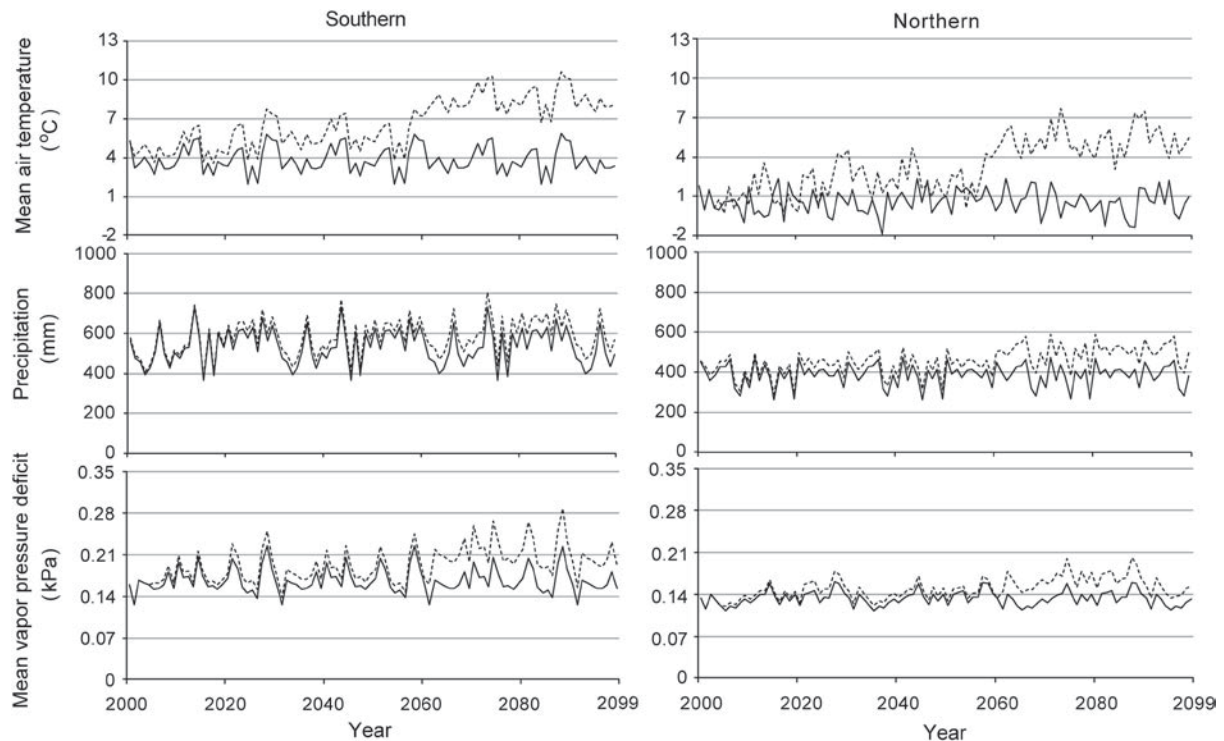
Figure 3. Variation in annual mean temperature (top panel), annual precipitation (middle panel) and mean vapor pressure deficit (bottom panel) for the current (solid line) and changing (dashed line) climate on the southern and northern sites.
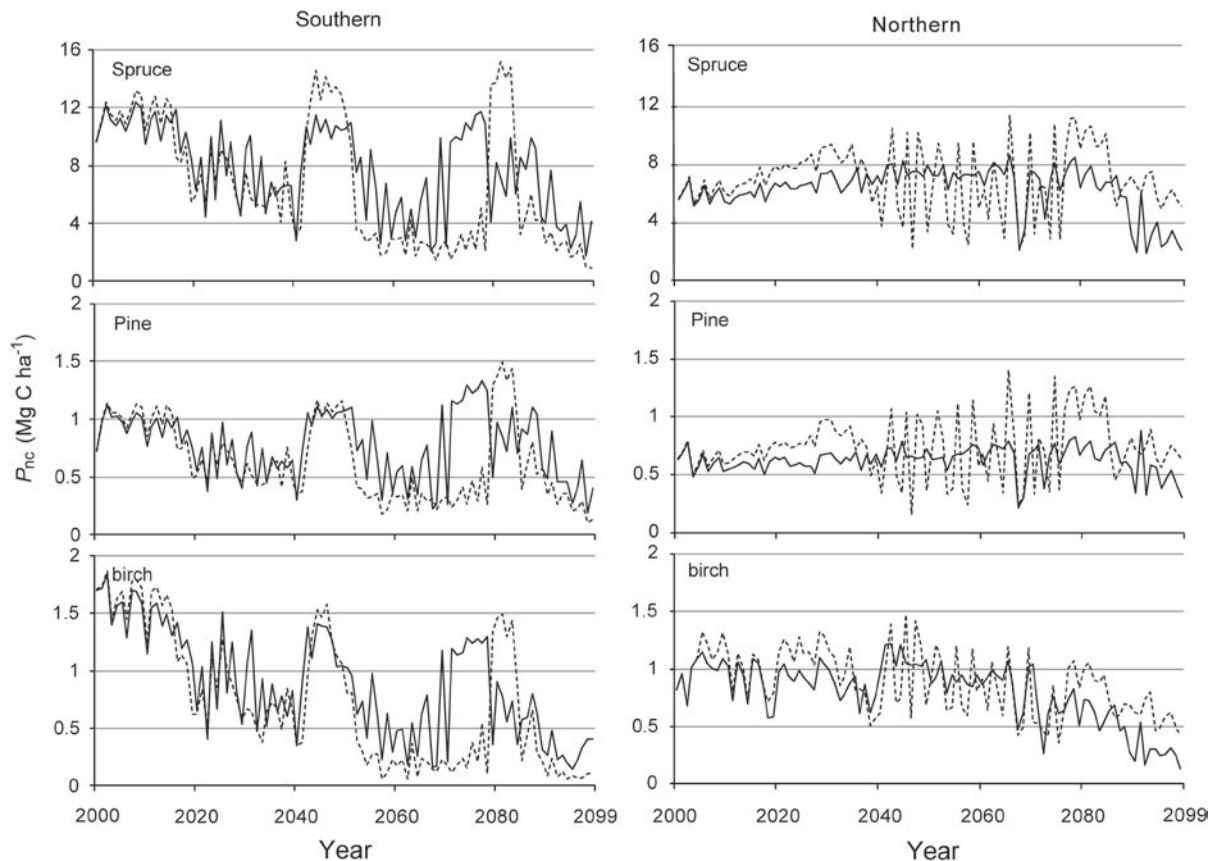

Figure 4. Annual net photosynthesis (P_{nc}) for each of the three species grown in mixed stands on the southern (left panel) and northern (right panel) sites under the current (solid line) and changing (dashed line) climate over the 100-year rotation.

Table 2. Cumulative net photosynthesis and total stem wood growth in mixed stands for different tree species under the current and changing climate on the southern and northern sites over the simulation period.

Sites and species	Net photosynthesis (P_{nc}, Mg C ha^{-1})		Stem wood growth (V_s, m^3 ha^{-1})	
	Current	Changing	Current	Changing
Southern site				
Norway spruce	780	676 (−15)	667	610 (−9)
Scots pine	78	69 (−12)	156	144 (−8)
Birch	84	74 (−13)	133	127 (−5)
Total	942	819 (−15)	956	881 (−8)
Northern site				
Norway spruce	634	715 (+11)	394	441 (+10)
Scots pine	63	80 (+21)	100	125 (+20)
Birch	79	88 (+10)	76	83 (+8)
Total	776	883 (+12)	569	649 (+12)

Figures in parenthesis show the percentage change (%) in total net photosynthesis and stem wood growth under the changing climate compared with the current climate.

under the changing climate than under the current climate. On the northern site, W_{in} was larger under the changing climate because precipitation increased more than water depletion.

The potential soil water deficit (W_d) increased along with the growth development of the tree stands regardless of climate scenario and site location (Figure 7, lower panel). When the changing climate was applied on the southern site, W_d was larger than under the current climate. On the northern site, the situation was the opposite.

Simulation of the mono-species stands

For analysis of the mono-species stands, P_{nc} and V_s in the pure Norway spruce stand were 18 and 13% lower, respectively, under the changing climate than under the current climate on the southern site (Table 3). The opposite was the case for the pure Scots pine and birch stands, where the changing climate increased the values of P_n and V_s. On the northern site, the values of P_n and V_s were higher under the changing climate for all the tree species. Regarding water depletion, the proportion of E_T to precipitation was higher in the pure Norway spruce stands than in the pure Scots pine and birch stands regardless of site location. On the other hand, the amount of water depleted was 11% larger under the changing climate than under the current climate (Table 3). On the southern site, cumulative water use efficiency increased by 11–14% under the changing climate compared with that under the current climate. In the northern site, the increase was 4–8% (Table 3).

Discussion and conclusions

Evaluation of approach

In this study, a process-based ecosystem model (FinnFor; Kellomäki and Väisänen 1997), considering the canopy and

plant-soil processes, was used to study whether climate change may change the growth of the main boreal tree species growing in mixtures compared with that under the current climate. The physiological core of the model is the Farquhar-type biochemical model developed by Farquhar et al. (1980) and von Caemmerer and Farquhar (1981). In parameterizing the photosynthetic model, data from several field experiments were utilized to identify photosynthetic and stomatal responses of Norway spruce (Roberntz and Stockfors 1998, Medlyn et al. 2001, 2002), Scots pine (Wang et al. 1995, 1996, Kellomäki and Wang 1996, 1997) and birch (Kellomäki and Wang 2001, Medlyn et al. 2001, 2002) to the elevation in temperature and CO_2. These experiments demonstrated that long-term CO_2 enrichment often leads to down-regulation in stomatal behavior and carboxylation efficiency (e.g., Stitt and Krapp 1999, Urban 2003), and combined elevation of temperature and CO_2 will decrease net photosynthesis compared with that under CO_2 enrichment alone (e.g., Wang et al. 1995, 1996, Tjoelker et al. 1998). On the other hand, environmental adjustment of physiological processes regarding the elevation of temperature and CO_2 has been reported (Kellomäki and Väisänen 1996, 1997, Roberntz and Stockfors 1998, Ge et al. 2010a). These previous findings are mostly considered in the parameterization and validation of the physiological core of the FinnFor model.

The Jarvis-type model was used for stomatal conductance. The model allows the simulation of how varying atmospheric and edaphic conditions affect stomata–photosynthesis interactions (McMurtrie and Wang 1993, Kellomäki and Wang 1999, 2000, Wang et al. 2004a). High vapor pressure deficit, for example, will stress stomatal behavior, which in turn will reduce carbon uptake, transpiration and consequent tree growth. Moreover, stomatal conductance is linked to the availability of soil water, which is controlled by precipitation, evaporation from canopy and soil surfaces, infiltration of water into the soil profile and transpiration (Kellomäki and Väisänen 1996, 1997). Data from several field experiments were used to parameterize the stomatal model for different tree species and to assess the performance of the model (Wang et al. 1995, 1996, Kellomäki and Wang 1996, 1999, 2000, Roberntz and Stockfors 1998, Medlyn et al. 2001, 2002). Processes of water/heat flow in the stand (evapotranspiration) have been parameterized and validated based on eddy flux measurements for a boreal Scots pine forest and sap flow measurements for Scots pine grown under the current and changing climate scenarios (Kellomäki and Wang 1999, 2000, Wang et al. 2004b).

In the long term, interactions between the physiological processes are manifested in terms of the growth of trees and development of tree stands. The model merges the methods to allocate biomass to different mass components that had undergone wide-ranging validation exercises using the observed
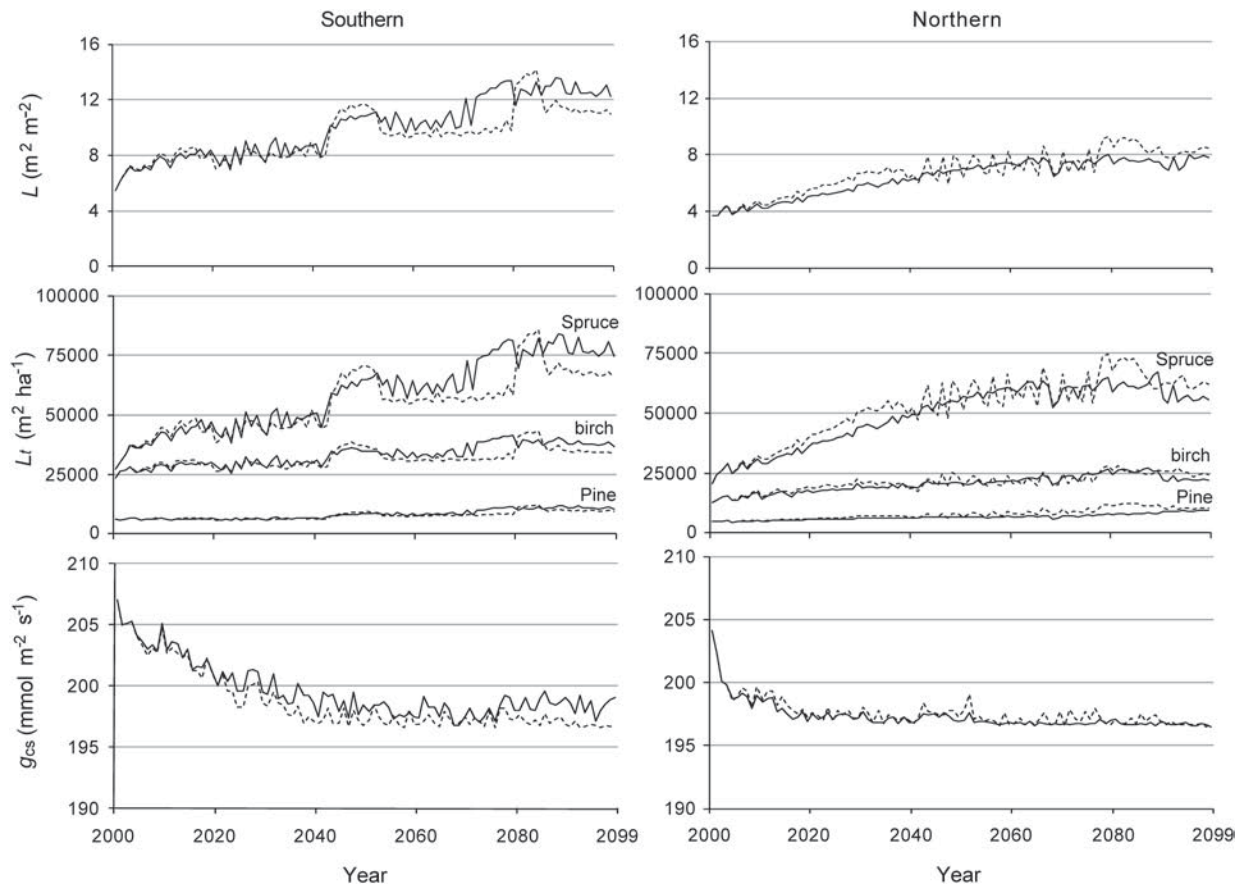
Figure 5. Annual leaf area index (*L*) for all tree species in the stand (top panel), development of leaf area (*L*$_t$) for each species (middle panel) and annual mean canopy conductance (*g*$_{cs}$) for the whole mixed stand (bottom panel) on the southern and northern sites over the 100-year rotation. Solid line means the current climate, and dashed line the changing climate.

growth data (Matala et al. 2003) and the intensive analysis of sensitivity of the model's performance to the changes in temperature, precipitation, CO$_2$ concentration and nitrogen content of foliage (Briceño-Elizondo et al. 2006). The current work also showed that the simulated growth agrees well with the measured stem wood growth. In this case, sample trees representing the permanent sample plots (by the Finnish NFI) situated throughout the country were utilized. The plots represented wide climatic and edaphic variability from southern to northern boreal conditions.

Evaluation of findings

In northern Finland, regardless of tree species, net carbon uptake and stem wood growth were higher under the changing climate compared with those under the current climate. This finding is in line with previous results for Sweden, where the BIOMASS model (Zheng et al. 2002, Bergh et al. 2003) was used to assess climate change impacts over the temperature gradient from southern to northern Sweden. In northern Finland, the elevation of temperature lengthened the growing season and increased total photosynthesis over the years. Photosynthetic production was further increased by the higher

atmospheric CO$_2$ in these conditions, where soil moisture seldom limits forest growth. Even in the future, increased precipitation in summertime could compensate for increased water consumption.

However, in southern Finland with its warmer climate, carbon uptake and stem wood growth were reduced under the changing climate regardless of tree species. This was mainly due to enhanced evapotranspiration as well as less summer precipitation. This led to a reduction in the infiltration of water into the soil profile and thus increased water deficit in the rooting zone, with the consequent decline in stomatal conductance and carbon uptake (e.g., Lu et al. 1995, 1996, Cienciala et al. 1998, Irvine et al. 1998). The elevation of CO$_2$ increased the water use efficiency, but it was not able to fully compensate for the effects of reduced soil moisture in the south (see Kellomäki and Wang 1998). Our findings regarding the water-limited growth of trees on the southern site under the changing climate are well in line with the previous findings of several field experiments and modeling studies for boreal conditions (Roberntz and Stockfors 1998, Bergh et al. 1999, Jyske et al. 2010).

Growth reduction was also predicted previously for Scots pine under climate change by Loustau et al. (2005), who
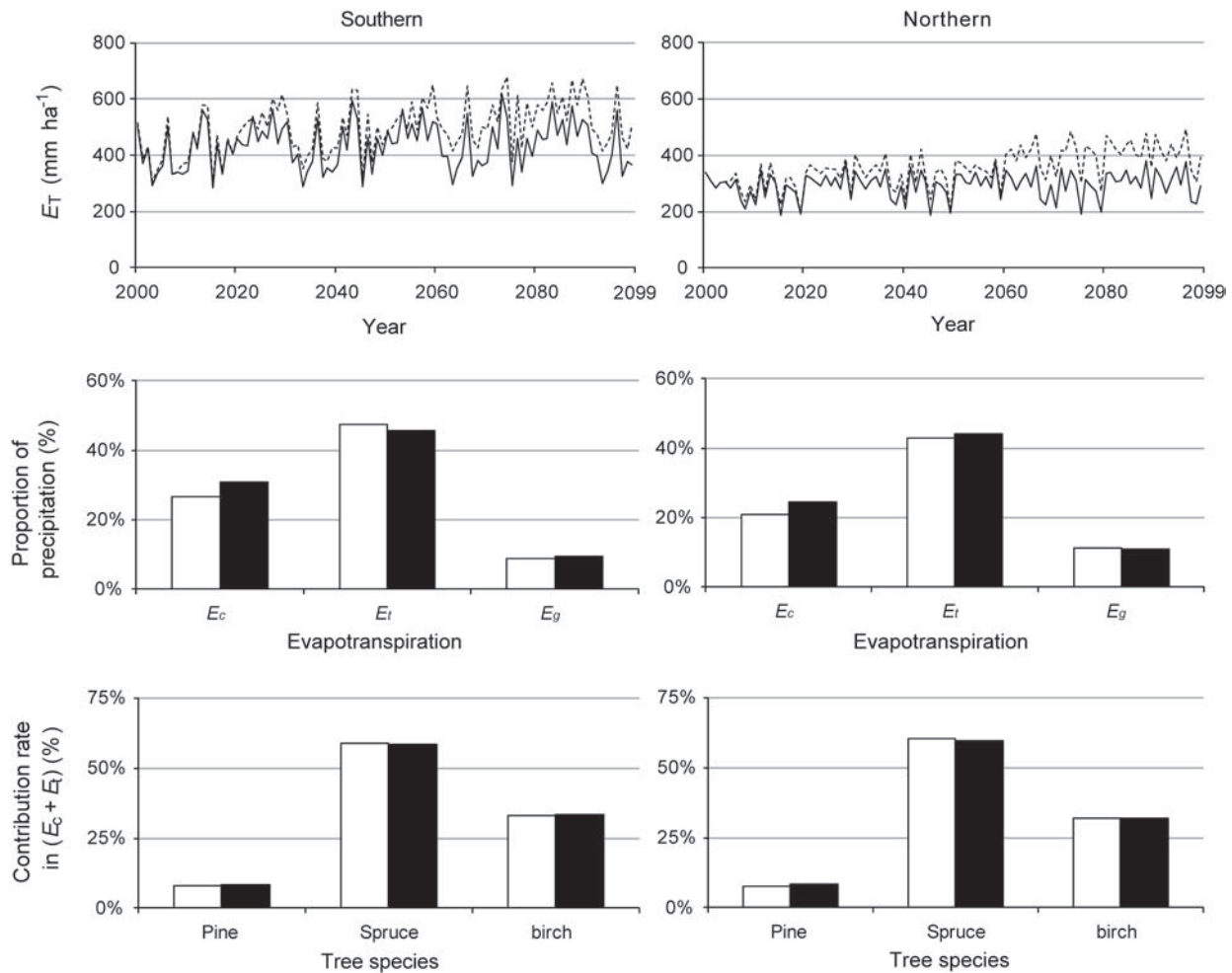
Figure 6. Annual mean evapotranspiration (E_T) (including canopy surface evaporation (E_c), transpiration (E_t) and ground surface evaporation (E_g)) (top panel), component E_T (components of E_c, E_t and E_g) as a proportion of precipitation (middle panel), and canopy evaporation (E_c) and transpiration (E_t) as a proportion of precipitation for each species in mixed stands (bottom panel) on the southern and northern sites, under the current (unshaded column and solid line) and changing (shaded column and dashed line) climate over the 100-year rotation.

used process-based models (i.e., CASTANEA, GRAECO and ORCHIDEE) to study the impact of climate change on gross productivity of forests in France. The expected positive effect of CO_2 elevation on growth was overcompensated 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). Regarding the ecotone between temperate and boreal zones, Bergh et al. (2005) demonstrated that for Denmark and southeastern Sweden the demand for water in a Norway spruce forest is normally larger than the surplus during the growing season. In southern Finland, forest growth could clearly be limited by climate change, despite the increase in atmospheric CO_2, if there is insufficient soil water (e.g., Ge et al. 2010a). Furthermore, the predicted soil drought would result in the reduction of litter and humus production, at the same time affecting the nitrogen availability for tree growth in the long run (Ge et al. 2010a). Concurrently, if the soil water conditions are not well initialized and the hydrological processes

are calculated at the same time, predictions may also lead to biased estimates of carbon gain and unrealistic predictions of the effects of climatic change on boreal forest ecosystems (Bergh et al. 2005).

Parallel to the simulations for mixed stands, the response of pure stands of single species was assessed in order to determine whether growth success in the tree species mixture would deviate from that in the mono-species stands. In the case of Norway spruce, the reduction in the carbon uptake and growth was even higher than in the mixed stand due to higher water depletion and reduction of soil water. In the pure stands of Scots pine and birch, carbon uptake and growth increased even in the southern site, which was opposite to the growth in the mixtures. This was because, in the pure stands of Scots pine and birch, the total leaf area was assumed to be much smaller than that of Norway spruce (see Waring et al. 1982, Whitehead et al. 1984, Oker-Blom 1985, 1986). Accordingly, leaf-area-dependent canopy interception and intrinsic water consumption (transpiration) of Norway spruce under the same
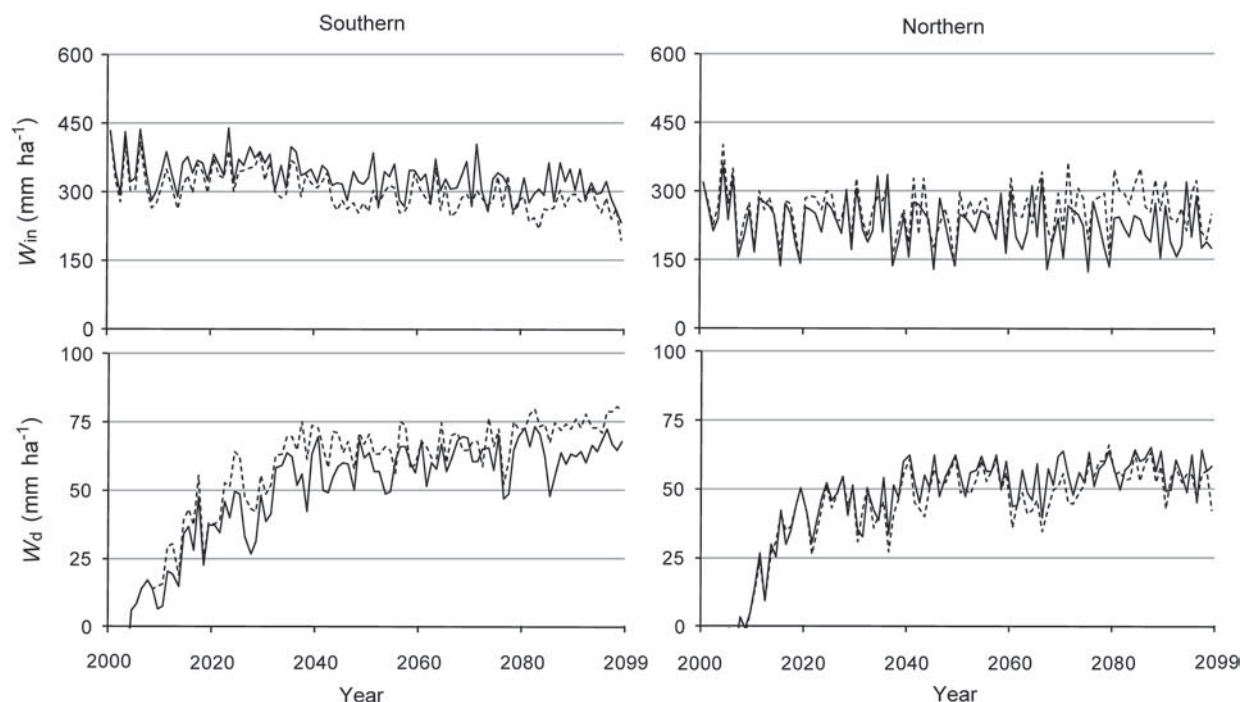
Figure 7. Annual mean water infiltration into the soil profile (W_{in}, top panel) and potential soil water deficit (W_d, bottom panel) in mixed stands on the southern and northern sites under the current (solid line) and changing (dashed line) climate over the 100-year rotation.

Table 3. Cumulative net photosynthesis, total stem wood growth, evapotranspiration (E_T) as a proportion of precipitation and water use efficiency (the ratio between net photosynthesis and transpiration) in the mono-species stands of Norway spruce, Scots pine and birch, under the current and changing climates on the southern and northern sites over the simulation period.

Mono-species stand	Net photosynthesis (P_{nc}, Mg C ha^{-1})		Stem wood growth (V_s, m^3 ha^{-1})		Proportion of E_T to precipitation (%)		Water use efficiency (Mg C mm^{-1})	
	Current	Changing	Current	Changing	Current	Changing	Current	Changing
Southern site								
Norway spruce	940	795 (−18)	834	738 (−13)	85	94 (+10)	0.043	0.049 (+14)
Scots pine	807	926 (+13)	902	984 (+8)	66	67 (+1)	0.047	0.052 (+11)
Birch	1026	1198 (+14)	1274	1311 (+7)	73	75 (+2)	0.054	0.060 (+11)
Northern site								
Norway spruce	753	842 (+12)	507	562 (+11)	78	84 (+7)	0.058	0.061 (+5)
Scots pine	685	896 (+24)	745	957 (+22)	66	66 (+0.3)	0.062	0.067 (+8)
Birch	869	1090 (+20)	865	1044 (+17)	70	71 (+0.5)	0.074	0.077 (+4)

Figures in parenthesis shows the percentage change (%) under the changing climate compared with the current climate.

growing conditions were larger than for other species. Under the changing climate, the simulated high ratio of evapotranspiration to precipitation with the increment in soil water deficit was especially evident for the pure and mixed stands of Norway spruce on the southern site. This finding on the relationship between stand water budget and leaf area supports the claim of Sun et al. (2008), who reported that evapotranspiration loss from a forest is largely controlled by leaf area (also, e.g., Gholz and Clark 2002, Chen et al. 2004). Nevertheless, leaf area alone could not fully explain the differences in evapotranspiration among forests of different types (Sun et al. 2008). Our simulations also indicated that annual evapotranspiration was not greatly sensitive to leaf area development during the 100-year period. The cause was that evapotranspiration, and in turn the soil water deficit, was controlled by a combination of annual precipitation, leaf area, water extraction, throughfall and other factors in climatic dynamics. In this context, the contribution of different tree species to the total leaf area is an important factor in explaining how different tree species are growing in mixed stands under the changing climate.

Evaluation of uncertainties in simulations

The FINADAPT climate scenario used in this study included only changes in temperature, precipitation and atmospheric

CO_2 (Carter et al. 2005, Ruosteenoja et al. 2005). This may result in uncertainties regarding details of future weather patterns. In particular, uncertainty in estimating atmospheric water vapor may be a problem for simulating future conditions as discussed by Amthor et al. (2010). They pointed out that some studies did not assume or set up any control of atmospheric water content (relative air humidity). This might lead to large increases in air vapor pressure deficit and hence evapotranspiration in the warmed ecosystem and to an overestimation of the occurrence of drought. We tried to avoid this by assuming that relative air humidity will be conserved under the changing climate relative to that under the current climate (e.g., Dessler and Sherwood 2009) in order to have a reasonable increase in the atmospheric vapor pressure deficit for model running. The values of missing climatic factors were provided by the weather generators including relative air humidity (see Strandman et al. 1993).

Species differences regarding the response of growth to climate change are of interest because they could provide causal links between climate change and the performance of trees under the predicted conditions. There are differences between tree species in the values of the key parameters of the main physiological processes (e.g., photosynthesis, respiration, transpiration and stomatal functions) in the model, leading to potential uncertainties in the simulations. Photosynthesis capacity indicates the potential of a species to be successful under a particular climate. For the three boreal C_3 tree species, the discrepancy of species-specific parameters for the Farquhar model is typically found to vary little (see Table A1), by which the uncertainty in estimating the photosynthesis per unit leaf area among the species could be neglected. Stomatal aperture, in combination with light, is an indirect measure of photosynthesis and therefore of the potential carbon income of a tree (Leuning et al. 2003). In other words, stomatal conductance reflects the climate-related physiological performance of a tree as a percentage, and can be compared across species. Based on previous environment-acclimation experiments (see Kellomäki and Wang 1996, 2001, Wang et al. 1996, Roberntz and Stockfors 1998, Medlyn et al. 2001), the characters of stomata-environment regulation patterns revealed that Norway spruce, Scots pine and birch need good or moderate soil water conditions to different extents, in order to keep their stomata open and to remain productive. Potentially, canopy photosynthesis regulation by stomatal parameters could induce overestimation of the effects of soil water. Nevertheless, the most common soil textures among the forest soils are sand and fine sand with low water-holding capacity in Finland (Urvas and Erviö 1974). In these conditions forest growth could, therefore, be further limited (Kellomäki 1995, Kellomäki and Väisänen 1996).

Despite the large potential influence of parameters other than climate and tree physiology, total leaf area is an important variable in terms of the stand water and carbon dynamics in the simulations (Kellomäki and Väisänen 1997). As discussed above, differences in physiological processes have only a minor impact on the growth success of different species in mixed and mono-species stands compared with the impact of differences in crown structure and leaf area. This was previously found by Wang et al. (2004a), who studied the sensitivity of annual net canopy photosynthesis of Scots pine stands to varying values of leaf area, maximum carboxylation velocity (V_{cmax}) and maximum rate of electron transport (J_{max}). The variability by ±20% done independently for each parameter showed that the annual net canopy photosynthesis was most sensitive (±13%) to the change in leaf area, and the variability in J_{max} and V_{cmax} resulted in much less variation (±1.5–2.7%) in the annual net canopy photosynthesis. Total leaf area appeared to be the main factor behind the differences in growth success between Norway spruce, Scots pine and birch in mixed stands.

Interspecific competition for light is also of importance regarding the dynamics of mixed species forests (e.g., Bartelink 2000, Stadt and Lieffers 2000). Leverenz and Hinckley (1990) and Ellenberg (1996) rated Scots pine and birch as light-demanding, shade-intolerant species with relatively small and shallow root systems. The FinnFor model includes species-specific parameters of leaves and needles, distribution of foliage in the tree canopy and canopy shape in order to calculate the light absorbed in different parts of the tree canopy of cohorts (Kellomäki and Väisänen 1997). When mixed with Norway spruce with a dense canopy, the growth of Scots pine and birch would be restricted due to the reduction in available light. In this study, the Poisson distribution was assumed regardless of trees in the different cohorts, which may create uncertainty regarding the degree of light competition. Nonetheless, these effects were assumed to be the same for both sites and climate scenarios with no impact on the comparisons.

Conclusion

Mixed stands dominated by Norway spruce are common in Finland, particularly in the southern parts of the country, where drought episodes may become more frequent in summer periods (Carter et al. 2005, Ruosteenoja et al. 2005). Our findings indicate that appropriate tree species mixture is of importance for avoiding the negative impacts of reduced soil moisture on forest growth in these conditions. Previous studies have indicated that thinning with wider spacing may reduce the occurrence of drought effects and mitigate detrimental impacts on growth (e.g., Bréda et al. 1995). However, proper thinning (and initial spacing) regimes, considering even reduction in the dominance of Norway spruce on sites with low water-holding capacity, are needed to mitigate the

adverse impacts of climate change (e.g., Ge et al. 2010b) in order to sustain the productivity of Norway spruce-dominant mixed stands.

Acknowledgments

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Appendix

Table A1. Values for the main parameters when V_{cmax}, J_{max}, R_{day}, Γ_*, K_c and K_o for the Farquhar model are calculated as a function of temperature as described by Kellomäki and Wang (1996, 2001), Wang et al. (1996), and Medlyn et al. (2002) for Norway spruce, Scots pine and birch under the current climate.

Parameters	Unit	Values for tree species			Explanation
		Norway spruce	Scots pine	Birch	
V_{cmax}	μmol m^{-2} s^{-1}				Maximum carboxylation velocity
ΔH_a		52.75	52.71	52.75	
ΔH_d		202.6	202.3	202.6	
ΔS		669	672	669	
C		25.12	25.80	25.12	
J_{max}	μmol m^{-2} s^{-1}				Maximum rate of electron transport
ΔH_a		61.75	61.74	61.75	
ΔH_d		185.6	185.2	185.6	
ΔS		621	624	621	
C		30.6	30.43	30.6	
R_{day}	μmol m^{-2} s^{-1}				Daytime respiration rate
ΔH_a		33.87	33.87	33.87	
C		13.68	17.08	13.68	
K_c	μmol mol^{-1}				Michaelis constant for CO_2
ΔH_a		67.32	67.32	67.32	
C		33.25	40.59	20.32	
K_o	μmol mol^{-1}				Michaelis constant for O_2
ΔH_a		36	36	36	
C		20.32	20.32	20.32	
Γ_*	μmol mol^{-1}				CO_2 compensation point in the absence of dark respiration
ΔH_a		0.05	0.049	0.052	
C		20.32	19.16	20.32	

ΔH_a (kJ mol^{-1}) is the activation energy for CO_2 and light-saturated assimilation, ΔH_d (kJ mol^{-1}) the energy of deactivation, ΔS (kJ K^{-1} mol^{-1}) the entropy of the denaturation equilibrium of CO_2 and light-saturated assimilation, and C a constant.

For the gradient changing climate, the parameters of each year were re-calculated with the listed values using the linear functions concluded by Kellomäki and Wang (1996) and Wang et al. (1996), based on climate-acclimation (combined elevation in temperature and CO_2) experiments.