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ORIGINAL PAPER

Simulated climate change impacts on fluxes of carbon in Norway spruce ecosystems along a climatic transect in Sweden

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Abstract A simulation study based on recent regional climate scenarios for Sweden investigated possible changes in carbon (C) dynamics and net ecosystem exchange (NEE) of Swedish Norway spruce forest ecosystems. Four sites, representative of well-drained soils in four regions, were included. Stand development was simulated for a 100-year rotation period using a coupled model describing abiotic and biotic processes in the soil-plant-atmosphere system. Two IPCC climate change scenarios, corresponding to a mean annual temperature increase of about 2°C (A2) or 3°C (B2) from the reference period 1961–1990 to a new period 2061–2090, were considered. Annual maximum snow depth decreased with the increase in air temperature, whereas maximum soil frost depth and mean annual soil temperature showed only small changes, especially for the sites in northern Sweden. Simulations suggested that in the warmer climate, gross primary production (GPP) increased by 24–32% in northern Sweden and by 32–43% in the south. In the north, the increase was related to the combined effect of air and soil temperature extending the growing season, whereas in the south it was mainly governed by increased N availability due to increased soil temperature. NEE increased by about 20% (A2) or 25% (B2) at all sites, more or less solely due to increased accumulation of C in the tree biomass (including harvest residues), since changes in soil C were small compared with the current climate. Both light use efficiency and water use efficiency were improved in the future climate scenarios, despite increases in atmospheric CO_2 not being considered.

Keywords Air temperature · Boreal · CoupModel · Net ecosystem exchange · Nitrogen · Soil temperature · Soil frost · Soil respiration

Introduction

A number of attempts have been made to simulate the response of boreal forest ecosystems to climate change. It seems reasonable to expect a substantial increase in forest production as a consequence of increased temperature and CO_2 concentrations in the atmosphere (Kellomäki and Väisänen 1997; Mäkipää et al. 1999; Briceno-Elizondo et al. 2006). The corresponding change in soil organic carbon (C) is more uncertain because it is the net result of changes

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in two large fluxes, the influx of litter to the soil and the efflux of CO_2. Some losses also occur as leaching of dissolved organic C (DOC), which in some soils could make a significant contribution in a long-term perspective (Michalzik et al. 2001). Some studies have reported an increase in forest growth and a simultaneous decrease in soil C (Mäkipää et al. 1999), whereas other have emphasized that the increased respiration from soil may stimulate growth and input of litterfall to the same extent, with the result that no net change in soil C can be expected (Melillo et al. 1996). Thus an approach coupling abiotic conditions in the atmosphere with the corresponding conditions in the soil is needed to evaluate the interaction between different processes in the soil-plant-atmosphere system. Recently, Lal (2005) discussed and demonstrated the potential for a further increase in soil C storage as a result of appropriate soil management in combination with climate change.

Sweden has a pronounced climatic gradient, with mean annual temperatures increasing from about 0.5–8°C north to south. National inventories also show forest productivity and soil C pools increasing from north to south (Olsson et al.2007), indicating a link to the climate variation within the country. However, nitrogen (N) deposition also increases from north to south. Deposition of N (sum of ammonium and nitrate N) to spruce forests was estimated at >20 kg ha^{-1} yr^{-1} in southern Sweden and 3–6 kg N ha^{-1} yr^{-1} in northern Sweden during the early 1990s (Lövblad et al. 1995). Hyvönen et al. (2006) estimated that N deposition increased from 6 to 20 kg ha^{-1} yr^{-1} in southern Sweden and from 1 to 4 kg ha^{-1} yr^{-1} in northern Sweden in the period 1900–1990. Swedish forest ecosystems are in general N deficient, indicating a strong link between N supply and tree growth/litter production (Linder 1987). Thus, it is not only future climate change that will affect the size of the C pool in Swedish soils, but also the soil N pools present and future changes in N deposition. One way to resolve the role of climate versus ecosystem N status in controlling the C build-up in forest soils is to use ecosystem models. Arain et al. (2006) demonstrated recently how such a coupling of C with N processes improved model performance in a 5-year study of eddy covariance flux measurements of net ecosystem productivity (NEP) in Canada. Previously, such coupled ecosystem models were mostly calibrated on relatively short time series and with the emphasis on the plant response to environmental conditions, without accounting for the long-term changes in the entire ecosystem (Matala et al. 2006). Models such as the FINNFOR model of Kellomäki and Väisänen (1997), which includes a coupling between N and C, use a simplified uptake sub-model for nitrogen without linking the change in GPP to differences in soil N and C turnover on a mechanistic level. The study by Mäkipää et al. (1999) demonstrates for example how uptake of N and decomposition were coupled with an empirical multiplier that was related to annual values of transpiration as the forcing conditions for the decomposition of soil organic material. In recent work, Svensson et al. (2007) applied the CoupModel (Jansson and Karlberg 2004) with a daily time step for estimating decomposition rates and N supply in order to evaluate effects of climate and N on ecosystem productivity in Sweden. They concluded that it was not possible to explain the tree growth rate in northern Sweden with the conventional decomposition mineralization model. Nitrogen input had to be linked with an enhanced decomposition rate and/or an organic uptake rate. The CoupModel focuses on the climate and abiotic processes of the soil-plant-atmosphere system and has previously been demonstrated to describe crucial processes of snow, frost and heat exchange with the atmosphere for Swedish conditions (Jansson et al. 1999; Stähli et al. 2001; Gustafsson et al. 2004; Mellander et al. 2005), and to estimate the hydrological effects of climate change (Gärdenäs and Jansson 1995).

The main objective of the present work was to estimate long-term changes in carbon fluxes and pool sizes, taking the link between nitrogen and carbon into account, when managed Norway spruce stands were exposed to two of the IPCC climate scenarios (A2 and B2) according to SWECLIM (Rummukainen et al. 2004) based on the Hadley centre GCM model. Simulations were made for well-drained soils in 4 selected regions in Sweden, representing differences in the current climate and N deposition rates, using the CoupModel, previously parameterized on a regional-based dataset (Svensson et al. 2007). Specific objectives were to: (i) Identify how a change in climate affected abiotic factors of importance for ecosystem C dynamics; (ii) analyze how a change in climate affected the rate of processes governing the accumulation of carbon in vegetation and litter production, compared to the rate of processes regulating the rate of SOC decomposition; and (iii) identify the extent to which limiting factors for key ecosystem processes are expected to change, for instance the role of moisture and nitrogen.

Materials and methods

Brief description of the CoupModel

The CoupModel, an integrated version of the SOIL and SOILN-models (Jansson and Halldin 1979; Johnsson et al. 1987), is a coupled ecosystem model simulating abiotic and biotic processes in a soil-plant-atmosphere system. The basic structure of the model is a depth profile of the soil, and calculations of water and heat flows are based on common soil properties. C and N balances and the dynamics of plant development are simulated, as are the interactions between plants and physical driving forces, e.g., how the plant cover influences both aerodynamic conditions in the atmosphere and the radiation balance at the soil surface. The only dynamic input data necessary are precipitation, air temperature, wind speed, air humidity and radiation. As two (or more) plant layers are simulated, the equations used are calculated for the respective plant layer. Competition is enabled between different plant layers with respect to the interception of light, uptake of water and N.

Model assumptions and setting of relevance for the present paper are briefly described below. More details are given in Svensson et al. (2007).

Soil organic matter

Soil organic matter was represented by two pools; litter (fast turnover rate) and humus (slow turnover rate). Microbes were only implicitly represented in the substrate. Decomposition of the litter and humus pools was described as first order rate processes governed by response functions of soil temperature and soil moisture. The products of litter decomposition are CO_2 (respiration), humus and, conceptually, microbial biomass and metabolites, whereas CO_2 is the only product of humus decomposition. The fraction of C and N being transformed from the litter to the humus pool was determined by a humification factor, set to 0.2 in all simulations. Temperature and moisture effects on the turnover of soil organic matter were accounted for using standard functions suggested by Ratkowsky et al. (1982) and Johnsson et al. (1987), respectively. The same temperature and moisture sensitivity was assumed for the litter and humus pools.

Gross primary production

The photosynthetic rate was calculated as proportional to global radiation adsorbed by the canopy. The proportionality constant, i.e., light use efficiency, was calculated as a function of three multiplicative response functions taking into account air temperature, and the plant availability of water and nitrogen. The air temperature response was set to be optimal within the range 10–25°C and was reduced in a linear way both above and below the optimal range. The water response was expressed as the ratio between actual water uptake and potential transpiration. Water uptake was controlled both by soil temperature and due to soil moisture. The soil temperature response was given as a power function that showed a rapid increase in the water uptake rate around 5°C to reach values close to unity when the soil temperature was above 10°C (Mellander et al. 2006). Nitrogen response was assumed to be linear in relation to the nitrogen content of leaves (Robertz and Stockfors 1998).

Nitrogen uptake by plants

Plant N uptake is driven by N demand, which is related to the C assimilation rate and assumed CN ratios of different plant components. Mineral N is taken up from nitrate and ammonium pools in proportion to the relative sizes of these pools. In cases of N deficiency, i.e. when estimated uptake is less than the estimated demand, N is allowed to be extracted in organic form (Näsholm et al. 1998). The organic N uptake rate is assumed to be proportional to the pool size of N in the humus pool. Both mineral and organic N uptake are related to the root distribution in the soil profile. The fluxes of inorganic N from the litter and humus pools are driven by C turnover, and are related to the CN ratio of the decomposed product and the substrates. Thus, there is a strong link between C and N mineralization rates in the model.

Climatic and N deposition data

Simulations were run for four different regions in Sweden covering mean annual air temperatures from 0.7°C to 7.1°C. Climatic data were taken from four representative sites, Lycksele in the north, Mora and Nässjö in central Sweden and Ljungbyhed in the south (Table 1). For these sites, mean daily values of air temperature, humidity, wind speed, cloudiness and precipitation were available from the Swedish Meteorological and Hydrological Institute (SMHI) for 1961–1986. In the reference simulations, this dataset was duplicated to cover a 100-year period. Nitrogen deposition was based on official data reported by IVL (2006) and was taken from a regionally representative measuring point for each region. The N deposition values were assumed to remain constant during the whole simulation period (Table 1).

Two climate scenarios for the climate 2071–2100 were obtained from the SWECLIM project, using the Hadley Centre simulations of scenario A2 and B2 according to IPCC. Both scenarios correspond to increased emissions of greenhouse gases during the next 100 years, with the largest increase with scenario A2. The major characteristics of the climate scenarios are increased mean annual air temperatures and increased total annual precipitation for all sites included in the study. However, whereas air temperature increases at all times of the year at all sites, precipitation decreases during summer at the southern sites while increasing all year round at the northern sites. New climate series based on the reference period (Table 2) were generated using monthly-based delta functions to transfer the current climate to the new climate, using multiplicative factors for precipitation and additive values for air temperature. These coefficients have previously been used in hydrological studies by Graham (2004). Other climatic variables were not changed following the procedures suggested by Gärdenäs and Jansson (1995), i.e., cloudiness, windspeed, relative humidity and N deposition remained the same in the climate scenarios as in the reference simulations (Table 1).

Table 2 Annual mean air temperature and precipitation, simulated for 3 climate scenarios and 4 regions of Sweden

Variable	Scenario	Latitude			
		65°N	61°N	58°N	56°N
Temperature (°C)	Present	0.7	3.3	5.2	7.1
	B2	2.6	5.2	7.7	9.4
	A2	3.3	5.8	8.4	10.1
Precipitation (mm)	Present	613	629	711	838
	B2	671	683	709	868
	A2	704	701	717	890

Initial conditions for vegetation and forest management practices

Initial conditions were chosen as clear cutting with two plants similar in size but with different characteristics, allowing them to develop as a tree canopy and an understorey. General guidelines from the Swedish Forest Agency (2005) regarding forest management were used in the simulations, i.e., one cleaning after 10 years, followed by the first thinning after 40 years and the second and last thinning after 80 yrs. These management practices were only applied to the tree layer. During cleaning, all residues were left on the ground but at the following thinning the stems were harvested and the remaining roots and leaves were added to the normal litter input to the soil.

Table 1 Selected sites with some general characteristics

Name	Lycksele	Mora	Nässjö	Ljungbyhed
Latitude	64°N 35′	60°N 58′	57°N 38′	56°N 05′
Altitude (m.a.s.l)	223	161	305	76
Mean annual air temperature (°C)	0.7	3.3	5.2	7.1
Mean annual precipitation (mm yr^{-1})	613	630	712	838
Mean annual N deposition (gN m^{-2})	0.15	0.35	0.75	1.25
Mean annual Tree growth (g C m^{-2})	54	78	104	115

Table 3 Parameters and initial conditions that have been set to different values for the different latitudes

Parameter				
Latitude	64°N35’	60°N 58’	57°N 38’	56°N 05’
Initial C soil	7006	8576	9995	10666
Initial N soil	223	295	367	539
CN ratio soil	31.5	29.1	27.2	19.8
Decompositon rate coefficient humus, K_h (1/day)	3.7E−4	2.8E−4	1.9E−4	1.1E−4
Organic uptake rate coefficient humus, O_H (1/day)	0.65E−4	0.4E−4	0.22E−4	0

Initial conditions for soil carbon and nitrogen

Initial soil C and N stocks are reported in Table 3. These data are representative of their respective region of Sweden and represent the statistical values of complete rotation periods (Skogsdata 2003).

Modeling approach and parameterization

The simulations were run over a 100-year period, enabling the simulated system to develop from a young newly established forest to a mature closed forest. The general approach chosen was to use the same parameterization for all regions, i.e., with a minimum of site-specific data, in order to evaluate the general applicability of the model. The parameter values used in the simulations are equal to those obtained by ‘calibration approach III’ presented in Svensson et al. (2007) for these same regions. The parameters represent values that were shown to be reasonable explanation of the regional long term behavior of the model as it was run during a 100-year period. On the other hand we have demonstrated that these values are not expected to be correct for individual sites and for shorter periods of time (Berggren Kleja et al. 2007). Parameters that are obtained from short-term calibration of the model are probably more precise for the dynamic behavior within the year and within the days but on the other hand such values are less reliable for the long term coupling between N and C pools of the ecosystem. No precise interpretation of the model against soil biological processes or tree physiological processes is claimed.

In this approach, the rate constant for humus decomposition (k_h) and the uptake coefficient for rate of organic N uptake by plants (O_H) were allowed to vary on a regional basis in order to match measured standing stock volumes in the respective region. A full list of parameter values used in the present simulations are presented by Svensson et al. (2007) but here only parameters that were set to different values for the different regions are reported (Table 3).

The soil physical properties used in the simulations were based on mean values from measurements of soil texture in 37 soil profiles at different forest sites located in northern, central and southern Sweden. The soil texture data originated from studies at the Swedish Agricultural University (Wiklert et al. 1977–1983) and are available in a database published with the CoupModel (URL: ftp//www.lwr.kth.se/CoupModel). The same soil physical properties were used in all simulations and dry and mesic conditions were simulated through a drainage level of 1.5 m. Parameter values describing hydrology, radiation and snow were taken from previous simulations made in similar environments, i.e., a Norway spruce forest on sandy silty till (Alavi and Jansson 1995; Gustafsson et al. 2004).

Estimation of sensitivities in relation to latitude and climate change

To allow a comparison between current climate variation with latitude and climate change, a virtual shift to more southern latitudes that corresponded to climate change was calculated. The climate variation with latitude for the current climate was estimated using simple linear regression. The mean value of the change from the current climate to the new climate for the four points in the transect was then divided by the slope from the linear regressions to allow the change to be expressed as the mean shift in latitude.

Results and discussion

Abiotic conditions

The two major abiotic inputs to the model were air temperature and precipitation, which were closely related to simulated snow depth, soil temperature and frost depth. There were significant variations between the different sites and the degree of change in these variables because of the climate change introduced (Figs. 1, 2 and Table 2). The mean annual air temperature change of about 2–3°C corresponded to a latitudinal shift of approximately 3° and 4° southward for the two scenarios, respectively. Due to the higher air temperature, the maximum annual snow depth decreased for all sites, even when precipitation was assumed to increase in the climate scenarios. The mean annual soil temperature deviated from the

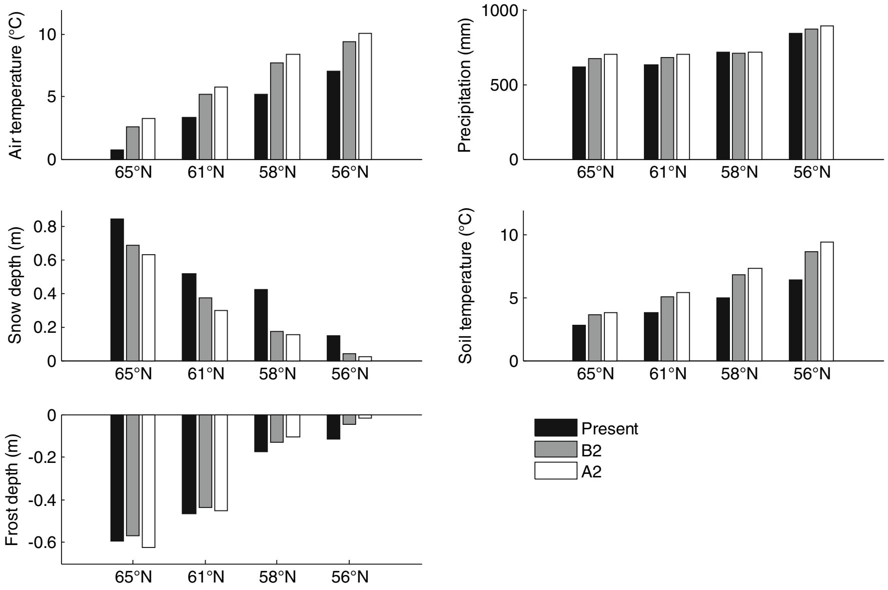

Fig. 1 Abiotic variables used as input to the model, (**a**) annual mean air temperature, and (**b**) annual precipitation, together with corresponding simulated (**c**) mean annual maximum of snow depth, (**d**) soil temperature at 30 cm depth, and (**e**) annual mean maximum frost depth for 4 positions in a north-south transect through Sweden, representing present climate and scenarios B2 and A2

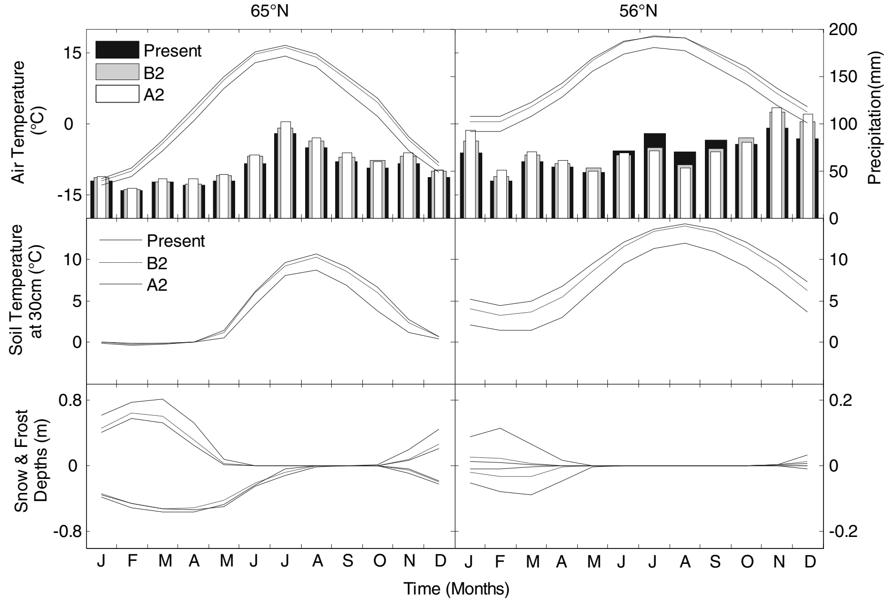

Fig. 2 Air temperature and precipitation as assumed to the model (top panels), simulated soil temperatures (middle), snow depths and frost depths (lower) as a function of mean monthly values during 100 years according to present climate, scenarios B2 and A2, representing 2 positions in a transect from north (left panels) to south (right panels) through Sweden

corresponding air temperature in two interesting ways. The current range in soil temperature from the north to the south was substantially smaller than the range in air temperature. The simulated mean annual soil temperature was 2°C warmer than air temperature in the north, but slightly colder than air temperature in the south. The explanation for this asymmetrical relationship between air and soil temperature between northern and southern sites was mainly the snow insulating effect in the north preventing the soil from cooling in proportion to air temperature during winter (Fig. 2). In the south, neither snow depth nor soil frost had any major influence on the soil temperature in the winter (Figs. 1, 2). Instead, the air to soil temperature relationship was mainly a result of the simulated closed forest canopy preventing the soil warming up during the summer. In the climate change scenarios, the differences between the mean annual air and soil temperature at the different latitudes was less pronounced. The reduced snow depth and shorter snow cover period counteracted the increased air temperature at the northern sites, which resulted in scarcely any changes during winter and relatively small increases in mean annual soil temperatures (Figs. 1, 2). Consequently, the maximum annual frost depth was not affected at the two more northern positions in the transect. The combination of the remaining relatively deep soil frost and the increased soil temperatures during the vegetation period were obviously important for the functioning of the northern ecosystem. On the other hand, with insignificant influence of snow cover, the most substantial changes in mean annual soil temperature occurred in the south, where temperatures increased both during summer and winter (Fig. 2). The fact that soil temperature remained above 0°C during winter is important for the functioning of the southern ecosystem, since it would have a major impact on the soil carbon dynamics.

Gross primary production

Fluxes of carbon showed different seasonal patterns, which are important to consider when interpreting the results of the different scenario simulations (Fig. 3). In this section we focus on the largest flux, GPP, which governed the input of carbon to the ecosystem. In our climatic transect, GPP showed differences both with respect to its duration and to its mean monthly rates during the year (Fig. 3). The length of the growing season increased from north to south, with a peak in GPP earlier at the southern positions of the transect compared to the northern. The relative contributions of air temperature, water and nitrogen as limiting factors for GPP, given as an average for the entire 100-year period, are presented in Fig. 4. In the simulated current climate, a water supply shortage occurred during spring, especially in the north (Fig. 4). The main restriction in the early spring was low soil temperature, which restricted water uptake in the model. This effect has also been demonstrated in experimental studies conducted in

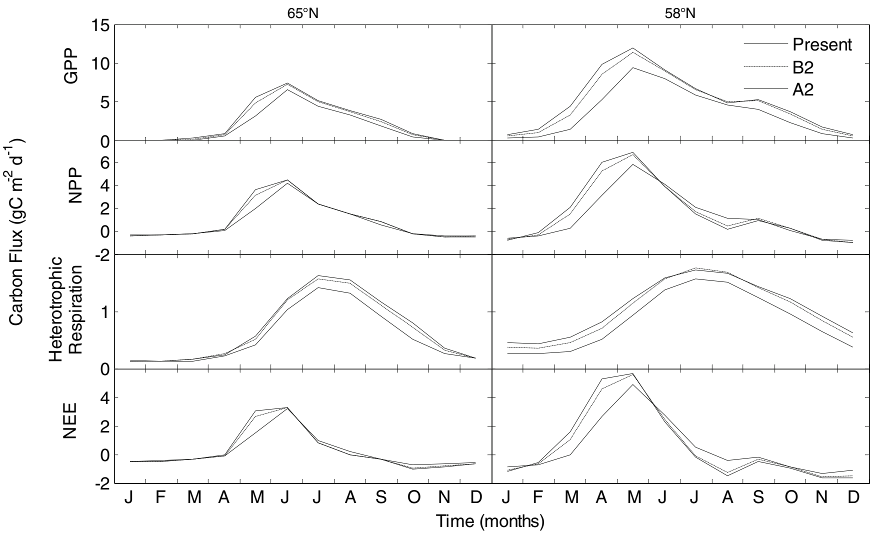

Fig. 3 Simulated GPP (upper panels), NPP (upper middle) soil heterotrofic respiration (middle lower), and NEE (lower) as a function of mean monthly values during 100 years according to present climate, scenarios B2 and A2, representing 2 positions in a transect from north (left panels) to south (right panels) through Sweden

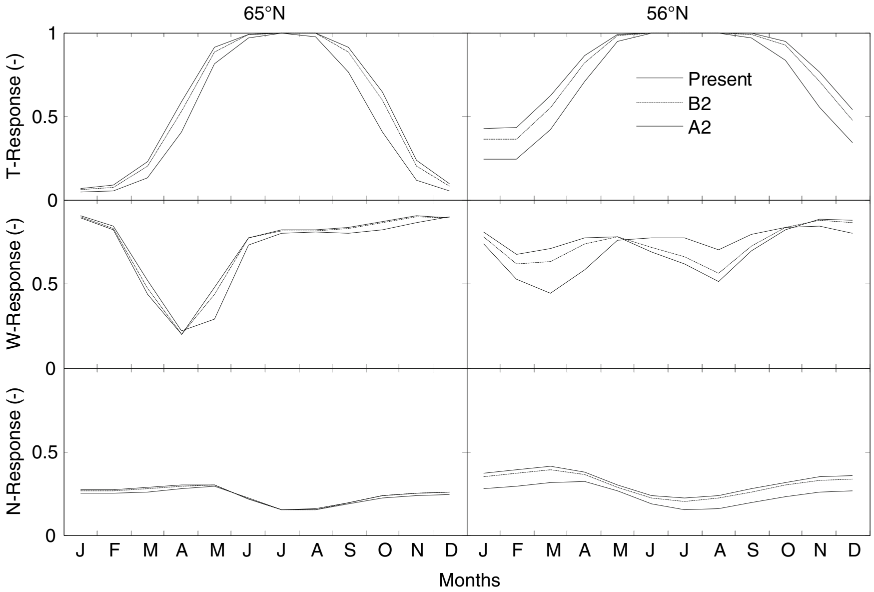

Fig. 4 Simulated monthly mean response functions for GPP, i.e. multiplicative scaling functions, for two positions in a transect from north (left) to the south (right), according to present climate, scenarios B2 and A2. The different responses originate from air temperature (upper), transpiration (middle) and nitrogen (lower)

the northern part of Sweden (Mellander et al. 2006). The overall most important limiting factor for GPP at all sites, in all climatic scenarios, was N supply rate, which was particularly true during the vegetation period (Fig. 4). Substantial increases in annual GPP were obtained for both climate scenarios at all sites, ranging from 24% to 32% in the north to 32–43% in the south. Air temperature effects were relatively similar at all latitudes with a mean increase from 4.5% to 6.5% for the respective scenarios, whereas the effects of changed water and nitrogen stress showed large differences between the sites.

The water shortage was modified in a warmer climate (Fig. 4). For the most northerly site, the water shortage remained at a high stress level in April but a substantial improvement occurred in May. As a consequence of enhanced soil temperature, much less water stress was seen during this month, corresponding to a shift of 2–3 weeks. For the most southerly site, the previous water stress in March and April more or less disappeared but on the other hand this southern site suffered increased water stress during the summer, which was only slightly indicated for the current climate simulations. This increase in summer water stress in the south counteracted the improved nitrogen conditions so that the July GPP was only slightly increased compared to the current climate. The summer water stress in the south was of course a result of the reduced summertime precipitation rates (Fig. 2), but also a result of the longer growing season, increased LAI values and increased evaporative demand from the atmosphere. On average the water stress was reduced in the north and slightly enhanced in the south.

The N limitation on GPP shifted, so that the southern sites became less N limited due to increased mineralization of the soil N pools especially during late winter and spring (Fig. 4). On average, the mean N limitation on GPP decreased at all sites, but only by about 5% in the north, whereas it decreased by more than 30% in the south. The simulations suggested that GPP is to a large extent governed by indirect effects of climate factors on nitrogen availability, and to a lesser extent by the direct effects of temperature and water conditions. These results agree with those of soil heating experiments conducted in a northern Norway spruce forest in Sweden, reporting increased GPP related to an increased soil N supply (Strömgren and Linder 2002). The results are also in agreement with the general role of nitrogen limitation as a main factor for reduced growth in the Sweden (cf. Tamm 1991). The seasonal pattern of the N-response as simulate corresponds to the CN ratio of the “big canopy leaf” as respresented in the model. Few or no studies exist on a stand level demonstrating the integrated N-response on GPP but detailed studies on N concentrations of Foliar contents for Norway spruce in the north of Sweden exist (Linder 1995). Our simulated decrease of N response corresponds were well to such measurements from Flakaliden for both unfertilized and fertilized stand of Norway spruce. The relative N-stress corresponds to simulated N concentrations of leaf concentrations that are similar to concentrations that have been reported from Skogaby in SW of Sweden with high nitrogen deposition (Persson and Nilsson 2001). However it is important to clarify that are simulated N-response is not an experimental N-response since additional limiting nutrients are not considered in the model. Instead the simulated N-response represents the limitations of all nutrients and not only nitrogen. The experimental and pratical N-deficiency as reported by Bergh et al (2004) is consequently indicating less N-stress in south compared to the north but also in that study it was suggested that forest production could be increased by 100% in the south and by 300% in the north by nutient optimization. The lower potential to increase the production in the south was partly related to a water deficiency effect at the experimental site at Asa (Bergh et al. 1998) that was not of such importance for this regional study.

The overall simulation results of increased GPP are similar to what has previously been reported by Kellomäki and Väisänen (1997). However, Kellomäki and Väisänen (1997) explained their increase mainly as a result of CO_2 increase in the atmosphere and not as increased nitrogen availability.

Net primary production

The large differences between the most northerly and southerly sites regarding changes in GPP compared to the current climate were much less pronounced for NPP, with changes between 17–22% in the north and 20–26% in the south. This indicates the importance of considering plant respiratory losses in order to understand changes in NEE. The increased GPP in May and June was also apparent as increased NPP during the same period (Fig. 3). However, during late summer and autumn the enhanced influx of C to the ecosystems through climate change was more or less lost due to increased maintenance respiration in the north, while for the same period in the south it decreased the NPP. The importance of considering maintenance respiration was also apparent regarding litter production, as the change in litter production and NPP were of the same magnitude at the respective sites, compared to the larger changes in GPP.

Soil carbon dynamics

As shown in the current climate change simulations, and discussed in detail by Svensson et al. (2007), soil respiration varies from north to south in Sweden

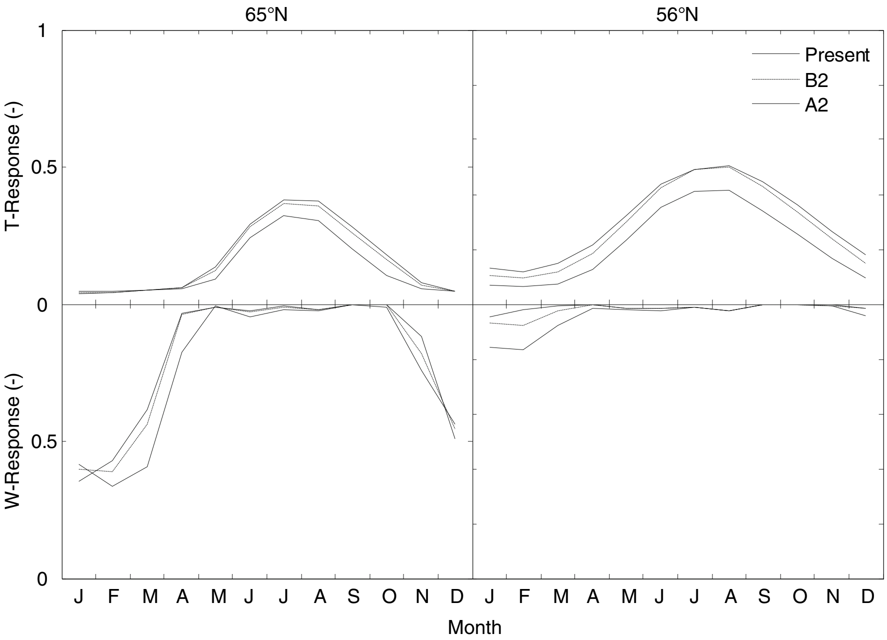

Fig. 5 Simulated monthly mean response functions for soil heterotrofic respiration, i.e. multiplicative scaling functions, for two positions in a transect from north (left) to the south (right), according to present climate, scenarios B2 and A2. The different responses originate from soil temperature (upper), and soil moisture (lower)

because of the different pool sizes and the different climatic conditions. The maximum rate of heterotrophic soil respiration occurred in July at all sites, irrespective of climate scenario (Fig. 3).

The annual pattern in soil heterotrofic respiration followed the soil temperature to a large extent and was less affected by water than the corresponding GPP (Fig. 5). This was also clear when the relative contributions of soil moisture and soil temperature to heterotrophic respiration were considered. The fact that soil temperature was more important than soil moisture in these results may be a consequence of the restriction of the study to well-drained soils, and it is likely that results would be different if a wider moisture regime were considered. The strong link between heterotrophic respiration and soil temperature found in this study is in accordance with results from a girdling experiment performed in a boreal pine forest ecosystem on well-drained soils, which showed heterotrophic respiration to be directly related to temperature (Högberg et al. 2001). Soil temperature changes could potentially be more important in the south than in the north as a result of the non-linear response function (Ratkowsky et al. 1982) used in the simulations. However, for the soil temperature ranges occurring in these simulations, the difference in temperature increase between the north and south was more important than the shape of the response function.

One difference in seasonal pattern between north and south was that the most northerly site did not have altered respiration during the winter period, whereas the most southerly site increased respiration losses substantially during the winter period. This was a direct effect of the asymmetry in the relationship between air temperatures and soil temperature, caused by the influence of snow depth and soil frost as discussed above (Fig. 2). Relative changes because of climate change during the summer, when the highest respiration losses take place, were similar for both the northern and the southern sites (Fig. 5).

In these simulations, we assumed the same temperature sensitivity of the litter and humus pools. At present, it is clear that the labile fraction of soil organic matter (‘litter’) seems to respond rapidly to temperature changes. This has been shown in both laboratory incubation experiments (Fang et al. 2005) and in situ soil-warming experiments (Knorr et al. 2005; Eliasson et al. 2005). In contrast, the decomposition rate of stable soil organic matter is difficult to measure because of its slowness, and is currently a matter of scientific debate. Some researchers claim that the decomposition rate of stable soil organic matter is even more sensitive to temperature than that of labile soil organic matter (Ågren 2000; Knorr et al. 2005), whereas others claim that it is fairly insensitive to temperature (Giardina and Ryan 2000; Liski et al. 2005). Thus, considering these uncertainties, we believe that our approach of assuming the same temperature sensitivity for both types of soil organic matter pools was justified.

Net ecosystem exchange

The simulated net ecosystem flux showed a pattern that was logical as the net results of GPP and respiration losses (Fig. 3). The major influx of CO_2 occurred in May to June for the current climate conditions and slight losses could be seen for autumn and winter. The climate change simulations showed increased positive values, especially during March to June. Both sites gained more net influx during the early part of the season. A shift from slightly negative NEE values during April to May for the current climate to large positive values in the simulations for the climate change scenarios occurred at the northern sites. Higher losses in July and August were also noted for the southern site, which was explained by the decreased NPP. The water shortage effect was simulated to be more pronounced for GPP than the corresponding effect on soil heterotrophic respiration (cf. Figs. 4 & 5). When considering the total net ecosystem exchange a major annual increase occurred for all sites, with smaller changes at 58°N compared to the other latitudes. The net ecosystem exchange consisted mainly of a change in tree biomass and in export of stem biomass at the thinning that was included in the simulations (Fig. 6). The change in soil storage was a small fraction that showed small negative values at the two northern sites and small positive values at the southern sites (Fig. 6). The same general tendency remained for the different components of the net ecosystem flux before and after the climate change. There could be many reasons for a change in the net carbon flux from the soil storage, as discussed intensively in the global change community during recent years. The factors

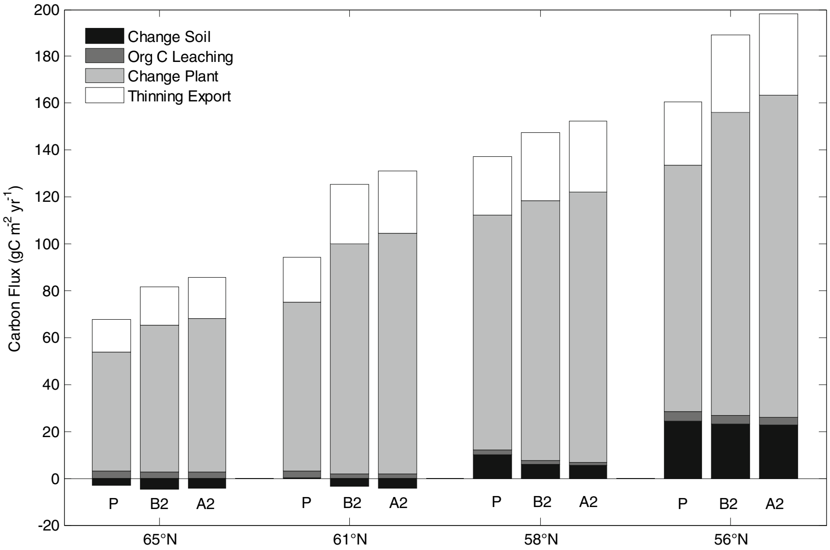

Fig. 6 Simulated mean annual values of net ecosystem exchange with their correspondent partitioning into change in soil storage, export of dissolved organics, change in tree biomass and export of stem in connection to thinning for 4 positions in the transect according to present climate (P), scenarios B2 and A2

governing photosynthesis are not the same as those governing soil heterotrophic respiration losses. However, there is a very strong link between decomposition, mineralization, nutrient supply, and photosynthesis that may give the whole ecosystem a more inert behavior than could be expected from the individual processes. This was clearly indicated (see Fig. 6), where the change in soil C was shown as the result of two counterbalancing fluxes so that the increased litter production was mirrored in increased soil heterotrophic respiration, resulting in only small changes in soil C as a consequence of climate change.

It was interesting to note that the enhanced heterotrophic soil respiration in the south showed an effect similar to that of N-response on photosynthesis (Figs. 3 & 4). The increased soil respiration in the south was important for an increase N uptakte. However, the large differences in the N-response from the north to the south were only partly seen in the soil temperature response functions as such that govern soil respiration. N mineralization is also a function of amount of organic material and CN ration. A possible explanation was that the current larger CN ratio of the soil in the north compared to the south did not respond with the same rate of N supply to the trees as was the case in the south. The strong N limitation of the northern sites persisted, whereas the southern sites with lower CN ratios could benefit from the enhanced soil respiration more efficiently than the northern sites.

Comparison between different variables

To illustrate the general sensitivity of a number of important ecosystem variables in relation to climate, we estimated their dependence on latitude position for the current climate and their expected virtual transition to southern latitudes as the result of a simulated climate change (Fig. 7). The results could be compared with the same values for the abiotic climate variables that were partly input to and partly simulated by the model (Fig. 1).

The sum of air temperatures during the growing season has been used in many ecological contexts and was included here for comparison with the other variables. The air temperature sum has no direct impact in the model but was calculated for use as a reference. It was interesting to find that this index showed the largest virtual change in latitude of all variables, probably because it combines the longer duration of the growing season with the higher temperature in a way that makes a larger change according to the air temperature scenarios. When considering the GPP governing variables as used in the model, we noticed that adsorbed radiation had a small change that was related to the increased leaf area index. In other words, the light use efficiency increased according to the simulations, based on the more favorable nitrogen, temperature and water conditions. Evapotranspiration and transpiration also showed very small changes compared to the

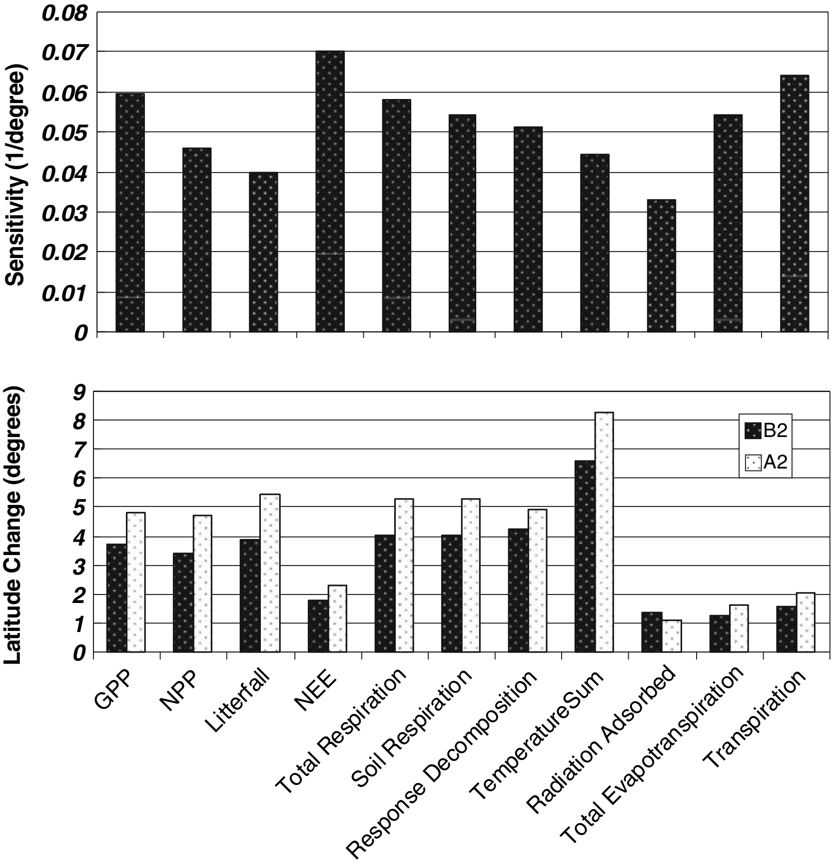

Fig. 7 Present relative change with latitude of a number of selected variables (upper) and their correspondent transition of virtual latitude changes to the south for because of changed climate according to scenarios B2 and A2 (lower)

substantially increased NPP, which indicates that not only light use efficiency but also water use efficiency will be improved with climate change. This was independent of the change in CO_2 in the atmosphere, which has been emphasized as strong evidence for improved light and water use efficiencies.

The virtual change in GPP to southern latitudes corresponded to a larger change than that given by the annual air temperature. Similar results were obtained for NPP and litterfall rates, which were closely related to GPP.

The conditions governing heterotrophic soil respiration were represented by the simulated response functions (multiplicative scaling functions taking values between 0 and 1) as estimated from simulated temperature and moisture conditions in the soil, respectively, and the combined total response. In this case we obtained a result that was approximately similar to the virtual transition of latitudes as for soil temperature. However, the transition was larger than the corresponding transitions in both GPP and air temperature, which indicates that soil heterotrophic respiration losses were slightly more sensitive to climate change than GPP. This was further reflected in a smaller change in NEE as a transition of latitude. The NEE showed the largest change with latitude during current climate from north to south, but had a relatively small virtual change to southern latitudes as a result of climate change.

Concluding remarks

Climate change according to recent SWECLIM scenarios caused substantial effects on the functioning of Swedish forest ecosystems in the scenarios simulated here. A coupled model of abiotic and biotic ecosystem processes was useful for demonstrating how the different variables of the ecosystem may be influenced. Increased N availability was found to be more important for tree growth in the south of Sweden than in the north. The increased soil temperature did not enhance soil respiration losses substantially more than it increased GPP. Climate change in winter conditions in the north, causing a longer growing season and a shortening of winter-related reduction in transpiration, was highly important for carbon turnover, whereas the corresponding increase in nitrogen availability in combination with summer-related water shortage was most important in the south. This study used parameters established from Swedish regional statistics on pools in the soil and in biomass and can be expected to be reliable for the current climate conditions. The assumed regional differences in the humus decomposition rates and in the organic uptake rates would be of major interest to investigate further, as would water availability for tree growth during periods of climate change - especially related to the changing winter conditions that are expected to cause new physical environmental conditions. Finally, studies with more comparisons of different management options as a means to change the carbon balance of Swedish forest ecosystems would be of interest.

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