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Modelling the short-term effects of climate change on the productivity of selected tree species in Nordic countries

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Abstract

A boreal version of the process-based simulation model, BIOMASS, was used to quantify the effect of increased temperature and CO_2-concentrations on net primary production (NPP). Simulations were performed for both coniferous (*Pinus sylvestris*, *Picea abies*) and deciduous broad-leaves stands (*Fagus sylvatica*, *Populus trichocarpa*), growing in different Nordic countries (Denmark, Finland, Iceland, Norway and Sweden), representing a climatic gradient from a continental climate in Finland and Sweden to a maritime in Denmark, Norway and Iceland. Simulations with elevated temperature increased NPP by ca. 5–27% for the coniferous stands, being less for a Scots pine stand growing in a maritime climate (Norway) compared with a continental (central Sweden, eastern Finland). The increase in NPP could largely be ascribed to the earlier start of the growing season and more rapid recovery of the winter-damaged photosynthetic apparatus, but temperature-driven increases in respiration reduced carbon gain. The effect of elevated temperature on NPP was similar in the *P. trichocarpa* stand on Iceland, mainly caused by an earlier budbreak and a more rapid leaf development in spring. Increased temperature reduced, however, NPP for the *F. sylvatica* stand in Denmark, since elevated temperature had no effect on budbreak but increased the water deficit and water demand during the summer and lowered photosynthesis. Increased CO_2-concentrations had an additional effect on NPP by 25–40% for the conifers and beech, which originated from increased photosynthesis, through enhanced carboxylation efficiency in summer and improved water use efficiency (beech). The effect of elevated CO_2 on NPP was somewhat less for the *P. trichocarpa* by 13%.

Keywords: Boreal forest; Climate change; Net primary production; Photosynthesis; Respiration

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1. Introduction

After the meetings in Kyoto (1997) and Haag (2000), the carbon balance of terrestrial ecosystems has been discussed more vividly. All countries who signed the Kyoto-protocol (UNFCCC, 1997) have undertaken to reduce the emissions of greenhouse gases and establish national carbon budgets. In the Nordic countries, where the boreal and cold-temperate forest ecosystems covers more than 40% of the land surface, the forests have a critical part in a national carbon budget. The large northern coniferous belt, Taigan, to which the Nordic coniferous forests belong, is assumed to play an important role in the global

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carbon balance, since the boreal coniferous forests are considered to constitute a major sink for atmospheric CO_2 (cf. Kirschbaum and Fischlin, 1996).

The boreal and cold-temperate forests are characterised by low productivity and long rotation periods, especially in the northern part of the boreal zone. The low productivity primarily results from climatic constraints with long period of sub-zero temperatures together with low photon flux densities (Troeng and Linder, 1982) and low nutrient availability (Tamm, 1991). Low-temperature constrains photosynthesis directly and indirectly, e.g. by way of soil freezing, stomatal closure, freezing of needles, early decline of photosynthesis and damage to the photosynthetic apparatus in winter (see Havranek and Tranquillini, 1995 and references therein). Low nutrient availability is also known to be a major limitation to forest yield in most boreal forests (see review by Tamm (1985) and Linder (1987)). The lack of nutrients is partly a consequence of low soil temperatures, which inhibit mineralisation and decomposition rates in soil organic matter (Van Cleve et al., 1981; Berg et al., 1993).

A temperature increase, as a result of an increasing atmospheric CO_2, is predicted to take place in this century. Recent simulations, over the period 2000–2100, predict a global warming at Nordic latitudes of 5–6 °C in winter and 2–3 °C in summer (Räisänen, 2000; IPCC, 2000). Climate change, with elevated CO_2-concentration and especially increased temperature, would certainly change many aspects of the environment in the cold-temperate and boreal forests and influence a number of physiological processes in both coniferous and deciduous stands as well as in the soil. The cold-temperate and boreal forests are therefore likely to be particularly sensitive to climatic change (cf. Kirschbaum and Fischlin, 1996). It is therefore important for a correct estimation of the carbon balance in the future, to include how global change would effect the ability of the boreal forest to assimilate CO_2, produce biomass, and sequester carbon.

Models are often used as tools to predict responses of vegetation to environmental change, and a number of models of forest ecosystem production are currently available at patch and regional scales (cf. Rastetter et al., 1991; Ryan et al., 1996). Many of these models are, however, not suitable for predicting the carbon gain of conifers in boreal and cold-temperate environments, since they do not include essential low-temperature effects on physiological processes. To be able to make reliable predictions how global warming might affect productivity in boreal coniferous forests, certain temperature-dependent processes, such as soil freezing/thawing, phenology, seasonality of photosynthetic capacity and soil nutrient availability must be considered. Some of these effects such as soil frost, phenology and seasonal changes in photosynthetic capacity, have been included in the process-based growth model BIOMASS (McMurtrie et al., 1990; Bergh et al., 1998) to simulate the annual course of photosynthesis in boreal coniferous ecosystems.

The recovery of photosynthetic capacity in spring is a likely key-process for the annual carbon assimilation in the boreal coniferous forest (Bergh et al., 1998) and particularly sensitive to elevated temperature. Spring recovery might also respond differently to elevated temperature in a mild maritime climate compared with colder continental one. For deciduous stands these processes in spring are not applicable, but instead many deciduous species may show an earlier leaf flush and hence increase NPP in warmer climate. The response of elevated CO_2 on NPP, might give large differences (Freeman, 1998), since water availability during the growing season varies from a water deficit in Denmark and southern Sweden to a surplus for the rest of the Nordic area.

To make clear the differences within the Nordic countries and between species, the boreal version of the process-based simulation model, BIOMASS, is used in this paper to quantify and compare the effect of increased temperature and elevated CO_2-concentration on net primary production (NPP) for Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*) and black cottonwood (*Populus trichocarpa*), growing in the Nordic countries (Denmark, Finland, Iceland, Norway and Sweden), representing a climatic gradient from a continental to a maritime climate.

2. Material and methods

2.1. Experimental sites

The BIOMASS simulations are focused on six different sites in the Nordic countries, representing a climate gradient from a maritime climate in Denmark, Iceland and Norway to a more continental climate in Finland, central and northern Sweden. There is also a transition from a cold-temperate climate in the south (55°59′N) to a boreal in the north (64°07′N). The length of the growing season is approximately 220 days in Denmark and ca. 125 days in eastern Finland and northern Sweden. The winter in Finland and Sweden is characterised by low negative temperatures and frozen soils with a persistent snow cover. The precipitation varies from ca. 600 to 800 mm per year in Finland, Denmark and Sweden to more than 1100 mm in Iceland and Norway. In general it is only in Denmark and southeastern Sweden, where the demand (evapo-transpiration) of water normally exceeds surplus (rainfall) during the growing season, and the water deficit limits the potential photosynthesis and growth in mature forests. The sites in Finland (Mekrijärvi), Norway (Aamli) and central Sweden (Jädraås) are dominated by relative young stands of Scots pine (*P. sylvestris* L.), while the Norway spruce (*P. abies* (L.) Karst) stand, at the site in northern Sweden (Flakaliden), was planted in 1963. The site in Denmark (Gribskov) is a middle-aged European beech (*F. sylvatica* L.) stand, while a plantation of black cottonwood (*P. trichocarpa* Torr. and Gray, clone Iðunn) is found on Iceland (Gunnarsholt). A more detailed description for each site is found in Table 1.

2.2. Scenarios used in the simulations

Three years of current climate, 1994–1996, were used from each of the six Nordic sites for the reference simulation of NPP. Two climatic warming scenarios were then used, with increased mean annual air temperatures of +2 and +4 °C. In both scenarios, the temperature increase was stepwise, with higher temperature elevation in winter compared to spring, summer and autumn (Fig. 1). These temperature scenarios are close to the predictions of elevated temperature presented in Räisänen (2000). However, changes in precipitation are not taken into account in the simulations. A scenario with increased CO_2 (700 ppm) alone and in combination with the two temperature scenarios, were also used in the simulations of NPP. The reference simulation was used for comparison with the results of simulations with elevated CO_2, temperature and the combination of elevated CO_2 and temperature. The annual course of NPP for the scenarios are in relation to current climate and are referred henceforth as ΔNPP.

2.3. The BIOMASS model with boreal features

The BIOMASS model describes processes of radiation absorption, canopy photosynthesis, phenology, allocation of photosynthate among plant organs,

Table 1
Stand descriptions for each site[a]

	Site					
	Flakaliden (Sweden)	Mekrijärvi (Finland)	Jädraås (Sweden)	Aamli (Norway)	Gunnarsholt (Iceland)	Gribskov (Denmark)
Longitude	64°07′N	62°47′N	60°49′N	58°55′N	63°51′N	55°59′N
Latitude	19°27′E	30°58′E	16°30′E	8°30′E	−20°12′E	12°15′E
Altitude (m a.s.l.)	310	145	185	155	78	15
Mean annual air temperature (°C)	2.0	2.1	2.6	7.9	3.6	8.8
Annual precipitation (mm)	590	690	780	1350	1120	660
Growing season PAR (GJ m^{-2})	0.97	0.92	1.14	1.17	0.96	1.55
Length of growing season (days)	125	125	145	190	150	220
Species	*P. abies*	*P. sylvestris*	*P. sylvestris*	*P. sylvestris*	*P. trichocarpa*	*F. sylvatica*
Stand age (years)	31	24	24	24	4	34
Stocking (stems ha^{-1})	2570	2500	2500	2500	10000	800
Initial height (m)	4.29	4.6	4.6	4.6	0.33	13.4
Initial basal area (m^2 ha^{-1})	7.82	3.1	3.1	3.1		19.7
Initial LAI (projected)	2.04	2.0	2.0	2.0	0.25	5.1

[a] Meteorological data are means of 3 years (1994–1996). For deciduous species (*P. trichocarpa* and *F. sylvatica*), initial LAIs are peak values during the first year of simulation. Stand age given for first year of simulation.

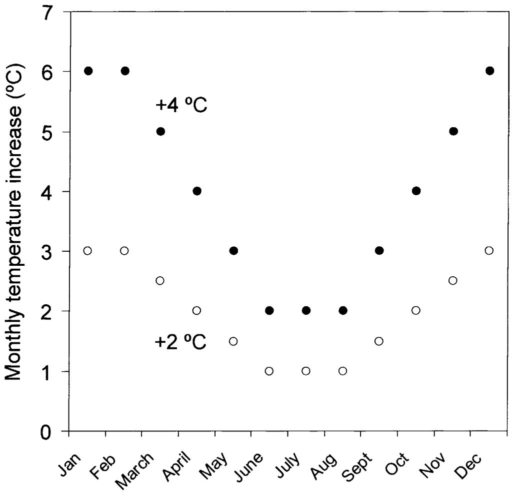

Fig. 1. Monthly temperature increase used in simulations in the +2 and +4 °C global warming scenario. Values shown were added to the measured monthly mean temperatures.

litterfall, and stand water balance. BIOMASS consists of a series of equations, some processes being described by a single equation, others by several. The equations are based on established theories of plant-physiological processes and soil-water dynamics. For a detailed description of the BIOMASS model, see McMurtrie et al. (1990). A boreal version of BIOMASS is described in Bergh et al. (1998), in which effects of frozen soils, post-winter recovery of photosynthetic capacity, frost-induced decline of photosynthetic capacity, and phenology pattern have been included.

The start of photosynthesis and recovery of the photosynthetic apparatus in spring, can be delayed and reduced by a frozen soil. The date of soil thawing is required as an input to BIOMASS, and can be obtained direct from soil measurements or by modelling soil thawing processes. The recovery of light-saturated photosynthesis and quantum yield is strongly temperature dependent (Pelkonen, 1980; Linder and Lohammar, 1981; Lundmark, 1996; Bergh, 1997) and the recovery is related to an accumulated day-degree sum in BIOMASS. Frost-nights and cold days with sub-zero temperatures can slow and even set back photosynthetic recovery. BIOMASS simulations of the post-winter recovery has been compared and validated against measured gas exchange data in the field (Wallin pers. communication). The autumn decline of photosynthetic capacity is reduced by severe frost-nights (Bamberg et al., 1966; Strand, 1995) and declines progressively after each successive frost until it is reduced below a "dormancy level", which is set at approximately 20% of potential capacity. The decline is irreversible until recovery occurs the following spring (for more detailed information concerning the boreal features in BIOMASS see Bergh et al. (1998)). The control of budburst in Norway spruce and Scots pine has been incorporated into BIOMASS as a sub-model. As recommended by Heide (1993a), the onset of budburst is determined by a thermal sum, which accumulates when daily mean air temperature exceeds 0 °C. The accumulation of the thermal sum can be slowed down and delayed by night frosts. This simplified approach to simulation of budburst, whereby the chilling requirement is not taken into account (Bergh et al., 1998), seems to be reasonably accurate in predicting budburst (Bergh, 1997).

2.4. Parameterisation of BIOMASS

Budburst for Norway spruce, Scots pine and black cottonwood were simulated with BIOMASS in current climate conditions (1994–1996) and then compared with budburst in field for the three consecutive years. Simulated date of budburst corresponded well with observed budburst and BIOMASS was used to predict budburst in the two scenarios with elevated temperature. The earlier budburst in the climatic-warming scenarios was included in BIOMASS, by changing parameters in the development of leaf area at the beginning of the growing season. The flush of leaves in beech has been reported by Heide (1993b) to be almost entirely determined by day-length, which is supported by field observations (Freeman, pers. commun.). Therefore no change was made for the flush of leaves in the two temperature scenarios.

Earlier soil thawing, as an effect of increased air temperatures, was either estimated from simulations of soil thawing using the SOIL model (Jansson and Halldin, 1980) or from records of soil-temperature data in the field. An earlier soil thawing by 2 and 4 weeks were used, for Norway spruce, Scots pine and black cottonwood, in BIOMASS for the +2 and +4 °C scenario, respectively. No changes in earlier soil thawing were made for beech in Denmark, since soil is usually unfrozen long before budburst with present climate conditions.

The optimum temperature for net photosynthesis in evergreen conifers growing in cold climates has been reported to be ca. 15 °C (Tranquillini, 1959; Vorwinckel et al., 1975; Teskey et al., 1984, 1994), which agrees well with the observed temperature response for Norway spruce at the site in northern Sweden (Bergh, 1997). An optimum temperature for net photosynthesis of 18 °C (Kellomäki, pers. commun.) was used for the sites with Scots pine, while it was considerably higher for beech and black cottonwood, 24 (Freeman, 1998) and 22 °C (Sigurdsson, 2001a), respectively.

Parameters related to phenology, gas exchange, stand and tree characteristics were derived from direct measurements and a number of studies performed at each specific site: Flakaliden (Linder and Flower-Ellis, 1992; Flower-Ellis, 1993; Linder, 1995; Stockfors, 1997; Bergh, 1997; Roberntz, 1998), Mekrijärvi (Wang et al., 1996; Wang and Kellomäki, 1997; Laitinen et al., 2000; Kellomäki, pers. commun.); Gunnarsholt (Sigurdsson, 2001a; Sigurdsson, pers. commun.) and Gribskov (Freeman, 1998; Freeman, pers. commun.). In the simulations of the three sites with Scots pine (Mekrijärvi, Aamli and Jädraås), we have used parameters from studies at Mekrijärvi, but with local climate data for each site. For a more detailed list of essential stand, tree and model specific parameters used in the simulations, see Appendix A.

3. Results

3.1. Simulated change in NPP for the coniferous species

BIOMASS predicted budburst for Scots pine and Norway spruce to occur approximately 2 and 5 weeks earlier in the +2 and +4 °C scenario, respectively. The between-year variation ranged from 5 to 20 days for the +2 °C and 16–46 days for the +4 °C scenario. Results of the annual course of ΔNPP of the Norway spruce stand in northern Sweden (Flakaliden) for elevated CO_2 and +4 °C scenario, are shown in Fig. 2. Elevated temperature increased ΔNPP mainly in spring, while elevated CO_2 increased ΔNPP in summer. This general pattern of the annual course of ΔNPP is valid for all coniferous stands. The large increase of ΔNPP in Norway spruce in spring by 14 and 31% (Fig. 3a and b) for the +2 and +4 °C scenario, respectively, was mainly caused by the earlier and more rapid recovery of the photosynthetic capacity. Earlier date of soil thawing made it possible for the recovery of the photosynthetic capacity to begin earlier in spring. Earlier budburst for Norway spruce in the temperature scenarios had only a minor effect on ΔNPP, by 1–2%. Increased temperature delayed the first frost-nights in autumn and reduced their frequency and severity. This resulted in a later

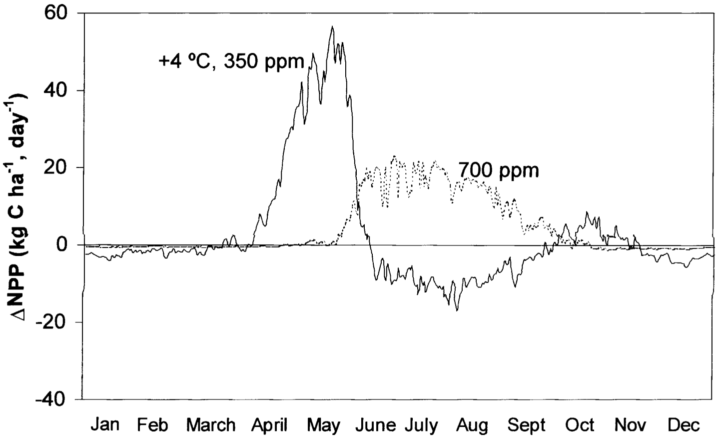

Fig. 2. The effect of global change, in relation to current climate, on the seasonal course of NPP of Norway spruce at Flakaliden. Simulations were performed with the boreal version of BIOMASS and the scenarios were: elevated CO_2 (dotted line) and +4 °C scenario at ambient CO_2 (solid line), respectively. For further explanations, see text.

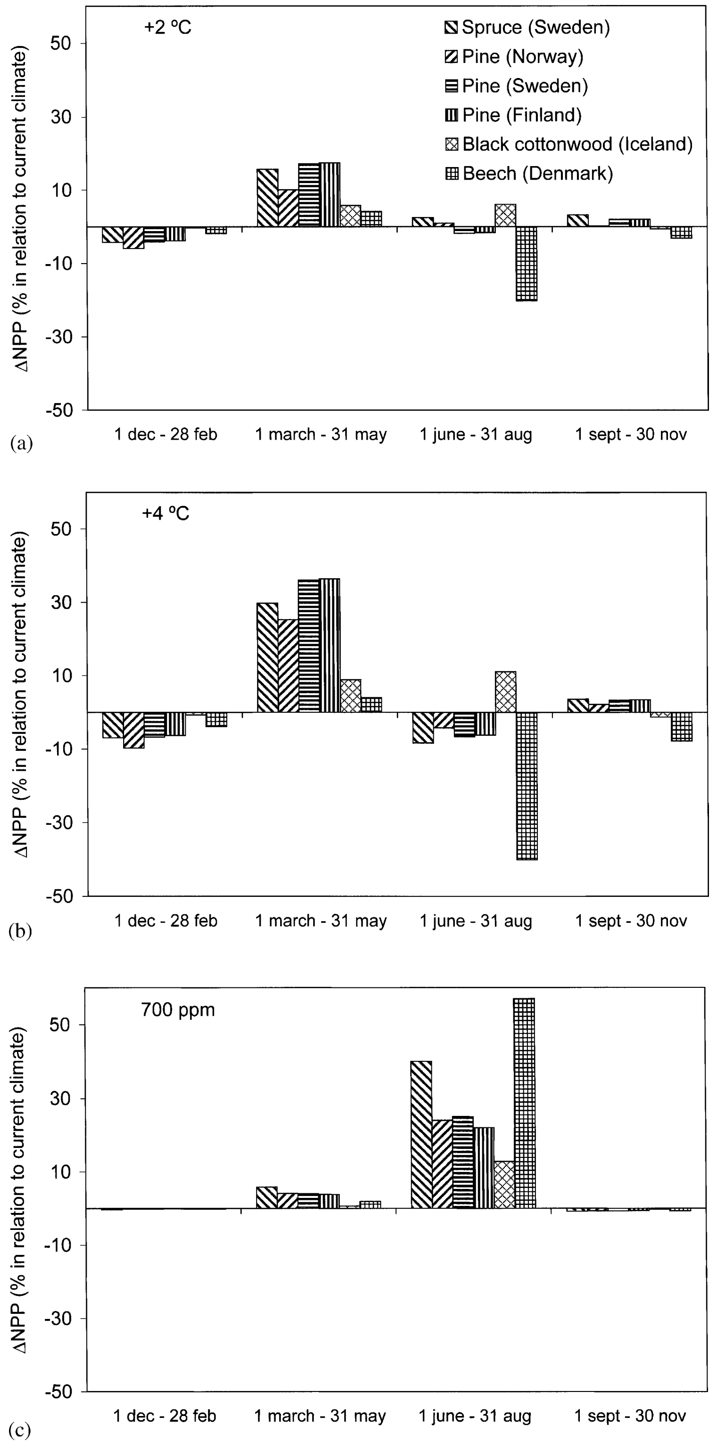

Fig. 3. The effect of global change, in relation to current climate, on the seasonal course of NPP for the six different Nordic sites. Simulations were performed with the boreal version of BIOMASS and the scenarios were: (a) +2 °C; (b) +4 °C; (c) elevated CO_2 (700 ppm). For further explanations, see text.

and slower decline of photosynthetic capacity and increased ΔNPP by 3–4% during autumn. The moderate effect on ΔNPP is largely explained by the low light intensities in October and November.

The +2 and +4 °C scenario caused also an increase in rates of respiration of the various tree components throughout the year. Increased respiration resulted in a reduction in ΔNPP during late autumn, winter, early spring and during summer (Fig. 2). Increased respiration was counterbalanced by increased photosynthetic rates in late spring and early autumn. The decrease of ΔNPP in summer was not only caused by increased respiration, but also by temperatures being supra-optimal for photosynthesis. The scenario with elevated CO_2 increased rates of photosynthesis by more than 40% in late spring and summer (Fig. 3c), caused by enhanced carboxylation efficiency (the leaf protein Rubisco, is more efficient as a carboxylase). The very small decrease of ΔNPP in autumn, winter and early spring was an effect of increased respiration caused by increased biomass production in summer. Elevated CO_2 combined with the +4 °C scenario gave a large increase in NPP by 75% (Table 2).

The seasonal course of ΔNPP and the underlying processes behind the temperature and CO_2 effect, was similar for Scots pine in Norway, central Sweden and Finland. The effect of +2 and +4 °C scenarios on ΔNPP during spring was, for the Norwegian site (Aamli) with a maritime climate, 11 and 24%, respectively (Fig. 3a and b). The effect of +2 and +4 °C scenarios was more pronounced by 18 and 37% in Finland (Mekrijärvi) and 17 and 36% in central Sweden (Jädraås). In the reference simulations with current climate the maritime climate in Norway gave a much earlier start of the recovery of the photosynthetic capacity (March) compared with the continental climate in Finland and Sweden (April–May). Elevated temperature with an earlier start of recovery results therefore in a larger gain in photosynthesis and ΔNPP if it occurs in April–May, instead of March, since light intensities are much higher in late spring. An earlier budburst in the temperature scenarios increased ΔNPP by 3–5% for Scots pine. Elevated CO_2 increased photosynthesis and ΔNPP by 25–28% (Fig. 3c) in summer. The increase in NPP as an effect of both elevated CO_2 and the temperature scenarios varied from 34 to 62% (Table 2) for the Scots pine sites in Norway, Finland, and central Sweden.

3.2. Simulated change for deciduous species

The predicted start for leaf development in spring for black cottonwood was approximately 7 and 22 days earlier in the +2 and +4 °C scenario, which is similar to the observed interannual variation in budburst at the site (Sigurdsson, 2001b). The course of ΔNPP in spring for the two temperature scenarios was similar for the black cottonwood stand in Iceland (Gunnarsholt), compared with the coniferous stands. The increase of photosynthesis and ΔNPP by 6–9% (Fig. 3a and b), originated though from an earlier and a more rapid leaf development in spring instead of an earlier and more rapid recovery. The temperature scenarios increased rates of photosynthesis and ΔNPP

Table 2
Predicted changes in NPP (kg C ha^{-1} a^{-1}), for each site and for a 3-year period (1994–1996), using two different temperature scenarios (+2 °C, +4 °C) at a CO_2-concentration of 350 and 700 ppm[a]

	Site (country) [species]					
	Flakaliden (Sweden) [*P. abies*]	Mekrijärvi (Finland) [*P. sylvestris*]	Jädraås (Sweden) [*P. sylvestris*]	Aamli (Norway) [*P. sylvestris*]	Gunnarsholt (Iceland) [*P. trichocarpa*]	Gribskov (Denmark) [*F. sylvatica*]
Scenarios						
Reference NPP	2677 (100)	5004 (100)	5718 (100)	6185 (100)	1612 (100)	3331 (100)
+2	2953 (110)	5693 (114)	6458 (113)	6492 (105)	1786 (111)	2631 (79.0)
+4	3218 (120)	6364 (127)	7233 (126)	7078 (114)	1898 (118)	1740 (52.2)
700 ppm	4249 (140)	6249 (125)	7343 (128)	7863 (127)	1822 (113)	5247 (158)
+2, 700 ppm	4721 (157)	7136 (143)	8267 (145)	8299 (134)	2032 (126)	4552 (137)
+4, 700 ppm	5182 (175)	8000 (160)	9282 (162)	9072 (147)	2178 (135)	3658 (110)

[a] The changes (%), in relation to the reference simulations (current climate), are given within brackets.

by 11% in summer, since temperatures are normally well below optimal for photosynthesis in reference simulations with current climate (Sigurdsson, 2001a). This increase of ΔNPP in summer is in contrast to all other sites and species. Increased temperature increased respiration and therefore reduced ΔNPP in late autumn, winter and early spring. Elevated CO_2 enhanced photosynthesis and increased ΔNPP by 14% for the black cottonwood stand (Fig. 3c), as a result of increased carboxylation efficiency during the growing season. The combined effect of elevated CO_2 and the +4 °C scenario caused an increase in NPP by 35% (Table 2).

Elevated temperature had no effect on the start of leaf development in beech in spring, but caused a faster leaf development. This had a minor positive effect on photosynthesis and ΔNPP in spring by 4–6% (Fig. 3a and b). The +2 and +4 °C scenario caused a major reduction on ΔNPP in summer for the beech stand in Denmark (Gribskov) by 16–43%. The large reduction in ΔNPP was mainly an effect of an enhanced demand of water, which lowered photosynthetic rates in summer. The reduction in ΔNPP was also an effect of increased respiration rates. Elevated CO_2 had a large positive effect on photosynthesis and ΔNPP increased with 58% (Fig. 3c). The large effect on photosynthesis can be ascribed, besides the increased carboxylation efficiency, by increased water use efficiency, which lowered water demand in summer. The combination of elevated CO_2 and the +4 °C scenario increased NPP for beech by 10% (Table 2).

4. Discussion

In the Nordic countries, elevated temperature would most likely lead to earlier and more rapid recovery of photosynthetic capacity in spring and a prolonged photosynthetic active season in autumn for both Norway spruce and Scots pine and was demonstrated in this study by model simulations. This extension of the growing season is likely to increase the potential carbon gain and growth of the cold-temperate and boreal coniferous forests (Bergh, 1997; Zheng et al., 2002). Previous model simulations have also indicated that climatic change in terms of rising temperature can increase the yield of boreal Scots pine stands in Finland (Kellomäki and Kolström, 1993). The enhanced production was more pronounced in northern Finland (Kellomäki et al., 1988), where the increase in dry mass production was ca 30%, compared to ca 15% in the southern Finland. Experiments with elevated temperature in whole-tree chambers with Scots pine in Finland has also shown that a temperature increase of +4–5 °C resulted in 4–8 weeks earlier budburst (Hänninen, 1995). Simulation results for Scots pine for the three different sites in Finland, Norway and central Sweden, indicate that the response of elevated temperature is less in a milder maritime climate (5–14% in Norway), where the current mean temperature rises above 0 °C in February–March, compared with a colder continental (13–27% in Finland and central Sweden).

In this simulation exercise the deciduous species were less responsive to elevated temperature, compared to the coniferous species. The gain in NPP for black cottonwood, as an effect of elevated temperature, originated from earlier leaf flush and more rapid leaf development in spring, but was also an effect of the air temperatures, which came closer to the temperature optimum for photosynthesis in the two temperature scenarios. Most deciduous species would respond in a similar way to elevated temperature as black cottonwood with earlier leaf development. The leaf flush for beech, however, seems to be more closely related to day-length (Heide, 1993b) and the date of leaf flush for beech would therefore only change marginally with elevated temperatures. Milder winters and warmer spring are likely to cause earlier budburst (Cannell and Smith, 1986; Murray et al., 1989). Earlier budburst could increase the risk of frost injury, unless the incidence of frost periods in spring changes (Cannell, 1985, 1989; Hänninen, 1991). The magnitude of this risk can be debated, because climatic warming could also reduce the risk of late frosts as spring progresses (Kramer, 1994).

The temperature optimum for light-saturated photosynthesis was set in the simulations to 15 °C for Norway spruce, 18 °C for Scots pine, 22 and 24 °C for black cottonwood and beech, respectively. To some extent, the optimum can be acclimated to seasonal changes in temperature (Nielson et al., 1972; Strain et al., 1976) as indicated in Fig. 4. However, a seasonal adjustment does not always occur (Vorwinckel et al., 1975; Teskey et al., 1994). A seasonal adjustment of temperature optimum, however, is not included in these

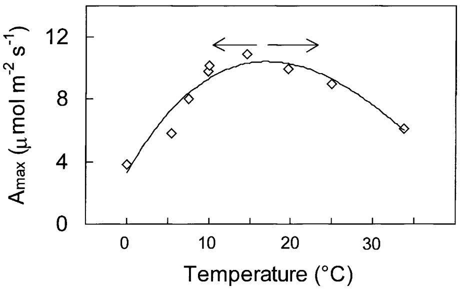

Fig. 4. Temperature response of light-saturated rates of net photosynthesis in current shoots of Norway spruce (after Bergh, 1997). Arrows indicate seasonal changes in temperature optimum for photosynthesis. For further explanations, see text.

simulations and might have introduced minor errors into the results of NPP.

The +2 and +4 °C scenario increased rates of respiration of the various tree components throughout the year for all sites and species, which agrees with earlier reports (e.g. Penning de Vries, 1972; Ryan et al., 1994; Stockfors, 1997). Plant maintenance respiration is largely an exponential function of temperature (Ryan et al., 1994) and the 'losses' of ΔNPP is logically the largest in summer when air temperatures reach their peak values. The relative increase of respiration was higher in winter, for the +2 and +4 °C scenario, in a maritime climate compared to continental. This was likely caused by the milder winters in a maritime climate compared with a colder continental climate, since an elevation, i.e. from −2 to +4 °C ($\Delta + 6$ °C) in winter (maritime) gives a more substantial increase in respiration rates, compared with an elevation from −10 to −4 °C (continental). The +2 and +4 °C scenario gave also higher respiration rates in relative numbers for Gribskov in Denmark, with higher prevailing temperatures in summer compared with the other sites.

Elevated temperature leads to increased evapo-transpiration and the demand of water increases. This was evident for the simulations of the beech site in Denmark, where the water deficit reduced NPP by more than 40%. The demand of water is normally larger than the surplus, through rainfall, during the growing season in Denmark and southeastern Sweden. If global warming is not followed by increased rainfall, water could limit growth to larger extent than today in primarily cold-temperate but also boreal forest ecosystems.

Elevated CO_2 alone increased NPP for the coniferous species in Finland, Sweden and Norway by 25–40%. Similar findings of the effect of elevated CO_2, through enhanced carboxylation efficiency and increased photosynthesis, was found in studies of Norway spruce at Flakaliden (Roberntz, 1998; Roberntz and Stockfors, 1998) and in studies of Scots pine at Mekrijärvi in Finland (Wang et al., 1996; Laitinen et al., 2000). Elevated CO_2 increased photosynthesis and NPP by 58% for the beech site in Denmark. This large increase was caused by enhanced carboxylation efficiency, but also by the improved water use efficiency (Freeman, 1998), since water limits photosynthesis for this stand.

Photosynthetic capacity has in some experiments been acclimated to long-term CO_2 enrichment. The reason to this "down-regulation" of photosynthesis is still debated, but the phenomenon is more common in experiments, where nutrient availability is limiting growth (Curtis, 1996). Long-term experiments (3–5 years) with CO_2 enrichment in branch bags, conducted at Flakaliden, Mekrijärvi, Gunnarsholt and Gribskov, showed no down-regulation of A_{sat} (light-saturated photosynthesis) and the photosynthetic rates were ca 49–114% higher at elevated CO_2 (700 ppm) compared to ambient. At Gunnarsholt, however, whole trees were treated with and without elevated CO_2 and growing at high and low nutrient availability (Sigurdsson et al., 2001). Those trees were harvested and the relative growth rate of trees treated with elevated CO_2 was significantly higher only when nutrient availability was high. This was explained by nutrient-driven change in allocation patterns and leaf phenology when nutrient availability was too low to meet increased demand in elevated CO_2 (Sigurdsson et al., 2001; Sigurdsson, 2001b).

An increase in carbon gain and growth of trees leads to increased demand of nutrients. The increased demand must be met by increased mineralisation, nutrient availability and uptake by roots, otherwise will the growth response to elevated temperature and CO_2 stagnate at a lower level (Bonan and van Cleve, 1991; Melillo et al., 1993; Houghton et al., 1998; Medlyn et al., 2000; McMurtrie et al., 2001), compared with the simulation results and CO_2 enrichment studies in the Nordic countries. An increased mineralisation and nutrient availability, however, has been found in several studies with elevated temperature

(Van Cleve et al., 1990; Peterjohn et al., 1994; Lückewille and Wright, 1997; Jarvis and Linder, 2000). However, no feed-back mechanism on mineralisation and soil nutrient dynamics is included in the BIOMASS model.

5. Conclusions

The start of the recovery of photosynthetic capacity and the length of the recovery period in spring for coniferous stands are very sensitive to increased temperature. Simulations showed an increase of NPP in spring for Scots pine and Norway spruce by 24–37% for the +4 °C scenario. Earlier bud burst and sub-optimal temperature for photosynthesis contributed to this increase, but to a minor extent compared with the spring recovery. The simulation study also gives significant differences in terms of NPP for Scots pine, comparing a continental climate with a maritime, where a continental climate is more favoured by increased temperature.

In Iceland black cottonwood responded to elevated temperature by earlier and more rapid development of leaf area in spring, while beech in Denmark gave only a more rapid leaf area development. Beech is not favoured by increased temperature in spring to same extent as other deciduous species. The effect of CO_2, however, was more pronounced for the beech stand in Denmark, since elevated CO_2 improved water use efficiency drastically for the water limited stand. Those areas with a substantial water deficit in summer might be more favoured by elevated CO_2 than others.

It is important to quantify the magnitude and durability of the nutrient effects in field studies, for estimation of the combined effect of increased temperature, CO_2-concentration, and nutrient availability. To achieve more realistic predictions from models of long-term responses of cold-temperate and boreal forests to elevated temperature and CO_2, a combination of low-temperature effects and soil nutrient feed-back mechanisms are needed. Without these processes, simulations will lead to biased estimates of carbon gain and unrealistic predictions of the effects of climatic change in boreal forest ecosystems.

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Appendix A

Parameters used in the simulations of annual NPP in both coniferous and deciduous stand, growing in five different Nordic countries. All rates of photosynthesis and foliage respiration are expressed per unit projected leaf area, and amounts of biomass in terms of dry mass per unit ground area. Parameters are derived for Scots pine (Aamli, Jädraås, Mekrijärvi) from Wang et al. (1996), Wang and Kellomäki (1997), Laitinen et al. (2000) and Kellomäki (pers. commun.); Norway spruce (Flakaliden) from Linder and Flower-Ellis (1992), Flower-Ellis (1993), Linder (1995), Stockfors (1997), Bergh (1997) and Roberntz (1998); black cottonwood (Gunnarsholt) from Sigurdsson (2001a,b) and Sigurdsson (pers. commun.); European beech (Gribskov) from Freeman (1998) and Freeman (pers. commun.).

	Flakaliden (SE)	Aamli (NO), Jädraås (SE), Mekrijärvi (FIN)	Gunnarsholt (IS)	Gribskov (DK)
Canopy and soil characteristics				
Specific leaf area (projected) of foliage in the upper canopy ($m^2\,kg^{-1}$)	2.52	2.80	11.1	15.5
Specific leaf area (projected) of foliage in the mid-canopy ($m^2\,kg^{-1}$)	3.20	3.00	12.6	15.5
Specific leaf area (projected) of foliage in the lower canopy ($m^2\,kg^{-1}$)	3.43	3.10	14.4	15.5
Green height at the start of the simulation (m)	3.80	2.70	0.33	6.0
Number of branches per tree	68	24	9	120
Fraction of foliage dry mass in top third of canopy height (%)	20	19	29	30
Fraction of foliage dry mass in middle third of canopy height (%)	30	55	47	60
Fraction of foliage dry mass in bottom third of canopy height (%)	50	26	24	10
Initial dry mass of foliage at the start of the simulation ($Mg\,ha^{-1}$)	5.99	0.93	0	0
Initial dry mass of stem at the start of the simulation ($Mg\,ha^{-1}$)	6.82	3.55	0.070	67.2
Initial dry mass of branches at the start of the simulation ($Mg\,ha^{-1}$)	3.11	1.02	0.13	34.6
Initial dry mass of roots at the start of the simulation ($Mg\,ha^{-1}$)	7.25	4.81	0.243	13.0
Assumed depth of rooting zone (mm)	0.55	0.90	0.55	1.00
Soil water storage (mm)	173	81	350	250
Photosynthesis and respiration				
V_{cmax} in the upper canopy	23.5	37	41.2	110.5
V_{cmax} in the mid-canopy	23.5	37	41.2	110.5
V_{cmax} in the lower canopy	21.2	37	30.9	82.9
J_{max} in the upper canopy	76.1	67	92.8	189.6
J_{max} in the mid-canopy	76.1	67	92.8	189.6
J_{max} in the lower canopy	68.4	67	69.6	142.2
V_{cmax} temperature function coefficients				
First order	−0.017	0.042	0.073	0.0334
Second order	−0.0027	−0.00025	−0.0035	−0.0025
Third order	−0.00004	−0.0002	0	−0.0000881
J_{max} temperature function coefficients				
First order	−0.017	0.0223	0.073	0.00424
Second order	−0.0027	−0.0035	−0.0035	−0.00352
Third order	−0.00004	−0.0001	0	−0.0000867
Maximum stomatal conductance ($mol\,m^{-2}\,s^{-1}$)	0.165	0.17	0.75	0.30
Temperature optimum for photosynthesis (°C)	15	18	22	24
Temperature lower limit for positive photosynthesis (°C)	−3	−3	5	5

Appendix A. (*Continued*)

	Flakaliden (SE)	Aamli (NO), Jädraås (SE), Mekrijärvi (FIN)	Gunnarsholt (IS)	Gribskov (DK)
Temperature upper limit for positive photosynthesis (°C)	43	43	45	35
Foliage Q_{10} for temperature dependence of foliar maintenance respiration	2.3	2.0	3.38	2.2
Stem Q_{10} for temperature dependence of stem maintenance respiration	2.3	2.0	2.5	2.2
Branch Q_{10} for temperature dependence of branch maintenance respiration	2.3	2.0	2.5	2.2
Root Q_{10} for temperature dependence of root maintenance respiration	2.3	2.0	3.07	2.2
Foliar maintenance respiration rate at 0 °C (μmol m^{-2} (projected area) s^{-1})	0.18	0.1	0.16	0.13
Stem maintenance respiration rate at 0 °C (μmol m^{-2} (surface area) s^{-1})	0.19	0.1	0.05	0.04
Branch maintenance respiration rate at 0 °C (μmol m^{-2} (surface area) s^{-1})	0.19	0.1	0.05	0.04
Root maintenance respiration rate at 0 °C (kg C Mg^{-1} (dry mass) per day)	0.40	0.13	0.154	0.16
Parameters related to boreal features				
Day-degree sum required for full photosynthetic recovery	150	150		
Level of photosynthetic capacity at the start of spring (%)	15	15		
Maximum reduction in day-degree sum after a severe spring frost event (%)	30	30		
Maximum reduction in photosynthesis after an autumn frost event (%)	10	10		
Mean daily temperature below which stomatal closure begins (°C)	0	0		
Mean daily temperature below which stomata are fully closed (°C)	−1	−1		
Minimum daily temperature below which stomatal closure begins (°C)	0	0		
Minimum daily temperature below which stomata are fully closed (°C)	−2	−2		

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