MODELLING REGIONAL CLIMATE CHANGE EFFECTS ON POTENTIAL NATURAL ECOSYSTEMS IN SWEDEN

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Abstract. This study aims to demonstrate the potential of a process-based regional ecosystem model, LPJ-GUESS, driven by climate scenarios generated by a regional climate model system (RCM) to generate predictions useful for assessing effects of climatic and CO_2 change on the key ecosystem services of carbon uptake and storage. Scenarios compatible with the A2 and B2 greenhouse gas emission scenarios of the Special Report on Emission Scenarios (SRES) and with boundary conditions from two general circulation models (GCMs) – HadAM3H and ECHAM4/OPYC3 – were used in simulations to explore changes in tree species distributions, vegetation structure, productivity and ecosystem carbon stocks for the late 21st Century, thus accommodating a proportion of the GCM-based and emissions-based uncertainty in future climate development. The simulations represented in this study were of the potential natural vegetation ignoring direct anthropogenic effects. Results suggest that shifts in climatic zones may lead to changes in species distribution and community composition among seven major tree species of natural Swedish forests. All four climate scenarios were associated with an extension of the boreal forest treeline with respect to altitude and latitude. In the boreal and boreo-nemoral zones, the dominance of Norway spruce and to a lesser extent Scots pine was reduced in favour of deciduous broadleaved tree species. The model also predicted substantial increases in vegetation net primary productivity (NPP), especially in central Sweden. Expansion of forest cover and increased local biomass enhanced the net carbon sink over central and northern Sweden, despite increased carbon release through decomposition processes in the soil. In southern Sweden, reduced growing season soil moisture levels counterbalanced the positive effects of a longer growing season and increased carbon supply on NPP, with the result that many areas were converted from a sink to a source of carbon by the late 21st century. The economy-oriented A2 emission scenario would lead to higher NPP and stronger carbon sinks according to the simulations than the environment-oriented B2 scenario.

1. Introduction

Terrestrial ecosystems, particularly forests, provide a variety of essential goods and services to humankind (Costanza et al., 1997; Daily, 1997; Daily et al., 1997; Drake et al., 1997). For example, they supply timber, fuel and food, regulate the climate, contribute to soil and water quality, maintain biodiversity, and provide opportunities for recreational and cultural activities (Ewel et al., 1998; Alcamo et al., 2003). The role of ecosystems in regional and global carbon balance has received particular attention, and carbon budgeting of all major ecosystems types

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is expected to become a legally binding commitment of Annex I countries to the Kyoto Protocol. Climate changes and higher levels of atmospheric CO_2 in the coming century (IPCC, 2001a), are likely to cause changes in ecosystems, and this will affect the goods and services they provide to society (Melillo, 1999; IPCC, 2001b). Advance notice of likely effects is desirable, both to enable planning and the development of adaptive strategies. Provision of useful projections will require climate change scenarios and simulation models encapsulating relevant ecosystem properties and their responses to changes in climate and other associated drivers of ecosystem processes, such as atmospheric CO_2 concentrations (IPCC, 1996). To be useful for planning, projections must be delivered at policy-relevant spatial scales, typically scales at which differences between countries, counties, municipalities or other administrative regions can be resolved (Nijkamp, 1999).

Dynamic global vegetation models (DGVMs) have been used to simulate biogeochemical cycling, particularly carbon cycles, and vegetation dynamics under climate change at continental-global scales (Cramer et al., 2001; Bachelet et al., 2003). DGVMs incorporate more-or-less mechanistic representations of key ecosystem processes, and may therefore remain valid even when applied to the novel climatic conditions of the future (Cramer et al., 2001; Bachelet et al., 2003). However, as DGVMs are intended to be applicable primarily at the global scale, they incorporate rather simplified representations of vegetation and vegetation dynamic processes (Smith et al., 2001) and cannot, for example, resolve landscape-scale heterogeneity in vegetation type, structure or development stage, nor distinguish individual tree species. This would restrict their utility in regional studies. Here we apply a model similar to a DGVM in its treatment of physiological and biogeochemical ecosystem processes but with more detailed representations of vegetation and its dynamics, similar to "gap" models (Bugmann, 2001). The model is capable of providing the spatial, temporal and biological detail necessary to generate output of value to stakeholders such as regional and national land-use planning agencies.

Studies of climate change impacts on ecosystems are typically based on climate scenarios generated by general circulation models (GCMs), operating on resolutions in the order of 200–300 km, which are coarse in comparison to the scales of interest in regional studies. In addition, coarse GCM grids may omit physiographic detail which significantly affect climate in the region of interest, e.g. the Baltic Sea, Fenno-Scandian mountain range, and river and lake systems in Scandinavia (Mearns et al., 2001). Regional climate models (RCMs) attempt to overcome these shortcomings, providing greater spatial detail, and taking regional physiography into account, e.g., by dynamical downscaling of GCM output (McGregor, 1997).

The aim of this study is to demonstrate the potential of process-based regional ecosystem models driven by RCM-generated climate scenarios as an approach to assessing effects of future climate and CO_2 change on ecosystem goods and services at the regional scale. We apply a process-based regional ecosystem model to explore changes in vegetation dynamics and ecosystem carbon cycling under a number of alternative RCM scenarios for the late 21st century. Our study area is Sweden, and our focus is on ecosystem capacity for carbon storage and exchange. Sweden constitutes an interesting case study because a large proportion (c. 60%) of the country is covered by forest .(National Board of Forestry, 2003), an ecosystem type with a high carbon storage capacity and predominantly natural dynamics. Sweden spans a comparatively broad latitude range (c. 55–70° N) with vegetation zones ranging from cool temperate forest to boreal forest and alpine and subarctic tundra. Like other northerly regions, Sweden is projected to experience greater warming in the coming century than many lower-latitude regions (Cubasch et al., 2001).

2. Materials and Methods

2.1. ECOSYSTEM MODEL

We employed the LPJ-GUESS ecosystem modelling framework (Smith et al., 2001), which integrates the mechanistic representations of plant physiological and biogeochemical processes of Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ-DGVM) (Sitch et al., 2003) with detailed representations of vegetation dynamic processes, similar to forest gap models such as FORSKA (Leemans and Prentice, 1989; Prentice et al., 1993). The model simulates the growth of individual trees on a number of replicate patches, corresponding in size approximately to the area of influence of one large adult tree on its neighbours. Herbaceous vegetation is also represented, but individuals are not distinguished. Dynamic changes in individual size and form influence the resource uptake and growth of neighbours. Photosynthesis and carbon allocation to leaves, fine roots and sapwood are modelled on an individual basis. Height and diameter growth are regulated by carbon allocation, conversion of sapwood to heartwood, and a set of prescribed allometric relationships. The biological units simulated may be plant functional types (PFTs; e.g., boreal needle leaved tree, C_3 grass) or species. In the present study the model was configured to simulate the major Swedish forest tree species and a generic herbaceous PFT (C_3 grass). Litter and soil organic matter (SOM) carbon dynamics (three pools) follow first-order kinetics and are sensitive to temperature and soil water. Leaf and root turnover and plant mortality replenish the litter pool. Climate changes influence plant growth in LPJ-GUESS via temperature effects on the kinetics of photosynthesis and maintenance respiration, the influence of soil water content on stomatal conductance and photosynthesis, and changes in phenology, e.g., in association with an increased growing-season heat sum. Increased atmospheric CO_2 concentrations result in biochemical stimulation of photosynthesis (in C_3 plants), and can lead to improved water relations due to enhanced water use efficiency (WUE) (Drake et al., 1997). A full description of LPJ-GUESS is given by Smith et al. (2001). Further details of the physiological, biophysical and biogeochemical components of the model are given by Sitch et al. (2003). The version used in this study includes improved representations of soil hydrology, snow pack dynamics and soil-vegetation-atmosphere exchange of water, as documented by Gerten et al. (2004).

Modelled PFT/species compositions, biomass and distributions have been tested against data in a number of studies. Badeck et al. (2001) showed that the model simulated correctly the dominant PFT at five European pristine forests sites. It also predicted correctly the PFT composition of observed natural vegetation at various sites across Europe (Smith et al., 2001). Hickler et al. (2004) successfully simulated vegetation dynamics, tree species composition and biomass at three sites in the U.S. Great Lakes region. The model has also been validated with respect to seasonal and interannual variation in carbon and water vapour fluxes at 15 forest sites across Europe (Morales et al., In press) and by comparison to regional forest inventories (Koca et al., unpublished). The closely-related model LPJ-DGVM has also been subjected to extensive validation, particularly with respect to spatial (Lucht et al., 2002; Sitch et al., 2003) and temporal (Heimann et al., 1998; Sitch et al., 2003) variation in ecosystem carbon balance.

The model was applied over a window covering the entire landmass of Sweden at a resolution of 0.5° longitude and latitude. Ecosystem properties in each grid cell were taken as the average over 100 patches of 0.1 ha area, representing random samples of the overall vegetation of the grid cell. A disturbance regime with an average return time of 100 years – the approximate average for natural disturbances in Sweden (Zackrisson, 1977) – was prescribed. The main output variables of interest were gridded values of biomass (ecosystem total and by tree species), ecosystem annual net primary production (NPP), and annual net ecosystem carbon exchange (NEE). In this study, the simulations represent the potential natural vegetation that would exist in equilibrium under changing climate and site conditions with natural disturbances. Direct human intervention (i.e. land use and silvicultural management practices), and the impacts of air pollution and deposition from neighbouring countries were not included in the simulations.

2.2. TREE SPECIES PARAMETERISATION

Assignment of species-specific parameters for trees followed the approach of Hickler et al. (2004). Seven of the most important native tree species of Swedish forests were distinguished, namely *Picea abies* (Norway spruce), *Pinus sylvestris* (Scots pine), *Betula pendula* (silver birch), *Betula pubescens ssp. czerepanovii (=tortuosa)* (mountain birch), *Fagus sylvatica* (beech), *Quercus* spp. (oak), and *Tilia cordata* (lime) (nomenclature follows Tutin et al. (1964–1980)).

For parameters concerning the physiology and life-history of species (Fulton, 1991; Haxeltine and Prentice, 1996; Smith et al., 2001; Sitch et al., 2003; Gerten et al., 2004; Hickler et al., 2004) generic values for the corresponding plant functional types (trees versus grasses; gymnosperms versus angiosperms; boreal versus temperate trees; trees of differing shade-tolerance class) were used. Bioclimatic limits for establishment or survival (Skre, 1972; Prentice and Helmisaari, 1991; Sykes et al., 1996; Bradshaw et al., 2000) and maximum non-stressed longevity (Prentice and Helmisaari, 1991; Bugmann, 1994) were specified for each tree species (Table I).

2.3. CLIMATE AND CO_2 DATA

Monthly climatology (temperature, precipitation and cloudiness), annual atmospheric CO_2 concentration, and soil type – derived from the FAO global soil data set (FAO, 1991) – were used as input data to drive the model.

The CRU05 global dataset of monthly surface climate (temperature, precipitation, cloudiness) extending from 1901 to 1998 (New et al., 2000) was used for the historical time period of the simulations. A time-series comprising the first 30 years of data (1901–1930), detrended in the case of temperature, was used repeatedly for the first 300 years of the simulations as a "spin up" period to allow the vegetation and soil+litter pools to come to equilibrium with the long-term climate. Equilibrium sizes of the two soil carbon pools (turnover times 33 and 1000 years, respectively, at 10 °C) were determined analytically, based on average litter inputs for the final years of the spin up.

Climate data for the period 1999–2100 were based on regional climate scenarios for the late 21st Century from the SWECLIM programme (Räisänen et al., 2003). These scenarios were generated by the regional climate modelling system RCAO, which comprises the RCA2 atmospheric model (Bringfelt et al., 2001) coupled to the three dimensional 11 km horizontal resolution Baltic Sea model RCO (Meier et al., 1999; Meier, 2002a, b) and the PROBE lake model (Ljungemyr et al., 1996). Boundary conditions for the RCM simulations are taken from global simulations with atmosphere-ocean general circulation models (AOGCMs). Scenarios based on two alternative AOGCMs, ECHAM4/OPYC3 and HadAM3H, were used in this study. In each case, scenarios consistent with both the A2 ("regional-economic") and B2 ("regional-environmental") greenhouse gas (GHG) emission scenarios of the IPCC Special Report on Emissions Scenarios (SRES) (Nakicenovic et al., 2000) were used, giving four scenarios in total (Table II). All four scenarios correspond to an overall increase in mean annual temperature and precipitation for the Swedish study area. More specifically, the A2 scenarios predict temperature increases of 3.6–4.5 °C, and an overall increase of 12–13% in annual mean precipitation. The B2 scenarios show generally similar trends as for A2, but with somewhat lower amplitude (Table I). All of the scenarios represent a slightly decreasing mean summer precipitation with a more pronounced decrease in the south and a slight increase in the north (Räisänen et al., 2003). These changes, both in annual average and seasonal climate, are consistent with the average trend for the north European region obtained from a suite of nine AOGCMs driven by SRES preliminary marker emission scenarios A2 and B2 (Giorgi et al., 2001), which also suggest that precipitation

TABLE I
Plant functional type and species parameters for simulations with the ecosystem model LPJ-GUESS

Parameter	Details					
Growth form	*Tree*			*Grass*		
min PAR flux for establishment (MJ m^{-2} day^{-1})	—			2.5		
fraction of roots in upper/lower soil layer	0.67/0.33			0.9/0.1		
Tree type	*Gymnosperm*			*Angiosperm*		
leaf phenology	evergreen			summergreen		
Min. canopy conductance (mm s^{-1})	0.3			0.5		
leaf area/sapwood area (m^2 cm^{-2})	2			4		
leaf turnover (yr^{-1})	0.5			1		
fine root turnover (yr^{-1})	0.5			1		
specific leaf area (cm^2 $[gC]^{-1}$)	220			410		
nopy interception parameter[1]	0.06			0.02		
Climate zone	*Boreal*			*Temperate*		
Optimal temperature range for photosynthesis (°C)	10–25			15–25		
Shade-tolerance class	*Intolerant*		*Intermediate*		*Tolerant*	
sapwood conversion (yr^{-1})	0.1		0.075		0.05	
growth efficiency threshold for stress mortality (kgC m^{-2} yr^{-1})	0.12		0.10		0.0001	
max establishment (saplings ha^{-1} yr^{-1})	2500		1875		1250	
Recruitment shape parameter[2]	10		6		3	
Tree taxon	*Spruce*	*Pine*	*Birch*[3]	*Beech*	*Oak*	*Lime*
Type	gymnosperm	gymnosperm	angiosperm	angiosperm	angiosperm	angiosperm
climate zone	boreal	boreal	boreal	temperate	temperate	temperate
shade-tolerance	tolerant	intermediate	intolerant	tolerant	intermediate	tolerant
max non-stressed longevity (yr)	900	760	220 / 300	430	1060	940
Min T_c for survival (°C)[4]	—	—	—	−18	−18	−18
Min T_c for reproduction (°C)	—	—	—	−3.5	−16	−18
Max T_c for reproduction (°C)	−2	−1	−/− 15.0	—	—	—
Min GDD_5 for reproduction[5]	600	500	700 / 150	990	1100	830

[1] in Gerten et al. (in press)

[2] α in Fulton (1991); larger values indicate greater suppression of establishment at low forest-floor NPP.

[3] lowland/mountain taxa or ecotypes

[4] T_c = mean temperature of coldest month

[5] annual growing degree days on 5°C base; $GDD_5 = \Sigma_d \max(T_d - 5, 0)$; T_d = mean temperature of Julian day d (1–365) (°C).

TABLE II

Predicted changes in mean annual temperature and precipitation in Sweden by 2071–2100 compared with 1961–1990, according to four regional climate scenarios (RCAO forced by ECHAM4/OPYC and HadAM3H, for SRES A2 and B2 greenhouse-gas emission scenarios; see text)

	Temperature (°C)		Precipitation (%)	
A2	B2	A2	B2	
ECHAM4 + RCAO	4.5	3.5	23	17
HadAM3H + RCAO	3.6	2.5	12	8

Source: (SWECLIM, 2003)

will increase in northern mid-latitude regions under both SRES scenarios in winter, and slightly decrease in the summer months.

For each scenario, monthly climate values were available for a 30-year control period (1961–1990) in addition to the 30-year scenario period (2071–2100). Anomalies calculated from the difference between observed data and RCM-generated data for the 30-year control run were applied (added) to the scenario data to provide model input for the scenario period. Temperature and precipitation data for the period between the end of the historical record in 1998 and the beginning of the scenario period in 2071 were derived by interpolation between means for the final 30 years of the historical data and the scenario, superimposing on this the detrended interannual variability for the last 30 years of the historical record. For cloudiness data, the final 30 years of CRU historical data were repeated until the end of the simulation.

Global atmospheric CO_2 concentrations derived from ice-core measurements and atmospheric observations (c.f., Sitch et al., 2003) were used for the historical period of the ecosystem model simulations. For the first 300 years of the simulations the 1901 value of 296 ppmv was used. CO_2 concentrations projected by the 'reference' version of Bern Carbon Cycle Model (Joos et al., 2001) and compatible with the SRES A2 and B2 scenarios were used in conjunction with the corresponding RCM climate scenarios the period of 1999–2100. These concentrations amount to 836 ppmv by year 2100 under the A2 scenario and 611 ppmv under the B2 scenario.

3. Results

3.1. POTENTIAL NATURAL VEGETATION

Under modern climate [throughout this paper "modern climate" denotes mean climatic and atmospheric CO_2 conditions for the period 1969–1998] LPJ-GUESS correctly estimated that Norway spruce and Scots pine were the most widespread species over Sweden and achieved the highest biomass in boreal and boreo-nemoral regions (Figure 1). Deciduous broadleaved tree species occurred in all forest areas,

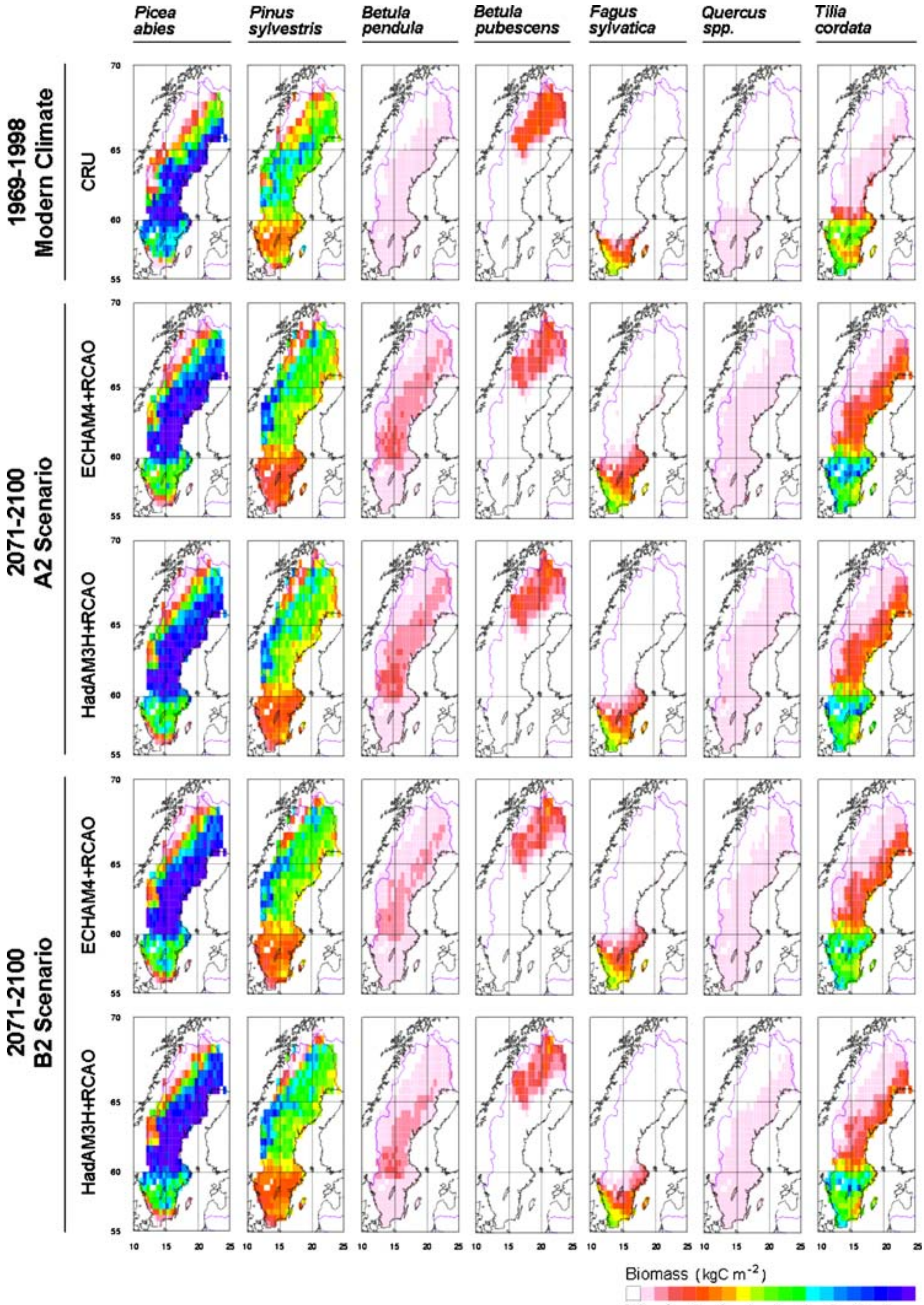

Figure 1. Biomass distributions of major tree species in Sweden according to simulations of potential natural vegetation with LPJ-GUESS under the modern climate (1969–1998) and four regional climate scenarios (2071-2100) (RCAO forced by ECHAM4/OPYC and HadAM3H, for SRES A2 and B2 greenhouse-gas emission scenarios; see text).

but were a minor component except in the southern nemoral region. Mountain birch, which in reality forms the treeline in Scandinavia, was correctly predicted to occur mainly in the mountain areas of the northwest. Oak was predicted to occur as far north as 62° N, where the Limes Norrlandicus – the northern boundary for many deciduous tree species in Europe (Sjörs, 1956) – lies. Beech and lime dominated in the south, lime extending as a minor component to forest areas north of Limes Norrlandicus.

Under all four climate scenarios [hereinafter, “climate scenario” denotes both climate and associated atmospheric CO_2 for the RCM scenario period 2071–2100], LPJ-GUESS predicted extension of the boreal forest northward and to higher elevations, Scots pine and Norway spruce joining mountain birch at a higher alpine treeline. Pine and spruce remained the dominant species in the boreal zone; however, a shift in dominance from Scots pine to deciduous broadleaved trees (lime, silver birch and some oak) was predicted for the Baltic coast and the central boreal region. The dominance of spruce and pine in the boreo-nemoral zone was reduced in favour of deciduous species, especially beech and lime. The northern boundary of the boreo-nemoral forest zone, i.e. Limes Norrlandicus, was displaced northwards in association with increased temperatures, a longer growing season and an apparent shift in competitive balance between conifers and broadleaved trees, favouring the latter.

3.2. NET PRIMARY PRODUCTION

Under modern climate, the model estimated average NPP values ranging from 2 g C m^{-2} yr^{-1} for herbaceous vegetation in the northern Swedish mountains to 0.548 kg C m^{-2} yr^{-1} for spruce-dominated areas of the boreo-nemoral forest region in southern and western Sweden. Intermediate productivity was predicted for the boreal region, with a declining trend in association with colder temperatures and a shorter growing season towards the north and northwest and the alpine zone (Figure 2).

Substantial increases in productivity were predicted under all four climate scenarios, central Sweden tending to become more productive compared to both southern and northern areas. In the southeast, NPP remained unchanged or declined slightly under the ECHAM4-B2 and both HadAM3H scenarios, the result of vegetation water deficits caused by increased summer evapotranspiration not compensated for by increased rainfall. On average for the study area, NPP increased by about 30% under the climate scenarios compared with the modern climate. NPP enhancement was somewhat greater under the A2 scenarios, with their higher atmospheric CO_2 levels compared with the B2 scenarios, and for the wetter ECHAM4-based scenarios compared with the HadAM3H-based scenarios (Table III).

The modelled productivity of spruce and pine, averaged over Sweden, increased throughout the past century, attaining a maximum c. 2030–2040 and declining

TABLE III

Area-weighted 30-year averagenet primary production (NPP) for Sweden under the modern climate (1969–1989) and the four regional climate scenarios (2071–2100) according to simulations with LPJ-GUESS

	Area Weighted avg. NPP (kgC m^{-2} yr^{-1})	Change in Percentage (%)
Modern climate	0.416	–
ECHAM4 + RCAO, A2	0.564	35
ECHAM4 + RCAO, B2	0.524	26
HadAM3H + RCAO, A2	0.548	32
HadAM3H + RCAO, B2	0.509	22

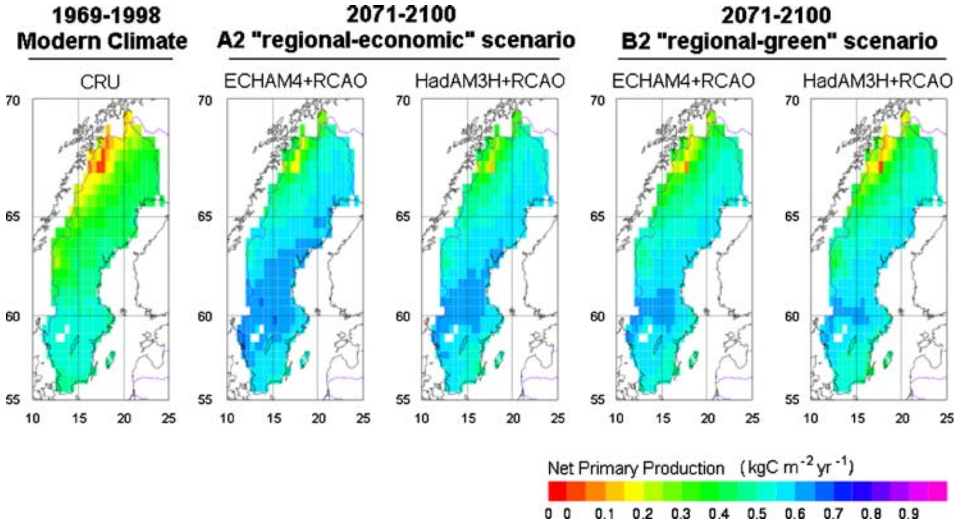

Figure 2. Distribution of net primary production (NPP) by potential natural vegetation in Sweden according to simulations with LPJ-GUESS under the modern climate (1969–1998) and the four regional climate scenarios (2071–2100).

by the late 21st Century (Figure 3; results for ECHAM4-A2 climate scenario; results from simulations driven by the other climate scenarios were similar and are not shown). The decline can apparently be explained by increasing competition with deciduous broadleaved tree species. With the exception of silver birch, which attained maximum productivity around 2020 and thereafter declined, deciduous trees appeared to generally benefit from recent historical and projected changes in climate and CO_2 levels. There was a continuous decrease in NPP of C_3 grass, apparently as a result of increased shading by a denser forest canopy.

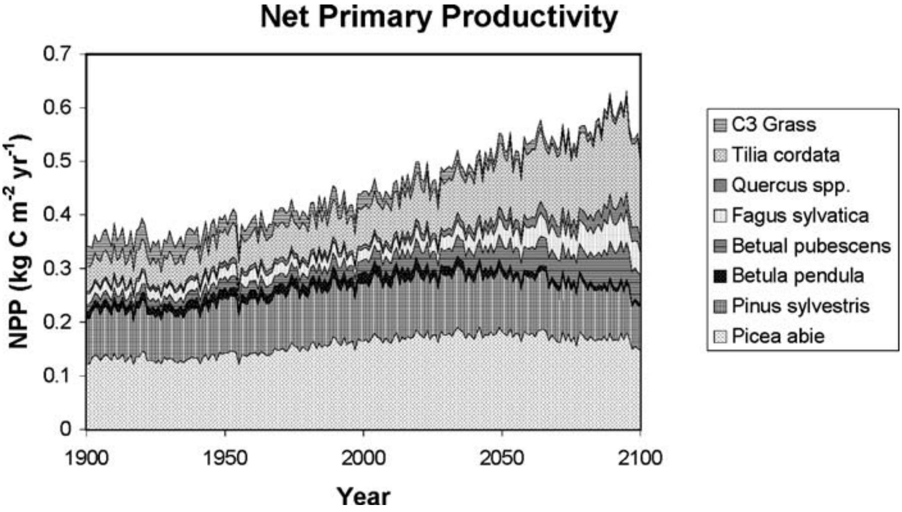

Figure 3. Changes in area-weighted average NPP for Sweden through the simulation period 1901–2100, in total and for each species, according to simulations with LPJ-GUESS. Values for 1999–2100 are from the simulation driven by the ECHAM-A2 regional climate scenario (see text).

3.3. NET ECOSYSTEM EXCHANGE

According to LPJ-GUESS, Swedish natural ecosystems would, in general, sequester carbon from the atmosphere under the modern climate (Figure 4). The carbon sink is strongest in the boreal forest region, with a few grid cells in the southern and western part of the country showing a weak net release of carbon to the atmosphere.

Under all four climate scenarios, the model predicted that the modern boreo-nemoral region would become a weak source of carbon to the atmosphere by the end of the 21st Century (Figure 4), while northern Sweden, particularly the mountain areas in the northwest, would become a greater sink, approximately maintaining modern average NEE levels on a country basis (Table IV; Figure 5). Although carbon uptake by vegetation (NPP) tended to increase under all climate scenarios (Figure 2; Table IV), this was approximately balanced by carbon release through a temperature-driven increase in decomposition rates of soil organic matter (Table IV).

Although NEE varies from year to year (depending mainly on interannual variation in climatic conditions), the model simulations indicate that the carbon sequestration capacity of Swedish natural ecosystems would have generally increased through the 20th century, reaching a maximum by the late 20th Century which is maintained to the end of the scenario period. Throughout the coming century, carbon stored in Swedish natural ecosystems would continue to increase according to the simulations (Figure 5; results for ECHAM4-A2 climate scenario; results from simulations driven by the other climate scenarios were similar and are not shown).

TABLE IV

Area weighted 30-year average net ecosystem carbon exchange (NEE), vegetation carbon exchange and soil carbon exchange under the modern climate (1969–1989) and the four regional climate scenarios (2071–2100) according to simulations with LPJ-GUESS (negative values represent a net uptake and positive values a net release of carbon by ecosystems)

	Carbon Exchange ($kgC\ m^{-2}\ yr^{-1}$)			Change in Percentage (%)			Total Carbon Sink/Source ($PgC\ yr^{-1}$)		
	NEE	Veg.	Soil	NEE	Veg.	Soil	NEE	Veg.	Soil
Modern climate	−0.040	−0.421	0.383	—	—	—	−0.0164	−0.1730	0.1574
ECHAM4 + RCAO, A2	−0.044	−0.570	0.534	11.6	35.4	39.6	−0.0181	−0.2343	0.2195
ECHAM4 + RCAO, B2	−0.042	−0.530	0.493	6.1	25.9	28.9	−0.0173	−0.2178	0.2026
HadAM3H + RCAO, A2	−0.048	−0.554	0.516	19.8	31.6	34.7	−0.0197	−0.2277	0.2121
HadAM3H + RCAO, B2	−0.045	−0.515	0.474	12.5	22.4	23.9	−0.0185	−0.2117	0.1948

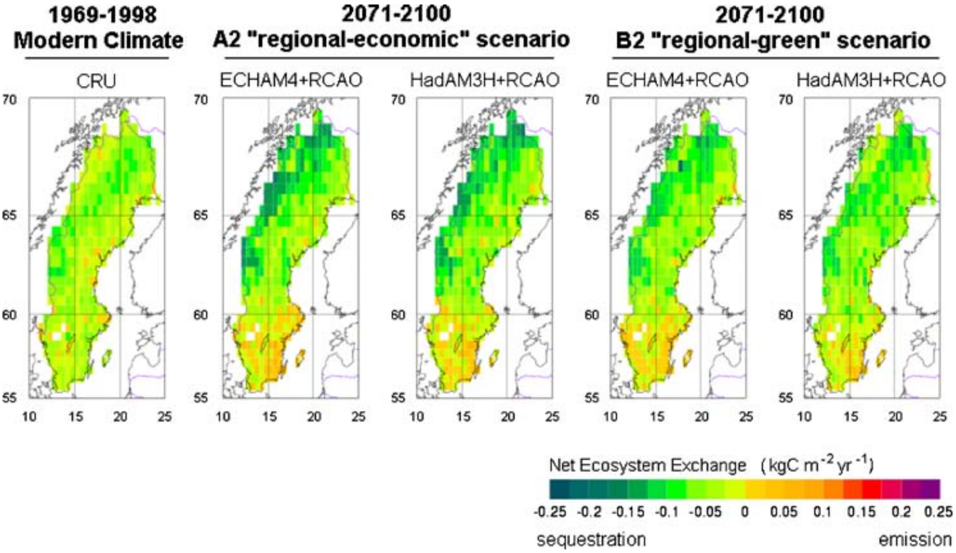

Figure 4. Distribution of net ecosystem carbon exchange (NEE) according to simulations with LPJ-GUESS under the modern climate (1969–1998) and the four regional climate scenarios (2071–2100) (negative values represent a net uptake and positive values a net release of carbon by ecosystems).

4. Discussion

4.1. POTENTIAL NATURAL VEGETATION DISTRIBUTION

Simulated tree species distributions for the modern climate compare well to the actual natural distributions .(Jalas and Suominen, 1972–1999) and projections are

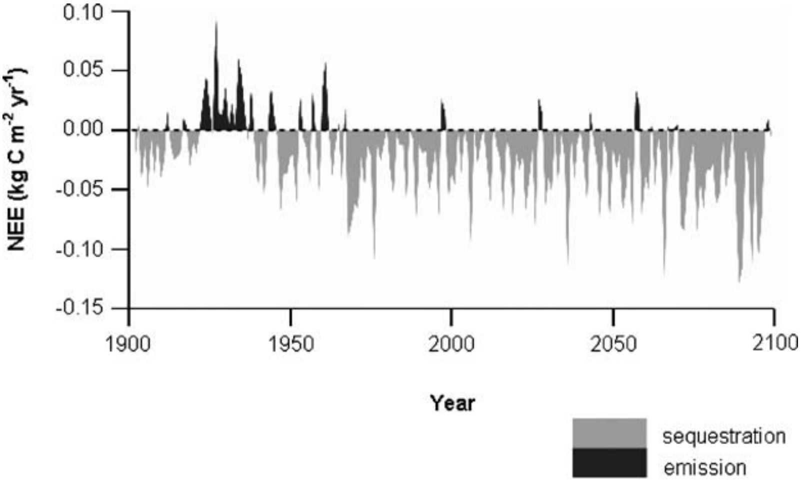

Figure 5. Changes in area-weighted average NEE for Sweden through the simulation period 1901–2100 according to simulations with LPJ-GUESS. Values for 1999–2100 are from the simulation driven by the ECHAM-A2 regional climate scenario (see text) (see Figure 4 for sign convention).

similar to the results of previous modelling efforts (Sykes and Prentice, 1995, 1996b; Sykes et al., 1996). The northern limits of the boreal forest dominants Norway spruce and Scots pine are considered to correspond to minimum growing season heat sums (Odin et al., 1983; Prentice and Helmisaari, 1991). These are enhanced by general temperature increases under the climate scenarios and lead to an extension of the boreal forest northwards and into the northwestern mountain areas, displacing mountain birch in some areas (Figure 1). Increased temperatures and a longer growing season also allow oak, beech, silver birch and lime to expand northwards. South of 60° N, Norway spruce and Scots pine are inferior in competition with deciduous trees and are eventually replaced by beech and lime. Spruce regeneration is curtailed in the model when coldest month temperatures rise above −2 °C; indeed, the increased likelihood of late spring frosts in association with increased winter temperatures has been suggested to interfere with regeneration of this species (Sykes and Prentice, 1996b, 1999).

The predicted shifts in tree species range limits are over smaller distances than suggested by some previous studies. Using the static bioclimatic model STASH (Sykes et al., 1996), Sykes and Prentice (1995) predicted substantial northward and eastward displacements for Norway spruce and Scots pine under a GCM-based climate scenario based on doubled greenhouse forcing. The warm limits of both species were predicted to retreat some 1200 km towards the far north of Sweden. The climate scenario used in the latter study was of generally stronger warming than the SWECLIM scenarios and other current assessments describe. A more recent study with the same model suggested that the range shift for spruce would be qualitatively similar but smaller (Bradshaw et al., 2000). However, an important additional difference between the present study and previous ones is the use of a dynamic vegetation model able to capture the transient effects of climatic change on forest composition and structure. Although spruce and pine exhibit regeneration failure in the southern part of the study area according to LPJ-GUESS, they remain present in declining abundance to the end of the 21st Century. Similar transient responses of mixed forest to a rapid climate warming were simulated using a gap model for a site near Stockholm by Prentice et al. (1991).

Under the constant and infrequent disturbance regime implemented in the simulations, pine is disadvantaged in competition with deciduous trees because of its lower shade-tolerance. However, it is conceivable that disturbance by forest fires might increase under natural conditions in a warmer and drier future (Stocks et al., 1998) and this would tend to favour the early successional and fire-adapted pine over deciduous trees, particularly beech (Bradshaw et al., 2000).

4.2. ECOSYSTEM CARBON DYNAMICS

The model estimates of NPP under the modern climate are comparable to or possibly somewhat higher than values for Swedish boreal forests derived from field measurements and remote sensing. Zheng et al. (2004) estimated a mean NPP of 0.578 ± 0.154 (s.d.) kg m^{-2} yr^{-1} (dry weight) for coniferous forest areas south of 66° N in Finland and Sweden. This corresponds to an NPP in carbon mass units of approximately 0.3 kgC m^{-2} yr^{-1}, assuming that half of ecosystem biomass is carbon (UN-ECE/FAO, 2000). Similarly, multi-year field measurements from 1973 to 1981 in six evergreen conifer forest sites in Sweden and Finland (Gower et al., 2001) suggest that NPP ranged from 0.215 to 0.462 kg C m^{-2} yr^{-1} during this period. These data compare reasonably well to the results of the present study (Figure 2).

Under all four scenarios, combined effects of warmer and wetter climate and higher levels of CO_2 in the atmosphere lead to a general increase in NPP in most areas. Regional differences are mainly associated with water availability. Reduced or unchanged NPP in the southeast, for example, can be explained by increased vegetation water stress as a consequence of increased evapotranspiration not counterbalanced by increased rainfall (Räisänen et al., 2003). Growing season drought may decrease photosynthesis rates in the model through reduced stomatal conductance. Increased water use efficiency as a result of reduction in stomatal conductance in response to higher atmospheric CO_2 concentrations (Drake et al., 1997) may compensate somewhat. The greatest NPP enhancement was simulated in the central forested region, where neither precipitation nor low temperatures limit enhancement of productivity.

Previous modelling studies generally suggest that future climate change should lead to increased forest production in Sweden and other, climatically similar, regions. Using a physiological growth model and a suite of warming and CO_2 elevation scenarios, Bergh et al. (2003) predicted increases in net production of Norway spruce and Scots pine at boreal forest sites in Sweden, Norway and Finland, identifying growing season changes and CO_2-enhancement of carboxylation efficiency as primary causes of the enhanced productivity. A warming scenario alone decreased NPP of beech in Denmark, in part due to impaired water balance and increased respiration. Positive effects of rising temperatures on boreal forest growth have also been predicted by model studies in Finland (Kellomäki and Kolström, 1993), although Karjalainen et al. (1996) predicted decreased NPP for most tree species under a scenario of increasing temperature and precipitation in southern Finland.

Regional differences are apparent in the simulated responses of NEE to the climate scenarios. Northern and central regions tend to become stronger sinks for carbon in the future, while southern Sweden, a weak sink under the modern climate according to the model, becomes a source in the future. The explanation for this lies mainly in regional differences in the development of vegetation carbon stocks, which remain relatively constant in the south but increase elsewhere in conjunction with increased NPP and the northward and upslope expansion of forest (see Section 4.1). Heterotrophic respiration, mainly associated with microbial metabolism of soil organic matter, increases in all areas due to the warmer climate and in the south generally exceeds NPP by the late 21st Century, leading to net release of carbon by ecosystems there.

The predicted increase in the carbon sequestration capacity by vegetation in central and northern parts of Sweden is in agreement with a larger-scale modelling study (White et al., 2000), in which NPP and NEE were predicted to increase at high northern latitudes ($>50^\circ$ N) globally until at least 2100. Using a gap-type model including biogeochemical components, Karjalainen et al. (1996) predicted a decline in ecosystem carbon storage capacity under climate warming for a site in southern Finland, while in northern Finland, net carbon sequestration increased. At the southern site, NPP declined for most tree species while SOM and litter decay rates increased due to higher temperatures. At the northern site, a positive growing-season effect on tree production outweighed the temperature effect on SOM and litter decay. A similar north/south contrast in future NEE was seen for Sweden in the present study, even though NPP changes were positive in all areas.

A complicating factor for the assessment of changes in carbon sequestration capacity in reality may be changing land use in the future, which would affect the distribution of sinks and sources of carbon, but which is not taken into consideration in the present study.

The model simulates a generally increasing net sink of carbon for Sweden through the 1900s. This general trend is interrupted by a period of net carbon release (positive NEE) from the late 1920s until the 1940s (Figure 5). This anomaly is associated with the interruption of a trend of generally rising temperatures since the mid 19th century (Moberg and Alexandersson, 1997; SMHI, 2004) and with a period of decreasing precipitation in Sweden. In the model, these conditions lead to sporadic water stress and a general decline in forest NPP (carbon uptake) and biomass. At the same time, carbon release through heterotrophic respiration (decomposition of soil organic matter and litter) remains relatively unaffected or increases due to the influx of litter resulting from vegetation dieback. The net result, on average over Sweden, is a general release of carbon from ecosystems over two decades or so. The mechanism underlying this feature is plausible, but it remains unproven in the absence of observations at regional scales.

4.2.1. *Differences Among Scenarios*

Scenarios compatible with the A2 and B2 greenhouse gas emission scenarios of the SRES and with boundary conditions from two GCMs were used in simulations to explore changes in tree species distribution, vegetation structure, productivity and ecosystem carbon stocks for the late 21st Century, thus accommodating a proportion of the GCM-based and emission-based uncertainty in future climate development.

Only small differences between the four RCM scenarios were apparent, in terms of simulated effects on species composition and distribution, production and carbon storage. Species potential range limits in LPJ-GUESS were defined by the temperature-based indices minimum and maximum temperatures of the coldest month, and minimum growing season heat sum (Table II). As temperature changes are similar under all scenarios, differences in their effects on species distributions were small.

The A2 scenarios were associated with generally greater NPP, biomass and carbon sequestration than the B2 scenarios. The main explanation for the modelled differences in ecosystem carbon balance lies in the modelled stimulation of photosynthesis by CO_2, which is stronger under the high-CO_2 A2 scenarios.

There are numerous sources of uncertainty associated with the climate scenarios, the ecosystem model and their underlying assumptions. Some of the major sources of uncertainty are discussed later in Section 4.3.1. Nevertheless, the general consistency among the predicted ecosystem responses to the range of possible future conditions represented by the four scenarios seems noteworthy. To the extent that the ecosystem model can be regarded as realistic, and assuming that the four scenarios encapsulate a proportion of the uncertainty in the regional climate development, overall patterns of change in Swedish natural ecosystems in the coming century may qualitatively and quantitatively resemble those simulated in the present study.

4.2.2. *Future Carbon Storage by Swedish Ecosystems in a Global Context*

Boreal forest ecosystems, with low rates of decomposition, store nearly 50% of the total carbon in all forests ecosystems (corresponding to 20% of total terrestrial ecosystem carbon stocks) (Prentice et al., 2001). It is likely that boreal forests will experience greater changes in climate over the coming century compared to temperate and tropical forests (Giorgi et al., 2001). Responses of plant physiological processes, as well as vegetation composition and structure, may affect the productivity of boreal forests, and, in turn, their capacity to sequester carbon, with implications for the global carbon cycle (Schimel et al., 2000; Cramer et al., 2001). Results of the present study suggest that Swedish ecosystems may generally maintain a currently positive carbon sequestration capacity to the end of the next century, though with some regional variation. The most important explanation for these sinks lies in the enhancement of NPP by rising CO_2 levels and an extended growing season. A number of earlier studies have arrived at similar conclusions for high-latitude ecosystems as a whole (White et al., 2000; Cramer et al., 2001). However, as forests reach maturity, fertilization effects of elevated CO_2 saturate, and decomposition rates catch up with increased growth, the capacity of ecosystems to sequester excess carbon must eventually decline (IPCC, 2001c).

4.3. MODELLING REGIONAL CLIMATE CHANGE EFFECTS ON ECOSYSTEMS

In this paper we simulated vegetation dynamics and distributions throughout Sweden with a process-based regional scale ecosystem model driven by RCM-generated climate scenarios. RCMs take regional physiography into account (e.g., the Baltic Sea, Fenno-Scandian mountain range, river and lake systems for Sweden) to give scenarios with greater spatial detail compared to GCMs. With such detailed spatial patterns, the high resolution RCM simulations of temperature, distribution of precipitation intensities and surface hydrology (i.e. runoff and snow cover) are more realistic than coarse resolution GCM output for the Scandinavian region (Christensen et al., 1998).

Forest gap models are usually applied at the site scale, where they use empirical relationships based on observations of individual species. These relationships, however, may not hold true under future climates or different CO_2 levels (Norby et al., 2001). LPJ-GUESS, as a general process-based ecosystem model incorporating gap-phase dynamics, has already been applied (at the species level) at specific sites in the Great Lakes region USA, to simulate the transition zone between prairie, northern hardwoods and boreal forest (Hickler et al., 2004). Because of the generality of the process representations in the model, it can also be applied to different regions and on different scales with little or no change in parameter values. In this present paper, the model was applied at the regional scale and thus was able to simulate, for example, changing treeline and its effect on regional carbon storage; or how a change from conifer to deciduous forest could affect phenology and thereby regional NPP and NEE.

4.3.1. *Model Limitations and Uncertainties*

Even though there are studies suggesting that, in the past, fires have occurred at 50–150 year intervals in northern Sweden and as frequently as every 20 years in southern

Sweden (Niklasson and Granstörm, 2000; Niklasson and Drakenberg, 2001), in the present study, modelling of disturbances was restricted to a generic mean disturbance interval of 100 years in all areas. This interval corresponds to the approximate return time for natural disturbances under modern conditions (Zackrisson, 1977) and has also been used previously in other similar modelling studies (Prentice et al., 1991; Sykes, 2001). In fact, climate changes may be expected to impact disturbance regimes, and this would have implications for vegetation structure and ecosystem carbon cycling. Stocks et al. (1998), for example, simulated increased fire frequencies in boreal forests under a warmer climate. Similarly, diseases and pests might have significant effects on boreal forests due to warmer climate (Fleming and Volney, 1995) and/or increased levels of CO_2 (Ceulemans et al., 2002) in certain areas. Factors associated with changing patterns of extreme weather events such as droughts, floods, and windstorms could also potentially lead to severe changes in the structure and dynamics of boreal forest ecosystems.

In LPJ-GUESS, the extension of the treeline, as simulated, is a result of the general temperature increases under the climate scenarios. However, in reality, temperature may not be the only factor involved in treeline movements; for example, increased CO_2 concentrations may improve tree growth at high altitudes (LaMarche et al., 1984; Hättenschwiler et al., 2002) and may themselves enable advancement of treeline (Körner, 1998). In contrast, climatic events such as exceptionally cold winters with poor snow cover in high altitude boreal forests may also affect treeline species negatively, leading to a retreat in the treeline. Such events occurred in some regions of Scandinavia during the period 1970–95, despite increasing temperatures generally (Kullman, 1997). However, treelines have been extending upslope in the southern Swedish Scandes since the early 1950s (Kullman, 2002). A possible reservation concerning the displacement of the boreal tree line and other vegetation changes predicted by the model is the potential for dispersal limitations causing species ranges to lag behind changes in their climatological niche. The model assumes that no such limitations operate, so that species begin to establish in new areas as soon as conditions there become suitable. The main reason for adopting this assumption is that suitable models of tree species dispersal on regional scales are lacking (Canadell et al., 1998). In the event that dispersal limitations operate, the model is likely to overestimate the rate of change in tree species distributions beyond their current limits; including the replacement of mountain birch by Norway spruce and Scots pine in the northwestern mountainous areas.

The simulations presented in this study were of the potential natural vegetation, ignoring direct anthropogenic effects such as land use or silvicultural management. Forest management practices constitute an important factor that shapes the species composition of forest ecosystems and hence influences carbon sequestration. However, changes in species ranges of the natural vegetation form the basis for understanding the dynamics of carbon sequestration in managed forests and also provide the background for comparisons of the carbon sequestration potentials of managed and natural forests (Karjalainen, 1996).

Even though the model version applied in this study does not take into account possible nutrient limitations on plant production (McGuire et al., 1992; Finzi et al., 2002), nor stimulation of production by nitrogen deposition (Aber, 1992; Bergh et al., 1999), i.e., without explicitly modelling the nitrogen cycle, it appears to predict reasonable overall NPP levels for Sweden. However, Hungate et al. (2003) argued that models lacking an explicit representation of the nitrogen cycle may exaggerate the amount of carbon that terrestrial ecosystems can sequester, due to nitrogen constraints on NPP. It may be important to include nitrogen cycling in process-based ecosystem models to address this possible bias.

A great number of experimental studies have shown that increased CO_2 concentrations typically stimulate production in individual plants, populations and ecosystems (Poorter and Navas, 2003; Ainsworth and Long, 2005). Higher levels of CO_2 can stimulate production directly via increased carboxylation efficiency, and indirectly through improved WUE (Drake et al., 1997). Both mechanisms are represented in LPJ-GUESS, which has been shown to reproduce correctly the observed NPP enhancement from the high-CO_2 treatments of a number of forest FACE experiments (Hickler, 2004; T. Hickler et al., unpublished). However, not all ecosystems exhibit increased growth under elevated CO_2 (Ainsworth and Long, 2005), and there are indications that in some ecosystems, complex interactions among multiple global change drivers may produce an unexpected *suppression* of NPP under elevated CO_2 (Shaw et al., 2002). These effects are unlikely to be captured by the model in its current form. In addition, it has been hypothesized that in many ecosystems, negative biogeochemical feedbacks, in particular, reduced nitrogen mineralization, may inhibit plants from fully utilising the additional assimilates resulting from CO_2 fertilisation on time scales of decades or more (McGuire et al., 1992; Prentice et al., 2001). These mechanisms are not represented in the model, and might result in smaller NPP increases by the late 21st century than simulated in this study.

There are several sources of uncertainties underlying future regional climate changes and ecosystem responses to such changes. These include uncertainty in anthropogenic greenhouse forcing and in responses of atmospheric circulation to a given level of greenhouse forcing, and uncertainties due to missing or misrepresented physical processes in GCMs (Cubasch et al., 2001). There are also considerable uncertainties associated with parameterisation and process representations in the ecosystem model (Zaehle et al., In press) resulting from limited knowledge of the underlying processes or the correct parameter values for scaling them. Model assumptions concerning carbon allocation and allometry, for example, are based on a limited understanding of the underlying physiology (Landsberg, 2003) and have been shown to have a strong influence on biomass (Badeck et al., 2001).

To our knowledge, this study is the first to use a *process-based ecosystem model* to explore how possible shifts in climatic zones according to a range of *regional climate scenarios* may lead to changes in the structure and function of natural ecosystems on *species level* and at the *regional scale*. Previous studies using physiological growth models, or forest gap models, have examined the effects of climate change on productivity (e.g. Bergh et al., 2003) and carbon storage (e.g. Sykes and Prentice, 1996a) at selected Swedish sites. The present study generally supports the overall trend towards increasing NPP and ecosystem carbon storage identified in such earlier studies, but is the first to demonstrate that the trend holds at the regional scale, and under a range of possible future climates.

Although the uncertainties in the model, and as to the realism of the various assumptions of the study, are substantial, some differences in the model predictions between scenarios are likely to be robust to the actual course of future climate development. The stronger overall NPP response under the higher-CO_2 A2 scenarios is likely to be realistic, since the model has been shown to correctly reproduce observed patterns of NPP enhancement from the above-ambient CO_2 treatments of forest FACE experiments (Hickler, 2004: T. Hickler et al., unpublished). The significance of growing season length for productivity in cold climates is well-understood and clearly brought out by earlier modelling studies of boreal ecosystems (e.g. White et al., 2000; Bergh et al., 2003), like the present one. At least for northern parts of Sweden, where moisture availability is unlikely to limit production increases on most sites, greater NPP enhancement may be expected in response to stronger warming, assuming that temperature increases are relatively uniform throughout the year (and thus lead to an increased growing season). Similarly, northern and altitudinal distributional limits of the simulated tree species are clearly linked to temperatures, so that, in the absence of dispersal limitations, range shifts may be expected to be larger in the event of stronger warming, as predicted by LPJ-GUESS for the A2 scenarios in comparison to the B2 scenarios.

An important issue within the future development of the approach demonstrated by this study would be to include direct anthropogenic drivers of ecosystem dynamics (i.e., land use change, forest management, atmospheric deposition etc.) in addition to climate change scenarios, as well as addressing other services provided to society by ecosystems apart from carbon uptake and sequestration. A prerequisite for such a study is the development of scenarios that are consistent in terms of change in the (largely interdependent) driving variables (e.g., Schröter et al., In press). Further, the involvement of stakeholders would help to ensure policy relevance of the study and the dissemination of its findings to the wider community affected by the potential consequences of climate change for Swedish ecosystems.

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