Increased accuracy in climate impact studies by incorporating forest management practices within a process-based regional ecosystem modelling framework

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ABSTRACT

Process-based simulation models of terrestrial ecosystem dynamics are increasingly being applied as practical tools in forest management. Regional applications of such models are, however, very limited to date. This study presents and tests the performance of a process-based regional ecosystem modelling framework, LPJ-GUESS, which incorporates forest management practices. The model is driven by historical climate data and applied on a grid across Sweden to simulate the influence of recent historical management practices on the forest structure and its productivity. The study focuses on species-level interactions and investigates how stem wood volume increment has changed during the historical time period. The performance of the model is evaluated by comparing the simulated forest composition and growth with the observed forest inventory data from Swedish forest regions. The model estimates tend to be somewhat low in the southern and high in the northern part of the country, but generally comparable with observations in all regions of Sweden. Our results emphasize the potential that models like LPJ-GUESS offers to support forestry practice, especially with regard to the choice of species and management regime in a changing environment.

Keywords: managed forest ecosystems, process-based ecosystem modelling, LPJ-GUESS, Sweden, stem wood volume increment, net primary productivity

1. INTRODUCTION

Projected climate change and higher levels of atmospheric CO_2 concentrations (IPCC, 2001a) are likely to have significant impacts on forest ecosystems, and the goods and services they provide to society (IPCC, 2001b). This may have serious implications for non-market ecological attributes such as biodiversity, as well as socio-economic implications for forest related sectors like timber production and carbon storage (Shugart *et al.*, 2003).

There is a need to develop adaptive strategies, which can provide decision makers with the information they need at policy-relevant regional to national scales (Renn *et al.*, 1998). Development of such strategies, however, requires a good understanding of the potential responses of forest ecosystems to future scenarios of climate and atmospheric CO_2 change on such scales (Lexer *et al.*, 2002).

During the past two decades, a number of computer simulation models have been developed for terrestrial ecosystem research purposes and applied to investigate mainly the long term effects of climate and CO_2 changes on vegetation dynamics (Johnsen *et al.*, 2001). Forest gap models (Bugmann, 2001), for example, have been widely employed to simulate the consequences of changing climate on the structure and dynamics of potential natural vegetation from stand level (Prentice *et al.*, 1993; Bugmann *et al.*, 1996; Sykes *et al.*, 1996a; Badeck *et al.*, 2001) to regional scales (Lindner *et al.*, 1997). There are some applications of these models to managed forest ecosystems on stand levels (Kellomäki *et al.*, 1993; Lindner, 2000), but regional applications are very few (Lasch *et al.*, 1999; Lindner *et al.*, 2000; Lasch *et al.*, 2002; Lasch *et al.*, 2005). Similarly, a number of physiological growth models have recently been applied as practical tools in forest management, yet all applications are on stand level (Monserud, 2003) as these types of models contain many site-specific parameters, restricting their utility for regional applications (Battaglia *et al.*, 1998a; Johnsen *et al.*, 2001). Dynamic global vegetation models (DGVMs), on the other hand, with rather simplified representations of vegetation and vegetation dynamic processes (Smith *et al.*, 2001) have been applied to simulate biogeochemical cycling and vegetation dynamics under climate change at larger spatial scales, primarily continental to global scales (Cramer *et al.*, 2001; Bachelet *et al.*, 2003; Sitch *et al.*, 2003). However, as they cannot, for example, resolve landscape-scale heterogeneity in vegetation type, structure or development stage, nor distinguish individual tree species, their applicability in regional studies is very limited. Moreover, like the majority of gap model studies, simulation results of most DGVM investigations are only of the potential natural vegetation.

Many of world's forest regions have been managed intensively and in these ecosystems it is management activities that have determined the species composition rather than natural factors (IPCC, 2001b). Hence, if we want models to be useful for regional level planning and policy making processes, they should include direct anthropogenic drivers of ecosystem dynamics *i.e.* forest management and land use change, and be applied on regional/national scales.

In this study, we present and test a modified version of LPJ-GUESS (Smith *et al.*, 2001), a process-based ecosystem 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 forest gap models. The modified model integrates a statistics-based forest management module, which specifies the species mix and management regime most likely to be adopted on a site with a given quality class. We expect the model to perform better at the national/regional level compared with the unmodified version of LPJ-GUESS, which lacks a forest management scheme, and compare results to a similar study with the original version of the model (e.g. Koca *et al.*, in press). The model is applied on a grid over Sweden driven by observed climate and atmospheric CO_2 concentrations to simulate changes in forest species composition and stemwood production over the last 150 years. Performance of the model is evaluated by comparing the simulated results with observed data provided from the Swedish National Forest Inventory (Swedish National Forest Inventory, 2005).

2. MATERIALS AND METHODS

2.1 Ecosystem model

LPJ-GUESS is a process based terrestrial ecosystem modelling framework (Smith *et al.*, 2001), which is applicable at landscape to regional/global scales. Mechanistic representations of plant physiological and biogeochemical processes (*i.e.* carbon assimilation and allocation, canopy-atmosphere exchange of water and CO_2, plant water uptake, soil hydrology and snow pack dynamics, and litter and soil biogeochemistry) are inherited from Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ-DGVM) (Sitch *et al.*, 2003). Tree populations and process governing their dynamics are represented in similar ways to patch and individual-oriented forest gap models such as FORSKA (Leemans *et al.*, 1987; Prentice *et al.*, 1993; Sykes *et al.*, 1996b). 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. 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.

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 (Drake *et al.*, 1997).

Both LPJ-GUESS and the closely related model LPJ-DGVM have been tested against observational data in a number of studies, demonstrating reasonable success in reproducing major global and regional patterns of PFT or species composition, distribution, biomass and productivity of potential natural vegetation, as well as ecosystem-level carbon stocks and fluxes. LPJ-DGVM has 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. LPJ-GUESS has been shown to simulate correctly the dominant PFT in a number of pristine forests (Badeck *et al.*, 2001) and PFT composition of potential vegetation at a range of sites across Europe (Smith *et al.*, 2001). Hicker *et al.*, (2004) successfully simulated vegetation dynamics, tree species composition and biomass at three sites in the U.S. Great Lakes region. LPJ-GUESS has been demonstrated to simulate spatial patterns and interannual variation in satellite-based measurements of maximum vegetation "greenness" (leaf area index, LAI) and growing season length over global land areas north of 40°N (Lucht *et al.* 2003). The model has also been validated with respect to seasonal and interannual variation in carbon and water vapour fluxes at 15 eddy-covariance flux sites of the CarboEuroflux campaign (Morales *et al.*, 2005).

The original version of LPJ-GUESS is fully described by Smith *et al.* (2001). Sitch *et al.* (2003) provide the further details of the physiological, biophysical and biogeochemical components of the model, which are common also to LPJ-DGVM.

In the present study the model simulated six major Swedish forest tree species and a generic herbaceous plant functional type (PFT; C_3 grass). The version used in here includes improved representations of soil hydrology, snow pack dynamics and soil-vegetation-atmosphere exchange of water, as documented by Gerten *et al.* (2004) in addition to the novel forest management module, presented below.

2.2 Forest management module

The newly-implemented forest management module incorporates a "species choice algorithm" (Table 1) and a "forest management scheme" (Table 2), which are both developed and provided by the Swedish University of Agricultural Science. Both components are based on traditional statistical models of forest growth and yield, which were applied on various forest sites in Sweden, particularly in the south (Fries, 1964; Carbonnier, 1971; Carbonnier, 1975; Eriksson, 1976; Agestam, 1985; Ekö, 1985). In the present model application, these two components utilise a prognostic "site quality class", quantified as the expected mean productivity of Norway spruce during one rotation period.

Five site quality classes are distinguished, ranging from least productive "1" to most productive "5" (Table 1). The current quality class is determined in conjunction with the start of a new rotation on a simulated patch by "planting" spruce saplings at a density of 2000 saplings ha^{-1} and simulating the development of the stand during one rotation period in the absence of disturbances, natural establishment or competition with other species. Climate and CO_2 data from the year of plantation and forward in time are used to drive the model during this phase. The quality class is determined based on the mean annual wood volume increment over the simulated rotation period, according to the scheme shown in Table 2. Following the determination of site quality, simulation time is reset to the current planting date.

2.2.1 Species choice algorithm

Regardless of the quality class of the patch, the species choice algorithm (Table 1) first decides whether a monoculture or a mixed-species forest will be planted. This is determined stochastically based on expected probabilities of 70% and 30% for monocultures and mixed stands, respectively. In the case of mixed stands, the number of different tree species to be planted is chosen at random based on expected probabilities of 80%, 15% and 5% for 2, 3 or 4 species, respectively. The identity of the planted species is likewise determined based on species-specific expected probabilities (Table 1). The same probabilities apply both for monocultures and mixed stands. In mixed stands, the relative proportions of different species (in terms of sapling densities) are determined once again based on the site quality classes (Table 1). A constant plantation density of 2000 saplings ha^{-1} (sum across all species in mixed stands) was implemented. An understory population of C_3 grasses was permitted to coexist with the tree community.

2.2.2 Forest management scheme

Species-specific thinning and harvesting regimes were implemented by the forest management scheme (Table 2). The number, interval and intensity of thinning, and rotation periods for each tree species were based on the site quality class of the patch as determined in conjunction with plantation (see above). Biomass removed by thinning and harvesting was transferred to the litter pools (which are also replenished by shed roots and leaves and biomass lost through natural mortality). No separate carbon pools for forest products or forestry residues were implemented. The effects of different types of harvesting methods were not considered in the model simulations.

2.3 Environmental data and simulations

The model was applied on a grid covering the entire landmass of Sweden at a resolution of 0.5º longitude and latitude. The simulations were spanned 400 years, comprising a 300-year initialisation/spinup period, and a 100-year historical period. The model was driven by monthly mean climate (temperature, precipitation and cloud cover) and annual global atmospheric CO_2 concentration data. Interannual time-series of the climatic variables for 1901-1998 were extracted from the CRU05 global dataset of monthly surface climate (New *et al.*, 1999; New *et al.*, 2000). Cloud cover data for 1997 and 1998 were taken as averages over the previous 30 years. The initial 30 years (1901-1930) of CRU climate data, detrended in the case of temperature, were used repeatedly for the spinup phase of the simulations in order to establish vegetation at approximate equilibrium with climate conditions at the start of the historical time-series. Temperature and precipitation data for 1999, 2000 (as a part of historical period) and beyond (to be used in the quality class determination) were derived by interpolation between means for the final 30 years (1969-1998) of the historical data and a 30 year (2071-2100) regional climate model scenario (HadAM3H-A2) data, by superimposing on this the detrended interannual variability of the last 30 years of the historical record. The final 30 years of CRU historical data were repeated for the simulations beyond 1998.

In the present study, each modelled grid cell was represented by 100 replicate patches of 0.1 ha area. Ecosystem properties in each of these grid cells were taken as the average over all patches. A generic mean disturbance interval of 100 years – the approximate average for natural

Table 1. Tree species choice algorithm based on site quality class.

Patch type (probability)	Tree species choice procedure							
Monoculture (70%)	Mean potential productivity of Norway spruce (m^3 ha^{-1} yr^{-1})	Site quality class	Probability of respective tree species choice (%)					
			Spruce	Pine	Birch	Oak	Beech	Lime
	1-3	1	10	60	20	5	-	5
	3-6	2	30	40	20	5	-	5
	6-9	3	55	20	10	5	5	5
	9-12	4	65	5	10	5	10	5
	>12	5	75	-	-	10	10	5
Mixed (30%)	No of species in the patch (probability)		Proportion of different tree species					
			Species 1	Species 2	Species 3	Species 4		
	2 (80%)		70	30	-	-		
	3 (15%)		60	30	10	-		
	4 (5%)		50	30	15	5		

disturbances in Sweden (Zackrisson, 1977) – was assumed and implemented by destroying all vegetation on a particular patch with an annual probability of 0.01. Non-management disturbances were implemented only during the spinup phase of the simulations. Management practices were begun in each patch on a randomly selected year between 1850 and 1900. The output variables of interest were gridded values of biomass (ecosystem total and by tree species) and wood volume increment.

Soil characteristics within each grid cell were based on nine texture classes derived from the FAO global soil data set (Zobler, 1986; FAO, 1991) and the scheme given by Sitch *et al.* (2003). Atmospheric CO_2 concentrations for 1901-1998 were taken from a data set based on ice-core measurements and atmospheric observations, documented by Sitch *et al.* (2003). The 1901 value of 296 ppmv was used for the 300-year spinup phase of the simulations.

2.4 Species parameters

Species-specific parameters for trees followed Koca *et al.* (in press), which in turn followed the approach of Hickler *et al.* (2004). The two most common needleleaved tree species of Swedish

Table 2. Silvicultural programme for different yield classes and tree species.

Site quality class	Tree species	Stand age at thinning (yrs)	Percent of the volume thinned (%)	Rotation length (yrs)
1	Spruce, pine	74	30	139
	Birch	54	30	89
	Oak, beech, lime	74,89,109,124	20,20,30,30	144
2	Spruce, pine	54,74,104	25,25,20	124
	Birch	44,54,64	30,30,25	74
	Oak, beech, lime	64,74,84,94,104,119	20,20,20,20,30,30	134
3	Spruce, pine	39,59,74	30,30,30	104
	Birch	29,34,44,49	28,25,24,21	64
	Oak, beech, lime	54,59,64,74,84,94,104,114	15,15,15,15,20,20,30,30	129
4	Spruce, pine	29,39,49,59	30,30,25,25	79
	Birch	19,24,29,34,39	28,25,24,22,21	49
	Oak, beech, lime	49,54,59,64,69,74,84,94,104,114	15,15,15,15,15,15,20,20,30,30	124
5	Spruce, pine	19,29,39,49	30,30,25,25	64
	Birch	19,24,29,34,39	28,25,24,22,21	49
	Oak, beech, lime	44,49,54,59,64,69,74,79,89,99,109	15,15,15,15,15,15,20,20,20,30,30	119

Table 3. 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		
canopy 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 (kg C 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*. (2004)

[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).

forests, *Picea abies* (Norway spruce) and *Pinus sylvestris* (Scots pine), and four broadleaved species, *Betula pendula* (silver birch), *Fagus sylvatica* (beech), *Quercus* spp. (oak), and *Tilia cordata* (lime) were distinguished in the simulations (nomenclature follows Tutin *et al.* (1964 -1980)). Each tree species was assigned bioclimatic limits for establishment or survival (Skre, 1972; Prentice *et al.*, 1991; Sykes *et al.*, 1996c; Bradshaw *et al.*, 2000) and maximum non-stressed longevity (Prentice *et al.*, 1991; Bugmann, 1994). Concerning parameters relating to the physiology and life-history of species (Fulton, 1991; Haxeltine *et al.*, 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 (Table 3).

2.5 Model-data comparison

Simulation results of annual stem wood volume increments, averaged over consecutive 5-year time slices from 1983 to 1997, were compared to data from the Swedish National Forest Inventory for 29 forestry administrative regions (see inset map in Figure 1) (Swedish National Forest Inventory, 2005). For each 0.5° × 0.5° grid cell, model predictions of annual stem wood volume increment on a grid cell area basis were weighted by the fraction of the grid cell occupied by forest according to a gridded land use database (Schröter *et al.*, 2004), then aggregated to totals for forestry administrative regions in a geographic information system. For conversion to stem wood volume increments it was assumed that 65% of the total simulated wood volume increment (which implicitly includes coarse roots and fine branches) would contribute to measurable increases in stem volume (Shvidenko *et al.*, unpublished). A universal wood density of 250 kg C m^{-3}, the same value as used by the model, was assumed in the conversion of the simulated increment from mass to volume units.

3. RESULTS

3.1 Tree species composition, net primary productivity and LAI

Results showing the composition of managed forest ecosystems, averaged over the 15-year period of 1983-1997, suggested that some 58.3% of tree biomass in Sweden was Norway spruce, 31.3% Scots pine, giving a total of 89.6% needleleaved species. Broadleaved species accounted for 10.4% of the tree biomass (Table 4).

Over the 30 year period of 1969-1998, the model estimated average NPP values ranging from 0.033 kg C m^{-2} yr^{-1} in the northern Swedish mountains to 0.461 kg C m^{-2} yr^{-1} in the very south of Sweden (Figure 2). The geographic pattern is similar for LAI (Figure 3).

3.2 Net annual stem wood volume increment

The model estimated an area weighted mean net annual wood volume increment of 6.09 m^3 ha^{-1} yr^{-1} for Swedish managed forests during the period 1983-1997, somewhat overestimating the value of 5.11 m^3 ha^{-1} yr^{-1} reported in forest inventory statistics. Broken down regionally, the model estimates tend to be somewhat low in the south and high in the north, but generally comparable with observations in all regions of Sweden (Figure 1a).

Table 4. Comparison of tree species composition (area-averaged percentage of total biomass) – modelled vs observed (1983-1997).

Tree species	Tree species composition (%)	
	Modelled	Observed
Needleleaved	89.6	84.9
Spruce	58.3	46.4
Pine	31.3	38.5
Broadleaved	10.4	15.1

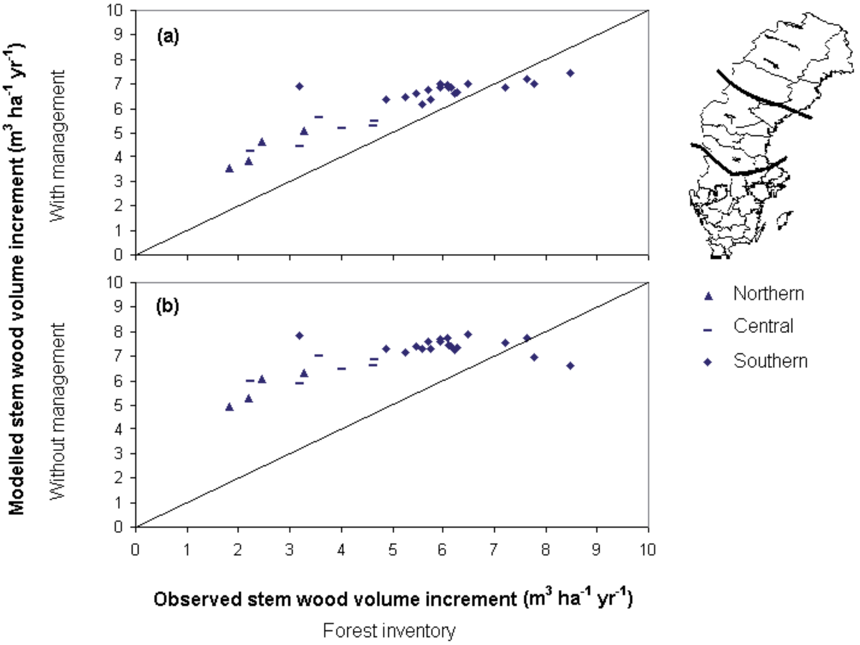
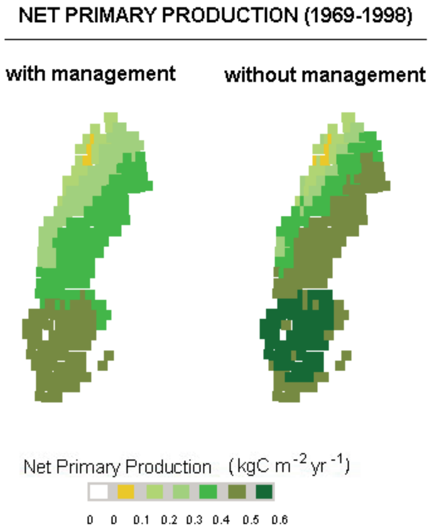


Figure 1. LPJ-GUESS model validation comparing simulated stem wood volume increment (m^3 ha^{-1} yr^{-1}) of managed (1a) and potential natural (1b) forests to Swedish National Forest Inventory data for 29 forestry administrative regions averaged over 15 years between1983-1997.



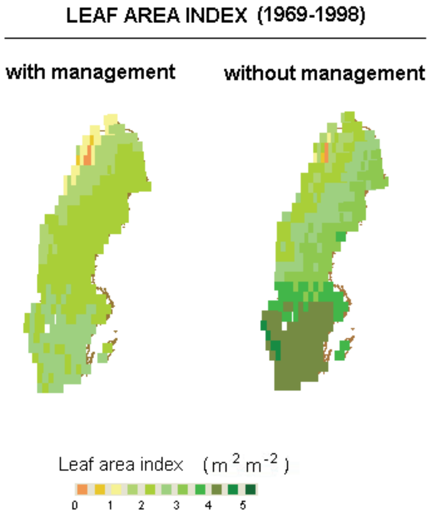


Figure 2. Spatial distribution of net primary production (NPP) of forest ecosystems in Sweden with and without forest management according to simulations with LPJ-GUESS, averaged over the time period 1969-1998. The results for unmanaged forests are reproduced from Koca *et al.* (in press).

Figure 3. Spatial distribution of leaf area index (LAI) of forest ecosystems in Sweden with and without forest management according to simulations with LPJ-GUESS, averaged over the time period 1969-1998. The results for unmanaged forests are reproduced from Koca *et al.* (in press).

4. DISCUSSION

4.1 Consequences of forest management practices on tree species composition and NPP

4.1.1 Tree species composition

Model estimates of the relative cover of needleleaved versus broadleaved tree species in Sweden compares well with the forest inventory data (Table 4). However, the tree species choice algorithm used in the model tends to favour spruce strongly, which resulted in about 10% higher values as compared to observations. The algorithm was developed based on forest statistics for the southern part of Sweden and application of it over the whole country appears to be causing an overestimate of the importance of this species, especially in northern forests in which Scots pine is of greater relative importance compared with southern areas.

4.1.2 Net primary productivity

The model results suggested highest NPP values in the southern part of Sweden and lowest values in the northern mountainous regions. For the boreal region, the model predicted intermediate productivity with a tendency to decline towards the north and northwest and the alpine zone in association with colder temperatures and a shorter growing season (Figure 2). The patterns of the spatial distribution of NPP are similar to a previous modelling study (Koca *et al.*, in press), where LPJ-GUESS was applied to assess the impacts of changing climate on the productivity of potential natural vegetation (which was simulated to be predominantly forest) for the same study area. Compared to the results of that study, simulated NPP values of managed forests are generally lower throughout Sweden (Figure 2). LAI is likewise lower in most areas when management is enabled, while the spatial distribution is similar with and without management. Spatial patterns are also similar for LAI and NPP (Figure 3). As light interception and utilization are key factors affecting the growth of forests, the LAI plays an important role in determining the productivity (Battaglia *et al.*, 1998b). The lower LAI in the management-enabled simulations is a result of differences in species composition, stem density and stand age resulting from the simulated forest management, as natural driving factors for production (*i.e.* climate, atmospheric CO_2 concentrations and soil type) were common to both studies.

Nevertheless, the model estimates of NPP for managed forests, averaged over 1969-1998, show closer agreement with estimates from remote sensing and field measurements, compared with model estimates for potential natural forests (Koca *et al.*, in press). Multi-year field measurements between 1973 and 1981, for example, showed that NPP was within the range of 0.215 to 0.462 kg C m^{-2} yr^{-1} in six evergreen conifer forest sites in Sweden and Finland (Gower *et al.*, 2001). In a remote sensing study, a mean NPP of 0.578±0.154 (s.d.) kg m^{-2} yr^{-1} (dry weight) was estimated for coniferous forest areas south of 66°N in Finland and Sweden (Zheng *et al.*, 2004). Assuming that half of ecosystem biomass is carbon (UN-ECE/FAO, 2000), this figure corresponds to an NPP in carbon mass units of approximately 0.3 kg C m^{-2} yr^{-1} (c.f. Figure 2).

4.2 Comparison of modelled and observed stem wood volume increment

The model estimates of annual wood volume increments of Swedish managed forests compare better with the forest inventory data (Figure 1a), than the estimates of volume increments of potential natural vegetation do (Figure 1b). When the model estimates are compared with the inventory statistics for each forestry region separately, the model seems to generally overestimate growth in northern and central Sweden, and underestimate growth in the very south (Figure 1). One likely explanation for model bias could be the existence of nitrogen limitations on production, which would tend to become more pronounced with lower average temperatures towards to the north (Bergh *et al.*, 1999). Direct constraints of nitrogen availability on production are not taken into account by LPJ-GUESS. The apparent underestimation of the annual wood volume increment in the very south of Sweden might, conversely, be the result of the fertilization effect of the high atmospheric deposition loads of reactive nitrogen there (Aber, 1992; Bergh *et al.*, 1999). It should be noted that the model nevertheless seems to predict reasonable overall levels of NPP and volume growth for Swedish forests. However, it has been argued that, due to nitrogen constraints on NPP, models lacking an explicit representation of the nitrogen cycle may amplify the carbon sequestration capacity of terrestrial ecosystems under future climates and CO_2 concentrations (Hungate *et al.*, 2003).

A relatively exceptional region is the Gotland Island located in the southeast, where the model overestimated the annual net stem wood volume increment (Figure 1). This is most probably due to negative effect of wind on productivity (Worrell, 1987), which is not included in the model.

4.3 Limitations and uncertainties in relation to the forest management module

There are a number of important limitations associated with the management module implemented in this study. The tree species choice algorithm and management scheme are based on the forest yield and growth statistics provided from various forest sites, primarily in southern Sweden (Fries, 1964; Carbonnier, 1971; Carbonnier, 1975; Eriksson, 1976; Agestam, 1985; Ekö, 1985). In the present study, however, the management scheme was applied not only in the south, but other parts of the study area, which may not be so reliable. The forest management module, in its current form, assumes that a fixed proportion (65%) of total biomass is in stem wood and this proportion is same for all tree species, quality classes and ages. However, in reality the percentage varies depending on the above three factors (Shvidenko *et al.*, unpublished).

Another important issue is the determination of the site quality, which is a poorly understood and ill-defined factor (Mäkelä *et al.*, 2000). In the simulations, site quality of a grid cell was assumed to be same everywhere in a grid cell (i.e. heterogeneity in a grid cell was not taken into account). However, in reality the site quality not only depends on water content and fertility of the soil, but topographic factors such as altitude, slope and proportion of rocks, and varies across the grid cell.

The current version of the model assumes that the tree choice algorithm and the management scheme remain same throughout the simulation periods. In the present study, the model did not consider, for example, a possible control of tree species composition to meet the changing needs and expectations (i.e. plantation of tall trees may not be preferred due to the risk of wind damage, or deciduous trees and Scots pine may not be preferred at certain areas due to increasing browsing etc.) during the simulation period. Similarly, modifications in thinning practices (timing and intensity) and changes in rotation lengths to meet a possible enhancement or decrease in the productivity were not considered in the simulations. This may be an important issue to consider, especially if the model is to be applied to investigate the managed forest dynamics in relation to changing climate and atmospheric CO_2 concentrations. Other sources of uncertainties include the parameterisation and process representations in LPJ-GEUSS resulting from limited knowledge of the underlying processes or the correct parameter values for scaling them, which have been discussed in detail in Zaehle et al., (2005) and Koca et al., (in press).

5. CONCLUSIONS

Comparison of the results of simulations by LPJ-GUESS with and without forest management for the same time period, demonstrated that the inclusion of prognostic forest management events in the simulations led to results showing closer agreement with the forest inventory data. In a subsequent study, the modified model can be applied under future scenarios of regional climate changes, exploring the potential consequences for the composition, growth and carbon sequestration of managed forests of Sweden. Results of such a study might be of key importance for decision/policy makers in developing better and more sustainable forest management strategies at regional and national level.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge the financial support from the Swedish Research Council for Environment, Agricultural Science & Spatial Planning (FORMAS), which is the Swedish National Member Organisation of International Institute for Applied Systems Analysis (IIASA). This research was carried out at IIASA, as part of the 2005 Young Scientists Summer Programme (YSSP). Dr. Markku Rummukainnen and Dr. Jouni Räisäsenen from the Rossby Centre of the Swedish Meteorological Office, are thanked for providing the regional climate model output. Land use data for Sweden were assembled by the European Union project ATEAM (Contract No. EVK2-2000-00075). The CRU05 climate data were kindly supplied by the Climate Research Unit, University of East Anglia.

REFERENCES

Aber, J.D., 1992. Nitrogen cycling and nitrogen saturation in temperate forest ecosystems, Trends in Ecology and Evolution, pp. 220-224.

Agestam, E., 1985. A growth model for mixed stands of pine, spruce and birch in Sweden., Department of Forest Yield Research. Swedish University of Agricultural Science. Report 15. 150 pp., Umeå.

Bachelet, D., Neilson, R.P., Hickler, T., Drapek R, J., Lenihan, J.M., Sykes, M.T., Smith, B., Sitch, S., Thonicke, K., 2003. Simulating past and future dynamics of natural ecosystems in the United States. Global Biogeochemical Cycles 17, 1045.

Badeck, F.W., Lischke, H.K., Bugmann, H., Hickler, T., Hönninger, K., Lasch, P., Lexer, M.J., Mouillot, F., Schaber, J., Smith, B., 2001. Tree species composition in European pristine forests. Comparison of stand data to model predictions, Climatic Change, pp. 307-347.

Battaglia, M., Sands, P.J., 1998a. Process-based forest productivity models and their application in forest management, Forest Ecology and Management, pp. 13-32.

Battaglia, M., Cherry, M.L., Beadle, C.L., Sands, P.J., Hingston, A., 1998b. Prediction of leaf area index in eucalypt plantations: effects of water stress and temperature. Tree Physiology 18, 521-528.

Bergh, J., Linder, S., Lundmark, T., Elfving, B., 1999. The effect of water and nutrient availability on the productivity of Norway spruce in northern and southern Sweden. Forest Ecology and Management 119, 51-62.

Bradshaw, R.H.W., Holmqvist, B.H., Cowling, S.A., Sykes, M.T., 2000. The effects of climate change on the distribution and management of Picea abies in southern Scandinavia, Canadian Journal of Forest Research, pp. 1992-1998.

Bugmann, H.K.M., 1994. On the ecology of mountainous forest in a changing climate: A simulation study, Swiss Federal Institute of Technology, Zurich, pp. 258.

Bugmann, H.K.M., 2001. A review of forest gap models, Climatic Change, pp. 259-305.

Bugmann, H.K.M., Yan, X., Sykes, M.T., Martin, P., Lindner, M., Desanker, P.V., Cumming, S.G., 1996. A comparison of forest gap models: model structure and behaviour., Climatic Change, pp. 289-313.

Carbonnier, C., 1971. Yield of beech in Sweden. Studia Forestalia Suecica 91.

Carbonnier, C., 1975. Yield of oak plantations in southern Sweden. Studia Forestalia Suecica 125.

Cramer, W., Bondeau, A., Woodward, F.I., Prentice, I.C., Betts, R.A., Brovkin, V., Cox, P.M., Fisher, V., Foley, J.A., Friend, A.D., Kucharik, C., Lomas, M.R., Ramankutty, N., Sitch, S., Smith, B., White, A., Young-Molling, C., 2001. Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. Global Change Biology 7, 357-373.

Drake, B.G., Gonzales-Meler, M.A., Long, S.P., 1997. More efficient plants: a consequence of rising atmospheric CO_2?, Annual Reviews of Plant Physiology and Plant Molecular Biology, pp. 609-639.

Ekö, P.-M., 1985. A growth model for Swedish forests, based on data from the national forest survey, Department of Silviculture. Swedish University of Agricultural Sciece. Report 16, Umeå.

Eriksson, H., 1976. Yield of Norway spruce in Sweden, Dept of Forest Yield Research. Swedish University of Agricultural Science. Report 41, Stockholm.

FAO, 1991. The digitized soil map of the world (release 1.0). World Soil Resources Report 67/1. Food and Agriculture Organization of the United Nations, Rome.

Fries, J., 1964. Yield of Betula verrucosa Ehrh. in middle Sweden and southern north Sweden. Studia Forestalia Suecica 14.

Fulton, M.R., 1991. Adult recruitment as a function of juvenile growth rate in size-structured plant populations, Oikos, pp. 102-105.

Gerten, D., Schaphoff, S., Haberlandt, U., Lucht, W., Sitch, S., 2004. Terrestrial vegetation and water balance—hydrological evaluation of a dynamic global vegetation model, Journal of Hydrology, pp. 249-270.

Gower, T., Krankina, O., Olson, R.J., Apps, M., Linder, S., Wang, C., 2001. Net primary production and cabon allocation patterns of Boreal forest ecosystems. Ecological Applications 11, 1395–1411.

Haxeltine, A., Prentice, I.C., 1996. BIOME3: an equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types, Global Biogeochemical Cycles, pp. 693-709.

Heimann, M., Esser, G., Haxeltine, A., Kaduk, J., Kicklighter, D.W., Knorr, W., Kohlmaier, G.H., McGuire, A.D., Melillo, J., Moore, B., Otto, R.D., Prentice, I.C., Sauf, W., Schloss, A., Sitch, S., Wittenberg, U., Wurth, G., 1998. Evaluation of terrestrial carbon cycle models through simulations of the seasonal cycle of atmospheric CO_2 - First results of a model intercomparison study, Global Biogeochemical Cycles, pp. 1-24.

Hickler, T., Smith, B., Sykes, M.T., Davis, M.B., Sugita, S., Walker, K., 2004. Using a generalized vegetation model to simulate vegetation dynamics in the western Great Lakes region, USA, under alternative disturbance regimes, Ecology, pp. 519-530.

Hungate, B.A., Dukes, J.S., Shaw, M.R., Luo, Y., Field, C.B., 2003. Nitrogen and Climate Change, Science, pp. 1512-1513.

IPCC, 2001a. Intergovernmental Panel on Climate Change. Climate Change 2001: The Scientific Basis. In: Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K., Johnson, C.A. (Eds.). Cambridge University Press, Cambridge.

IPCC, 2001b. Intergovernmental Panel on Climate Change. Climate Change 2001: Impacts, Adaptation and Vulnerability. In: McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J., White, K.S. (Eds.). Cambridge University Press, Cambridge.

Johnsen, K., Samuelson, L., Teskey, R., McNulty, S., Fox, T., 2001. Process models as tools in forestry research and management, Forest Science, pp. 2-8.

Kellomäki, S., Kolström, M., 1993. Computations on the yield of timber by Scots pine when subjected to varying levels of thinning under a changing climate in southern Finland. Forest Ecology and Management 59, 237-255.

Koca, D., Sykes, M.T., Smith, B., in press. Modelling regional climate change effects on potential natural ecosystems in Sweden. Climatic Change.

Lasch, P., Lindner, M., Erhard, M., Suckow, F., Wenzel, A., 2002. Regional impact assessment on forest structure and functions under climate change - the Brandenburg case study. Forest Ecology and Management 162, 73-86.

Lasch, P., Badeck, F.W., Suckow, F., LIndner, M., P., M., 2005. Model-based analysis of management alternatives at stand and regional level in Brandenburg (Germany). Forest Ecology and Management 207, 59-74.

Lasch, P., Lindner, M., Ebert, B., Flechsig, M., Gerstengarbe, P.-W., Suckow, F., Werner, P.C., 1999. Regional impact analysis of climate change on natural and managed forests in the Federal State of Brandenburg, Germany, Environmental Modelling and Assessment, pp. 273-286.

Leemans, R., Prentice, I.C., 1987. Description and simulation of tree-layer composition and size distributions in a primaeval *Picea-Pinus* forest. Vegetatio 69, 147-156.

Lexer, M.J., Honninger, K., Scheifinger, H., Matulla, C., Groll, N., Kromp-Kolb, H., Schadauer, K., Starlinger, F., Englisch, M., 2002. The sensitivity of Austrian forests to scenarios of climatic change: a large-scale risk assessment based on a modified gap model and forest inventory data. Forest Ecology and Management 162, 53-72.

Lindner, M., 2000. Developing adaptive forest management strategies to cope with climate change. Tree Physiology 20, 299-307.

Lindner, M., Lasch, P., Erhard, M., 2000. Alternative forest management strategies under climatic change - prospects for gap model applications in risk analyses. Silva Fennica 34, 101-111.

Lindner, M., Bugmann, H., Lasch, P., Flechsig, M., Cramer, W., 1997. Regional impacts of climatic change on forests in the state of Brandenburg, Germany. Agricultural and forest meteorology 84, 123-135.

Lucht, W., Prentice, I.C., B. Myneni, R., Sitch, S., Friedlingstein, P., Cramer, W., Bousquet, P., Buermann, W., Smith, B., 2002. Climatic Control of the High-Latitude Vegetation Greening Trend and Pinatubo Effect, Science, pp. 1687-1689.

Mäkelä, A., Landsberg, J., Ek, A.R., Burk, T.E., Ter-Mikaelian, M., Ågren, G.I., Oliver, C.D., Puttonen, P., 2000. Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. Tree Physiology 20, 289–298.

Monserud, R.A., 2003. Evaluating forest models in a sustainable forest management context. Forest Biometry, Modelling and Informations Sciences 1, 35-47.

Morales, P., Sykes, M.T., Prentice, I.C., Smith, P., Smith, B., Bugmann, H., Zierl, B., Friedlingstein, P., Viovy, N., Sabaté, S., Sánchez, A., Pla, E., Gracia, C.A., Sitch, S., Arneth, A., Ogee, J., 2005. Comparing and evaluating process-based ecosystem model predictions of carbon and water fluxes in major European forest biomes. Global Change Biology 11, 2211-2233.

New, M., Hulme, M., Jones, P.D., 1999. Representing twentieth century space-time climate variability. Part1: development of a 1961-90 mean monthly terrestrial climatology. Journal of Climate 12, 829-856.

New, M., Hulme, M., Jones, P.D., 2000. Representing twentieth-century space-time climate variability. Part 2: development of 1901-1996 monthly grids of terrestrial surface climate. Journal of climate 13, 2217-2238.

Prentice, I.C., Helmisaari, H., 1991. Silvics of north European trees: Compilation, comparisons and implications for forest succession modelling, Forest Ecology and Management, pp. 79-93.

Prentice, I.C., Sykes, M.T., Cramer, W., 1993. A simulation model for the transient effects of climate change on forest landscapes. Ecological Modelling 65, 51-70.

Renn, O., Goble, R., Kastenholz, H., 1998. How to apply the concept of sustainability to a region. Technological Forecasting and Social Change 58, 63-81.

Schröter, D., Acosta-Michlik, L., Arnell, A.W., Araújo, M.B., Badeck, F., Bakker, M., Bondeau, A., Bugmann, H., Carter, T., de la Vega-Leinert, A.C., Erhard, M., Espiñeira, G.Z., Ewert, F., Fritsch, U., Friedlingstein, P., Glendining, M., Gracia, C.A., Hickler, T., House, J., Hulme, M., Kankaanpää, S., Klein, R.J.T., Krukenberg, B., Lavorel, S., Leemans, R., Lindner, M., Liski, J., Metzger, M.J., Meyer, J., Mitchell, T., Mohren, F., Morales, P., Moreno, J.M., Reginster, I., Reidsma, P., Rounsevell, M., Pla, E., Pluimers, J., Prentice, I.C., Pussinen, A., Sánchez, A., Sabaté, S., Sitch, S., Smith, B., Smith, J., Smith, P., Sykes, M.T., Thonicke, K., Thuiller, W., Tuck, G., van der Werf, G., Vayreda, J., Wattenbach, M., Wilson, D.W., Woodward, F.I., Zaehle, S., Zierl, B., Zudin, S., Cramer, W., 2004. Advanced Terrestrial Ecosystem Analysis and Modelling (ATEAM) final report 2004 - Detailed report related to overall project duration. Potsdam Institute for Climate Impact Research (PIK), Potsdam, Germany.

Shugart, H., Sedjo, R., Sohngen, B., 2003. Forests & Global Climate Change: Potential Impacts on U.S. Forest Resources, Pew Center on Global Climate Change, Arlington, VA.

Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer W., Kaplan, J., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K., Venevsky, S., 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ Dynamic Global Vegetation Model. Global Change Biology 9, 161-185.

Skre, O., 1972. High temperature demands for growth and development in Norway spruce (Picea abies (L.) Karst.) in Scandinavia. Agricultural University of Norway, pp. 29.

Smith, B., Prentice, I.C., Sykes, M.T., 2001. Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. Global Ecology and Biogeography 10, 621-637.

Swedish National Forest Inventory, 2005. Department of Forest Recource Management and Geomatics, Swedish University of Agricultural Sciences, Umeå. Statistics home page http://www-nfi.slu.se/

Sykes, M.T., Prentice, I.C., 1996a. Climate change, tree species distributions and forest dynamics: A case study in the mixed conifer/northern hardwoods zone of northern Europe. Climatic Change 34, 161-177.

Sykes, M.T., Prentice, I.C., 1996b. Climate change, tree species distributions and forest dynamics: a case study in the mixed conifers / northern hardwoods zone of northern Europe. Climatic Change 34, 161-177.

Sykes, M.T., Prentice, I.C., Cramer, W., 1996c. A bioclimatic model for the potential distribution of north European tree species under present and future climates, Journal of Biogeography, pp. 203-233.

Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M., Webb, D.A., 1964 -1980. Flora Europaea. Cambridge University Press, Cambridge.

UN-ECE/FAO, 2000. Forest Resources of Europe, CIS, North America, Australia, Japan and New Zealand. Main Report. Geneve Timber and Forest Study Papers, No. 17. United Nations Economic Commission for Europe (Geneva), Food and Agriculture Organization of the United Nations, Rome.

Worrell, R., 1987. Geographical variation in sitka spruce productivity and its dependence on environmental factors. Ph.D. Thesis, Edinburgh University, Edinburgh.

Zackrisson, O., 1977. Influence of forest fires on the North Swedish boreal forest, Oikos, pp. 22-32.

Zaehle, S., Sitch, S., Smith, B., Hatterman, F., 2005. Effects of parameter uncertainties on the modeling of terrestrial biosphere dynamics. Global Biogeochemical Cycles 19, GB3020, doi:3010.1029/2004GB002395.

Zheng, D., Prince, S., Hame, T., 2004. Estimating net primary production of boreal forests in Finland and Sweden from field data and remote sensing. Journal of Vegetation Science 15, 161–170.

Zobler, L., 1986. A world soil file for global climate modelling. NASA Technical Memorandum 87802. NASA Goddard Institute for Space Studies, New York.