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Partitioning direct and indirect human-induced effects on carbon sequestration of managed coniferous forests using model simulations and forest inventories

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Abstract

Temperate forest ecosystems have recently been identified as an important net sink in the global carbon budget. The factors responsible for the strength of the sinks and their permanence, however, are less evident. In this paper, we quantify the present carbon sequestration in Thuringian managed coniferous forests. We quantify the effects of indirect human-induced environmental changes (increasing temperature, increasing atmospheric CO_2 concentration and nitrogen fertilization), during the last century using BIOME-BGC, as well as the legacy effect of the current age-class distribution (forest inventories and BIOME-BGC). We focused on coniferous forests because these forests represent a large area of central European forests and detailed forest inventories were available.

The model indicates that environmental changes induced an increase in biomass C accumulation for all age classes during the last 20 years (1982–2001). Young and old stands had the highest changes in the biomass C accumulation during this period. During the last century mature stands (older than 80 years) turned from being almost carbon neutral to carbon sinks. In high elevations nitrogen deposition explained most of the increase of net ecosystem production (NEP) of forests. CO_2 fertilization was the main factor increasing NEP of forests in the middle and low elevations.

According to the model, at present, total biomass C accumulation in coniferous forests of Thuringia was estimated at $1.51\,t\,C\,ha^{-1}\,yr^{-1}$ with an averaged annual NEP of $1.42\,t\,C\,ha^{-1}\,yr^{-1}$ and total net biome production of $1.03\,t\,C\,ha^{-1}\,yr^{-1}$ (accounting for harvest). The annual averaged biomass carbon balance (BCB: biomass accumulation rate-harvest) was $1.12\,t\,C\,ha^{-1}\,yr^{-1}$ (not including soil respiration), and was close to BCB from forest inventories ($1.15\,t\,C\,ha^{-1}\,yr^{-1}$). Indirect human impact resulted in 33% increase in modeled biomass carbon accumulation in coniferous forests in Thuringia during the last century. From the forest inventory data we estimated the legacy effect of the age-class distribution to account for 17% of the inventory-based sink. Isolating the environmental change effects showed that these effects can be large in a long-term, managed conifer forest.

Keywords: carbon sequestration, climate change, forest inventory data, Kyoto protocol, managed forests, modeling, stand age

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Introduction

During the last decades it has become more and more obvious that anthropogenic CO_2 emissions in the world must be reduced to diminish global warming. The Kyoto protocol (UNFCC-United Nations Framework Convention on Climate Change – http://unfccc.int/) allows accounting for increased carbon sinks related to direct human-induced activities such as afforestation and reforestation as well as additional agricultural or forestry activities leading to CO_2 reduction. The increase in carbon sequestration associated with

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indirect human-induced effects, i.e. increased temperature, CO_2 and nitrogen fertilization, however, is not accountable. It is a challenge although to separate direct from indirect human-induced carbon sources and sinks.

A number of recent studies demonstrated that European forests have been a significant carbon sink over the last decades and presented several explanatory variables such as CO_2 fertilization, increased temperatures and increased nitrogen deposition as well as forest management (Kauppi *et al*., 1992; Spiecker *et al*., 1996; Townsend *et al*., 1996; Delucia *et al*., 1999; Nadelhoffer *et al*., 1999; Beck, 2000; McGuire *et al*., 2001; Mund *et al*., 2002; Houghton, 2003; Nabuurs *et al*., 2003). However, they have not been able to determine relative contributions of those factors. Mund *et al*. (2002) showed that the standing biomass of a spruce chronosequence in Central Germany was 150–300% higher than the one indicated in standard yield tables, and attributed this discrepancy to the synergistic effects of management and environmental changes. Nabuurs *et al*. (2003) suggested that the increased European forest carbon sink might be associated with a large area of managed young forest age classes, which typically accumulate carbon at high rates. At the same time, management of the European forests has also improved site quality through fertilization and peat-land drainage programs (Kauppi *et al*., 1992; Spiecker *et al*., 1996; Beck, 2000). Many forest sites strongly degraded by litter raking in the past are still recovering. Furthermore, timber harvest has been reduced from 90% to 95% of annual increment in 1950 to about 55% at present, leading to increasing vegetation carbon stocks in European forests. Environmental changes (increased temperature, increased CO_2 and nitrogen fertilization), may also contribute to the faster site recovery, but the magnitudes of the effects are uncertain (Spiecker *et al*., 1996; Townsend *et al*., 1996; DeLucia *et al*., 1999; Nadelhoffer *et al*., 1999; Caspersen *et al*., 2000; McGuire *et al*., 2001; Houghton, 2003). A recent estimate of the forest carbon sink of Europe is 363 Tg carbon per year (Janssens *et al*., 2003). This estimate suggests that the European carbon sink absorbs about 20% of the European anthropogenic emissions (Janssens *et al*., 2003).

To distinguish between direct and indirect human impacts on forest carbon sequestration, it is necessary to look at the appropriate spatial and temporal scales where anthropogenic influences become quantifiable. Studies at larger scales have frequently investigated the impact of environmental changes on carbon sequestration (Churkina *et al*., 1999; Churkina & Running, 2000; Nabuurs *et al*., 2002), but failed to discriminate the direct human influence because indirect and direct effects overlap. Studies at local scales indicate that young and old stands react differently to environmental conditions (Law *et al*., 2001; Anthoni *et al*., 2002; Mund *et al*., 2002), probably because tree physiology changes with age (Ryan *et al*., 2000). On the other hand it is difficult to isolate the factors contributing to changes in forest carbon sequestration by experiments alone. Hence, very few experiments deal with this separation. Ecosystem models offer a possibility to 'translate' knowledge gained in field experiments to landscape or biome scales.

With this study we present a regional quantification of the relative contribution of different aspects of forest management and climatic and atmospheric forcing to changes in carbon stocks and fluxes using coniferous forests in Thuringia (confederate state of Germany) as a study area. Norway spruce covers 68% of the coniferous forest and 49% of the total forest area. The only other important coniferous is Scots pine comprising 31% of the coniferous forests and 22% of the total forest area. In Thuringia, the current structure and age-class distribution of coniferous forests is the result of more than two centuries of intense forest management. Knowledge of site history is thus essential for understanding carbon dynamics and for simulating carbon sequestration in these ecosystems. We combine model simulations performed with the ecosystem model BIOME-BGC (Thornton *et al*., 2002) and detailed analyses of geographic information system (GIS)-based soil and forest inventories (Thuringian State Institute for Forestry, Game and Fishery; TLWJF) to investigate both the effect of climate and changing environmental factors on carbon sequestration in coniferous forests during the last century. We address the following questions: What was the magnitude of the biomass carbon sink during the last 20 years (1982–2001)? How well do model simulations and inventory-based estimates match? What fraction of this sink is induced by climatic and atmospheric changes and how much of it can be explained by forest management?

Methods

Separating the indirect and direct human-induced effects on the carbon sequestration of a managed forest is not straight forward. As suggested by IPCC (2003) the environmental effect is relatively easy to separate with the help of model simulations. Our model scenarios represent cases C and D according to IPCC (2003). The direct human-induced effects are estimated using the age-class distribution from the forest inventories. Table 1 shows an overview of how the different scenarios and how the indirect and direct human-induced effects on the carbon sequestration are resolved. A more detailed description of the methods is given below.

Initialization of climate and soil conditions

The GIS of the Thuringian forest service (TLWJF, Thuringian State Institute for Forestry, Game and Fishery, unpublished) was used to extrapolate detailed point measurements of climate and soil texture to environmental strata at the landscape level. The forest–GIS encompasses a forest area of more than 500 000 ha (92% of total forest area) and lists entries for over 300 000 individual stands. The site conditions are characterized by six environmental layers, which provide qualitative information on climate and soil conditions for each stand.

In the forest–GIS combinations of elevation (five classes) and exposition in relation to the main wind direction (six classes) are used to define a total of 18 topographic climate classes. Each of these is characterized by a 50 years average of mean annual temperature (MAT) and precipitation based on data which were recorded in climate stations throughout Thuringia between 1900 and 1950 (Fig. 1a – open triangles). The 18 classes were further aggregated to three climate strata based on their position in the precipitation–temperature space (Fig. 1a – boxes). Note that the topographic climate classes do not exactly correspond to altitudinal bands, because of the differentiating effect of exposition. Hourly climate data from 11 stations covering the period from January 1972 to December 2001 (temperature, relative humidity and daily precipitation sum) were acquired from the German Meteorological Society (DWD, Offenbach, Germany) with the aim to construct mean climate series representative for each of the three climate strata. However,

Table 1 Methods used for estimating direct and indirect human-induced effects on carbon sequestration of a managed forest using forest inventories and model simulations

	Forest inventories	Model simulations
Baseline (B)		1
Present (P)	Growth harvest (1993)	2
Indirect human-induced effects	Actual vs. ideal age-class distribution (legacy age effect)	2-1 and legacy age effect
Direct human-induced effects	Age class shift (1993–2001)	Age class shift (1993–2001)

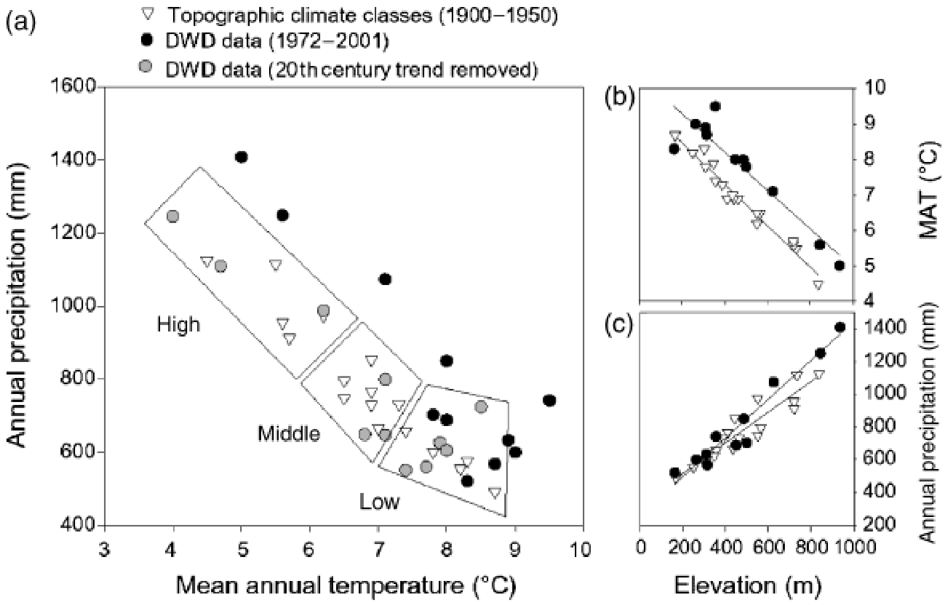

Fig. 1 Elimination of trend in climate data from German Weather Service (DWD) in climate space (mean annual temperature vs. mean annual precipitation), with the aim to make DWD data and climate data from the Forest Service comparable. The DWD data were grouped in the climate groups based on quality site maps (the eclipses marked the three climate classes and indirectly the high, middle and low elevation classes).

Table 2 Average values of temperature and precipitation of the DWD climate stations defining the elevation classes. The measurement period was from 1972 until 2002

Class	Annual averaged temperature (°C)	Precipitation (mm)	Elevation (m a.s.l.)	Stations
High	5.9	1243.3	802 (626–937)	Schmücke, Neuhaus am Rennweg, Sonneberg
Middle	8.4	764.6	448 (356–487)	Kaltennordheim, Schleiz, Leinefelde
Low	8.5	601.6	297 (164–450)	Gera, Meiningen, Weimar, Artern

climate change in Thuringia during the 20th century has complicated the assignment of stations to the three climate classes (note position of filled circles in Fig. 1a outside the boxes). An ANCOVA, with elevation as covariate, revealed a significant increase in MAT by 0.93 °C (95% CI 0.64−1.21, $F_{[1]} = 44.8$, $P < 0.001$, Fig. 1b) between the two measurement periods independent of elevation. At the same time precipitation increased by 100–150 mm only at higher elevation (interaction between elevation and measurement period: $F_{[2]} = 128.0$, $P < 0.001$, Fig. 1c). These models were used to remove the 20th century climate change trend from the DWD data in order to reconcile the position of the thus transformed mean values of MAT and precipitation (grey circles in Fig. 1a) with the historical climate classes. The resulting assignment of stations to climate strata which form the link to the GIS database is shown in Table 2.

Soil texture is an important driver variable in BIOME-BGC because it affects the ability of soil to store water. The water status of the soil influences the transpiration rate and thus the productivity and the microbial activity. Data on particle size distribution exist for 132 soil profiles in Thuringia (VEB Forstprojektierung Potsdam, 1987) which were established to characterize the substrate group which is one of four site quality indicators in the forest–GIS. On a ternary plot (percentage clay vs. silt vs. sand) the profiles fall into three distinct clusters (Fig. 2). Profiles of the substrates 'carbonate-rich', 'silt/loam' and 'clay' were pooled to form the texture stratum '*fine*'. Profiles of the substrate group 'loam' and 'silicaceous' form the texture stratum 'medium' and profiles on the substrate 'sand' or 'sandstone' form the texture stratum 'coarse' (Table 3).

Combining the three topographic climate classes ('low', 'middle' and 'high' elevation) and the three soil texture classes ('fine', 'medium' and 'coarse') the coniferous forest area of Thuringia (383 400 ha) is divided into nine environmental strata. Since in four of those the forest area was less than 0.5% of the total, we analyzed only the five most important environmental strata: high elevation/medium soil texture, middle elevation/medium soil texture and low elevation class with the texture strata coarse, medium and fine (Table 4). In the following we define these strata as elevation classes.

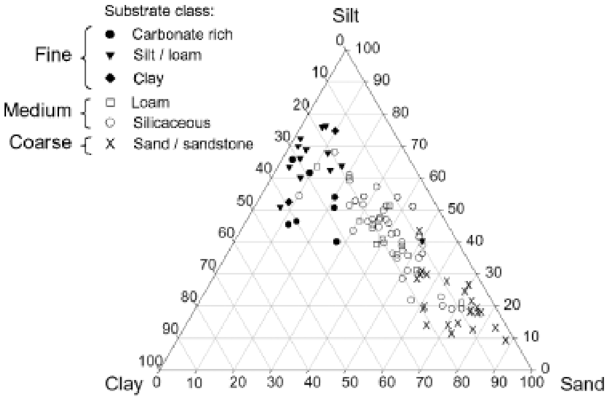

Fig. 2 The percentage of sand, silt and clay content of the 132 soil profiles in Thuringia (VEB Forstprojektierung Potsdam, 1987) fall into three distinct clusters. Profiles of the substrates 'carbonate-rich', 'silt/loam' and 'clay' form the texture stratum '*fine*'. Profiles of the substrate group 'loam' and 'silicaceous' form the texture stratum 'medium' and profiles on the substrate 'sand' or 'sandstone' form the texture stratum 'coarse'.

The Present environmental scenario

To simulate the present biomass carbon pool for all age classes at all elevations we needed to estimate long-term climate time series. For each of the elevation classes defined above, we ran MT-CLIM (Thornton *et al.*, 2000) for each station, then averaging the time series spatially over the stations for each elevation class. To achieve a long-term climate record, we looped the 30 years of data (present time series) for each elevation class. To account for the fact that the MAT has increased by about 1 °C during the 20th century, the DWD temperature series was progressively lowered by 1 °C over a 60-year ramp phase from 1972 back to 1912.

Table 3 Definition of soil texture classes based on 132 soil profiles from Thuringia (VEB, 1987) used in the model simulations

Soil classes	Associated substrate groups	Sand fraction (%)	Silt fraction (%)	Clay fraction (%)
Coarse	Sand	65.6 ± 12.5	22.7 ± 10.1	11.7 ± 6.2
Medium	Silica, loam, clay	40.5 ± 13.8	42.4 ± 11.9	16.6 ± 5.3
Fine	Carbonate, silt, loam, clay	14.7 ± 12.4	58.1 ± 11.3	27.2 ± 8.7

Table 4 The area distribution of needle-leaf forest in percent of the nine possible elevations (EC) and soil texture (SC) classes (numbers in parentheses are area in hectares)

	SC coarse	SC medium	SC fine
EC 'high'	0.4	23.7 (88 439)	0.2
EC 'middle'	0.1	17.0 (59 147)	0.2
EC 'low'	28.8 (106 233)	12.8 (61 433)	16.9 (124 882)

Only five combined classes contributed significantly to the total area occupied by the needle-leaf forest.

Before 1912 the DWD climate series was looped with the reduced temperature.

The precipitation did not change during the last century (slight increase in the highest elevation class) and we therefore selected the station matching best the annual averaged precipitation over all stations belonging to the actual elevation class. Water vapor deficit and radiation were estimated with MT-CLIM (Thornton *et al.*, 2000). Because we only had the long-term series for the averaged maximum and minimum temperature, we ran MT-CLIM with these averaged temperatures and received VPD and radiation values corresponding with the reduced temperatures. Because these values were biased towards too low values of radiation and VPD compared with the present climate series described above, we adjusted the long-term climate series with a correction obtained from running the present climate series with the averaged max and min values as done in the long-term series then correlating it to the present climate series. We obtained a linear correlation line for both VPD and radiation. High elevation: $\text{rad} = 0.99\text{rad}_1 + 86$, $R^2 = 0.93$; $\text{VPD} = 0.71\text{VPD}_1 + 133$, $R^2 = 0.76$; middle elevation: $\text{rad} = 0.94\text{rad}_1 + 85$, $R^2 = 0.82$; $\text{VPD} = 0.85\text{VPD}_1 + 97$, $R^2 = 0.64$; low elevation: $\text{rad} = 0.97\text{rad}_1 + 46$, $R^2 = 0.94$; $\text{VPD} = 0.98\text{VPD}_1 + 70$, $R^2 = 0.84$. This way, we obtained an artificial long-term climatic record, describing the temperature increase in the last century and still covering the typical climate conditions in Central Europe. CO_2 concentrations have steadily increased since the preindustrial time. From 1642 until present, we used an exponential increase of CO_2, from 276.9 reaching 368 ppm in 2000 (Prentice *et al.*, 2001). We used the actual CO_2 development during the three rotational periods of each 120 years reaching 370 ppm in 2001. The nitrogen deposition first started to increase strongly in the second half of the last century mainly because of increased burning of fossil fuel. In the Present scenario the N deposition was kept constant on the preindustrial level ($2\,\text{kg}\,\text{ha}^{-1}\,\text{yr}^{-1}$) until 1959 and then continuously increased to $\sim 32\,\text{kg}\,\text{ha}^{-1}\,\text{yr}^{-1}$ in 2001 for all elevations. The N-deposition scenario was taken from the EMEP model (Jonson *et al.*, 1998) based on measurements of the total N deposition in Tharandt (Germany) and Brasschat (Belgium) during the 1990s (Churkina *et al.*, 2003).

The Baseline environmental scenario

The Baseline scenario represents preindustrial conditions for our model estimates. Subtracting the Baseline scenario from the Present scenario, we estimate the effect of the increasing temperature and increasing CO_2 and nitrogen fertilization during the last centuries. The Baseline climate time series was obtained by reducing the temperature by 1 °C for each elevation class compared with the 'Present' climate time series from 1972 to 2001. The long-term Baseline climate series was obtained by looping this reduced time series from 1642 until 2001. Precipitation did not change during the last century, so precipitation was used as measured in the period 1972–1971. The atmospheric CO_2 concentration was set constant at 276.9 ppm (before 1642) (Prentice *et al.*, 2001). The atmospheric nitrogen deposition in the Baseline scenario was initialized at $2\,\text{kg}\,\text{ha}^{-1}\,\text{yr}^{-1}$ which is the highest preindustrial estimate reported by Holland *et al.* (1999).

Model and model simulations

The model. We used the biogeochemical model BIOME-BGC (version 4.1) which simulates carbon, nitrogen and water fluxes in a terrestrial ecosystem (Running, 1994; Hunt *et al.*, 1996; Thornton *et al.*, 2002). The model was successfully evaluated for a wide range of hydrological and carbon ecological components (Nemani & Running, 1989; Band *et al.*, 1993; Churkina *et al.*, 1999; Churkina & Running, 2000). In recent years, the model has been validated with eddy-covariance data (Anthoni *et al.*, 2002; Law *et al.*, 2002; Thornton *et al.*, 2002; Churkina *et al.*, 2003; Law *et al.*, 2003). The general ecophysiological parameter scheme for evergreen needle leaf forest was used.

The BIOME-BGC model was originally developed for natural forest ecosystems (Running & Gower, 1991). Owing to the fact that the forests of Europe have been managed for centuries, we chose to adjust the whole-plant mortality rate to reflect the mortality regime imposed by density regulation, which is an integral part of the German management practice (Assmann, 1968): Forest inventory data (FID) from the beginning of the 20th century were used to achieve the mortalities of a natural and a managed forest under almost preindustrial conditions (temperature and CO_2 concentration only moderately increased, no increase in nitrogen deposition: Baseline scenario). The stronger mortality regime in managed forests was achieved in the model by adjusting the mortality parameter (0.03 years^{-1}).

To simulate natural forest dynamics in an undisturbed forest, we reviewed the literature on long-term thinning experiments (Carbonnier, 1957; Franz, 1983; Kramer, 1988; Wenk *et al*., 1990). We assumed a moderate thinning level as characteristic for the past forest management in Thuringia. At the end of the rotation period, control plots typically exceeded the standing volume of moderately thinned stands by 25–50% (Gingrich, 1971; Kramer, 1988; Nyland, 1996). The whole-plant mortality was tuned (decreased to 0.015 years^{-1}) to approximate the dynamics in control plots. Spinup was done using the natural whole-plant mortality of 0.015 years^{-1} together with the preindustrial climate scenario, constant preindustrial CO_2 concentration (276.9 ppm) and N deposition ($2\,\text{kg C ha}^{-1}\,\text{yr}^{-1}$).

Simulation of the forest age dynamics. A large fraction of the Thuringian forest area (95.5%), is dominated by even-aged forests forming a mosaic of age classes at landscape level. This implies that depending on their age today's forests have experienced the recent changes in climatic and atmospheric forcing during different developmental stages. It is well documented although that young stands are more reactive towards environmental changes than mature stands (Mund *et al*., 2002). To account for differences in sensitivity, we performed age-class-specific model runs. In Europe (or Thuringia), coniferous forests are managed in rotations of up to 120 years. Only 2.6% of coniferous forests exceed a stand age of 120 years. Following the inventory scheme we grouped the population of stands into 20-year age classes and simulated the development of the resulting six cohorts (today 20, 40, 60, 80, 100 and 120 years old) starting in the years 1882, 1902, 1922, 1942, 1962 and 1982, respectively.

All state variables of interest to our study, such as various carbon pools, net primary production (NPP), heterotrophic respiration (R_h) and net ecosystem production (NEP) as the difference between NPP and R_h reveal a distinct age pattern (Heinsdorf *et al*., 1986; Janisch & Harmon, 2002; Wirth *et al*., 2002) (i.e. stand age is an indispensable predictor for scaling up stocks and fluxes to the landscape level). For consistency, we averaged the annual biomass C pool, annual biomass accumulation and NEP over the last 20 years (from 1982 to 2001) for each run to the actual stand age. To investigate the relative effect of environmental changes (*E*) for the modeled fluxes on each age class, we used a normalization formula as follows:

$$E = \frac{|\text{flux}_{\text{Present}} - \text{flux}_{\text{Baseline}}|}{|\text{flux}_{\text{Present}}| + |\text{flux}_{\text{Baseline}}|},$$

where E ranges between 1 and 0, where 1 means a strong effect and 0 means no effect of environmental changes on the specific age class.

The total coverage area for each modeled age class was obtained from FID established in the beginning of the 1980s (TLWJF, Thuringian State Institute for Forestry, Game and Fishery, 1992).

Simulation of site history. The conventional harvest through clear cutting constitutes a disturbance of the natural succession of coniferous forest. First, a large fraction of the carbon pool is lost through the extraction of merchantable wood (Kreutzer, 1979; Krapfenbauer & Buchleitner, 1981). Second, the microbial activity in the soil is boosted by the input of logging residues (Hakkila, 1989) and an increase in soil temperatures and moisture (Wittich, 1930; Hager, 1988). As a consequence, heterotrophic respiration and mineralization of nutrients is strongly increased causing a reduction in soil carbon stocks and an increase of nutrient availability. In addition, there is a reduced litter input after clear cut, which is also leading to a reduction of the soil carbon over time, and a reduced plant demand for mineral N immediately after harvest which can produce a big increase in net N mineralization but has little direct impact on gross N mineralization. A net loss of nutrients may occur if the nutrient availability exceeds uptake rates of the regenerating plant cover. To account for the ecological legacy of repeated harvests in the past (Johnson & Curtis, 2001; Churkina *et al*., 2003), we implemented a 'management' scheme: We let the model spinup with the mortality of a natural forest (0.015). After spinup, we initialized litter pools with site-specific data from Thuringia representative for managed forests (Table 5). This was necessary since the model, originally developed for natural forests, yielded unrealistically low litter pools compared with measured values. This disequilibrium causes a higher soil respiration than without initializing the litter pools. We then 'harvested' the forest according to the biomass allocation patterns in Wirth *et al.* (2004): 60% of the biomass pool was exported from the system as stem carbon. Forty percent of the biomass before harvest remained in the system redistributed in the following way: Branches, in total comprising 14% of the total biomass, were redistributed 7% to the litter pool. The other 7% was transferred to the coarse woody debris pool together with 20% of the root carbon pool. All of the leaf carbon pool (6% of biomass carbon pool) was transferred to the litter carbon pool. We 'replanted' the forest with plant pools equivalent to 1% of the biomass carbon and nitrogen pools of a mature stand before harvest. The leaf carbon pool was initialized with $0.06\,\mathrm{kg\,m^{-2}}$ at each planting. After cutting, the forest was allowed growing for 120 years. We repeated the harvest three times according to Pietsch & Hasenauer (2002), and then let the forest grow to the different stand ages (always ending in 2001, Fig. 3).

Simulation of C fluxes at landscape level. Because of the age and site dependence of carbon stocks and fluxes (e. g. NPP, NEP, R_a, R_h) the age-class distribution as well as the distribution of environmental strata has a strong influence on the landscape level estimates of these quantities. The total simulated fluxes of the conifer forests (Table 6) were calculated from the area fraction of the different age and site classes as follows:

$$\mathrm{flux}_{\mathrm{average}} = \frac{\sum_{j=1}^{j=5}\sum_{i=1}^{i=6}\mathrm{flux}_{ij}A_{ij}}{\sum_{j=1}^{j=5}\sum_{i=1}^{i=6}A_{ji}},$$

where A is the area (ha), j the indicator of the environmental strata (1–5: high–medium, middle–medium, low–coarse, low–medium and low–fine), and i the indicator of the age classes (1–6). Stands older than 120 years were assigned to the sixth age class.

To estimate the net change in carbon stocks at the landscape level (net biome productivity (NBP) since fire is not relevant in Thuringia NBP is not including fire), carbon losses through harvest H_C have to be subtracted from NEP (i.e. $\mathrm{NBP} = \mathrm{NEP} - H_C$). H_C was calculated assuming that 60% of the biomass of mature trees at age 120 years is extracted. To account for the fact that stands are harvested exactly at age 120 years, 60% of the total biomass carbon of the sixth age class (spanning 20 years) was divided by 20 to arrive at an annual flux. Since the mortality rates in the model were adjusted to reflect the age trend of biomass carbon in the inventories, carbon that would in reality be extracted by thinning operations remains in the stand in form of litter and CWD. Because harvest statistics include an unknown proportion of thinning, applying them in calculating NBP would overestimate losses through double counting and thus underestimate NBP.

Table 5 Initial values of the litter carbon pools from measurements for the five combined elevation and soil classes used to adjust the simulated values as well as the original model values

Elevation class	Soil texture class	Litter layer measured ($\mathrm{t\,C\,ha^{-1}}$)	Litter layer (original model values) ($\mathrm{t\,C\,ha^{-1}}$)
High	Medium	32.4	7.9
Middle	Medium	30.4	6.9
Low	Coarse	21.5	6.2
Low	Medium	33.0	6.2
Low	Fine	35.6	5.9

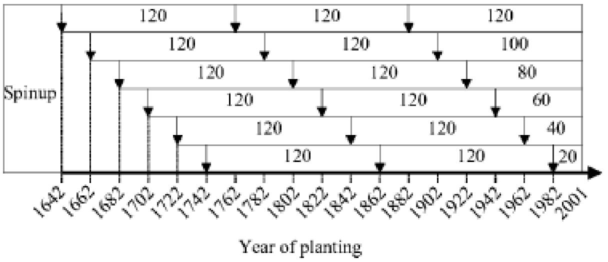

Fig. 3 Protocol of the model simulations. Each simulation was started with a 'spinup run' towards a steady state. Arrows indicates forest harvest and reallocation of the biomass not exported out of the system. The numbers indicates the number of years in each iteration.

Carbon fluxes from FID

The Thuringian forest inventory system serves to guide small-scale management decisions and is based on stand-level estimates of stand age, species composition, mean diameter, mean height and basal area. Standing stock and volume increment is estimated based on local yield tables with the above-mentioned quantities as input data. Unlike gridded point inventories based on permanent sample plots, the inventory here is exhaustive, and comprises data entries for all existing stands ($>300\,000$ stands in Thuringia with an average area of 1.5 ha). Since it takes about 7 years to acquire this large amount of data, there is no fixed reference date. However, in a single effort after the reunion of the two German states the complete database was synchronized for the year 1993 using a yield table-based extrapolation scheme for those stands that lacked recent measurements.

To convert increment of merchantable volume into carbon accumulation rates at the whole-tree level, new

Table 6 Important modeled components of the carbon cycle in the Thuringian coniferous forest under Baseline and Present scenarios divided into the five climate/soil classes

Site classes	Biomass ($\mathrm{t\,C\,ha^{-1}}$)	*GPP* (1)	R_a (2)	*NPP* (3) = (1)−(2)	R_h (4)	NEP (5) = (3)−(4)	H_C* (6)	NBP (7) = (5)−(6) ($\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$)	Biomass accumulation rate (8)	BCB (9) = (8)−(6)	Soil accumulation rate	Litter accumulation rate
Baseline												
High middle	107.03	17.43	9.87	7.56	6.13	1.43	0.27	1.17	1.78	1.51	−0.13	−0.18
Middle medium	99.14	15.93	9.46	6.47	5.91	0.56	0.19	0.37	1.19	1.00	−0.21	−0.31
Low coarse	84.13	13.68	8.20	5.48	4.99	0.49	0.17	0.32	1.02	0.84	−0.17	−0.26
Low middle	90.80	14.17	8.52	5.65	5.13	0.52	0.38	0.14	0.91	0.54	−0.15	−0.16
Low fine	98.56	14.57	8.79	5.79	5.19	0.59	0.62	−0.03	0.75	0.13	−0.08	0.00
Weighted average	**95.77**	**15.06**	**8.92**	**6.14**	**5.42**	**0.72**	**0.35**	**0.37**	**1.10**	**0.75**	**−0.14**	**−0.16**
Present												
High middle	124.67	21.80	12.71	9.10	6.71	2.39	0.30	2.09	2.28	1.99	0.05	0.12
Middle medium	107.71	18.53	11.19	7.33	6.21	1.13	0.20	0.93	1.58	1.38	−0.12	−0.20
Low coarse	95.60	16.97	8.44	6.57	5.44	1.13	0.19	0.94	1.40	1.21	−0.05	−0.11
Low middle	102.71	17.54	10.78	6.76	5.60	1.16	0.42	0.74	1.30	0.88	−0.03	0.001
Low fine	110.88	17.99	11.08	6.91	5.67	1.23	0.69	0.54	1.13	0.44	0.04	0.15
Weighted average	**108.39**	**18.52**	**10.74**	**7.30**	**5.89**	**1.42**	**0.39**	**1.03**	**1.51**	**1.12**	**−0.01**	**0.01**

The values constitute the area-weighted averages of the carbon fluxes of the different forest age classes in each class, respectively. The differences between classes not only arose through differences in the climate and soil texture, but also through differences in the age-class distribution. The area-weighted averages for the total Thuringian spruce forest are given in bold font.

*The carbon loss through harvest were calculated based on 60% of the carbon pool, that were reached after 120 years for the five classes, respectively. The calculations were based on modeled values.

GPP, gross primary production; NPP, net primary production; NEP, net ecosystem production; NBP, net biome production; BCB, biomass carbon balance.

generic biomass functions were developed for Norway spruce based on biomass data from 688 trees. These were combined with data on stand structure (309 fully inventories stands) to develop age- and site-specific conversion factors F_G (Wirth *et al.*, 2003, 2004). For Scots pine the age-specific conversion factors of Burschel *et al.* (1993) were used. We define the net change in biomass carbon resulting from growth and harvest as biomass carbon balance (BCB) (or the biomass component of NBP). BCB was quantified as the difference between the volume increment G in 1993 and the average growing stock volume H extracted annually as recorded in harvest statistics during the 1990s expressed in carbon units (termed G_{C} and H_{C}, respectively). For any given tree species,

$$\mathrm{BCB} = G_{\mathrm{C}} - H_{\mathrm{C}} = \sum_{i=1}^{n}\sum_{j=1}^{m}(AGF)_{ij} - HF_{\mathrm{M}},$$

where j indicates the m site quality classes (here different from environmental strata introduced above), i indicates the n age classes (here 1-year bins), A is the area (ha), G the growth as volume increment per unit area predicted by yield table based on inventoried growing stock and site quality ($\mathrm{m^3\,ha^{-1}\,yr^{-1}}$), F_G the site- and age-specific conversion factor from volume increment to biomass carbon accumulation ($\mathrm{t\,C\,m^{-3}}$) and H the state-wide estimate of harvest volume ($\mathrm{m^3\,ha^{-1}\,yr^{-1}}$) converted into carbon units with a generic conversion factor for mature trees F_{M} which is not site specific ($\mathrm{t\,C\,m^{-3}}$). It has been reported that yield tables tend to underestimate growth rates (Mund *et al.*, 2002; Pretzsch, 2002). BCB calculated as above therefore provides a minimum estimate of carbon accumulation.

Partitioning indirect and direct human-induced effects

The terms 'direct' and 'indirect' human-induced effects have been used in the Kyoto protocol to separate between increases in forest carbon sink size that result from deliberate (direct) management activities and those which come as windfall profit being indirectly caused by nitrogen deposition, $\mathrm{CO_2}$ fertilization, climate change or the legacy of past forest management (especially with respect to the age-class distribution) (Schulze *et al.*, 2002). The indirect effects of nitrogen deposition, $\mathrm{CO_2}$ fertilization and climate change are simply calculated as the difference between the modeling results of the Baseline and the Present scenario. Since there is no standard way to quantify the age-class effect we present two different approaches. First, we quantify the imprint of the current observed age-class distribution ($A_{\text{obs.}}$) on biomass carbon accumulation rates in comparison with an ideal even distribution of age classes ($A_{i=1,\dots,n} = 1/n\sum_i^n A_i = A_{\text{even}}$) with a rotation period of 100 years for spruce and 120 years for pine. A departure from an even age-class distribution will influence BCB because growth rates are age dependent with young forests exhibiting higher rates than old ones. Assuming that H_{C} is largely unaffected by changes in the age-class distribution this 'legacy' age effect is calculated as

$$\mathrm{BCB}_{\mathrm{age1}} = \sum_{i=1}^{n}\sum_{j=1}^{m}(A_{\text{obs.}}GF_G)_{ij} - \sum_{i=1}^{n}\sum_{j=1}^{m}(A_{\text{even}}GF_G)_{ij}.$$

A different age effect ($\mathrm{BCB}_{\mathrm{age2}}$) results from current shifts in the age-class distributions. Since mature forests generally have higher biomass carbon densities c per unit area than young forests any shift in the age-class distribution towards higher ages results in a positive $\mathrm{BCB}_{\mathrm{age2}}$ given that site-and age-specific carbon densities c_{ij} stay constant. Tracking the change in the age-class distribution requires a repeated inventory, which was not available for a large enough area. We therefore, projected the age-class distribution in 1993 forward into 2001 with constant c_{ij} of 1993 under the assumption that stands are harvested at 100 years for spruce and at 120 years for pine and thereafter replanted. Stands older than 120 years in 1993 (2.6% of the area) were left unharvested. This age effect is calculated as

$$\begin{aligned}\mathrm{BCB}_{\mathrm{age2}} &= (C'_{01} - C_{93})/\Delta t\\ &= \left(\sum_{i=1}^{n}\sum_{j=1}^{m}(A_{01}c)_{ij} - \sum_{i=1}^{n}\sum_{j=1}^{m}(A_{93}c)_{ij}\right)/\Delta t,\end{aligned}$$

where C'_{01} and C_{93} are landscape biomass carbon stocks in 2001 and 1993 (t C), and $\Delta t = 9$ years. These calculations were performed with 1-year bin age classes. $\mathrm{BCB}_{\mathrm{age1}}$ could be viewed an indirect human-induced effect, whereas, $\mathrm{BCB}_{\mathrm{age2}}$ operates on a shorter timescale and, therefore, has the quality of a direct human-induced effect.

Results

Carbon dynamics at stand level

In our simulation experiment, we investigated the effect of global change on standing biomass, biomass accumulation rate and NEP of different forest age classes for both Baseline and Present environmental scenarios. With this information, it was also possible to investigate the effects of stand age dynamics on biomass and NEP for each elevation/soil class and how these fluxes changed under changing environmental conditions.

The model simulations with the Present environmental scenario suggested that the growth of managed coniferous forests significantly increased relative to

Baseline scenario during the last century. Even 100-year-old forests continued to accumulate biomass (Fig. 4a). In contrast, the biomass of forests simulated with the Baseline scenario saturated already after 60 years. Sixty-year-old forests under Present scenario had accumulated almost the same amount of carbon as 100-year-old forests under Baseline conditions. Twenty-year-old forests had 20% higher biomass when simulated with the Present rather than with the Baseline scenario.

For both scenarios, the simulated biomass of all forest age classes increased with increasing elevation. For the Present scenario, the biomass of mature (100–120 years) stands in the high, middle, and low elevations reached 170, 150 and 130 $\mathrm{t\,C\,ha^{-1}}$, respectively. The simulated biomass was lower for Baseline scenario (150, 140 and 120 $\mathrm{t\,C\,ha^{-1}}$) than for Present scenario, but higher than the biomass estimates from forest inventories (100, 115 and 110 $\mathrm{t\,C\,ha^{-1}}$), where no such elevation trend was observed.

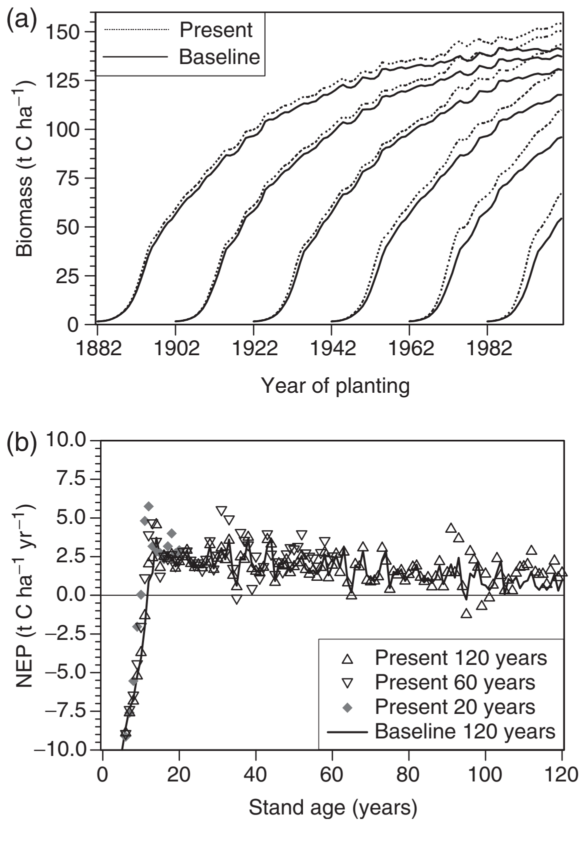

Fig. 4 (a) Changes in the biomass through the last 120 years for the six modeled forest age classes under Baseline (solid line) and Present (dotted line) conditions. (b) Changes in the net ecosystem production (NEP) as a function of forest age (years) over the last 120 years. Thick solid line shows the development of NEP under Baseline environmental conditions.

In all environmental strata and age classes, biomass accumulation rates were higher under the Present scenario with the relative effect (*E*) ranging from near zero to almost 0.6 (Fig. 5). With exception of the youngest age class at high elevation, the relative effect of environmental changes increased towards higher ages. This was mainly because under the Baseline scenario biomass in mature stands was close to equilibrium after a stand age of 80 years. The highest relative changes in mature forests were seen at high elevations. Absolute biomass accumulations rates were also highest at high elevations with a peak of 4 $\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$ in 20–40-year-old stands. Variability related to different substrates was generally very low.

The modeled NEP followed a typical age pattern for both scenarios (Fig. 4b). Young forests were a source of carbon to the atmosphere. The source strength reduced, as the forests grew older, turning into a carbon sink after 15 years. The NEP of forests reached a maximum after approximately 15–20 years and then decreased continuously. Depending on climate variability there is strong interannual variability of the NEP also for older age classes. Under Baseline conditions NEP decreased to values close to zero after about 100–120 years, the 120 years old forest under the Present scenario still functioned as a significant carbon sink of 1.4 $\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$. Forests turned from a carbon source into a sink about 3 years earlier under Present scenario than under Baseline scenario.

Under the Baseline scenario the highest amplitude and absolute values of NEP were found at high elevation forests. Here, an initial source of about 5 $\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$ turned into close to being carbon neutral. In contrast, the initial swing was less pronounced at low and middle elevations and mature forests acted as carbon sinks of 0.7 $\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$ (Fig. 6, left panel). As for the biomass accumulation rates the variability related to different substrates was low. Under the Present scenario increased biomass accumulation rates reduced the strength of the initial source and all mature forests sequestered carbon at rates of about 1.7 $\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$ under the Present scenario. The relative response of NEP to the environmental changes (*E*) showed an age pattern similar to the biomass accumulation rates (Fig. 6, right panel) but less pronounced. Also, for NEP the highest elevations showed a stronger relative effect of the environmental changes than middle and low elevations.

Carbon dynamics at landscape level

The average NEP of the Thuringian conifer forests from 1982 to 2001 was simulated at 1.42 $\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$ with the Present scenario and at 0.72 $\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$ with the

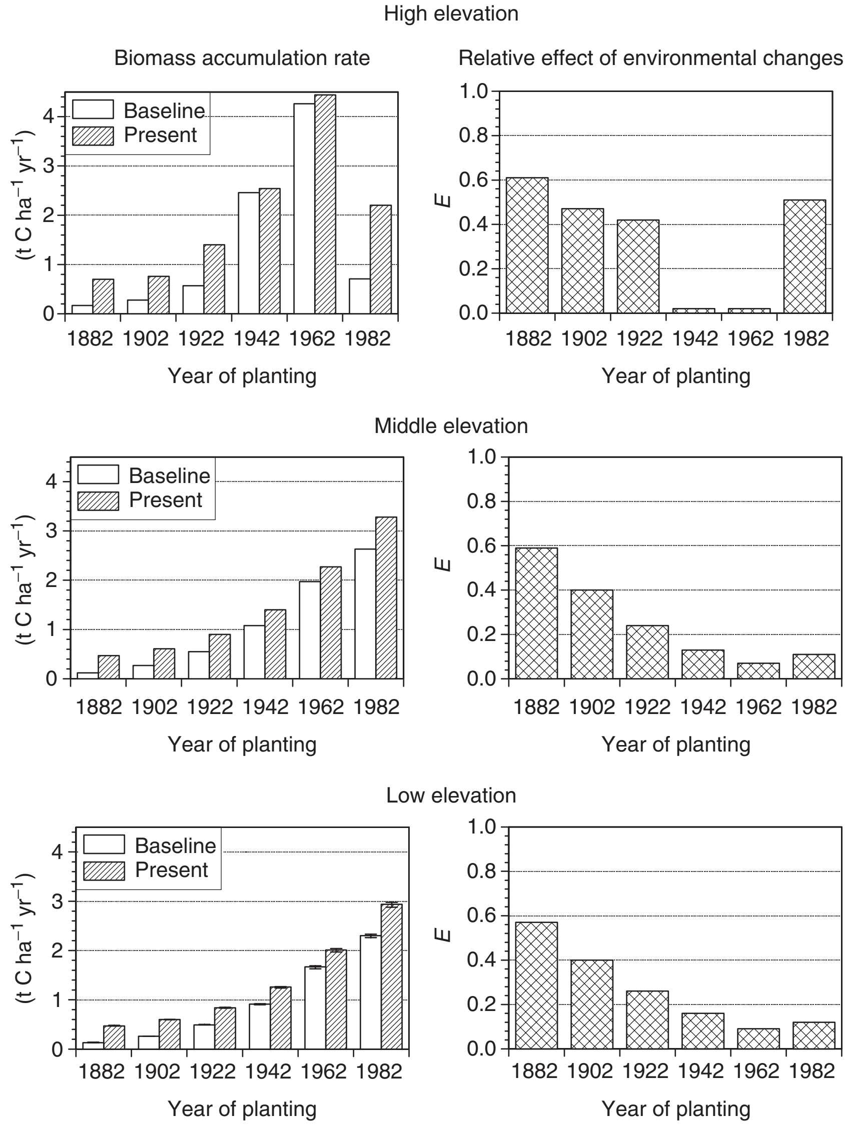

Fig. 5 Modeled annual biomass accumulation rate and the relative effect of environmental changes on the biomass accumulation rate at high (upper panels), middle (middle panels) and low (lower panels) elevation classes for the period 1982–2001. The deviation bars in the lower panels are showing the effect of coarse, middle and fine soil structure on the biomass accumulation rate.

Baseline scenario (Table 6). There were, however, distinct differences between the contributions of different elevation/soil classes to this total. The contribution of the class 'high medium' to the total NEP was high, because of the combined effect of high NEP and regenerating of forests planted in the middle of the 20th century after major snow breaks and reparation cutting after world war II, which occupied large areas at all elevations (Fig. 9). These age classes are exactly those with the highest NEP (Fig. 6, left panel).

Rates of changes in carbon sequestration at landscape level were quantified through NBP, which is the difference between NEP and forest harvest (Schulze, 2000). Fire is not relevant for the Thuringian forests and is not included in the simulations. The NBP simulated with Baseline scenario was estimated as 0.37 t C ha^{-1} yr^{-1} (Table 6). For the Present scenario, the average NBP of Thuringian forests was 1.03 t C ha^{-1} yr^{-1} (= NEP$-H_C$ = 1.42$-$0.39 t C ha^{-1} yr^{-1}).

The higher atmospheric CO_2 concentration, elevated temperatures, and N deposition led to an increase in NEP by 49% under Present scenario compared with Baseline conditions (Table 6). While NPP increased by approximately 16% (from 6.1 to 7.3 t C ha^{-1} yr^{-1}), heterotrophic respiration increased only by 8% (from 5.4 to 5.9 t C ha^{-1} yr^{-1}) despite increased temperature.

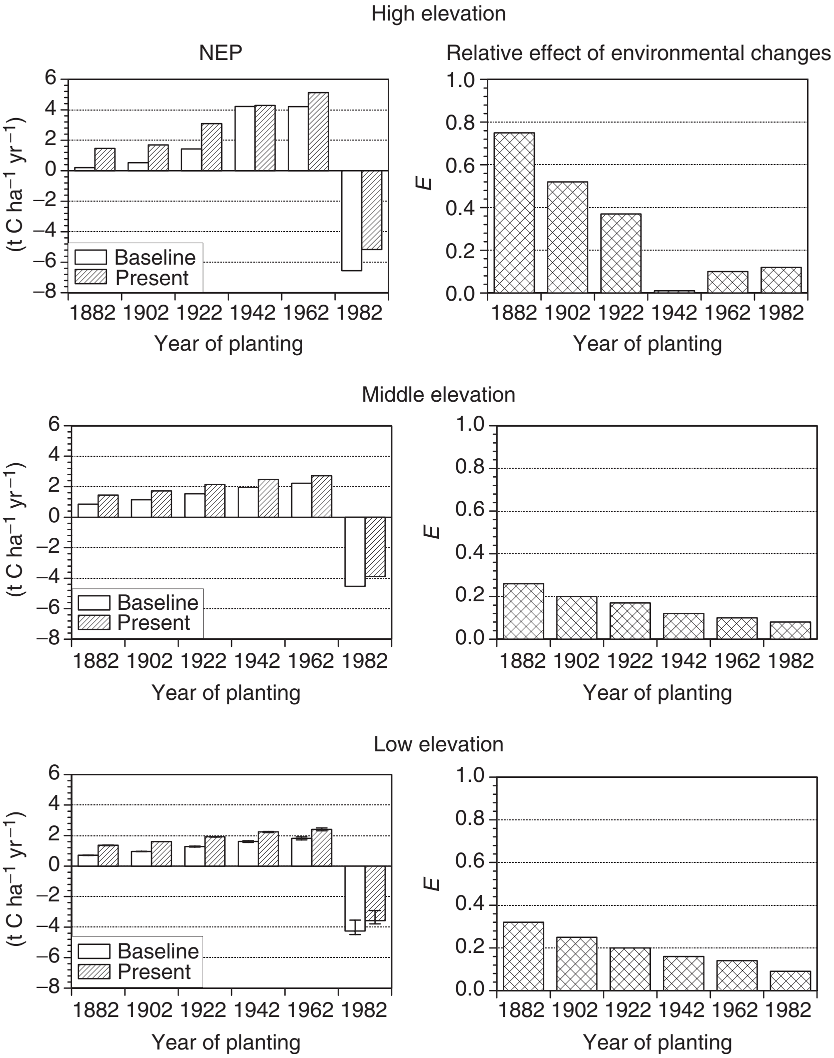

Fig. 6 Modeled annual net ecosystem production (NEP) and the relative effect of environmental changes on the NEP at high (upper panels), middle (middle panels) and low (lower panels) elevation classes for the period 1982–2001. The deviation bars in the lower panels are showing the effect of coarse, middle and fine soil structure on the NEP.

The environmental changes led to a shift of the ratio between carbon uptake (NPP) and carbon loss (R_h) in favor of the uptake (Schulze *et al.*, 2001).

To investigate the impact of the different environmental factors such as increased temperature, increased atmospheric CO_2 and increased nitrogen deposition (added in this sequence), we calculated the rates of annual biomass accumulation and NEP at landscape level using the assumption of equally distributed age classes (Fig. 7). In the high elevation/soil class the increase of temperature and CO_2 led to an increase in biomass accumulation rates (Fig. 7, upper panel), but the strongest increase in biomass accumulation rate was found by accounting for N deposition. In the middle and lower elevation/soil classes the temperature and CO_2 increase showed the strongest increase in carbon sequestration, while additional increasing N deposition did not cause any further increase of the carbon accumulation rate.

A slightly different picture was found for NEP. All elevations showed an increase in NEP because of increased temperature (Fig. 7, lower panel). The combined effect of increasing temperature and CO_2 resulted in a further increase of NEP in all elevation/soil classes being highest in the lower and middle elevations. N deposition in addition to the other factors had the strongest impact on NEP at high elevation/soil classes. In the middle and lower elevation/soil class, it led to only small changes in the NEP as compared with the other scenarios. At middle elevations, as well as, at lower elevations with medium and fine soil texture, we observed no change in NEP related to N deposition.

Table 7 The biomass carbon balance BCB estimated from model simulations and forest inventories (t C ha^{-1} yr^{-1}) for Thuringia as well as the contribution of age-class effects

	Model simulations (t C ha^{-1} yr^{-1})	Forest inventories (t C ha^{-1} yr^{-1})
BCB (Present)	1.12	1.15
BCB (Baseline)	0.75	–
BCB$_{\text{age1}}$ (legacy)	0.09	0.18
BCB$_{\text{age2}}$	0.25	0.31

The age-class effect is calculated based on different assumption: BCB$_{\text{age1}}$, the age-class effect based on even-aged distribution; BCB$_{\text{age2}}$, the age-class effect based on forest growing one age-class older with 'business as usual' (new planting of age-class 1).

In comparison the lower elevation with coarse soil structure showed a small increase in NEP. The effect of different environmental changes may be summarized as follows: For the high elevation, the most important factors for elevated biomass accumulation rates and NEP were increasing N deposition followed by increasing CO$_2$ concentration. For the middle and lower elevations, increased temperatures and CO$_2$ concentrations had the greatest impact on NEP. The most pronounced change in the carbon sequestration was found for high elevations.

Comparison with inventory-based carbon fluxes and partitioning in direct and indirect effects

The inventory-based BCB was 1.15 t C ha^{-1} yr^{-1} (Table 7) and resulted from the difference of biomass increment G_{C} of 2.58 t C ha^{-1} yr^{-1} and carbon export through harvest H_{C} of 1.43 t C ha^{-1} yr^{-1} (Norway spruce alone: 1.35 = 2.86–1.51 t C ha^{-1} yr^{-1} (BCB = G_{C}–H_{C}) and Scots pine: 0.66 = 1.90–1.24 t C ha^{-1} yr^{-1}). The modeled BCB for coniferous forests (based on the annual averaged accumulated biomass rates) was estimated to be 1.12 t C ha^{-1} yr^{-1} (Table 7) and was therefore, close to the estimate based on the FID. In Fig. 8 a direct comparison between forest inventories and model simulations (with Present environmental scenario) of the age classes shows that the age-class-dependent biomass curves were similar, but that total modeled biomass was too high compared with the forest inventories. The discrepancy between model prediction and inventory were greatest for the 20–40 and 100–120-year-old trees.

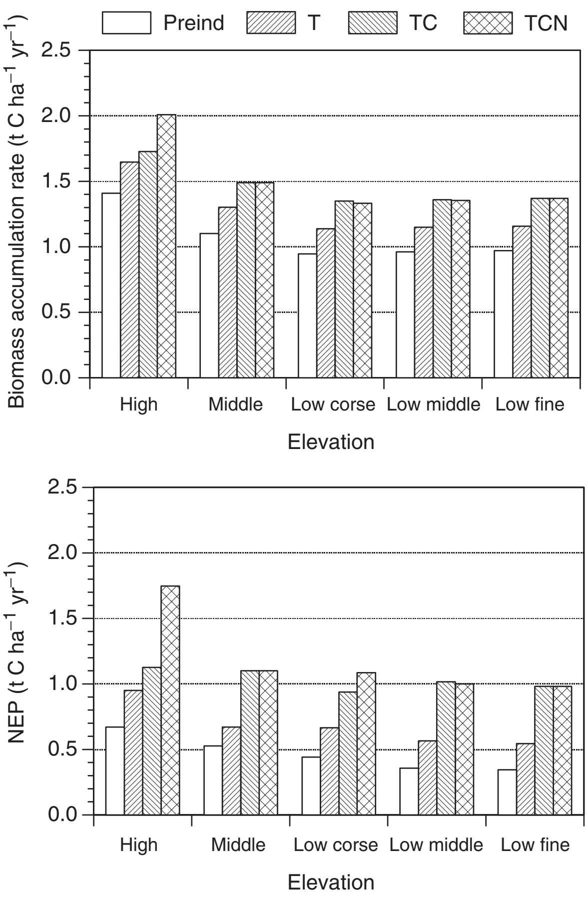

Fig. 7 Impact of temperature (*T*), carbon dioxide (CO$_2$) and N deposition (N) on the biomass accumulation rate and net ecosystem production (NEP) for five climate/texture classes. To investigate the effect of the environmental changes without considering the age-class effect the forest age classes were assumed to have equal areas. The major changes occur at high and middle elevation by adding N deposition. In the lower elevation class the increasing CO$_2$ caused the greatest changes.

In our numerical experiment, we estimated indirect (changed environmental conditions during the last century and age-class legacy effect, BCB$_{\text{age1}}$) and direct human-induced effects (short-term shift in age-class distribution, BCB$_{\text{age2}}$) on the carbon sequestration (Table 7). The total increase in biomass carbon because of environmental changes was 0.4 t C ha^{-1} yr^{-1} (Present–Baseline). This indirect human-induced effect counted for 33% of the BCB at present. The 'legacy' age effect BCB$_{\text{age1}}$ based on the modeled growth rates was small and amounted to 0.09 t C ha^{-1} yr^{-1} or 8% of total BCB at present. Projected shifts in the age-class distribution between 1993 and 2001 with constant carbon densities induce a BCB$_{\text{age2}}$ of 0.25 t C ha^{-1} yr^{-1} or 22% of total BCB. The corresponding values for BCB$_{\text{age1}}$ and BCB$_{\text{age2}}$ based on inventory data are 0.18 and 0.31 t C ha^{-1} yr^{-1} (17% and 27%, respectively) and were thus, higher in both cases. This is because of the difference in age-class-dependent biomass

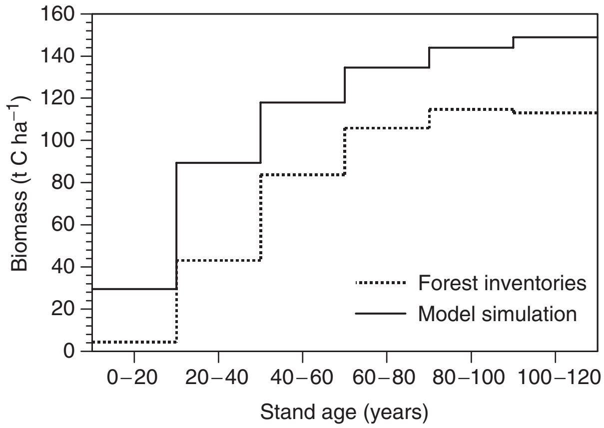

Fig. 8 Comparison of the biomass carbon accumulation from model simulation (Present scenario) and the inventory data for the class 'middle–middle'. The rate of change between the age classes is similar, the modeled age classes having the greatest rate of change.

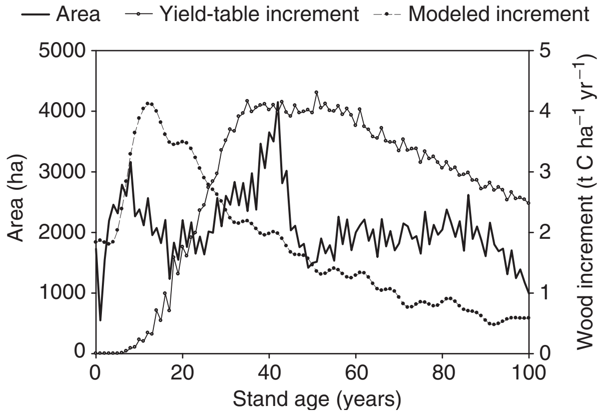

Fig. 9 Age-class distribution of coniferous forests (1–100 years) according to the inventory in 1993 (thick line). The average wood increment predicted by BIOME-BGC (dotted line-smoothed to remove the variability induced by climate) peaks much earlier than the wood increment predicted by local yield tables (white dotted line). The marked peak in the age-class distribution at stand age 45 years is related to postwar reparation logging and coincides with the time of highest yield table growth rates inducing a legacy age-class effect on the contemporary carbon sink.

accumulation between forest inventory and model simulations (Fig. 9).

Discussion

Carbon dynamics at stand and landscape level

Results from other studies (eddy-covariance measurements) demonstrated that mature forests (>70 years) were by no means carbon neutral, but net sinks with up to 5 t C ha^{-1} yr^{-1} (Schulze *et al.*, 1999; Carey *et al.*, 2001; Law *et al.*, 2002). Studies of age-dependent development of biomass, NEP, respiration and NEE in Oregon also support the findings of our study (Law *et al.*, 2001, 2003). Under the Present scenario mature stands showed the strongest increase in biomass accumulation in all elevations. This is because of the fact that these stands saturated at an age of approximately 80 years under Baseline conditions. The young stands also showed a positive response to the environmental changes were as the middle-aged stands showed least response. These stands are already close to their maximum growth rate and are not strongly limited by nutrients. The middle and low elevations did not respond to the increased nitrogen deposition. This is probably because of higher temperature and large inputs of CWD and litter directly after clear-cutting resulting in a high nutrient input and plant available N. Additionally, the new planted trees have less demand of N. Nadelhoffer *et al.* (1999) also found that temperate forests only shows a minor contribution to the carbon sequestration in temperate forests. For middle and low elevations the increase of CO_2 showed the strongest increase in biomass accumulation mainly because of improved water-use efficiency. Compared with high elevations, the low elevation has less than half of the precipitation in the high elevation, and 150 mm less than the middle elevation. At the same time, the annual averaged temperature is more than 2 °C higher. The increased temperature in low and middle elevations caused the increased CO_2 to be the strongest effect on biomass accumulation as well as NEP (Fig. 7). At higher CO_2 concentrations, the stomata conductance is reduced and less water is respired, hence the stands are less limited by water. At high elevations, the additional increase in N deposition gave an increased biomass accumulation and NEP may be because of lower temperature and N mineralization and higher N leaching because of higher soil water content at this elevation.

The effect of global warming has been shown to be significant, resulting in increased soil respiration, N mineralization and plant productivity (Rustad *et al.*, 2001). In the European Alps, temperature-driven changes were responsible for forest belt changes at wet sites and that boreal and temperate forests have a high sensitivity to changes in precipitation (Badeck *et al.*, 2001). The effect of CO_2 fertilization on forest growth has been studied in several cases. The FACE study from the Duke forest suggests that gradually increasing atmospheric CO_2 concentrations also led to a gradually increase in carbon sequestration at shorter time scales (Lou *et al.*, 2003). At larger time scales this seems to level off because of an increased nitrogen demand at higher CO_2 concentrations (Finzi & Schlesinger, 2003). Our simulations followed those patterns: The effect of temperature led to increased biomass accumulation in all elevations. The effect of increased atmospheric CO_2 concentration led to increased biomass accumulation in all elevations. Adding increased nitrogen deposition confirmed this pattern as the high elevation showed the greatest increase of carbon sequestration whereas middle and low elevations showed almost no increase (only a small increase for coarse soil structure). The difference between the responses of high and low elevations to increased N deposition may be partly because of temperature differences inferring a less nitrogen limited forest at lower elevations (compare Rustad *et al*., 2001).

The differences in age development are important, because they have an effect on using the age-class distribution on landscape level averages of BCB and NBP. The discrepancy between model simulations and forest inventories arose because the mortality in BIOME-BGC was set constant during the simulation, which is not mirroring the real forest development (mortality may be age dependent). The total carbon pool is in this way overestimated, but the annual averaged changes were in range (a further increase of the modeled plant mortality would lead to an increased carbon loss of old forests, which would be a model artifact). The biomass accumulation rate estimated from the model simulations peaked much earlier than the accumulation rate estimated from the inventories (Fig. 9).

The absolute magnitude of the modeled carbon fluxes for Thuringian forests agreed well with other published data. Schulze (2000) estimated an averaged NPP for European spruce forests of $9\,t\,C\,ha^{-1}\,yr^{-1}$, while our simulations yielded an actual NPP on landscape level of $7.3\,t\,C\,ha^{-1}\,yr^{-1}$. The averaged NPP in a spruce chronosequence in Fichtelgebirge (Bavaria, south of Thuringia) was found to be $9.1 \pm 2.5\,t\,C\,ha^{-1}\,yr^{-1}$ (range: $6.1–13.4\,t\,C\,ha^{-1}\,yr^{-1}$) (Mund *et al*., 2002). Other model studies achieved lower NPP values in the range of $6–7\,t\,C\,ha^{-1}\,yr^{-1}$ (Milne *et al*., 2001, EuroBiota-model, mixed forest in Europe: $6.0\,t\,C\,ha^{-1}\,yr^{-1}$; Karjalainen *et al*., 2002, EFISCEN-model, mixed forest in Germany: $6.1\,t\,C\,ha^{-1}\,yr^{-1}$; LTEEF-project site Harz, TREEDYN3-model, spruce forest: $7.0\,t\,C\,ha^{-1}\,yr^{-1}$, http://www.usf.uni-kassel-de/ecosys/projects/abschluss.htmt). The ratio NPP to gross primary production (GPP) of 0.4 corresponded with statements of Makela & Valentine (2001), whereas the calculated ratio of NEP to GPP of 0.08 in our study was lower than the value of 0.2 calculated for European forest sites from eddy-covariance measurements in the Euroflux project. This discrepancy was probably because of an underestimation of the modeled NEP in the old stands in the model simulations.

The modeled value of the NBP (landscape average $1.03\,t\,C\,ha^{-1}\,yr^{-1}$) was in a very realistic range. Other published values ranged from 0.3 to $4.7\,t\,C\,ha^{-1}\,yr^{-1}$ with an average of $1.16 \pm 1.12\,t\,C\,ha^{-1}\,yr^{-1}$ and a median of 0.77 ($n = 21$; based on literature listings of Böswald, 1996; Nabuurs *et al*., 2003). In agreement with Valentini *et al*. (2000), particularly heterotrophic respiration and its changes had the greatest effect on the sinks. At the same time, the simulation showed that N deposition was the major factor responsible for an increasing NEP in higher altitudes. The primary effect of the N deposition was certainly to increase the GPP and in a similar way the NPP as well, while the heterotrophic respiration could not follow this trend. This is in agreement with results observed in the CANIF project (Schulze *et al*., 2001). Against previous assumptions, it appears that increased N deposition does not increase the decomposition of organic material as much as the plant production at this elevation.

Indirect and direct human-induced impact on carbon sequestration

Because warmer temperatures and fertilizing effects of increased CO_2 and nitrogen deposition may have generally a positive effect on the carbon sequestration of Central European forests, the amount of this additional carbon sink would not be accountable under article 3.4 of the Kyoto protocol (Schulze *et al*., 2002). In contrast, to deliberate contemporary forest management activities, CO_2 fertilization, nitrogen deposition and climate change represent unintentional indirect human influences. The same is true for sinks that arise from the current age-class distribution and, therefore, represent a legacy of management decision in the past. Comparing the carbon sink under the Present ($1.12\,t\,C\,ha^{-1}\,yr^{-1}$) and Baseline scenario ($0.75\,t\,C\,ha^{-1}\,yr^{-1}$) (Table 7) a contribution of the above-mentioned environmental changes was quantified as 33%. This indirect effect had the strongest impact on high elevation sites with cold climate where temperature and nutrient limitations can be expected. The result of this study suggests that care should be taken when selecting sites for investigating effect of environmental changes in field studies since substantial variability may exist at the landscape level.

The inventory-based sink was very close the modeled sink under the Present scenario ($1.15\,t\,C\,ha^{-1}\,yr^{-1}$). This estimate represents a minimum estimate since conventional yield tables on which the growth predictions are based have been to underestimate contemporary growth rates (Mund *et al*., 2002; Pretzsch, 2002). The current age-class distribution induced a carbon sink of 0.18 $\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$ if compared with an even age-class distribution ($\mathrm{BCB_{age1}}$). This is because of a high proportion of 50-year-old stands, which were replanted after the postwar reparation loggings. This pronounced peak in the age-class distribution coincides with the time of maximum growth rates. The legacy-age effect accounts for 17% of the inventory-based flux estimate from 1993 of 1.15 $\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$ (growth minus harvest).

Simulating the effect of a shift in the age-class distribution on the changes in carbon stocks ($\mathrm{BCB_{age2}}$) during the time period from 1993 to 2001 in a business as usual fashion (harvest of spruce at age 100 and pine at age 120 years and replanting thereafter) we obtained an additional sink of 0.25 and 0.31 $\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$ for the modeled and inventories biomass carbon densities, respectively. This indicates that the sink size has probably increased since 1993.

Caspersen *et al*. (2000) correlated that the aboveground biomass accumulation because of enhanced growth caused by environmental changes was only approximately 2%, the rest being driven by land-use changes. In contrast, our model results suggest a 33% increase. These results highlight the idea that particular caution should be used in defining land-use changes and site history when estimating the impact of environmental changes and human management on forest ecosystems.

Conclusions

From the synthesis of our results we conclude that the mean sink strength of Thuringian coniferous forests on the order of 1.1 $\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$ with a range of 0.6–1.3 $\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$. The major uncertainty was found to originate from the discrepancy of different methods used in estimating biomass accumulation from forest inventories and model. This study demonstrates that it is possible to separate the direct and indirect human-induced effects on carbon sequestration in a managed coniferous forest by combining model simulations and forest inventories. Moreover, this study showed that older forests had the strongest relative increase in carbon sequestration at Present scenario. All elevations showed an increase in biomass accumulation in response to Present scenario with the highest elevation showing the greatest increase. We conclude that the greatest effect of climate change on forest growth will be found at higher elevations. Thus, we suggest designing experiments to investigate vegetation response at higher elevations (here 600–900 m a.s.l.) where changes are more prominent.

This study showed that modeling should go hand in hand with measurements because none of the techniques leads to satisfying results alone. Experimental data alone (frequently too cost expensive) cannot distinguish between the impacts of environmental changes and direct human influence on the carbon sequestration of forests. However, models are powerful tools for this purpose if the scenarios are clearly defined in the model input data. Information about forest area and age-class structure, from the forest inventories, was essential for the model results. Success of separating between direct and indirect human-induced carbon sequestration is dependent on choosing the appropriate spatial and temporal scale. On a global scale the effect of the direct human-induced carbon sequestration will overlap with the indirect effects. Human activities in forests take place on a much smaller scale, thus on this scale we can most easily distinguish direct and indirect effects on carbon sequestration, e.g. through a combination of model simulations and forest inventories as we did in this study.

In this paper, we succeeded for the first time distinguishing between direct and indirect human impacts on carbon sequestration in a managed coniferous forest. The procedure is not simple, and requires a well-known knowledge of the site history and environmental heterogeneity. Our study showed results stating that 33% of the carbon sink can be related to environmental changes during the past century and 8% and 17% origin from management (legacy) estimated by model simulations and forest inventories, respectively.

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References

Anthoni PM, Unsworth MH, Law BE *et al*. (2002) Seasonal differences in carbon and water vapor exchange in young and old-growth ponderosa pine ecosystems. *Agricultural and Forest Meteorology*, **111**, 203–222.

Assmann E (1968) Zur 'theorie der grundflächenhaltung'. *Forstwissenschaftliches Centralblatt*, **87**, 321–330.

Badeck FW, Lischke H, Bugmann H *et al*. (2001) Tree species composition in European pristine forests: comparison of stand data to model predictions. *Climatic Change*, **51**, 307–347.

Band LE, Patterson P, Nemani R *et al*. (1993) Forest ecosystem processes at the watershed scale – incorporating hillslope hydrology. *Agricultural and Forest Meteorology*, **63**, 93–126.

Beck W (2000) *Silviculture and stand dynamics of Scots pine in Germany.* Investigacion agravia: Sistemas y recursos Forestales: Fuera de Serie no. 1, 199–212.

Böswald K (1996) *Zur Bedeutung des Waldes und der Forstwirtschaft im Kohlenstoffhaushalt, eine Analyse am Beispiel des Bundeslandes Bayern*. Schriftenreihe der Forstwissenschaftlichen Fakultät der Universität München und der Bayerischen Landesanstalt für Wald und Forstwirtschaft, Lehrstuhl für Waldbau und Forsteinrichtung der Ludwig-Maximilian-Universität, 147 pp.

Burschel P, Kürsten E, Larson BC (1993) Present role of German forests and forestry in the national carbon budget and options to its increase. *Water, Air and Soil Pollution*, **70**, 325–340.

Carbonnier C (1957) Ett Gallringsförsök I planterad granskog. *Svenska SkogsvFören Tidskrift*, **55**, 463–476.

Carey EV, Sala A, Keane R *et al*. (2001) Are old forests underestimated as global carbon sinks? *Global Change Biology*, **7**, 339–344.

Caspersen JP, Pacala SW, Jenkins JC *et al*. (2000) Contributions of land-use history to carbon accumulation in U.S. forests. *Science*, **290**, 1148–1151.

Churkina G, Running SW (2000) Investigating the balance between timber harvest and productivity of global coniferous forests under global change. *Climatic Change*, **47**, 167–191.

Churkina G, Running SW, Schloss AL *et al*. (1999) Comparing global models of terrestrial net primary productivity (NPP): the importance of water availability. *Global Change Biology*, **5** (Suppl. 1), 46–55.

Churkina G, Tenhunen J, Thornton P *et al*. (2003) Analyzing the ecosystem carbon dynamics of four European coniferous forests using a biogeochemistry model. *Ecosystems*, **6**, 168–184.

DeLucia EH, Hamilton JG, Naidu SL *et al*. (1999) Net primary production of a forest ecosystem with experimental CO_2 enrichment. *Science*, **284**, 1177–1179.

Finzi AC, Schlesinger WH (2003) Soil–nitrogen cycling in a pine forest exposed to 5 years of elevated carbon dioxide. *Ecosystems*, **6**, 444–456.

Franz F (1983) Effects of stand treatment on the growth of pine (*Pinus sylvestris*) – results of a yield study based on growth-model calculations. *Forstwissenschaftliches Centralblatt*, **102**, 18–36.

Gingrich SF (1971) *Management of young and intermediate stands of upland hardwoods*. US forestry Services Research Papers, NE-195.

Hager H (1988) Stammzahlreduktion - Die Auswirkungen auf Wasser-, Energie-und Nährstoffhaushalt von Fichtenjungwüchsen. In: *Österreichische Gesellschaft für Waldökosystemforschung und experimentelle Baumforschung*. Universität für Bodenkunde, Wien.

Hakkila P (1989) *Utilization of Residual Forest Biomass*. Springer Verlag, Berlin.

Heinsdorf D, Kraus H-H, Tölle H (1986) Entwicklung der C-und N-Vorräte nach Kahlschlag auf ärmeren anhydromorphen Sandböden unter Kiefer. *Beiträge zur Forstwirtschaft*, **20**, 8–13.

Holland EA, Dentener FJ, Braswell BH *et al*. (1999) Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry*, **46**, 7–43.

Houghton RA (2003) Why are estimates of the terrestrial carbon balance so different. *Global Change Biology*, **9**, 500–509.

Hunt ER, Piper SC, Nemani R *et al*. (1996) Global net carbon exchange and intra-annual atmospheric CO_2 concentrations predicted by an ecosystem process model and three-dimensional atmospheric transport model. *Global Biogeochemical Cycles*, **10**, 431–456.

IPCC (2003) IPCC meeting on current Scientific understanding of the processes affecting terrestrial carbon stocks and human influences upon them. In: *Expert Meeting Report* (eds Schimel D, Manning M), IPCC Working Group – Technical Support Unit, http://ipcc-wg1.ucar.edu/.

Janisch JE, Harmon ME (2002) Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. *Tree Pysiology*, **22**, 77–89.

Janssens IA, Freibauer A, Ciais P *et al*. (2003) Europe's terrestrial biosphere absorbs 7–12% of European anthropogenic CO_2 emissions. *Science*, **300**, 1538–1542.

Johnson DW, Curtis PS (2001) Effects of forest management on soil C and N storage: meta analysis. *Forest Ecology and Management*, **140**, 227–238.

Jonson E, Bartnicki J, Olendrzynski K *et al*. (1998) EMEP Eularian model for atmospheric transport and deposition of nitrogen species over Europe. *Environmental Pollution*, **102**, 289–298.

Karjalainen T, Pussinen A, Liski J *et al*. (2002) An approach towards an estimate of the impact of forest management and climate change on the European forest sector carbon budget: Germany as a case study. *Forest Ecology and Management*, **5910**, 1–17.

Kauppi PE, Mielikainen K, Kuusela K (1992) Biomass and carbon budget of European forests, 1971–90. *Science*, **256**, 70–74.

Kramer H (1988) Waldwachstumslehre. In: *Ökologische und anthropogene Einflüsse auf das Wachstum des Waldes, seine Massen und Wertleistung und die Bestandessicherheit* (eds Karmer H, Gussone HA, Schober R), Paul Parey, Hamburg.

Krapfenbauer A, Buchleitner E (1981) Holzernte, biomassen-und nährstoffaustrag, nährstoffbilanz eines fichtenbestandes. *Centralblatt des gesamten Forstwesen*, **98**, 193–223.

Kreutzer K (1979) Ökologische fragen zur vollbaumernte. *Forstwissenschaftliches Centralblatt, München*, **98**, 298–308.

Law BE, Falge E, Gu L *et al*. (2002) Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agricultural and Forest Meteorology*, **113**, 97–120.

Law BE, Sun OJ, Campbell J *et al*. (2003) Changes in carbon storage and fluxes in a chronosequence of ponderosa pine. *Global Change Biology*, **9**, 510–524.

Law BE, Thornton PE, Irvine J *et al*. (2001) Carbon storage and fluxes in ponderosa pine forests at different developmental stages. *Global Change Biology*, **7**, 755–777.

Lou Y, White LW, Ganadell JG *et al*. (2003) Sustainability of terrestrial carbon sequestration: a case study in Duke forest with inversion approach. *Global Biogeochemical Cycles*, **17**, 1021.

Makela A, Valentine HT (2001) The ratio of NPP to GPP: evidence of change over the course of stand development. *Tree Physiology*, **21**, 1015–1030.

McGuire AD, Sitch S, Clein JS *et al*. (2001) Carbon balance of the terrestrial biosphere in the twentieth century: analyses of CO_2, climate and land use effects with four process-based ecosystem models. *Global Biogeochemical Cycles*, **15**, 183–206.

Milne R, Mobbs D, Grace J (2001) The EuroBiota forest ecosystem model. In: *Long-Term Effects of Climate Change on Carbon Budgets of Forests in Europe* (eds Kramer K, Mohren GMJ), pp. 234–239. Alterra – Green World Research, Wageningen.

Mund M, Kummetz E, Hein M *et al*. (2002) Growth and carbon stocks of a spruce forest chronosequence in central Europe. *Forest Ecology and Management*, **171**, 275–296.

Nabuurs GJ, Pussinen A, Karjalainen T *et al*. (2002) Stemwood volume increment changes in European forests due to climate change – a simulation study with the EFISCEN model. *Global Change Biology*, **8**, 304–316.

Nabuurs GJ, Schelhaas MJ, Mohren GMJ *et al*. (2003) Temporal evolution of the European forest sector carbon sink from 1950 to 1999. *Global Change Biology*, **9**, 152–160.

Nadelhoffer KJ, Emmett BA, Gundersen E *et al*. (1999) Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature*, **398**, 145–148.

Nemani RR, Running SW (1989) Testing a theoretical climate soil leaf-area hydrologic equilibrium of forests using satellite data and ecosystem simulation. *Agricultural and Forest Meteorology*, **44**, 45–260.

Nyland RD (1996) *Silviculture – Concepts and Applications*. McGraw-Hill Series in Forest Resources, New York.

Pietsch SA, Hasenauer H (2002) Using mechanistic modelling within forest ecosystem restoration. *Forest Ecology and Management*, **159**, 111–131.

Prentice IC, Farquhar GD, Fasham MJR *et al*. (2001) The carbon cycle and atmospheric carbon dioxide. In: *Climate Change 2001: The Scientific Basis. Countribution of Working Group I to the Third Assesment Report of the International Panel on Climate Change* (eds Houghton R, Griggs DJ, Noguer PJ, van der Linden PJ, Dai XY, Maskell CA, Johnson CA), pp. 183–237. Cambridge University Press, Cambridge.

Pretzsch H (2002) *Grundlagen der Waldwachstumsforschung*. Parey, Berlin.

Running SW (1994) Testing forest–BGC ecosystem process simulations across a climatic gradient in Oregon. *Ecological Applications*, **4**, 238–247.

Running SW, Gower ST (1991) Forest–BGC, a general model of forest ecosystem processes for regional applications. 2. Dynamic carbon allocation and nitrogen budgets. *Tree Physiology*, **9**, 147–160.

Rustad LE, Campbell JLGCTE-NEWS *et al*. (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and above ground plant growth to experimental warming. *Oecologia*, **126**, 543–562.

Ryan MG, Bond BJ, Law BE *et al*. (2000) Transpiration and whole-tree conductance in ponderosa pine trees of different heights. *Oecologia*, **124**, 553–560.

Schulze ED (2000) *Carbon and Nitrogen Cycling in European Forest Ecosystems*. Springer Verlag, Berlin.

Schulze ED, Dolman AJ, Jarvis P *et al*. (2001) *The carbon sink: absorption capacity of the European terrestrial biosphere*. Directorate Gernera for research/1.2.

Schulze ED, Loyd J, Kelliher FM *et al*. (1999) Productivity of forests in the Eurosiberian boreal region and their potential to act as a sink – a synthesis. *Global Change Biology*, **5**, 703–722.

Schulze ED, Valentini R, Sanz MJ (2002) The long way from Kyoto to Marrakesh: implications of the Kyoto Protocol negotiations for global ecology. *Global Change Biology*, **8**, 505–518.

Spiecker H, Mielikainen K, Köhl M, Skovsgaard JP (eds) (1996) *Growth trends in European forests*. Research Report No. 5, European Forest Institute, Joensuu, Finland, 372 pp.

Thornton PE, Hasenauer H, White MA (2000) Simultaneous estimation of daily solar radiation and humidity from observed temperature and precipitation: an application over complex terrain in Austria. *Agricultural and Forest Meteorology*, **104**, 255–271.

Thornton PE, Law BE, Gholz HL *et al*. (2002) Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agricultural and Forest Meteorology*, **113**, 85–222.

TLWJF, Thuringian State Institute for Forestry, Game and Fishery (1992) *Datenspeicher Wald*. TLWJF, Forstbeschreibung.

TLWJF, Thuringian State Institute for Forestry, Game and Fishery (unpublished) *Forsteinrichtung des Staatswaldes in Thüringen*.

Townsend AR, Braswell BH, Holland EA (1996) Spatial and temporal patterns in terrestrial carbon storage due to deposition of fossil fuel derived nitrogen. *Ecological Applications*, **6**, 806–814.

Valentini R, Matteucci G, Dolman AJ *et al*. (2000) Respiration as the main determinant of carbon balance in European forests. *Nature*, **404**, 861–865.

VEB Forstprojektierung Potsdam (1987) *Ökologische Waldzustandskontrolle. 2. Richtlinien zum Basisnetz*. VEB Forstprojektierung, Potsdam.

Wenk G, Antanaitis V, Smelko S (1990) *Waldertragslehre. Forest Growth and Yield*. Deutscher Landwirtschaftsverlag, Berlin.

Wirth C, Czimzik CI, Schulze ED (2002) Beyond annual budgets: Carbon Flux at different temporal scales in Five-prone Siberian Scots pine Forests. *Tellus Series, B-Chemical and Physical Micrology*, **54**, 611–630.

Wirth C, Schulze ED, Schwalbe G *et al*. (2003) *Dynamik der Kohlenstoffvorräte in den Wäldern Thüringens. Abschlussbericht zur 1. Phase des BMBF-Projektes 'Modelluntersuchung zur Umsetzung des Kyoto-Protokolls'*. Max-Planck Institute for Biogeochemistry, Jena.

Wirth C, Schumacher J, Schulze ED (2004) Generic biomass functions for Norway spruce in Central Europe – a meta-analysis approach towards prediction and uncertainty estimation. *Tree Physiology*, **24**, 121–139.

Wittich W (1930) Untersuchungen über den Einfluß des kahlschlags auf den Bodenzustand. *Mitteilungen aus Forstwirtschaft und Forstwissenschaft*, **1**, 438–506.