

# Analyzing the Ecosystem Carbon Dynamics of Four European Coniferous Forests Using a Biogeochemistry Model

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## ABSTRACT

This paper provides the first steps toward a regional-scale analysis of carbon (C) budgets. We explore the ability of the ecosystem model BIOME-BGC to estimate the daily and annual C dynamics of four European coniferous forests and shifts in these dynamics in response to changing environmental conditions. We estimate uncertainties in the model results that arise from incomplete knowledge of site management history (for example, successional stage of forest). These uncertainties are especially relevant in regional-scale simulations, because this type of information is difficult to obtain. Although the model predicted daily C and water fluxes reasonably well at all sites, it seemed to have a better predictive capacity for the photosynthesis-related processes than for respiration. Leaf area index (LAI) was modeled accurately at two sites but overestimated at two others (as a result of poor long-term climate drivers and uncertainties in model parameterization). The overestimation of LAI (and consequently gross photosynthetic production (GPP)), in

combination with reasonable estimates of the daily net ecosystem productivity (NEP) of those forests, also illustrates the problem with modeled respiration. The model results suggest that all four European forests have been net sinks of C at the rate of 100–300 gC/m<sup>2</sup>/y and that this C sequestration capacity would be 30%–70% lower without increasing nitrogen (N) deposition and carbon dioxide (CO<sub>2</sub>) concentrations. The magnitude of the forest responses was dependent not only on the rate of changes in environmental factors, but also on site-specific conditions such as climate and soil depth. We estimated that the modeled C exchange at the study sites was reduced by 50%–100% when model simulations were performed for climax forests rather than regrowing forests. The estimates of water fluxes were less sensitive to different initializations of state variables or environmental change scenarios than C fluxes.

**Key words:** carbon cycle; eddy covariance; ecosystem model; evapotranspiration; net ecosystem exchange.

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## INTRODUCTION

It is important that we gain more knowledge of the carbon (C) dynamics of terrestrial ecosystems, given that terrestrial ecosystems together with marine environments limit atmospheric carbon dioxide (CO<sub>2</sub>) concentrations and consequently the extent of atmospheric and climate change. Data on atmospheric CO<sub>2</sub> and oxygen (O<sub>2</sub>) confirm that the terrestrial biosphere was largely neutral with respect to net C exchange during the 1980s but became a net C sink in the 1990s (Schimel and others 2001). A number of scientists have expressed concern about the high uncertainty concerning the residual terrestrial C sink in the 1990's (2–4 Gt C per year). Uncertainties, they say, arise from the magnitude of regional responses of terrestrial ecosystems to spatially heterogeneous nitrogen (N) deposition, climate anomalies, and land-use change.

Future projections will rely on our understanding of the mechanisms controlling the terrestrial C sink. Although the spatial distribution of C sinks and sources of terrestrial vegetation remains an important area of scientific investigations, it also has policy relevance in conjunction with the Kyoto Protocol (UNFCCC 1997). According to this protocol, more than 100 signatory countries are required to have in place by 2008 a national system for the estimation of anthropogenic emissions from all sources and removals by all sinks of the greenhouse gases not controlled by the Montreal Protocol. This system has to provide estimates of each nation's C stocks in 1990 and enable an estimation of C stock changes in subsequent years.

The established methods for measuring the various components of the terrestrial C budget over large areas include global atmospheric CO<sub>2</sub> sampling networks (inverse modeling, global scale) (Francey and others 1995; Fan and others 1998), forest inventories (national scale) (Kauppi and others 1992; Turner and others 1995; Rodriguez-Murillo 1997), eddy covariance methods (ecosystem scale) (Baldocchi and others 1996; Aubinet and others 2000), and satellite observations (from ecosystem to global scale) (Running and others 1994; Justice and others 1998). Each of these methods allows some insight into certain components of the terrestrial C budget, but none of them provides complete information about the C budget. Thus, the best solution is to use these methods in a complementary way. Although integration is possible (Running and others 1999), it is not a straightforward process because each of these methods estimates different components of the C budget (net ecosystem productivity [NEP], net primary produc-

tivity [NPP], biomass) at different spatial and temporal scales.

A simulation model, which is able to estimate the relevant C budget components separately at different spatial and temporal scales and includes anthropogenic influences, can serve as an integrative tool. Simulation models corroborated with actual measurements of C fluxes can be used to interpolate and extrapolate C flux measurements in time and space. Models can also help to investigate the C sequestration potential of various vegetation types, especially forests at different stages of their growth cycles.

In recent years, numerous models have been developed to estimate various aspects of the C budget and forest growth. A traditional method for estimating forest growth and yield is based on statistical relationships among stand age, density, and site index. Although this method works well for natural stands and individual trees, where historical data can be used to predict future growth, it is not very useful under changing environmental conditions.

New generation (process-based) *forest growth models* (Sonntag 1998) are more sensitive to environmental conditions, but they are based on the same basic method and inherently rely on forest inventories for initialization. Forest inventories are not taken every year. Their frequency differs from country to country (5–10 per year). Therefore, they have dubious reliability. Inventory-based models alone cannot provide accurate estimates of the current C budget. Most models of this type are highly specialized because they were developed for certain applications (forest management, forest succession study, and so on) or certain forest sites. Thus, they may include a detailed description of the forest ecosystem processes relevant to the specific application but descriptions of other processes are schematic or nonexistent.

There are also more general forest models that can be applied to different forest types; these models also represent various ecosystem processes at comparable levels of complexity. For instance, *gap forest modeling* is based on the dynamics (disturbance, recruitment, and mortality processes) of individual trees or small patches of land, where each can have a different age and succession stage (Bugmann 2001). Given that traditional gap models follow the fate of individual trees and the formulations of establishment and mortality are stochastic, these models are of limited use at a regional scale because of the increasing complexity of simulations (Bugmann and others 1996). Gap models also do not always adequately simulate biogeochemical responses to changing industrial atmospheric condi-

tions (for example, elevated CO<sub>2</sub> concentrations) (Reynolds and others 2001).

*Biogeochemical models estimate C fluxes using seasonal dynamics of ecosystem C and N balances.* An advantage of the biogeochemical modeling approach is that it not only allows spatially explicit estimates of the C budget over large heterogeneous areas, but it also quantifies the causes of possible changes in C stocks by changes occurring at the ecosystem level. Models of this type, in conjunction with remote sensing data, can be used to monitor the forest C budget in a spatially explicit way. Model simulations with various scenarios provide valuable predictions that can be used to determine the most effective management strategies to increase C sequestration at a given site. Although long-term measurements of C fluxes (Goulden and others 1996a; Aubinet and others 2000) are under way and can describe the interannual variability of the C flux (Goulden and others 1996b), they cannot project the future C dynamics of a site. General representation of plant physiology is essential for successful regional- to global-scale applications of the model because species-specific information is usually lacking at regional and global scales.

In this paper, we explore the ability of a mechanistic ecosystem model, BIOME-BGC (Running and Hunt 1993; Hunt and others 1996; Thornton 1998), to estimate the C dynamics of coniferous forest stands growing in different climates. This paper provides *the first steps toward a regional-scale analysis of the C budget.* We start with an evaluation of the uncertainty in the model estimates associated with different initializations of vegetation successional stages (C and N state variables). We then analyze the effect of changes in environmental conditions (atmospheric CO<sub>2</sub> concentrations and N deposition) on the simulated C dynamics of forests and discuss the uncertainty arising from imprecise information about input variables. Finally, we corroborate modeled daily ecosystem productivity and actual evapotranspiration across the sites using eddy covariance measurements of net CO<sub>2</sub> and water fluxes.

## METHODS AND DATA

### Model

*Model Description.* In this study, the biogeochemical model BIOME-BGC was applied to four coniferous forest stands that are part of the EUROFLUX network (Aubinet and others 2000; Valentini and others 2000). BIOME-BGC is a mechanistic model that simulates C, N, and water fluxes of terrestrial ecosystems. Much of the fundamental logic for BIOME-BGC springs from the FOREST-

BGC family of models (Running and Coughlan 1988; Running and Gower 1991; Running 1994). The BIOME-BGC model is an extended version for use with different vegetation types, which may be identified and partially characterized by remote sensing methods. The basic structure of the model incorporates the long-term experience of established forest ecosystem scientists (Waring and Running 1998) and at the same time has been modified for spatial simulations—that is, it is prepared for use in a landscape or regional context. With respect to forest ecosystem simulations, the model has been corroborated for a number of hydrological and C cycle components (Nemani and Running 1989; Korol and others 1991; Band and others 1993; Running 1994; Cienciala and others 1998; Thornton and others 2002). It is difficult, however, to corroborate every aspect of an ecosystem model because not all relevant ecosystem components can be measured in the field.

The model structure is based on some key simplifying assumptions that have proven to be particularly valuable in extending ecosystem analyses to regional levels. *Trees are not defined individually, as in a typical forest stand growth model. Only the cycling of C, water, and N are expressed in mass units.* Species are also not identified explicitly, although species-specific physiological characterization can be represented. *Geometric complexities of different tree canopies are reduced to a simple quantification of the sum of all leaf layers as leaf area index (LAI).* All biogeochemical processes are simulated within the vertical extent of a vegetation canopy and its rooting system. For computational convenience and to keep the model parameters and outputs dimensionally consistent with observations, an arbitrary unit of horizontally projected area is defined, over which all fluxes and storage are quantified. Complete horizontal homogeneity is assumed within that unit area. This horizontal area and the vertical extent of the canopy and its rooting system define the maximum physical boundaries of the simulation system. This includes all living and dead plant materials, leaf or shoot boundary layer, the litter and soil surfaces, all mineral and organic matters making up the soil and litter down to a depth at which root penetration is negligible, all water held in the soil down to that same depth, and any snow cover.

The temporal framework of the BIOME-BGC model (version 4.1.1) (Thornton and others 2002) consists of a dual discrete time step approach, which is slightly different from the implementation in previous versions of the BGC logic (Running and Hunt 1993; Hunt and others 1996). In the latest version

of BIOME-BGC, most simulated ecosystem activity occurs at a daily time step, driven by daily values for maximum and minimum temperatures, precipitation, solar radiation, and air humidity. Examples of processes assessed daily are soil water balance, photosynthesis, allocation (which was assessed annually in the previous version), litterfall, and C and N dynamics in the litter and soil. Phenological timing of the budburst is determined once a year using long-term thermal sums and soil moisture status for deciduous forests and grasslands (White and others 1997). For evergreen vegetation, current climatic conditions determine the beginning and end of the growing season.

Finally, the model is designed to require only standard meteorological data—namely, daily maximum–minimum temperature, precipitation, solar radiation, vapor pressure deficit, and daylength—so that the model may be applied beyond those sites with sophisticated instrumentation.

In this study, we used BIOME-BGC to simulate daily net ecosystem productivity (NEP), daily actual evapotranspiration (AET), and projected leaf area index (LAI). NEP was computed as the difference between gross photosynthesis and respiration (autotrophic and heterotrophic). Gross photosynthesis (gross photosynthetic production) was calculated based on absorbed photosynthetically active radiation, atmospheric CO<sub>2</sub> concentration, air temperature, vapor pressure deficit, precipitation, atmospheric N deposition, LAI, and available N content in soil.

Autotrophic respiration was the sum of maintenance and growth respiration of the different parts of the plant (canopy, stem, roots). Maintenance respiration of each plant compartment was computed as a function of the compartment's N content and temperature. Growth respiration was calculated on the basis of construction costs by plant compartment. Different construction costs were applied to woody and nonwoody plant tissues. Heterotrophic respiration included decomposition of both litter and soil and was related to their chemical composition (cellulose, lignin, and humus), to their C:N ratios, to soil mineral N availability, and to soil moisture and temperature. Thus, BIOME-BGC was able to simulate the effects of a number of abiotic (temperature, vapor pressure deficit, soil water, solar radiation, atmospheric CO<sub>2</sub> concentration, and atmospheric N deposition) and biotic (LAI, soil C and N contents) controls on net C flux.

AET was estimated as the daily sum of plant transpiration and evaporation from soil and canopy. The Penmon-Monteith equation (Monteith 1973) was used to calculate both the evaporation

and transpiration rates. These computations were based on absorbed photosynthetically active radiation, daily average surface temperature (soil or canopy), and surface (soil or canopy) resistances to the transport of sensible heat and water vapor, respectively. In the transpiration function, canopy resistance to sensible heat was dependent on canopy boundary layer conductance. Canopy resistance to water vapor was calculated as the inverse of stomatal conductance. In the soil evaporation function, constant soil resistance to water vapor and latent heat were used to calculate potential evaporation, which was consequently modified by a function of time since rain or snowmelt event. Canopy evaporation was dependent on interception and the potential evaporation rates.

*Model Parameterizations.* The BIOME-BGC model was initialized for four coniferous EUROFLUX sites with a single set of ecophysiological parameters (Table 1) and with four site-specific sets of parameters, including geographic coordinates, elevation above sea level, atmospheric N deposition, and soil texture and depth (Table 2). This parameterization reflects two important model assumptions: (a) that evergreen coniferous forest stands have the same physiology, and (b) that the difference in forest functioning stems from site-specific environmental conditions and forest age. With a view to the future regional applications of the model, it was important to test those assumptions. In this study, the simulated coniferous forest stands differed by climate, elevation, age, soil depth, and soil texture, as well as by amount of atmospheric N deposition.

*Model Simulations.* C and N state variables of the BIOME-BGC model represent the amounts of C or N stored in simulated plant and soil pools. Unless variables for the initialization of the model's state variables are available from measurements, model simulations are required for their initialization (spin-up run). In the spin-up run, the model is run to a steady state to obtain the size of the ecosystem's C and N pools under the assumption that the ecosystem is in equilibrium with the long-term climate.

However, most of the world's ecosystems are far from the equilibrium. Harvesting, grazing, replanting, as well as other natural and anthropogenic disturbances affect the ecosystems and consequently the sizes of their C and N pools. On one hand, ignoring management impacts in the model usually leads to overestimation of state variables. On the other, it is rare that all state variables are measured in the field simultaneously, and land-use or management history becomes harder to obtain as we move from site to regional model simulations. Therefore, we have to learn how to simulate dis-

**Table 1.** Ecophysiological Parameterization for Evergreen Needleleaf Forest

Parameter	Unit	Description
0.3	DIM	Transfer growth period as fraction of growing season
0.3	DIM	Litterfall as fraction of growing season
0.26	1/yr	Annual leaf and fine-root turnover fraction
0.7	1/y	Annual live wood turnover fraction
0.005	1/y	Annual whole-plant mortality fraction
0.005	1/y	Annual fire mortality fraction
1.4	DIM	(ALLOCATION) ratio of new fine-root C to new leaf C
2.2	DIM	(ALLOCATION) ratio of new stem C to new leaf C
0.071	DIM	(ALLOCATION) ratio of new live wood C to new total wood
0.29	DIM	(ALLOCATION) ratio of new coarse root C to new stem C
0.5	DIM	(ALLOCATION) ratio of current growth to storage growth
42	kgC/kgN	C:N of leaves
93	kgC/kgN	C:N of leaf litter, after retranslocation
58	kgC/kgN	C:N of fine roots
50	kgC/kgN	C:N of live wood
730	kgC/kgN	C:N of dead wood
0.31	DIM	Leaf litter labile proportion
0.45	DIM	Leaf litter cellulose proportion
0.24	DIM	Leaf litter lignin proportion
0.34	DIM	Fine-root labile proportion
0.44	DIM	Fine-root cellulose proportion
0.22	DIM	Fine-root lignin proportion
0.71	DIM	Dead wood cellulose proportion
0.29	DIM	Dead wood lignin proportion
0.00025	1/LAI/day	Canopy water interception coefficient
0.51	DIM	Canopy light extinction coefficient
2.6	DIM	All-sided to projected leaf area ratio
8.2	m <sup>2</sup> /kgC	Canopy average specific leaf area (projected area basis)
2	DIM	Ratio of shaded SLA to sunlit SLA
0.07	DIM	Fraction of leaf nitrogen in Rubisco
0.006	m/s	Maximum stomatal conductance (projected area basis)
0.00006	m/s	Cuticular conductance (projected area basis)
0.09	m/s	Boundary layer conductance (projected area basis)
-0.63	MPa	Leaf water potential: start of conductance reduction
-2.3	MPa	Leaf water potential: complete conductance reduction
610	Pa	Vapor pressure deficit: start of conductance reduction
3100	Pa	Vapor pressure deficit: complete conductance reduction

*DIM, dimensionless; SLA, specific leaf area*

*The BIOME-BGC model was initialized for four coniferous EUROFLUX sites with a single set of ecophysiological parameters. This parameterization reflects the model assumption that coniferous forest stands have similar physiology.*

turbed ecosystems as well as how to estimate the errors that we make by simulating mature ecosystems instead of disturbed ones if land-use history is not available.

Because we considered only managed forest ecosystems, we simulated disturbed forest ecosystems and then compared the results with simulations of mature ecosystems to estimate the error caused by simulating mature ecosystems instead of disturbed ones. To initialize the model state variables representing disturbed ecosystems, we used a combina-

tion of results from steady-state runs as well as our knowledge of each site's history—in this case, the year of forest planting. First, the model was run to a steady-state condition (spin-up run) for each forest site. Given that we were interested in the simulations of a forest stand of a certain age, the tree C and N pools were consequently reinitialized with the minimum initial values possible to represent a young stand. Then, the model was run for the number of years equal to the age of the specific stand (stand growth run). To check the sensitivity

**Table 2.** Site-specific Parameterization of the BIOME-BGC Model

Site	Lat	Long	Elevation (m)	Soil Texture (%)			Soil Depth (m)	Stand Age in 1997 (y)	Average N Deposition in the 1990s (kg/ha)
				Sand	Silt	Clay			
Tharandt	50°58'	13°38'	380	20.7	41.4	37.9	1.5	96	40
Loobos	52°10'	05°44'	25	96	2.1	1.9	0.5	80	40
Brasschaat	51°18'	04°31'	16	93	5	2	1.8–2.3	70	40
Hyytiala	61°51'	24°17'	181	52	14	7	0.4	35	3

The BIOME-BGC model was initialized for four coniferous EUROFLUX sites with four site-specific sets of parameters, including geographic coordinates, elevation above sea level, atmospheric N deposition, and soil texture and depth.

**Table 3.** Protocol of the BIOME-BGC Model Run

Scenario	After 1860		Before 1860
	Steady-State Initialization	Young Stand Initialization	
Preindustrial	Mature stand run	Stand growth run	Spin-up run
Industrial	Mature stand run	Stand growth run	—

First, the spin-up runs for preindustrial conditions for each site were performed. Then the model was initialized for a young stand and run for the number of years equal to the stand age with both preindustrial and industrial scenarios. Finally, the model was initialized with steady-state conditions and run for the same number of years with both scenarios.

of the model outputs to the initial values of the C and N pools, the model simulations were also performed for the same number of years with all C and N pools initialized from the steady-state condition (mature stand run). Then the differences between the two outputs were analyzed.

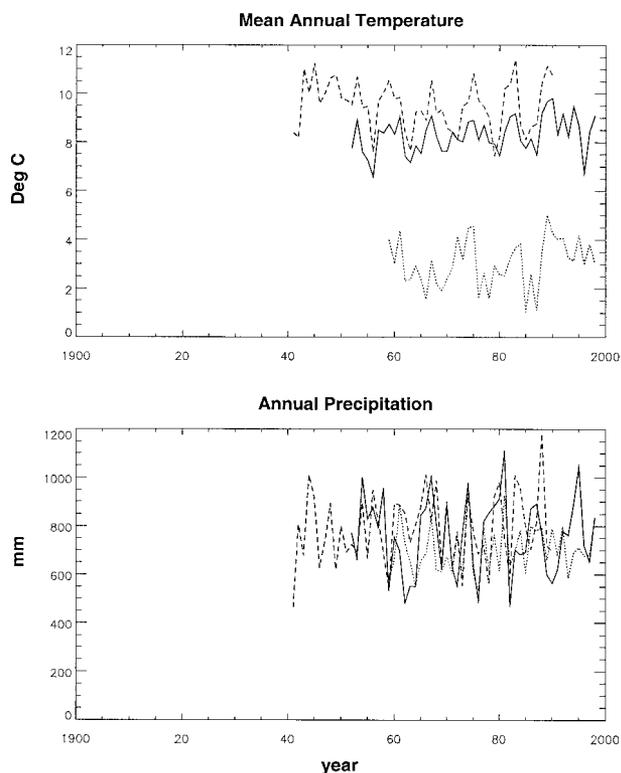
The spin-up run was performed with preindustrial parameterization of atmospheric CO<sub>2</sub> concentration and atmospheric N deposition (Table 3). The spin-up run required long-term climatic variables, which would represent long-term interannual climate variability of the sites necessary to generate plausible values for C and N pools. The daily climate data used for the spin-up run were from 40 to 50 years long on average (Figure 1). Meteorological data were available for the Tharandt site for 1952–98 and for the Hyytiala site for 1959–98. Site-specific, long-term meteorological data were unattainable for Brasschaat and Loobos. The long-term climatologies for these two sites were generated from monthly values obtained from the database of the Climate Research Unit at the University of East Anglia in England (New and others 1999, 2000). The monthly time series for the years 1941–90 were selected for the 0.5° × 0.5° pixel, including both tower sites and then desegregated to daily values with the C2W weather generator

(Bürger 1997). Then the daily data were adjusted for the site conditions (for example, elevation, precipitation pattern) using MTCLIM (Running and others 1987; Kimball and others 1997; Thornton and Running 1999; Thornton and others 2000).

**Environmental Change Scenarios.** To estimate the effects of anthropogenic forcing on the C sequestration capacity of coniferous forest stands, the stand growth and mature ecosystem run were executed with two scenarios: preindustrial and industrial (Table 3).

The preindustrial scenario aimed to reproduce potential forest development and functioning with preindustrial levels of atmospheric CO<sub>2</sub> concentrations and N deposition. In this scenario, atmospheric CO<sub>2</sub> concentrations were set to 290 ppm, approximating the levels at the end of the 19th century (from Gates 1993). Atmospheric annual N deposition was initialized at 2 kg/ha, the highest preindustrial estimate reported in Holland and others (1999).

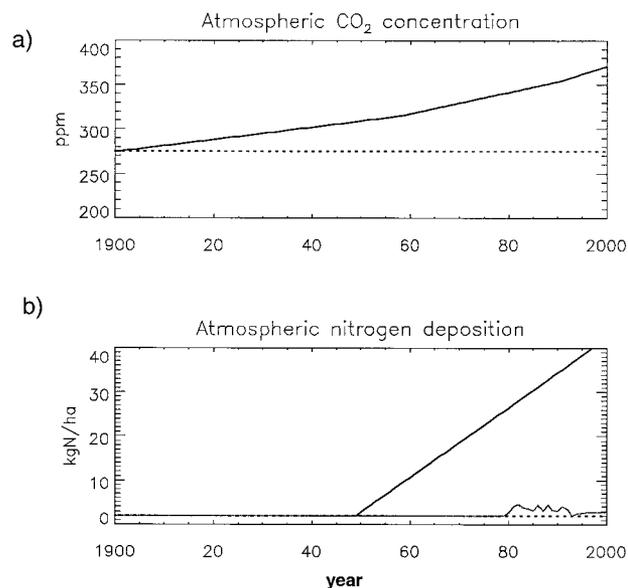
The effects of ongoing environmental changes on coniferous forests in Europe were reflected in the industrial scenario. Stand growth was simulated with continuously increasing atmospheric CO<sub>2</sub> concentrations (Figure 2a) and N deposition (Figure 2b) in the 20th century. The CO<sub>2</sub> concentration in



**Figure 1.** Mean annual temperature and precipitation variabilities for Tharandt (*solid line*), Hyytiala (*dotted line*), and Brasschaat and Loobos (*dashed line*) (differences between the latter two sites were too small to draw two lines). Although the four sites have comparable mean annual precipitation (824, 640, 750, and 772 mm, respectively), their annual temperatures are quite different. Loobos and Brasschaat have slightly higher mean annual temperatures (10 and 10.3°C, respectively) than Tharandt (7.5°C). Hyytiala has a significantly lower mean annual temperature than the other sites (3.4°C), with relatively high interannual variability.

the atmosphere has increased from the preindustrial value of 290 ppm at the end of the 19th century to the average value of 360 ppm measured in 1997. Atmospheric N deposition was assumed to be at a preindustrial level of 2 kg/ha before 1959 and has increased continuously since that time. N deposition increase rates were from the EMAP model (Jonson and others 1998) for Tharandt, Brasschaat, and Loobos; they were averaged from Kulmala (1998) for the Hyytiala site. A sensitivity test of the initialization of the state variables was performed for both the preindustrial and the industrial scenarios.

Other environmental factors that might influence the C dynamics of the studied forests are elevated ozone levels in the atmosphere and N saturation in the soils, both of which may lead to forest decline



**Figure 2.** The environmental change (industrial) scenario assumes increases in both (a) atmospheric CO<sub>2</sub> concentrations (*solid line*) and (b) N deposition (*solid black line* for Loobos, Brasschaat, and Tharandt; *solid gray line* for Hyytiala). Dotted horizontal lines represent preindustrial conditions.

(Schulze 1989; Larcher 1995). The damage manifests as needle yellowing and loss, with subsequent tree and stand mortality (Schulze and Lange 1990). Given that no such damage was observed at the studied sites, these factors were excluded from the scope of the paper. However, it does not mean that they should be ignored in future research, since tropospheric levels of ozone (Lelieveld and Dentener 2000) and atmospheric wet and dry N deposition may well continue to increase in the future.

### Model Corroboration

There is no single measurement technique that can provide information on all of the major C budget components (C uptake, plant respiration, soil microbial respiration). This is a problem that complicates model corroboration. Therefore, we focused on three variables projected LAI, NEP, and AET, integrating C and water cycles at the ecosystem level, because measurements were available for these factors simultaneously at all four sites. Projected LAI is a measure of canopy density and size and is defined as the projected area of leaves over a unit of land. It can serve as a possible measure of carbon accumulation. NEP integrates ecosystem processes occurring at different time scales. "Slow" processes include allocation, soil decomposition, and so on; the "fast" processes are photosynthesis

and maintenance respiration. In terms of magnitude, NEP is the small difference between two large fluxes (photosynthesis and respiration) and approaches zero for climax vegetation. The water balance integrates precipitation input, soil water storage, and atmospheric evaporative demand, and appears to be a dominant control of variation in plant productivity. AET is the net flux of water from the land surface back to atmosphere, integrating evaporation from soil and plant surfaces with transpiration of the plants, and can serve as an indicator of water balance in the ecosystem. The water and C cycles of the ecosystems are closely linked. In the model, they are coupled through a control on stomatal conductance.

In this study, LAI, NEP, and AET were simulated with preindustrial and industrial scenarios and with different initializations of the C and N pools to generate a range of possible values and to provide estimates of uncertainty in model estimates. Then these ranges were compared with observed data.

*Long-term C Dynamics: LAI.* LAI, which represents the hypothetical number of leaf layers in a tree canopy, is often used as a simplified measure of canopy geometry. The ability to simulate an LAI that is comparable to observations is an important test of the model algorithm to integrate numerous processes that occur at longer time scales and are responsible for forest growth and canopy development. Accurate simulations of changes in vegetation structure are the next step after simulations of daily C and water balances with prescribed vegetation structure. In our case, only one observation of LAI, taken around 1997, was available for each of the four EUROFLUX sites (Vesala and others 1998; Kowalski and others 1999; Aubinet and others 2000). For each site, we compared the maximum LAI simulated with the different scenarios and averaged over the last 5 years (1995–98) to the available data from actual observations. For accurate corroboration of annual C dynamics, we would need time series of observed LAI.

*Daily C and Water Balance: NEP and AET.* The eddy covariance technique offers an exceptional opportunity to assess C and water fluxes between terrestrial ecosystems and the atmosphere at the ecosystem level. The flux footprint (the area where the fluxes come from) depends on (a) the height of the tower (the sensor) relative to the zero plane displacement of the vegetation, (b) the wind speed, and (c) the atmospheric stability (Horst and Weil 1994). In general, the daytime flux footprint extends about 100 m for every meter measured above the reference level and can cover an area located as far as 100–1000 m away from the tower (Baldochi

and others 1996). The flux footprint is smaller in the daytime and larger at night. However, the eddy covariance method is not free from errors. A number of errors of atmospheric, surface, and instrumental origin contribute to uncertainty in the flux estimation (Moncrieff and others 1996). In addition, instrument failures associated with adverse weather conditions result in data gaps. Various methods exist for filling the data gaps, but they can yield substantially different results (Falge and others 2001). Systematic overestimation of NEP is also possible using the eddy covariance technique, because nonturbulent phases occur more often during the respiration-dominated periods. The latter hypothesis is currently being tested at the Tharandt site.

BIOME-BGC estimates of NEP and AET were corroborated using eddy correlation measurements from the four EUROFLUX sites. The observed half-hourly values of NEP and AET were aggregated to the daily values to match the temporal resolution of the model estimates. For correlations between simulated and observed data, we used only data for days without measurement gaps to avoid bias introduced by gap-filling techniques.

## RESULTS AND DISCUSSION

Variations in climates, site-specific variables (atmospheric N deposition, site elevation, soil texture), and forest ages resulted in the differences between simulated LAI as well as net C and water fluxes among the sites.

### Effect of Model Initialization and Environmental Changes on Simulated Annual C Dynamics

Model simulations of LAI are an important test of our understanding of how climate controls vegetation growth and critical canopy processes and to show whether the simplified representation of tree canopy development in the model is adequate. For the industrial scenario, BIOME-BGC simulated LAI accurately for Tharandt and Hyytiala but overestimated it for Loobos and Brasschaat (Table 4). The poor long-term climate data (representing a larger area around the site [ $0.5^\circ \times 0.5^\circ$ ]), uncertainties in site-specific parameterizations (for examples rooting depth), or allocation parameters could have contributed to these overestimations. The LAI simulated with the industrial scenario was higher than that simulated with the preindustrial scenario for all sites because all ecosystems under normal conditions are limited by C and N availability. The sim-

**Table 4.** Comparison of Measured Leaf Area Index (LAI, Dimensionless) to Modeled LAI under Different Scenarios

Site	Observed LAI	Modeled LAI			
		IND/YNS	IND/STS	PRE/STS	PRE/YNS
Tharandt	5	5.0	4.7	3.2	3.6
Loobos	3	4.0	4.0	2.6	3.4
Brasschaat	3	5.5	4.8	3.2	4.0
Hyytiala	3	3.3	3.2	3.2	3.1

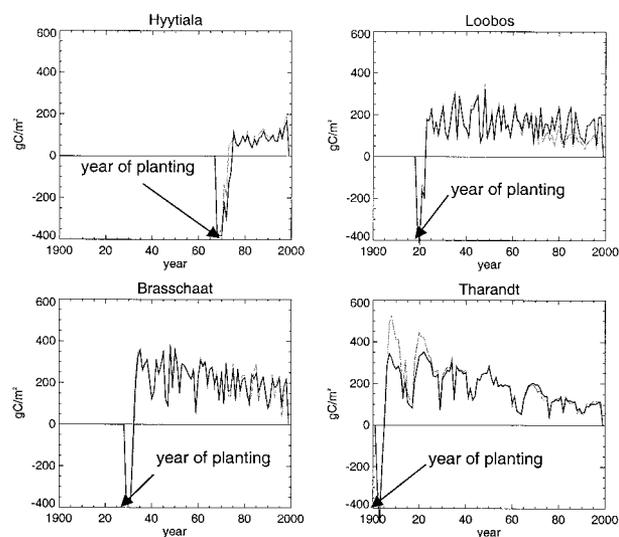
The model provided accurate estimates of LAI for Tharandt and Hyytiala but overestimated it for Loobos and Brasschaat (second versus third column, PRE/STS scenario). For comparison, predicted LAI is also given for other scenarios.

IND, industrial; PRE, preindustrial; YNS, young stand; STS, steady-state

ulated LAI was higher for the stand growth run than for the mature stand run, which follows the ecosystem theory that mature or climax ecosystems have a lower LAI than growing ones. The Loobos site was the only exception to this rule; LAI was the same for both the mature stand run and the stand growth run under the industrial scenario. This finding can be explained by the fact that it stands reached maturity after only 80 years due to conditions of high N availability and low soil depth.

Except for the few years needed for the trees to establish themselves and grow a canopy, the NEP for the stand growth run was higher than the NEP for the mature stand run, resulting in positive differences between the two states (Figure 3). The negative differences in NEP at the beginning of the simulations derived from the negative NEP simulated in the stand growth run, because right after planting the trees have a low LAI and take up considerably less C than the soil releases. The positive difference between NEP simulated using different initializations of plant state variables ranged from 50 to 500 gC/m<sup>2</sup> per year, depending on climate conditions. The difference was greater in years with favorable climatic conditions (higher temperature and precipitation) and dropped to 50 gC/m<sup>2</sup> in cold or dry years. Although the difference declined with the age of the forest (equivalent to the number of model iterations in our case), it still fluctuated between 50 and 100 gC/m<sup>2</sup> per year after 97 simulation years for the oldest forest stand considered (Tharandt). Hyytiala, the site with the lowest mean annual temperature (3.5°C) and the least precipitation (640 mm), had the smallest differences between the NEP values simulated with the two different model initializations. The effect of increased atmospheric CO<sub>2</sub> concentrations and N deposition on both the magnitude and the decline rate of the difference was not pronounced.

This study showed that enhanced atmospheric CO<sub>2</sub>



**Figure 3.** Difference between annual net ecosystem productivities modeled with different initializations of state variables (stand growth NEP minus steady-state NEP) for four coniferous forest stands. Differences in NEP decline slowly with time for both the industrial (*gray line*) and preindustrial (*black line*) scenarios. The difference varies from year to year depending on climate conditions.

concentrations and especially increased N deposition had a marked effect on the simulated C sequestration capacity of the forest stands (Figure 4). This result was similar to the patterns that have been observed for global coniferous forests (Churkina and Running 2000). The effect of environmental changes on simulated NEP was comparable for both initializations of state variables (young stand and steady state) at all sites except Loobos (Figure 5). In the case of Loobos, the difference between NEP simulated with the industrial and preindustrial scenarios was higher for the model run with a steady-state initialization, most

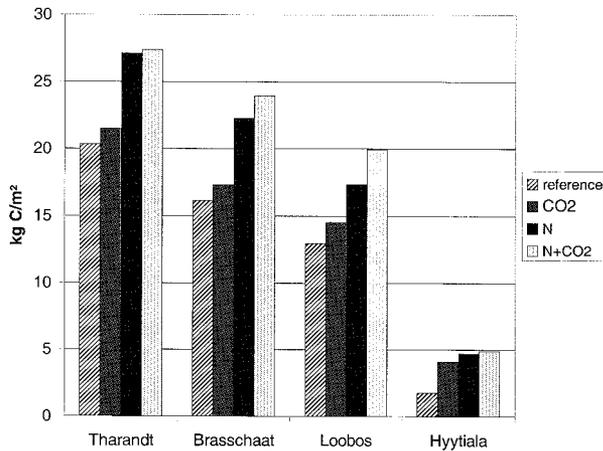


Figure 4. Effects of elevated  $\text{CO}_2$ , increased N deposition, and the combination of both on cumulative NEP ( $\text{kg C/m}^2$ ) for four coniferous forest stands. Each bar on the figure represents NEP summed over the number of years equal to the stand age. A combination of elevated N deposition and increased atmospheric  $\text{CO}_2$  has the largest effect on C sequestration potential of the sites. Reference, both N deposition and atmospheric  $\text{CO}_2$  concentrations are constant; N, increasing N deposition, atmospheric  $\text{CO}_2$  is constant;  $\text{CO}_2$ , increasing atmospheric  $\text{CO}_2$ , N deposition is constant; N+ $\text{CO}_2$ , both N deposition and atmospheric  $\text{CO}_2$  are increasing.

likely because simulated LAI differences were higher at steady state than for young plant initialization.

Differences in NEP estimates increased for both the young stand and steady-state initializations of the vegetation state variables and were mostly associated with the steady increase in N deposition that began in 1950. These differences varied from year to year depending on climate conditions. The forest stand at the Hyytiala site had the lowest increase in NEP in response to elevated atmospheric  $\text{CO}_2$  and N deposition because the industrial N deposition there was an order of magnitude lower than that at the other sites. For forest stands at Loobos, Brasschaat, and Tharandt, increases in N deposition at an average rate of  $0.08 \text{ gN/m}^2$  per year and in  $\text{CO}_2$  at  $1.3 \text{ ppm}$  per year resulted in enhanced C uptake by vegetation at a rate of  $4.2 \text{ gC/m}^2$  per year. The model results suggest that the magnitude of response to environmental changes was dependent on the site's climate variability, site-specific parameters (for example, soil depth), as well as the character and magnitude of environmental changes.

### Daily NEP and AET

Daily NEP modeled with the industrial scenario and with young stand initializations (gray line at the top

of the uncertainty range in Figure 6) gave the closest estimate of the observed NEP and was used in the correlation plots. Although corresponding modeled AET values did not always provide the closest estimates of the observed AET (Figure 7), for consistency, these daily AET estimates were used in the regression analysis.

Linear regression analysis of modeled and observed daily average NEP showed a good relation ("All NEP" rows in Table 5) for all four sites, with  $0.676 < R^2 < 0.823$ . In-depth analysis of the two seasonal subsets (data pairs with modeled NEP  $> 0$  and modeled NEP  $\leq 0$ ) provided interesting insights into the model behavior. During the C uptake period (modeled NEP  $> 0$ ), the model still provided good estimates of the observations for all four sites with  $R^2$  in the range of 0.45–0.73, with underestimation for Hyytiala and Tharandt ( $b > 1$ ). The underestimation of NEP, combined with the accurate LAI (accurate GPP) for Hyytiala and Tharandt and the accurate NEP simulated with overestimated LAI (inflated GPP) for Loobos and Brasschaat, suggest that the model overestimates soil respiration. The overestimation of soil respiration may result either from overestimated C content in soil, because the management history was not available, or from the respiration algorithm used in the model. Both hypotheses should be tested with chamber measurements of soil respiration and a comparison of the simulated and observed C stocks in the soils.

During the C release period (modeled NEP  $\leq 0$ ), the model explained fluxes well only for the forest stand at the Loobos site ( $R^2 = 0.723$ ). There was a weak correlation between the modeled and measured fluxes at Brasschaat ( $R^2 = 0.319$ ) and at Tharandt ( $R^2 = 0.266$ ). At Hyytiala, the model failed to simulate the variance in the observed fluxes ( $R^2 = 0.003$ ) during the C release period. Therefore, the BIOME-BGC model seems to have a better predictive capacity for the photosynthesis-related processes than for respiration. The algorithm used in the model for simulations of respiration fluxes with air temperature below freezing and with snow cover is worth revisiting, given recent findings (Marico and others 2000).

The model, as well as the flux observations, could be responsible for the weak correlation between the observed and modeled daily NEP during negative NEP periods. In the model, the reason for this can most likely be traced to the simulations of soil respiration, which is the largest source of respired C in winter. The initialization of soils from steady state tends to overestimate soil C and consequently respiration. The method used to simulate the soil temperature and respiration could be another source of

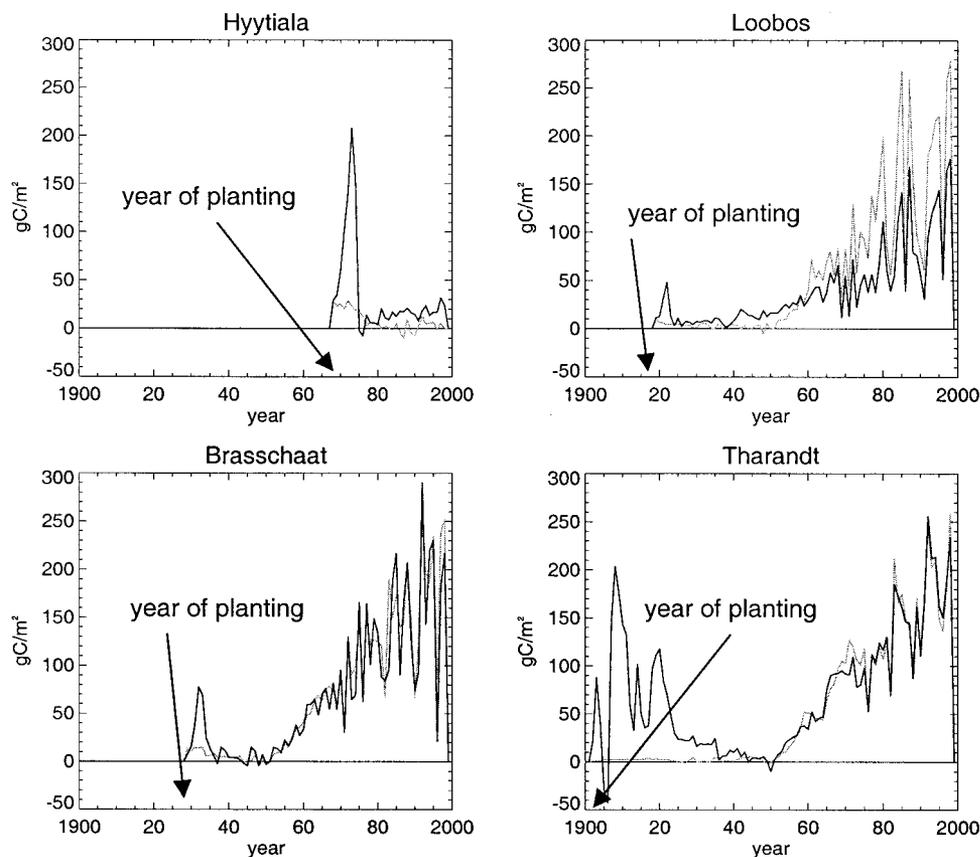


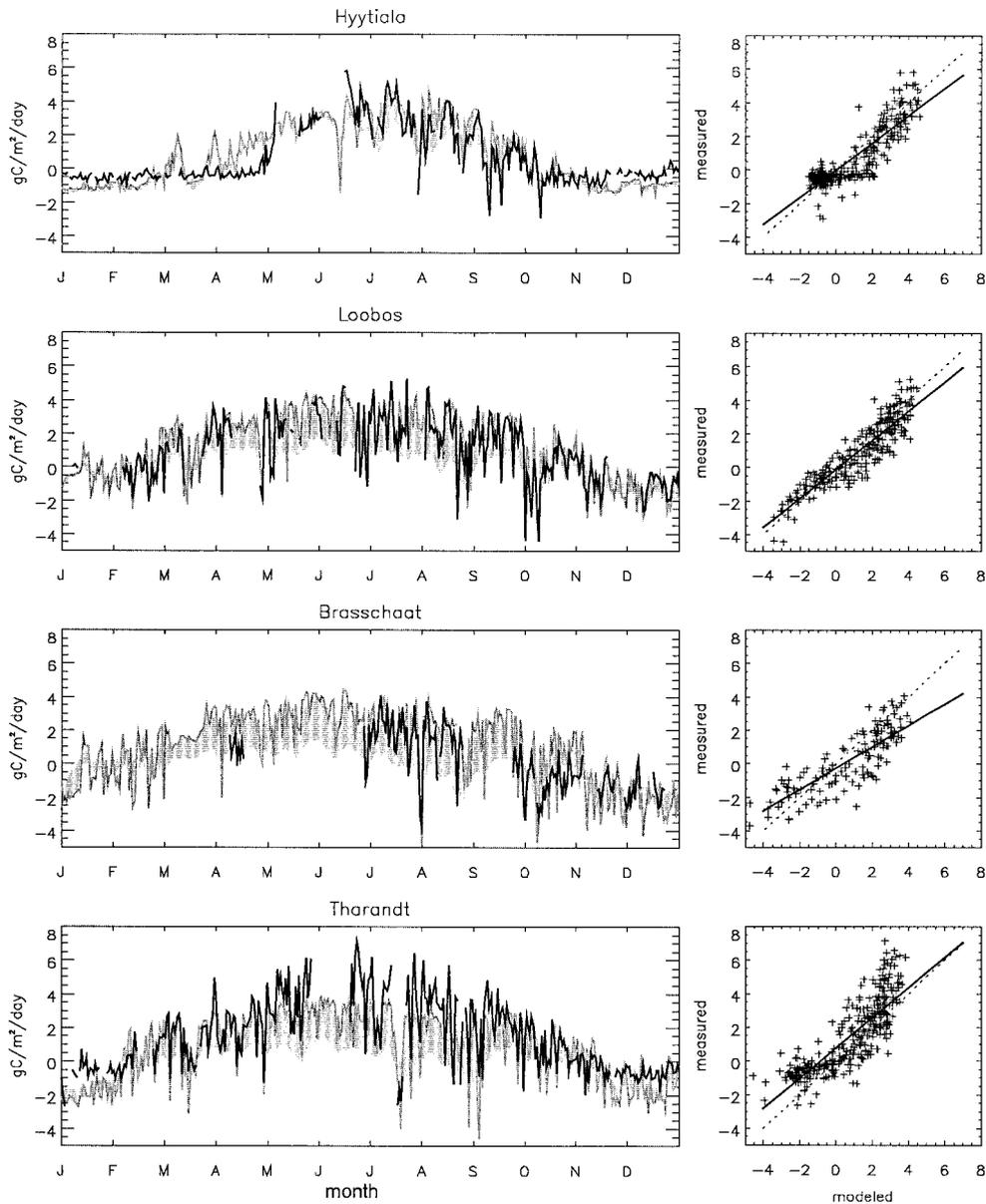
Figure 5. Difference between annual net ecosystem productivities modeled with different environmental conditions (industrial minus preindustrial NEP) for four coniferous forest stands. Differences in NEP increase with time for both young plant (*black line*) and steady-state (*gray line*) initializations of the vegetation state variables and is associated mostly with steadily increasing N deposition, starting in 1950. The difference varies from year to year depending on climate conditions.

the problem. Checking the validity of the method at near-freezing temperatures and in the presence of snow cover against the chamber respiration measurements would be worthwhile.

Flux measurements in winter could also have contributed to the problem. During the winter, nights are significantly longer than days and the contribution of nighttime flux to the cumulative daily flux becomes more significant. However, the nighttime eddy fluxes are often dubious, because at night the turbulent flux is partially inhibited by stable stratification of the atmospheric surface layer above the canopy. The overnight accumulation is released after sunrise with the onset of convection, resulting in a prominent spike of  $\text{CO}_2$  in the morning (Moncrieff and others 1996). Although at a daily time step, this spike should compensate for the stratification effect under conditions of ideal terrain and system design, real conditions are far from ideal, and site-specific corrections are applied to compensate for the lost fluxes (Aubinet and others 2000).

There is still a debate as to whether such site-specific corrections should include an empirical  $u^*$  correction, or a consideration of advection, or something else. At an annual time step, the  $u^*$  correction applied to half-hourly flux values can result in an increase of 77–185  $\text{gC/m}^2$  per year for temperate forests, accounting for nearly the average NEP of a temperate forest (Falge and others 2001).

Analysis of the modeled and observed daily average AET showed that the BIOME-BGC model explained 60%–88% of variance in the measured water fluxes (Table 6). The model overestimated AET at the high end (Figure 7). A clustering of data points between 0 and 1 complicated the regression analysis in the cases of Hyytiala and Tharandt. Clustering revealed that there were many days with a low AET, which was most likely related to the relatively humid climates at the sites. Overestimation of water fluxes, combined with underestimation of the C fluxes during the C uptake period, suggests that the water-use efficiency of the forests is most likely higher than that simulated by the model.



**Figure 6.** Comparison of modeled and observed daily net ecosystem productivities (NEP,  $\text{gC/m}^2$ ) of four coniferous forest stands for 1997. For each site, seasonal courses and a scatterplot between observed and modeled net ecosystem productivity are shown. Gray-shaded areas on the plots with seasonal courses show uncertainty ranges in model estimates of NEP, which are caused by different environmental conditions and initializations of the state variables. NEP modeled with the industrial scenario and with young plant initializations of the state variables (*gray line*) is at the top of the uncertainty range. It is the closest estimate to the observed NEP (*black line*) and is used in the correlation plots.

The uncertainties in the model estimations of daily C and water fluxes arising from different state variable initializations and from different environmental change scenarios were higher during the summer and lower during the winter (Figures 6 and 7). In the summer, the discrepancy in the model estimates of NEP reached as high as  $2 \text{ gC/m}^2$  per day, an average C uptake per day.

The estimates of AET were less sensitive than NEP to different initializations of state variables or environmental change scenarios. More information about the sites' history, as well as the availability of accurate long-term climate data, measured biomass, and soil C and N contents, could improve the initialization of the state variables. Site-specific information about the anthropogenic

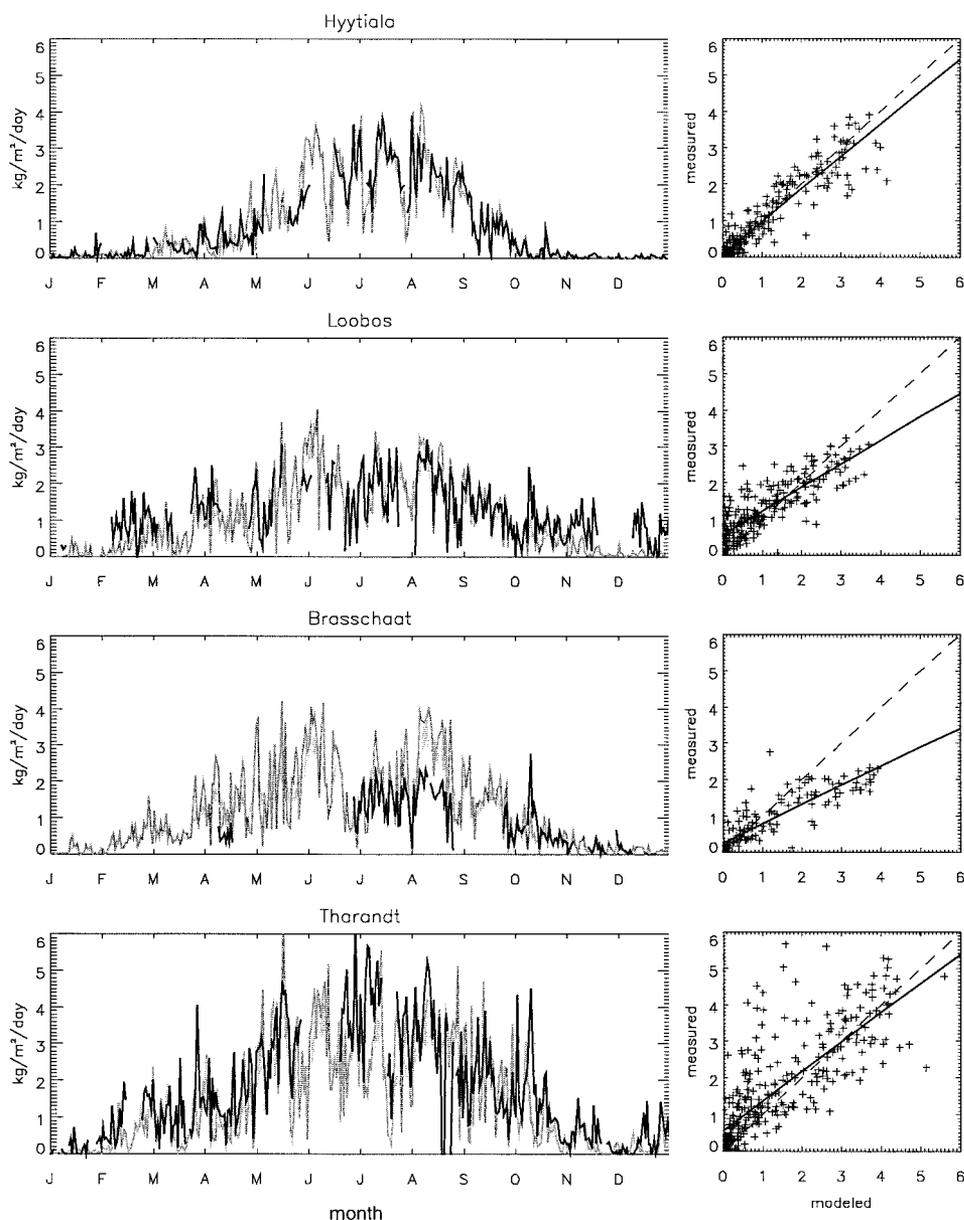


Figure 7. Comparison of modeled and observed daily actual evapotranspiration (AET,  $\text{kg}/\text{m}^2$ ) of four coniferous forest stands for 1997. For each site, seasonal courses and a scatterplot between observed and modeled actual evapotranspiration are shown. Gray-shaded areas on the plots with seasonal courses show uncertainty ranges in model estimates of AET, which are caused by different environmental conditions and initializations of the state variables. AET modeled with the industrial scenario and with young plant initializations of the state variables (*gray line*) is at the top of the uncertainty range. For consistency with the previous plot, this AET was used in the correlation plots, although it was not always the closest estimate to the observed AET (*black line*).

factors influencing ecosystems would improve current predictions of C dynamics.

The model results suggest that after the initial 10–15 years of C loss during stand establishment, the forests at all four sites have been sequestering C at an average rate of  $100\text{--}300\text{ gC}/\text{m}^2$  per year (Figure 8). Surprisingly, the NEP rate at the almost 100-year-old stand at Tharandt was as high as the

NEP at the 70–80-year-old stands at Loobos and Brasschaat, most likely as a result of increasing N deposition. Despite the significantly different LAI, annual mean NEP did not vary as much between the sites (excluding Hyytiala), because forests with a higher LAI also generate more litter and consequently have higher respiration rates. Hyytiala had a considerably lower LAI and NEP than the other

**Table 5.** Linear Regression ( $y = a + b \cdot x$ ) Results for Comparisons between Modeled and Observed Daily Average NEP

	$n$	$R^2$	b (Std. Err.)	a (Std. Err.)
Tharandt				
All NEP	316	0.683	0.899 (0.035)	0.773 (0.071)
NEP > 0	206	0.461	1.302 (0.099)	-0.040 (0.216)
NEP ≤ 0	110	0.131	0.266 (0.066)	-0.200 (0.120)
Loobos				
All NEP	248	0.823	0.867 (0.026)	-0.123 (0.060)
NEP > 0	180	0.659	1.017 (0.055)	-0.524 (0.139)
NEP ≤ 0	68	0.723	0.954 (0.073)	0.159 (0.120)
Brasschaat				
All NEP	136	0.676	0.639 (0.038)	-0.257 (0.093)
NEP > 0	85	0.450	1.026 (0.124)	-1.124 (0.299)
NEP ≤ 0	51	0.319	0.386 (0.080)	-0.747 (0.196)
Hyytiala				
All NEP	310	0.755	0.808 (0.026)	-0.022 (0.052)
NEP > 0	163	0.733	1.203 (0.057)	-1.082 (0.147)
NEP ≤ 0	147	0.003	0.065 (0.099)	-0.461 (0.090)

Only observations without gaps ( $n$ ) were included in the regression. The regression was performed for all pairs of observed and modeled NEP, for data pairs with modeled NEP > 0 (C uptake processes dominate) and for data pairs with modeled NEP ≤ 0 (C release processes dominate). In most cases, the BIOME-BGC model estimated NEP during the C uptake period (high  $R^2$ , low standard errors) better than during the C release period (low correlation or lack of correlation).

**Table 6.** Linear Regression ( $y = a + b \cdot X$ ) Results for Comparisons between Simulated and Observed Daily Average AET

	$n$	$R^2$	b (Std. Err.)	a (Std. Err.)
Tharandt	316	0.605	0.803 (0.037)	0.577 (0.073)
Loobos	248	0.693	0.647 (0.028)	0.577 (0.040)
Brasschaat	136	0.745	0.528 (0.027)	0.266 (0.045)
Hyytiala	310	0.887	0.890 (0.018)	0.088 (0.024)

Only observations without gaps ( $n$ ) were included in the regression. Strong clustering of data points between 0 and 1 complicated regressions in the cases of Hyytiala and Tharandt and led to heteroskedastic results. The model explained 60%–88% of the variance. The BIOME-BGC model overestimated AET at the high end.

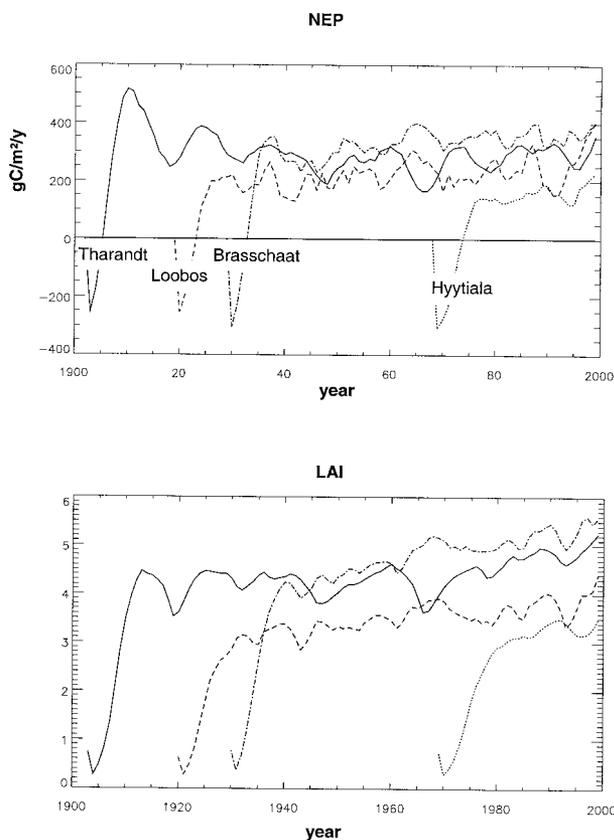
sites because of its lower mean annual temperatures (see Figure 1).

## CONCLUSIONS

In this study, we evaluated the ability of the BIOME-BGC ecosystem model to estimate the daily and annual C dynamics of four European coniferous forests, shifts in these dynamics in response to increasing atmospheric N deposition and CO<sub>2</sub> concentrations, and uncertainties in the model estimates related to the initialization of forest successional stage. Although the model predicted daily C and water fluxes reasonably well ( $R^2 \approx 0.60$ – $0.80$ ) at all sites, it seems to have a better predictive ability for the photosynthesis-related processes (NEP > 0,

$R^2 = 0.45$ – $0.73$ ) than for the respiration-related processes (NEP ≤ 0,  $R^2 = 0.003$ – $0.72$ ). Overestimations of LAI (and consequently Gross Photosynthetic Production), in combination with reasonable estimates of daily NEP for two sites, also illustrate the problem with modeled respiration. Either the estimates of autotrophic respiration are similarly inflated, or the estimates of heterotrophic respiration are inflated, or both components of respiration are inflated. Measured soil respiration, C contents in vegetation and soils, and site management histories would be helpful to identify the reasons and improve the model behavior.

The model results suggest that all four European forests have been net sinks of C at the rate of 100–300 gC/(m<sup>2</sup>/y) and that this C sequestration ca-



**Figure 8.** Annual net ecosystem productivity (moving average over 5 years) and maximum leaf area index (LAI) simulated by the BIOME-BGC model for four sites. Both variables were generated with the stand growth run and industrial scenario. After the initial 10–15 years of C loss during the stand establishment, forests at all sites have been sequestering C at an average rate of 100–300 gC/m<sup>2</sup> per year. Hyttiala had the lowest NEP and LAI because of considerably lower mean annual temperatures (see Figure 1). Shallow soils resulted in significantly lower LAI and NEP at Loobos than at Brasschaat, despite similar climate conditions.

capacity would be 30%–70% lower without the increasing N deposition and CO<sub>2</sub> concentrations. Elevated anthropogenic N deposition played a prominent role in increasing this capacity; therefore, this factor should not be neglected either in the modeling of European ecosystems or in field experiments. Simultaneous measurements of C and N pools of the ecosystems will improve our understanding of C–N interactions, help to refine model algorithms, and eventually reduce uncertainty in the global C budget.

We estimated that the modeled C exchange at the study sites was reduced by 50%–100% when model simulations were performed for climax forests rather than for regrowing forests. The stand age

appeared to be a critical parameter for accurate estimations of forest C exchange. Although simulations of C dynamics of climax vegetation provide insights into its interannual variability, they do not provide accurate estimates of the current C exchange. Because it is not feasible to take into account different successional stages of vegetation or forest age distribution at a regional scale, regional estimates of biomass and soil C contents can be used as substitutes for model initialization. New algorithms, which allow real-time adjustment in the model's state variables using on-ground and remote observations of vegetation structure and processes (for example, data assimilation), should reduce uncertainty in the model estimates and improve its accuracy.

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#### REFERENCES

- Aubinet M, Grelle A, Ibrom A, Rannik Ü, Moncrieff J, Foken T, Kowalski A S, Martin P H, Berbigier P, Bernhofer C, and others. 2000. Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. *Adv Ecol Res* 30:113–175.
- Baldocchi DD, Valentini R, Running SW, Oechel W, Dahlman R. 1996. Strategies for monitoring and modeling CO<sub>2</sub> and vapor fluxes over terrestrial ecosystems. *Global Change Biol* 2:159–168.
- Band LE, Peterson DL, Nemani RR, Running SW. 1993. Forest ecosystem processes at the watershed scale: incorporating hill-slope hydrology. *Agric For Meteorol* 63:93–126.
- Bugmann H. 2001. A review of forest gap models. *Clim Change* 51:259–305.
- Bugmann HKM, Xiaodong Y, Sykes MT, Martin P, Lindener M, Desanker PV, Cumming SG. 1996. A comparison of forest gap models: model structure and behaviour. *Clim Change* 34:289–313.
- Bürger G. 1997. On the disaggregation of climatological means and anomalies. *Clim Res* 8:183–194.
- Churkina G, Running SW. 2000. Investigating the balance between timber harvest and productivity of the global coniferous forests under global change. *Clim Change* 47:167–191.
- Cienciala E, Running SW, Lindroth A, Grelle A, Ryan MG. 1998. Analysis of carbon and water fluxes from the NOPEX boreal forest: comparison of measurements with Forest-BGC simulations. *J Hydrol* 212–3:62–78.
- Falge E, Baldocchi D, Olson R, Anthoni P, Aubinet M, Bernhofer C, Burba G, Ceulemans R, Clement R, Dolman H, and others. 2001. Gap filling strategies for defensible annual sums of net

- ecosystem sums of net ecosystem exchange. *Agric For Meteorol* 2912:1–27.
- Fan S, Gloor M, Mahlman J, Pacala S, Sarmiento J, Takahashi T, Tans P. 1998. A large terrestrial carbon sink in North America implied by atmospheric and carbon dioxide data and models. *Science* 282:442–446.
- Francey RJ, Tans PP, Allison CE, Enting IG, White JWC, Troller M. 1995. Changes in oceanic and terrestrial carbon uptake since 1982. *Nature* 373:326–330.
- Gates DM. 1993. *Climate change and its biological consequences*. Sunderland (MA): Sinauer.
- Goulden ML, Munger JW, Fan S-M, Daube BC, Wofsy SC. 1996a. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. *Global Change Biol* 2:169–182.
- Goulden ML, William MJ, Fan S-M, Daube BC, Wofsy SC. 1996b. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science* 271:1576–1578.
- Holland EA, Dentener FJ, Braswell BH, Sulzman JM. 1999. Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry* 46:7–43.
- Horst TW, Weil JC. 1994. How far is far enough? The fetch requirements for micrometeorological measurement of surface fluxes. *J Atmos Oceanic Technol* 11:1018–1025.
- Hunt ER Jr, Piper SC, Nemani RR, Keeling CD, Otto RD, Running SW. 1996. Global net carbon exchange and intra-annual atmospheric CO<sub>2</sub> concentrations predicted by an ecosystem process model and three-dimensional atmospheric transport model. *Global Biogeochem Cycles* 10:431–456.
- Jonson JE, Bartnicki J, Olendrzynski K, Jakobsen HA, Berge E. 1998. EMEP Eulerian model for atmospheric transport and deposition of nitrogen species over Europe. *Environ Pollut* 102:289–298.
- Justice CO, Vermonte E, Townshend JRC, Defries R, Roy DP, Hall DK, Salomonson VV, Privette JL, Riggs G, Strahler A, and others. 1998. The Moderate Resolution Imaging Spectroradiometer (MODIS): land remote sensing for global change research. *IEEE Trans Geosci Remote Sens* 36:1228–1249.
- Kauppi PE, Mielikäinen K, Kuusela K. 1992. Biomass and carbon budget of European forests, 1971 to 1990. *Science* 256:70–74.
- Kimball JS, Running SW, Nemani R. 1997. An improved method for estimating surface humidity from daily minimum temperature. *Agric For Meteorol* 85:87–98.
- Korol RL, Running SW, Milner K, Hunt ER. 1991. Testing a mechanistic carbon balance model against observed tree growth. *Can J For Resources* 21:1098–1105.
- Kowalski AS, Overloop S, Ceulemans R. 1999. Eddy fluxes above a Belgian, Campine forest and relationships with predicting variables. In: Ceulemans R, Veroustrate F, Gond V, Van Rensbergen J, editors. *Forest ecosystem modelling, upscaling and remote sensing*. The Hague: SPB Publishing. p 3–18.
- Kulmala A, Leinonen L, Ruoho-Airola T, Salmi T, Waldén J. 1998. *Air quality trends in Finland*. Helsinki: Finnish Meteorological Institute.
- Larcher W. 1995. *Physiological plant ecology*. 3rd ed. Berlin: Springer-Verlag.
- Lelieveld J, Dentener FJ. 2000. What controls tropospheric ozone? *J Geophys Res* 105:3531–3551.
- Marico S, Nishimura N, Mo W, Matsui Y, Kibe T, Koizumi H. 2000. Winter CO<sub>2</sub> flux from soil and snow surfaces in a cool-temperate deciduous forest, Japan. *Ecol Res* 15:363–372.
- Moncrieff JB, Mahli Y, Leuning R. 1996. The propagation of errors in long-term measurements of land-atmosphere fluxes of carbon and water. *Global Change Biol* 2:231–240.
- Monteith JL. 1973. *Principles of environmental physics*. New York: Elsevier.
- Nemani RR, Running SW. 1989. Testing a theoretical climate-soil-leaf area hydrologic equilibrium of forests using satellite data and ecosystem simulation. *Agric For Meteorol* 44:245–260.
- New M, Hulme M, Jones P. 2000. Representing twentieth century space-time climate variability. Part II. Development of 1901–1996 monthly grids of terrestrial surface climate. *J Clim* 13:2217–2238.
- New M, Hulme M, Jones PD. 1999. Representing twentieth century space-time climate variability. Part I. Development of a 1961–90 mean monthly terrestrial climatology. *J Clim* 12: 829–856.
- Reynolds JF, Bugmann H, Pitelka LF. 2001. How much physiology is needed in forest gap models for simulating long-term vegetation response to global change? Challenges, limitations, and potentials. *Clim Change* 51:541–557.
- Rodriguez-Murillo JC. 1997. Temporal variations in the carbon budget of forest ecosystems in Spain. *Ecol Appl* 7:461–469.
- Running SW. 1994. Testing FOREST-BGC ecosystem process simulations across a climatic gradient in Oregon. *Ecol Appl* 4:238–247.
- Running SW, Baldocchi DD, Turner DP, Gower ST, Bakwin PS, Hibbard KA. 1999. A global terrestrial monitoring network integrating tower fluxes, flask sampling, ecosystem modeling and EOS satellite data. *Remote Sens Environ* 70:108–127.
- Running SW, Coughlan JC. 1988. A general model of forest ecosystem processes for regional applications I. Hydrologic balance, canopy gas exchange and net primary production processes. *Ecol Model* 42:125–154.
- Running SW, Gower ST. 1991. FOREST-BGC, a general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiol* 9:147–160.
- Running SW, Hunt ERJ. 1993. Generalization of a forest ecosystem process model for other biomes, Biome-BGC, and an application for global-scale models. In: Ehleringer JR, Field CB, editors. *Scaling physiological processes: leaf to globe*. San Diego (CA): Academic Press. p 141–158.
- Running SW, Justice CO, Salomonson V, Hall D, Barker J, Kaufmann YJ, Strahler AH, Huete AR, Muller J-P, Vanderbilt V, and others. 1994. Terrestrial remote sensing science and algorithms planned for EOS/MODIS. *Int J Remote Sens* 15:3587–3620.
- Running SW, Nemani RR, Hungerford RD. 1987. Extrapolation of synoptic meteorological data in mountainous terrain and its use for simulating forest evapotranspiration and photosynthesis. *Can J For Resources* 17:472–483.
- Schimel DS, House JJ, Hibbard KA, Bousquet P, Ciais P, Peylin P, Braswell BH, Apps MJ, Baker D, Bondeau A, and others. 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature* 414:169–172.
- Schulze ED. 1989. Air pollution and forest decline in a spruce (*Picea abies*) forest. *Science* 244:776–783.

- Schulze ED, Lange OL. 1990. Die Wirkungen von Luftverunreinigungen auf Waldökosysteme. *Chem Z* 3:117–130.
- Sonntag M. 1998. Klimaveränderungen und Waldwachstum: TREEDYN3-Simulationen mit einer Analyse modellstruktureller Unsicherheiten. Kassel: Universität Kassel.
- Thornton PE. 1998. Regional ecosystem simulation: combining surface- and satellite-based observations to study linkages between terrestrial energy and mass budgets [dissertation]. Missoula: University of Montana.
- 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. *Agric For Meteorol* 104:255–271.
- Thornton PE, Law BE, Gholz HL, Clark KL, Falge E, Ellsworth DE, Goldstein AH, Monson RH, Hollinger DY, Falk M, and others. 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agric For Meteorol* 113:185–222.
- Thornton PE, Running SW. 1999. An improved algorithm for estimating incident daily solar radiation from measurements of temperature, humidity, and precipitation. *Agric For Meteorol* 93:211–228.
- Turner DP, Koerper GJ, Harmon ME, Lee JJ. 1995. A carbon budget for forests of the conterminous United States. *Ecol Appl* 5:421–436.
- [UNFCCC] United Nations Framework Convention on Climate Change. 1997. Kyoto Protocol to the United Nations Framework Convention on Climate Change. Conference of the Parties, Kyoto, Japan. <http://unfccc.int/resource/docs/convkp/kpeng.pdf>
- Valentini R, Mateucci G, Dolman AJ, Schulze E-D, Rebmann C, Moors EJ, Granler A, Gross P, Jensen NO, Pilegaard K, and others. 2000. Respiration as the main determinant of carbon balance in European forests. *Nature* 404:861–865.
- Vesala T, Haataja J, Aalto P, Altimir N, Buzorius G, Garam E, Hämeri K, Ilvesniemi H, Jokinen V, Keronen P, and others. 1998. Long-term field measurements of atmosphere–surface interactions in boreal forest combining forest ecology, micrometeorology, aerosol physics and atmospheric chemistry. *Trends Heat Mass Momentum Transfer* 4:17–35.
- Waring R, Running SW. 1998. *Forest ecosystems: analysis at multiple scales*. 2nd ed. New York: Academic Press.
- White MA, Thornton PE, Running SW. 1997. A continental phenology model for monitoring vegetation responses to interannual climatic variability. *Global Biogeochem Cycles* 11: 217–234.