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Biomass of forest stands under climatic change: a German case study with the Frankfurt biosphere model (FBM)

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ABSTRACT

In this contribution, we perform a case study of the German forests. We couple the Frankfurt biosphere model (FBM) with a model of the age class development (AGEDYN). The coupled model is applied to simulate the temporal development of carbon pools in German forests under the influence of climate change taking into account changes in the age class structure. In the base case, the growth of forest stands is simulated using a temporally averaged climate dataset, being representative for the contemporary climate conditions. To assess the sensitivity of forest growth to changes in environmental conditions, the FBM is run in several scenarios. In these simulations the effects both of climate change and of the direct effect of increased levels of atmospheric CO_2 on photosynthesis (CO_2 fertilization) on forest growth are assessed. In another simulation run with the FBM both effects — climate change and CO_2 fertilization — are combined. In simulations under present day's climate conditions a good agreement is gained between simulation results and statistical data of the present standing stock carbon density of Germany's forests. A pure climate change leads to a decrease of the annual increments as well as to the climax standing stocks. The negative effect of climate change alone is overcompensated by enhanced photosynthesis in the simulations with combined climate change and CO_2 fertilization. In the transient case, the coupled model is used in two scenarios describing first a continuation of present day's climate conditions and second a transient climate change from present conditions (1990) to $2 \times CO_2$ conditions in 2090. Here, the simulations indicate that changes in the forest's age class structure can have a stronger influence on the future carbon balance of the forests in the considered region than the combined effect of climate change and CO_2 fertilization.

1. Introduction

The net sink strength of the terrestrial biosphere was estimated by the IPCC (Melillo et al., 1996) as 0.5 to 1.9 GtC/yr in the 1980s. Possible causes were identified as "*post-harvest regrowth of mid- and high-latitude forests, enhanced vegetation growth due to physiological effects of increasing CO_2 and nitrogen deposition and probably a substantial range of interannual variation due to climatic anomalies*".

In this paper, we estimate the magnitudes of the first two points mentioned (forest regrowth and CO_2 fertilization) using the Frankfurt biosphere model (FBM) for German forests. The assessment of the effect of interannual climatic variation with the FBM is the subject of another study (Kindermann et al., 1996). The implementation of a nitrogen cycle submodule in the Frankfurt biosphere model is still in progress.

Due to the fact that young and middle-aged forests accumulate carbon, while old-growth forests

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are balanced in respect to the carbon cycle, changes in the age class structure of forest stands must be considered when estimating the global carbon budget. From all the processes which can affect forest growth, disturbances like fire, severe storms, insect infestations and forest management practices are the ones which alter the age class distribution most effectively (Li and Apps, 1996). Climate, CO_2-fertilization and nitrogen deposition show a more physiologically-based influence. However, fire frequency and the susceptibility to insect infestations can also be altered by climatic conditions such as warming or drought. Therefore it is difficult to separate increases in carbon uptake caused by post-harvest forest regrowth (and a change in the age class structure of a stand) from increases due to changes in the environmental conditions.

Up to now, terrestrial biogeochemical biosphere models have been focussed on the influence of the physiologically-based processes (Raich et al., 1991; Kindermann et al., 1993; Warnant et al., 1994; Kaduk and Heimann, 1995), while forest inventories give estimates of age-specific carbon accumulation rates and the age class distribution of forest stands. For the projection of future changes in carbon storage, both approaches — mechanistic description of biosphere processes and simulation of changes in forests age class structure — must be combined in one model. The approach used here combines two previously documented models:

- a model to calculate the development of forest's age-class distribution under influence of disturbancies, AGEDYN (Kohlmaier et al., 1995a);
- a global process-oriented biosphere model, the Frankfurt biosphere model (FBM, Janecek et al., 1989; Kindermann et al., 1993; Lüdeke et al., 1994; Kohlmaier et al., 1997).

The first step towards the combination of both approaches was a version of the FBM with which vegetation growth can be simulated. With this model version, carbon pools and fluxes between vegetation in regrowing states and the atmosphere can be simulated (Häger et al., 1996). In a second step the results of these transient calculations were carefully validated by Würth et al. (1997). The modifications of FBM version 2.2 (described by Kohlmaier et al., 1997) leading to FBM version 2.2.2, which is used in this study, can be found in Section 8.

In this paper we describe the coupled model, and discuss the temporal development of age class and biomass distribution in German forests from 1990 to 2090. We have chosen the forest sector in Germany because there exists comprehensive statistical material that describes the present state of German forests. As shown by Würth et al. (1997) the FBM simulates biomass carbon stocks under currrent environmental conditions that are very consistent with the carbon stocks based on the data from German forest inventories and yield tables.

2. Methods

The idea of the study is illustrated in Fig. 1 with hypothetical data and normalized units. We calculate the total standing biomass of a given forest complex by multiplying its age class distribution (forest area per age class) with its specific growth curve (biomass per area and age class). The result is an age dependent biomass distribution. By summing up over all age classes the total biomass can be calculated for any year in which the age class distribution is known.

The age class distribution can be derived from forest inventories, while the growth curve is taken either from the inventory datasets or simulated. There are many approaches to simulate forest growth curves, e.g., the Richards equation, which we used in a previous examination (Kohlmaier et al., 1995a); in this study we use the Frankfurt biosphere model (FBM). Due to the fact that the prognostic model FBM is climate driven, the influence of climate on forest growth can be examined, too. Additionally, the influence of atmospheric CO_2 is described in the FBM by an approach based on leaf physiology developed by Kirschbaum and Farquhar (1987). On the other hand the future development of the age class structure can be simulated with a matrix approach using the AGEDYN model. The combination of these models can then be used as a prognosis tool for the future development of carbon pools and fluxes in forest complexes which considers climate, CO_2-fertilization and changes in the age class distribution.

2.1. *The Frankfurt biosphere model (FBM)*

The Frankfurt biosphere model (FBM), a mechanistic and prognostic compartment model of the terrestrial biosphere, has been developed to simu-

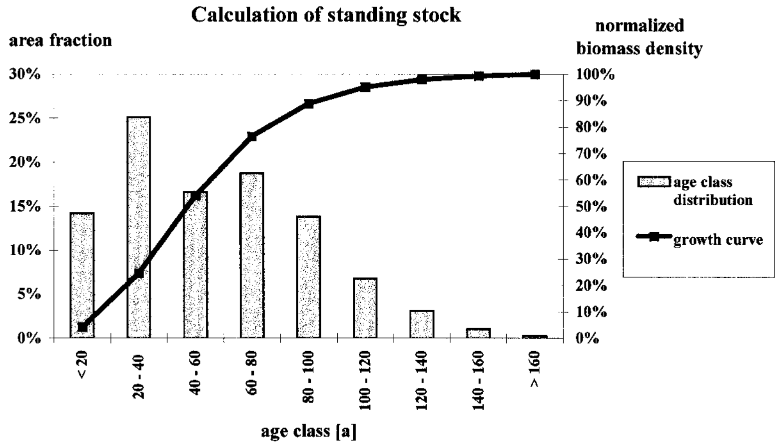

Fig. 1. Example of how the model works: calculation of standing biomass using the distribution of stand ages (areas versus age class; bars) in Germany's forest and a specific growth curve (biomass density versus time; line).

late the carbon exchange fluxes between the vegetation and the atmosphere with a spatial resolution of 0.5° × 0.5° (long × lat) on a global scale. The versions 2.1 and 2.2 of the FBM are described in full detail by Lüdeke et al. (1994) and Kohlmaier et al. (1997).

The FBM calculates CO_2 uptake by photosynthesis and release by autotrophic and heterotrophic respiration as a function of climatic conditions (temperature, precipitation and irradiation) and internal states of the ecosystem (soil water content, carbon in leaves and fine roots, and carbon in structural compartments, as well as in leaf/fine root litter, carbon in woody litter and soil carbon). A short description of the model can be found in Section 8.

Although originally designed to model uptake and release of CO_2 by vegetation and soil in a steady state, simulations with the FBM have been performed in this study using the transient version of the model as described in Häger et al. (1996). Here we are interested in the temporal development of standing biomass in forest stands. Interannual changes in carbon fluxes between regrowing vegetation and the atmosphere are simulated. The vegetation's carbon content from an initial seedling state to the climax state is also calculated. According to the assumptions of the FBM the climax state in a constant climate is reached when annual net primary productivity (NPP) equals annual litter production.

The FBM simulates the dynamics of carbon pools within the natural vegetation. Natural mortality (shedding of leaves and branches and also dying of old trees near the climax) is accounted for within the modelling of litterfall.

Lüdeke et al. (1997) performed steady state simulations with the model under contemporary climate conditions and compared it with the normalized difference vegetation index derived from satellite measurements. The model approach of the FBM was tested in respect to its sensitivity against changes of climatic variables by Kindermann et al. (1996). In the latter study the simulation results of the FBM were compared with results from two $^{12}C/^{13}C$ deconvolutions. Together with the regional comparison of growth simulations with two independent datasets of forest's standing stock in Germany (Würth et al., 1998) the model has been validated with very different and independent datasets giving convincing results.

All simulations presented in this paper are performed without a modification of the free parameters determined in the calibration process (see Section 8) for the complete set of vegetation types in the global model.

2.2. *The age class distribution development model (AGEDYN)*

The complete model is described by Kohlmaier et al. (1995a), here we will recapitulate only the basic ideas of the model.

Data on age class distributions of an ensemble of forest stands are conventionally given with a class width ranging from 10 to 30 years. For mathematical convenience an algorithm has been developed to have a smoothed continuous distribution which conserves the area of the original data set.

The interpolated distribution is arranged in a normalized vector N with n elements. For convenience a cut-off is chosen at age 400. Each stand that reaches the age of 400 years is harvested and the area is reforested in the following year. Each of its 400 elements N_i gives the area fraction that is covered by stands of a certain age in the reference year, with the normalization condition:

$$\sum_{j=1}^{400} N_j = 1. \tag{1}$$

To propagate the age class vector N into the future we use a matrix concept in which we introduce a so called mortality matrix **M**. The mortality matrix **M** contains the probability of the mortality in each age class, m_j (similar to the Leslie matrix, Lewis, 1942; Leslie, 1945, 1948; Usher, 1966, 1972). The calculation of the probabilities is shown below. We can write the equation for the temporal development of the age class vector N:

$$N^{t+1} = MN^t. \tag{2}$$

The assumption that an area fraction which is disturbed by harvesting is set back to the age class $j=1$ can be formulated using the following equations:

$$N_1^{i+1} = \sum_{j=1}^{n} m_j \cdot N_j^i, \tag{3}$$

$$N_j^{i+1} = (1 - m_{j-1}) \cdot N_{j-1}^i, \qquad j = 2, \ldots, n. \tag{4}$$

These equations describe the temporal development of N^i, where i denotes the actual year. As only a relatively small number of matrix elements are nonzero, the quadratic matrix **M** with rank n is sparse and of singly-bordered band diagonal form: only the elements in the first line ($M_{1,i}$; $i = 1, \ldots, n$) and in the lower diagonal ($M_{i+1,i}$; $i = 1, \ldots, n-1$) are nonzero.

In the publication by Kohlmaier et al. (1995a) some examples for the application of this matrix equation are given. There are some assumptions necessary in respect to the future practices of wood harvesting. Here we follow the most simple assumption, that the amount of wood harvested will not change significantly in the future. We also assume that there are no land cover changes: Land covered by one forest type will be covered by this type during the whole simulation period. At least we assume that harvest intensity (percentage of harvested wood on a unit of ground area) follows a *tangens hyperbolicus* curve with stand age. A more detailed description of the harvest function is given by Kohlmaier et al. (1995a).

2.3. *Description of simulations*

As a case study, we perform simulations with three different vegetation types in Germany under the influence of changes in climate variables and ambient CO_2 concentration. Due to the lack of data giving the forest's age class structure in a gridded format, specific climate conditions can not be attributed to a particular age class distribution. The effect of climate on grid base is therefore aggregated in the form of a mean biomass density for German's needleleaved and mixed stands.

To assess the possible effect of global change on the German forests five different scenarios are assumed:

1. present climate, no CO_2 fertilization
2. $2 \times CO_2$ climate, no CO_2 fertilization
3. present climate, CO_2 fertilization
4. $2 \times CO_2$ climate and CO_2 fertilization
5. transient change from present climate (1990) to conditions of scenario 4 (2090).

The simulations according to scenarios 2 to 4 represent the growth of forests in the new climate regime and not the transition from the present to the future CO_2 greenhouse climate. These simulations are a kind of sensitivity analysis of the FBM. In transient scenario 5, the transition is studied with the coupled FBM-AGEDYN model.

3. Data

3.1. *Input data for the FBM*

On the global scale, the FBM distinguishes 32 natural vegetation types for which the geographical distribution is given according to the vegetation map of Matthews (1983, 1984). According to Matthews, vegetation types 8 (temperate/subpolar evergreen needleleaved forest), 10 (cold-deciduous forest with evergreens) and 11 (cold-deciduous forest without evergreens) are the major types of potential vegetation in Germany. The first vegetation type is addressed within this study as "needleleaved stands" while the latter two are combined to the type "mixed stands" (which mainly consists of deciduous species in Germany).

As a first approximation, for the grid elements in Germany we use the vegetation type which was assigned to them by Matthews. Simulations of these grid elements with the FBM result in biomass density (carbon per unit area) for each grid cell dependent on different climate regimes. These densities are averaged giving a mean biomass density for Germany. Then, total pools are calculated in the AGEDYN-model by multiplication with the area actually covered by specific vegetation type. Therefore, actual land use is accounted implicitly in this study.

The climate used to drive the ecosystem model is based on the climate database CLIMATE V2.1 (W. Cramer, Potsdam, personal communication). Instead of historic weather data of the considered grid elements a continuous repetition of the averaged climate data is applied.

The simulation for a future greenhouse climate used the anomalies calculated by the Max Planck Institute of Metereology in Hamburg (ECHAM, Roeckner et al., 1992; Cubasch et al., 1992). These calculations were performed by the Deutsches Klimarechenzentrum and the Max-Planck-Institut für Meteorologie in Hamburg (Cubasch et al., 1995) under the assumption of the "business-as-usual-scenario" (Houghton, Callander and Varney, 1992). From the results of these GCMs scenario runs and the results of control runs under normal conditions we calculate regional climate anomalies and add them to the contemporary climate. The result is a map of climatic variables representing the changed climate. The anomalies with respect to a CO_2 doubling are added to the CLIMATE V2.1 dataset and then used as new input for the FBM. The monthly values of both datasets are interpolated as described in Lüdeke et al. (1994), resulting in a climate dataset with $0.5° \times 0.5°$ (long × lat) resolution. We superimpose onto the temperature data a diurnal cycle derived from the daily maxima and minima typical for a particular vegetation type. In Fig. 2, the climate diagrams of contemporary and the assumed climate in 2090 in Germany are shown. The figure shows the mean values averaged over all 193 grid cells covering the area of whole Germany.

3.2. The German forest's age class distributions

The most recent German forest inventory is very detailed, but it was only performed in former Western Germany. There are some datasets describing the forests of the former German Democratic Republic, but the methods of data collection in both parts of Germany were inconsistent. For this reason

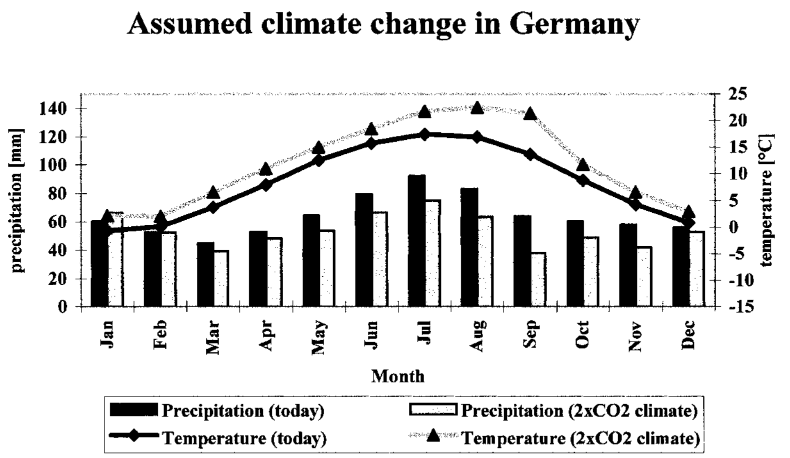

Fig. 2. Assumed climate change in Germany as simulated by the ECHAM-model of general atmosperic circulation (Cubasch et al., 1995). Shown here are the monthly mean values averaged over the whole examination area (Germany).

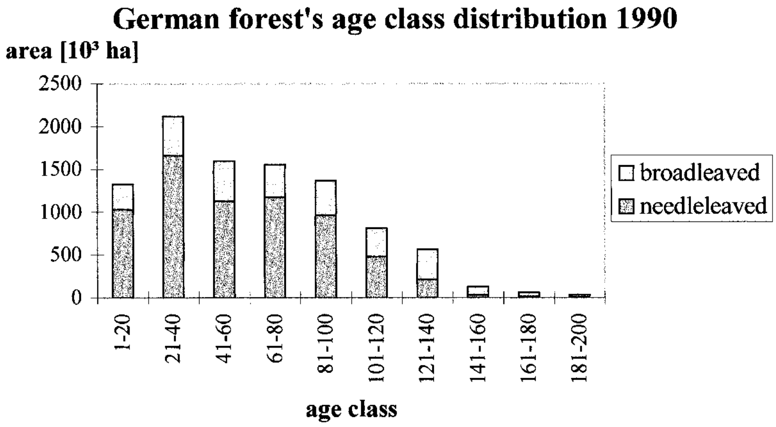

Fig. 3. Age class distribution of German forests: dark grey: Needleleaved forests, light grey: broadleaved forests (data according to FAO, 1992).

we use the ECE/FAO database (FAO, 1992) based on the national inventories which provides information of forests both in former Eastern and Western Germany. These data are processed using the same statistical methods and are therefore comparable. The age class distribution of Germany's forests is shown in Fig. 3.

The available German forest datasets give only the age class distributions on a whole country scale. This confines the spatial resolution of the model to the same scale, though other input data (climate data or vegetation type) are available in much higher resolutions.

4. Results

4.1. Present state

Using the method described in Section 2, it is possible to calculate the total biomass of Germany's forests in the year 1990. The input data, which are taken from FBM simulations (biomass density per area) and the ECE/FAO study (forest stand areas of different age classes, FAO, 1992), are shown in the upper row of Fig. 4. In the lower row of this figure, the calculated biomass in each of the age classes is shown.

In Table 1, the sum of all age classes is given. The result of this study is compared with two other studies, both of which are based on inventory data of Germany's forests. Our result of 778 MtC of total biomass is a little bit lower than the results of the other studies, but inspecting the total biomass density (81.4 tC/ha) there is a discrepancy of only about 6% compared with the results of the most recent study of the German Ministry of Agriculture and Forestry (86.5 tC/ha; BML 1996). Although we used the map of natural vegetation given by Matthews, good agreement is gained between simulation results and statistical data of present day's standing stock carbon density of Germany's forests.

4.2. Future development

Based on the results of the previous section the future development of biomass in Germany can be simulated either climate-dependent with the FBM or dependent on forest management with AGEDYN.

4.2.1. Sensitivity to environmental changes. The growth curves shown in Fig. 5 were obtained by simulating regrowth under different conditions in all grid cells covered by forests in Germany. For the sake of clarity we show only the average biomass density of each scenario for needleleaved (above) and for mixed stands (below). In both forest types, a pure climate change (scenario 2) leads to a decrease of the annual increments as well as to the climax standing stocks. In a detailed analysis Häger et al. (1996) showed that this is due to a decreased soil water availability under climate change conditions caused by an increased evapotranspiration. It can be seen in Fig. 2 that

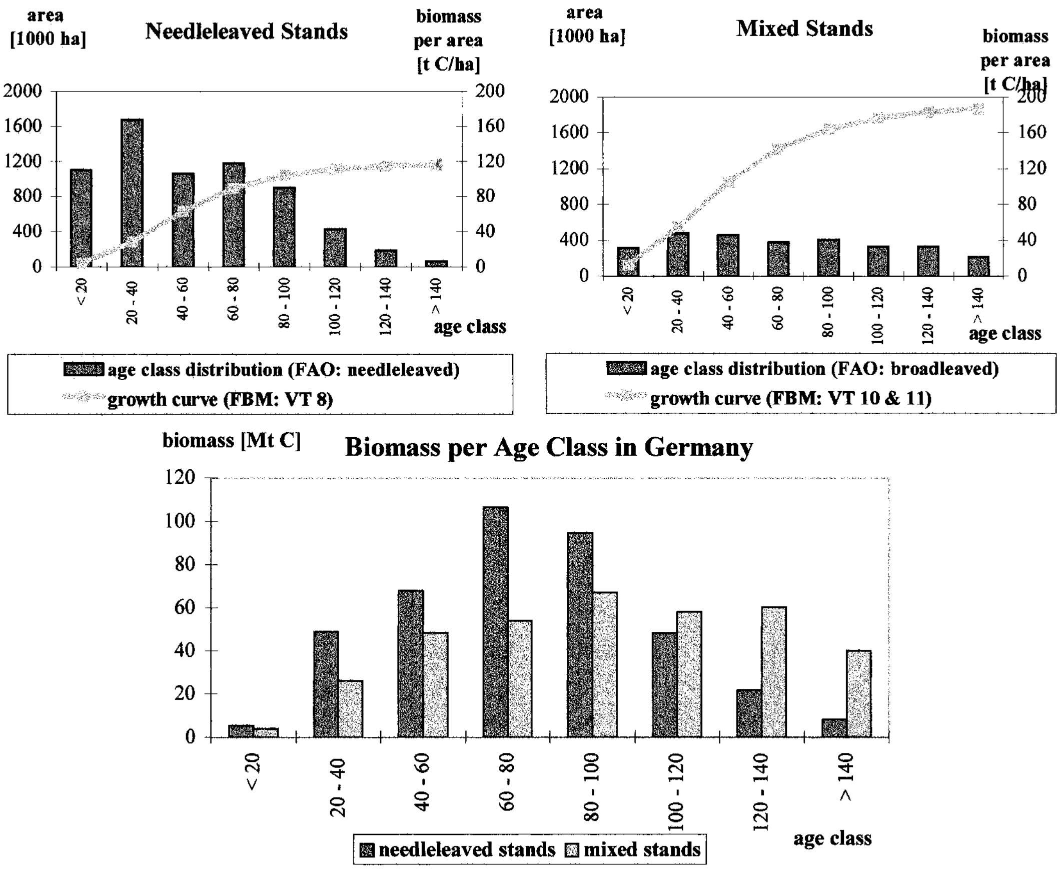

Fig. 4. Present carbon pools in German forests. Upper row: input data for calculations with needleleaved stands (left) and broadleaved/mixed stands (right). Areas according to FAO (1992), biomass density values according to FBM simulations. Lower row: calculated biomass per age class in Germany.

Table 1. *Calculation of standing stock and biomass density in standing stock in Germany's forests following this study compared with the studies of Burschel et al. (1993) and the study of the German Ministry of Agriculture and Forestry (BML, 1996); the areas of this study are according to FAO (1992)*

	This study	Burschel et al. (1993)	BML (1996)
standing stock [MtC]	778	890	877
total area [1000 ha]	9563	10030	10143
total carbon density [tC/ha]	81.4	88.7	86.5

precipitation is predicted to decrease while temperature is predicted to increase in the ECHAM simulations for Germany. This leads to a lack of soil water calculated by the FBM which causes water stress for the vegetation in the simulations.

If CO_2 fertilization is included (scenario 4) the climax biomass of the needleleaved stands is still below those for the present climate (scenario 1) while the contrary is true for the mixed stands. These results suggest that conifers are more sensitive to a climate change because the potential extension of these forests is limited by the temperatures as they occur in central Europe. Thus a further increase in temperature will go beyond the temperature optimum of net photosynthesis for these species even when the atmospheric CO_2 levels are enhanced.

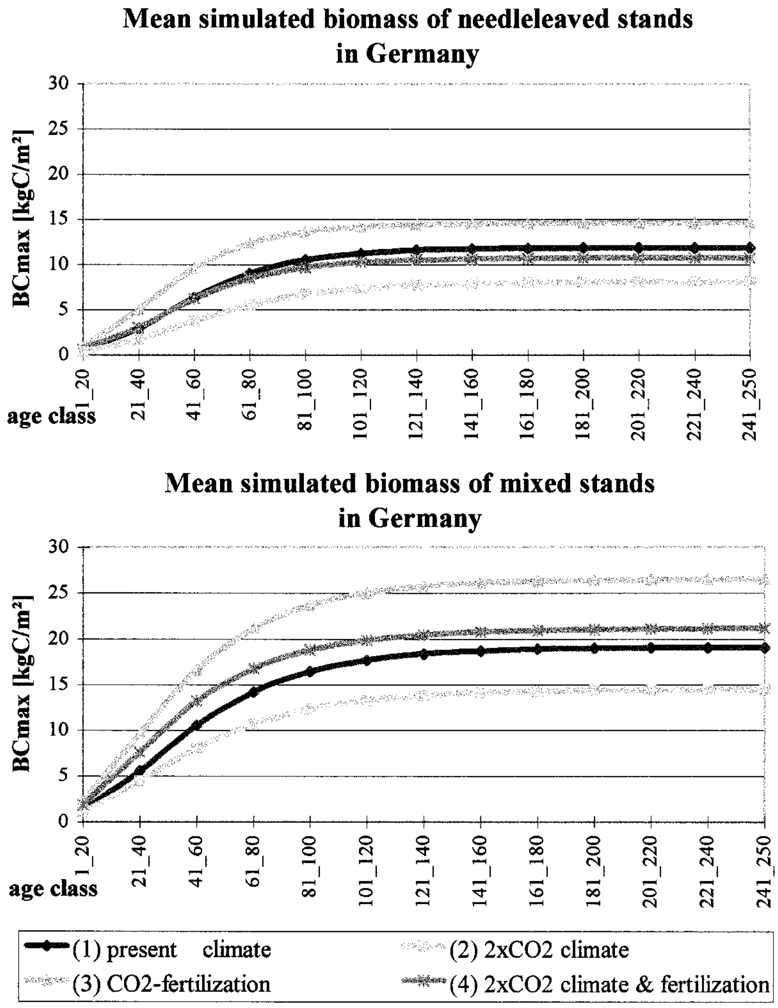

Fig. 5. Comparison of the growth curves within the present climate and the $2 \times CO_2$ climate with and without CO_2 fertilization of needleleaved and mixed stands in Germany according to scenarios 1 to 4.

4.2.2. Sensitivity to changes in age class structure. The present age class distribution can be projected into the future by using the age class development model AGEDYN.

In Fig. 6, the resulting age class distributions are shown for needleleaved and mixed forest stands in Germany following the simulations in scenario 1. The initial age class distribution as presented in Fig. 5 can be seen in the front of the three-dimensional graph. In Fig. 6, it can be seen that the peak of the age class 20–40 (years) is shifted towards higher age classes and is only slighly smoothed during the future projection. The assumptions of scenario 1 imply that the simulation results show only the effect of changes in the age class structure. The assumed forestry practice will result in very old forests in the future. Following our assumptions aging is not compensated by felling and there is not sufficient regeneration.

4.2.3. Results of transient simulations. Transient simulations are performed following the assumptions of scenario 5. In Fig. 7, a sequence of biomass

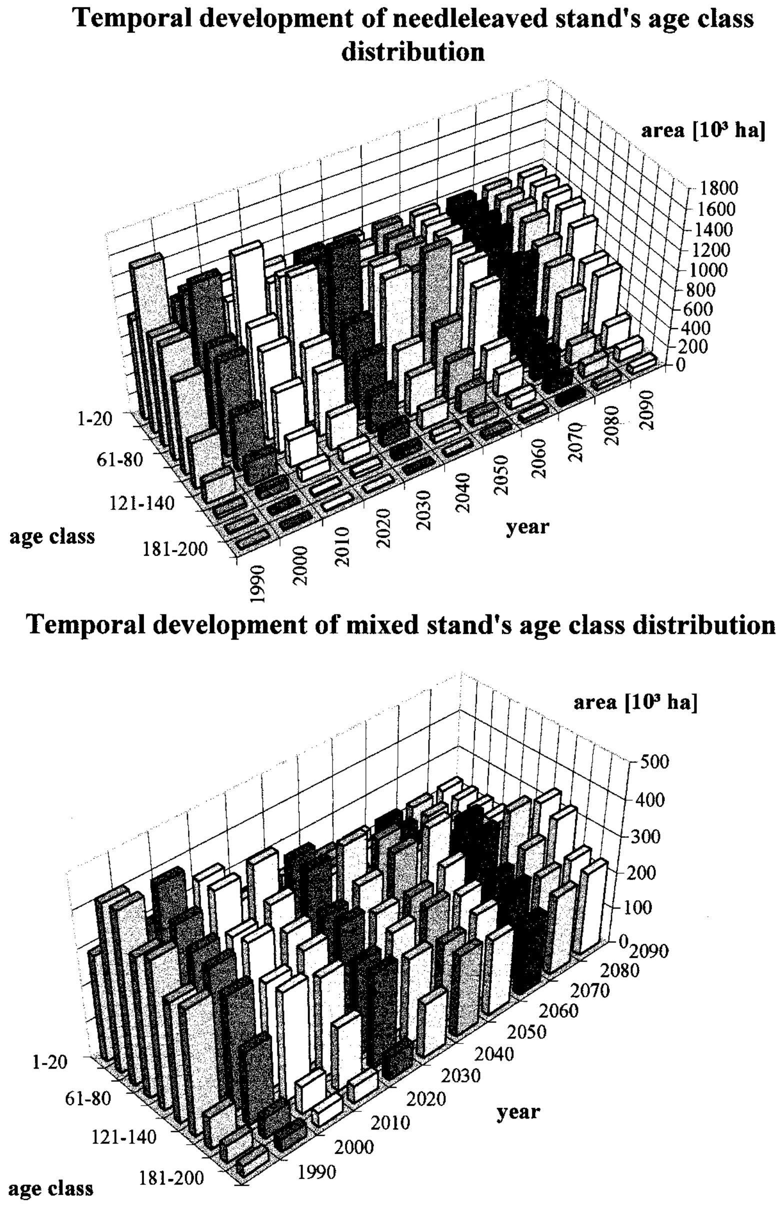

Fig. 6. Development of the age class distribution of Germany's forests in the period from 1990 to 2090. (Needleleaved stands in the upper figure, mixed stands below). Assumptions: constant rate of harvested wood; no climate change and no CO_2 fertilization (continuation of scenario 1).

distributions in some selected years can be seen. The shift of the age class with highest amount of stored biomass towards higher ages is obvious. This leads to a smaller amount of accumulated biomass in the last years of the simulation, as can be seen in Fig. 8b. Nevertheless following our simulations the carbon balance of German forests remains positive in the future (i.e., there will be carbon accumulated). Under the assumptions, that neither forest management nor climate will change

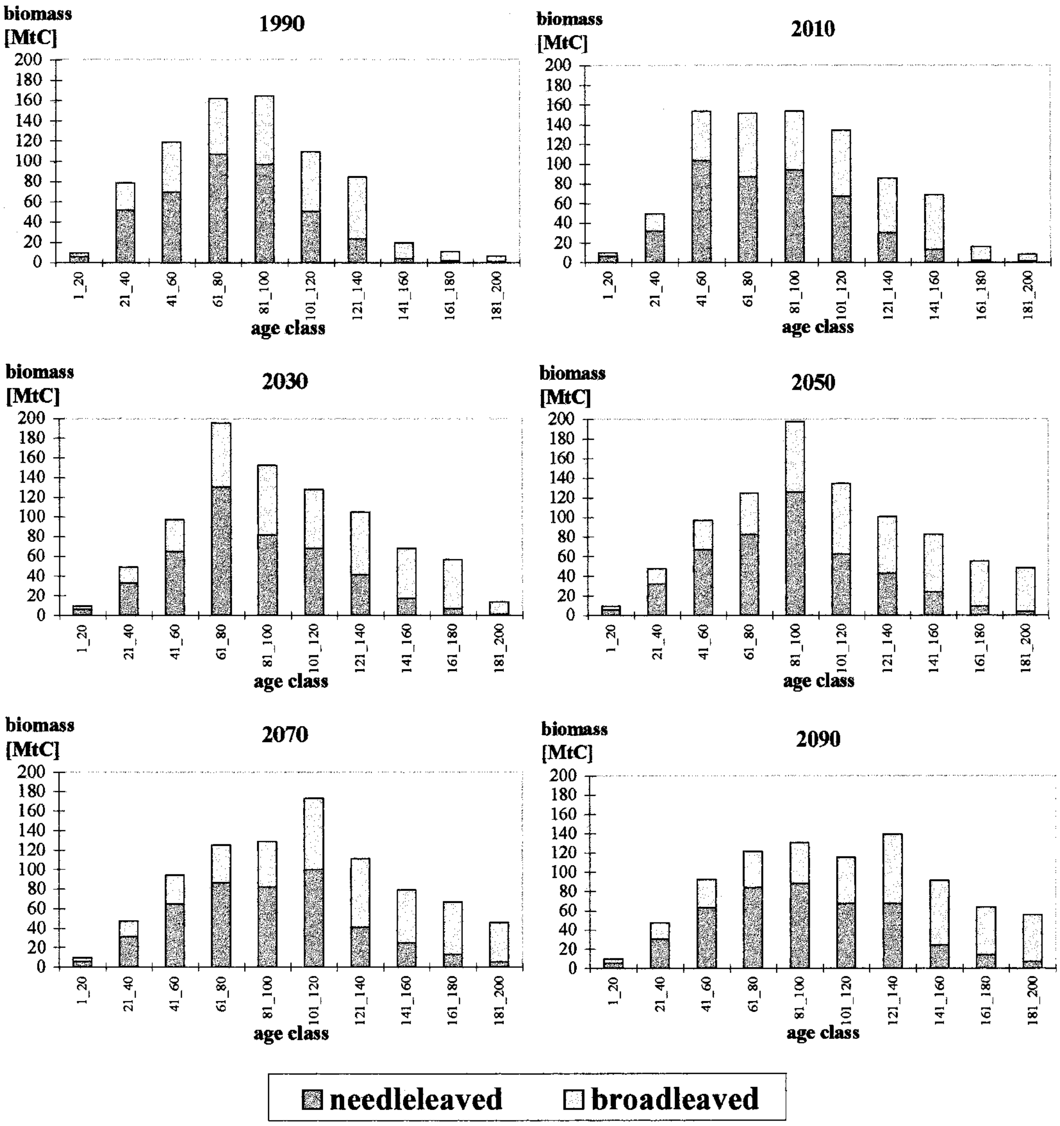

Fig. 7. Sequence of simulated biomass distributions in the years 1990, 2010, 2030, 2050, 2070 and 2090. Assumptions: constant rate of harvested wood and stimulation of forest growth due to climate change and CO_2 fertilization (scenario 5). (Dark grey: needleleaved stands; light grey: broadleaved stands.)

drastically (scenario 1) the total amount of carbon stored in the forest's biomass will increase from 777.8 MtC in 1990 to 925.9 MtC in 2090 (Table 2). This increase in biomass is only due to aging of forest, because in the considered scenario 1, no changes in environmental conditions are assumed.

The most interesting result is the comparison between simulations under different scenarios, e.g., scenario 1 and 5. The results can be seen in Fig. 8 and Table 2. Under the assumptions of scenario 5 (climate change and CO_2 fertilization effect) there will be an increased carbon accumulation. The biomass of German forests will increase from 777.8 MtC in 1990 to 955.7 MtC in 2090. In this case the assumed CO_2 fertilization effect is responsible for the enhanced carbon storage. The

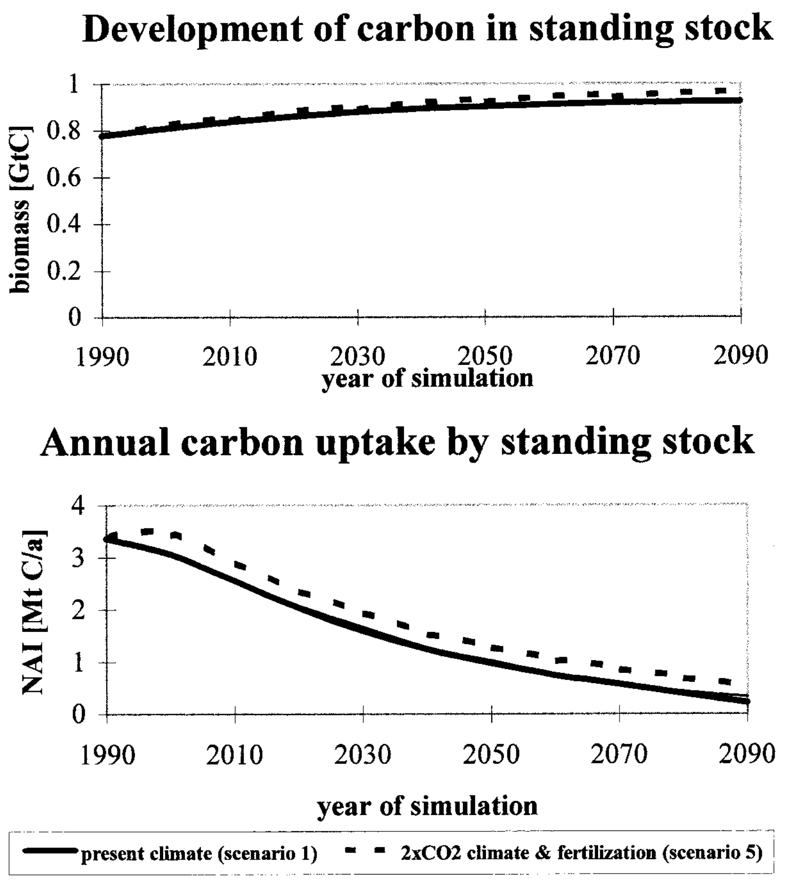

Fig. 8. Comparison of changes in carbon content in Germany's standing stock under two different transient climate scenarios (1 and 5). (a) Time series of total carbon in standing stock; (b) time series of annual carbon uptake (net annual increment).

Table 2. *Biomass pools and net annual increment in german forests between 1990 and 2090 according to the simulations following the scenarios 1 and 5*

	1990	2090		
		scen. 1	scen. 5	difference (scen. 5– scen. 1)
biomass [MtC]	777.8	925.9	955.7	29.8
NAI [MtC/a]	3.355	0.328	0.509	0.181

difference in biomass between these two simulations is 29.8 MtC at the end of the simulations in the year 2090. In the same year an amount of 0.29 MtC/a is accumulated (see Table 2).

5. Discussion

One of the major aims of this study is to understand the consequences of possible changes in environmental conditions on forest resources, another one is to evaluate carbon mitigation potentials of forests and possible strategies of forest management and the wood industry to strengthen this potential. With respect to changes in environmental conditions the prognostic model FBM predicts that without consideration of the CO_2 fertilization effect of a rising atmospheric CO_2 content, changes in climate (here from the results of the ECHAM model) lead to a lowering of the annual increments as well as to the climax standing stock in German forests.

Inclusion of CO_2 fertilization can overcompensate the effect of climate in the simulations of the mixed forests of Germany. Conifers, which need lower temperatures as optimal conditions for net photosynthesis (Larcher, 1980) are more stressed by the predicted warming than deciduous trees and even with CO_2 fertilization, growth is still impaired. A similar trend was detected in the global analyses made by Cao and Woodward (1998). In both analyses biosphere models were driven by a GCM output simulating the future climate. But in the global context the worse climate conditions are overcompensated by the effects of CO_2 fertilization.

While the simulations of the FBM have already been evaluated and validated using data from measurements and intercompared with other models several times (Heimann et al., 1998; Kicklighter et al.; 1998; Kindermann et al., 1996; Lüdeke et al., 1994, 1996; Würth et al., 1998), the AGEDYN-model is still based on simple assumptions which should be improved during future model development. Here, we considered only the anthropogenic disturbance of forest stands through harvesting and reforestation. But the impact of human disturbances will control the future carbon balance in an important way, at least in a country with such a long tradition in forestry as Germany. These first results suggest that the changes in the age class structure without changes in harvesting practice have a greater influence than changes in environmental conditions. Nevertheless, predictions of changes in forest practices should be included as well as changes in the area reforested. Besides human disturbances, natural disturbances should be included in future studies. The effect of wildfires, insect outbreaks, diseases and windthrow on forest stands should not be underestimated. In boreal, mediterranean and tropical forests, wildfires can reach a devastating extent affecting biomass and carbon dynamics quite substantially. As Li and Apps (1996) pointed out, the boreal forest has not only be structured by man through planting and harvesting, natural disturbances have also shaped the age class distribution of forests. Therefore, it is necessary to include at least a fire module into the combined model before this model is applied to forests often affected by wildfires.

Referring to Germany, we have decided to neglect this influence in this first study, because wildfires occur very rarely in this country. Nevertheless, we are aware of the fact, that changes in the future climate may change this situation. Especially under dryer and warmer conditions, wildfires can be enkindled more easily (Kurz and Apps, 1995). Thus, further investigations will consider mortalities due to natural disturbances in the matrix approach, too.

Referring to changes in forest management, Burschel et al. (1993) for example found that German forestry could relieve the atmosphere by an additional amount of 3 to 10 Mt C annually (out of a total of 290 $\mathrm{Mt\,C\,yr^{-1}}$ emission from fossil fuel burning) within the next 20 years if several possibilities such as lengthening rotation periods, afforestation of agricultural land and intensive utilization of wood waste and thinnings were included in forest management practices.

It should be stressed, that the proposed combination of the models is not confined to Germany. It can be applied to any forest region with sufficient information about the age class distribution.

6. Summary and conclusions

The Frankfurt biosphere model (FBM), a mechanistic and prognostic compartment model of the terrestrial biosphere, has been developed to simulate carbon exchange fluxes between terrestrial vegetation and the atmosphere with a spatial resolution of $0.5^\circ \times 0.5^\circ$ on a global scale. The FBM also offers the opportunity to simulate either interannual fluctuations of carbon exchange fluxes or the long-term development of the vegetation under the influence of climate change, the latter of which is performed in this study. We used the FBM to simulate the present carbon pools and fluxes of the German forests. It should be stressed again that the model was not tuned to special German conditions, we used FBM version 2.2.2 without any changes in parametrization.

In order to quantify possible contributions to the terrestrial carbon sink we have concentrated in this study on two subjects: "post-harvest regrowth of mid- and high-latitude forests" and "enhanced vegetation growth due to physiological effects of increasing CO_2", both of which were addressed in the most recent IPCC report (Melillo et al., 1996). We have shown in this case study, that it is possible to use the Frankfurt biosphere model (FBM) coupled with the age-class distribution development model (AGEDYN) to investigate these problems. Applying the method proposed in this study on a global scale it should be possible to clarify the role of the terrestrial biosphere within the global geo-biosphere cycles.

We did not use the FBM results of litter and soil carbon pools in this study. When investigating a longer timeframe the changes of these compartments are of great importance and should not be neglected (Kohlmaier et al., 1998).

In subsequent studies, the influence of natural and anthropogenic disturbances should be included directly in the model. For the moment, there is no fire module implemented. Also the modelling of human influence on natural ecosystems is subject of model improvements. A first attempt of a combined model approach to assess carbon balances of forestry and wood utilization by coupling the FBM with the Graz/Oak ridge carbon accounting model (GORCAM) has been proposed (Häger and Schlamadinger, private communication). Results of the proposed model will be subject of a later publication.

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8. Appendix

8.1. *Mathematical description of the FBM*

Versions 2.1 and 2.2 of the Frankfurt biosphere model, the latter of which was used with several modifications (implementation of growth respiration and CO_2 fertilization) in this study, are described in full detail by Lüdeke et al. (1994) and Kohlmaier et al. (1996). Here we will give only a very short description of the main assumptions and equations.

Carbon allocation. Here and in the following, bold capital letters represent the reservoirs of carbon or water, resp., while normal letters represent model parameters (Table 4). As shown in Fig. 9, it is assumed that the assimilate production C_{ASS} is determined by the mass of compartment **GC**, reflecting the amount of leaves, the actual soil water content **SW**, as well as by the external driving variables temperature T and irradiance I. This flux is to be partitioned according to present needs of the plant organs, namely, the buildup and maintenance of the photosynthesizing tissue and of the feeder roots (represented by **GC**), on the one hand, and the buildup and maintenance of stems, branches, and coarse roots (represented by **RC**) on the other. Furthermore, assimilates have to be translocated in order to fill particular storage organs, which are included in the carbon mass of the **GC** compartment as well.

Calculation of fluxes. The net uptake of CO_2 by plants is determined by a balance of two processes: carbon assimilation C_{ASS} (i.e., the gross photosynthetic carbon fixation) and autotrophic respiration, C_{GA} and C_{RA}. As assimilation and respiration show different seasonal courses and different temperature responses, we think it is more convenient to model these processes separately instead of simulating NPP directly.

Uptake of CO_2. The effective carbon assimilation rate C_{ASS} can be considered as a product function of the maximum canopy production (α LAI) and a term dependent on light and canopy structure (h_1), a temperature dependent term (h_2), a soil water dependent term (h_3), and a term which is dependent on the atmospheric CO_2 concentration (h_4).

$$C_{\mathrm{ASS}} = \alpha\,\mathrm{LAI}(\mathbf{GC}) \cdot h_1(I, \mathrm{LAI}(\mathbf{GC})) \times h_2(T) \cdot h_3(\mathbf{SW}) \cdot h_4(\mathrm{CO_2}) \quad (5)$$

The first three "h" terms range between 0 and 1; h_1 and h_3 are saturation curves, and h_2 is an optimum function. The fourth "h" term is steady increasing with $[CO_2]$ and is normalized to a CO_2 concentration of $CO_2^0 = 350$ ppmv. The functional dependencies are:

$$h_1(I, \mathrm{LAI}(\mathbf{GC})) = \frac{1}{k\,\mathrm{LAI}} \ln\left(\frac{\dfrac{\alpha}{\Phi} + I}{\dfrac{\alpha}{\Phi} + I\,\mathrm{e}^{(-k\mathrm{LAI})}}\right), \quad (6)$$

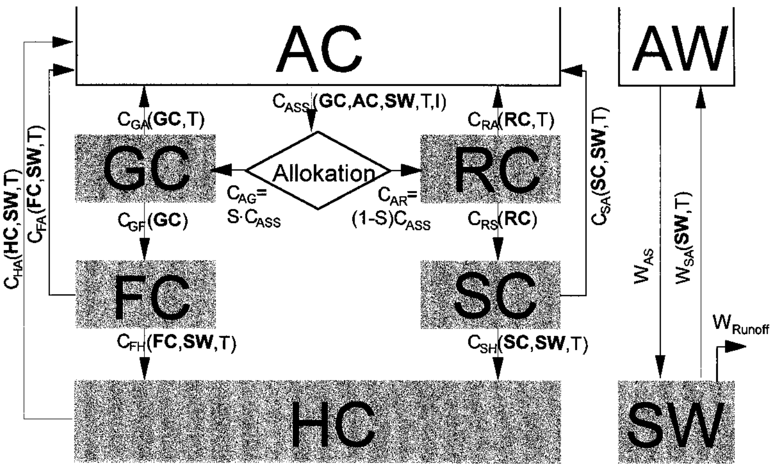

Fig. 9. Flow chart and model structure. Bold capital letters represent the reservoirs of carbon (second letter **C**) and water (second letter **W**): **AC**, atmospheric carbon; **GC**, carbon content of green biomass and feeder root biomass plus assimilate store; **RC**, carbon content of remaining biomass of biota; **HC,** carbon content of humus and soil layer; **SC**, carbon content of litter with slow decay rate; **FC,** carbon content of litter with fast decay rate; **AW**, water in the atmosphere; **SW**, soil water in the rooting zone. The capital letters C and W represent carbon and water fluxes. The indices indicate sources and sinks of these fluxes. The functional dependence of the fluxes on the driving variables and pool sizes is given in parentheses (T: hourly air temperature, I: hourly photosynthetic active radiation (PAR)). W_{AS} is the daily precipitation, W_{SA} is daily actual evapotranspiration. The factor S represents the fraction of total assimilation C_{ASS} that is allocated to **GC**.

$$h_2(T) = b_T \left\{ a_T \frac{(T-T_{min})(T-T_{max})}{(T-T_{min})(T-T_{max})-(T-T_{opt})^2} + \beta\, e^{\omega(T-T_0)} \right\}, \quad (7)$$

$$h_3(\mathbf{SW}) = \frac{\tanh\left(1.946\,\dfrac{\mathbf{SW}-\mathrm{PWP}}{\mathrm{FC}-\mathrm{PWP}}\right)}{\tanh(1.946)}, \quad (8)$$

$$h_4(CO_2) = \frac{c_i - \Gamma^*(T)}{c_i + 2\Gamma^*(T)} \bigg/ \frac{c_i^0 - \Gamma^*(T^0)}{c_i^0 + 2\Gamma^*(T^0)}, \quad (9)$$

with

$$\Gamma^*(T) = 40.6 \cdot e^{9.46(T-25.0/T+273.15)}.$$

A description of the variables and parameters of the four functions is given in Tables 3, 4.

Eq. (9) was originally derived by Kirschbaum and Farquhar (1987) for the enhancement of photosynthesis per unit leaf area due to increased CO_2. As the **GC** is increased by this process, LAI also increases causing the net effect of CO_2 fertilization to be larger than that given by the factor h_4 by itself (see discussion of this topic in the paper by Kohlmaier et al., 1998).

Table 3. *Description of variables in eqs. (6) to (9); for parameters see Table 4*

Variable	Description
I	incident radiation above canopy
LAI	leaf area index
PWP	permanent wilting point (soil parameter)
FC	field capacity (soil parameter)
CO_0^2	reference CO_2 concentration (350 ppmV)
T^0	reference temperature (293 K)
c_i	CO_2 concentration inside the leaves
Γ^*	CO_2 compensation point for gross photosynthesis and photorespiration
a_T	normalization factor for h_2

Release of CO_2: autotrophic respiration. Autotrophic respiration C_{GA} and C_{RA}, respectively, are modeled similarily for both compartments, **GC** and **RC**, depending on the compartment size and an exponential function of temperature corresponding to a constant Q_{10} value for each ecosystem type. Maintenance respiration is calculated from

$$C_{GA}^{M} = \beta\, \mathbf{GC}\, e^{\omega(T-T^0)}, \quad (10)$$

$$C_{RA}^{M} = \gamma\, \mathbf{RC}\, e^{\omega(T-T^0)}, \quad (11)$$

Table 4. *Set of parameters of the Frankfurt biosphere model (vers. 2.2.2) used in the simulations presented here (vegetation types 8, 10, 11); for detailed information and description see Kohlmaier et al. (1997)*

Parameter	Short description	VT 8	VT 10	VT 11
SLA [$m^2\,kg^{-1}\,C$]	specific leaf area	12.0	40.0	40.0
T_{min} [K]	minimum temperature of net photosynthesis	270.6	273.0	273.0
T_{max} [K]	maximum temperature of net photosynthesis	311.6	313.0	313.0
T_{opt} [K]	optimum temperature of net photosynthesis	290.6	294.0	294.0
ω [K^{-1}]	Q_{10} related parameter of autotrophic respiration	0.0642	0.0642	0.0642
RG [−]	soil respiration group	3	2	2
ξ [$(kg\,C\,m^{-2})^{1/\kappa}$]	parameter in allometric relation	5.49	96.38	96.38
κ [−]	parameter in allometric relation	1.6	1.6	1.6
ν [$(kg\,C\,m^{-2})^{1/\kappa}$]	parameter in allometric relation	—	1694.42	1694.42
GC_{max} [$kg\,C\,m^{-2}$]	maximum biomass of GC compartment	1.026	0.324	0.324
RC_{max} [$kg\,C\,m^{-2}$]	maximum biomass of RC compartment	5.724	15.880	15.880
SC_{max} [$kg\,C\,m^{-2}$]	maximum biomass of SC compartment	14.000	12.000	12.000
NPP [$kg\,C\,m^{-2}\,yr^{-1}$]	net primary production	0.310	0.540	0.540
Res G [$kg\,C\,m^{-2}\,yr^{-1}$]	annual integral of respiration fluxes of GC	0.155	0.270	0.270
Lp G [$kg\,C\,m^{-2}\,yr^{-1}$]	litter production of GC compartment	0.155	0.270	0.270
Φ [$kg\,J^{-1}$]	initial quantum yield	$2.56 \cdot 10^{-10}$	$2.56 \cdot 10^{-10}$	$2.56 \cdot 10^{-10}$
k [−]	light absorption coefficient per leaf layer	0.5	0.5	0.5
Y_G	growth efficiency	0.73	0.73	0.73
Calibration parameters:				
α [$kg\,C\,m^{-2}\,s^{-1}$]		$1.7801 \cdot 10^{-08}$	$4.7803 \cdot 10^{-08}$	$6.0455 \cdot 10^{-08}$
β [s^{-1}]		$8.8882 \cdot 10^{-17}$	$5.4359 \cdot 10^{-16}$	$7.0248 \cdot 10^{-16}$
γ [s^{-1}]		$3.2672 \cdot 10^{-18}$	$1.5021 \cdot 10^{-18}$	$1.9793 \cdot 10^{-18}$
δ [s^{-1}]		$6.0515 \cdot 10^{-05}$	$4.6863 \cdot 10^{-05}$	$4.6892 \cdot 10^{-05}$
δ [s^{-1}]		$5.1483 \cdot 10^{-04}$	0	0
η [s^{-1}]		$6.5266 \cdot 10^{-05}$	$6.3214 \cdot 10^{-05}$	$8.3738 \cdot 10^{-05}$

where the rate constants β and γ have to be determined by calibration and $T^0 = 293$ K is the reference temperature. The parameter ω is related to the common Q_{10} values by $\omega = {}^1/_{10} \ln Q_{10}$.

In the simulations presented, here we use an explicit description of growth respiration. Following the study of Wagner (1995), which is described in more detail by Häger et al. (1996), we use a modification of the equations given by Thornley (1970).

$$C^G_{BA} = (1 - Y_G)(C_{ASS} - C^M_{GA} - C^M_{RA}), \quad (12)$$

where Y_G is the growth efficiency (Table 4) and C^G_{BA} is the growth respiration for both vegetation compartments (**BC** = **GC** + **RC**). Total autotrophic respiration is then calculated by summing maintenance and growth respiration:

$$C_{BA} = C^G_{BA} + C^M_{GA} + C^M_{RA}. \quad (13)$$

Litter production. Litter production, C_{GS} and C_{RS}, is assumed to be proportional to the respective compartment size. For the **GC** compartment of the deciduous vegetation types an additional constant rate of litter production occurs during the abscission phase.

Release of CO_2: heterotrophic respiration. Based on the model of Fung (1987), a linear dependence on compartment size and a soil moisture factor analogous to the moisture dependence of photosynthesis is assumed. As the focus of the present study was the model part describing the living vegetation we consider neither the humus layer and the soil compartments nor the heterotrophic respiration fluxes.

Water fluxes. We use a simple bucket model with daily precipitation (W_{AS}) as input and actual evapotranspiration (W_{SA}) as output. Owing to the close relation between assimilation and transpiration, the actual evapotranspiration is calculated by the product of potential evapotranspiration according to Thornthwaite (1948), W_{PET}, and the soil water dependent function h_3 as used in the calculation of assimilation. W_{runoff} comprises both surface runoff and drainage. It is taken as the surplus water when the soil water content reaches field capacity but assumed to be 0 for SW < FC.

8.2. FBM parametrization

The parameter set of the Frankfurt biosphere model as used in the simulations presented here is given in Table 4.

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