Effects of the age class distributions of the temperate and boreal forests on the global CO_2 source-sink function

By G. H. KOHLMAIER*, CH. HÄGER, G. WÜRTH, M. K. B. LÜDEKE, P. RAMGE, F.-W. BADECK, J. KINDERMANN and T. LANG, *Institut für Physikalische und Theoretische Chemie, Johann Wolfgang Goethe-Universität Frankfurt, Marie-Curie-Straße 11, D-60439 Frankfurt/M, Germany*

ABSTRACT

The rôle of the temperate and boreal forests as a global CO_2 source or sink is examined, both for the present time and for the next hundred years. The results of the Forest Resource Assessment for 1990 of the Economic Comission for Europe and the Food and Agricultural Organisation of the United Nations (1992) serve as the main database in this study. Out of the estimated total area of approximately $20 \cdot 10^6$ km^2 of forests and wooded lands in the temperate and boreal zone only approximately fifty percent is documented within the category of exploitable forests, which are examined in detail here. In this study, a general formalism of the time evolution of an ensemble of forests within an ecological province is developed using the formalism of the Leslie matrix. This matrix can be formulated if the age class dependent mortalities which arise from the disturbances are known. A distinction is made between the natural disturbances by fire, wind throw and insect infestations and disturbances introduced through harvesting of timber. Through the use of Richards growth function each age class of a given biome is related to the corresponding biomass and annual increment. The data reported on the mean net annual increment and on the mean biomass serve to calibrate the model. The difference of the reported net annual increment and annual fellings of approximately $550 \cdot 10^6$ m^3 roundwood correspond to a sink of 210–330 Mt of carbon per year excluding any changes in the soil balance. It could be shown that the present distribution of forest age classes for the United States, Canada, Europe, or the former Soviet Union does not correspond to a quasi-stationary state, in which biomass is accumulated only due to a stimulated growth under enhanced atmospheric CO_2 levels. The present CO_2 sink function will not persist in the next century, if harvesting rates increase with 0.5 % annually or even less. The future state will also be influenced by the effect of the greenhouse climate, the impact of which may range from a stimulating effect on growth, which is calculated by the Frankfurt biosphere model, up to a transitional negative effect through a shift in vegetation zones.

1. Introduction

The CO_2-source-sink problem of the biosphere has a long record within the history of modeling the atmospheric response to a fossil fuel CO_2 input. One question is whether the ensemble of all terrestrial ecosystems has been neutral with respect to CO_2 exchange with the atmosphere before humans had a significant impact on the

biota. The other problem is connected with the land use changes since the beginning of global industrialization as well as all other effects which may have changed the balance between growth of vegetation and autotrophic and heterotrophic respiration.

Tans et al. (1990) suggested that the terrestrial biosphere of the northern temperate latitudes may act as a CO_2 sink, a conclusion they drew from the comparison of observed atmospheric signals with the results of an atmospheric transport model combined with source-sink distributions. The

---

* Corresponding author.

evaluation of forest statistic data by different working groups (Kauppi et al., 1992; Kolchugina and Vinson, 1993b; Kurz and Apps, 1993; Birdsey et al., 1993; Heath and Birdsey, 1993; and Sedjo, 1992) supports the conclusion that the temperate and boreal forests of the northern hemisphere could be a sink for atmospheric CO_2 at present. In contrary the analyses by Houghton (1993) and Melillo et al. (1988) using terrestrial biosphere models resulted in the suggestion that the northern regions are approximately in balance with the atmosphere with respect to carbon.

One aspect of estimating the carbon budget of northern forests concerns the influence of the age class structure on carbon sequestering since young and growing trees accumulate more carbon than elder trees which have nearly reached their climax state. Therefore a study of the carbon budget of the temperate and boreal forests should also take into consideration the distribution of the age classes as done by Kurz and Apps (1991, 1993) and Kurz et al. (1992) for the forests of Canada, by Kolchugina and Vinson (1993a, b) for the forests of the former USSR, and by Heath and Birdsey (1993) for private timberlands in USA.

Naturally growing forests are assumed to show an age class distribution with a high amount of area covered with stands of the youngest age class and an exponential decrease as stand age increases. For instance such a distribution has been observed in pure stands of Abies in Japan (Tadaki et al., 1977). This age class structure results from disturbance regimes caused mainly by fire but also by storms and insect infestation. According to Runkle (1985) the average rate of disturbance in temperate forests do usually vary between 0.5 and 2.0% per year (the average value is 1% per year) despite great differences in vegetation and types of disturbance. The examination of the age class distribution in exploitable forests of about thirty countries as given by the UN-ECE/FAO Assessment (United Nations, 1992) shows that a natural age class structure as mentioned above is very rare in the forests affected by anthropogenic disturbance regimes. There are only two countries where the proportion of exploitable forest area is largest in the youngest age class and decreases in older age classes, namely Italy and Bulgaria. Forest management accompanied by fire control, logging, land clearing and afforestation decisively modifies the age class structure of forests as can be seen for the

selected age class distributions as depicted in Fig. 1.

In an ongoing study we investigate the natural disturbances which, in principle, can be extracted from the differences of gross and net annual increments given in some selected country studies. We have not succeeded, however, to do this on a global scale and refer here to the study of Kurz et al. (1992) for the Canadian forests who have addressed this topic in detail. Although we do not consider the history and impacts of natural disturbances of particular forest complexes here, we do present a general analytical approach in form of the Leslie matrix which could describe this phenomenon if the corresponding mortalities of the disturbances are defined. We concentrate in this study on the future development of the forest lands under human disturbances, mainly through fellings, because these impacts will control in an important way the future carbon balance. The increasing levels of carbon dioxide and the possible change to a greenhouse climate will be considered through the modification of the growth functions of the forest stands.

2. Temporal development of forest stands

Within the temperate and boreal forests we can distinguish a number of ecological provinces, in which climate and soil determine the diversity, the growth, and the standing biomass of the forest ecosystems. Within the ecological provinces not all stands will have equal age, here determined by the age of the dominant trees, but indeed will differ depending on the time span and the strength of the previous disturbance. The successional stages following a disturbance are well characterized within an ecological province. This allows us to distinguish between several maturity classes: a regeneration stage (1–20 years), an immature stage (21–60 years), a mature stage (61–100 years) and an overmature stage (101–180 years and more), following the classification according to Kurz et al. (1992).

As we are interested in an assessment of the vegetation's carbon source or sink strength growth functions are needed to relate the area covered by a given age class to a particular carbon content. The net annual increment in growth of the stem as well as the whole tree and the standing biomass
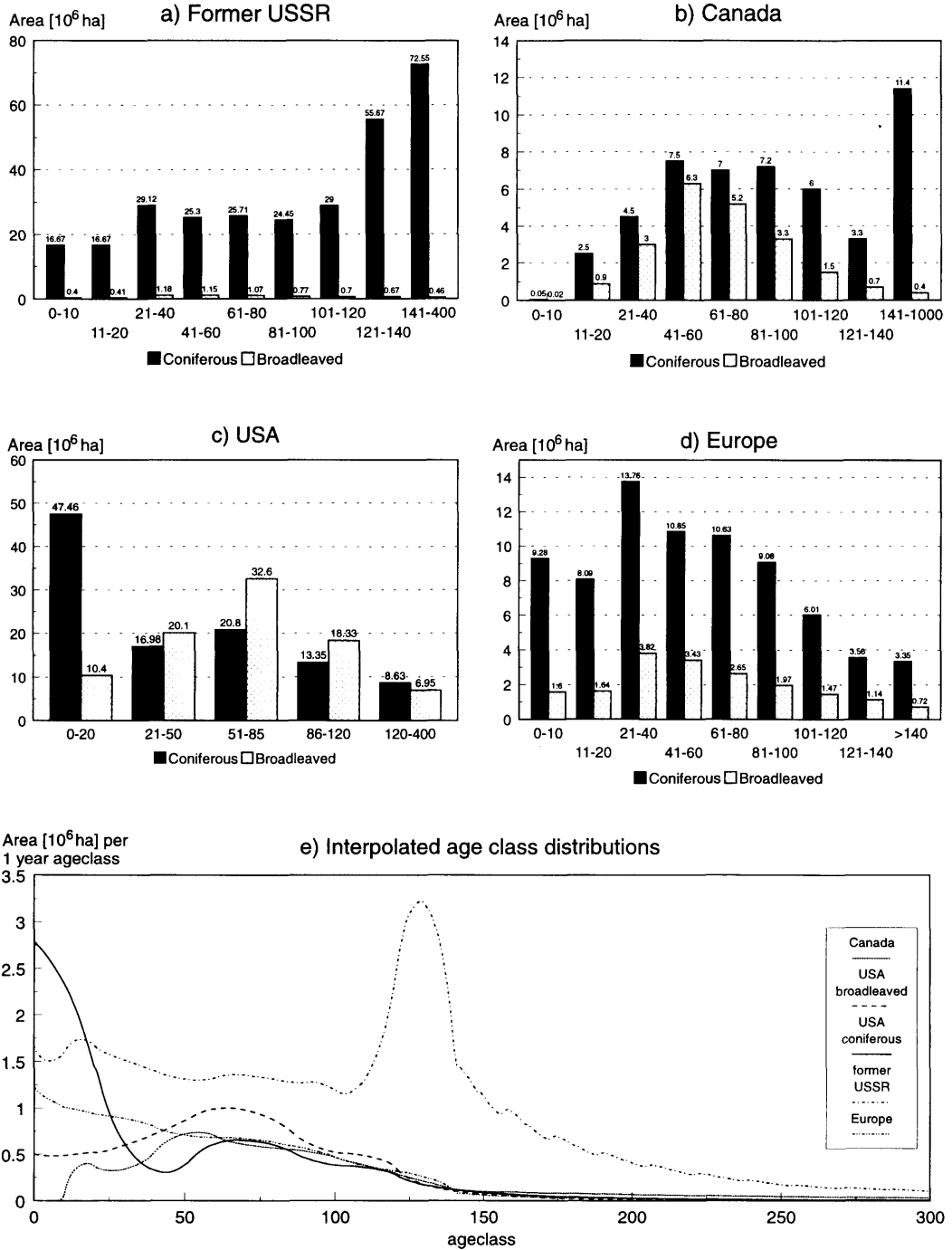
Fig. 1. (a–d) Age class distributions of the investigated exploitable forest complexes according to the UN-ECE/FAO-Assessment (United Nations, 1992). (e) Interpolated age class distributions.

can be described by a number of growth functions. Zeide (1993) has recently summarized about 15 growth functions with 2, 3 and 4 parameters out of which we have selected the s-shaped growth function of Richards. The three-parameter Richards equation of type I and II was also suggested by Cooper (1983) for the use in simulation of forest growth and yielded the best results in fitting the data given by the UN/ECE-FAO assessment. Our formulation of the two types of Richards equation is given by:

$$\text{Type I:} \quad \frac{dB}{dt} = NPP_{max} \left\{ \left(\frac{B}{B_{max}} \right)^{\delta} - \left(\frac{B}{B_{max}} \right) \right\}$$

$$0 \leqslant \delta < 1, \tag{1}$$

$$\text{Type II:} \quad \frac{dB}{dt} = NPP_{max} \left\{ \left(\frac{B}{B_{max}} \right) - \left(\frac{B}{B_{max}} \right)^{\delta} \right\}$$

$$\delta > 1, \tag{2}$$

where B is the living biomass per unit area and B_{max} is the corresponding maximum biomass achieved in the climax state, while NPP_{max} refers to the net primary production of stemwood, roots, leaves, feeder roots and fruits in the same asymptotic state. The first term in braces, multiplied by NPP_{max} can be identified with the net primary production at any time t, while the second term, again multiplied by NPP_{max}, is interpreted as the corresponding litter production, all terms per unit area.

We use $NPP_{max}/B_{max} = 1/\tau$, where τ can be interpreted as the mean carbon residence time in the climax state, which is much shorter for the total biomass than for stemwood alone. For growth, which is initially very slow the Richards functions of type II give a better fit than those of type I.

The integration of the differential equations leads to the following results:

Type I:

$$B(t) = B_{max} \left[1 - CIN \exp \left\{ -\frac{1-\delta}{\tau} t \right\} \right]^{1/(1-\delta)}$$

$$\text{for} \quad 0 \leqslant \delta \leqslant 1 \tag{3}$$

Type II:

$$B(t) = B_{max} \left[1 - CIN \exp \left\{ -\frac{\delta-1}{\tau} t \right\} \right]^{1/(1-\delta)}$$

$$\text{for} \quad \delta > 1, \tag{4}$$

with the constant CIN being in both cases is given by:

$$CIN = 1 - \left(\frac{B(0)}{B_{max}} \right)^{1-\delta}, \qquad B(0) > 0, \tag{5}$$

where $B(0)$ is the initial carbon mass at time $t = 0$.

In most cases, the Richards equations have been applied to managed forests where the overmature stage is never reached. If we want to apply these equations also to the carbon dynamics of old growth forests we need to consider that the closed canopy of even-aged trees will eventually break up by falling dead trees, such that the living standing biomass per unit area will decrease on the average. We introduce a correction factor of the type of a hyperbolic tangent to reduce the maximum biomass by a fraction of 10–35%. We then use the composite function by modifying the Type I Richards expression in eq. (3):

$$B(t) = B_{max} \left[1 - CIN \exp \left\{ -\frac{1-\delta}{\tau} t \right\} \right]^{1/(1-\delta)}$$
$$\times \left[f + (1-f) \left(1 - \tanh \left\{ \frac{t-t_{eff}}{T} \right\} \right) \right], \tag{6}$$

where f is chosen to range between 0.65 and 0.9, and where t_{eff} and T are parameters which are chosen for the best agreement with the empirical data. By analogy, the modified Type II Richards equation can be obtained from eq. (4). As eq. (6) needs to be weighted by the corresponding age class distributions of forest ensembles, as will be shown in the next chapter, the difference in the mean properties, like for instance the mean annual increment, are not very great for the two functions. Even for the former USSR where there is a lot of old growth the deviations in mean standing biomass and mean net annual increment ranged only between 1 and 3% for the original and the extended Richards equation.

One of the main concerns is the fate of the forests in a changing greenhouse climate. While the details will be described below it shall suffice to say that the analytical form of the Richards

function can be modified to include the expected greenhouse effect in an approximate way. One possibility is an increase in the net annual increment, while the same asymptotic biomass is reached. This can be described by:

Type I:

$$\frac{dB}{dt} = NPP_{max} \, C_{fert} \left\{ \left(\frac{B}{B_{max}}\right)^{\delta} - \left(\frac{B}{B_{max}}\right) \right\}, \qquad (7)$$

(for type II correspondingly).

The right-hand sides of the differential eqs. (1) and (2) are simply multiplied by the factor C_{fert}:

$$C_{fert}(t) = 1 + \beta \ln \left(\frac{CO_2(t)}{CO_2^0}\right), \qquad (8)$$

where it is assumed that growth increases logarithmically with increasing CO_2 levels, as originally suggested by Keeling (1973). β is the growth factor, which defines the relative increase in NPP following the corresponding increase in atmospheric CO_2.

Following the data collected and evaluated by Kimball (1983a, b) the value of the factor β was calculated to range between 0.15 and 0.60 (Kohlmaier et al., 1987). If atmospheric CO_2 increased from 280 ppmv in preindustrial times to 352 ppmv in 1990 the function C_{fert} (1990) takes on values between 1.034 to 1.137 for $\beta = 0.15$ and 0.60, corresponding to a 3 to 14% increase. For the complex of all exploitable forests in the temperate and boreal zone the FAO/ECE study gives a net annual increment of 1251 Mt C out of which, according to eq. (7) or eq. (23) correspondingly, 3–14%, or 40 to 150 Mt C yr^{-1} could be due to a CO_2 fertilization effect.

Considering a second limiting case of the effects of CO_2 fertilization the same formal factor C_{fert} can be used as a multiplier of the first term in braces, which leads to an increasing climax biomass as well:

Type I:

$$\frac{dB}{dt} = NPP_{max} \left\{ C_{fert} \left(\frac{B}{B_{max}}\right)^{\delta} - \left(\frac{B}{B_{max}}\right) \right\}, \qquad (9)$$

(for type II correspondingly).

In this particular case, B_{max} refers to the original climax state with pre-industrial CO_2 level and a new climax state is reached in which both NPP_{max} and B_{max} are increased by the factor $C_{fert}^{1/(1-\delta)}$. As δ for functions of type I is smaller than 1 the obtained fertilization effect is stronger than in the reference case, where the climax biomass remains constant.

3. The time evolution of an ensemble of forest stands

The analysis of the temperate and boreal forests presented in this paper is based on the following concepts:

• The growth of forests of a given species composition or their aggregates (hard woods, soft woods) under similar climatic and edaphic conditions can be described by a s-shaped growth curve, which is parameterized to follow the observations.

• The growth of an even-aged forest stand continues until a severe disturbance sets the forest back to the initial regeneration stage. A distinction is made between severe natural and direct anthropogenic disturbances. Fires, heavy storms or insect infestations as well as clearcut harvesting can have considerable areal extent. The still relatively rare selective cutting of tree species is not considered in the model. Natural breakup of the canopy in old-growth forests, however, is taken into consideration.

• Forests, within one region or ecological province, but different stages of temporal development are united to one ensemble. The ensemble is characterized by an age class distribution. For a world study of the temperate and boreal forests the ensembles are by necessity rather large, either because the local or regional data are not available or because the computational input can not be justified when still the basic phenomena need to be explored.

• The mathematical framework used here is the concept of a mortality and birth matrix of the Leslie type, which projects a normalized age class vector into the future according to some prescribed scenarios, or back into the past, when data are available. The mortality elements m_i refer to the mortality of a given age class i. They can be chosen to be functions of the time evolving with climate change, forest management and harvesting.

• In the basic case, the total area of the forest stand ensemble is conserved. Area fractions taken out of a given age class by mortality are transferred to the first age class in the next time step. Therefore the implicit assumption is made, that all disturbed areas will regrow either by natural rejuvenation or by tree planting. Land use changes like the conversion of forest land to agriculture or to bad lands and vice versa, transformation of surplus agricultural land, originally forested, to forests via natural succession or by reforestation need to be considered separately.

3.1. The Leslie matrix formalism applied to an ensemble of forest ecosystems

Data on age class distributions of an ensemble of forest ecosystems are conventionally given with a class width ranging from ten to thirty 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. The maximum value of n is suggested to represent the oldest age class as a mean value for all forest stands considered in different countries and regions. There are older trees in post-climax stands, where the canopy is broken by falling dead trees, and here some single trees may reach the age of 1000 years, or in some extreme situations even several thousand years. Each of its 400 elements N_i gives the area fraction which is covered by exploitable forests of a certain age in the reference year, with the normalization condition:

$$\sum_{j=1}^{400} N_j = 1. \tag{10}$$

To propagate the age class vector N into the future we use a matrix method which was first applied by Lewis and Leslie independently in the mid fourties to calculate the population dynamics of animals (Lewis, 1942; Leslie, 1945, 1948). Usher (1966, 1972) was the first to describe the application of this method to vegetation dynamics and especially to forest dynamics.

In our matrix concept we introduce a so called mortality matrix M which contains the probability of the mortality in each age class (similar to the Leslie matrix). The calculation of the probabilities is shown below. We can write the equation for the temporal development of the age class vector N:

$$N^{t+1} = MN^t \tag{11}$$

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:

$$N_1^{i+1} = \sum_{j=1}^{n} m_j N_j^i, \tag{12}$$

$$N_j^{i+1} = (1 - m_{j-1}) N_{j-1}^i, \qquad j = 2, ..., n. \tag{13}$$

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 $(M_{1,i}; \ i = 1, ..., n)$ and in the lower diagonal $(M_{i+1,i}; \ i = 1, ..., n-1)$ are non-zero.

The formulation with matrix elements can be written as:

$$\begin{pmatrix} N_1 \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ N_n \end{pmatrix}^{t+1} = \begin{pmatrix} m_1 & \cdot & m_i & \cdot & \cdot & m_{n-1} & 1 \\ 1-m_1 & 0 & \cdot & & \cdot & 0 & 0 \\ 0 & \cdot & \cdot & & & \cdot & \cdot \\ \cdot & \cdot & 1-m_i & \cdot & & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & & \cdot & \cdot \\ \cdot & & & \cdot & 0 & & \cdot \\ 0 & \cdot & \cdot & \cdot & 0 & 1-m_{n-1} & 0 \end{pmatrix} \begin{pmatrix} N_1 \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ N_n \end{pmatrix}^{t} \tag{14}$$

where $n = 400$, and $0 < m_i < 1$.

3.2. Some general properties of the Leslie matrix approach applied to forest ecosystems

Some of the general properties of the Leslie matrix approach are perhaps best illustrated in an example, where only three age classes exist, which for instance range for class 1 from 1 to 25 years, for class 2 from 26 to 50 years and for class 3 from 51 to 75 years. Beyond the age of 75 years no trees exist, because the mortality in the last age class (cut-off) is chosen equal to one. If the mortalities do not change in time, we expect that the age class vector will eventually become stationary ($t \to \infty$), that is the age class vector at steady state becomes an eigenvector of the Leslie matrix with the eigenvalue equal to 1.

$$\begin{pmatrix} m_1 & m_2 & 1 \\ 1-m_1 & 0 & 0 \\ 0 & 1-m_2 & 0 \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \\ N_3 \end{pmatrix}^{\infty} = 1 \begin{pmatrix} N_1 \\ N_2 \\ N_3 \end{pmatrix}^{\infty} . \quad (15)$$

The matrix vector multiplication clearly shows that

$$N_2 = (1-m_1)* N_1,$$
$$N_3 = (1-m_2)* N_2. \quad (16)$$

As the mortalities range between 0 and $+1$ it becomes evident that $N_3 \leqslant N_2 \leqslant N_1$. We conclude that there is a monotonous decrease in the relative weights from the lowest to the highest age class fraction. In an intensively managed ecosystem the mortalities m_1 and m_2 can, at least in principle, be reduced to zero; in such a case all three age classes have the same weight (case a). This ensures the forester that he can harvest every year the same amount of timber. In natural forests, where the mortalities are finite we expect an exponential decrease from the lowest to the highest age classes, when the mortalities are chosen equal to one another as shown in case b ($m_1 = m_2 = 1/2$).

Case a

$$\begin{pmatrix} N_1 \\ N_2 \\ N_3 \end{pmatrix}^{\infty}_{m_1 = m_2 = 0} = \frac{1}{3} \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}$$

Case b

$$\begin{pmatrix} N_1 \\ N_2 \\ N_3 \end{pmatrix}^{\infty}_{m_1 = m_2 = 1/2} = \frac{1}{7} \begin{pmatrix} 4 \\ 2 \\ 1 \end{pmatrix}$$

If the mortalities are just non-zero we still have a monotonously decreasing function. The principle outlined here with three age classes can be easily extended to the general case of a large number of age classes, where the general property for the eigenvector is still valid in the form of:

$$N_{i+1}^{\infty} = (1 - m_i)* N_i^{\infty}. \quad (17)$$

This result should still be valid if the mortality of age class i is decomposed into a sum of two terms:

$$m_i = m_i^{n} + m_i^{h} \quad (18)$$

where m_i^{n} refers to the natural mortality and m_i^{h} to the mortality due to harvesting. The two terms may not be completely independent but can influence each other. Intensive forest management can reduce the natural mortalities in age classes which are lower than the one harvested, on the other hand harvesting prior to old growth can avoid the effect of increasing old growth mortalities. The consideration of m_i^{h} without m_i^{n} will lead to asymptotic age class distributions which are falling off less steeply than the ones which include this effect. In transient states the effect of the omission of natural mortalities may be less pronounced.

Mortalities are usually not time independent, if their change is low enough there will be a corresponding moving stationary state age class vector. As, for instance, fire prevention has increased from the turn of the century to the present time in most industrialized nations, e.g., in the United States (Williams, 1992) it will reflect itself in a reduction of the mortalities. The original eigenvector, if it had been established at all, is no longer an eigenvector to a matrix with reduced mortalities but will tend to be substituted by an an eigenvector of the new mortality matrix after a sufficiently large period of time. In such a case we expect that the distribution in age classes becomes less steep which implies that there is a gain in area fractions occupied by higher age classes and at the same time an increase in standing biomass as long as the overmature stage is not reached yet. Numerical experiments with different non-equilibrium distributions with respect to a new mortality matrix have shown that it takes a rather long time for the forest to adjust to the new situation, anywhere from 1 to several life times of the trees making up the forest. It further could be shown that a

dramatic event in a paticular year where the mortalities of some selected age classes had been raised can lead to a non monotonous age class distribution which persists over several rotation periods. It is, however, still rather difficult to deconvolute past events from the present age class distribution.

A careful distinction should be made between situations where the total forested area of a particular ensemble stays constant and the case where the total forested area increases or decreases in time. This is the case when two ensembles of forest ecosystems are considered in which, for instance, broadleaved trees after harvest will be replaced by coniferous trees. The total area covered by coniferous forests will increase and the increment will be added to the lowest age classe of this ensemble. At the same time the stands taken out of the harvestable age class of the broadleaved forests are not transferred to the lowest class in this ensemble. The age class vector of each of the forest ensembles is therefore to be renormalized with respect to the total area. Similarly reforestation of marginal agricultural land leads to the additional increments in the lower age classes while at the same time the total forested area increases.

It is very difficult to determine the past time course of natural mortalities in detail for most forests. Usually data are only available for some extreme events in the past which are difficult to unite into a continuous record. In the present study we shall focus our attention on the measured standing biomass data and their net annual increments, out of which all natural disturbances have been implicitly subtracted.

4. Description of input data and calibration procedure for the Richards functions

4.1. Description of the input data

The main database used in this study is the UN-ECE/FAO Assessment (United Nations, 1992) of the temperate and boreal forests. The basic information is on area coverage, growing stock of roundwood over bark, net annual increment (NAI), net annual fellings, and the age class distribution of forests within a given country or continent. This study has its main emphasis on exploitable forests, which are forests not being withdrawn from timber utilization by statute or administrative regulation and at the same time

producing at least 1.4 m^3 of industrial wood per hectare and year. Forests which do not fulfil these criteria are termed "unexploitable forests". Wooded lands are intermediates between forests and grasslands where the areal coverage with trees ranges from 5 to 20%. Age class distributions are given only for the exploitable forests and therefore this study will exclusively cover this fraction of forests. In Table 1, the areal extent of both the total and the exploitable forests is given for the great forest formations in the United States, Canada, the former USSR, Europe, and the Pacific Countries (Japan, Australia and New Zealand). The mean standing biomass in this table is derived from the growing stock by using a corresponding expansion factor. Birdsey (1992) has shown that an expansion factor between 1.675 and 2.651 may be used to convert the stem biomass into the total above and below ground biomass of the tree (stem, branches, roots and leaves). In this study we use an average value of 2.0 for this conversion. This total biomass needs to be converted to carbon and it is common to use a factor of $0.27t$ C/m^3 to convert one cubic meter of wood into $0.27t$ of carbon (Birdsey, 1992). The data presented in Table 1 have been obtained by multiplying the standing stock in m^3 of round wood over bark or the corresponding net annual increment by $0.54t$ C/m^3 (Sampson, 1992 and Kolchugina and Vinson, 1993b suggest a similar multiplier of $0.534t$ C/m^3). It is remarkable that the mean standing biomass per unit area (t C ha^{-1}) is nearly the same for all five regions while this is not true for the mean net annual increment which is highest in Europe and the United States. The total standing biomass for the five world regions serves as one of the calibration parameters. Its sum over all exploitable temperate and boreal forests is 60.6 Gt C, which falls well within the expected range of constituting about 10% of the worlds standing biomass. Again the total NAI of the different regions serves as input data as will be shown in the next chapter. The sum of the NAI-values for the five regions is 1250 Mt C yr^{-1} which is, of course, much smaller than the estimated net primary production, NPP, because litter formation and disturbances must be subtracted from the NPP. Heath et al. (1993) estimate the NPP to be 4–5 times as high as the net annual increment (for the temperate forests), thus the total NPP for the exploitable forests is estimated to lie between 5 and 6 Gt C yr^{-1}. The

Table 1. (a) *Area, standing biomass, and net annual increment (NAI) for 5 world regions of the exploitable forests*; (b) *Resulting carbon balance (1990) from the difference in NAI and annual fellings (AF)*

	Former USSR	Canada	USA	Europe	Pacific	Total
Total area of forests and other wooded land [10^6 ha]	942	453	296	195	178	2064
(a) Area of exploitable forests [10^6 ha]	414	112*	196	133	43	898
Mean standing biomass per unit area [t C/ha]	66	72	64	75	63	67.5
and total standing biomass [Gt C]	27.3	8.0	12.5	10.0	2.7	60.6
Mean NAI [t C/ha yr]	0.91	1.03	2.03	2.34	1.13**	1.38
(a/b) Total NAI [Mt C/yr]	378	115	397	312	49	1251
(b) Total annual fellings [Mt C/yr]	280	85	335	222	28**	950
Resulting carbon balance [Mt C/yr]	98	30	62	90	21	301

* $223 \cdot 10^6$ ha after Kurz et al., 1992 for productive forests: Boreal east + west, cool + moderate temperate, Cordilleran forests.
NAI (net annual increment), AF (annual fellings) refer here to total biomass.
Conversionfactor: 0.54 t C m^{-3} roundwood (Birdsey, 1992).
Pacific includes Australia, New Zealand and Japan.
** Data only available for Australia; New Zealand and Japan extrapolated.

values of the NAI reported here serve not only as the calibration for the model but determine together with the annual fellings the present carbon balance which will be discussed in detail in Subsection 5.1.

For the future carbon balance the age class distributions are a significant factor. The country data often make a distinction between coniferous trees (soft wood) and broadleaved trees (hard wood). We retain this distinction in our study only for the United States, where there is a great difference in the age class structure between these categories. In the former USSR there are practically only coniferous trees while in Canada the coniferous trees prevail. The class widths applied by the foresters differ from country to country as becomes apparent from Fig. 1, where data on the four extensive forest biomes of Russia, USA, Canada, and Europe are shown.

As the temporal resolution of the given age class distributions is rather coarse and the age classes do not have the same width for each country, the distribution has been interpolated. This interpolation is also necessary as we use a general growth equation for determining biomass. The iterative numerical interpolation-algorithm used here exactly preserves the area of the 10 or 20 years class range and produces a smooth course between the given age classes. The input data as well as the interpolated distribution are documented in Fig. 1. In Fig. 1e, the great peak in the age classes 121–140 in the forests of the former USSR attracts attention. As Fig. 1a outlines, the area covered with age class 121–140 is nearly twice the area covered by stands of the age between 101–120. The area of about 72 Mha covered by the highest age class is distributed over the range of 141–400. A relatively great area of stands which belong to the highest age class (141–400 years) can also be found in Canada (see Fig. 1b) resulting in a peakless distribution after interpolation. Further information about the age class distribution of the former

USSR were available from Kolchugina and Vinson (1993a) but their classification in young stands 1st and 2nd class, middle age, premature and mature/overmature does not give more details about the highest age class. However, it should be mentioned that they also notice an extensive area covered with mature/overmature stands which amounts nearly to 323 Mha including all forest biomes while in other age classes the areas have the extent of 50–150 Mha.

4.2. Calibration procedure for the Richards function

The calculation of the carbon balance for each forest biome requires both the age class distribution and the growth function of biomass, described by the Richards function of type I and type II. The parameters of the Richards function B_{max}, $\mathrm{NPP}_{\mathrm{max}}$ and δ need to be chosen in such a way that the total standing stock and the total net annual increment, which are the only data given in the ECE-FAO Report, correspond with the model derived values. We therefore need to satisfy the following conditions:

total standing stock:

$$B = \sum_{j=1}^{400} N_j B(j),\qquad(19)$$

measured either in round wood or total biomass;

total net primary production:

$$\mathrm{NPP} = \sum_{j=1}^{400} N_j\,\mathrm{NPP}_{\mathrm{max}}\,C_{\mathrm{fert}} \left(\frac{B(j)}{B_{\mathrm{max}}}\right)^{\delta};\qquad(20)$$

and

total net annual increment:

$$\mathrm{NAI} = \sum_{j=1}^{400} N_j \left\{ \mathrm{NPP}_{\mathrm{max}}\,C_{\mathrm{fert}} \right. $$
$$\left. \times \left[\left(\frac{B(j)}{B_{\mathrm{max}}}\right)^{\delta} - \left(\frac{B(j)}{B_{\mathrm{max}}}\right) \right] \right\}.\qquad(21)$$

We note that within the calibration routine, we have the problem of dealing with aggregated data over large areas under different growth conditions and age class distributions within differing ecological provinces. We have been able to show, as presented in the Appendix, that the aggregation problem does not lead to any serious distortions if either the Richards equations or the age class distributions are very similar for the different provinces. However, it can be observed that the aggregated growth curve may considerably differ, if both the age class distributions and the Richards function differ, too. We attribute the delayed growth curves, presented within the mathematical

Table 2. (a) *Parameters* τ, δ *and* B_{max} *of the Richards functions for the examined regions and* t^* *of the harvest function.* (b) *Evaluation of the given age class distributions* (*1990*) *with the parameters of the Richards functions displayed in Table 2a*

(a)	Type	$\tau[1/a]$	δ	B_{max} (Gt C)	$t^*[a]$
Canada	I	10	0.75	16	93.5
USA, broadleaved	II	7.6	1.59	25	122.5
USA, needleleaved	I	15.75	0.65	39	82.3
former USSR	II	8	1.35	72	158.8
Europe	II	3.8	1.149	74	80[#]

(b)	Biomass increment [Gt C/yr]	Total biomass [Gt C]	Total fellings [Gt C/yr]
Canada	0.11 (0.12)	8.55 (8.02)	0.085 (0.085)
USA, broadleaved	0.17 (0.17)	5.84 (5.38)	0.122 (0.122)
USA, needleleaved	0.20 (0.24)	11.4 (7.09)	0.190 (0.190)
former USSR	0.38 (0.38)	28.1 (27.17)	0.291 (0.291)
Europe	0.22 (0.22)	7.9 (7.07)	0.157 (0.157)

Values in brackets are estimates according to the UN-ECE/FAO-Assessment (United Nations, 1992).
[#] The hyperbolic tangent harvesting function (eq. (24)) is used with $t^{**} = 80$.
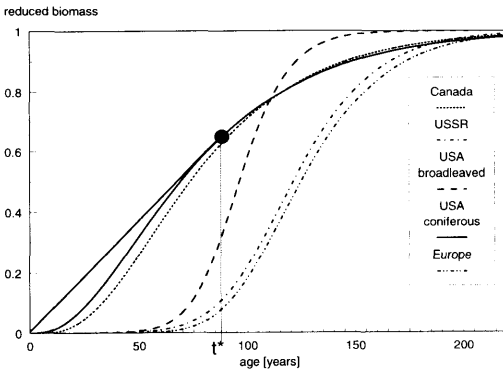
reduced biomass

Fig. 2. Richards functions of type I (US coniferous forests, Canadian forests) and of type II (former USSR, US broadleaved, and European forests). The optimal felling time *t** is illustrated for US coniferous forests.

formulation of the Richards function of type II, to such an aggregation problem.

To determine an average growth equation for each of the selected forest complexes USA, Canada, Europe, and former USSR the values of standing biomass, net annual increment (NAI), and the distribution of age classes are used as they are reported in the UN-ECE/FAO Assessment (United Nations, 1992). Table 2a shows the parameters defining the Richards equation which fits best to these prescribed values from the UN-ECE/FAO-Assessment given in Table 2b. The forest complex of the USA is divided into broadleaved and needleleaved stands because the strongly differing age class distribution makes it difficult to find well fitting parameters.

A graphical representation of the calibrated Richards functions is given in Fig. 2. It is noticed that Europe and the former USSR have growth curves which are very similar, as may be perhaps expected by the geographical proximity. For the example of US coniferous forests the optimal felling time *t** is presented as being determined by the tangent to the growth curve.

5. Present CO_2 balance of the temperate and boreal forests and its expected change in the future

5.1. Present CO_2 sink function

The inventory of the ECE/FAO presented in the preceeding chapter can not only be used to

calibrate the growth functions of the forests, but also to evaluate the current carbon balance when the data of the annual fellings in 1990 are taken into consideration. The net annual balance, as given in Table 1, serves as a starting point of our projected CO_2 source/sink function under different economic conditions as well as possible future climate changes.

The carbon stored annually in the forest formations is given by the difference between the net annual increment and the annual fellings. With the mean expansion factor used here the total carbon stored in living biomass is 300 Mt C yr^{-1}. Considering the given range of a weighted expansion factor between 1.4 and 2.2 one arrives at 210–330 Mt C yr^{-1}. In the present model we have not included changes in soil carbon which can be associated with the increase in living biomass, as has been suggested by Sedjo (1992), referring to a study of Jenny (1980). This effect could be important as the soil carbon storage is on the average 2–4 times higher than the corresponding stock of carbon in the living biomass. According to Sedjo's studies the carbon balance of both the biotic and the soil component should increase by a factor lying between 1.2 and 1.6 of the carbon in the biota alone. If the suggested soil factor would be applied to our balance, the range of carbon annually stored in the exploitable forests could range between 240 and 530 Mt C with a mean value of 385 Mt C. In a still ongoing study we included the unexploitable forests and wooded lands as well and came to the conclusion that the total annual carbon storage in trees and soils of the temperate and boreal region could range between 460 and 960 Mt C with a mean value of 710 Mt C. We note here that our country estimates as well as the global estimate, given in Table 1 represent a lower boundary for the carbon sequestration. While there is good agreement with the Canadian forests the values for the US forests, both productive and unproductive, lie between 152 Mt C yr^{-1} (Sedjo, 1992) and 230 Mt C yr^{-1} (Birdsey et al., 1993). Kauppi et al. (1992) estimate for Europe a carbon sink strength of 85–120 Mt C yr^{-1} while Kolchugina and Vinson (1993) give an approximate estimate of a carbon sink of 485 Mt C yr^{-1} for the productive and unproductive forests of the former USSR.

We also do not consider the effects of a carbon storage pool in forest products and its input and

decay, but we conclude from other studies (Apps et al., 1993; Heath et al., 1993; Heath and Birdsey, 1993) that the forest products pool does not change the carbon balance significantly. Kurz et al. (1992) estimate an increase in the product pool of 21 Mt C yr^{-1} for Canada while for the United States Birdsey et al. (1993) give an estimate of 36 Mt C yr^{-1}.

5.2. Initialization of the calculations of the future carbon balance

Within the theoretical framework described above the net annual increment within an ensemble of forest ecosystems was obtained by the summation of the products of the age class fraction and the particular biomass increment. Similarly the net annual balance will be described as a difference between the annual growth increments and the corresponding mortalities. A distinction is made between mortalities introduced by natural disturbances and mortalities caused by harvesting. In the statistical information on forests a distinction is often made between gross and net annual increment, whereby the gross annual increment is the production prior to the consideration of natural disturbances. Most of the statistical information, however, is only on the net annual increments, such that the mortalities due to natural disturbances and their change in time cannot be considered explicitly. We therefore fitted the parameters of the Richards function in such a way that they satisfied the net annual increment of 1990 as the initial value. For the different scenarios into the future the expected climatic changes are considered in a smoothed fashion in the change of the Richards functions, while the future mortalities contain only the anthropogenic component, namely harvesting. The net annual balance in 1990 and the future is given by

$$\text{NAB} = \sum_{j=1}^{400} N_j \left\{ \text{NPP}_{\max} C_{\text{fert}} \times \left[\left(\frac{B(j)}{B_{\max}} \right)^{\delta} - \left(\frac{B(j)}{B_{\max}} \right) \right] - m_j^{\text{h}} B(j) \right\}, \quad (22)$$

where m_j^{h} is the mortality in age class j due to harvesting. The net annual fellings (NAF) are consequently given by

$$\text{NAF} = \sum_{j=1}^{400} N_j m_j^{\text{h}} B(j). \quad (23)$$

6. Description of scenarios and results of simulations

The future fate of the forests will depend on their growth under a changing greenhouse climate, on the economic activities of forest management and harvesting as well as on the land use changes, which will convert forests into areas of other use or vice versa. In our simulations the change of the growth of forests is considered formally through the time dependent factor C_{fert}, which can change productivity alone conserving the climax standing stock or both productivity and standing stock in the same direction. The latter behaviour has been found in the Frankfurt Biosphere Model, while other authors have suggested that only the growth to the final state is accelerated in a CO_2 rich atmosphere. In a recent review Rogers et al. (1994) have summarized the response of agro- and forest ecosystems to elevated levels of CO_2 and the still ongoing controversy about the CO_2-fertilization effect. The only economic activities considered explicitly are harvesting, the scenarios are chosen in such a way that the initial conditions in 1990 are given by the present rate of harvesting, while the future development is expressed either through a decrease or an increase in harvesting or through a level which is frozen in at the present rate.

The shape of the harvesting function with respect to the age classes is expected to look differently for intensively managed forests and for felling of old growth forests, which had little management in the past. In either case environmental pressures are supposed to be presently and in the future strong enough that all areas harvested will be reforested or at least helped to regenerate quickly through natural rejuvenation.

6.1. Description of the harvest function

The elements $M_{1,i}$ of the mortality matrix M used in the scenario studies represent the mortality probability m_j^{h} due to harvesting. The harvesting is described by two alternative approaches. In managed forests harvest occurs at an optimal time t^* in which the net annual growth is equal to the average growth from the time of the seedling state to the felling state. We extend this general concept to all forests managed or unmanaged by replacing the δ-function at time t^* by a Gaussian function. To calculate the felling rate within every age class we center the Gaussian function around an

optimal felling time t^*, which maximizes the mean harvest over the whole growth interval (Cooper, 1983). A geometrical construction to yield the value of t^* can be seen in Fig. 2. The mortality m_j^h of the jth age class according to fellings is calculated as follows:

$$m_j^h = A\, e^{-\{(j-t^*)/\sigma\}^2}, \qquad (24)$$

where A is the amplitude and σ the standard deviation from the mean of the Gaussian distribution. Additionally we assume an exponentially increasing natural mortality probability in the oldest age classes (200–400). The biomass of these dead old trees also contributes to the annual replacement of them. In a second harvesting scenario a given convenient time of harvesting is chosen (e.g., 60–90 years for coniferous trees and 80–160 years for broadleaved species) independent of the growth curve. Here we propose the hyperbolic tangent function as a convenient tool:

$$m_j^h = \tfrac{1}{2}C\{1 + \tanh[\alpha(j - t^{**})]\}, \qquad (25)$$

where C is chosen to reproduce the prescribed amount of harvesting, α to determine the steepness of the transition at the chosen time of harvesting, t^{**}.

6.2. Description of the scenarios

The Leslie matrix approach allows us to follow the time development of the age class structures of a particular ensemble of forests. If the natural mortalities are included in the growth function and its change in time, then the corresponding mortalities in the Leslie matrix reflect only losses due to harvesting. As an example we should like to present here the evolution of the age class distribution of the broadleaved forests of the USA, represented in 3-dimensional plots (Fig. 3). The initial age class distribution as presented in Fig. 1e can be seen in the front of the three-dimensional graph. Pointing to the back in the graph the temporal development of the age class distribution is shown. The simulation yields a discontinuity in the temporal development of the youngest age classes (see Fig. 3a), when the area reforested corresponds exactly to the area harvested. This is so, because for most of the forests considered the present area annually reforested is either smaller or larger than the area of harvesting, prescribed by the harvesting func-

tion. However, if overall forest management and planning is included in the future scenario building in such a way that the future rate of reforestation is smoothly adapted to today's rate of reforestation, then the discontinuity disappears, as shown in Fig. 3b.

If the time evolution of the age class distribution is combined with the Richards equation then the corresponding biomass development can be predicted. In the reference scenario 1 the hypothetical case is studied in which both the growth properties of the forests and the rate of fellings are kept constant. Here the characteristic growth parameters of the Richards function remain constant in time, which implies that neither a change in climate nor a direct effect of CO_2 fertilization is considered. The fellings in the future are constrained to the same timber volume as given by the UN-ECE/FAO Assessment for 1990 (United Nations, 1992). A constant rate of harvest, however, can result in a change of area harvested, as harvesting may proceed from higher stocked forests to those, which have a lower standing stock. Within the model simulation the amplitude of the harvest functions (normalization constant A in eq. (24) and C in eq. (25)) is adjusted accordingly. We further assume that all areas affected by fellings will be reforested or will be helped to regrow by natural succession. Any gains or losses in forest area are omitted in the scenario. Scenario 1 thus will predominantly reveal the effect of the nonequilibrium distribution in age classes of the great complexes of forests of the former Soviet Union, of Canada, Europe, and the United States.

For the decade from 1980 to 1990, there was a net gain in 2 million hectares of forest area and other wooded lands for Europe. The data on the former USSR are very uncertain, a net gain of 22.6 million hectares is reported for the same period. Unfortunately no data on the United States and Canada are available.

The consequences of changes in forestry practices on the carbon budget are estimated in two further scenarios. The felling rate could be affected in two directions, either through an increasing demand in timber in a world, in which population is still growing by more than 1.6% annually or through governmental restrictions of fellings, environmental concerns, economic constraints. In scenario 2 the fellings are increased at a constant rate each year. In our simulation, however, an
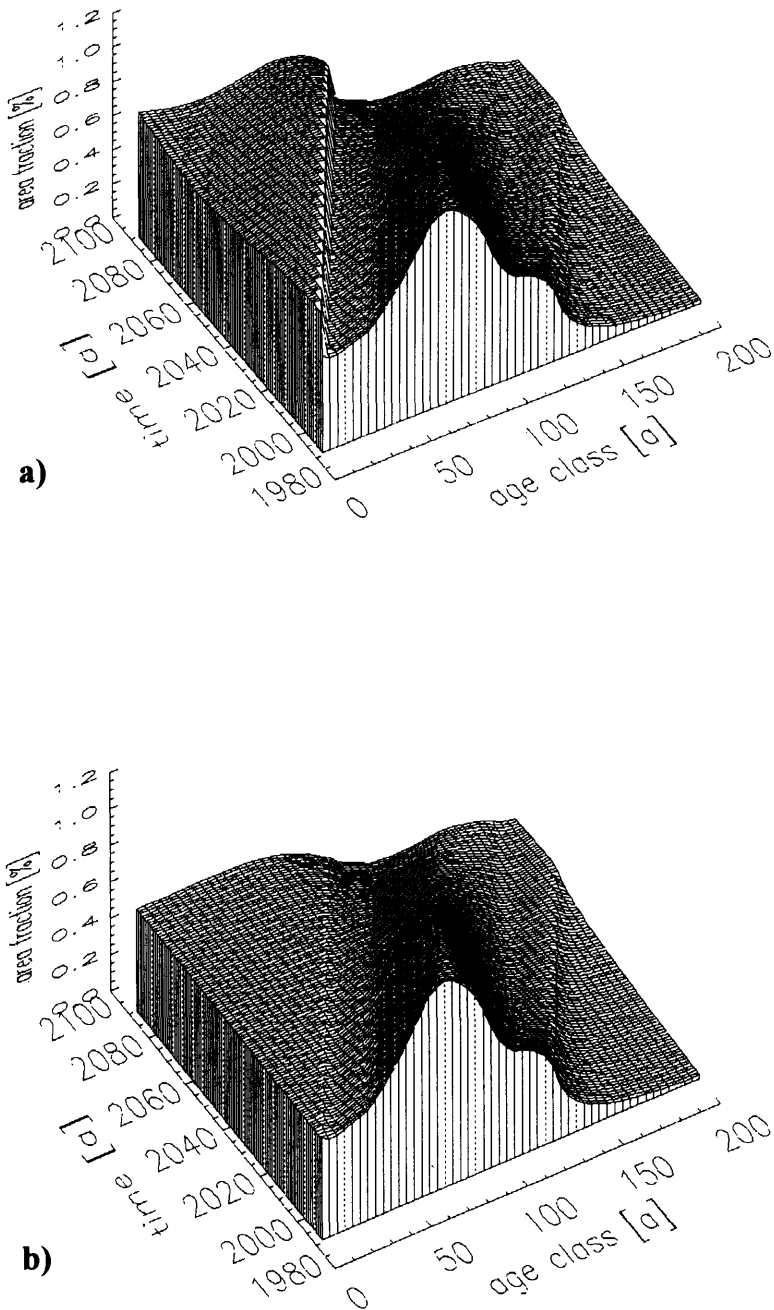
Fig. 3. Possible future age class distributions, simulated under assumption of 2 forest management scenarios. (a) Constant amount of annual fellings, all cleared areas will be reforested in the following year. Depending on the chosen time t^* for optimal felling, the area fraction available for reforestation can be larger or smaller than the fraction in previous years. (b) Constant amount of annual fellings, with area reforested chosen to corespond to the previous history.

assumed rate of only 1 % per year leads to a total clearing of some of the forest complexes already after several decades. As this scenario seemed to be rather unrealistic and certainly not wanted, we therefore proposed as scenario 2 an increase of only 0.5 % per year. By contrast in scenario 3 the fellings are decreased at a rate of 0.5 % per year.

The reference scenario 1 was then modified to include the effect of a climate change and the direct effects of CO_2 fertilization. From the studies with the Frankfurt Biosphere Model (Lüdeke et al., 1994b), which is a process model with high temporal and spatial resolution, we concluded, that within the next 30–100 years the stimulating effects of a direct CO_2 fertilization effect together with a climate change should be more important than the reducing effects occurring with a shift in climatic zones as suggested by Smith and Shugart (1993). There we could clearly show, that a consideration of changing temperature and precipitation alone as derived from the Hamburg $3 \times CO_2$ model results (Perlwitz, 1992) leads to a decrease in production due to the enhanced autotrophic respiration and increased water limitation. In particular the net primary production of the forests of the temperate and boreal zone was reduced by 22 %. This effect, however, was overcompensated by the direct CO_2 fertilization effect which resulted then in an overall increase in productivity by approximately 10 %. If an upward shift in the optimum temperatures for photosynthesis as postulated by Long and Drake (1992) in their exploration of the Farquhar photosynthesis model is considered then the stimulating effect in NPP increased to approximately 30 %. To include the combined CO_2/climate effect in this study we simply introduced the time dependent factor C_{fert} into the Richards equations. For the time dependence of atmospheric CO_2 we chose a scenario as proposed by Kohlmaier et al. (1991) in which the atmospheric CO_2 level rises from $CO_2(1850) = 280$ ppm to $CO_2(2090) = 620$ ppm with $CO_2(1990) = 352$ ppm. This scenario in which CO_2 rises by a factor of 2.2 relative to preindustrial times has a somewhat slower increase than the Hamburg business as usual scenario where an effective $3 \times CO_2$ concentration (corresponding approximately to a doubling in direct CO_2 concentrations) relative to the present time is reached in 100 years from now. To make the results of the detailed FBM study comparable to this investiga-

tion $C_{fert}(2090)/C_{fert}(1990)$ was evaluated for the factors $\beta = 0.15$, 0.40, and 0.60 with the result 1.082, 1.21, and 1.30. As the value $\beta = 0.40$ gave the best correspondance for a mean stimulation effect without and with a shift in optimum temperature we chose this value to be representative of a future greenhouse climate.

6.3. Results of the simulations

The net annual carbon balance of the three scenarios calculated for each of the selected regions is presented in Fig. 4, where for the United States the broadleaved and coniferous forests were considered in separate simulations. Scenario 1, which presupposes a constant felling rate, has been calculated with and without consideration of a climate change effect on the net primary production and respiration. Formally both the direct effect of the rising atmospheric CO_2 concentration and the change in temperature and precipitation are included in the stimulation factor β, which originally was defined for the direct CO_2 fertilization effect only. We formally included in our simulation also the stimulation factor $\beta = 0$ to show the effect of the age class distribution on the future development.

The range between the results of both simulation runs ($0 \leqslant \beta \leqslant 0.4$) is outlined by the hatched area. The exploitable forests of Canada appear to turn from a sink to a source for atmospheric carbon within the next 20 years and similarly the same holds true for the exploitable forests of the former USSR. The situation for the United States appears to be considerably different. Here the coniferous forests, which are at present nearly balanced, become a sink of CO_2 for the next century, while the broadleaved forests may turn from their present sink function to a source function by the middle of the next century, if there is no CO_2 stimulation effect. Europe shows a development in which the small but significant carbon sink function remains for a longer period of time.

It is remarkable that the economic decisions on harvesting have a strong effect on the future source/sink behaviour of those forests. It can be clearly seen from Fig. 4 that only an increase of 0.5 % in harvesting per year (scenario 2) brings all forest complexes except the European to a source function at the latest by the middle of the next century. It can be estimated from the areal extent of the hatched area that even a positive response

of the forests to the greenhouse climate can not overcome the intensified harvest and with that the rising CO_2 source function. On the other hand we explored in scenario 3 the influence of a decreasing rate of harvesting, again of 0.5 % per year. Here in all cases the present sink function can be main-

tained or even increased after the middle of the next century.

The results are summarized in Fig. 5 for the net annual carbon balance of the exploitable forests examined in this study, i.e., the forests of the United States, Russia, Canada, and Europe. Here
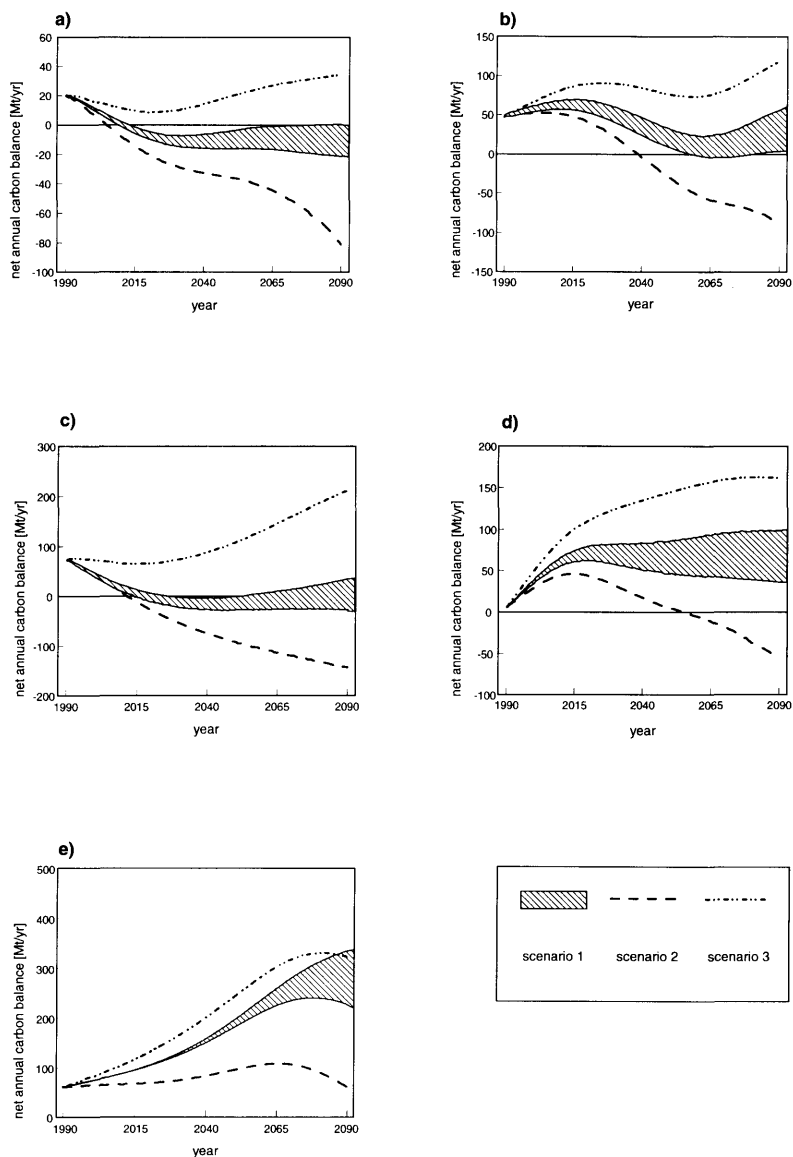

Fig. 4. Comparison of the possible future evolution of net carbon balance in four regions according to the assumptions of three scenarios regarding forest management as described in the text. (a) Canada; (b) USA (broadleaved); (c) former USSR; (d) USA (coniferous); (e) Europe.
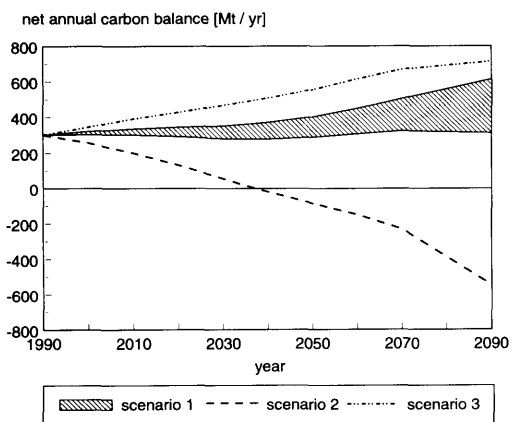
net annual carbon balance [Mt / yr]

Fig. 5. Sum of the net annual carbon balance of the investigated exploitable forest complexes according to the different assumptions concerning the amount of fellings.

again the strong influence of the harvest rate and its change is evident. It can overpower the importance of the response of the forests to an expected climate change.

7. Conclusions

It has been a question of long standing whether the biota have been in a stationary state at the beginning of the industrialization and later on, where man exerted considerable influence on the biosphere. The role of the temperate and boreal forests is particularly interesting in this respect as they certainly have been a source of CO_2 during the pioneer phase of industrialization. Due to the long life time of trees and forest stands it is to be expected that any change in the disturbance regime will express itself in a changing age class distribution for a rather long time. Using the Leslie matrix formalism to project an age class vector into the future we could show that there is a tendency for this vector to become stationary or, expressed differently, there is an eigenvector to any given Leslie matrix in which the mortalities remain constant. The properties of this eigenvector are such that there is a monotonous decrease in the age class fraction going from the lowest to the highest age class. The present distribution of age classes as reported by the ECE/FAO study shows

considerable deviation from the expected steady state distribution and thus indicate that the carbon balance will change in time even if the productivity of the forests remained constant.

The results presented in this study refer to the data given for the exploitable forests of Canada, USA, Europe, and the former USSR. Considering these complexes of the temperate and boreal forests the sink strength amounts to about 300 Mt carbon excluding soil changes. According to our simulations this sink strength will remain or will become weaker within the following 100 years. The magnitude of the sink strength depends on the influence of the rising CO_2 concentration on forest growth and expected greenhouse climate change. However, the development of carbon exchange between atmosphere and biosphere shows different trends for each country due to the particular age class distributions. The results lead to the assumption that an age class distribution like the one of the coniferous forests of the USA will ameliorate the sink function in the future development. The characteristics of this age class structure is a large area covered with rather young trees similar to the natural distribution. Instead of the exponential decrease with age this structure shows a smaller second peak in the middle ages. Regions having a high fraction covered with older stands will loose their sink function.

The changes in the forest management, the modifications of the felling rate, decisively affects the carbon balance. In this case all countries show the same trends.

It should be emphasized that our present analysis of the major forest complexes of the temperate and boreal zones include a number of assumptions which on the one hand are due to the incomplete data basis and the high aggregation level of different forest provinces and on the other hand due to our present uncertainty in modelling the impact of a future climate change. But leaving aside all these open questions we can conclude that the carbon source-sink functions of the temperate and boreal forests will not remain at the present level but most probably will change in such a way that the sink function will be diminished. The second most important conclusion is that the scenarios on harvesting have a very great effect on the future carbon store of the forests. Even small changes in the annual rate of harvesting of as little as 0.5 % seem to be more important for the

carbon balance than any anticipated future climate change, at least for the next 100 model years.

However, our examination of the age class structure does not include the unexploitable part of the temperate and boreal forests and a change in climate with distinctive regional patterns. In some areas net primary production and standing biomass may rise while in other locations the opposite may be true. We are therefore developing a detailed regional and seasonal model describing the CO_2 exchange between the biota and the atmosphere, the Frankfurt Biosphere Model (Kindermann et al., 1993; Lüdeke et al., 1994a), in which the physiological response of trees and ecological response of soils is examined in detail.

8. Acknowledgements

9. Appendix

Some remarks to the problem of aggregating forest complexes

Let us assume that the considered forest complex consists of m provinces p, $p = 1, ..., m$, each characterized by a normalized age class distribution vector n^p and a mean growth dynamics $b^p(t)$, representing the total standing biomass of age t in the province p. For convenience we additionally define a biomass vector b^p of the dimension s (number of age classes):

$$b^p = \begin{pmatrix} b^p(1) \\ \cdot \\ \cdot \\ \cdot \\ b^p(s) \end{pmatrix}, \qquad n^p = \begin{pmatrix} n_1^p \\ \cdot \\ \cdot \\ \cdot \\ n_s^p \end{pmatrix}. \tag{A1}$$

For the total biomass B and the total increment Z we obtain:

$$B = \sum_{p=1}^{m} b^p \cdot n^p$$

$$Z = \sum_{p=1}^{m} \left(\frac{d}{dt} b^p \right) \cdot n^p. \tag{A2}$$

To discuss the effects of aggregation of the provinces to the whole forest complex we investigate the results for B and Z obtained by using the dynamics of the total biomass, B, and the mean age class distribution N:

$$B = \sum_{p=1}^{m} b^p,$$

$$N = \frac{1}{m} \sum_{p=1}^{m} n^p. \tag{A3}$$

Assuming that the age class distributions in the different provinces are similar, $n^p \approx N$, while the growth dynamics b^p may be completely different, we conclude that there occurs only a slight error in the result for B:

$$B = \sum_{p=1}^{m} b^p \cdot n^p \approx \sum_{p=1}^{m} b^p \cdot N$$

$$= N \sum_{p=1}^{m} b^p = N \cdot B. \tag{A4}$$

The same can easily be shown for the total increment Z and for the situation that the b^p are similar while the n^p are different.

In the case that both the courses of b^p and n^p are varying significantly with p the calibration procedure described in Section 4 yields a vector B which is not simply the sum of the b^p. It has to be interpreted as an effective biomass dynamics accounting for the information losses by averaging the age class distributions.

REFERENCES

Apps, M. J. and Kurz, W. A. 1991. Assessing the rôle of Canadian forests and forest sector activities in the global carbon balance. *World Resource Review* **3**, 333–344.

Apps, M. J., Kurz, W. A., Luxmoore, R. J., Nilsson, L. O., Sedjo, R. A., Schmidt, R., Simpson, L. G. and Vinson, T. S. 1993. Boreal Forests and Tundra. *Water, Air and Soil Pollution* **70**, 39–53.

Birdsey, R. A., Plantinga, A. J. and Heath, L. S. 1993. Past and prospective carbon storage in United States forests. *Forest Ecology and Management* **58**, 33–44.

Birdsey, R. A. 1992. *Carbon storage and accumulation in United States forest ecosystems*. General Technical Report WO-59, US Department of Agriculture: Forest Service.

Burschel, P., Kürsten, E. and Larson, B. C. 1993. Die Rolle von Wald und Forstwirtschaft im Kohlenstoffhaushalt. *Forstliche Forschungsberichte München*, nr. 126.

Cooper, F. C. 1983. Carbon storage in managed forests. *Canadian Journal of Forest Research* **13**, 155–166.

Heath, L. S., Kauppi, P. E., Burschel, P., Gregor, H.-D., Guderian, R., Kohlmaier, G. H., Lorenz, S., Overdieck, D., Scholz, F., Thomasius, H. and Weber, M. 1993. Contribution of temperate forests to the world's carbon budget. *Water, Air and Soil Pollution* **70**, 55–69.

Heath, L. S. and Birdsey, R. A. 1993. Carbon trends of productive temperate forests of the coterminous United States. *Water, Air and Soil Pollution* **70**, 279–293.

Houghton, R. A. 1993. Is carbon accumulating in the northern temperate zone? *Global Biogeochemical Cycles* **7**, 611–617.

Jenny, H. 1980. The soil resource. *Ecological Studies* **37**. Springer, New York.

Kauppi, P. E., Mielikäinen, K. and Kuusela, K. 1992. Biomass and carbon budget of european forests, 1971 to 1990. *Science* **256**, 70–74.

Keeling, C. D. 1973. The carbon dioxide cycle: Reservoir models to depict the exchange of atmospheric carbon dioxide with the oceans and land plants. In: Rasool, S. I., (ed.): *Chemistry of the lower atmosphere*. Plenum Press, New York/London, 251–329.

Keeling, C. D., Bacastow, R. B. and Tans, P. P. 1980. Predicted shift in the $^{13}C/^{12}C$ ratio of atmospheric carbon dioxide. *Geophysical Research Letters* **7**, 505–508.

Kimball, B. A. 1983a. Carbon dioxide and agricultural yield: An assemblage and analysis of 430 prior observations. *Agron. J.* **75**, 779–788.

Kimball, B. A. 1983b. *Carbon dioxide and agricultural yield: An assemblage and analysis of 770 prior observations*. US Water Conservation Laboratory, 71 pp.

Kindermann, J., Lüdeke, M. K. B., Badeck, F.-W., Otto, R. D., Klaudius, A., Häger, Ch., Würth, G., Lang, T., Dönges, S., Habermehl, S. and Kohlmaier, G. H. 1993. Structure of a Global and Seasonal Carbon Exchange Model for the Terrestrial Biosphere. The Frankfurt biosphere model (FBM). *Water, Air and Soil Pollution* **70**, 675–684.

Kohlmaier, G. H., Bröhl, H., Siré, E. O., Plöchl, M. and Revelle, R. 1987. Modelling stimulation of plants and ecosystem response to present levels of excess atmospheric CO_2. *Tellus* **39B**, 155–170.

Kohlmaier, G. H., Lüdeke, M. K. B., Janecek, A., Benderoth, G., Kindermann, J. and Klaudius, A. 1991.

Land biota, source or sink of atmospheric CO_2: Positive and negative feedbacks within a changing climate and land use development. In: *Scientists on GAIA*, S. H. Schneider and P. J. Boston (eds.), MIT Press, Cambridge, 223–239.

Kolchugina, T. P. and Vinson, T. 1993a. Carbon sources and sinks in forest biomes of the former Soviet Union. *Global Biochemical Cycles* **7**, 291–304.

Kolchugina, T. P. and Vinson, T. 1993b. Comparison of two methods to assess the carbon budget of the forest biomes in the former Soviet Union. *Water, Air and Soil Pollution* **70**, 207–221.

Kurz, W. A., Apps, M. J., Webb, T. M. and McNamee, P. J. 1991. The contribution of biomass burning to the carbon budget of the Canadian forest sector: a conceptual model. In: *Global biomass burning*. J. S. Levine (ed.), MIT Press, Cambridge & London: 339–344.

Kurz, W. A., Apps, M. J., Webb, T. M. and McNamee, P. J. 1992. *The carbon budget of the Canadian forest sector: Phase I*. For. Can., Northwest Reg., North. For Cent., Edmonton, Alberta. Inf. Rep. NOR-X-326.

Kurz, W. A. and Apps, M. J. 1993. Contribution of Northern Forests to the Global C Cycle: Canada as a Case Study. *Water, Air and Soil Pollution* **70**, 163–176.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. *Biometrika* **35**, 183–212.

Leslie, P. H. 1948. Some further notes on the use of matrices in population mathematics. *Biometrika* **35**, 213–245.

Lewis, E. G. 1942. On the generation and growth of a population. *Sankhya* **6**, 93–96.

Long, S. P. and Drake, B. G. 1992. Photosynthetic CO_2 assimilation and rising atmospheric CO_2 concentrations. In: *Crop photosynthesis: spatial and temporal determinants*. N. R. Baker, H. Thomas (eds.), Elsevier: 69–103.

Lüdeke, M. K. B., Badeck, F.-W., Otto, R. D., Häger, C., Dönges, S., Kindermann, J., Würth, G., Lang, T., Jäkel, U., Klaudius, A., Ramge, P., Habermehl, S. and Kohlmaier, G. H. 1994a. The Frankfurt Biosphere Model. A global process oriented model for the seasonal and longterm CO_2 exchange between terrestrial ecosystems and the atmosphere. *Climate Research* **4**, 143–166.

Lüdeke, M. K. B., Dönges, S., Otto, R. D., Kindermann, J., Badeck, F.-W., Ramge, P., Jäkel, U. and Kohlmaier, G. H. 1994b. Responses in NPP and carbon stores of the northern biomes to a CO_2-induced climatic change, as evaluated by the Frankfurt biosphere model (FBM). *Tellus* **47B**, 191–205.

Melillo, J. M., Fruci, J. R., Houghton, R. A., Moore, B. III and Skole, D. L. 1988. Land-use change in the Soviet Union between 1850 and 1980: causes of a net release of CO_2 to the atmosphere. *Tellus* **40B**, 116–128.

Perlwitz, J. 1992. Preliminary results of a global SST anomaly experiment with a T42 GCM. *Annales Geophysicae Assembly of the European Geophysical Society*. Edinburgh, Apr. 6–10, 1992.

Rogers, H. H., Runion, G. and Krupa, S. V. 1994. Plant

responses to atmospheric CO_2 enrichment with emphasis on roots and the rhizosphere. *Environ. Pollut.* **83**, 155–189.

Runkle, J. 1985. Disturbance regimes in temperate forests. In: Pickett, S. T. A. and White, P. S. (eds.): *The ecology of natural disturbance and patch dynamics.* Academic Press, San Diego.

Sampson, R. N. 1992. Forestry opportunities in the United States to mitigate the effects of global warming. *Water, Air and Soil Pollution* **64**, 157–182.

Sedjo, R. A. 1992. Temperate forest ecosystems in the global carbon cycle. *Ambio* **21**, 74–277.

Smith, T. M. and Shugart, H. H. 1993. The potential response of global terrestrial storage to a climate change. *Water, Air and Soil Pollution* **70**, 629–642.

Tadaki, Y., Sato, A., Sakurai, S., Takeuchi, I. and Kawahara, T. 1977. Studies on the production structure of forest. XVIII. Structure and primary production in subalpine "Dead Tree Strips" abies forest near Mt. *Asahi. Jap. J. Ecol.* **3**, 83–90.

Tans, P. P., Fung, I. Y. and Takahashi, T. 1990. Observa-tional constraints on the global atmospheric CO_2 budget. *Science* **247**, 1431–1438.

United Nations, 1992. *The forest resources of the temperate zones.* The UN-ECE/FAO 1990 Forest Resource Assessment, vol. 1. General Forest Resource Information, New York.

Usher, M. B. 1966. A matrix approach to the manage-ment of renewable resources, with special reference to selection forests. *J. Appl. Ecol.* **3**, 355–367.

Usher, M. B. 1972. Developments in the Leslie matrix model. In: N. R Jeffers (ed.): *Mathematical models in ecology.* Blackwell, Oxford.

Williams, M. 1992. *Americans and their forests. A histori-cal geography.* Cambridge University Press, ch. 14, pp. 466–494.

Zeide, B. 1993. Analysis of growth equations. *Forest Science* **39**, 594–616.

Ziska, L. H., Chamberlain, S. and Drake, B. G. 1990. Long-term photosynthetic response in single leaves of a C_3 and C_4 salt marsh species grown in elevated atmospheric CO_2 in situ. *Oecologia* **83**, 469–472.