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Modelling stimulation of plants and ecosystem response to present levels of excess atmospheric CO_2

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ABSTRACT

Rising atmospheric CO_2 concentrations (16–26% above the preindustrial value) along with other anthropogenically released nutrients (especially nitrogen as well as phosphate compounds) may already have induced a fertilization effect of the biosphere. A great number of greenhouse and phytotron experiments along with only a few field observations suggest a stimulation of the net primary production which may be expressed by an experimental stimulation factor β between 0.25 and 0.50 on the average. Using these data, a global CO_2 fertilization effect can be calculated, which is supported at present by one open field observation at high altitude pines where an increase in tree ring width is correlated with the atmospheric CO_2 increase. The ecological response to increased biomass production in different ecosystems is still debated; global estimates for long-term storage of carbon range from zero to the order of several Gt C. A 3-compartment model for living biota, litter and humus is discussed for a global 1-biome as well as a global 4-biome aggregation of the land vegetation. Different kinetic models for NPP have been studied, of which the most realistic appeared to be dependent both on atmospheric CO_2 concentration and on standing biomass level. For a global 4-biome model, it was estimated that the annual carbon sequestering in the biota pool corresponds to a net ecosystem production of $NEP_b = 0.7 \pm 0.3$ Gt C/a, in the litter pool to $NEP_l = 0.07 \pm 0.03$ Gt C/a and in the humus pool to $NEP_h = 0.60 \pm 0.35$ Gt C/a, adding up to a present total carbon storage of $NEP = 1.4 \pm 0.7$ Gt C/a, assuming a β value of 0.25 to 0.50.

1. Introduction

The amplitude of the seasonal cycle of atmospheric CO_2 has been rising steadily over the past 25 years (Bacastow et al., 1985) at various stations, averaging $0.75 \pm 0.09\%$ a^{-1} relative to the amplitude in 1958 at Mauna Loa Observatory. Since the amplitude of the seasonal CO_2 cycle in the northern hemisphere is dominated by the uptake and release of CO_2 by the land vegetation, it has been postulated by Keeling (1983), that the observed amplitude increase is correlated to the increased activity of land plants. From the atmospheric data alone it cannot be decided whether this increase in plant activity implies an increase in carbon storage by the land biosphere, or whether it implies only an increased turnover of carbon with no additional storage.

Strain (1985) distinguishes between physiological controls and ecological controls for additional carbon assimilation and carbon sequestering. For a deeper understanding of the global carbon cycle at present time it is not only important to understand the carbon sequestering as an additional sink of atmospheric CO_2 but also the stimulation of plant communities with respect to anthropogenically released trace gases like CO_2, NO_x and ammonia, SO_2 and others, since other dynamic processes like regrowth from forest clearing or other detrimental effects depend on it.

Stimulation of the terrestrial vegetation by

anthropogenically released nutrients may depend on 3 factors.

(1) The additional availability of the nutrient factors at the site of the ecosystem.

(2) The stimulation of photosynthesis and net primary production (NPP) by the combination of the nutrient factors.

(3) The response of the ecosystem to the additional NPP and nutrient load affecting the community respiration and thus the release of CO_2 or the storage of carbon in the living and dead biotic compartments.

As far as CO_2 is concerned, its atmospheric levels have been rising homogeneously worldwide by 16 to 26% relative to the assumed pre-industrial value in 1860 of about 295 ppmV or 270 ppm resp. (Neftel et al., 1985).

According to Strain (1985) an enhanced carbon dioxide level leads to a hierarchy of plant physiological processes of photosynthesis, the secondary processes of photosynthate accumulation, composition and translocation and the tertiary whole plant responses given by growth rate, growth form and reproduction. Net primary production enhancement is one of the physiological responses examined and will be used in the following model analysis.

The response of net primary production to increased level of CO_2 is most conveniently expressed by an experimental factor β which describes a relative increase in net primary production with respect to the relative increase in CO_2 levels. As discussed below β values have been found to depend on the individual plant species or the plant community with a mean response being given by β between 0.25 and 0.5 (Strain and Cure, 1985). As the influence of present CO_2 and nutrient levels are examined, the question of a future global warming and change in precipitation patterns due to a greenhouse effect and their influence on gross primary production and carbon sequestering is not examined in this investigation. The ecological controls of plant stimulation have been described by Strain (1985) by plant/plant interaction in plant communities with one or several species and the plant/animal interactions of the herbivory food chain and in the plant/microbe interaction both within living plants and dead plant material in the litter and in the soil. It is clear that for some plant communities which already have a high leaf area index stimulation of photoproduction can lead to competitive shading unless the allocation of the assimulates is preferentially directed towards the roots and the stem of the plant. Plant/animal and plant/microbe interactions as well as natural fires will be of great importance in the question of additional carbon sequestering. Systems with a short turnover time of carbon like most natural grassland eco-systems and agricultural systems will have a much smaller ability to store additional carbon than those with larger carbon turnover times like forest ecosystems characterized by small ratio of NPP to standing biomass. The turnover time is also important in the question of additional storage of carbon in the litter and soil pool, since soil with its large carbon storage capacity is an important sink for carbon. Distinction of a CO_2 fertilization effect have also been made for systems which are in a quasi steady state, for upgrowing and for continuously harvested systems.

2. Response of annual and perennial plant stands to CO_2 fertilization

A great number of CO_2 stimulation experiments have been performed which show that there is a primary response of plants to elevated CO_2 concentrations: partial stomatal closure, increased photosynthesis per unit leaf area, decreased photorespiration and decreased transpiration (Strain, 1985). The secondary effects of CO_2 stimulation include a change of photosynthate concentration, composition and allocation, increased growth rate, and changed growth form, reproduction and plant water status, often increased water use efficiency, as well as an altered tolerance to gaseous atmospheric pollutants (Gifford, 1979; Strain, 1985; Strain and Cure, 1985). CO_2 studies have been performed at the leaf level in leaf chambers measuring gas exchange, or at the whole plant or plant stand level in controlled environments like phytotrons, portable growth chambers, sunlit controlled environment chambers as well as greenhouses. Very few open field studies are available at present time except the semicontrolled environments of open top cylinders (Rogers, 1983a, b) and one field tracking

chamber study of a tundra community (Oechel and Strain, 1985).

In these studies, short-term (<2 weeks) and long-term (>2 weeks) responses to elevated CO_2 concentrations of mostly annual plants of economic importance (crops, vegetables, weeds) are distinguished. Both the carbon exchange rate (CER) and the net assimilation rate (NAR) are often found higher in the short term response. For the question of carbon sequestering, the ultra-long term response (1 to the order of 100 years) is needed for which field experiments are virtually non-existent, except for the high altitude tree ring measurements on pine species (La Marche et al., 1984), which show a $\simeq 100\%$ increase relative to preindustrial times, and the yield measurements of managed forest ecosystems in Central Europe (Seibt, 1981), which for the period between 1950 and 1975 show a considerable (30–50%) gain relative to the time between 1880 and 1920. However, it is doubtful whether these changes are caused by the CO_2.

Since for the ecosystem model developed in the next chapter only one aggregated level of living biomass (B) is considered, the net primary production (NPP) of a given stand of plants is the most important quantity to be considered in response to CO_2 elevation. The annual production NPP is equal to the annual biomass accumulation plus all litter formation and herbivory consumption. Only if the latter two processes can either be excluded or accounted for, the experimentally determined biomass accumulation equals NPP. With this precaution, in analogy to biomass accumulation or yield measurements, a fertilization factor β is defined:

$$\beta(CO_2) = \frac{\Delta NPP/NPP^0}{\Delta CO_2/CO_2^0}, \qquad (1a)$$

where the upper index ^{0} refers to the standard conditions of CO_2, which is, for instance, the 1980 value of atmospheric CO_2, 340 ppm. β is, in general, a function of the increment ΔCO_2, due to the observed saturation response of NPP with respect to CO_2. Conversely, for a known β, any NPP may be modelled as a function of CO_2, which like atmospheric CO_2, may be a function of time.

$$NPP(CO_2) = NPP^0(1 + \beta \Delta CO_2(t)/CO_2^0), \qquad (1b)$$

where in this case the reference state "0" is the preindustrial atmospheric CO_2 value of 270 or 295 ppm, resp., and where β may be assumed constant, if the change in CO_2 is relatively small, as, e.g., is the case when we consider the rise in atmospheric CO_2 concentrations from the preindustrial to the present time. β values or corresponding quantities have been determined for a great number of annual and a few perennial plant stands at near ambient concentrations up to 5 times the present value.

Table 1 gives an example of 4 selected species at 4 different CO_2 concentrations studied in semicontrolled environments (Rogers et al., 1983a, b). It is seen that β is positive for all cases but one, and that stimulation occurs at all higher concentrations and shows saturation behaviour except for the case of sweet gum seedlings.

Table 1. *Determination of the fertilization factors β and β from CO_2 stimulation experiments in semi-controlled (open-top cylinder) environments*

CO_2/CO_2^0	529/340		718/340		910/340	
Growth factor	β	β	β	β	β	β
Soybean	1.03	1.30	0.92	1.05	0.51	0.87
Corn	0.45	0.57	0.20	0.29	0.15	0.26
Loblolly pine	0.41	0.52	0.26	0.39	0.17	0.29
Sweet gum	−0.19	−0.25	0.06	0.08	0.20	0.35

Data: Rogers et al. (1983a, b).

Originally a β factor was suggested by Bacastow and Keeling (1973), to take into account that the vegetation may sequester part of the CO_2 released by fossil fuels. They modelled the levelling off behaviour of stimulation with increasing CO_2 levels by a logarithmic curve:

$$NPP = NPP^0(1 + \beta \ln(CO_2(t)/CO_2^0)), \qquad (2a)$$

where β was a parameter to give a best balance between the CO_2 of atmosphere, oceans, and land. If this expression is expanded in a Taylor series with respect to CO_2, then we obtain:

$$NPP \simeq NPP^0(1 + \beta \Delta CO_2(t)/CO_2^0 + \cdots) \qquad (2b)$$

such that the parameter β may be identified with the experimentally measured β values at small $\Delta CO_2/CO_2^0$ values. In Table 1, β, as defined in eq. (2a), was also evaluated. It is seen, that also β varies with CO_2 concentration although not as

much as β. Ideally a form of saturation type behaviour is sought, which may be described, e.g., by a Michaelis-Menton type expression (Gates, 1985). We investigated a power expression to express the declining response of NPP to CO_2, which, however, has no saturation plateau:

$$NPP = NPP^0(CO_2(t)/CO_2^0)^{\bar{\beta}} \quad \text{with } 0 < \bar{\beta} \leqq 1 \quad (3a)$$

which when expanded in a Taylor series yields

$$NPP = NPP^0(1 + \bar{\beta}\Delta CO_2(t)/CO_2^0 + \cdots), \quad (3b)$$

which is identical with the logarithmic form ($\bar{\beta} = \beta$) for small CO_2 variations. Both equations (2a), (2b) and (3a), (3b) lack the dynamical feedback between expanded leaf biomass and additional photosynthesis. The CO_2 fertilization experiments show clearly that the relative increase in NAR, net assimilation rate per unit leaf area, i.e., is usually smaller than the relative accumulation in biomass, suggesting a concurrent expansion of the leaf canopy. Dynamically the proportion of leafs to the total biomass B may be modelled by:

$$(B/B^0)^{\delta} \quad \text{where } 0 \leqq \delta < 1,$$

and where B^0 is the reference climax state at standard CO_2 concentration (Kohlmaier, 1981). It is therefore suggestive to model NPP both as a function of B and CO_2 (Keeling, 1973):

$$NPP(B, CO_2) = NPP^0(B/B^0)^{\delta}(CO_2(t)/CO_2^0)^{\bar{\beta}}, \quad (4)$$

where $\bar{\beta}$ is distinguished from β, since part of the measured increase is incorporated in the biomass term. Eq. (4) is of the form, that any given level of B, which may, e.g., be the different stages of the development of the plant from the seedling state to the climax state, is stimulated by the same factor, provided that the CO_2 concentration is the same. Indications from the short term and long term response of some plant stands to CO_2 make it probable, that some plant growth is just accelerated, reaching faster the final development state, which in the extreme case may be identical with the reference state. To model this behaviour within the same formalism we suggest to use alternatively:

$$NPP(B, CO_2) = NPP^0(B/B^0)^{\delta(CO_2(t))}, \quad (5)$$

where

$$\delta(CO_2(t)) = \delta^0 e^{-\beta_\delta \Delta CO_2(t)/CO_2^0}$$

and where $\beta_\delta > 0$ is a characteristic parameter. In the limit of large CO_2 concentrations δ becomes zero such that NPP becomes independent of B.

3. Model structure for plant growth stimulation and ecosystem response to enhanced levels of CO_2 and other nutrient factors

In the following, we consider the response of a three level system B, L, H as shown in Fig. 1 to increased nutrient levels, where B describes the carbon mass of the living biota, L the carbon mass of the litter, and H the carbon mass of the soil humus of a particular ecosystem. The question which will be asked is in which way the levels B, L and H change in response to an enhanced NPP, which will depend both on the level of living biomass B and on an external fertilization function $f(t)$, depending on CO_2 and in general on the whole set of other nutrients like nitrogen, phosporus etc. The input term NPP is counteracted by an output term of living biomass, which is described by the annual litter formation LIT and the respiratory release of CO_2 in the herbivory food chain RES_b. Stochastic events like wildfires or storm damage as well as the planned events of harvest of annual or perennial plant communities shall be described by $F_{ex}(t)$.

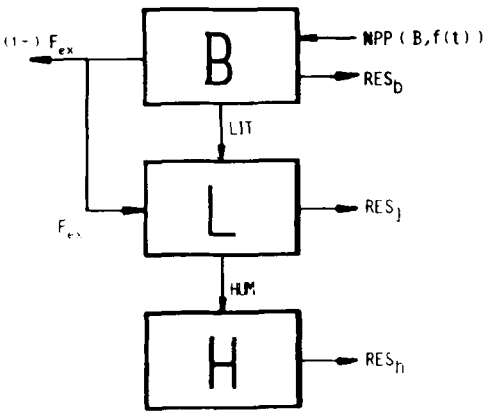

Fig. 1. 3-compartment model for living biota B, litter L and humus H. The respiration fluxes RES_i (i = b, l, h), the litter flux LIT and the humus flux HUM are internally controlled. Net primary production NPP is controlled both by the fertilization function $f(t)$ and by the standing biomass B. F_{ex} are externally controlled fluxes like harvest and natural catastrophic events.

Following these events the growth cycle can start again. With the above definitions the following set of non-autonomous differential equations for B as well as for L and H have the following structure:

$$dB/dt = NPP(B, f(t)) - LIT(B, f(t)) - RES_b(B, f(t)) - F_{ex}(t), \quad (6)$$

$$dL/dt = LIT(B, f(t)) + \kappa F_{ex}(t) - RES_l(L, f(t)) - HUM(L, f(t)), \quad (7)$$

$$dH/dt = HUM(L, f(t)) - RES_h(H, f(t)), \quad (8)$$

with

$$f(t) = (CO_2(t)/CO_2^0, x_j(t)/x_j^0), \quad (9)$$

where x_j/x_j^0 refers to the set of other nutrients with respect to a given reference state. κ is the fraction of the carbon flux that enters the litter system with respect to the total export flux F_{ex}, RES_l is the annual flux of CO_2 from litter, and HUM is the corresponding flux into the humus compartment, both of which are taken to be dependent on the litter level L and, in the most general case, on the fertilization function. For instance, $f(t)$ may influence both the rates and the relative proportions of RES_l and HUM when the quality of litter (i.e., a change of the ratio of C/N) is altered. Finally RES_h is the flux of CO_2 from the humus system which is taken to be dependent on the humus level H and on $f(t)$.

The fertilization function $f(t)$ describes the relative change in nutrient levels with respect to a preindustrial state.

According to the ecological terminology, the annual net ecosystem production, expressed as the annual net accumulation of carbon in the ecosystem, is defined as:

$$NEP(t) = NPP(t) - \sum_{i=b,l,h} RES_i(t) - (1-\kappa)F_{ex}(t), \quad (10)$$

or

$$NEP(t) = \dot{B}(t) + \dot{L}(t) + \dot{H}(t) = NEP_b(t) + NEP_l(t) + NEP_h(t). \quad (11)$$

We note, that $NEP(t)$ may be negative as well, in particular, when $F_{ex}(t)$ is positive; NEP_b, NEP_l and NEP_h are the corresponding net ecosystem productions with respect to the levels B, L and H.

4. Model A: Evaluation of the carbon storage in the living biota assuming a linear litter production and herbivory consumption response to a stimulated production of biomass. Initial considerations

In the following we examine the simple model for carbon storage in the living biota:

$$NPP = NPP^0(1 + \bar{\beta}\Delta CO_2(t)/CO_2^0)$$

as defined in eq. (3b),

$$LIT + RES_b = k_b B \quad (12)$$

and

$$F_{ex} = 0.$$

With the annual biomass change given by the time derivate of B,

$$\dot{B}(t) = NPP^0(1 + \bar{\beta}\Delta CO_2(t)/CO_2^0) - k_b B. \quad (13)$$

The fertilization effect on B within a perennial plant community is most clearly recognized, when NPP is chosen independent of the level of B, and when the litter production and herbivory consumption is assumed to be explicitly independent of fertilization. In the linear dependence of LIT and RES on B, however, an indirect fertilization response is considered, in as much as the increased biomass causes a proportionally higher respiration and litterfall.

If eq. (13) is applied to global considerations, then B represents the global standing biomass of the earth, NPP^0 the total annual net primary production at the reference concentration of CO_2 at preindustrial times, conventionally set at $\leqq 1860$. Ice core studies suggest that CO_2^0 may be as low as 270 ppm (Oeschger and Stauffer, 1986), appreciably lower than the value of 295 ppm used in modelling until recently. To account for this uncertainty the fertilization effect with respect to both reference states will be evaluated. The global NPP has been estimated between 53 and 68 Gt C/a (Whittaker and Likens, 1975; Ajtay et al., 1979; Olson, 1982); we adopt here the value $NPP^0 = 60 \pm 9$ Gt C/a. The living biota have experienced considerable changes since the early settlements with conversions of forests to agricultural lands being perhaps the most important. Although the potential (undisturbed) biomass may have been perhaps as high as 900 Gt C (Olson, 1982), we adopt here a hypothetical refer-

ence state value for B of 600 ± 120 Gt C, which is supposed to represent the present vegetation distribution (e.g., Ajtay et al., 1979) under the preindustrial CO_2 values. Disregarding at first the term F_{ex}, the preindustrial state in eq. (13) is described by a stationary state: $\dot{B} = 0$ in which the original steady state value of B is given by

$$B^0 = \mathrm{NPP}^0/k_b,$$

or vice versa, in which the rate constant k_b may be evaluated from NPP^0 and B^0

$$k_b = \mathrm{NPP}^0/B^0 = 0.1\ \mathrm{a}^{-1},$$

with the characteristic relaxation time

$$\tau_b = 1/k_b = B^0/\mathrm{NPP}^0 = 10\ \mathrm{a}. \qquad (14)$$

In reality, in a multibiome approach, there is a whole spectrum of τ_b-values, with $\tau_b \simeq 1$ a representing the stands of annual vegetation and with $\tau_b > 1$ a being characteristic of perennial plant formations.

The function $\Delta CO_2(t)/CO_2^0$ is well-known for the time period of the Mauna Loa measurements, but not for the reference state. It has increased by approximately 25 ppm in the 25 years from 1957 to 1982, or on the average 1 ppm annually, with $\Delta CO_2/CO_2^0 = 0.16$ ($CO_2^0 = 295$ ppm) and $\Delta CO_2/CO_2^0 = 0.26$ ($CO_2^0 = 270$ ppm). In agreement with many CO_2-fertilization studies, as summarized by Strain and Cure (1985), the model parameter $\overline{\beta}$ will be set equal to the experimental fertilization factor β of 0.25 to 0.5.

Case A.1. Response of the biota to a step function in CO_2

In the following we consider the dynamic response of B to a step function of CO_2

$$\Delta CO_2(t)/CO_2^0 = \begin{cases} 0 & \text{for } t < t_0 \\ \Delta CO_2/CO_2^0 = \text{const.} & \text{for } t > t_0, \end{cases} \qquad (15)$$

which may represent a rough model of the time evolution of atmospheric CO_2 from preindustrial times to present day. The time of switching t_0 is thought to lie in between today and 1860, the exact time is not important. Solving eq. (13) for this case, is given by

$$B(t) = B^0 e^{-k_b(t-t_0)} + B^0(1 + \overline{\beta}\Delta CO_2/CO_2^0) \times (1 - e^{-k_b(t-t_0)}) \quad \text{for } t \geqq t_0, \qquad (16)$$

with the asymptotic limit:

$$B^1 \equiv B(t \to \infty) = B^0(1 + \overline{\beta}\Delta CO_2/CO_2^0). \qquad (17)$$

With the assumed values for $\overline{\beta} = 0.25$ to 0.5 and $\Delta CO_2(1982)/CO_2^0 = 0.16$ to 0.26 the asymptotic value is given

$$B^1 = 624 - 678\ \mathrm{Gt\ C}$$

and

$$B^1 - B^0 = \Delta B = 24 - 78\ \mathrm{Gt\ C}.$$

It should be noted that this stationary state solution is obtained immediately from eq. (13) by setting $\dot{B} = 0$.

As illustrated in Fig. 2, the system will go from an initial steady state "0" to final steady state "1". The relative change in net primary production and standing biomass are equal to each other:

$$(\mathrm{NPP}^1 - \mathrm{NPP}^0)/\mathrm{NPP}^0 = (B^1 - B^0)/B^0 = \overline{\beta}\Delta CO_2/CO_2^0. \qquad (18)$$

Case A.2. Linearized CO_2 increase during the Mauna Loa period for a one-biome model

Knowing the explicit time behaviour of $\Delta CO_2(t)/CO_2^0$, eq. (13) may be solved analytically or numerically (Kohlmaier et al., 1985). A particular simple case arises if the CO_2 increase during the Mauna Loa Period (1958–1982) is represented by a linear function:

$$\Delta CO_2(t)/CO_2^0 = Ft \quad \text{and} \quad \overline{\Delta_a CO_2}/CO_2^0 = F, \qquad (19)$$

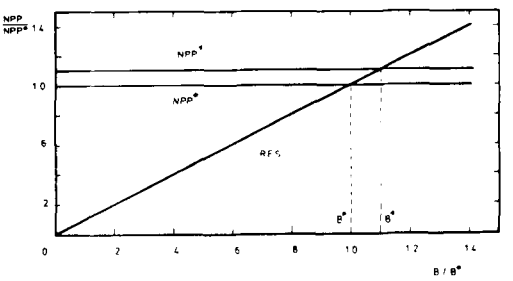

Fig. 2. Net primary production NPP and ecosystem respiration RES versus biomass assuming RES being proportional to B and NPP depending only on atmospheric CO_2 (Case A). Index "0" refers to the initial steady state, while index "1" refers to a final steady state after atmospheric CO_2 has increased by 16%. The fertilization factor is assumed to be $\overline{\beta} = 0.6$.

where $F \simeq 1/300\ a^{-1}$ represents the relative mean annual increase during the Mauna Loa Period, and where for a preindustrial value of CO_2^0 of 295 ppm, $t = 0$ corresponds to 1934, while for $CO_2^0 = 270$ ppm, $t = 0$ corresponds to 1904. The exact solution of eq. (13) is given by:

$$B^{lin}(t) = B^0 + \bar{\beta} F B^0 (t - \tau_b) + \bar{\beta} F B^0 \tau_b e^{-t/\tau_b} - [B^0 - B(0)] e^{-t/\tau_b}, \quad (20)$$

where the first term shows a time delay τ_b and the second and third terms are transient terms.

Differentiating B with respect to time, the net annual storage of carbon in the biota is given by:

$$\dot{B}^{lin}(t) = \bar{\beta} B^0 F (1 - e^{-t/\tau_b}) - \frac{1}{\tau_b} [B^0 - B(0)] e^{-t/\tau_b}, \quad (21)$$

or with the values adopted, the storage in the year 1982 ($t = 48$) is calculated for an original steady state B^0 to be:

$$\dot{B}^{lin}(1982) \simeq (0.25 - 0.5)(1/300)(600)(99/100)\ \text{Gt C/a} = 0.495 - 0.99\ \text{Gt C/a}.$$

Case A.3. Exponential CO_2 increase during the Mauna Loa period for a one-biome model

Similarly the Mauna Loa data of atmospheric CO_2 may be expressed by an exponential function of the form

$$\Delta CO_2(t)/CO_2^0 = C(e^{k_f t} - 1)$$

and (22)

$$\Delta_a CO_2(t)/CO_2^0 = k_f C e^{k_f t},$$

where $t = 0$ for 1860 and the average rate constant k_f between 1958 ($t = 98$) and 1982 ($t = 122$) was adjusted to describe a change from 0.08 to 0.16 ($CO_2^0 = 295$ ppm) or from 0.18 to 0.26 ($CO_2^0 = 270$ ppm). Adjusting the parameters k_f and C to those prescribed values we have:

$k_f = 0.027/a$,

$C = 6.16 * 10^{-3}$ and $CO_2^0 = 295$ ppm,

or

$k_f = 0.0104/a$,

$C = 0.1016$ and $CO_2^0 = 270$ ppm.

With eq. (22), eq. (13) can be integrated to give the following asymptotic relationship:

$$\dot{B}^{exp}(t) \simeq \bar{\beta} B^0 (\Delta_a CO_2(t)/CO_2^0)(1 + k_f/k_b)^{-1}, \quad t \gg 1/k_b, \quad (23)$$

or with $\bar{\beta} = 0.25 - 0.50$ and $B^0 = 600$ Gt C,

$\dot{B}^{exp}(1982) \simeq 0.53 - 1.06$ Gt C/a ($CO_2^0 = 295$ ppm),

$\dot{B}^{exp}(1988) \simeq 0.51 - 1.02$ Gt C/a ($CO_2^0 = 270$ ppm).

We conclude that the model carbon storage in the living biota (NEP_b) is insensitive to the particular time evolution (linear or exponential) of atmospheric CO_2.

We note that for the large-time scale observation of the variable B, the moving steady state (ss) approximation may be useful, provided that $\Delta CO_2(t)$ is a smoothly and slowly varying function. For our system this solution is obtained from eq. (13)

$$\dot{B}(t) = NPP^0(1 + \bar{\beta} \Delta CO_2(t)/CO_2^0) - k_b B,$$

by setting $\dot{B} = 0$ and solving for the moving steady state:

$$B^{ss}(t) = B^0(1 + \bar{\beta} \Delta CO_2(t)/CO_2^0), \quad (24)$$

using the values for B^0, $\bar{\beta}$, and ΔCO_2 as given above

$B^{ss}(1982) = 624 - 678$ Gt C.

The time derivate of B^{ss} is obtained from eq. (24):

$$\dot{B}^{ss} = \bar{\beta} B^0 \Delta_a CO_2(t)/CO_2^0, \quad (25)$$

and can be evaluated to approximate the same annual increase as the special cases already discussed.

5. Nonlinear models for stimulation of net primary production, and their effect on biomass storage

Case B

In the following treatment, we consider the two forms of NPP of eq. (4) and (5), both of which are dependent on $CO_2(t)$ and standing biomass $B(t)$, and discuss their effect on biomass accumu-

lation still retaining a linear response in litter production and herbivory consumption. Model B deals with the following Riccati's differential equation

$$\dot{B}(t) = \mathrm{NPP}^0 G(t)\left(\frac{B}{B^0}\right)^{\delta} - k_b B, \quad 0 \leqslant \delta < 1, \quad (26)$$

with

$$G(t) = \begin{cases} (1 + \bar{\beta}\Delta CO_2(t)/CO_2^0) & \text{or} \quad (26a) \\ (CO_2(t)/CO_2^0)^{\bar{\beta}} & \text{for large } CO_2 \text{ changes.} \quad (26b) \end{cases}$$

We expect that the dynamic behaviour of plant growth is described much better by this equation than, e.g., by NPP being independent of B and we know that in the limiting case $G(t) = 1$ (no additional fertilization) the Richards functions are obtained, which have been very successfully applied in forest dynamics.

In analogy to the cases A.1 to A.3 in Section 4, we give analytical results for the CO_2 step function, linear and exponential case, all of which result from the integrated form of eq. (26).

Case B.1. Response of the non-linear one-biome model to a step function in CO_2

Using the switching function of eq. (15) we obtain the time development of a system original in a climax state B^0,

$$B(t) = B^0\left(1 + \bar{\beta}\frac{\Delta CO_2}{CO_2^0}(1 - e^{-(t - t_0)/\tau_R})\right)^{1/(1-\delta)}, \quad (27)$$

with the relaxation time $\tau_R = \tau_b/(1 - \delta)$.

The asymptotic limit

$$B(t \to \infty) = B^0\left(1 + \bar{\beta}\frac{\Delta CO_2}{CO_2^0}\right)^{1/(1-\delta)} \quad (28)$$

is obtained, which is larger than in the corresponding case A.1, since $1/(1 - \delta) > 1$ for $0 < \delta < 1$, provided $\bar{\beta} = \beta$.

If, however, a CO_2 step experiment is evaluated where the relative change in accumulated biomass is measured, than the relative enhancement of cases A.1 and B.1 should be related to the same experimental quantity β. Expanding eq. (28) in a Taylor series and retaining terms to first order

$$B(t \to \infty) \approx B^0[1 + \bar{\beta}(1/(1 - \delta))(\Delta CO_2/CO_2^0)], \quad (29)$$

and comparing it to eq. (17), it becomes clear that

$$\bar{\beta} = \beta(1 - \delta) = \hat{\beta}(1 - \delta). \quad (30)$$

Case B.2. Response of the non-linear one-biome model to a linearized CO_2 increase during the Mauna Loa period

Solving eq. (26) for the linear CO_2 increase defined in eq. (19) we obtain:

$$B^{\mathrm{lin}}(t) = B^0\left(1 - \left(1 - \left(\frac{B(0)}{B^0}\right)^{1-\delta}\right)e^{-t/\tau_R} + \bar{\beta}F((t - \tau_R) + e^{-t/\tau_R})\right)^{1/(1-\delta)}, \quad (31)$$

which includes the special case of the integrated form of the Richards growth function for $F = 0$ and $B(0) \approx 0$ which shows the sigmoid growth form of a generalized logistic function. Formally case A.2 is also included in this solution, when setting $\delta = 0$. The asymptotic solution for large observation times, where still τ_R may not be neglected with respect to t, is given by:

$$B^{\mathrm{lin}}(t_{\mathrm{large}}) \approx B^0(1 + \bar{\beta}\bar{F}(t - \tau_R))^{1/(1-\delta)}, \quad (32)$$

or when expanded in a Taylor series, retaining terms only to first order

$$B^{\mathrm{lin}}(t_{\mathrm{large}}) \approx B^0(1 + \bar{\beta}\bar{F}(t - \tau_R)), \quad (33)$$

noting that $\bar{\beta}/(1 - \delta) = \bar{\beta}$.

Case B.3. Response of the non-linear one-biome model to an exponential increase in atmospheric CO_2

Solving eq. (26) for the exponential function given in eq. (22) we obtain:

$$B^{\exp}(t) = B^0\left(1 - \left(1 - \left(\frac{B(0)}{B^0}\right)^{1-\delta}\right)e^{-t/\tau_R} + \bar{\beta}C\left(\frac{1}{1 + k_f \cdot \tau_R}(e^{k_f t} - e^{-t/\tau_R}) - 1 + e^{-t/\tau_R}\right)\right)^{1/(1-\delta)}. \quad (34)$$

Again the asymptotic form for large observation times is a useful approximation for the experimental observations:

$$B^{\exp}(t_{\mathrm{large}}) = B^0\left(1 + \bar{\beta}C\left(\frac{e^{k_f \cdot t} - 1}{1 + k_f \cdot \tau_R}\right)\right)^{1/(1-\delta)} = B^0\left(1 + \bar{\beta}\frac{\Delta CO_2(t)/CO_2^0}{1 + k_f \cdot \tau_R}\right)^{1/(1-\delta)}. \quad (35)$$

This expression can be best compared with case A.3 when expanded into a Taylor series, retaining only terms to first order:

$$B^{exp}(t_{large}) \approx B^0\left(1+\overline{\beta}\frac{\Delta CO_2(t)/CO_2^0}{1+k_f\cdot\tau_R}\right), \qquad (36)$$

which is different from case A.3 since τ_b is replaced by τ_R.

The linear and exponential model in the limit for large t may be compared with the corresponding moving stationary state expressions which are simply obtained from eq. (26) and (26a) by setting $\dot{B}(t)=0$

$$B^{ss}(t) = B^0\left(1+\overline{\beta}\frac{\Delta CO_2(t)}{CO_2^0}\right)^{1/(1-\delta)}, \qquad (37a)$$

or when expanded into a Taylor series, retained only first-order terms

$$B^{ss}(t) = B^0\left(1+\overline{\beta}\frac{\Delta CO_2(t)}{CO_2^0}\right), \qquad (37b)$$

which is the same as corresponding case A. Although the asymptotic states in the limit of large observation times are similar in the moving steady state approximation, they differ for the exact solutions, in as much as τ_R replaces τ_b. The time dependence of upgrowing ecosystems is however, considerably different in the cases A and B, as will be shown in the next chapter.

Case C

Up to now, model A as well as model B represented results, where the stimulation of NPP was proportional to $\Delta CO_2/CO_2^0$ independent of the stages of development of the particular plant communities considered and summarized to one biome. In model C, we present the results of an ecosystem model, in which the plant dynamics are described by an extended Richards equation

$$\dot{B} = NPP^0\left(\frac{B}{B^0}\right)^{\delta(CO_2(t))} - k_b B,$$

$$\text{with } 0 \leqslant \delta(CO_2) < 1, \qquad (38a)$$

where now δ is a monotonously decreasing function with increasing CO_2:

$$\delta = \delta_0\, e^{-\beta_\delta \Delta CO_2(t)/CO_2^0} \quad \text{and } \beta_\delta > 0, \qquad (38b)$$

noting that decreasing δ values imply a greater relative net primary production of the younger stages of development. Lacking detailed experimental data this model C is still very rudimentary, choosing ad hoc $\beta_\delta = \ln 2$, which implies for a CO_2 doubling a decrease in the original δ_0-value by a factor of two. δ_0 itself if not very well known, however, it may be related to the regrowth time $\tau_{0.9}$ from the seedling state $B(0)$ to 90% of its climax state (Kohlmaier, 1981) in the implicit form

$$\tau_{0.9} = \frac{1}{1-\delta_0}\,\tau_b\cdot\ln\left(\frac{1-\left(\frac{B(0)}{B^0}\right)^{1-\delta_0}}{1-0.9^{1-\delta_0}}\right), \qquad (39)$$

averaging typically the value $\delta_0 = 0.5$ for forest ecosystems with $\tau_{0.9} = 90$–130 a.

By inspection of eq. (38), it becomes clear that the same climax value B^0 is reached, independent of $\Delta CO_2/CO_2^0$.

Fig. 3 shows the difference between model B and C, assuming for simplicity in both cases a step function increase of $\Delta CO_2/CO_2^0$ by 50%.

Choosing

$$\overline{\beta}\frac{\Delta CO_2}{CO_2^0} = \begin{cases} 0 & \text{for } t < t_0 \\ 0.1 & \text{for } t > t_0, \end{cases}$$

an increase in CO_2 of 50% with a corresponding $\overline{\beta} = 0.2$ may be simulated, or similarly any corresponding product like, e.g., 25% and $\overline{\beta} = 0.4$. With this assumption, model B reduces asymptotically to

$$NPP = \begin{cases} NPP^0(B/B^0)^{0.5} & \text{for } t < t_0 \\ NPP^0(B/B^0)^{0.35} & \text{for } t > t_0. \end{cases}$$

For a global biota one-biome model ($NPP^0 = 60$ Gt C·a^{-1}, $B^0 = 600$ Gt C) and $\delta = 0.5$, this implies a transition from $B^0 = 600$ Gt C to $B^1 = 726$ Gt C, or a corresponding 21% increase.

For model C using $\delta_0 = 0.5$, δ becomes 0.35 for $\Delta CO_2/CO_2^0$, such that

$$NPP = \begin{cases} NPP^0(B/B^0)^{0.5} & \text{for } t < t_0 \\ NPP^0(B/B^0)^{0.35} & \text{for } t > t_0. \end{cases}$$

Because of the larger difference between NPP and $k_b B$, the higher CO_2 case ecosystem grows up faster, in agreement with eq. (39).

6. Periodically harvested ecosystems

Considering the fertilization effect on systems disturbed in a more-or-less periodic manner, eq. (6) needs to be solved for special forms of the

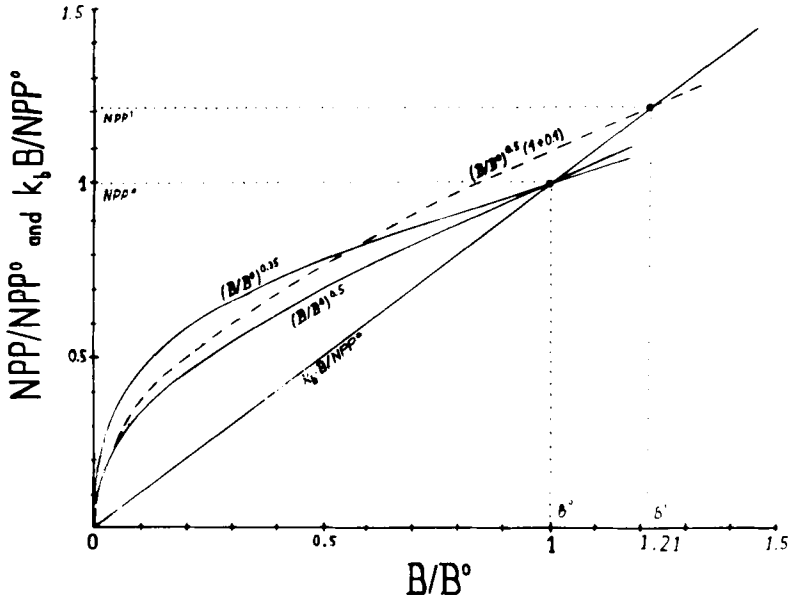

Fig. 3. Illustration of cases B and C in a plot of net primary production versus standing biomass (reduced units). NPP/NPP^0 is increased in case B by a constant factor of 10%. The original steady state B^0 is shifted towards a final steady state B^1, which is 21% higher. For case C, NPP is increased at any level except the climax state by replacing $\delta = 0.5$ with $\delta = 0.35$, again corresponding to a step increase in CO_2 concentration.

output term F_{ex}. For managed forests this output term F_{ex} may be assumed to be strictly periodic, i.e., the forests are always harvested at a given age τ_h. Such a forest ecosystem may be described either by the model case B or C, using the discrete version for the corresponding computer solution:

$$\Delta B(\tau_i)/\Delta\tau = \mathrm{NPP}^0\,\theta(\Delta\tau_0 + \tau_i)(B(\tau_i)/B^0)^{\delta} - k_b B(\tau_i) - F_{ex}(\tau_i) \quad (40a)$$

or

$$\Delta B(\tau_i)/\Delta\tau = \mathrm{NPP}^0(B(\tau_i)/B^0)^{\delta(\Delta\tau_0 + \tau_i)} - k_b B(\tau_i) - F_{ex}(\tau_i), \quad (40b)$$

where τ_i is the age of the plant stand, and $\Delta\tau_0$ is the time difference between the start of a fertilization effect and the start of the regrowing ecosystem from the seedling state. Using discrete constant time steps of size $\Delta\tau \gg \tau_h$, where τ_h is the age of harvesting, and where $\tau_i = i\Delta\tau$, ($i = 0, 1, 2, \ldots, h$), $F_{ex}(\tau_i)$ equals zero for all $\tau_i \neq \tau_h$, whereas at the time of harvest F_{ex} is equal to the total biomass of the system at that time, reduced by a factor $c = 0.999$ a^{-1}, which was introduced to allow for restoring a small amount of biomass necessary to initiate new growth:

$$F_{ex}(\tau_i) = cB(\tau_i)\int_{-\Delta\tau/2}^{\Delta\tau/2}\delta(\tau + \tau_i - \tau_h)\,d\tau, \quad (41)$$

where $\delta(\tau + \tau_i - \tau_h)$ is the well known delta function, not to be confused here with the growth factor δ in eqs. (40a, b). In the actual simulations presented below an ensemble of equal ecosystems but different age classes was chosen to represent a stationary state of harvested systems. To simplify the calculations, it was assumed that each age class was represented with the same weight, such that each year the same number of systems could be harvested, which after harvest returned to the lowest age class. In the unfertilized state such an ensemble of forests is characterized by a persistent total biomass and net ecosystem production in time, because the total harvest is equal to the net ecosystem production of all systems. Introducing fertilization an additional standing biomass as well as an additional NEP arises, which may be expressed as a fraction of the potential biomass B^0 as shown in Fig. 4.

Here, the results of a numeric simulation of two ensembles of ecosystems are shown, one typical for a forest biome (upper set of curves; parameter set: $\mathrm{NPP}^0/B^0 = 0.07$ a^{-1}, $\tau_h = 100$ a,

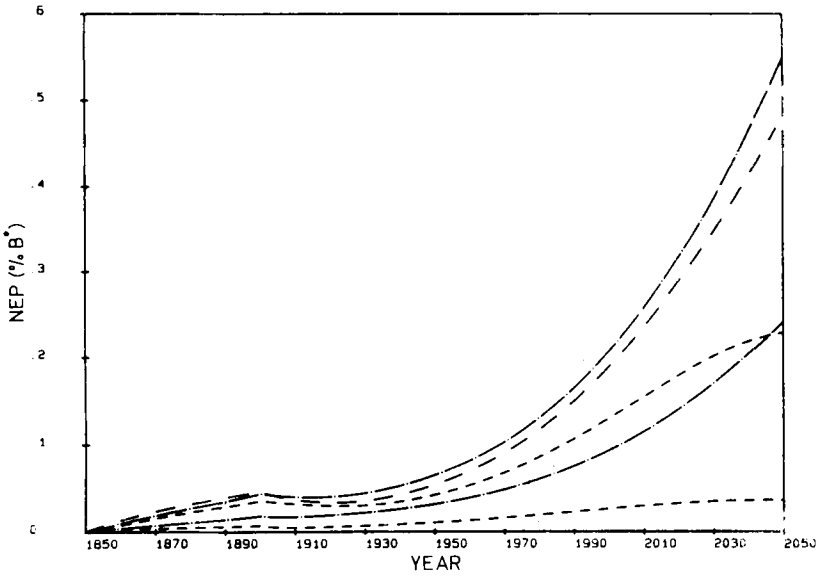

Fig. 4. Increase of net ecosystem production NEP for an ensemble of continuously harvested systems (expressed in relative units of B^0) as a function of time, stimulated by increasing atmospheric CO_2 concentration. The upper set of three curves refer to a forest ecosystem, the lower two curves to a grassland ecosystem. The dash-dotted curves refer to case B, the short-dashed curves to case C and the long-dashed curve to a forest system in its climax state.

$\delta = 0.5$, $\overline{\beta} = 0.25$), the other typical for a grassland biome (lower set of curves; $NPP^0/B^0 = 0.3\ a^{-1}$, $\tau_h = 14$ a, $\delta = 0.2$, $\overline{\beta} = 0.25$), where 'harvest' may occur due to natural events like fires in savannas. Harvest times τ_h were chosen to reach 95% B^0 at time of harvest. The atmospheric CO_2 concentration was calculated using data given by Oeschger and Stauffer (1986) for the time period 1850–1980 and was extrapolated using a modified logistic function. The dash-dotted curves represent the results obtained using eq. (40a) while the dashed curves are obtained using eq. (40b). The upper set of curves includes the total net ecosystem production of a climax forest biome (case B) for comparison (long dashes).

The numerical calculations were started with an ensemble of systems constituting a homogeneous age distribution (100 and 14 age classes for forests and grasslands, resp.) at the reference state for atmospheric CO_2 (1850). For model B (eq. (40a), dash-dotted curves) NEP shows the same qualitative time behaviour as atmospheric CO_2. The peaks around the year 1900 indicate the so-called pioneer-effect caused by extensive forest clearings in the temperate zone. The response of the climax forest and the forest ensemble to increasing CO_2 is quite similar and only slightly higher for the forest ensemble. The response of the forest ensemble in model C (short dashed curves) is significantly reduced showing a saturation behaviour. Accelerated growth leads to a shift in age distribution towards higher age classes with lower CO_2 response; in the limit of a climax system this response will reach zero.

It may be concluded that the climax forest system (case B) does not differ greatly in biomass storage compared to the forest ensemble harvested at constant age. However, a change in harvest practises, e.g., by lowering τ_h, will influence the storage of living biomass.

7. A more realistic estimate of the CO_2 fertilization effect: 4-biome model for agriculture, grasslands, tropical forests and temperate/boreal forests

In the preceding Sections, 3 models (A, B and C) were developed for systems in their near climax state (Sections 4 and 5) and for system ensembles kept in a steady state by harvest (Section 6). For an estimation of the fertilization

effect of carbon sequestering three factors have been shown to be important: First the assumed stimulation of NPP, expressed by $\bar{\beta}$ or the combination of $\bar{\beta}$ and δ; second the system dynamics, depending on the assumed kinetics of carbon input and output into a particular ecosystem i, with the parameters potential climax biomass B_i^0, net primary production NPP_i^0, their ratio, the carbon turnover time τ_b^i and the relaxation time $\tau_R^i = \tau_b^i/(1-\delta)$; third the external forces like changes in the systems environment (CO_2 rise, change of nutrient and water status) and external fluxes F_{ex} caused by humans and natural events, disturbing these systems. Therefore it is necessary to disaggregate the biota into vegetation units, which have distinct properties with respect to the factors mentioned above.

As a minimum set, 4 biomes were chosen, as shown in Fig. 5, with B_i^0, NPP_i^0 and τ_b^i derived from Ajtay et al. (1979), rounding numbers for simplicity. Each biome is certainly characterized by a specific mean CO_2 fertilization factor $\bar{\beta}_i$, however, very little experimental evidence is available to evaluate these factors. Therefore we prefer at this time to use the same $\bar{\beta}$ value of 0.25–0.50 for all biomes.

In the following, we consider the more realistic case of exponentially increasing atmospheric CO_2 concentrations, characterized by $k_f = 2.7\%/a$, and a relative cumulated increase $\Delta CO_2(1982)/CO_2^0 = 0.16$ ($CO_2^0 = 295$ ppm) and $k_f = 1.04\%/a$ and a relative cumulated increase $\Delta CO_2(1982)/CO_2^0 = 0.26$ ($CO_2^0 = 270$ ppm).

We calculate $\Delta B_i(1982)$ and $\dot{B}_i(1982)$ first in the near climax state ($F_{ex} = 0$) in the moving steady state approximation

$$B_i^{ss}(t) = B_i^0(1 + \bar{\beta}(1-\delta)\Delta CO_2(t)/CO_2^0)^{1/(1-\delta)} \quad (42a)$$

$$\dot{B}_i^{ss}(t) \approx B_i^0 \bar{\beta} \Delta_a CO_2(t)/CO_2^0, \quad (42b)$$

and in the asymptotic form of the exact solutions for models A ($\delta = 0$) and B ($\delta \neq 0$)

$$B_i(t_{large}) \approx B_i^0 \left(1 + \frac{\bar{\beta}(1-\delta)\Delta CO_2/CO_2^0}{1 + k_f \tau_b/(1-\delta)} \right)^{1/(1-\delta)}, \quad (43a)$$

$$\dot{B}_i(t_{large}) \approx \frac{B_i^0 \bar{\beta} \Delta_a CO_2/CO_2^0}{1 + k_f \tau_b/(1-\delta)}. \quad (43b)$$

From Table 2 we note that the steady state approximation is best for short carbon turnover times τ_b, but becomes inadequate for $\tau_b \gtrsim 10$ a, as e.g., for forests, which sequester less carbon than calculated by the stationary state assumption. Furthermore it is seen that the aggregated one-biome model with $B^0 = 600$ Gt C and $\tau_b = 10$ a leads to a total increase which is 15% higher than the disaggregated multibiome model.

In the above multibiome model, we have not considered harvest or catastrophic natural events which remove or destroy part of the biomass. In the agricultural sector, the annual cropping removes a greater part of the accumulated biomass each year, such that this sector cannot contribute significantly to the long-term storage of carbon in living biomass. Since this sector contributes only about 1% of the global biomass, its contribution is insignificant anyway.

Fire, drought, heavy storms or frost are natural catastrophic events which may affect ecosystems or biomes from time to time, such that they may not reach or stay in the respective climax states. However, under the assumption that the frequency of these events has not been changed significantly by CO_2, the relative change still should be proportional to the corresponding steady state biomass. The relative fertilization may be equal or larger for upgrowing systems, as was shown in Section 6.

Permanent land use changes, as they occur at present times in the tropics by forest clearings for shifting cultivation, permanent agriculture and timber harvest are of great significance for the carbon balance. Lanly (1982) has estimated the present deforestation to amount to 11.3 million ha annually. This may cause an annual flux of CO_2 to the atmosphere between 1 and 2 Gt C (Kohlmaier et al., 1985, Houghton et al., 1983).

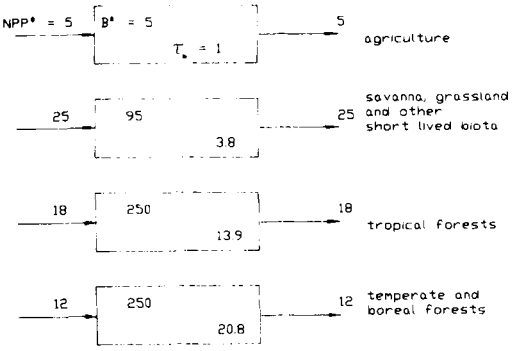

Fig. 5. A 4-biome model for the land vegetation with characteristic values of NPP^0, B^0 and τ_b in their initial climax state.

Table 2. *Accumulated biomass, $\Delta B_i(1982)$ in [Gt C] and annual biomass increase $\dot{B}_i(1982)$ [Gt C·a^{-1}] for 4 biomes following an exponential CO_2 rise*

		Steady state approximation		Case A $\delta = 0$		Case B $\delta_1 = \delta_2 = 0.2$; $\delta_3 = \delta_4 = 0.5$	
		$\dot{B}_i$	ΔB_i	$\dot{B}_i$	ΔB_i	$\dot{B}_i$	ΔB_i
Agriculture	I	0.006–0.012	0.2–0.4	0.006–0.012	0.19–0.39	0.006–0.012	0.19–0.39
	II	0.005–0.01	0.3–0.65	0.005–0.012	0.32–0.64	0.005–0.012	0.32–0.65
Grasslands	I	0.11–0.22	3.8–7.6	0.10–0.20	3.5–6.9	0.10–0.20	3.4–6.8
	II	0.09–0.18	6.2–12.4	0.09–0.18	5.9–11.9	0.09–0.18	5.9–11.9
Tropical forests	I	0.28–0.56	10–20	0.20–0.41	7.3–14.5	0.16–0.32	5.7–11.5
	II	0.23–0.47	16.3–32.5	0.20–0.41	14.2–28.4	0.18–0.36	12.8–25.8
Temperate/boreal forests	I	0.28–0.56	10–20	0.18–0.36	6.4–12.8	0.13–0.26	4.7–9.5
	II	0.23–0.47	16.3–32.5	0.19–0.39	13.6–26.7	0.16–0.33	11.5–23.2
Sum of 4 biomes	I	0.67–1.34	24–48	0.49–0.98	17.4–34.6	0.40–0.79	14.8–28.2
	II	0.56–1.13	39–78	0.49–0.99	34.0–67.6	0.44–0.88	30.5–61.6
One-biome model	I	0.67–1.34	24–48	0.53–1.05	18.9–37.8	0.44–0.87	15.7–31.6
	II	0.56–1.13	39–78	0.51–1.01	35.3–70.7	0.46–0.92	32.7–66.3

I $CO_2^0 = 295$ ppm and $k_f = 0.027$; $\Delta_a CO_2(1982)/CO_2^0 = 0.0037$, $\Delta CO_2(1982)/CO_2^0 = 0.16$.
II $CO_2^0 = 270$ ppm and $k_f = 0.0104$; $\Delta_a CO_2(1982)/CO_2^0 = 0.0045$, $\Delta CO_2(1982)/CO_2^0 = 0.26$.

The flux from the atmosphere to the biota caused by CO_2 fertilization, can only partially counterbalance the clearing flux. Using eq. (43b), an amount of carbon sequestering is calculated, which lies well below the release of CO_2 from deforestation:

$\dot{B}_{tf}(1982) \approx 0.16$–$0.41$ Gt C/a.

Periodic clearing in managed forests of the temperate zone will also influence the additional carbon storage in this sector. Though there is an indication that the total biomass of temperate zone forests has been increasing within the last forty years (Armentano and Hett, 1979), this effect is not yet established. Forest dieback caused by air pollution, as observed in Central Europe within the last years, may even reverse this trend in the future.

8. Response of soil and litter system to increased CO_2

For small increase levels of atmospheric CO_2, as they have occurred up to now, we expect that the increase in plant production will lead to increased litter availability and in the following to increased humus production as shown in Fig. 1.

Starting with the system of coupled differential eqs. (6–8) we define (with $F_{ex} = 0$) the following fractionations for the assumed linear decay terms:

$$\mathrm{LIT} = \rho_b k_b B, \tag{44a}$$

$$\mathrm{RES_b} = (1 - \rho_b) k_b B, \tag{44b}$$

$$\mathrm{HUM} = \rho_l k_l L, \tag{44c}$$

$$\mathrm{RES_l} = (1 - \rho_l) k_l L, \tag{44d}$$

$$\mathrm{RES_h} = k_h H. \tag{44e}$$

For a global one biome model, the fractionation coefficients ρ_b may be chosen to vary between 0.8 and 0.9, ρ_l to vary widely between 0.05 and 0.30. The litter pool L has a very short carbon turnover time $\tau_l = 1/k_l$, which varies approximately between 0.5 (tropical systems) and five years (temperate/boreal systems). The global standing litter biomass at reference conditions is estimated to be $L^0 = 60$ Gt C, (Schlesinger, 1984) in accordance with a weighted mean turnover

time $\tau = 1.2$ a. Since $B(t)$ is dynamically separated in our model system, eqs. (7) and (8) can be expressed as a function of B.

$$\dot{L} = \rho_b k_b B(t) - k_l L, \tag{45}$$

$$\dot{H} = \rho_l k_l L - k_h H. \tag{46}$$

Since the considered observation times are much larger than τ_l, we use the moving steady state approximation for eq. (45) to give:

$$L^{ss}(t) = (\rho_b k_b / k_l) B(t). \tag{47a}$$

The annual change of L in the stationary state approximation is given

$$\dot{L}^{ss}(t) = (\rho_b k_b / k_l) \dot{B} = (L^0/B^0) \dot{B}. \tag{47b}$$

Using the suggested data set: $L^0/B^0 = 0.1$ the annual change in litter is given by:

$$\dot{L}^{ss}(1982) = 0.1, \dot{B}(1982) = 0.04\text{–}0.10 \text{ Gt C a}^{-1}.$$

Inserting eq. (47a) into eq. (46), gives

$$\dot{H} = \rho k_b B(t) - k_h H, \tag{48}$$

where $\rho \equiv \rho_l \rho_b \simeq 0.15$. The initial unperturbed climax state of humus H^0 is given by:

$$H(0) = H^0 \equiv \rho k_b B^0 / k_h = \rho \text{NPP}^0 / k_h. \tag{49}$$

The humus pool has been estimated by Schlesinger (1984) to be approximately 1500 Gt C, which we adopt here as reference state. The turnover time of carbon is again very variable; using eq. (49)

$$k_h = \rho \text{NPP}^0 / H^0 \simeq 0.15 \bullet 60/1500 = 6 * 10^{-3} \text{ a}^{-1}.$$

Eq. (48) can be formally integrated to give:

$$H(t) = H^0 \{ e^{-k_h t} + k_h \int_0^t e^{-k_h (t-t')} (B(t')/B^0) \, dt' \}. \tag{50}$$

The first term is an exponential decay term which is counterbalanced by the driving term of humus formation. The annual increase in humus is derived from eq. (50):

$$\dot{H}(t) = H^0 k_h \int_0^t e^{-k_h (t-t')} (\dot{B}(t')/B^0) \, dt'. \tag{51}$$

An upper limit is derived from eq. (51) by setting the exponential function under the integral equal to one:

$$\dot{H} \leqq H^0 k_h \Delta B(t)/B^0 = k_b \rho \Delta B(t). \tag{52}$$

With the present estimate of $\Delta B(t)$ given in Table 2,

$$\Delta B(1982) \simeq 15\text{–}68 \text{ Gt C}$$

or

$$\overline{\Delta B}(1982) \simeq 42 \text{ Gt C},$$

and with $\rho = 0.15$ and $k_b = 0.1$ a^{-1}:

$$\overline{\dot{H}} \leqq 0.63 \text{ Gt C a}^{-1}.$$

As in the previous chapter we explore the humus response to a linearized CO_2 increase during the Mauna Loa period and to an exponential atmospheric CO_2 increase. Inserting the asymptotic solutions of $B(t)$, eqs. (42a, 42b), into eq. (50) we obtain for the linear CO_2 increase:

$$H^{lin}(t) \simeq H^0 \left\{ 1 + \overline{\beta} F \left[t - \frac{1}{k_h} (1 - e^{-k_h t}) \right] \right\}, \tag{53}$$

$$\dot{H}^{lin}(t) \simeq H^0 \overline{\beta} F (1 - e^{-k_h t}), \tag{54}$$

where t starts in 1934 ($CO_2^0 = 295$ ppm) or in 1904 ($CO_2^0 = 270$ ppm). If eq. (54) is evaluated, we find:

$$\dot{H}^{lin}(1982) \approx 0.31\text{–}0.93 \text{ Gt C a}^{-1}.$$

Similarly the exponential CO_2 increase within large observation times is given by:

$$H^{exp}(t) \simeq H^0 \left(1 + \frac{k_h}{k_h + k_f} \frac{\overline{\beta} C e^{k_f t}}{1 + k_f \tau_R} \right), \tag{55}$$

$$\dot{H}^{exp}(t) \simeq H^0 \frac{k_h k_f}{k_h + k_f} \frac{\overline{\beta} C e^{k_f t}}{1 + k_f \tau_R}. \tag{56}$$

This formula can again be evaluated, the resulting flux is:

$$\dot{H}^{exp}(1982) = 0.24\text{–}0.88 \text{ Gt C a}^{-1}.$$

Within the above mentioned assumptions the annual net ecosystem production with respect to the litter/soil system is given by:

$$\text{NEP}_l = 0.07 \pm 0.03 \text{ Gt C a}^{-1},$$

$$\text{NEP}_h = 0.60 \pm 0.35 \text{ Gt C a}^{-1},$$

where the error bars are perhaps even larger since the fractionation and the rate constants, as well as the levels of L and H, have a considerable range of uncertainty. Compared to the annual storage in living biota the litter/soil storage at present times is still a little smaller, but in the long time limit the humus pool will have the highest potential storage capacity unless other degrading soil processes take place.

9. Conclusions

A large number of CO_2 stimulation experiments with selected plant communities in controlled or semicontrolled environments suggest that the annual production and biomass accumulation is increased at elevated CO_2 concentrations, expressed by an experimental fertilization factor β of 0.25 to 0.50, which describes the relative increase in biomass in relation to the relative increase in CO_2 with respect to present atmospheric CO_2 concentrations.

If CO_2 stimulation of net primary production is a real effect in natural ecosystems as well, the dynamics of the presented models suggest that there may be an increase in standing biomass as well as in litter and humus carbon, which, however, is much smaller than the potential carbon accumulation when no ecosystem response is considered. Using three models (A, B and C) characterized by different ultra-long term responses of NPP to excess atmospheric CO_2, the annual and cumulative storage of carbon has been calculated for a 1-biome model ($B^0 = 600$ Gt C, $NPP^0 = 60$ Gt C/a) as well as for a 4-biome model distinguishing agriculture, grasslands, tropical and temperate/boreal forests on a global scale. Choosing $\beta = 0.25$ to 0.50, carbon annually sequestered in living biomass is given by $NEP_b = 0.7 \pm 0.3$ Gt C/a, using the 4-biome model, while the 1-biome model gives about 10% higher values. The global excess biomass in 1982 accumualted due to a CO_2 increase relative to the preindustrial value of 270–295 ppm has been calculated for the 4-biome model to range from 15 to 68 Gt C.

The global litter pool amounts to only 10% of the global standing biomass and is characterized by a correspondingly low annual accumulation of $NEP_l = 0.07 \pm 0.03$ Gt C/a. On the other hand, the global humus pool with a carbon mass of about 1500 Gt C and a long carbon turnover time is the greatest potential sink for additional plant production. We have calculated its annual change in 1982 to be $NEP_h = 0.60 \pm 0.35$ Gt C/a, i.e., an amount comparable to the annual storage in living biomass.

In summary, we can estimate the annual net ecosystem production at present to be NEP(1982) $= 1.4 \pm 0.7$ Gt C/a, using a fertilization factor β of 0.25 to 0.50 and assuming that the model B is best suited to describe a CO_2 fertilization effect.

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