SIMULATION OF ECOSYSTEM RESPONSE TO RISING CO₂, WITH SPECIAL ATTENTION TO INTERFACING WITH THE ATMOSPHERE

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How to approach the problem

The response of ecosystems to rising CO₂ may show a myriad of characteristics (Strain and Bazzaz, 1983), but only those aspects that concern interaction with the atmosphere will be considered here. The first aspect is that of primary productivity, because it provides the substrate for all other ecosystem components, and also because it may affect the carbon cycle. The second aspect is that of the physical interface characteristics, which determine energy exchange and evapotranspiration, by which vegetation affects the lower layer of the atmosphere. The third aspect is that of the geographical distribution. Interspecies relationships such as food-web relations, species composition, species behavior, competitive balances, etc. will not be considered here. They are of a second order character, and will follow the changes of primary productivity.

The time scales of these aspects are different. Energy exchange is usually considered as a diurnal process, for which vegetation characteristics such as leaf area are important. On the next time scale, primary productivity is expressed on an annual basis, and finally, natural geographical distribution of plant species only changes on time scales of decades. Processes on the shorter time scales operate on the background provided by the longer time scales. In this way CO₂, which is rising on a decadal time scale, will change the background of fast processes such as stomatal regulation and carbon uptake.

Primary productivity and biomass

A review of estimates of primary productivity in different ecosystems was given in Lange \underline{et} al. (1983). The dazzling amount of data from such studies can be put into a common framework by simulation modeling, which facilitates analysis of data and potential effects of increasing CO2. Some smoothing and streamlining is inevitable. To give an example of the method, a scheme (Fig. 1) is presented for the carbon flows in the modeling process in a temperate forest on an annual basis. This scheme shows a steady-state situation, in which the flows to the biomass components compensate for the losses through respiration, death and decay. We start with Gross Primary Production of a closed stand, (GPPclosed), here estimated as 2600 g dry matter m^{-2} yr $^{-1}$. This value was chosen from field observations, such as those reported in Lange \underline{et} al., or by Mohren et al. (1984). On the basis of available radiation alone much greater

GPP is possible, but nutrients and/or water limit growth to a large extent in natural ecosystems.

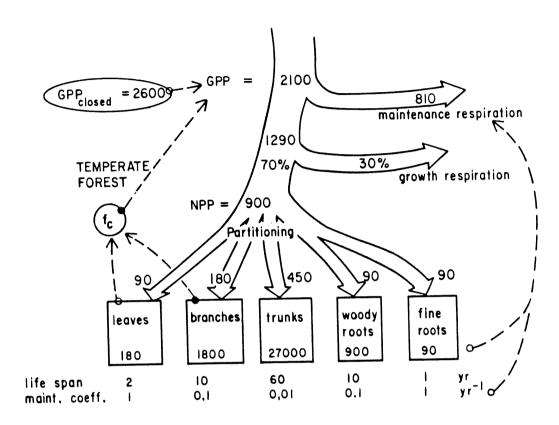


Figure 1. Flows of dry matter in g m^{-2} yr $^{-1}$, and the corresponding biomass in five major organs in a steady-state situation.

A first reduction in dry matter is applied to account for incomplete soil cover. The value of soil cover f_{C} is derived from leaf weight L, modified by clustering around branches:

$$f_c = f_B (1 - \exp(-L/(L_c * f_B)))$$
 (1a)

and

$$f_B = 1 - \exp(-B/B_C) \tag{1b}$$

where fB = branch clustering factor

L_C = leaf weight coefficient

B = branch weight

Bc = branch weight coefficient

When L_c is set at 90 and B_c at 800 g m⁻², f_c equals 0.81 and GPP is reduced to 2100 g m⁻² yr⁻¹:

$$GPP = f_{c} GPP_{closed}$$
 (2)

Total respiration is composed of growth respiration and maintenance respiration. Maintenance respiration, which is subtracted first, is calculated as the sum of the annual maintenance requirement of leaves and of fine roots (100% of their weight), branches and woody roots (10% of their weight), and of trunks (1% of their weight), leading to 810 g m 2 yr $^{-1}$ in the steady-state case:

$$M = \sum_{k=1}^{n} m_k O_k \tag{3}$$

where M = total annual maintenance requirement

 m_k = specific annual maintenance requirement of organ k

Ok = organ weight per ground area, such as leaf, branch or trunk weight

Growth respiration is expressed by a reduction of the remaining flow. The reduction factor is dependent on the chemical composition of the material formed (Penning de Vries, 1975). In the average situation, where the dry matter formed has a carbon content of 46%, a reduction to $70\%_1$ of the available carbohydrate flow may be used, so that only 900 g m⁻² yr⁻¹ remains as actual Net Primary Production (NPP):

$$NPP = 0.7 (GPP - M) \tag{4}$$

This flux is distributed according to a partitioning coefficient P_k over leaves (10%), branches (20%), trunks (50%), woody roots (10%), and fine roots (10%). With average lifetimes τ_k of 2, 10, 60, 10 and 1 yr respectively, the steady-state weights of these organs reach 180, 1800, 27,000, 900 and 90 g m⁻², respectively:

$$O_{k} = P_{k} \tau_{k} NPP \tag{5}$$

Schemes similar to this one for a temperate forest, can be set up for other ecosystems. The resulting allocation of the GPP shows a considerable shift towards maintenance requirements in the tropical forest, reaching as much as 70%. In grassland, on the other hand, the maintenance requirement is much less, primarily because of the much lower biomass accumulation.

The dynamics of this system become important after disruptions such as logging or fire and Eq. 5 must be replaced by its dynamic equivalent:

$$\frac{dO_k}{dt} = P_k NPP - O_k/\tau_k \tag{6}$$

A rather arbitrary guess for the initial biomass is $400~\rm g~m^{-2}$, which corresponds to a soil cover of about 10%. For a forest, the annual relative growth rate then equals about $0.35~\rm yr^{-1}$, so that a tenfold increase is reached after $10~\rm years$. From then on, the positive feedback with leaf area has disappeared and a negative exponential is followed which approaches the asymptote of the steady-state described above. In models with a decadal time scale, the exponential start phase can be neglected, and an immediate transition can be made to the asymptotic negative exponential (Goudriaan and Ketner, 1984).

The driving variable of the system is GPP. Other system parameters such as longevities may also change with increased CO_2 , but we know very little about that. Based on a detailed model, in which the physiology of the CO_2 effects is incorporated (Goudriaan et al., 1984), the use of a logarithmic response of GPP to CO_2 is permitted on an annual time scale. It should be noted that this logarithmic response has no physiological basis in itself, but that it is derived from results of the detailed physiological CO_2 model. The relative ecosystem sensitivity to CO_2 (sometimes ambiguously called the "biotic growth factor") around the present CO_2 content of 350 ppmv, may reach a value of up to O.7. Under nutrient limitations such as are especially predominant in tropical ecosystems, the response to CO_2 is much less. Water shortage will not diminish the CO_2 effect, but on the contrary, it will probably enhance it (Gifford, 1979).

In temperate zones, the climatic effect of CO₂ will almost certainly mean a longer growing season, and so GPP will increase once more. The size of this effect can be estimated by considering the annual temperatures. An increase of about 2°C will mean a growing season of 30 to 40 days longer, corresponding to an increase in GPP of about 20%. Although initially the full effect may not show up due to inadequate ontogenetic adaptation of species, especially of the woody ones, in the long run it will certainly express itself.

The flow of dry matter through biomass will continue through litter-fall, decay and humus formation. By adding boxes for litter, humus and stabilized carbon, the size of these ecosystem components can be estimated as well (Goudriaan and Ketner, 1984). These compartments are huge and exhibit large spatial variability. Therefore, it is hard to determine their rates of change by direct observations.

Some interface characteristics

Detailed models for the micrometeorology of crop plants and for forests have been developed and validated (Goudriaan, 1977; Halldin, 1979). It is possible to replace the vertically distributed models by a one-layered "big leaf" model, provided the descriptive interface characteristics are correctly adapted and interpreted (Chen, 1984; Goudriaan et al., 1984). In such models the most important characteristics for the energy balance of the vegetation surface are the reflection coefficient, interception reservoir, roughness length leading to boundary layer resistance, and canopy resistance. A separation between plant transpiration and soil evaporation is useful, but requires soil cover or leaf area index. Typical values for these characteristics are given in Table 1.

Table 1. Typical values for some physical characteristics of the ecosystematmosphere interface.

	Tropical Forest	Temperate Forest	Tropical Grassland	Grassland and Tundra	Agric. Land	Human Area	Desert
Plant type	C3	C3	C 4	C3	C3/C4	C3	C4
Reflection coefficient with snow	0.2	0.15 0.4-0.6	0.25	0.25 0.6-0.8	0.25 0.6-0.8	0.2 0.4-0.8	0.2
Interception reservoir(mm		0.5	0.5	0.5	0.5	0.1	0.1
Roughness length(m)	1	1	0.1	0.1	0.1	1	0.1
Baseline canopy resistance(s m ⁻¹) to be divide by soil cover) 30 ed	80 0 to 1	80 1	50 0 to 1	50 0 to 1	50 0.25	100 0.05
Rooting dept	h(m) 4	2	1	1	.1	1	1

The roughness length can be converted into a boundary layer resistance for the 10 meters above the vegetation, by equations such as given by Thom and Oliver (1977). When the entire mixed boundary layer is included (Driedonks, 1982; McNaughton and Spriggs, 1985), the simulation results are much more generalized and will also account for the feedback of the energy balance on the atmospheric weather conditions.

The baseline canopy resistance must still be modified to account for incomplete soil cover, which varies throughout the season in the temperate forest and in agricultural land. In most climatic zones, monthly values are probably sufficiently accurate.

The next reduction in canopy conductance is due to depletion of soil water. Maximum available soil water is about 25% of the rooted soil volume. About half of the maximum amount can be depleted without any effect on canopy conductance, but between this half-way point and wilting point a linear reduction in canopy conductance can be assumed.

In forests, a deeper profile of soil is available for rooting than in other vegetation types, and so forests are better able to continue transpiring in dry periods. In simulations, the soil water content must be kept track of by updating the amounts of precipitation, transpiration and runoff. A single soil

layer may be sufficient for a rough description, but a stratification into a few layers is advisable.

It is also necessary to keep track of water intercepted by the canopy, because it enhances the rate of return of precipitated water to the atmosphere. Intercepted water is a much faster state variable than soil water, and may appear and disappear within a few hours.

Geographical distribution

The distribution of different types of ecosystems on earth is primarily governed by climate. The Holdridge classification system uses climate variables to map vegetation. This system is useful for an analysis of the effect of climatic change (Shugart et al., 1985; Warrick et al., 1985). However, it is difficult to estimate the path of change, and its dependence on local circumstances. The temperature increase will almost certainly be accompanied by changes in precipitation, humidity and radiation, along with a large effect on the potential evapotranspiration ratio.

This ratio may also be affected by the increase of CO2 through the reduction of stomatal aperture. With a doubling of atmospheric CO2, the potential evapotranspiration ratio may be effectively reduced by a factor up to 30%. Although this effect will be moderated by a negative feedback through atmospheric weather conditions, still the vegetation should be less water-stressed, even without any change in precipitation or evaporative demand. Especially in presently arid or semi-arid regions, where the vegetation cover is small, the atmospheric feedback is very weak, so that the stomatal effects of CO2 will be fully expressed. Both the increase in the precipitation/transpiration ratio and the photosynthetic effect of CO₂ will lead to an increased value of GPP_{closed}. Equations 1-5 imply some critical value for GPP where a transition from grassland to forest occurs. This critical value can be represented by a combination of clustering of leaves around branches, a fixed ratio between productive leaves and other tissue such as branches and trunks and the maintenance requirement that is connected with it. In the forest example, this limit is situated at about 1550 g $\rm m^{-2}$ (Fig. 2). Of course, in reality, this sharp boundary is blurred by ecological adaptations such as lower partitioning to the woody components, which result in more shrub-like vegetation. Where the geographical gradient of the climatologically determined GPP_{closed} crosses this threshold level, a natural boundary exists between grassland and forested land. Therefore an increase in $\mathsf{GPP}_{\mathsf{closed}}$ due to climatic change or due to rising CO_2 will result in transitions from grassland or tundra vegetation to forested land. In the Holdridge diagram, this effect will probably show up as a leftward trend in the ecosystem classification.

Most of the effects of rising CO₂ discussed above will be overshadowed by human activities, such as agriculture, logging, pollution, cattle-grazing, urbanization, etc., so that they will hardly be detected directly. In the long run, however, the background to such human activities and the response of natural vegetation to the anthropogenic changes will change due to CO₂. The background global trend will be towards more vegetation cover and more biomass, although, regionally, different changes may occur.

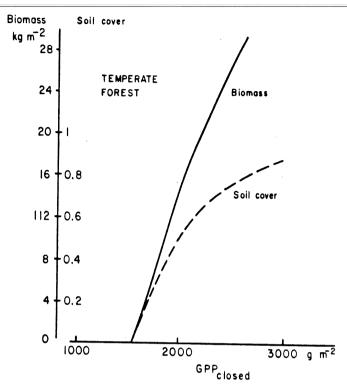


Figure 2. Forest biomass and soil cover in the steady state situation, simulated with Eqns. 1-5 for a temperate forest.

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