

STRUCTURE OF A GLOBAL AND SEASONAL CARBON EXCHANGE MODEL FOR THE TERRESTRIAL BIOSPHERE

THE FRANKFURT BIOSPHERE MODEL (FBM)

J. KINDERMANN, M. K. B. LÜDEKE, F.-W. BADECK, R. D. OTTO, A. KLAUDIUS,
CH. HÄGER, G. WÜRTH, T. LANG, S. DÖNGES, S. HABERMEHL,
AND G. H. KOHLMAIER

*Institut für Physikalische und Theoretische Chemie, J. W. Goethe-Universität
Frankfurt/M., Niederurseler Hang, D-6000 Frankfurt 50, Germany*

Abstract: Carbon exchange fluxes of terrestrial ecosystems are expected to depend on the internal dynamics of C stocks in vegetation and soils, on nutrient availability, and on the local climatic conditions / weather. The model structure which we present focuses on the internal dynamics in the living vegetation. The mathematical description is derived from two basic hypotheses: 1) vegetation tends to maximize photosynthesizing tissue, and 2) the relative amounts of C in pools with relatively short and long turnover times are given by allometric relations. The model can be calibrated for any vegetation type in a typical climate under the condition to meet mean ecological estimates of e.g. biomass and NPP. For C cycle modeling the FBM yields the net CO₂ flux between the grid elements and the atmosphere in a daily resolution. It is demonstrated that simulations with a 1°x1° spatial resolution reproduce the response of the time course of C fluxes to local climates.

1. Introduction

A full understanding of the importance of terrestrial biota within the global C cycle has not been achieved, yet. Positive and negative feedbacks must be taken into consideration with respect to the vegetation / climate interaction (Kohlmaier *et al*, 1991). The stimulation of ecosystem production and respiration by atmospheric trace constituents (Kohlmaier *et al*, 1987) as well as the effects of temperature and precipitation change play an important role in the determination of the feedback.

One may also argue that modeling the interaction of internal vegetation dynamics and climatic driving variables will capture some major traits of C exchanges in terrestrial ecosystems. Tight links between climate and vegetation have already laid the basis for numerous scientific approaches in the past (Holdridge, 1947; Box, 1981; Woodward,

Water, Air, and Soil Pollution 70: 675–684, 1993.

© 1993 Kluwer Academic Publishers. Printed in the Netherlands.

1987; Prentice *et al*, 1992). For these reasons we came to the conclusion that our model has to meet the following requirements:

- The major ecophysiological processes responsible for the reaction of the different ecosystem types to climatic variations must be included.
- The characteristic properties of these ecosystem types should be expressed in terms of (measurable) quantities like biomass, GPP, NPP, soil C, etc.
- A realistic response of the ecophysiological processes to climatic variables requires a time resolution in the range of hours/days.
- The basic structure of the model should be valid for all plant functional types.
- The model structure has to be as simple as possible in order to be manageable at a global scale.

We consider photosynthesis, autotrophic, and heterotrophic respiration as the major ecophysiological processes. Light intensity, temperature, and soil moisture (and in a further state of development: CO₂ concentration), among others, are regarded as the main driving variables.

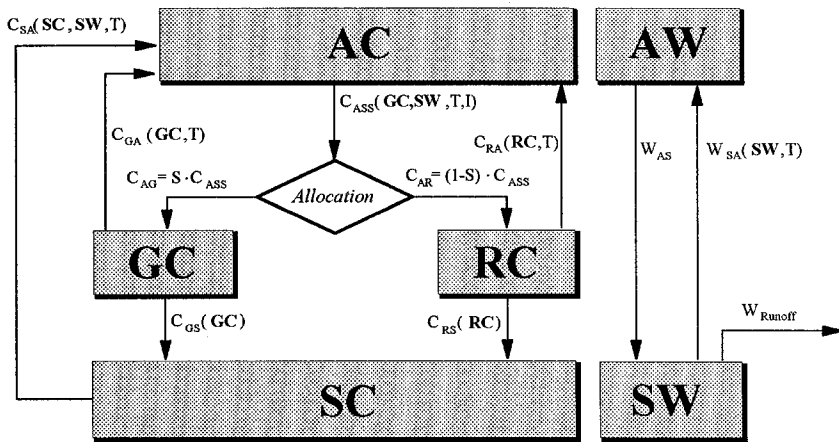


Figure 1: Flow chart and model structure. Bold capital letters represent the reservoirs of C (second letter C) and water (second letter W): AC, atmospheric C; GC, C content of green biomass and feeder root biomass plus assimilate store; RC, C content of remaining biomass of biota ($GC + RC = BC$); SC, C content of litter, humus and dead biomass; AW, water in the atmosphere; SW, soil water in the rooting zone. The capital letters C and W represent C and water fluxes. The indices indicate sources and sinks of these fluxes. The functional dependence of the fluxes on the driving variables and pool sizes is given in parentheses (T: hourly air temperature, I: hourly photosynthetic active radiation, PAR). W_{AS} is the daily precipitation, W_{SA} is daily actual evapotranspiration. The factor S represents the fraction of total assimilation C_{ASS} that is allocated to GC.

2. Compartmentation

According to Janecek *et al* (1989), for every ecosystem type we propose the same basic model structure, showing the minimal functional subdivision of the total C content of the living biomass (**BC**) into two compartments. Here we distinguish between the parts of the vegetation with a short turnover time (leaves, feeder roots, and stored assimilates, summarized in the **GC**-compartment) and mostly woody, structural material with a long turnover time (**RC**-compartment). To describe the decomposition processes of soil organic matter, a one-compartment model after Fung *et al* (1987) is used (C mass of litter and humus are summarized in the **SC**-compartment). Furthermore, the soil water compartment **SW** is introduced to calculate the actual soil water status. The C and water fluxes between these compartments and the atmosphere generally depend on the climatic variables and pool sizes, both varying in time (Figure 1). This structure is assumed to be sufficient to describe the major C uptake and release processes at any point of the terrestrial surface, the advantage of it being the limited and constant number of parameters required. Hence the local difference of the model source and sink strength is influenced externally by the climatic variables and internally by the vegetation properties, which are reflected by suitable parameter values and developmental state.

Figure 2 illustrates how the C part of the proposed model works for one grid element of a temperate deciduous forest in equilibrium. For C cycle modeling the net C exchange flux between the grid element and the atmosphere is the main output (Heimann and Keeling, 1989). Besides the net exchange flux a number of intermediate results is available for further examinations (Figure 2). A comparison of these intermediate results with available data on standing biomass in selected regions, with documentations of the seasonality of leaf biomass etc. may be used to corroborate the model.

3. Carbon Allocation and Phenology

As shown in Figure 1 it is assumed that the assimilate production C_{ASS} is determined by the mass of compartment **GC**, reflecting the amount of leaves, the actual soil water content **SW** as well as by the external driving variables temperature T and light intensity I . This flux is to be partitioned according to present needs of the plant organs, namely the build-up and maintenance of the photosynthesizing tissue and of the feeder roots, (represented by **GC**) on the one hand, and the build-up and maintenance of stems, branches and coarse roots (represented by **RC**) on the other. Furthermore, assimilates have to be translocated in order to fill particular storage organs, which are included in the C mass of the **GC** compartment as well.

The partitioning of the C assimilation flux C_{ASS} into the **GC** and **RC** compartment is derived in its seasonal and long term patterns from two basic assumptions:

- The vegetation tends to maximize the amount of photosynthesizing tissue (contained in the **GC** compartment).
- It is possible to identify a function $RC = \Omega(GC)$ determining the minimum amount of **RC** needed to support and maintain the given amount of **GC**.

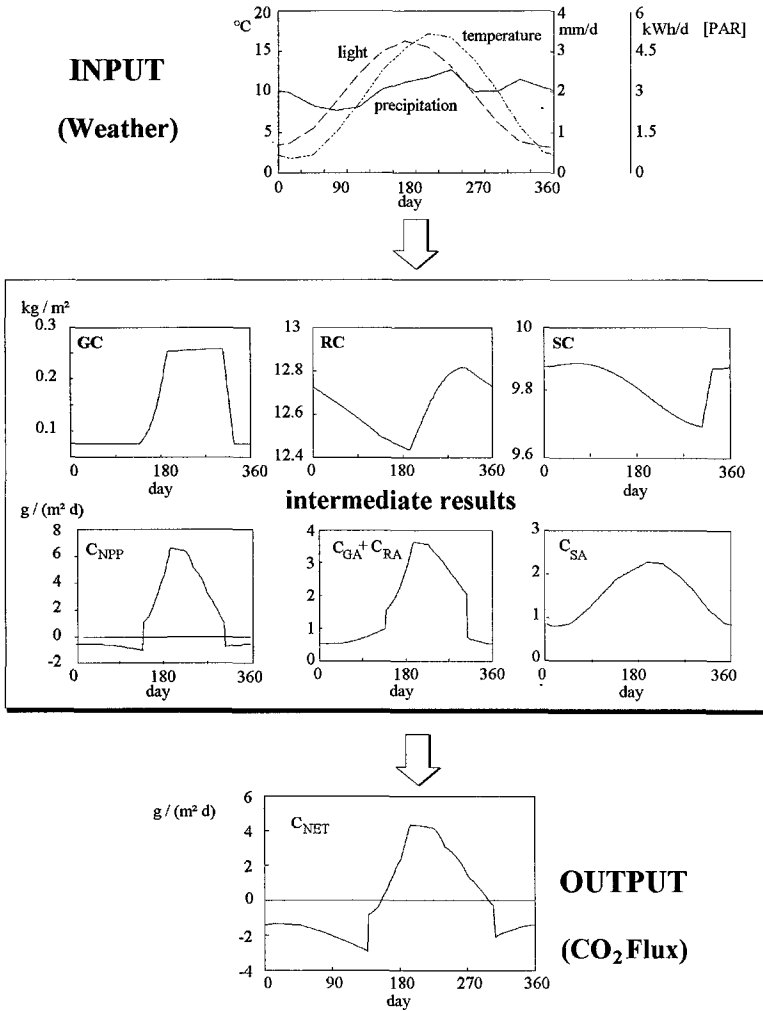


Figure 2: Driving climatic variables (input) and resulting annual course of the net C exchange flux C_{NET} between the whole ecosystem and the atmosphere (output) for a typical grid element of vegetation type 'cold-deciduous forest'. The annual courses of the C compartments and the fluxes $C_{NPP} = C_{ASS} - C_{GA} - C_{RA}$ (exchange flux between living vegetation and atmosphere), $C_{GA} + C_{RA}$ (autotrophic respiration), and C_{SA} (heterotrophic respiration) are displayed as intermediate results.

Data from field measurements (Reichle, 1981) and theoretical considerations suggest that a parabola type of function, the so-called allometric relation, is a suitable parametrisation (see Janecek *et al.*, 1989): $RC = \Omega(GC) = \xi \cdot GC^k$. For the functional types 'temperate broad leaved forest', 'coniferous forest', 'tropical evergreen forest', and 'grasslands' measurements of woody biomass and maximum leaf mass were used to determine the parameters in this function by least square fitting. For a cold-deciduous forest ecosystem a typical course of the allometric relation is shown in Figure 3. In order to comply with the basic assumptions, the system's development within the GC/RC plane is allowed to take place only in the region $RC \geq \Omega(GC)$. Furthermore the system passes through four phases during one annual cycle, as shown in Figure 3.

3.1. Shooting Phase

The C gain from photosynthesis is greater than the C loss. The system allocates most of the assimilates to the GC compartment until the trajectory reaches $\Omega(GC)$, maximizing its production ability.

3.2. Secondary Growth

The system is forced to allocate simultaneously into the GC and RC compartment according to the $\Omega(GC)$ function.

3.3. Leaf Shedding

At the end of the vegetation period, when unfavorable weather conditions do not allow biomass increase (e.g. drought, cold), a leaf abscission phase reduces the GC compartment to a remaining amount of feeder roots and assimilate store, which is proportional to the annual maximum of GC and characterized by the function $RC = \Theta(GC) = \nu \cdot GC^k$.

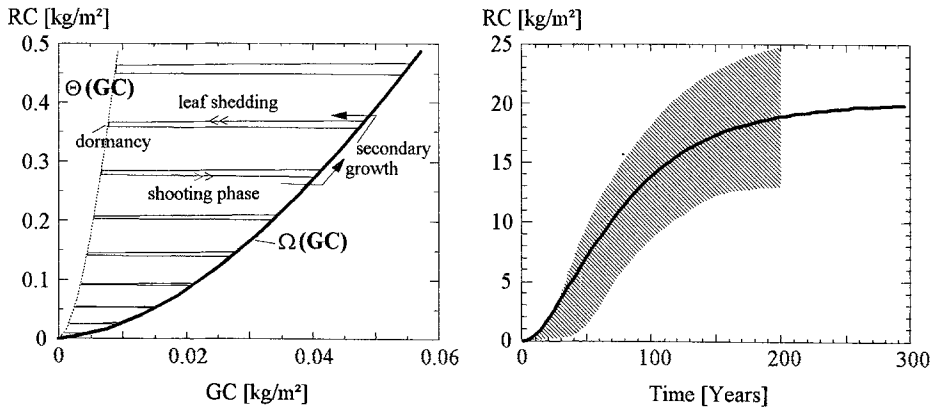


Figure 3: Trajectory in the G-R-space (left hand side) and long term development (right hand side). The hatched area indicates the range of field measurements (Schober, 1975).

3.4. Dormancy Phase

When the trajectory reaches the $\Theta(\text{GC})$ curve the dormancy phase starts. During this phase the biomass losses, as defined by the **RC** respiration and the total litter production C_{BH} , are distributed among the compartments so that the systems trajectory follows the $\Theta(\text{GC})$ curve. This phase ceases when the weather conditions allow a net biomass increase, assuming a total conversion of stored assimilates into leaf biomass and feeder roots.

These phases are described by the differential equations given in the appendix.

4. Calculation of Fluxes

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

4.1. Uptake of CO_2

The effective C assimilation rate, C_{ASS} , can be considered as a product function (Richter, 1985) of a term dependent on light and canopy structure, a temperature dependent term and a soil water dependent term. The dependence on incident light intensity and leaf area index, LAI, which is correlated with the **GC** compartment is modeled according to Monsi and Saeki (1953) taking into account the light attenuation in the canopy. For the temperature dependence an optimum curve is used characterized by the minimum, maximum, and optimum temperature of photosynthesis. The dependence of photosynthesis on water availability, represented by the soil water content **SW**, is assumed to follow a saturation curve which is zero at the permanent wilting point and approaches one for field capacity.

4.2. Release of CO_2 - Autotrophic Respiration

Autotrophic respiration, C_{GA} and C_{RA} respectively, is modeled similarly for both compartments, **GC** and **RC**, depending on the compartment size and an exponential function of the temperature corresponding to a constant Q_{10} value for each ecosystem type (Ryan, 1991).

4.3. Litter Production

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

4.4. Release of CO_2 - Heterotrophic Respiration

For the climate response of the decomposition of dead organic matter, C_{SA} , we extended the model of Fung *et al* (1987) taking into consideration a linear dependence on compartment size and introducing a soil moisture factor analogous to the moisture dependence of photosynthesis.

4.5. Water Fluxes

Due to the close relation between assimilation and transpiration, the actual evapotranspiration, W_{SA} , is calculated by the product of potential evapotranspiration after Thornthwaite (1948), W_{PET} , and the soil water dependent function as used in the calculation of assimilation.

W_{Runoff} comprises both surface runoff and drainage. It is taken as the surplus water when the soil water content reaches field capacity (Wilson and Henderson-Sellers, 1985).

5. Results and Discussion

Although the model is constructed to perform simulations on a global scale, in this paper we will only discuss some selected results. For this purpose we have chosen the ecosystem type 'cold-deciduous forest' from Matthews global vegetation map (Matthews, 1983).

Before running the model for a given ecosystem type, one free parameter per flux equation has to be determined. Therefore a calibration procedure is performed based on mean ecological estimates, e.g. of biomass (Matthews, 1984; Rodin *et al*, 1972), net primary production (Fung *et al*, 1987), annual respiration (Reichle, 1981) and an averaged climate which was generated conserving the typical phase relations between temperature, precipitation, and light of this vegetation type (data basis: climate atlas of Shea (1986)).

These parameters are equally used for all grid elements of this vegetation type. Yet, taking into consideration the real locally different climate as given in the Shea atlas, different fluxes in the different locations are achieved.

In Figure 4 the driving climatic variables and the corresponding equilibrium results for the annual courses of GC and the net C exchange fluxes for two grid elements of the considered vegetation type are displayed. The model reproduces the expected differences of vegetation dynamics comparing the results of a grid element with moderate ($8^{\circ}E$, $50^{\circ}N$) and of a location with continental climate ($50^{\circ}E$, $56^{\circ}N$):

In the moderate climate we obtain

- a greater maximum LAI-value
- a greater annual averaged standing biomass
- a longer vegetation period
- a greater amplitude of the annual course of the net C exchange flux.

The following table compares the calculated LAI and standing biomass with the ecological estimates used for the calibration.

	Leaf area index [m ² m ⁻²]	Standing biomass [kg C m ⁻²]
8°E, 50°N (W. Germany)	5.2	13.2
50°E, 56°N (Russia)	4.6	10.9
Ecological estimates (cold-decid. forest)	5	12.6

The evaluation of the whole ecotype results is in preparation and will be published soon. In addition to the discussed equilibrium calculations the model allows for the calculation of all these quantities not only in the steady state, but also under non stationary conditions, i.e. for non climax systems, or systems in transients induced by climate change.

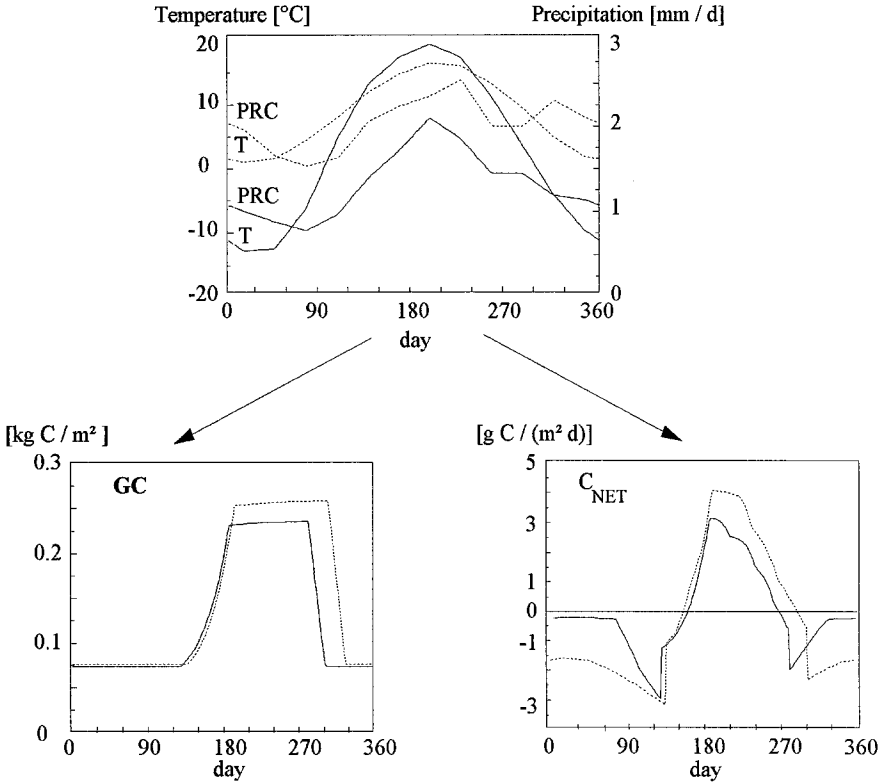


Figure 4: Driving climatic variables and resulting annual courses of the GC compartment and the net C exchange fluxes between ecosystem and atmosphere for two grid elements of vegetation type 'cold-deciduous forest'. Solid lines: 50°E, 56°N; dotted lines: 8°E, 50°N.

6. Acknowledgements

The authors thank the Bundesministerium für Forschung und Technologie and the European Communities for financial support. We also acknowledge the helpful comments of M. Bartel.

7. Appendix

DIFFERENTIAL EQUATIONS	DESCRIPTION OF PHASES; DETERMINATION OF S *)
$\frac{dGC}{dt} = S \cdot C_{ASS} - C_{GA} - C_{GS}$ $\frac{dRC}{dt} = (1 - S) \cdot C_{ASS} - C_{RA} - C_{RS}$	<p>Shooting phase: All assimilates are allocated to GC except for a flux for the compensation of the RC-respiration.</p> $S = \frac{C_{ASS} - C_{RA}}{C_{ASS}}$ <p>Secondary growth phase: Simultaneous allocation to the GC and RC compartment. The systems trajectory equals $RC = \Omega(GC)$.</p> $S = \frac{C_{ASS} + \frac{d\Omega}{dGC} \cdot (C_{GA} + C_{GS}) - (C_{RA} + C_{RS})}{\left(1 + \frac{d\Omega}{dGC}\right) \cdot C_{ASS}}$
$\frac{dGC}{dt} = -\Delta$ $\frac{dRC}{dt} = -C_{RA} - C_{RS}$	<p>Leaf shedding phase: Leaf abscission is performed with a constant rate Δ while leaf metabolism is assumed to be neglectable. The driving variables do not have any impact on the abscission rate. Once started this phase ends when the trajectory reaches the curve $RC = \Theta(GC)$.</p>
$\frac{dGC}{dt} = \frac{1}{1 + \frac{d\Theta}{dGC}} \cdot (-C_{RA} - C_{BS})$ $\frac{dRC}{dt} = \frac{\frac{d\Theta}{dGC}}{1 + \frac{d\Theta}{dGC}} \cdot (-C_{RA} - C_{BS})$	<p>Dormancy phase: Respiration and litter losses are distributed so that the systems trajectory equals $RC = \Theta(GC)$.</p>

*) In order to describe the allocation strategy during the vegetation period, we introduce an allocator S , $0 \leq S \leq 1$. As no assimilates are produced out of the vegetation period the allocator is not determined in the leaf shedding phase and in the dormancy phase.

8. References

- Box, E.O.: 1981, *Macroclimate and Plant Forms: An Introduction to Predictive Modeling in Phytogeography*, The Hague, Junk.
- Fung, I. Y.; Tucker, C. J.; Prentice, K. C.: 1987, *J. Geophys. Res.* **92**(D3), 2999.
- Heimann, M. and Keeling, C. D.: 1989, A Three Dimensional Model of Atmospheric CO₂ Transport Based on Observed Winds: Model Description and Simulated Tracer Experiments, in: D. H. Peterson (ed.), *Aspects of Climate Variability in the Pacific and the Western Americas*, Geophysical Monograph 55, Washington DC, pp. 237-275.
- Holdridge, L.R.: 1947. *Science*, **105**, 367.
- Janecek, A.; Benderoth, G.; Lüdeke, M. K. B.; Kindermann, J.; Kohlmaier, G. H.: 1989, *Ecological Modelling* **49**, 101.
- Kohlmaier, G. H.; Bröhl, H.; Siré, E. O.; Plöchl, M.: 1987, *Tellus* **39B**, 155.
- Kohlmaier, G. H.; Lüdeke, M.; Janecek, A.; Benderoth, G.: 1991, Land biota, Source or Sink of Atmospheric Carbon Dioxide, in: Schneider, S. H.; Boston, P. J. (eds.), *Scientists on Gaia*, MIT Press, Cambridge, pp 223-239.
- Matthews, E.: 1983, *J. Clim. Appl. Meteor.* **22**(3), 474.
- Matthews, E.: 1984, *Progress in Biometeorology* **3**, 237.
- Monsi, M. and Saeki, T.: 1953, *Jap. Journ. Bot.* **14**, 22.
- Prentice, I. C.; Cramer, W.; Harrison, S. P.; Leemans, R.: 1992, *J. Biogeogr.* **19**, 117.
- Reichle, D. E. (ed.): 1981, *Dynamic Properties of Forest Ecosystems. International Biological Programm*, **23**, Cambridge University Press, Cambridge.
- Richter, O.: 1985, *Simulation des Verhaltens ökologischer Systeme. Mathematische Methoden und Modelle*. VCH, Weinheim.
- Rodin, L. E.; Bazilevich, N. I.; Rozov, N. N.: 1972, Productivity of the World's Main Ecosystems, in: *Proc. of World Ecosystems*, Seattle Symp., pp. 13-26.
- Ryan, M. G.: 1991. *Ecological Applications* **1**(2), 157.
- Schober, R.: 1975. *Ertragstafeln wichtiger Baumarten*, Sauerländer, Frankfurt.
- Shea, D. J.: 1986, *Climatological Atlas: 1950-1979, NCAR Technical Note 269+STR*, NCAR, Boulder, Colorado.
- Thornthwaite, C. W.: 1948, *Geographical Review* **38**, 55.
- Wilson, M. F. and Henderson-Sellers, A.: 1985, *Journal of Climatology* **5**, 119.
- Woodward, F. I.: 1987, *Climate and Plant Distribution. (Cambridge Studies in Ecology)*. Cambridge University Press, Cambridge