

The effects of tree species grouping in tropical rain forest modelling

Simulations with the individual based model FORMIND

Peter Köhler¹ and Andreas Huth

*Center for Environmental Systems Research, Kurt-Wolters-Str. 3, University of Kassel,
D-34109 Kassel, Germany*

Abstract

Due to high biodiversity in tropical rain forests tree species are aggregated into functional groups for modelling purposes. In this article the influences of two different classifications of tropical tree species into functional groups on the output of a rain forest model are analysed. The used model FORMIND is documented. FORMIND simulates the tree growth of tropical rain forests. The model is individual based and developed from the FORMIX3 model. In the model trees compete for light and space in plots of 20 m × 20 m in size. A carbon balance is calculated based on the processes of photosynthesis and respiration. Using a tree geometry submodel typical tree variables (e. g. diameter, height, crown length) are calculated. The mortality process is mainly driven by falling trees and the canopy gaps they create. Trees of the same functional group and diameter class are represented in one cohort. Simulation results for a primary lowland dipterocarp rain forest in Sabah, Malaysia, are discussed. Detailed structural characteristics of the rain forest stands can be analysed, e.g. the simulation results support the hypothesis that rain forests grow in a layer structure. A comparison of results for the aggregation of 436 tree species into 5 or 22 functional groups respectively shows that typical results like total stem volume or crown closure achieved with 5 groups are as accurate as simulations with a huge number of groups. However some features like interspecific competition can only be analysed with a huge number (e. g. 22) of functional groups. The model has the potential to analyse extinction processes and spatial structure of gap formations in rain forests. The analysis of logging scenarios could estimate the effects of human impacts in tropical rain forests.

Keywords: Simulation, model, individual based, tropical rain forest, growth, functional groups, dipterocarp forest, Malaysia

Printed in *Ecological Modelling* (1998) 109(3), 301-321.

Copyright ©1998 Elsevier Science B.V.

¹Corresponding author. E-mail: koehler@usf.uni-kassel.de

1 Introduction

Globalisation with all its consequences like an increase in traffic, industrial output and pollution as well as population pressure is threatening ecosystems all around the world. Climate change is one result of this development. There is strong evidence that intact forests can play an important role in keeping the global system in balance. The reduction of the world's forests, mainly in the tropics, and their annual input in the atmosphere of 1 to 3 billion tons of carbon from tropical forest burning impairs their important functions as carbon sinks contributing significantly to the building of greenhouse gases (Riswan and Hartanti, 1995). Besides the importance of tropical rain forests for climate change, 75 to 90 % of the global biodiversity are to be found in this type of ecosystem (Terborgh, 1993).

A growth model for rain forests can be a tool to understand the important factors which are responsible for the longterm behaviour of the system. With this understanding, forest management can be applied in an intelligent way to minimize human impacts on the balance of the coexisting species. Growth models for forest ecosystems are well known for temperate forests. In the past decades they have been widely studied. The so-called gap models (Botkin et al., 1972; Shugart, 1984) have been able to establish themselves as important instruments in understanding forest growth from a scientific point of view as well as for estimating future wood productivity. Only in the past few years simulation models for tropical rain forests have been developed (Bossel, 1991; Vanclay, 1994). Some reasons are the huge number of coexisting species and the complex interaction in which they live. It is possible to find up to 400 tree species in one hectare of tropical rain forest (Terborgh, 1993). Another reason is the missing availability of data from field measurements, which are necessary to validate a growth model. The model structure for temperate and tropical forests is different. In the first case monospecific evenaged forests often are the object of research (Bossel, 1994). In tropical forests, however, we have to deal with the complex interactions and biodiversity and have to concentrate on particular processes, e. g. the falling of big trees and the creation of canopy gaps. In these gaps trees are growing in a cycle of succession. Light demanding species, the so-called pioneers, strongly depend on such gaps. They come up in the first cycle and suppress the main climax species. Because of the short lifetime of the pioneers the main canopy is filled up again with trees of the climax species after about 50 years (Whitmore, 1990).

Typical gap models simulate the succession process by dividing the simulation area in subareas with a size of the crown projection area of a dominant tree (Shugart, 1984). Several models have shown, that they can produce reasonable results by aggregating the species richness into a few functional groups (Bossel and Krieger, 1991, 1994; Bugmann, 1996; Huth et al., 1996; Ong and Kleine, 1995; Vanclay, 1994). Because of a monthly rainfall in the wet tropics above 100 mm all over the year (Whitmore, 1990) growth limitation due to water stress is not to be expected, seasonal differences can be omitted (Deutscher Forstverein, 1986; Terborgh, 1993).

A growth model for tropical rain forest, which takes all these aspects into account, is the FORMIX3 model (Huth et al., 1996). It calculates the numbers and biomasses of five different species groups. The trees are related to one of five layers according to their height and the position of their crowns. Growth is modelled and trees change to the next higher layer when reaching their present layers upper limit. As every species group is represented in each layer by a number of identical trees only, fixed transition are assumed when the representative tree reaches the layer limit. The following report documents a model called FORMIND which has some details in common with the FORMIX3 model. The new model is individual based, which FORMIX3 is not. That means no layers and no transition rates are considered and no calculations with average trees are performed.

Other advantages of individual based models are a higher transparency in some essential forest structures, e.g. crown closure (Huston et al., 1988; Judson, 1995; Liu and Ashton, 1995). For each tree the light received is calculated in a submodel. The model does not consider nutrient cycles other than the carbon cycle (Weidelt, 1993). The calculation is performed in a cohort structure (Bugmann, 1994; Vanclay, 1994) which reduces the simulation efforts as much as possible. In this paper we present and discuss results for a lowland dipterocarp rain forest in Sabah (Borneo), Malaysia following to a detailed documentation of the model. Simulation results for a parametrisation with 5 and 22 functional groups are compared. It is shown in which features a more precise group classification is necessary and where few functional groups achieve reasonable results.

2 Classification of Functional Groups

For modelling purposes it is necessary to aggregate the high biodiversity of tree species in tropical rain forests into functional groups (Whitmore, 1990). A common classification into two groups is made according to the light demand of the species. Shade tolerant species develop seedlings which can establish below a closed canopy. These trees are normally slow growing. Their crowns are found in the main canopy of the forest. They are also called climax species. The second group are shade intolerant species, or pioneers, whose seedlings need a certain minimum of light for germination. Adequate light conditions are only found in canopy gaps of a certain size. Sometimes a third group is distinguished with light demand inbetween that of pioneer and climax species. Studies have shown a linkage between ecology and physiology of functional groups in a tropical forest community (Ellis et al., 1997). Therefore classifications relying on certain physiological criteria support a modelling approach, where simplifications are necessary.

A classification of 436 tree species in Sabah into 22 functional groups was performed by Ong and Kleine (1995) on the basis of diameter growth characteristics and light demand. Tree species with the same light demand whose growth behaviour in terms of diameter increment are similar are aggregated into the same group. In Table 1 this grouping is presented. In the FORMIX3 model a further aggregation of these groups into five species groups was performed by using the potential height as third criteria (Ditzer and Huth, 1995) (see Table 2). The aggregation into these functional groups is analysed in Ditzer et al. (1997). The FORMIND model can work with both classifications. In section 5 we compare simulation results which are achieved with different numbers of functional groups.

3 FORMIND: A Model Description

A first description of the modelling concepts of FORMIND can be found in Köhler and Huth (1997). The simulation area is divided into plots of $20\text{ m} \times 20\text{ m}$ (see Fig. 1). All trees in a plot compete for the available light and space. The size of these plots (400 m^2) is restricted by two considerations. A lower limit is given by the resource competition and the possibilities of dominant trees to grow up to a correct maximum size, which is corresponding to the plot size. The consideration of correct gap-phase replacement in a succession process sets an upper limit on the plot size. By that the size of the plots should be between 0.04 and 0.08 ha (comp. Shugart, 1984).

The model is designed in a cohort structure, which means that trees of the same functional group and size (we chose a diameter discretisation of $\Delta d = 5\text{ cm}$) are represented by one typical

tree. A cohort model is characterised by three main components (Vanclay, 1994):

- growth increment is modelled by incrementing the size of the representative tree,
- mortality is simulated by reducing the number of trees represented by each cohort and
- recruitment is accommodated by initiating new cohorts from time to time.

3.1 Main Equations

In each plot l ($l = 1, \dots, m$) for each functional group j and diameter class of 5 cm width a cohort i ($i = 1, \dots, n(l, t)$) is generated, in which the tree number and the biomass of one tree are calculated.

For each timestep dt the changes in biomass $B_{i,l}$ (above ground) of each individual tree are calculated due to the actual photoproduction $\hat{P}_{i,l}$ and the losses for deadwood, respiration and investment into undergrowth structure R_i , (section 3.2.2).

$$\frac{dB_{i,l}}{dt} = \hat{P}_{i,l} - R_{i,l}. \quad (1)$$

Changes in the tree number $N_{i,l}$ can only occur through mortality $M_{i,l}$ (section 3.2.4). An input of new seedlings is modelled by generating a new cohort i (section 3.2.5).

$$\frac{dN_{i,l}}{dt} = -M_{i,l}. \quad (2)$$

This leads to a system of $2 \times m \times n(l, t)$ coupled ordinary nonlinear differential equations, for which an analytic solution is out of sight.

For keeping the equations easy to read we continue without using the index l for different plots.

3.2 Description of the different submodels

There are five submodels in which different processes of the model are described. They are named 'Tree Geometry', 'Carbon Cycle' (divided into 'Photoproduction' and 'Respiration'), 'Competition for Light', 'Mortality', and 'Recruitment of Seedlings'. In Fig. 2 the interactions between the submodels and the two main variables *biomass* and *tree number* in each cohort are shown.

3.2.1 Submodel Tree Geometry

For the calculation of processes such as shading and photoproduction we can not regard the tree biomass B_i as only descriptive variable but we need additional information about the tree. The relationship between tree height h_i and stem diameter d_i is often investigated and expressed as a second order polynom (see also Fig. 3B).

With the assumption of a conical stem, the relation between its diameter d_i and the biomass B_i is calculated in equation 3, where ρ_j is the wood density, τ_j the stem wood fraction and $\gamma_i(B_i)$ is a form factor which takes the difference to a cylinder into account. γ_i itself depends on the biomass of the tree (Fig. 3A),

$$B_i = \frac{\pi}{4} d_i^2 \cdot h_i(d_i) \cdot \rho_j \cdot \gamma_i(B_i). \quad (3)$$

Stem volume SV_i is of particular interest when forest management is applied on a model. SV_i is calculated with stem wood fraction τ_j and wood density ρ_j from the biomass B_i .

The crown projection area f_i can be calculated as a function of stem diameter using the ratio $s_j(d_i)$ of crown to stem diameter, which is shown in Fig. 3D:

The crown length c_i depends on the tree height. The relation from crown length to crown diameter is big in small trees and small in big trees (Burgess, 1961; Poker, 1993; Richards, 1952). Fig. 3C shows how the relative crown length c_P is varied with height h .

A typical tree with its dimensions is shown in Fig. 4.

3.2.2 Submodel Carbon Cycle

The photosynthetic production is computed using an approach developed by Monsi and Saeki (1953). The model is based on an exponential light distribution within the crowns as a function of the cumulative leaf area index and the photosynthetic active radiation I_i above the regarded tree. The light response curve for photosynthetic production P_i of leaves is assumed to be a saturation type curve expressed by:

$$P_i(I_i) = \frac{\alpha_j \cdot I_i}{1 + \frac{\alpha_j}{P_{Mj}} I_i}, \quad (4)$$

where α_j is the initial slope of the light response curve and P_{Mj} the maximum rate of net photosynthetic production per leaf area (Fig. 5A).

The solar radiation I_i received by a tree i is calculated from the cumulative leaf area index L_i above the tree and the average annual light intensity I_0 above the whole forest. The light attenuation within the canopy can be approximated by an exponential absorption with an absorption coefficient k (Kira, 1978),

$$I_i(L_i) = I_0 \cdot e^{-k \cdot L_i}. \quad (5)$$

The calculation for the cumulative leaf area index L_i is to be found in the submodel 'Competition for Light', section 3.2.3. The hypothetical maximum photosynthetic production rate \tilde{P}_i for trees whose crowns fill the plot completely can be calculated by integrating the productivity $P_i(I_i)$ vertically down the crown of the regarded tree and is given by (Thornley, 1978):

$$\tilde{P}_i = \frac{P_{Mj}}{k} \cdot \ln \left[\frac{1 + \frac{\alpha_j}{P_{Mj}} I_i}{1 + \frac{\alpha_j}{P_{Mj}} I_i \cdot e^{-k \cdot \widetilde{LAI}_j}} \right]. \quad (6)$$

where \widetilde{LAI}_j is the leaf area index of one single tree's crown.

\tilde{P}_i has to be multiplied by a correction factor δ_i (see section 3.2.3) for trees with their crown in overcrowded layers and must be applied at the actual crown projection area f_i (see section 3.2.1).

According to estimates for matured tropical rain forests approximately 13 – 16 % of the above-ground standing biomass is lost per year (Kira, 1978). These losses R_i include respiration, litter fall, increment of roots and renewal of stem, branches, leaves and roots. In case of leaf respiration only the losses at nighttime are considered. The respiration of leaves at daytime is included in the light response curve (Fig. 5A). To assure that trees do not exceed their maximum diameter

d_{Mj} a diameter-dependent term is included in the calculation of the respiration:

$$R_i = B_i \cdot R_{Pj} \cdot \left(1 - \left(\frac{d_i}{d_{Mj}} \right)^2 \right) + \hat{P}_i \cdot \left(\frac{d_i}{d_{Mj}} \right)^2, \quad (7)$$

with R_{Pj} as specific respiration rate. Parameter estimates are necessary for emergents. With a size independent respiration trees would not exceed a diameter of 90 cm. Therefore the specific respiration rate R_{Pj} is corrected depending on tree height (Fig. 5B).

3.2.3 Submodel Competition for Light

For the calculation of light attenuation of a single tree we have to know the distribution of leaves within the crown. The leaves in a crown are assumed to be homogeneously distributed. The whole canopy is divided into layers of the thickness Δz . For each layer between z and $z + \Delta z$ we calculate the fraction of leaf area index $LAI_i(z)$ of individual trees whose crown of the length c_i overlaps this layer. In the following we label the layer between z and $z + \Delta z$ with z .

The crown closure $F(z)$ of each layer is calculated by summing up the crown projection area f_i normalized over the plotsize A of all concerned trees. If crown closure $F(z)$ exceeds its maximum value of 1.0, a reduction factor $\delta(z) = 1/F(z)$ is calculated, from which the average reduction factor δ_i for each tree can be determined.

To calculate the leaf area $L(z)$ of a specific layer z , the crown closure $F(z)$ has to be multiplied by the LAI_i of that layer z .

Shading in the canopy is only considered within a plot with one exception. The emergents can shade neighbouring plots. If the crown projection area f_i of a emergent exceeds the plot size of 400 m², the four neighbouring plots are shaded in the same portion,

The cumulative leaf area index L_i above each individual tree is calculated by summing up the leaf area $L(z)$ of all layers above the height h_i of the tree.

It is also considered that trees with their crown at the same height are not able to shade each other. They are excluded in this calculation (Fig. 6).

3.2.4 Submodel Mortality

Tree mortality in tropical rain forests has a rate of about 1 % to 3 % annually (Condit et al., 1995; Phillips and Gentry, 1994; Swaine, 1989; Van der Meer and Bongers, 1996). Field measurements for climax species have shown a relation between the mortality rate M_{Ni} and the annual diameter increment d_{Zi} (Fig. 7). The average turn over rate for trees with $d \geq 10$ cm in the study of Swaine (1989) was 1.2 %. We additionally include a weighting factor M_{Wj} depending on the functional groups to calculate the mortality rate M_i :

$$M_i = M_{Wj} \cdot M_{Ni}(d_{Zi}). \quad (8)$$

Eq. 8 takes into account the well known (Whitmore, 1990) higher mortality rate for the shade intolerant pioneer species. In the measurements of Swaine (1989) big trees are underrepresented. Due to this, their mortality rate would be overestimated. For big trees ($d \geq 0.6$ m) mortality is reduced linearly in a way, that a tree with $d = 1.5$ m would have a mortality rate of 0.5 %.

Seedlings and small trees have a significantly higher mortality rate (Swaine, 1989; Whitmore, 1990). We assume an approximate mortality rate of 8 % for trees with $h_i \leq 1.3$ m.

It is supposed that overcrowded stands have a higher mortality. Crown closure is the indicator for crowding. If the average crown closure \bar{F}_i of a tree exceeds a certain threshold ($\bar{F}_i > 1$) the tree is assumed to stand in a crowded forest with a mortality rate of 4% (8% for pioneers) and 32% for small trees (with $h \leq 1.3\text{m}$).

An important mechanism for tree mortality and the whole growth dynamics is the so called gap dynamics (Brokaw, 1985). Up to 90% of tree mortality occurs due to falling trees that damage their neighbours (Van der Meer and Bongers, 1996). Therefore every dying tree with $d \geq 10\text{cm}$ has a possibility of $W = 40\%$ to fall and can smash other trees. The size of a gap created by a falling tree is as big as its crown projection area f_i .

Mortality is calculated deterministically in cohorts with huge tree numbers and stochastically in cohorts with tree numbers less than 100 which means in the stochastic case the mortality rate M_i is a longterm time average value.

3.2.5 Submodel Recruitment of Seedlings

The model works with the assumption of a constant seed bank in the forest ground. This is true for pioneers. Climax species do not build up a seed bank, but under normal conditions a constant number of seedlings is found on the forest floor (Whitmore, 1990). A former version of the FORMIX model simulated this seed bank as well (Bossel and Krieger, 1991). It is assumed that the simulation area is surrounded by intact forest, from which enough seeds of every species group can fill the seed bank in the calculated area. The approach with a constant seedling input restricts the application of the model to simulate parts of large forest areas, where extinction of tree species is not an important feature.

Conditions necessary for an input of seedlings are:

- Free crown space at the forest floor and
- the light intensity I_F at the forest floor must exceed a minimum amount I_{Sj} which is necessary for germination of seeds,

$$I_F \geq I_{Sj}. \quad (9)$$

If the conditions are fulfilled a new cohort is created. The variables biomass B_i and tree number N_i are initialized with the biomass of the seedlings B_{Sj} and a fixed number N_{Sj} of newly establishing seedlings per year and plot respectively. An input of seedlings occurs once a year.

4 Site and Parametrisation

Based on an extensive literature study a parametrisation for the simulation of dipterocarp evergreen tropical moist forest at Deramakot was developed for the FORMIX3 model (Huth et al., 1996). This parametrisation was developed for 5 functional groups. The Deramakot Forest Reserve is situated in Sabah (Borneo, Malaysia, 117°30' E, 5°25' N). Located just north of the equator, Deramakot has the perhumid climate typical for the inner tropics. Mean annual temperature is 27° C and mean annual rainfall is about 2800 mm. Geologically Deramakot is characterized by tertiary sediments, mostly sandstone. The soils are mainly Acrisols. They are poor in nutrients and easily eroded, especially when the protective plant cover is removed. The

Deramakot Forest Reserve lies in an altitude of 130 to 300 m. The prevailing forest type is dipterocarp lowland forest. The forest was kept rather undisturbed until this century. Commercial logging started in 1956. Intensity of logging and logging damages vary widely.

For FORMIND we adopt the parametrisation of FORMIX3. For details concerning the parameters see Huth et al. (1996). The parameter values are listed in Table 3. It should be noted that these parameters values are identical with those in FORMIX3 apart from the fall probability W and the new parameter *leaf area index of a single tree* \widetilde{LAI} .

The classification into 22 functional groups subdividing the 5 groups used in FORMIX3 demands a more specific determination of parameter values. We rely on field data and specify only a few characteristic parameters for which a data set for 22 groups is available or where realistic assumptions can be made. A whole data set for the leading species of all 22 functional groups exists for *wood density* ρ (Cockburn, 1980; Ong and Kleine, 1995). For the parameter of the light response curve (*maximum photoproductivity* P_M and *initial slope* α) field data for 8 functional groups are available (Eschenbach, 1994). For the missing 14 groups we make assumptions based on data for species with similar growth behaviour: The relative variation (P_{M22}/P_{M5}) of the *maximum photoproductivity* P_{M22} in the classification in 22 groups from its mean value P_{M5} for the classification in 5 groups is assumed to correspond to the relative variation (ρ_{22}/ρ_5) of the *wood density* ρ_{22} from the mean density ρ_5 for 5 group classification. Corrections in the *initial slope* α from the mean value for classification in 5 groups are done in cases where these groups dominate the stand in an unrealistic manner (Whitmore, 1990). For the *input of seedlings* N_S we simply use the parameter values for 5 groups for the corresponding groups of the 22 group classification. Parameters for the submodel 'Mortality' and the *minimal light intensity for germination of seedlings* I_S simply depend on the fact whether the group consists of climax or pioneer species. Some parameters do not vary at all with different functional groups (*crown-to-stem-relation* s , *fraction of stemwood to total biomass* τ , *biomass of seedlings* B_S , *leaf area index of single tree* \widetilde{LAI} and *specific respiration* R_P). In this first approach we continue working with five height-to-diameter relations. Table 4 contains the parameter set for 22 functional groups.

The stem diameter distributions at the beginning of the simulation are taken from inventory data (Schlensog, 1997).

5 Results and Discussion

In this section simulation results are presented and discussed. We simulate the growth of a primary lowland dipterocarp rain forest in Deramakot Forest Reserve, Sabah, Malaysia and compare the results achieved with 5 and 22 functional groups. Typical stand characteristics are shown, like the dynamic behaviour of the stem volume, stem number distribution and the distribution of plots in different stages of succession, called growth stages. We document how the cumulative leaf area index varies with height and what we can learn from the model output about the crown closure in vertical direction. The stem volume distribution with 22 functional groups gives us an idea of the interspecific competitions over time.

5.1 Simulation with 5 Functional Groups

For initialisation trees counted by an inventory (Schlensog, 1997) are distributed over the plots by a random scheme which takes the number of gaps in the forest into account and classified in 5 functional groups and different cohorts with a diameter width of $\Delta d = 5$ cm. Nine hectares

of rain forest have been simulated for minimizing stochastic effects of mortality. We chose a vertical discretisation of $\Delta z = 0.5$ m and a time step of $\Delta t = 0.1$ a. The equations have been numerically solved by an Euler - Cauchy integration by which the numerical error has the order of $(\Delta t)^2$.

The results for the development of a primary rain forest are given in Fig. 8. Some main features of the trees with $d \geq 10$ cm are seen there. The functional groups composition of the stand as well as the total stem volume are fairly the same at the beginning of the simulation and after 500 years. This result corresponds to a matured forest stand which has reached its equilibrium and stays constant in its biomass and species composition. This should be expected if the forest is undisturbed under constant environmental conditions (Weidelt, 1986; Whitmore 1988). The stem volume has an equilibrium at about $550 \text{ m}^3/\text{ha}$ (Fig. 8B). Kato (1978) measured stem volumes of 556 and $777 \text{ m}^3/\text{ha}$ in a matured dipterocarp forest in Pasoh, Malaysia on stand area of 0.1 ha in size. This fits well our simulation results. Field measurements in tropical forest are often made for a diameter threshold of $d = 10$ cm. Nicholson (1979) found 422 and 667 trees per hectare ($d \geq 10$ cm) in a forest in Sabah, Malaysia. In the same region Newbery et al. (1992) counted 470 trees/ha ($d \geq 10$ cm). In other lowland rain forests the tree numbers are of the same order. Van der Meer and Bongers (1996) found 526 trees/ha ($d \geq 10$ cm) in Amazonia, Crome et al. (1992) 664 trees/ha ($d \geq 10$ cm) in Australia, and Brokaw (1985) more than 1000 tree/ha with $h \geq 1$ m in Panama. In the simulation the stem number ($d \geq 10$ cm) has its equilibrium at 1200 1/ha, from which 800 1/ha belong to functional group 1 (Fig. 8D). This difference to literature values is due to high stem number in the lowest diameter classes (Fig. 8C). It can be understood as a very close packing of trees in the lowest layers. This phenomenon has to be analysed in future studies. One reason could be the assumptions in the submodel 'Tree Geometry', where there are only small differences between small and large trees. Field studies (Rollet, 1978) find an exponential decrease in stem numbers to bigger stem diameter, in which small trees ($d \leq 20$ cm) do not fit into. They behave rather irregular. The simulation results show the same exponential decrease (Fig. 8C).

The variation of the growth stages over time shows, that the forest reaches its equilibrium after about 200 years of simulation (Fig. 8A). Then about 5 % of the forest are in gap stage, which means, that in the regarded plot no trees larger than $h \geq 20$ m exist. About 30 % of the plots are in a building stage, where trees with a height up to 36 m exist. 65 % of the area is matured forest with trees bigger than 36 m. This classification corresponds to a gap definition by Van der Meer and Bongers (1996). Fluctuations are high (about 10 %). The equilibrium state is different from the initial situation, because the inventory (Schlensog, 1997) was measured on areas smaller than 0.81 ha, which might not represent all growth stages of primary rain forest. A measurement of different growth stages was done by Hubbel and Foster (1986) in a forest in Panama of 50 ha in size. They measured a forest with $34\% \pm 23\%$ in a gap stage (no trees with $h \leq 20$ m exist), $37\% \pm 19\%$ in a building stage (trees between 20 m and 30 m exist) and $29\% \pm 30\%$ in a matured stage (trees bigger than 30 m exist). The observed areas were $5 \text{ m} \times 5 \text{ m}$ in size (which is a quarter of the plotsize in the model). This higher resolution can be the reason for the differences in the results.

Leaf area index is another possibility to characterize a forest. In Fig. 9 the cumulative *LAI* for the different heights is shown. It can be seen that there are little differences between the initial stage and the one after 500 years of simulation. Due to unexpected behaviour of small trees we have distinguished two canopy sections. Trees with a diameter smaller than 10 cm are about 10 m high. Therefore the lower part in Fig. 9 should be regarded more critically than the upper. The cumulative *LAI* between the top of the canopy and $h = 10$ m (or the forest floor) has a value of 5 (or 10 respectively). Measurements in a Malaysian rain forest achieve $LAI = 7.3$

down to the forest floor (Kato et al., 1978). In a tropical rain forest in Thailand an $LAI = 11.4$ to the forest floor was measured (Kira, 1975). In the same forest where the inventory used for the initialisation of our simulations was taken Schlenso (1997) determined a $LAI = 5.1$ at 0.5 m above forest floor by measuring diffuse radiation. Using the approach of exponential absorption within the whole canopy (equation 5) Schlenso achieves LAI -values of 6.44 to 10.99 at 3 m above forest floor depending on the absorption coefficient k . By considering, that undergrowth can achieve a LAI of 1.2 to 4.0 (Rollet, 1978), the simulation results fall fairly good in the range of measurements.

Because of the fine solution of the model output in vertical direction the results can be analysed for a layer structure in the canopy. This is a controversial subject in literature (Richards, 1952; Rollet, 1978; Terborgh and Petren, 1991). In Fig. 10 the crown closure in different heights can be seen. We distinguish between forest in a mature (Fig. 10A) and in a building stage (Fig. 10B). The first one can be interpreted as primary forest where the second one corresponds to secondary forest.

In the results for primary forest maxima in crown closure can be seen at 42 m, 9 m, and three submaxima at 21 m, 15 m and 2 m. The secondary forest has maxima at 36 m, 18 m and 10 m but these are not well defined. With the assumption that a maximum in crown closure corresponds to a typical layer construction it can be said that an Malaysian rain forest tends to organize itself in a 2 to 5 layer structure, corresponding to statements of Richards (1936). But it must be mentioned that no rigid division between the layers exists, comparable to statements of Rollet (1978).

This corresponds to observations of Terborgh and Petren (1991). For a primary forest they found a layer structure but the height levels differ from our simulation results (30 m, 6 m, 3 m and 0.5 m). It has to be considered that these observations were made with different resolution of tree heights (Δz up to 5 m compared to $\Delta z = 0.5$ m in our simulations) in a forest formation in South America.

If we simulate different stands (e. g. a secondary forest with a huge clearing) after 400 years the same equilibrium state in terms of stem volume, species composition, growth stages and crown closure is reached. This is the case even if a clear cut is simulated where the forest grows up in a clear area. In this case impacts on the forest floor due to erosion are omitted. Forest regrowth after a stage of shifting cultivation can be simulated with that approach.

5.2 Simulation with 22 Functional Groups

The initialisation of the simulation is done similar to the last section. Schlenso's (1997) inventory data are distributed over the plot, followed by a classification into 22 functional groups and a cohort structure with a diameter width of $\Delta d = 5$ cm. For the simulations with 22 functional groups the same vertical discretisation and time step as in section 5.1 were chosen ($\Delta z = 0.5$ m, $\Delta t = 0.1$ a). This time we simulate only one hectare of rain forest for analysing the species composition.

In Fig. 11 the main simulation results are visualized. Because the classification in 5 groups relies on the one in 22 groups a comparison can be made easily. After simulation we aggregate the resulting stem volume of the 22 groups together to the 5 groups (Fig. 11B). Compared to direct simulations with 5 groups (Fig. 8B) no qualitative differences can be seen. The equilibrium of the total stem volume with $d \geq 10$ cm is $550 \text{ m}^3/\text{ha}$, from which $450 \text{ m}^3/\text{ha}$ belong to group 1 and $80 \text{ m}^3/\text{ha}$ to group 2. The pioneer species (group 3) vary between zero and $60 \text{ m}^3/\text{ha}$. This means that the species composition in terms of the aggregated 5 groups as well as the total stem

volume of the ecosystem do not depend on the classification of functional groups. The smoother behaviour of all time graphics for simulations with 5 functional groups in section 5.1 is caused by the larger simulation area used there (9 ha).

This result is confirmed by other variable outputs. The stem-diameter-distribution after 500 years of simulation (Fig. 11C) is qualitatively comparable to that resulting from the aggregated simulations (Fig. 8C). Compared to the primary forest inventory data initialising the simulation We have an increase in stem numbers at small diameters ($d \leq 40$ cm). The distribution of the plots in various growth stages (Fig. 11A) has a similar equilibrium (comp. Fig. 8A) which is reached after 200 years of simulation (65 % are matured area, 30 % are building area and 5 % are gap area). The growth stages (Fig. 11D) vary widely around the equilibrium because with 22 functional groups only one hectare (25 plots) of rain forest is simulated and therefore changes in a few plots have a remarkable influence on the output.

Even the crown closure in primary forest (Fig. 11D) is compareable. With 22 functional groups the maximum peaks are at 42 m and 15 m with submaxima at 21 m, 8 m and 2 m, where the simulations with 5 functional groups show maxima at 42 m, 9 m, and three submaxima at 21 m, 15 m and 2 m (see Fig. 10A).

The composition of species groups in the forest as simulated for the 22 functional groups is presented in Fig. 12 and 13. The stem volume of nearly every group varies widely. This happens due to competition processes for light and space on the small area of one hectare, and was expected in that way (Whitemore, 1990). Some groups (1, 3, 14 and 20) tend to dominate the stand while others (9, 11, 12, 18) are represented on a low level. The pioneer species (group 13) shows the typical behaviour which is a dramatic increase after the creation of a canopy gap (e. g. in year 105, 240 and 345) followed by a decline of stem volume within the next 25 years. In spite of the competitions with widely varying stem volumes for most functional groups it is surprising that the aggregated stem volumes (Fig. 11B) are very stable.

To understand how sensitive the model FORMIND reacts to the number of functional groups one might as well reduce this number down to one. In this case the modelled forest reaches the same steady state but much faster. It indicates that pioneer species seem to regulate the succession process, but the total amount of living biomass depends mostly on the functional groups which include mainly dipterocarp trees. This approach of simplification shows that first results can be achieved with rough assumptions but the more detailed the model is the more detailed information can be extracted out of the results. As far as accuracy is concerned one might like to model a rain forest with as much functional groups as possible. But the modeller has to consider as well the restrictions which are put onto his model by data and knowledge availability about rain forest growth and the possibilities of output analysis. Within this context it seems that a proper classification in few functional groups does not lead to results which are less precise but to a loss of information which is available with a classification in more functional groups.

It should be highlighted that the simulations with 22 species groups were undertaken with a parametrisation, in which only parameters were altered from the 5 species group situation for which data are available for 22 functional groups. This seems to be suitable because these altered parameters belong mainly to the submodel 'Photoproduction' which influences the results strongly as sensitivity analysis has shown. With this knowledge the results can be understood as a representation of trends in terms of dynamic development which might differ little in detail but not in their main features when further parameter research would be undertaken.

6 Conclusions

Simulations with the model FORMIND are able to describe the growth development of tropical rain forest. We have discussed in detail the results for a primary forest stand in Sabah, Malaysia.

The comparison between simulation results with different group classifications supports the approach of FORMIX3 which uses a classification into five species groups. Studies with only very few (here five) functional groups can lead to acceptable results in various important features of tropical rain forests. The capacity of the ecosystem in form of the total stem volume does not depend on the classification as well as the composition of the five functional groups in the stand. Even the diameter distribution and the crown closure are similar and independent of the classifications. Further studies show that the leaf area index is independent as well. A similar result concerning the approach of modelling with few functional groups was achieved by Bugmann (1996) for temperate and boreal forests. He classified 30 and 72 tree species respectively into 6 functional groups.

Nevertheless a simulation with significantly more groups can produce some additional features including interspecific competition and extinction processes, which can not be achieved with a small number of groups. Depending on the objective of a study one has to choose which is the most appropriate classification. As far as we understand modelling processes for tropical forests, results achieved with many functional groups are not automatically more precise than those obtained with few groups. For an appropriate choice of the number of groups to be distinguished one has to keep in mind that the effort of parametrising a classification into more than 10 groups is overwhelming.

In spite of the promising results discussed above some improvements of the model are desirable. With the approach of a constant seed bank (see section 3.2.5) functional groups can not become extinct. Extinction of species is observed in nature (Whitmore, 1990) even in large areas of 50 hectares (Condit, 1995). Therefore an improvement of the model involves new approaches concerning the recruitment of seedlings as well as further distinctions of some group parameters. Particularly the development of different height-diameter relations including the potential height h_M for all 22 groups would lead to a new model quality. Another improvable part of the model is the submodel 'Tree Geometry'. In this version the geometric relations are nearly independent of tree size. Modification in the relation of crown diameter to crown length is one approach to model size dependent changes. Further characteristics might include a variable leaf area index for the individual tree. Because the recruitment of small trees influences the longterm behaviour of the stand a lot, it is well worth improving the model parts which determine the stem number of small trees.

Based on the work presented here studies with different scopes can be performed with the model. The effects of tree logging can be examined as a function of logging strategy and logging cycle. If the recruitment of seedlings is coupled to the present stand a simulation of large areas can analyse the spatial structure of gap dynamics and the minimum size of undisturbed rain forest can be evaluated to guarantee a maximum species richness. Natural extinction processes can be analysed, especially through simulations with a large number of functional groups.

7 References

- Bossel, H., 1991. Modelling forest dynamics: Moving from description to explanation. For. Ecol. Manage., 42: 129-142.

- Bossel, H., 1994. TREEDYN3 Forest simulation model, mathematical model, program documentation, and simulation results. *Berichte des Forschungszentrums Waldökosysteme der Universität Göttingen*, Vol. B 35, Göttingen, 118 pp.
- Bossel, H. and Krieger, H., 1991. Simulation model of natural tropical forest dynamics. *Ecol. Model.*, 59: 37-71.
- Bossel, H. and Krieger, H., 1994. Simulation of multi-species tropical forest dynamics using a vertically and horizontally structured model. *For. Ecol. Manage.*, 69: 123-144.
- Botkin, D.B., Janak, J.F. and Wallis, J.R., 1972. Some ecological consequences of a computer model of forest growth. *J. Ecol.*, 60: 849-872.
- Brokaw, N.V.L., 1985. Gap-Phase regeneration in a tropical forest. *Ecology*, 66: 682-687.
- Bugmann, H.K.M., 1994. On the ecology of mountainous forests in a changing climate: A simulation study PhD thesis no. 10638, Swiss Federal Institute of Technology Zürich, Switzerland, 258 pp.
- Bugmann, H., 1996. Functional types of trees in temperate and boreal forests: Classification and testing. *Journal of Vegetation Science*, 7: 359-370.
- Burgess, P.F., 1961. The structure and composition of lowland tropical rain forest in North Borneo. *Malaysian Forestry* 1, 24: 66-80.
- Cockburn, P. F., 1980. Trees of Sabah I and II. In: *Sabah Forest Record*, 10. Forest Department, Sandakan, Sabah, 385 pp.
- Condit, R., 1995. Research in large, long-term tropical forest plots. *TREE*, 10(1): 18-21.
- Condit, R., Hubbell, S.P. and Foster, R.B., 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecol. Monogr.*, 65(4): 419-439.
- Crome, F.H.J., Moore, L.A. and Richards, G.C., 1992. A study of logging damage in upland rainforest in North Queensland. *For. Ecol. Manage.*, 49: 1-29.
- Deutscher Forstverein (Editor), 1986. *Erhaltung und nachhaltige Nutzung tropischer Regenwälder*. Forschungsbericht des Bundesministeriums für wirtschaftliche Zusammenarbeit, 74, Weltforum-Verlag, Köln, 246 pp.
- Ditzer, T. and Huth, A., 1995. Simulation of structural dynamics in Dipterocarp rain forest. Center for Environmental Systems Research, University of Kassel, Kassel, 41 pp.
- Ditzer, T., Huth, A. and Bossel, H., 1997. Modeling growth dynamics of tropical rain forest and its disturbance based on functional groups of tree species. *Ecology*, submitted.
- Ellis, A.E., Hubbell, S.P. and Potvin, C., 1997. A physiological basis for ecological groups in a tropical forest. *Ecology*, in press.
- Eschenbach, C., 1994. Photosynthesis rates of selected tree species. Malaysian-German Sustainable Forest Management Project, Sabah, Malaysia, Center for Environmental Systems Research, University of Kassel, Kassel, 62 pp.
- Hubbell, S.P. and Foster, R.B., 1986. Canopy gaps and the dynamics of a neotropical forest. In: M.J. Crawley (Editor), *Plant ecology*, Blackwell Scientific Publications, Oxford, pp. 77-96.

- Huston, M., DeAngelis, D. and Post, W., 1988. New computer models unify ecological theory. *BioSci.* 10, 38: 682-691.
- Huth, A., Ditzer, T. and Bossel, H., 1996. Simulation of the growth of tropical rain forests (final report for GTZ). Center for Environmental Systems Research, 9602, University of Kassel, Kassel, 180 pp.
- Judson, O.P., 1994. The rise of the individual-based model in ecology. *TREE*, 9: 9-14.
- Kato, R., Tadaki, Y. and Ogawa, H., 1978. Plant biomass and growth increment studies in Pasoh Forest. *Malay. National Journal*, 30: 211-224.
- Kira, T., 1975. Primary production of forests. In: J.P. Cooper (Editor), *Photosynthesis and productivity in different environments*, Cambridge University Press, Cambridge, pp. 5-40.
- Kira, T., 1978. Community architecture and organic matter dynamics in tropical lowland rain forests of Southeast Asia with special reference to Pasoh Forest, West-Malaysia. In: P.B. Tomlinson and M.H. Zimmermann (Editors), *Tropical Trees as Living Systems. Proceedings, 4th Cabot Symposium*, Harvard Forest, University Press, Cambridge, Mass., pp. 26-30.
- Köhler, P. and Huth, A. 1997. An individual based rain forest model - concepts and simulation results. In: A. Kastner-Maresch, W. Kurth and M. Sonntag (Editors), *Proceedings of the workshop on modelling approaches for forest ecosystems*, Wallenfels, 1996, Bayreuther Forum "Ökologie, 52, Bayreuth.
- Liu, J. and Ashton, P.S., 1995. Individual-based simulation models for forest succession and management. *For. Ecol. Manage.*, 73: 157-175.
- Monsi, M. and Saeki, T., 1953. Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Jap. J. Bot.*, 14: 22-52.
- Newbery, D.McC., Campbell, E.J.F., Lee, Y.F., Ridsdale, C.E. and Still, M.J., 1992. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia: structure, relative abundance and family composition. *Phil. Trans. R. Soc. Lond.*, B335, pp. 341-356.
- Nicholson, D.I., 1979. The effects of logging and treatment on the mixed dipterocarp forests of South East Asia. Food and Agriculture Organization of the United Nations, Rome, 65 pp.
- Ong, R.C. and Kleine, M., 1995. DIPSIM: A dipterocarp forest growth simulation model for Sabah. *FRC Research Papers 2*, Forestry Department, Sabah, Malaysia, 94 pp.
- Phillips, O.L. and Gentry, A.H., 1994. Increasing turnover through time in tropical forests. *Science*, 263: 954-958.
- Poker, J., 1993. Struktur und Dynamik des Bestandesmosaik tropischer Regenwälder Mitteilungen der Bundesanstalt für Forst- und Holzwirtschaft, Nr. 174, Wiedebusch Verlag, Hamburg, 221 pp.
- Richards, P.W., 1936. Ecological observations on the rain forest of Mount Dulit, Sarawak, Part I and II. *J. Ecol.*, 24: 1-37, 340-360.
- Richards, P.W., 1952. *Tropical rain forest*. Cambridge University Press, Cambridge, 450 pp.

- Riswan, S. and Hartanti, L., 1995. Human impacts on tropical forest dynamics. *Vegetatio* 121:41-52.
- Rollet, B., 1978. Organisation. In: UNESCO, UNEP and FAO (Editors), *Tropical forest ecosystems. A state of knowledge report.* UNESCO-UNEP, Paris, pp. 112-142.
- Schlenzog, M., 1997. Experimentelle Untersuchung des Lichtklimas in Urwaldparzellen Nordborneos. *Göttinger Beiträge zur Land- und Forstwirtschaft in den Tropen und Subtropen*, Verlag Erich Goltze, Göttingen, 152 pp.
- Shugart, H.H., 1984. *A theory of forest dynamics.* Springer, New York, 278 pp.
- Swaine, M.D., 1989. Population dynamics of tree species in tropical forests. In: L.B. Holm-Nielsen, I.B. Nielsen and H. Balslev, *Tropical forests: Botanical dynamics, speciation and diversity*, Academic Press, London, pp. 101-110.
- Terborgh, J., 1993. *Lebensraum Regenwald - Zentrum biologischer Vielfalt.* Spektrum Akademischer Verlag, Heidelberg, 253 pp.
- Terborgh, J. and Petren, K., 1991. Development of habitat structure through succession in an Amazonian floorplain forest. In: S.S. Bell, E.D. McCoy and H.R. Mushinsky, *Habitat structures: The physical arrangement of objects in space*, Chapman and Hall, London, pp. 28-46.
- Thornley, J.H.M., 1976. *Mathematical models in plant physiology.* Academic Press, New York, 320 pp.
- Vanclay, J.K., 1991. Aggregating tree species to develop diameter increment equations for tropical rain forest. *For. Ecol. Manage.*, 42: 143-168.
- Vanclay, J., 1994. *Modelling forest growth and yield: Applications to Mixed Tropical Forests.* CAB International, Wallingford, 312 pp.
- Van der Meer, P.J. and Bongers F., 1996. Patterns of tree-fall and branchfall in a tropical rain forest in French Guiana. *J. Ecol.*, 84: 19-29.
- Weidelt, H.-J., 1986. *Die Auswirkungen waldbaulicher Maßnahmen auf die Entwicklung exploitierter Dipterocarpaceen-Wälder.* Institut für Waldbau, Universität Göttingen, 166 pp.
- Weidelt, H.-J., 1993. Some effects of selective logging on forest productivity and ecology. In: H. Lieth, and M. Lohmann (Editors), *Restoration of tropical forest ecosystems*, Kluwer Academic Publishers, Amsterdam, pp. 155-161.
- Whitmore, T.C., 1988. The influence of tree population dynamics on forest species composition. In: A.J. Davis, M.J. Hutchings and A.R. Watkinson (Editors): *Population biology of plants.* Blackwell, Oxford, pp. 271-291.
- Whitmore, T.C., 1990. *Tropical rain forest.* Clarendon Press, Oxford, 226 pp.

A Figures

Fig. 1: Concepts used for dividing the simulation area in hectares and plots.

Fig. 2: Overview of the interactions of the submodels and the dependencies on the main variables *biomass* B and *tree number* N . Arrows indicate whether the results of one submodel influences the calculations of another submodel.

Fig. 3: Functional dependencies in the submodel 'Tree Geometry'; A: relationship between the form factor γ and biomass B of a tree; B: height-diameter-relation $h(d)$; C: relative crown length c_P as a function of tree height h ; D: modified crown diameter to stem diameter ratio $s(d)$ in relation to stem diameter.

Fig. 4: A typical tree of the model is shown including the relevant geometric dimensions.

Fig. 5: Functional dependencies in the submodel 'Carbon Cycle'; A: Light response curve and B: height depending specific respirationrate $R_P(h)$ of emergent trees.

Fig. 6: Shading of neighbouring trees in one plot. Tree 1 is shading tree 3, but not tree 2. Tree 2 is not shading tree 3.

Fig. 7: Mortality rate M_N as a function of diameter increment dz (after Swaine 1989).

Fig. 8: Simulation results for the development of primary dipterocarp rain forest with 5 functional groups; A: dynamic distribution of growth stages; B: dynamic behaviour of stem volume ($d \geq 10$ cm); C: stem number in diameter classes at the beginning of the simulation and after 500 years of simulation; D: dynamic behaviour of stem numbers ($d \geq 10$ cm). Discussion in the text.

Fig. 9: Cumulative leaf area index at different times of simulation. The height of $h = 10$ m marked by a line in the graph corresponds to trees with $d = 10$ cm. Discussion in the text.

Fig. 10: Crown closure at different times of simulation and different growth stages. A: primary forest; B: secondary forest.

Fig. 11: Simulation results for a primary dipterocarp rain forest with 22 functional groups; A: dynamic distribution of growth stages; B: dynamic behaviour of stem volume ($d \geq 10$ cm) for the aggregated 5 growth groups; C: stem number in diameter classes at the beginning of the simulation and after 500 years of simulation; D: crown closure in primary forest. Discussion in the text.

Fig. 12: Development of species composition over time in simulations with 22 functional groups (group 1-11), mainly dipterocarp. Dynamic behaviour of the stem volume ($d \geq 10$ cm).

Fig. 13: Development of species composition over time in simulations with 22 functional groups (group 12-22), mainly non-dipterocarp. Dynamic behaviour of the stem volume ($d \geq 10$ cm).

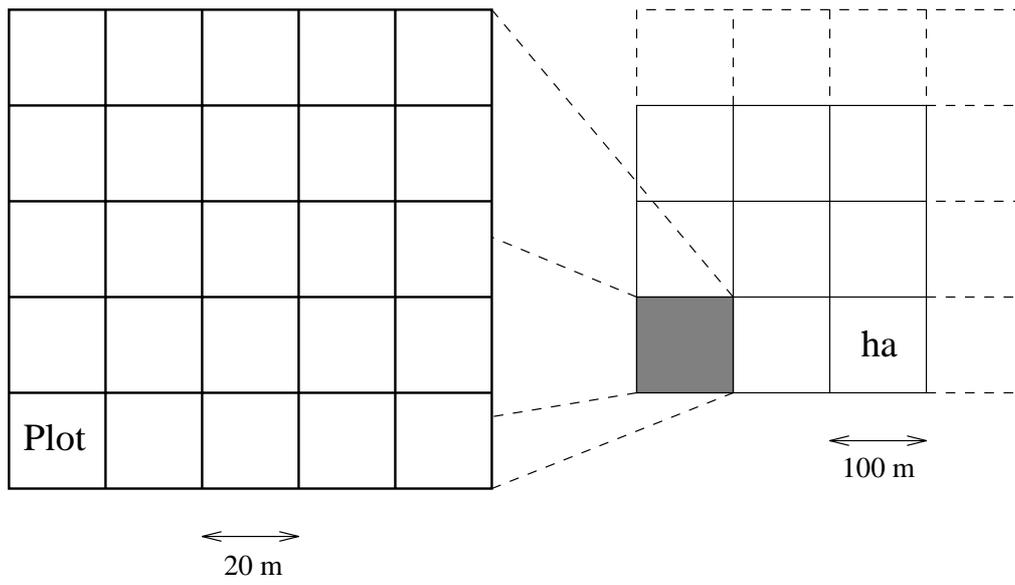


Figure 1:

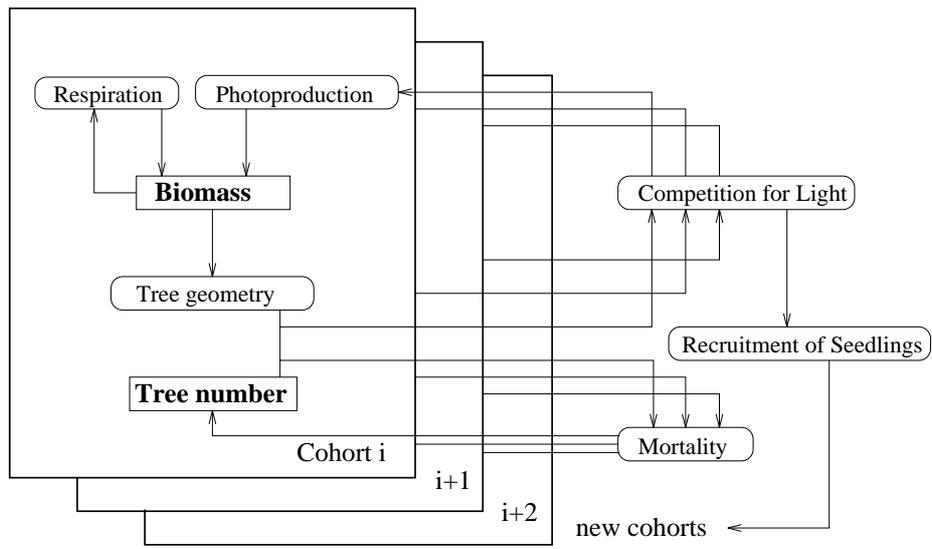


Figure 2:

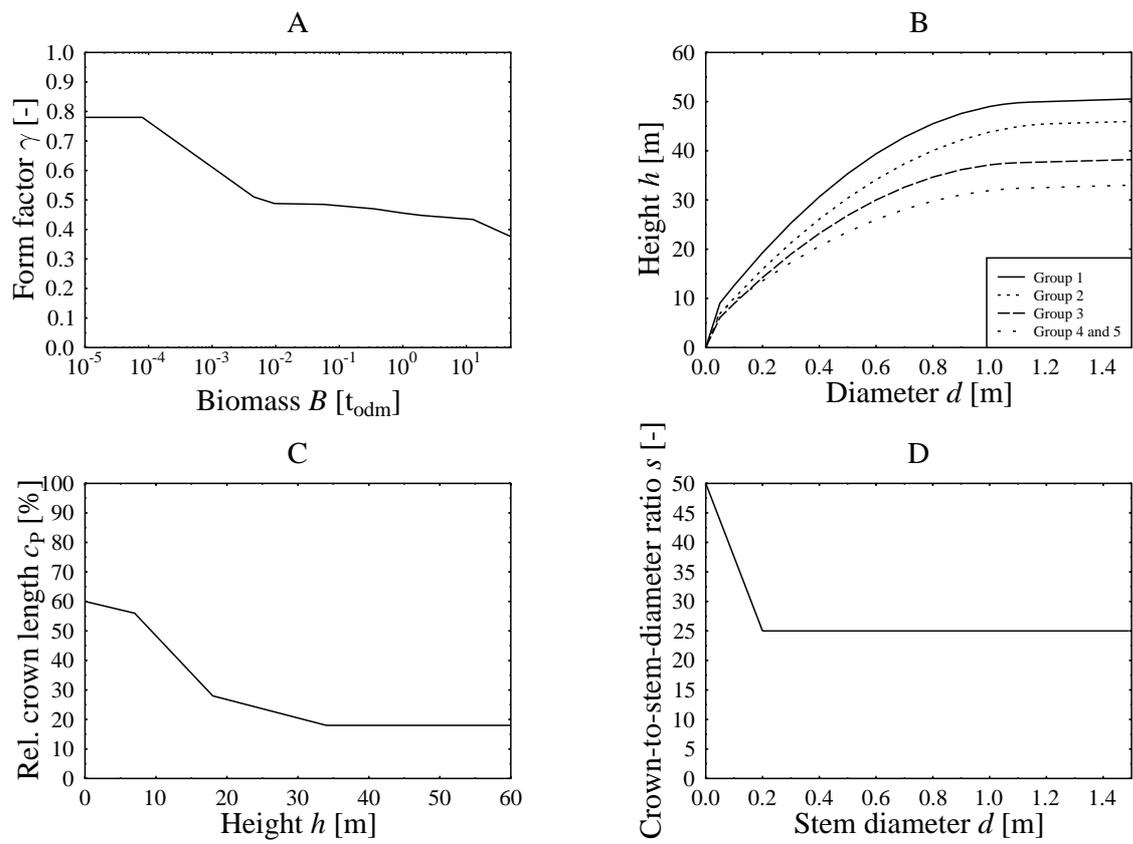


Figure 3:

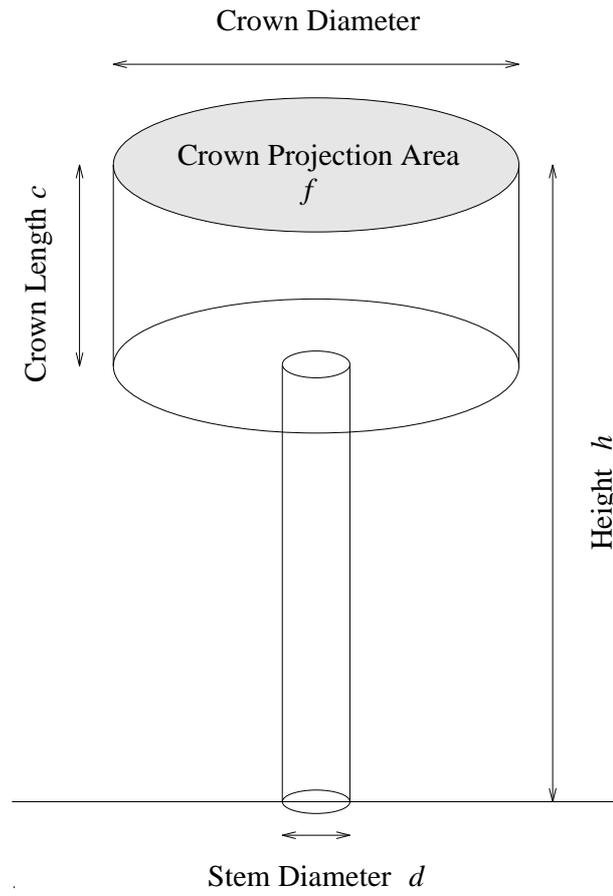


Figure 4:

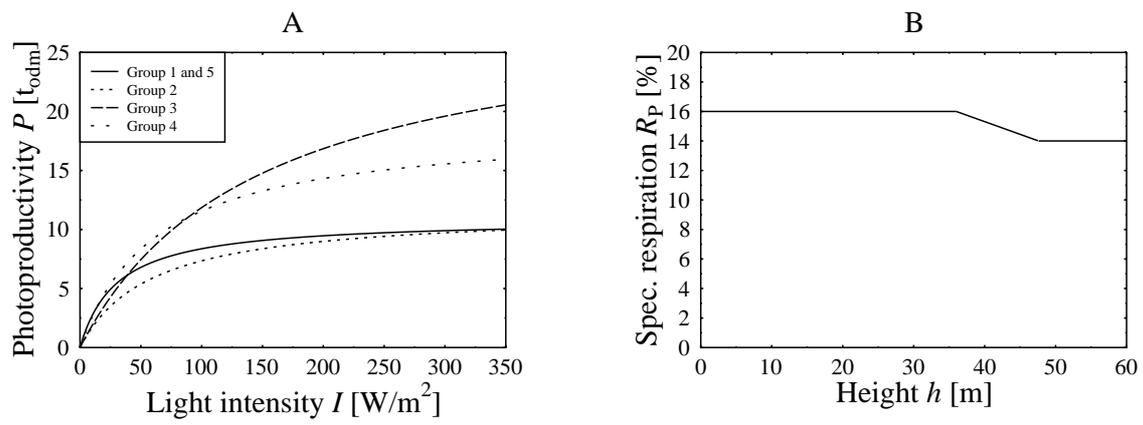


Figure 5:

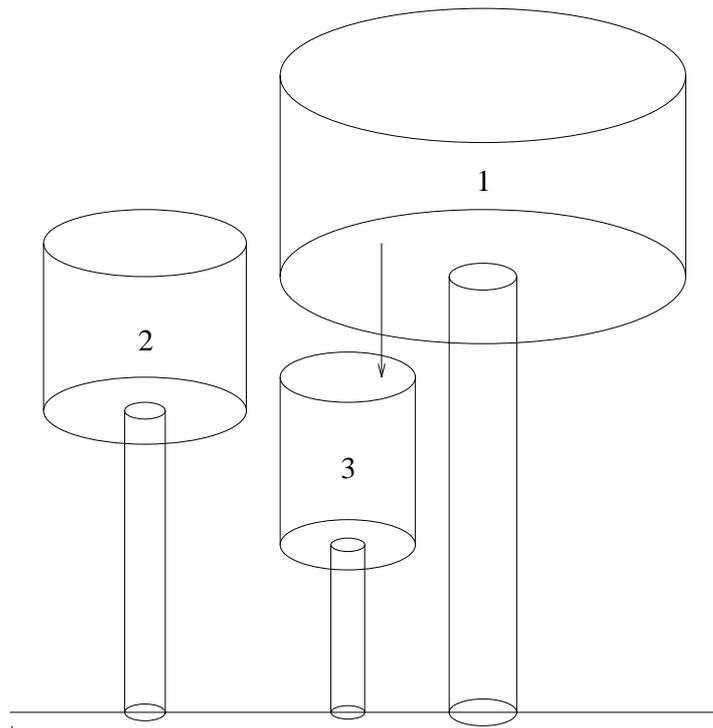


Figure 6:

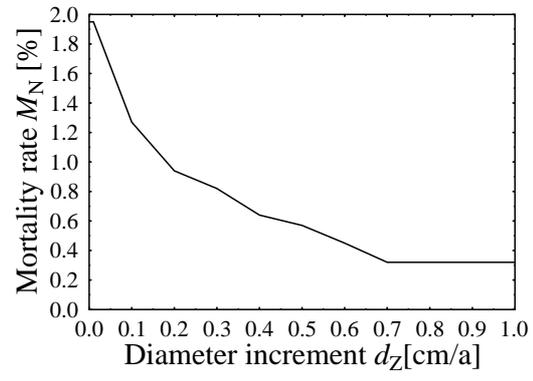


Figure 7:

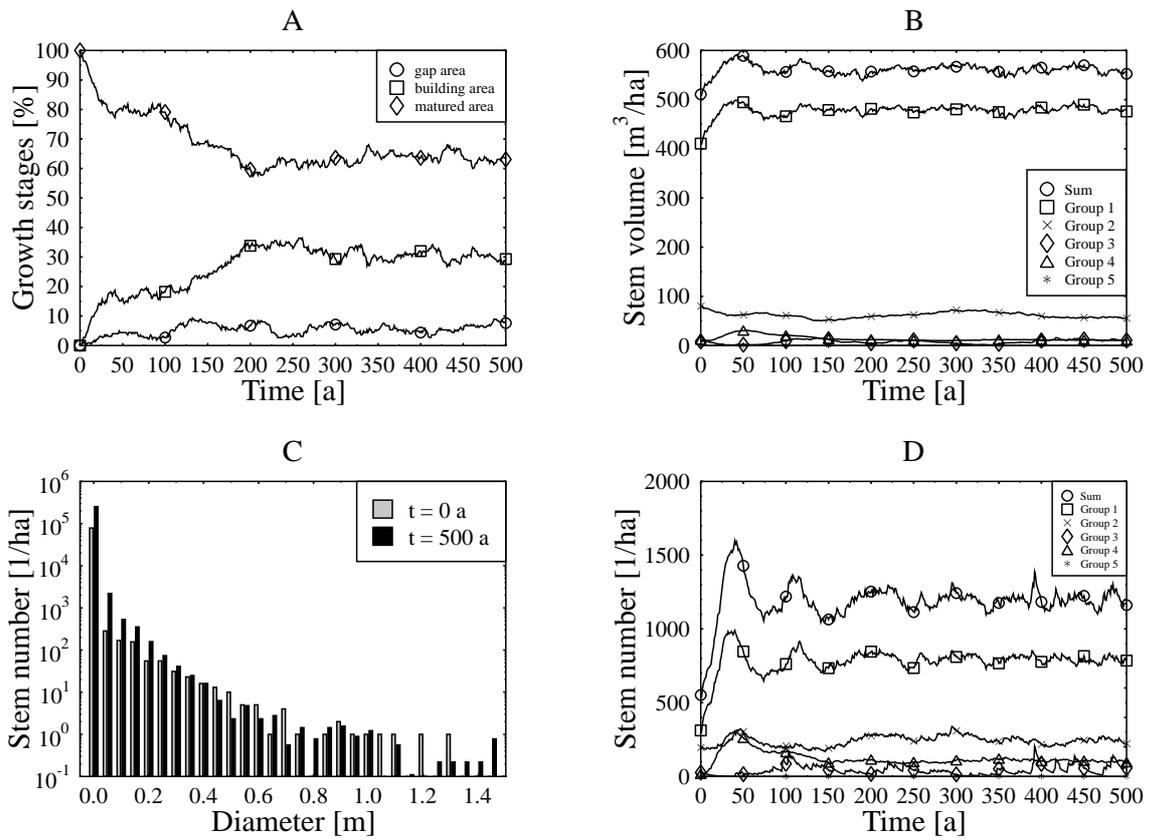


Figure 8:

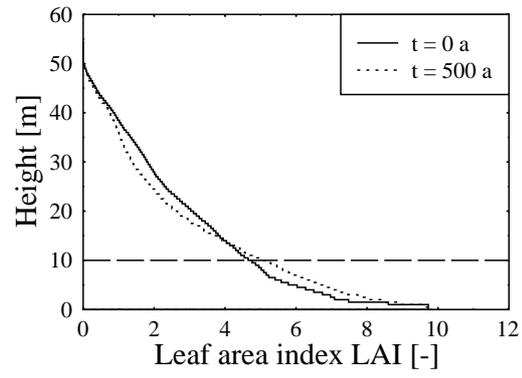


Figure 9:

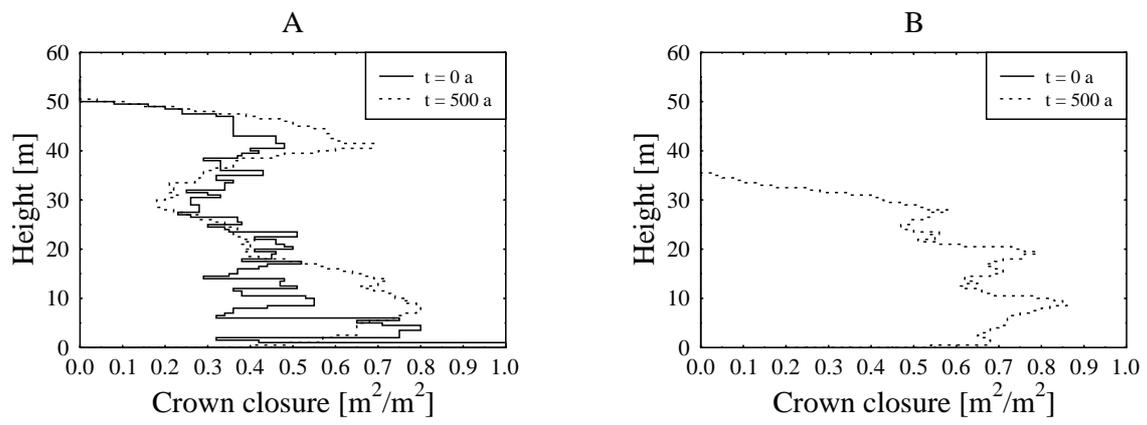


Figure 10:

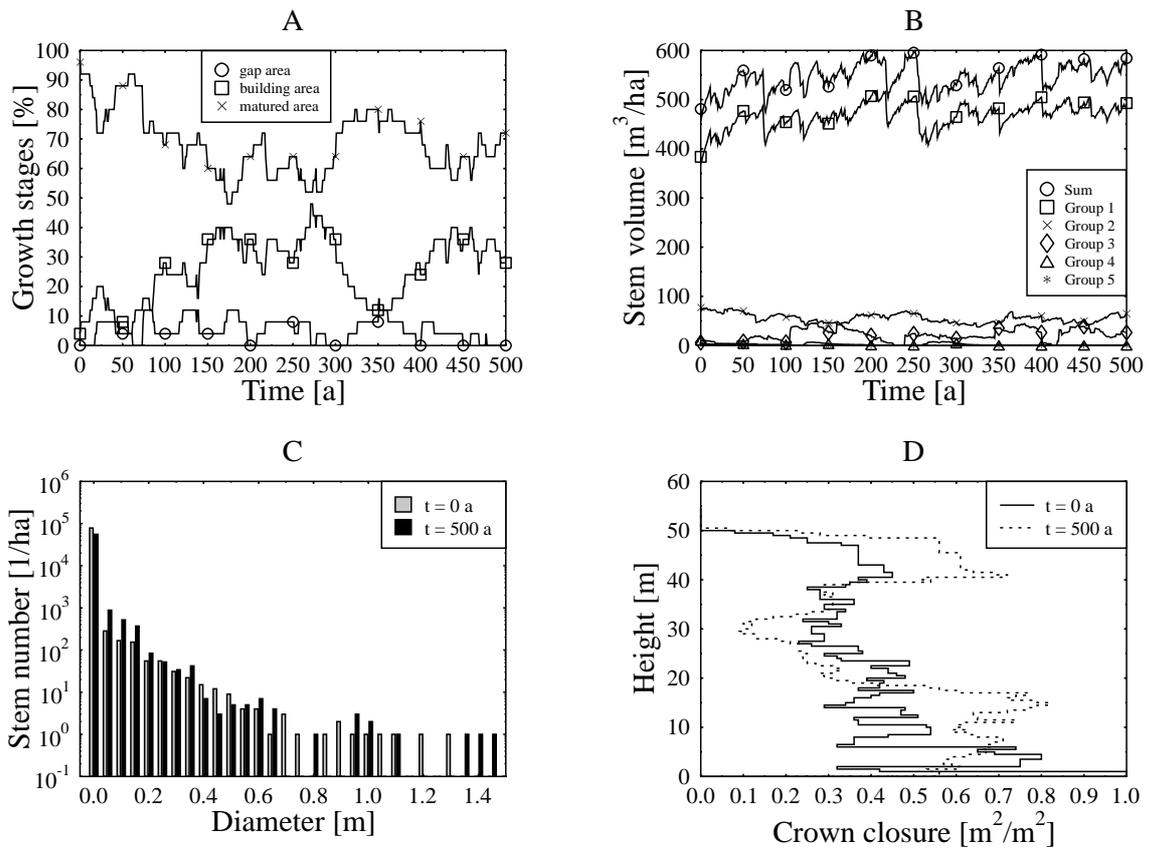


Figure 11:

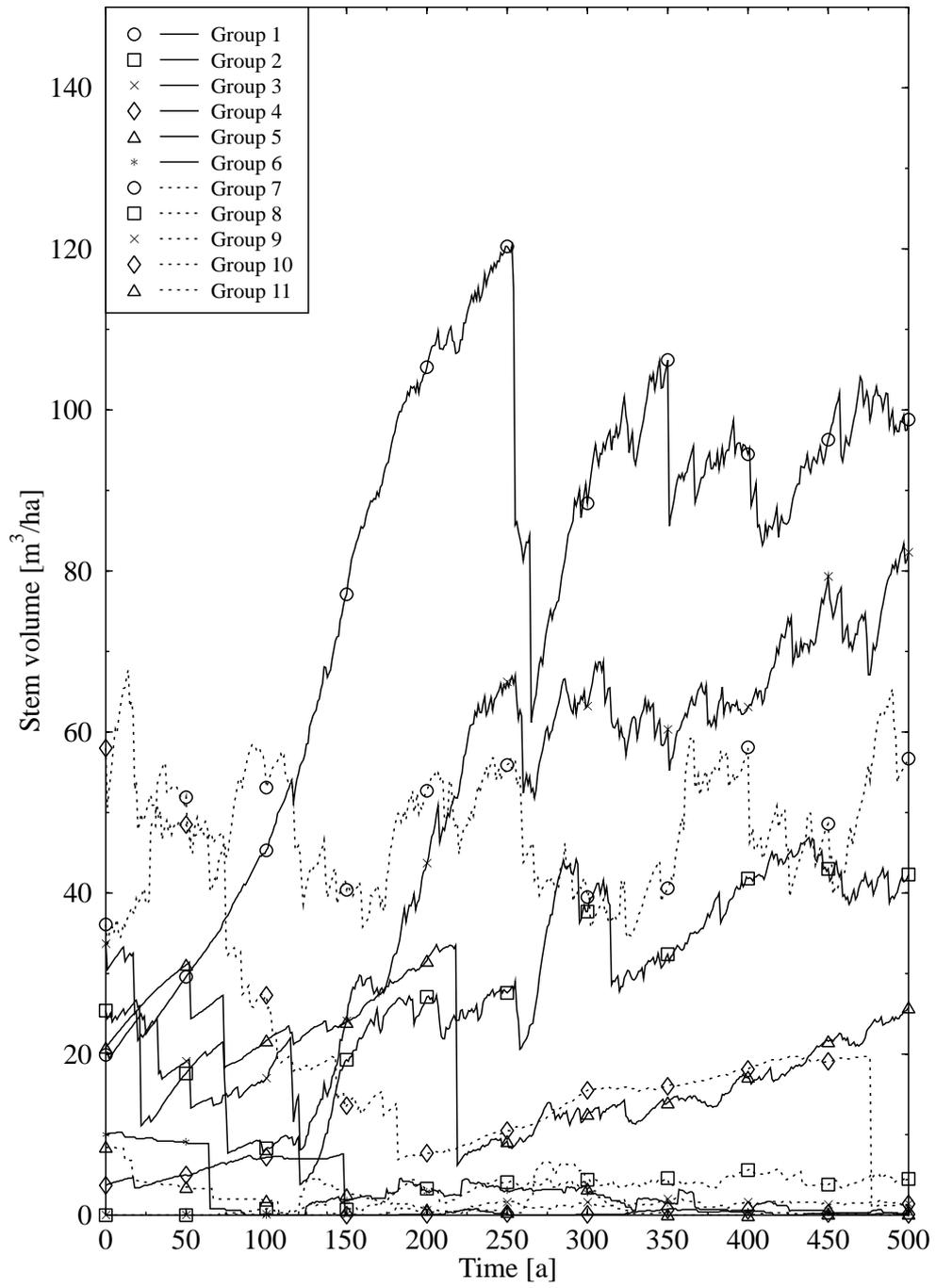


Figure 12:

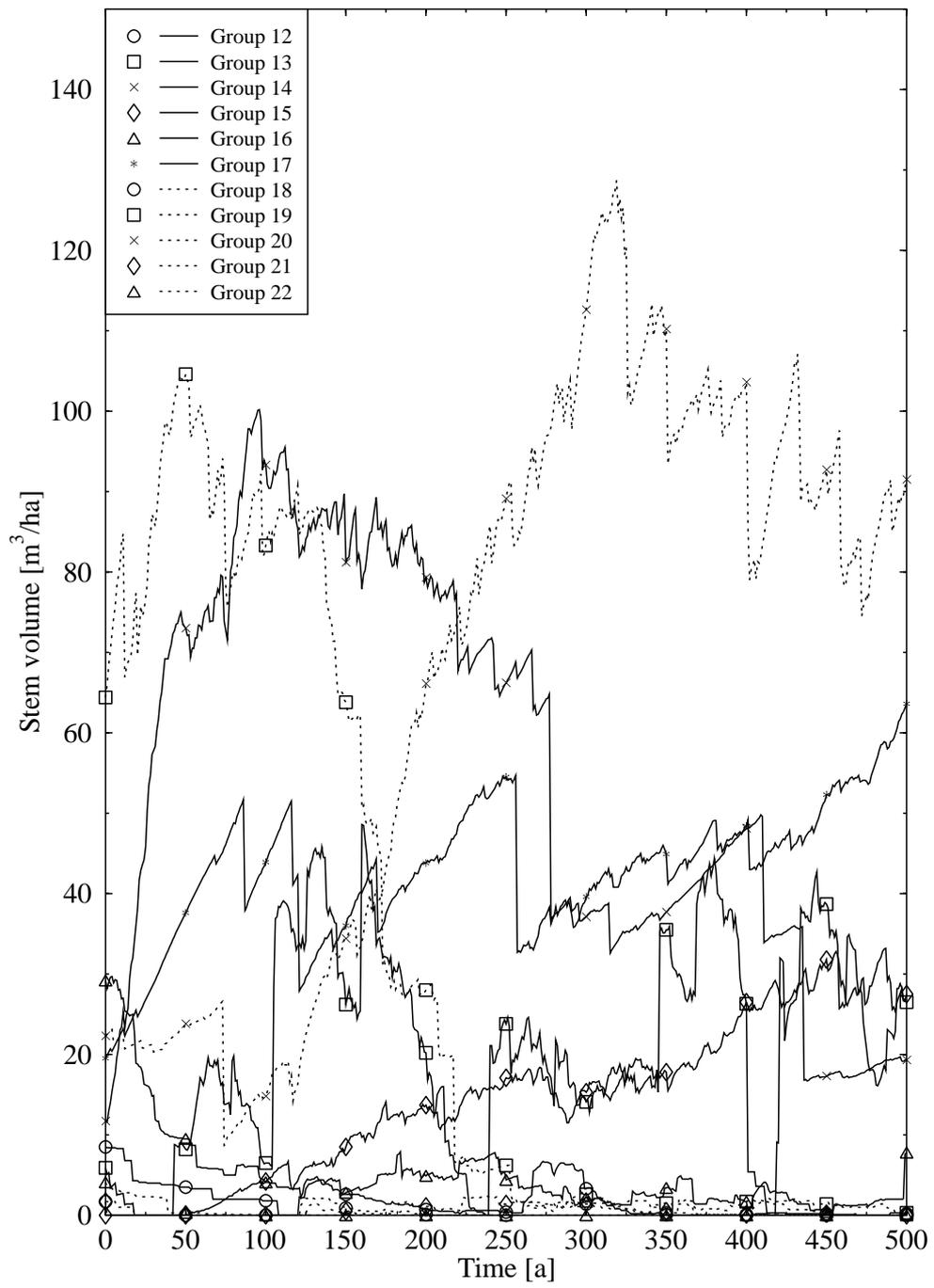


Figure 13:

B Tables

Table 1: Aggregation of tree species into growth groups after Ong and Kleine (1995), Ditzer and Huth (1995). The main species of the groups are mentioned by local and botanical name. The columns labeled No_5 and No_{22} correspond to the respective functional group in the model with a classification into 5 or 22 groups respectively. The column *Species* tells how many tree species are aggregated together in each group.

No_5	No_{22}	Local Name	Botanical Name	Family	Species	
1	1	Urat mata	Parashorea sp.	Dipterocarpaceae	4	
	2	Seraya majau	Shorea johorensis	Dipterocarpaceae	17	
	3	Seraya tembaga	Shorea leprosula	Dipterocarpaceae	9	
	4	Keruing putih	Dipterocarpus caudiferus	Dipterocarpaceae	25	
	5	Kapur paji	Dryobalanops lanceolata	Dipterocarpaceae	10	
	8	Seraya daun mas	Shorea argentifolia	Dipterocarpaceae	4	
	9	Seraya kelabu	Shorea waltonii	Dipterocarpaceae	4	
	10	Selangan batu	Shorea sp.	Dipterocarpaceae	22	
	11	Seraya melantai	Shorea macroptera	Dipterocarpaceae	14	
	14	Sepetir	Sindora irpicina etc.	Leguminosae	191	
	15	Terap	Artocarpus & Parartocarpus spp.	Moraceae	14	
	17	Takalis	Pentace sp.	Tiliaceae	12	
	19	Kembang	Heritiera simplicifolia etc.	Sterculiaceae	35	
	20	Berangan	Castanopsis sp.	Fagaceae	12	
	2	6	Seraya kuning barun	Shorea xanthophylla	Dipterocarpaceae	11
		7	Selangan jangkang	Hopea nervosa	Dipterocarpaceae	37
		16	Takalis daun halus	Pentace laxiflora	Tiliaceae	13
		21	Nyatoh	z.B. Ganua, Madhuca, Palaquium, Payena sp.	Sapotaceae	1
	3	13	Macaranga	Macaranga	Euphorbiaceae	10
	4	12	Obah	Eugenia sp.	Myrtaceae	7
18		Karpus	Hydnocarpus	Flacourtiaceae	16	
5	22	Miscellaneous				

Table 2: Characteristics of the aggregated functional groups, after Ditzer und Huth (1995). The column labeled No_5 corresponds to the groups in a classification in 5 functional groups.

Functional Group No_5	Potential Height	Lightdemand	Description
1	55 m	shade tolerant	emergents, climax species
2	36 m	shade tolerant	climax species
3	25 m	light demanding	pioneer species
4	15 m	shade tolerant	climax species
5	1.3 m	shade tolerant	herbs, farns, shrubs climbers, grases, etc.

Table 3: Parametrisation (5 growth groups) for a dipterocarp lowland rain forest in Deramakot Forest Reserve in Sabah (Borneo), Malaysia

Name	Description	Functional Groups				
		1	2	3	4	5
Submodel tree geometry						
a_{0j}	Coefficient of height-diameter relationship [m]	2.94	2.30	1.97	3.11	3.11
a_{1j}	Coefficient of height-diameter relationship [m/cm]	0.42	0.42	0.39	30	0.30
a_{2j}	Coefficient of height-diameter relationship [m/cm ²]	-0.002	-0.002	-0.002	-0.001	-0.001
s_j	Crown-to-stem-diameter-relation [-]	25	25	25	25	25
ρ_j	Wood density [t _{odm} /m ³]	0.62	0.57	0.37	0.71	0.62
τ_j	Fraction of stemwood to total biomass [-]	0.7	0.7	0.7	0.7	0.7
h_{Mj}	Potential height [m]	55	36	25	15	1.3
Submodel recruitment of seedlings						
B_{Sj}	Biomass of seedling [g _{odm}]	10	10	10	10	10
N_{Sj}	Number of seedlings per year and plot [1/a · 400 m ²]	2500	4000	6000	700	700
I_{Sj}	Minimal light intensity for germination [W/m ²]	1	1	50	1	1
Submodel carbon cycle						
P_{Mj}	Maximum photoproductivity [mgCO ₂ /(dm ² · h)]	10.9	11.6	29.1	18.8	10.9
α_j	Slope of light response curve [mgCO ₂ · m ² /(dm ² · h · W)]	0.36	0.20	0.20	0.30	0.36
\widetilde{LAI}_j	Leaf area index of single tree [-]	2	2	2	2	2
R_{Pj}	Spec. respiration (biomass losses relative to total biomass) [1/a]	0.16	0.16	0.16	0.16	0.16
Submodel mortality						
M_{Wj}	Weighting factor for normal mortality [-]	1	1	8	1	1
M_{Yj}	Spec. mortality rate of seedlings [1/a]	0.08	0.08	0.16	0.08	0.08
M_{Cj}	Spec. mortality rate due to crowding [1/a]	0.04	0.04	0.08	0.04	0.04
M_{CYj}	Spec. mortality rate of seedlings due to crowding [1/a]	0.32	0.32	0.32	0.32	0.32
Species independent parameters						
I_0	Light intensity above canopy [W/m ²]	335				
k	Light extinction coefficient [-]	0.7				
W	Probability for a dying tree to fall [-]	0.4				

Table 4: Parametrisation (22 growth groups) for a dipterocarp lowland rain forest in Deramakot Forest Reserve in Sabah (Borneo), Malaysia. The parameters of the height-diameter-relation of each of the 22 groups (No_{22}) are those of the respective 5 groups (No_5) denoted in Table 3. For detailed description of the parameters see Table 3.

Parameter	Unit	No ₂₂	1	2	3	4	5	6	7	8	9	10	11
		No ₅	1	1	1	1	1	2	2	1	1	1	1
Submodel tree geometry													
s_j	-		25	25	25	25	25	25	25	25	25	25	25
ρ_j	t _{odm} /m ³		0.55	0.48	0.55	0.72	0.67	0.54	0.60	0.60	0.50	0.94	0.47
τ_j	-		0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7
h_{Mj}	m		55.0	55.0	55.0	55.0	55.0	36.0	36.0	55.0	55.0	55.0	55.0
Submodel recruitment of seedlings													
B_{Sj}	g _{odm}		10	10	10	10	10	10	10	10	10	10	10
N_{Sj}	1/a · 400 m ²		180	180	180	180	180	1000	1000	180	180	180	180
I_{Sj}	W/m ²		1	1	1	1	1	1	1	1	1	1	1
Submodel carbon cyle													
P_{Mj}	mgCO ₂ /(dm ² · h)		9.7	8.4	9.7	12.6	11.8	11.0	12.2	10.5	8.8	16.5	8.3
α_j	mgCO ₂ · m ² /(dm ² · h · W)		0.36	0.31	0.36	0.36	0.41	0.20	0.30	0.36	0.28	0.41	0.26
LAI_j	-		2	2	2	2	2	2	2	2	2	2	2
R_{Pj}	1/a		0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16
Submodel mortality													
M_{Wj}	-		1	1	1	1	1	1	1	1	1	1	1
M_{Yj}	1/a		0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08
M_{Cj}	1/a		0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
M_{CYj}	1/a		0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32
		No ₂₂	12	13	14	15	16	17	18	19	20	21	22
		No ₅	4	3	1	1	2	1	4	1	1	2	5
Submodel tree geometry													
s_j	-		25	25	25	25	25	25	25	25	25	25	25
ρ_j	t _{odm} /m ³		0.68	0.37	0.63	0.56	0.48	0.65	0.737	0.65	0.70	0.67	0.62
τ_j	-		0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7
h_{Mj}	m		15.0	25.0	55.0	55.0	36.0	55.0	15.0	55.0	55.0	36.0	1.3
Submodel recruitment of seedlings													
B_{Sj}	g _{odm}		10	10	10	10	10	10	10	10	10	10	10
N_{Sj}	1/a · 400 m ²		350	6000	180	180	1000	180	350	180	180	1000	700
I_{Sj}	W/m ²		1	50	1	1	1	1	1	1	1	1	1
Submodel carbon cyle													
P_{Mj}	mgCO ₂ /(dm ² · h)		18.0	29.1	11.1	9.8	9.3	11.4	19.5	11.4	12.2	13.6	10.9
α_j	mgCO ₂ · m ² /(dm ² · h · W)		0.31	0.20	0.36	0.36	0.20	0.41	0.30	0.36	0.46	0.2	0.41
LAI_j	-		2	2	2	2	2	2	2	2	2	2	2
R_{Pj}	1/a		0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16
Submodel mortality													
M_{Wj}	-		1	8	1	1	1	1	1	1	1	1	1
M_{Yj}	1/a		0.08	0.16	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08
M_{Cj}	1/a		0.04	0.08	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
M_{CYj}	1/a		0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32
Species independent parameters													
I_0	W/m ²		335										
k	-		0.7										
W	-		0.4										