An individual based rain forest model - concepts and simulation results.[1]

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Abstract

In this article a model is presented to simulate the growth of tropical rain forests. The model is individual based. Trees of the same diameter class are performed in one cohort. The main part of the model is the competition for light in plots of 20 m × 20 m in size. A carbon cycle is calculated including processes like photosynthesis and respiration. Due to 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 are creating. Some simulation results for a primary lowland dipterocarp rain forest in Sabah, Malaysia are discussed. The results can be interpreted that rain forests grow in a layer structure. The model has the potential to analyse spatial structure of gap formation in rain forests as well as to simulate a huge number of different species groups. The analysis of logging scenarios can estimate the effects of human impacts in tropical rain forests.

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

1 Introduction

Global industrialisation, increase in population and the reduction of natural resources are threatening ecosystems all around the world. Climate change is one result of this development. There are strong evidences that intact forests can play an important role in keeping the global system in balance. They are the biggest carbon sink above the soil and include about 475 to 825 billion tons of carbon currently (Deutscher Bundestag 1990). The increasing input of carbondioxid in the atmosphere is estimated to seven billion tons per year, from which 20 % are caused by deforestation (Deutscher Bundestag 1994).

Beside the importance of tropical rain forests for climate change, 75 to 90 % of the global biodiversity are to be found in this ecosystem type (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 conserve 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. It only has been in the past few years, that 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

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of data from field measurements, which are necessary to validate a growth model. The model structures for temperate and tropical forests are different. In the first case monospecic evenaged forests are often 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 special processes, i. e. the falling of big trees and the creation of canopy gaps. In these gaps trees are growing in a cycle of succession. Lightdemanding species, the so called pioneers, are strongly depending on such gaps. They come up in the first cycle and suppress the main climax species. Because of the shortliving of the pioneers the main canopy is filled up again with trees of the climax species after about 50 years (Whitmore 1990).

It is possible to model this succession process by dividing the simulation area in subareas with a size of the crown projection area of a dominant tree (Shugart 1984). Models have shown, that they can produce some acceptable results by aggregating the species richness to a few growth groups (Ong and Kleine 1995; Bossel and Krieger 1991 1994; Huth et al. 1996). Relying on other results in tropical research it is not neccessary to consider nutrient cycles other than the carbon cycle in the regions on Borneo (Weidelt 1993). Because of the level of rain fall without any dry periods in the tropics (Deutscher Bundestag 1990) growth limitations due to water stress is not to be expected, saisonal differences can be omitted (Deutscher Forstverein 1986; Terborgh 1993).

A growth model for tropical rain forest, which takes all these into accout, is the FORMIX 3 - model (Huth et al. 1996). It is calculating the number of trees and their biomasses of five different tree species groups in different height layers, in which the trees have their crown. The following report documents a model, which has some details in common with the FORMIX 3 - model. The new model is individual based, which FORMIX 3 is not, which means, no layers are considered and no calculations with average trees are done. Other advantanges of individual based models are a higher transparency of the processes which are responsible for the forest growth (Huston et al. 1988; Liu and Ashton 1995; Judson 1995). For each tree the received light is calculated in a submodel. The calculation is performed in a cohort structure (Vanclay 1994) which reduces the simulation efforts as much as possible.

One advantage of the high resolution in the canopy is the possibility to discuss the controversial question if tropical forests do have a layer structure (Richards 1952; Terborgh and Petren 1991).

After a detailed documentation of the model some results for a lowland dipterocarp rain forest on Sabah, Malaysia are shown and discussed.

2 Classification of Growth Groups

Due to the high biodiversity in tropical rain forests, an aggregation of trees into growth groups is necessary. A common classification is made by the light demand of the species into two groups. Shade tolerant species are trees whose seedlings could establish under a closed canopy. These trees are normally slow growing. Their crowns are found in the main canopy of the forest and therefore they are called climax species. The second group are pioneers whose seedlings need a minimum of light for germantation which is only found in canopy gaps of a certain size (Whitmore 1990).

A classification in 20 growth groups was made by Ong and Kleine (1995). In table 1 a similar grouping into 22 groups is done. A further aggregation of these groups in five species groups was done by using the potential height and the carbon fixation as two further criteria (Bossel et al. 1993; Ditzer and Huth 1995) (see table 2).

No	Local Name	Botanic Name	Family
1	Urat mata	Parashorea sp.	Dipterocarpaceae
	Seraya majau	Shorea johorensis	Dipterocarpaceae
	Seraya tembaga	Shorea leprosula	Dipterocarpaceae
	Keruing putih	Dipterocarpus caudiferus	Dipterocarpaceae
	Kapur paji	Dryobalanops lanceolata	Dipterocarpaceae
	Seraya daun mas	Shorea argentifolia	Dipterocarpaceae
	Seraya kelabu	Shorea waltonii	Dipterocarpaceae
	Selangan batu	Shorea sp.	Dipterocarpaceae
	Seraya melantai	Shorea macroptera	Dipterocarpaceae
	Sepetir	Sindora irpicina etc.	Leguminosae
	Terap	Artocarpus & Parartocarpus spp.	Moraceae
	Takalis	Pentace sp.	Tiliaceae
	Kembang	Heritiera simplicifolia etc.	Sterculiaceae
	Berangan	Castanopsis sp.	Fagacae
2	Seraya kuning barun	Shorea xanthophylla	Dipterocarpaceae
	Selangan jangkang	Hopea nervosa	Dipterocarpaceae
	Takalis daun halus	Pentace laxiflora	Tiliaceae
	Nyatoh	z.B. Ganua, Madhuca, Palaquium, Payena sp.	Sapotaceae
3		Macaranga	Euphorbiaceae
4	Obah	Eugenia sp.	Myrtaceae
	Karpus	Hydnocarpus	Flacourtiaceae
5	Miscellaneous		

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 botanic name. *No* represents the growth group in the model.

Growth Group	Potential Height	Lightdemand	Description
1	55 m	shade tolerant	emergents, climax species
2	36 m	shade tolerant	mainly 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 2: Characteristics of the aggregated growth groups, after Ditzer und Huth (1995).

3 Model Description

The simulation area is divided into plots of $20\,\mathrm{m} \times 20\,\mathrm{m}$ (see figure 1). All trees in a plot compete for the available light. The size of these plots ($400\,\mathrm{m}^2$) 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. The consideration of gap-phase replacement in the model 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 size (we chose a diameter discretisation of $\Delta d = 5\,\mathrm{cm}$) are represented by one typical tree. A cohort model is characterised by three main components (Vanclay 1994):

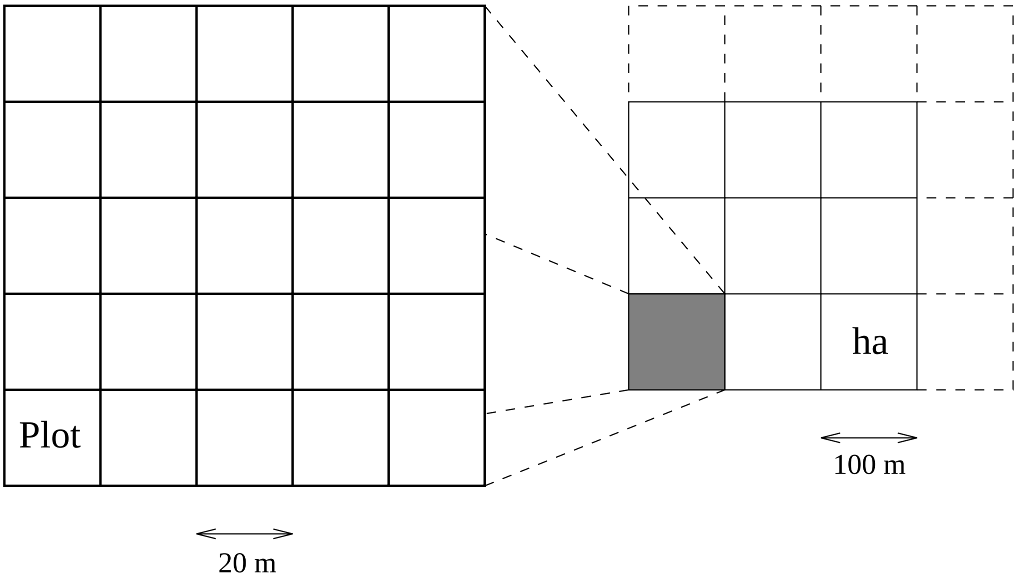

Figure 1: Dividing the simulation area in hectares and plots.

- diameter 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

The trees counted by an inventory (Schlensog 1995) are distributed into the plots by a scheme which takes into account the number of gaps in the forest. In each plot $l(l = 1, ..., m)$ for each diameter class of 5 cm width a cohort $i(i = 1, ..., n(l))$ 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 and respiration $R_{i,}$ (chapter 3.2.2).

$$\frac{\mathrm{d}B_{i,l}}{\mathrm{d}t} = \hat{P}_{i,l} - R_{i,l}. \tag{1}$$

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

$$\frac{\mathrm{d}N_{i,l}}{\mathrm{d}t} = -M_{i,l}. \tag{2}$$

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

3.2 Description of the different submodels

There are five submodels in which different processes of the model are described. They are tree geometry, carbon cycle (divided into photoproduction and respiration), competition for light,

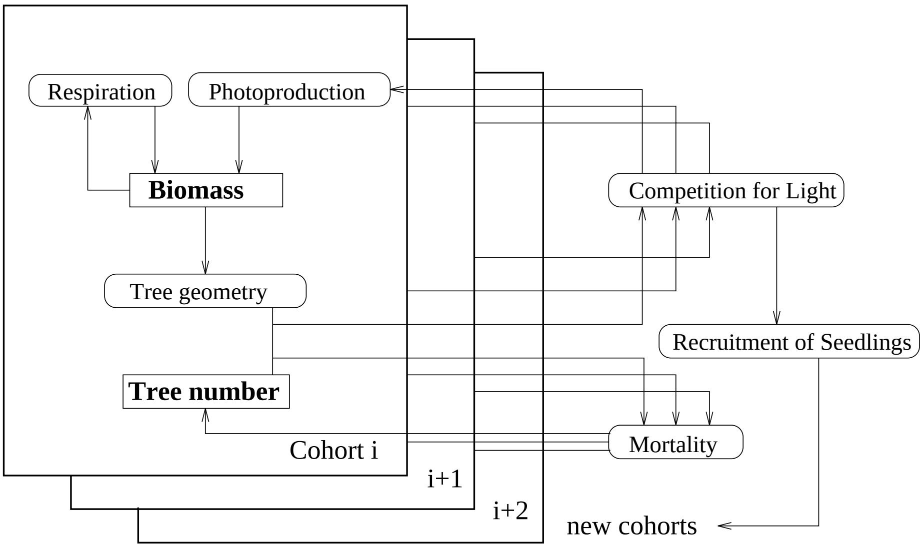

Figure 2: Overview at the interactions of the submodels and the dependencies on the main variables biomass B and tree number N.

mortality, and recruitment of seedlings. Each of the submodel can be discussed on its own. In figure 2 the interactions between the submodels and the two main variables biomass and tree number in each cohort are shown. The parametrisation for a Dipterocarp lowland rain forest in Sabah (Borneo), Malaysia is found in appendix A.

3.2.1 Submodel Tree Geometry

For the calculation of processes such as shading and photoproduction we need additional information about a tree. The relationship between tree height h_i and stem diameter d_i are often investigated and expressed as a second order polynom:

$$h_i = a_{2,j} d_i^2 + a_{1,j} d_i + a_{0,j}. \tag{3}$$

With the approach of a cylindrical stem, the relation between its diameter d_i and the stem biomass $B_{\mathrm{T}i}$ is calculated in equation 4, where ρ is the wood density and γ is a form factor which takes the differences to an ideal cylinder into account. γ itself depends on the biomass of the tree (figure 3),

$$B_{\mathrm{T}i} = \frac{\pi}{4} d_i^2 \cdot h_i(d_i) \cdot \rho_j \cdot \gamma_i. \tag{4}$$

The total biomass B_i of a tree can be calculated with the stem wood fraction τ_j:

$$B_i = \frac{B_{\mathrm{T}i}}{\tau_j}. \tag{5}$$

The crown projection area f_i can be calculated as a function of stem diameter with a relationship $s_j(d_i)$ between the crown and the stem diameter which is shown in figure 3:

$$f_i = \frac{\pi}{4} (s_j \cdot d_i)^2. \tag{6}$$

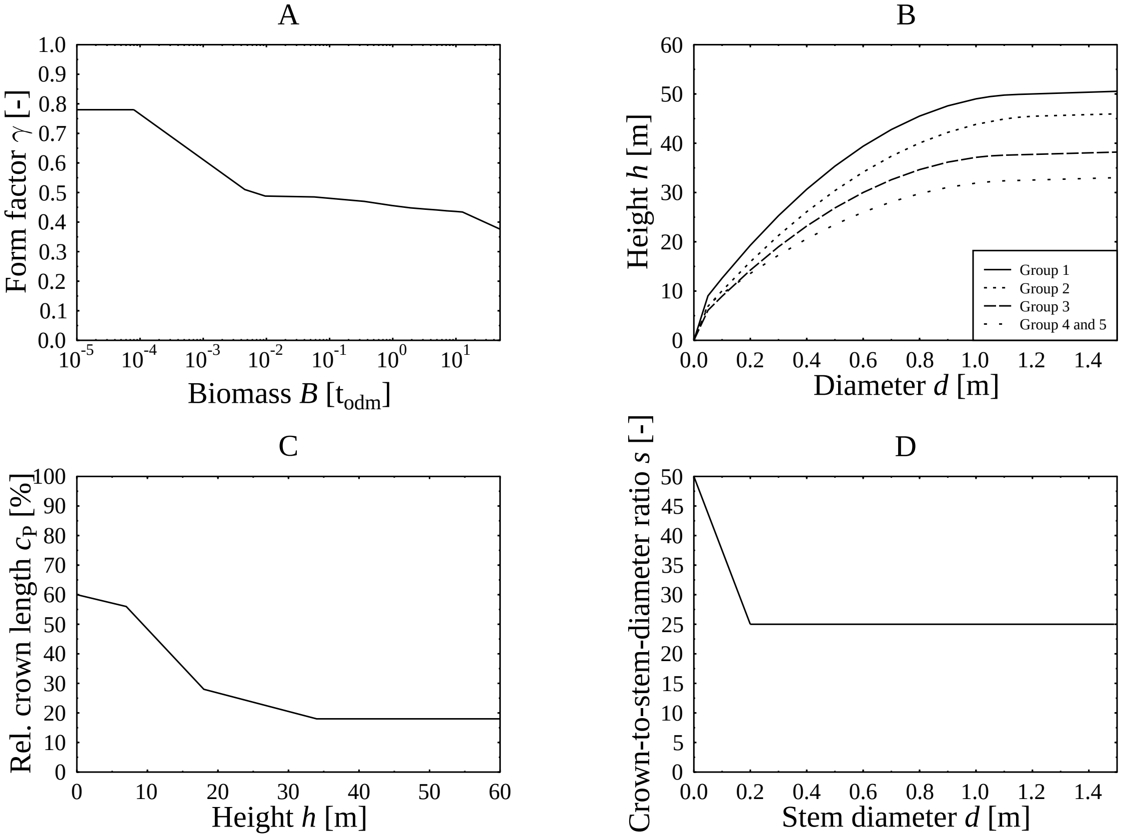

Figure 3: Functional dependencies in the geometry submodel; A: relationship of the form factor γ and biomass B; B: height-to-diameter-relation $h(d)$; C: relative crown length c_{P} as a function of tree height h (after Richards 1936; Burgess 1961; Poker 1993); D: modified crown diameter to stem diameter relation $s(d)$.

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 (Richards 1952; Poker 1993). Figure 3 shows how the relative crown length c_{S} is varied by height h.

$$c_i = c_{\mathrm{S}}(h_i) \cdot h_i. \tag{7}$$

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

3.2.2 Submodel Carbon Cycle

The photosynthetic production is computed using an approach given 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:

$$P_i(I_i) = \frac{\alpha_j \cdot I_i}{1 + \frac{\alpha_j}{P_{\mathrm{M}j}} I_i}, \tag{8}$$

where α_j is the initial slope of the light response curve and $P_{\mathrm{M}j}$ the maximum gross biomass production (figure 5).

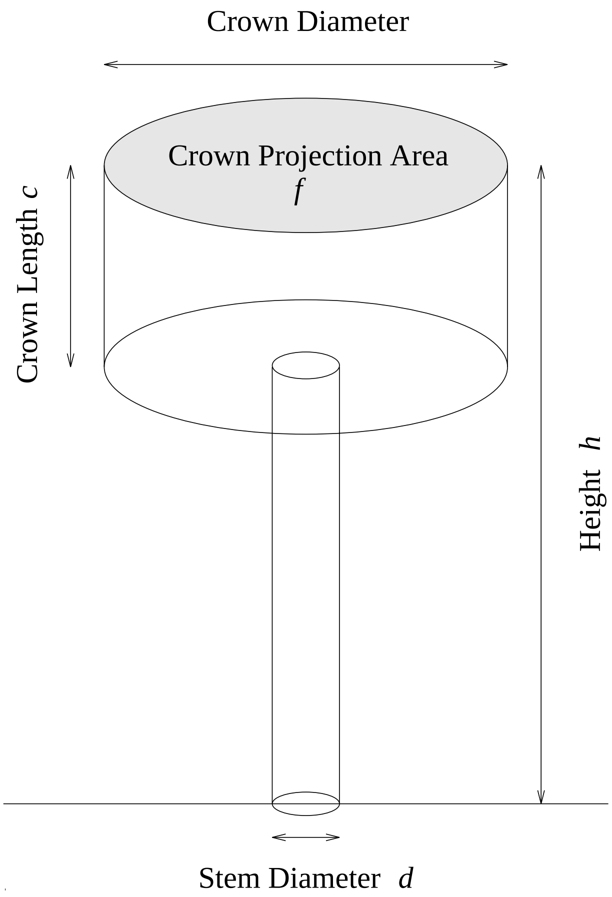

Figure 4: A typical tree of the model is shown including the relevant geometric dimensions.

The light attenuation within the canopy can be approximated by an exponential absorption with an absorption coefficient k (Kira 1978),

$$I_i(L_i) = I_0 \cdot \mathrm{e}^{-k \cdot L_i}. \tag{9}$$

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 light intensity I_0 above the whole forest. The calculation for the cumulative leaf area index L_i is to be found in the submodel *competition for light*, chapter 3.2.3. The hypothetical maximum photosynthetic production rate $\tilde{P}_i$ for trees with a crown which fills the plot completely is given by integrating down the canopy to the top of the regarded tree:

$$\tilde{P}_i = \int_0^{L_i} P_i(I_i(L))\mathrm{d}L. \tag{10}$$

The solution of equation 10 is given by (Thornley 1978):

$$\tilde{P}_i = \frac{P_{\mathrm{M}j}}{k} \cdot \ln\left[\frac{1 + \frac{\alpha_j}{P_{\mathrm{M}j}} I_i}{1 + \frac{\alpha_j}{P_{\mathrm{M}j}} I_i \cdot \mathrm{e}^{-k \cdot \widetilde{LAI}_j}}\right], \tag{11}$$

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

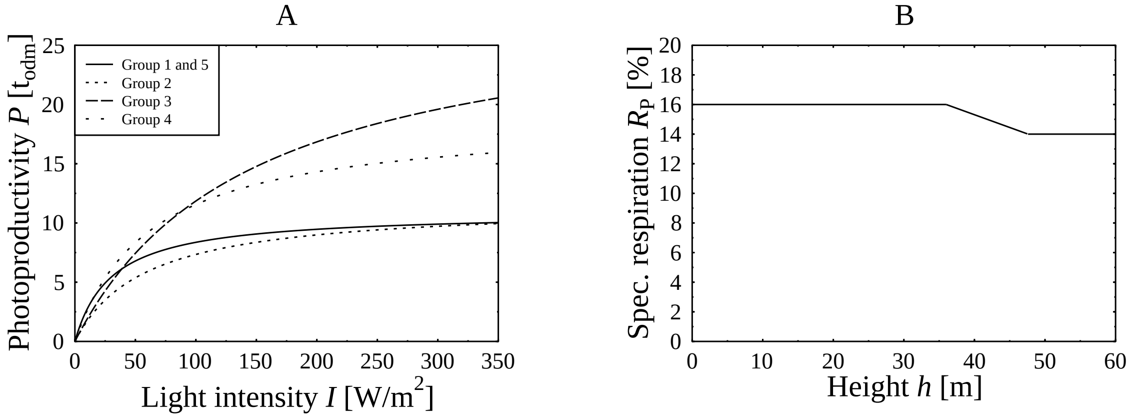

Figure 5: A: Light response curve (after an approach of Monsi and Saeki 1953) and measurements by Eschenbach (1994) and B: height depending specific respirationrate $R_{\mathrm{P}}(h)$ of emergents.

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

$$\hat{P}_i = \delta_i \cdot f_i \cdot \tilde{P}_i. \tag{12}$$

According to estimates for matured tropical rain forests approximately 13 % of the aboveground standing biomass is lost per year (Kira 1978). These losses R_i include respiration, litter fall, and renewal of stem, branches and leaves. In case of leaf respiration only the losses in nighttime are considered. The respiration of leaves at daytime is included in the light response curve (figure 5). To assure that trees do not exceed their maximum diameter $d_{\mathrm{M}j}$ a diameter-dependent term is included in the calculation of the respiration:

$$R_i = B_i \cdot R_{\mathrm{P}j} \cdot \left(1 - \left(\frac{d_i}{d_{\mathrm{M}j}}\right)^2\right) + \hat{P}_i \cdot \left(\frac{d_i}{d_{\mathrm{M}j}}\right)^2 \tag{13}$$

Special approaches are necessary for emergents. With this mechanism trees would not exceed a diameter of 90 cm. Therefore the specific respiration rate $R_{\mathrm{P}j}$ is corrected depending on tree height (figure 5).

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 homogeneous distributed. The whole canopy is divided in layers of the thickness Δz. For each z we calculate the leaf area index $LAI_i(z)$ of each tree with its crown of the length c_i in this layer:

$$LAI_i(z) = \widetilde{LAI}_j \cdot \frac{\Delta z}{c_i} \tag{14}$$

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:

$$F(z) = \sum_i \left(N_i \cdot \frac{f_i}{A}\right). \tag{15}$$

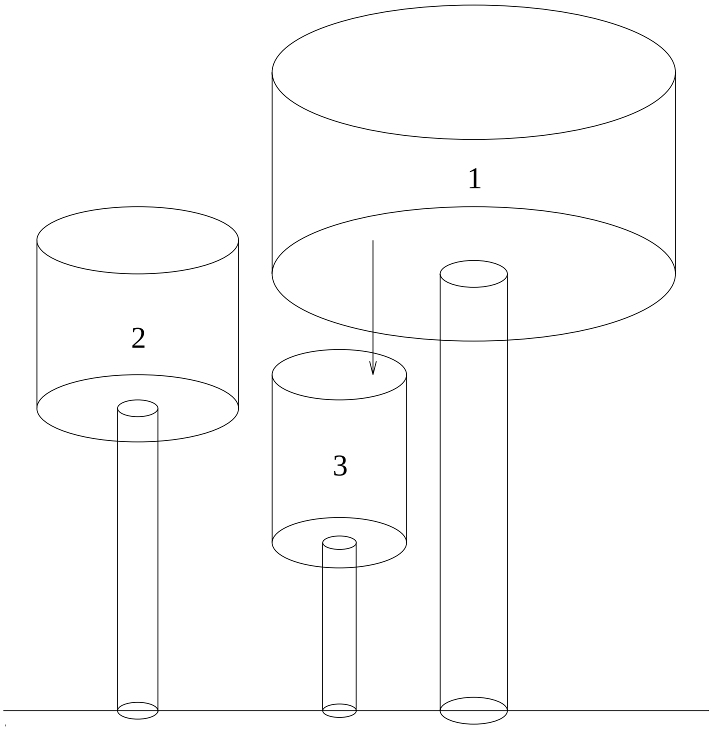

Figure 6: Shading of neighbouring trees in one plot. Tree 1 is shading tree 3, but not tree 2. Tree 2 is not shading tree 3.

If a crown closure $F(z)$ exeeds 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.

$$\delta_i = \frac{1}{Q} \cdot \sum \delta(z), \qquad \text{with } z \in [(h_i - c_i), h_i], \tag{16}$$

where Q is the number of layers in which the tree i has its crown.

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

$$L(z) = \sum_i \left(N_i \cdot \frac{f_i}{A} \cdot LAI_i(z) \right). \tag{17}$$

Shading in the canopy is only considered in a plot with one exception. Only the emergents can shade neighbouring plots. If the crown of a emergent is exeeding the plot size, 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.

$$L_i = \sum_z L(z), \qquad \text{with } z > h_i \tag{18}$$

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 (figure 6).

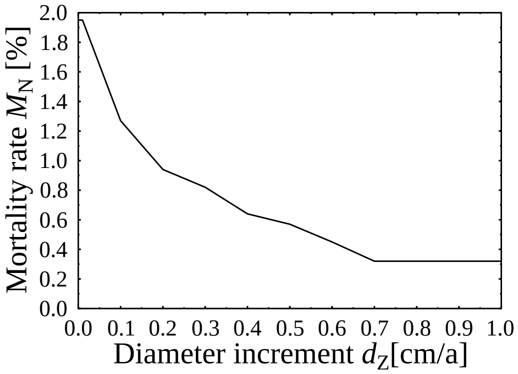

Figure 7: Mortality rate M_N as a function of diameter increment d_Z (after Swaine 1989).

3.2.4 Submodel Mortality

Tree mortality in tropical rain forests has a rate of about 1 % to 3 % annually (Swaine 1989; Condit et al. 1995; Van der Meer and Bongers 1996; Phillips and Gentry 1994). Field measurements for climax species have shown a relation between the mortality rate M_i and the annual diameter increment $d_{\mathrm{Z}i}$ (figure 7). The average turn over rate for trees with $d \geq 10\,\mathrm{cm}$ in the study of Swaine (1989) was 1.2 %:

$$M_i = M_{\mathrm{W}j} \cdot M_{\mathrm{N}i}(d_{\mathrm{Z}i}). \tag{19}$$

$M_{\mathrm{W}j}$ is a weighting factor depending on the growth group. It takes into account the higher mortality rate for pioneers. In the measurements of Swaine (1989) big trees are underrepresented. Due to this, their mortality rate would be overestimated. For big trees ($d \geq 0.6\,\mathrm{m}$) it is reduced linear in a way, that a tree with $d = 1.5\,\mathrm{m}$ would have a mortality rate of 0.5 %.

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

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

It is necessary to distinguish between climax species and pioneers. The mortality rate of pioneers is significant higher (Swaine 1989).

An important mechanism for tree mortality and the whole growth dynamic is the so called gap dynamic. Up to 90 % of tree mortality happens due to falling trees (Van der Meer and Bongers 1996). Therefore every dying tree with $d \geq 10\,\mathrm{cm}$ 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.

Mortality is calculated deterministically in cohorts with huge tree numbers and stochastically in cohorts with tree numbers less than 100.

3.2.5 Submodel Recruitment of Seedlings

The model works with an approach of a constant seed bank in the forest ground. This is true for pioneers. Climax species do not build up a seed bank, but a constant number of seedlings (Whitmore 1990). A former version of the FORMIX model was simulating 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.

Conditions necessary for an input of seedlings are:

- A lowest crown layer, which is not closed and
- the light intensity I_{F} on the forest floor must exeed a minimum amount $I_{\mathrm{S}j}$, which is necessary for germanation of the seeds,

$$I_{\mathrm{F}} \geq I_{\mathrm{S}j}. \tag{20}$$

If the conditions are fullfilled a new cohort is created. The variables biomass B_i and tree number N_i are initialized with the biomass of the seedlings $B_{\mathrm{S}j}$ and the number of seedlings per year and plot $N_{\mathrm{S}j}$ respectivly.

An input of seedlings occurs once a year.

4 Results and Discussion

In this section some first results are shown. We simulate the growth of a primary lowland dipterocarp rain forest in the Deramakot Forest Reservat, Sabah, Malaysia (Schlensog 1995).

The simulation results have been achieved with the parametrisation documented in the appendix. Nine hectare of rain forest have been simulated for minimizing stochastical effects of mortality. We chose a vertical discretisation of $\Delta z = 0.5\,\mathrm{m}$ and a time step of $\Delta t = 0.1\,\mathrm{a}$. The equations have been numerical solved by an Euler - Cauchy integration by which the numerical error has a size of $(\Delta t)^2$.

The results for a primary rain forest are given in figure 8. Some main features of the trees with $d \geq 10\,\mathrm{cm}$ are seen there. The stem volume[2] has an equilibrium at about $550\,\mathrm{m}^3/\mathrm{ha}$, where the rise from the inital value is due to an increase in the stem volume of growth group 1. It can be shown that this increase happens in trees with $d \leq 40\,\mathrm{cm}$. This increase is also seen in the diameter distribution. The tree number rises in the lower diameter classes during the simulation as well. It can be understood as a very close packing of trees in the lowest layers. This phenomenon has to be analysed in future studies. If it turns out that such a close packing is not to be found in nature the model has to be corrected, e. g. by increasing the mortality rate for small plants.

Field measurements in tropical forest are often made for a diameter threshold of $d = 10\,\mathrm{cm}$. Therefore it is difficult to compare simulation data with a different threshold with field studies. Nicholson (1979) found 422 and 667 trees per hectare in a forest in Sabah, Malaysia. In the same region Newbery et al. (1992) counted 470 trees/ha. In other lowland rain forests the tree numbers are of the same order. Van der Meer and Bongers (1996) found 526 trees/ha in

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[2] Stem volume SV is calculated from the biomass B by $SV = \frac{\tau}{\rho} \cdot B$, where τ is the stem wood fraction from the above soil part of the tree and ρ the wood density. Typical values for a dipterocarp rain forest are: $\tau = 0.7$, $\rho = 0.6\,\mathrm{g/cm}^3$. They are needed for comparisons with literature, where normally biomass is noted.

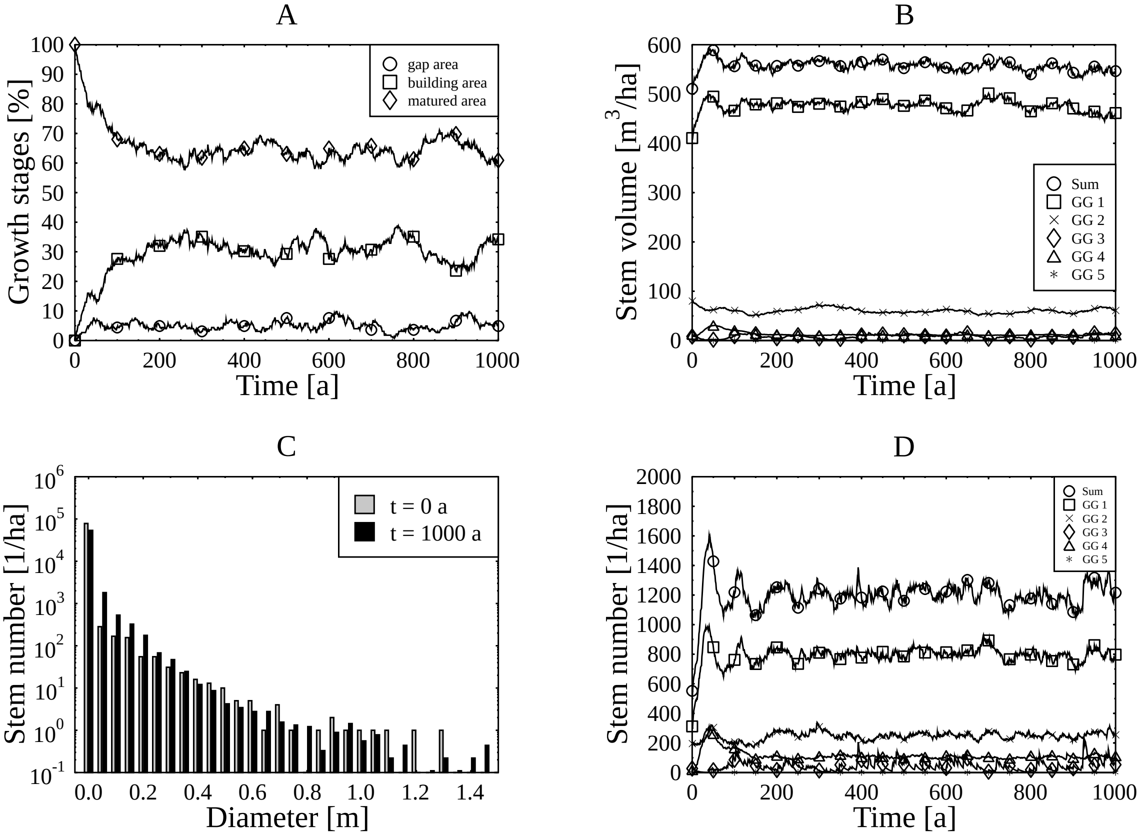

Figure 8: Simulation results for a primary diperocarp rain forest; A: dynamic distribution of growth stages; B: dynamic behaviour of the stem volume($d \geq 10\,\mathrm{cm}$); C: Stem number versus diameter distribution; D: dynamic behaviour of the stem numbers ($d \geq 10\,\mathrm{cm}$). Discussion in the text.

Amazonien, Crome et al.(1992) 664 trees/ha in Australia, and Brokaw (1985) more than 1000 tree/ha with $h \geq 1\,\mathrm{m}$ in Panama. In the simulation the stem number ($d \geq 10\,\mathrm{cm}$) has its equilibrium at 1200/ha, from which 800 belong to growth group 1. This difference to literature values is due to the increase in the lowest diameter classes as mentioned above.

Field data for stem volume or biomass are very seldom, because it is necessary to clear cut a certain area and measure every tree. The question which arises is, if the chosen areas are representive for a typical primary forest. Kato (1978) measured a stem volume of 556 and $777\,\mathrm{m}^3$/ha in a dipterocarp forest in Pasoh, Malaysia on an area of 0.1 ha in size. This fits well with our simulation results.

The variation of the growth stages over time show, that the forest reaches its equilibrium after about 200 years of simulation (figure 8A). Then about 5 % of the forest are in a gap area, which means, that in the regarded plot no tree bigger than $h \geq 20\,\mathrm{m}$ exists. 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[3]. Fluctuations are high (about 10 %). Hubbel and Foster (1986) found a similar composition in a forest in Panama of 50 ha in size. They measured a forest with 34 % ± 23 % in a gap stage (no trees with $h \leq 20\,\mathrm{m}$ exist), 37 % ± 19 % in a building

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[3] This classification was chosen due to a gap definition by Van der Meer and Bongers (1996) and a definition of emergents by Whitmore (1990).

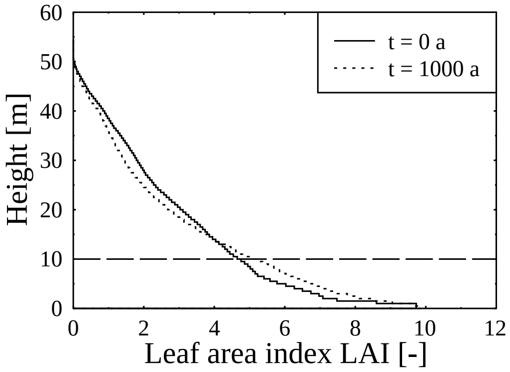

Figure 9: Cumulative leaf area index for different times. The line at $h = 10\,\mathrm{m}$ is corresponding to trees with $d = 10\,\mathrm{cm}$. Discussion in the text.

stage (trees between 20 m and 30 m exist) and 29 % ± 30 % in a matured stage (trees bigger than 30 m exist). The observed areas were 5 m × 5 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.

Similar results can be achived by simulating different stands (e. g. a secondary forest with a huge lightening). The equilibrium state of the forest after roughly 400 years is always the same. This is even the case if a clear cut is simulated where the forest grows up in a clear area[4].

Leaf area index is another possibility to characterize a forest. In figure 9 the cumulative LAI for the different heights is shown. It can be seen that there are little differences between the inital stage and the one after 1000 years of simulation. Due to small trees which behave critically we have devided the canopy in two sections. Trees with a diameter smaller than 10 cm are about 10 m high. Therefore the lower part in figure 9 should be regarded more critical than the upper one. The cumulative LAI gets up to 5 at $h = 10\,\mathrm{m}$ and to 10 on the forest floor. Measurements in a malaysian rain forest achieve $LAI = 7.3$ (Kato et al. 1978) and $LAI = 4.7 - 6.8$ (Schlensog 1995). In a tropical rain forest in Thailand an $LAI = 11.4$ was measured (Kira 1975). These differences occure because different methods are used to define the LAI. If it is considered, that small plants like shrubs and herbs can achieve a LAI of 2 (Rollet 1978), the simulation results are fairly good.

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; Terborgh and Petren 1991). In figure 10 the crown closure in different heights can be seen. We distinguish between forest in a mature and in a building stage. The first can be interpreted as primary forest where the second is corresponding to secondary forest.

In a primary forest maxima can be seen at 40 m, 10 m, and two submaxima at 21 m and 2 m. The secondary forest has maxima at 36 m, 18 m and 10 m but they are not well defined.

This is related to observations from 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 und 0,5 m). It has to be considered that these observations were done in a different forest formation in South America. In the measurement the solution of the upper canopy was with steps of 5 m

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[4] In this case impacts on the forest floor due to erosion are omitted. A reforestation after a stage of shifting cultivation can be simulated with that approach.

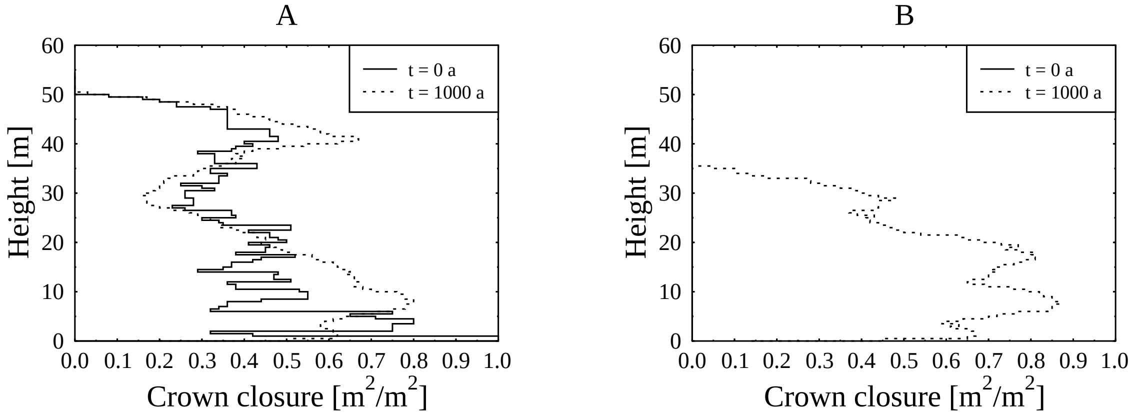

Figure 10: Crown closure in the equilibrium for different times and growth stages. A: Primary forest; B: Secondary forest.

very rough. The differences between the measurements and the simulation is probable due to the different forest types.

With the approach that a maximum in the crown closure is corresponding to a typical layer construction it can be said that an malaysian rain forest tends to organize itself in a 2 to 4 layer structure.

There are some considerations (Rollet 1978) that the distribution of the crowns within the canopy is a function of the diameter distribution. In the model this is true due to the tree geometry submodel. The question is whether there is selforganisation mechanism in the layer structure or in the diameter distribution.

5 Outlook

As mentioned in the discussion, the model has to be reconsidered for small trees. With some simple improvements the increase in stem numbers should become more realistic.

With the model a wide range of studies can be done. The effects of tree logging can be examined as a function of logging strategy and logging cycle. A model extension can simulate the coexistence of a large number of species groups (e. g. 20 growth groups). 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.

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A Parametrisation for a dipterocarp lowland rain forest in the Deramakot Forest Reservat on Sabah (Borneo), Malaysia

Name	**Description**	**GG 1**	**GG 2**	**GG 3**	**GG 4**	**GG 5**
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 [$\mathrm{t_{odm}/m^3}$]	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
$h_{\mathrm{M}j}$	Potential height [m]	55	36	25	15	1.3
Recruitment of seedlings						
$B_{\mathrm{S}j}$	Biomass of seedling [$\mathrm{g_{odm}}$]	10	10	10	10	10
$N_{\mathrm{S}j}$	Number of seedlings per year and plot [1/a $\cdot$ 400 m^2]	2500	4000	6000	700	700
$I_{\mathrm{S}j}$	Minimal light intensitiy for germenation [W/m^2]	1	1	50	1	1
Carbon cycle						
$P_{\mathrm{M}j}$	Maximum photoproductivity [$\mathrm{mg}_{CO_2}/(\mathrm{dm}^2\cdot \mathrm{h})$]	10.9	11.6	29.1	18.8	10.9
α_j	Slope of light response curve [$\mathrm{mg}_{CO_2}\cdot\mathrm{m}^2/(\mathrm{dm}^2\cdot \mathrm{h} \cdot \mathrm{W})$]	0.36	0.20	0.20	0.30	0.36
$\widetilde{LAI}_j$	Leaf area index of single tree[-]	2	2	2	2	2
$R_{\mathrm{P}j}$	Spec. respiration (part of biomass losses on total biomass) [1/a]	0.16	0.16	0.16	0.16	0.16
Mortality						
$M_{\mathrm{W}j}$	Weighting factor for normal mortality [-]	1	1	8	1	1
$M_{\mathrm{Y}j}$	Spec. mortality rate of seedlings [1/a]	0.08	0.08	0.16	0.08	0.08
$M_{\mathrm{C}j}$	Spec. mortality rate due to crowding [1/a]	0.04	0.04	0.08	0.04	0.04
$M_{\mathrm{CY}j}$	Spec. mortality rate of seedlings due to crowding [1/a]	0.32	0.32	0.32	0.32	0.32
Group independing parameter						
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				