

Simulation model of natural tropical forest dynamics

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ABSTRACT

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Assessments of the long-term natural regeneration of tropical forests following selective logging are today mostly based on extrapolation of limited empirical observations. Mounting evidence suggests that current logging policies overestimate forest regrowth by a wide margin, and are therefore not sustainable. The need for more reliable assessment of natural forest growth dynamics has led to the development of a vertically and spatially structured dynamic simulation model of natural forest development. The model accounts explicitly for biomass and tree numbers in five distinct canopy layers (seedlings, saplings, poles, main canopy, emergents). Energy accounting of assimilation and dissimulation rates leads to biomass, diameter, and height growth in each layer. Leaf mass in each layer determines photoproduction, and light and photosynthesis conditions in lower layers. Transitions to higher layers, mortalities in each layer, and seed events are accounted for. The basic model simulates the development dynamics of a forest gap. Parallel computation of spatially distributed single gap models with stochastic mortalities and seed dispersal provides a simulation of the spatial dynamics of the tropical forest mosaic. Simulation results are provided with parameters corresponding to unlogged and logged Malaysian lowland dipterocarp forest.

INTRODUCTION

Forest science has developed fairly reliable tools for long-term forest planning and management in temperate regions. These regions are distinguished by only about a dozen major forest tree species, long-term forest observations, silvicultural tradition and experience, as well as a relationship between tree age and growth clearly defined by seasonal increment (tree rings). Some of the tools of temperate forest science can be adapted to forest plantations in tropical and subtropical regions, but the correct

assessment of natural tropical forest growth dynamics requires more than the standard growth and yield table approach. This is because the development of tropical natural forests is largely determined by specific features which are not normally considered in traditional forest science: a vertically layered canopy including trees of all age groups and many different species (Golley, 1983); a spatial structure of forest gaps in which regeneration takes place; and often complex pollination, seed dispersal, and regeneration processes, in which animals, light conditions and microclimate play an important role (Jacobs, 1988). In addition, little is known concerning the growth histories of even the more common tree species of commercial interest: the absence of annual growth rings being one reason (Hallé et al., 1978; Whitmore, 1984).

Despite these gaps in knowledge concerning natural tropical forest development, forest planners in tropical countries have no choice but to make decisions about forest use strategies, often based on nothing more than educated guesses about future forest development (Lamprecht, 1986).

In the light of this dilemma, it is worthwhile investigating the potential contribution to forest planning of modelling and simulation of the dominant physiological processes of forest growth. Obviously, the complexity of the system calls for a very aggregated representation in the model. The question is whether essential features of forest development can be captured by such an aggregated model.

The objective of the modelling project therefore was to develop a valid representation of the long-term dynamics of logged natural tropical forest (specifically for lowland dipterocarp forest in Malaysia) over a period of several cutting cycles (several hundred years), with a reliable representation of short-term processes (e.g. dynamics induced by logging events or silvicultural treatments).

For forest management purposes, stem numbers per hectare for different diameter classes (diameter at breast height, DBH) are required. The DBH can be used to derive corresponding stem heights via known height-to-diameter (h/d) ratios, while DBH and stem numbers provide estimates of standing biomass (and timber volume).

Natural tropical forests have a definite vertical canopy structure, leading forest ecologists to distinguish (usually) between layers (e.g. Golley, 1983), namely (1) seedlings and herbs, (2) saplings and shrubs, (3) poles and understorey, (4) main canopy, and (5) emergents (Fig. 1). Each of these canopy layers absorbs a substantial fraction of the light it receives, thus determining light conditions and growth of lower canopy layers. Apart from the vertical structuring, natural forests also exhibit a distinct horizontal spatial structuring on the scale of the gaps produced by the death of large trees and subsequent regrowth in these gaps (Whitmore, 1984).

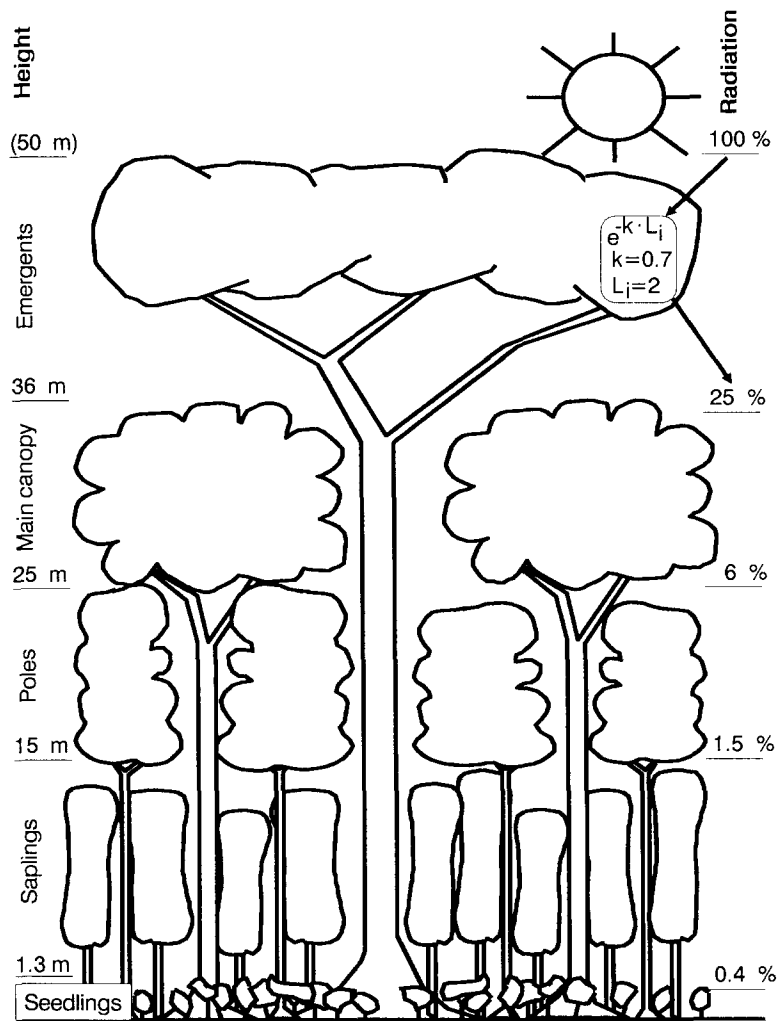


Fig. 1. Schematic representation of the vertical structure of tropical rain forests and the corresponding reduction of photosynthetic active radiation received.

Since the pronounced spatial structuring of natural tropical forests has a significant effect on light distribution and growth dynamics, candidates for natural tropical forest models must therefore be able to account for vertical canopy structure, layer-dependent photoproduction, and horizontal gap structure. Stem numbers and stem biomass are required for management purposes.

POSSIBLE MODEL FORMULATIONS

Various modelling approaches are possible candidates for modelling the dynamics of natural forests. However, they differ widely with regard to computational efficiency and model validity for the stated purpose. In the following, we compare the computational effect on a per hectare basis, even though the actual computational unit may be somewhat smaller.

Growth table models could in principle be used to compute growth for a mixed-species, uneven-aged stand, for a given initial spatial distribution of trees (e.g. Schober, 1975). Relative tree heights would have to be tracked in order to compute growth reductions due to shading. Some 10000 time paths per hectare of trees would have to be computed simultaneously in order to simulate natural forest development. Since the model dynamics are entirely driven by the time-dependent growth functions and not by explicit representations of the processes of assimilation, and partitioning and respiration, the approach has only descriptive validity at best, apart from the fact that such growth tables are unavailable for tropical trees.

In the *gap models* of the JABOWA and FORET type (Shugart, 1984), the predictive quality is improved over the previous approach by introducing empirical site and competition factors and stochastic elements, repeating the computations (usually) 100 times, and averaging the results (requiring the computation of some 1 million timepaths per hectare). Again, the a priori assumption of logistic time-dependent growth functions used here is descriptive in nature and cannot represent the adaptive response of growth processes to site and light conditions.

In *tree process models* the prescribed logistic growth functions of the previous models are replaced by a real-structure description of the major assimilation and dissimilation processes of an individual tree. This can be done with some 3 to 10 state variables per tree (Bossel, 1986; Bossel and Schäfer, 1989; Mäkelä, 1988; McMurtrie and Wolf, 1983; Mohren, 1987; Valentine, 1985). Representing 10 000 trees per hectare would therefore require the computation of 30 000 to 100 000 state variables per hectare.

In *canopy layer models* (Oikawa, 1985; Bossel and Krieger, 1990a) the physiological process description of tree process models is maintained, while individual trees are aggregated to units of gap size canopies representative of the five classes (seedlings, saplings, poles, main canopy, emergents). Each is characterized by the state variables biomass and height, which determine (for example) tree number, crown density, and light attenuation in the canopy. Assuming ten state variables per gap, and 100 gaps per hectare, simulating forest development then requires the computation of only 1000 time paths per hectare while still explicitly representing the essential processes of assimilation and dissimilation.

In *life cycle models* (Wissel, 1990) the forest mosaic is represented by gaps, each of which is currently in a particular state of its natural life cycle (seedling, sapling, pole, mature stage, death). The life cycle is affected by random events (tree death and tree fall, creating a new gap, and starting a new life cycle). The life cycle is prescribed as a function of time; the actual growth determining processes are not explicitly accounted for. The approach therefore lacks the detail of information and accuracy required for forest management. At 100 gaps per hectare, the life cycle approach only requires the computation of 100 state variables per hectare.

Age class models are common in ecological systems studies (Begon and Mortimer, 1986). The number of individuals in each age class (cohort) is computed annually as a function of mortality losses and seedling gains (first age class only). Age-dependent (distribution) functions are used to assign quantities like height, biomass etc. Relative height could be used to compute growth reduction factors. The approach is extremely data-intensive and unwieldy. A major drawback is the fact that in natural forests even for a given species, tree age is a poor indicator of tree height, biomass etc. Using annual age classes with 200 age classes per gap, and 100 gaps per hectare, it would require the computation of 20 000 time paths per hectare.

Height class models (or, equivalently, diameter class models) are closer to the thinking of forest managers. In addition, they allow in principle the computation of light attenuation in the canopy and the resulting growth of each height class. Transition probabilities to the next height class can be assigned and the transition process can be formulated as a Markov model. However, this approach (mathematically) allows instantaneous transition of biomass through all height layers which is (physically) impossible. For example, a large number of seedlings following a seed year will immediately also lead to a higher number of trees in the highest class. This dilemma can be avoided only by introducing time delays, or switching to the age class approach. After considerable analyses and modelling work we determined this approach to be unsuitable for a valid description of forest dynamics. If 1 meter height increments were used, it would require some 60 height classes per gap, and therefore the computation of 6000 state variables for 100 gaps per hectare.

(For more details on the relative merits and demerits of the different modelling approaches, see Bossel and Krieger, 1990b.)

'FORMIX' MODEL OF TROPICAL NATURAL FOREST GROWTH

A comparison of the different possible modelling approaches (previous section) reveals that for the modelling objectives stated, canopy layer models can be expected to combine high computational efficiency with

TABLE 1

Parameter list of the FORMIX model

(a) Parameters used for all layers

Name	Value	Unit	Description	Source
IS	335	W m^{-2}	Radiation rate above canopy	Kira, 1978
K_i	0.7	—	Light extinction coefficient	Kira, 1978
LAI_i	2	ha ha^{-1}	Maximum leaf area index for layer i	Kira, 1978
C	2.39	—	$1 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ $= 2.39 \text{ t}_{\text{ODM}} \text{ ha}^{-1} \text{ a}^{-1}$ (assuming 8760/2 daylight hours per year)	Own calculation
P_{max}	20	$\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$	Gross photosynthesis rate at light saturation	Kira, 1978
M	0.15	$\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1} \text{ W}^{-1} \text{ m}^2$	Initial slope of the light response curve	Kira, 1978
G	0.65	$\text{t}_{\text{ODM}} \text{ m}^{-3}$	Specific weight of wood	Estimate
TR_i	0.7	—	Stemwood fraction	Estimate
CD_i	25	m m^{-1}	Crown-to-stem diameter ratio	Assmann, 1961
PR_i	0.5	—	Leaf-proportional energy use efficiency	Kira, 1978
SR_i	0.06	a^{-1}	Biomass-proportional energy loss rate	Assmann, 1961
SS	0.25	a^{-1}	Specific seed survival rate	Estimate
BS	0.00002	t C	Specific initial seedling biomass	Estimate

(b) Parameters differing for the different layers

i	1	2	3	4	5	Unit	Description	Source
MN_1	0.1	0.005	0.01	0.008	0.005	a^{-1}	Specific mortality	Estimate
MC_1	0.5	0.5	0.2	0.15	0.1	a^{-1}	Specific mortality due to crowding	Estimate
TS_1	0.1	0.08	0.05	0.02	—	a^{-1}	Specific transition rates	Estimate
DM_1	0.01	0.1	0.25	0.45	—	m	Threshold diameter	Estimate

(c) Table function points for form factor F and h/d ratio HD as function of biomass per tree BT

Name	Value					Unit	Description	Source
BT	0	5	10	20	50	t_{ODM}	Tree biomass	
HD	140	67	56	48	40	—	Height-to-Diameter ratio	Kato et al., 1978
F	0.5	0.45	0.44	0.42	0.38	—	Form factor	Kato et al., 1978

good structural, behavioural, empirical, and application validity. We therefore choose this approach for describing natural forest dynamics, and in particular for computing the dynamic response to logging. The mathematical formulations below are generic, i.e. they can be adapted to other sites and situations by choosing appropriate parameters. The current list of parameters (for Malaysian lowland dipterocarp forest) is given in Table 1.

The FORMIX model is intended to represent the growth of tropical natural forest before and after logging. Since the dynamics of these forests are determined by gap formation and closure, the basic geometric unit must therefore represent a gap, with an area of the order of 0.01 to 0.1 hectare. Spatial patterns of forest development can then be computed by representing the forest mosaic by a large number of neighbouring gaps. Effects of neighbouring gaps on each other (shading, localized seed dispersal, microclimate etc.) can also be included.

Solar radiation and other climatological variables are the external inputs to the gap. At the present stage of development, the model assumes a constant ambient temperature (representing tropical conditions), and non-limiting water and nutrient supplies. These factors can be added to the model later as more or less elaborate submodels, in order to allow the study of water and nutrient stress, or effects of the microclimatic conditions in the gap.

Forest processes must obey the physical laws of energy and mass conservation. In ensuring strict adherence to these laws, energy and mass balance modelling (as practised here) provides a consistent framework of accounting, and therefore at least eliminates errors which can otherwise appear in traditional approaches, such as those based on growth and yield tables, which may violate the energy conservation principle when applied to sites and stands different from those which provided the empirical data for the tables.

Light energy absorption in the canopy is dependent on incident solar radiation, on light attenuation in the canopy, and on the specific photoproduction of the leaves of the species considered (light response curve). The light attenuation in a natural forest canopy causes different photoproduction rates and hence different growth potential at different canopy heights. The light distribution and corresponding photoproduction processes must therefore be properly accounted for.

The assimilated energy is partly used for chemical construction energy to form chemical compounds, partly for maintenance respiration of all tree parts, partly for the formation of temporary biomass (leaves, fine roots, deadwood losses etc.), and partly for increment of the permanent wood mass. All of these energy dissipation rates must be properly accounted for in the energy balance (or mass balance).

Canopy layers and canopy layer submodels

The model is composed of tree classes representing the five canopy layers recognized by forest ecologists as being functionally distinct development stages; seedlings, saplings, poles, main canopy, and emergent trees. Although parameters and light conditions differ for each of these classes, the processes at each stage are structurally identical: photoproduction, respiration, shading of lower classes, transfer of trees from lower to higher classes, etc. Hence it is sufficient to define a submodel structure for one of these classes, and 'copying' the structure for the remaining classes. Identification of a particular class-specific variable or parameter is achieved by adding an index: 1, seedlings; 2, saplings; 3, poles; 4, main canopy trees; 5, emergents.

Each of these submodels can be summarized as a 'box' containing the respective state variables (class biomass B_i and tree number N_i). The relationships between the submodels or 'modules' are shown in Fig. 2.

Seedlings enter the 'seedling class' at a rate which is a function of seed availability from mature trees in the main canopy and in the emergent layer, of germination rate (seed survival), and/or of planting. This means (1) a corresponding increase in seedling number, and (2) a corresponding increase in seedling biomass. Growth in the seedling layer is a function of the light reaching this layer after passing through – and being partially absorbed by – the emergent, main canopy, pole, and sapling layers. As seedlings grow, they eventually reach their transition diameter, and must be counted as saplings. A certain fraction of the seedlings then transfers from the seedling to the sapling layer, reducing seedling number and seedling layer biomass, and adding the corresponding tree numbers and biomass in the sapling layer.

The transfer processes between the other layers operate in the same way. Logging is accounted for by removing (or destroying) given fractions of the biomass and the tree numbers in each layer.

In the model, we distinguish the canopy layers by the following characteristics (Fig. 1):

i	Layer	Diameter (cm)	Height (m)
1	seedlings	0–1	0.0–1.3
2	saplings	1–10	1.3–15.0
3	poles	10–25	15.0–25.0
4	main canopy	25–45	25.0–36.0
5	emergents	> 45	> 36.0

This vertical structure of the development stages applies to Malaysian lowland dipterocarp forests. For other regions or other species composi-

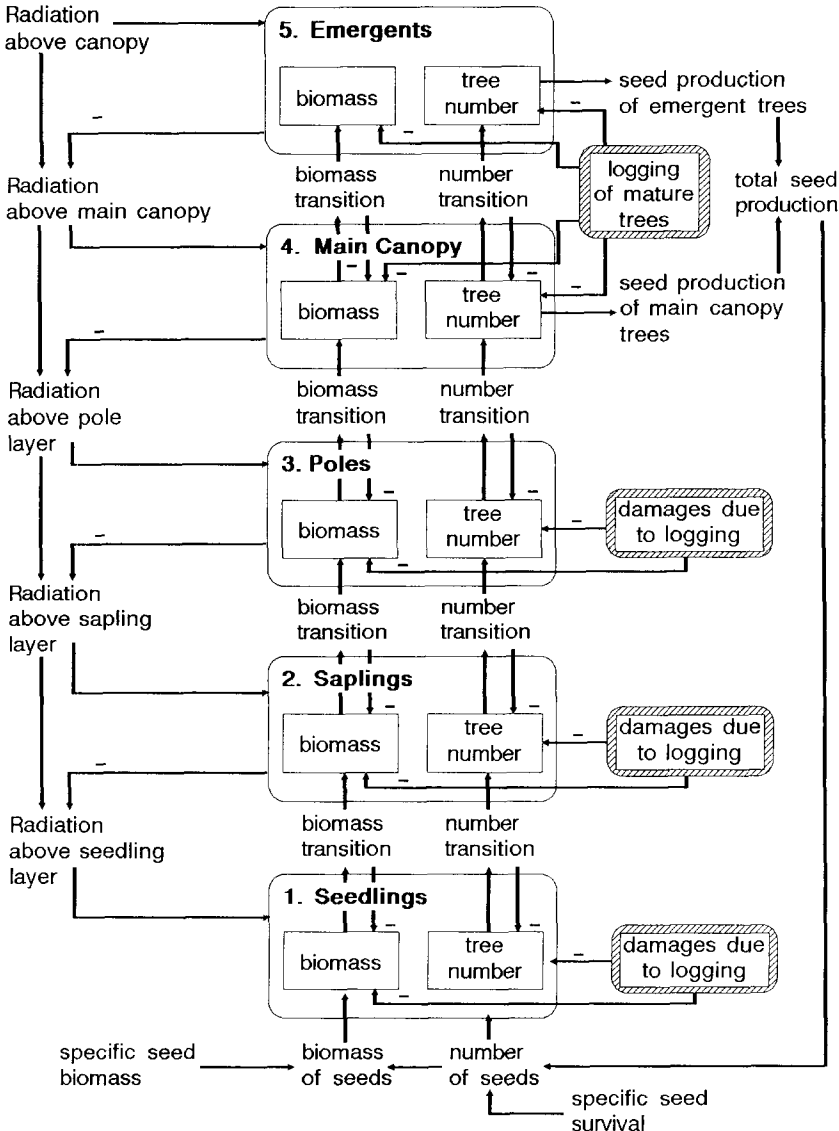


Fig. 2. Influence diagram for the system modules contained in the FORMIX forest dynamics model (seedling, sapling, pole, main canopy, and emergent layer).

tions, the number of layers as well as the absolute heights of the classes may differ from the above classification (Golley, 1983).

The model structure within each canopy layer is shown in Fig. 3.

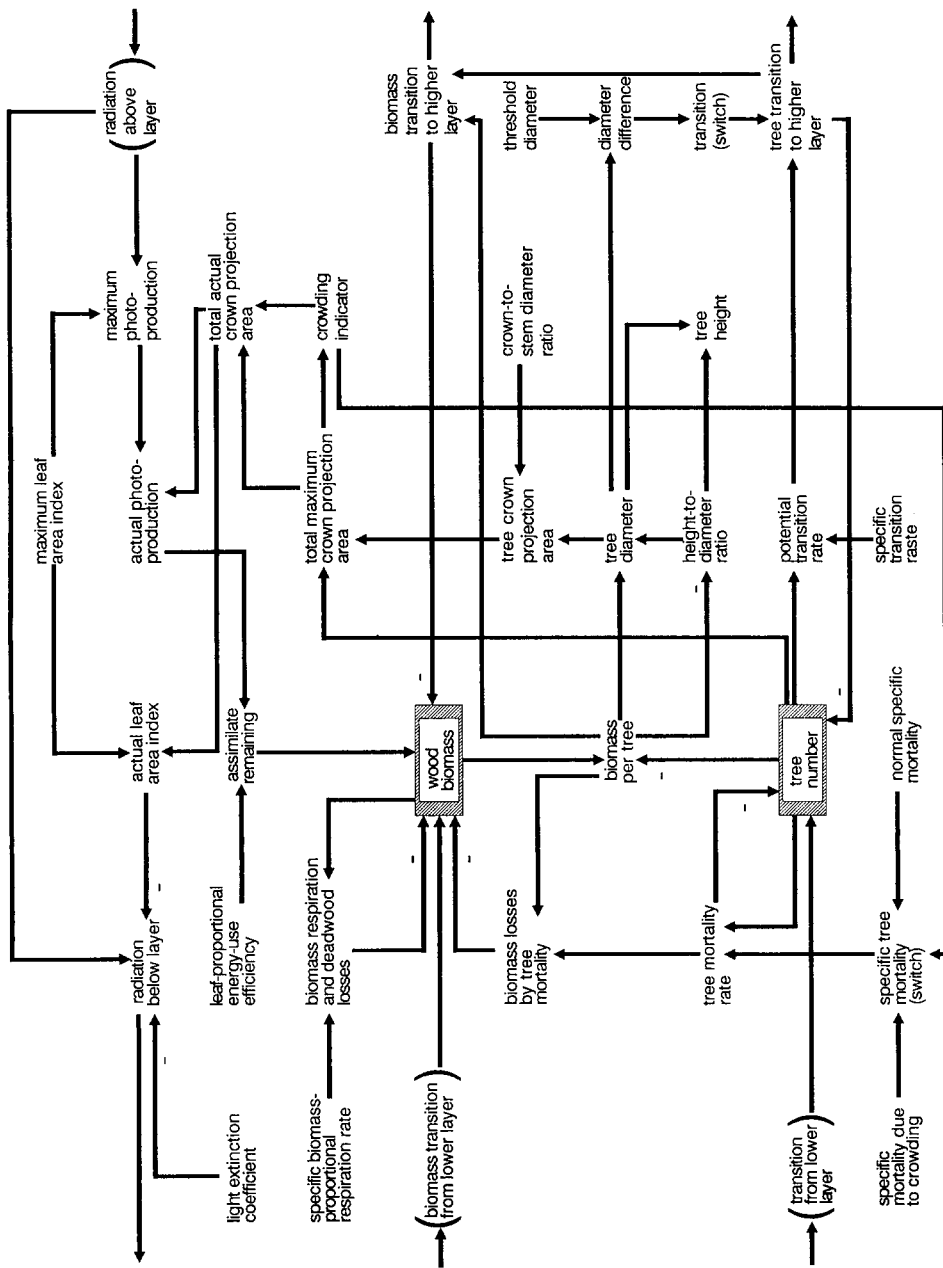


Fig. 3. Influence diagram for each canopy module of the FORMIX forest dynamics model.

Differential equations

Each canopy layer is represented by two differential equations describing the temporal development of wood biomass and stem number in that particular layer (units in brackets '[]').

Tree numbers N_i (numbers per hectare [ha^{-1}]) are calculated by integrating the transition rates TN_{i-1} and TN_i representing trees growing into this class from a lower stratum and leaving the class to the next canopy layer, and accounting for density-dependent tree mortality rates M_i . The transitions will be activated if the (average) height of trees-within a particular class exceeds a given threshold value, i.e. as trees grow into the next canopy layer:

$$dN_i/dt = \text{TN}_{i-1} - \text{TN}_i - M_i$$

Biomass B_i (metric tons of organic dry matter per hectare [$\text{t}_{\text{ODM}} \text{ha}^{-1}$]) increases at the rate of biomass production by photosynthesis PB_i . The biomass transfer TB_{i-1} is caused by ingrowth from the next lower level and can be derived directly from TN_{i-1} and tree specific biomass BT_i . Biomass is transferred to the canopy layer $i+1$ at the rate TB_i proportional to TN_i . Biomass losses occur due to biomass-proportional respiration and dead-wood losses R_i (respiration demands for maintaining stems, branches, coarse roots; losses of dead branches and coarse roots). B_i will also be affected by a density-dependent mortality rate MB_i derived from M_i :

$$dB_i/dt = \text{PB}_i + \text{TB}_{i-1} - \text{TB}_i - R_i - \text{MB}_i$$

For applying the model to a given initial situation, the user may enter different initial conditions for the tree numbers N_i ($i = 1, \dots, 5$) and the biomass values B_i ($i = 1, \dots, 5$) in the different layers. As the latter figures are often not available, the FORMIX user has to provide the initial average stem diameters (DBH) for the different tree classes; these will be recalculated automatically in terms of biomass.

Photosynthetic production

The photosynthetic production in the forest canopy is computed using a model given by Kira (1978) using light response data for dipterocarp and other trees which form the main portion of Malaysian tropical forests. This model is based on an exponential light distribution within the crown as a function of the cumulative leaf area index of this layer and the photosynthetic active radiation (PAR) above the canopy (or above the currently

evaluated canopy layer). The light response curve of the leaves is assumed to be a saturation type curve expressed by a Michaelis–Menten equation:

$$p = \frac{mI}{1 + \frac{m}{p_{\max}} I}$$

where p_{\max} is the light response (maximum gross photosynthesis [$\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$]) at light saturation, m is the initial production increase with increasing radiation (slope), and I is the photoactive solar radiation [W m^{-2}]. The parameters m and p_{\max} are determined by fitting experimental data. The parameters are species-dependent and differ in particular for shade-tolerant and light-seeking species (pioneers). For most shade-tolerant tropical trees, the light response is characterized by a maximum gross photosynthesis at light saturation of about $30 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ (Kira, 1978; Medina and Klinge, 1983; Pearcy, 1987). In the present aggregate model of tropical forest dynamics, the same photosensitivity function is applied in all canopy layers. For a more detailed description of natural forest dynamics, a distinction between functionally different species (pioneers, shade-tolerant, light-demanding, etc.) is appropriate and has been made in Bossel and Krieger (1990b).

The light attenuation within the canopy of a dense natural forest can be approximated by the Monsi–Saeki formulation of exponential attenuation (Lambert–Beer law):

$$I = I_0 e^{-kI}$$

where I is the radiation at a certain level in the canopy [W m^{-2}], I_0 is the radiation above the canopy [W m^{-2}], k the light attenuation parameter [$-$], and l the cumulative leaf area index [ha ha^{-1}] between the canopy surface and the height level considered.

Inserting the equation for I into the expression for p gives the specific photoproduction at each level. Integration over all levels of the canopy leads to an expression for total photoproduction which is of the form (see Kira, 1978, pp. 578–579):

$$p = \frac{p_{\max}}{k} \ln \frac{1 + \frac{m}{p_{\max}} I_0}{1 + \frac{m}{p_{\max}} I_0 e^{-k L_{\text{tot}}}}$$

Hence the incident solar radiation I_0 , the light extinction coefficient k , the parameters of the light response curve (m and p_{\max}), and the total leaf

area index LAI_i [$ha\ ha^{-1}$] of the forest canopy determine the total photo-production in the canopy.

Applying this formulation to the individual canopy layer (index i) and integrating vertically down into the canopy, that is integrating from 0 to the maximum leaf area index of a given layer, yields the specific (maximum) gross photosynthetic production rate PS_i for the i th layer (tons of ODM per hectare and year [$t_{ODM}\ ha^{-1}\ a^{-1}$]):

$$PS_i = C * P_{max}/K_i * \ln[(1 + (M/P_{max}) * I_i) / (1 + (M/P_{max} * \exp(-K_i) * LAI_i) * I_i)]$$

In the equation, I_i is the radiation [$W\ m^{-2}$] received by layer i (and therefore depends on shading by higher canopy layers). The parameters P_{max} and M describe the light response for *Dipterocarpus crinitus* and include a factor to recalculate the radiation input in units of Watt per square meter ($1\ W\ m^{-2} = 680\ lux$). The parameter P_{max} reflects the maximum gross photoproduction rate possible and was derived by Kira (1978) on the basis of a total annual gross photoproduction of approximately $80\ t_{ODM}\ ha^{-1}$ which is a reasonable figure for tropical rain forests. In our model $P_{max} = 20\ mg\ CO_2\ dm^{-2}\ h^{-1}$ and $M = 0.15\ mg\ CO_2\ dm^{-2}\ h^{-1}\ W^{-1}\ m^2$. The parameters K_i and LAI_i denote the light extinction coefficients of leaves within a particular crown layer and the appropriate cumulative leaf area index, respectively. Using Kira's (1978) data, we apply $K_i = 0.7$. Finally, the factor C recalculates photoproduction in units of tons of organic dry matter per hectare per year [$t_{ODM}\ ha^{-1}\ a^{-1}$]. Note that the actual annual production is the integral of PS_i over a constantly changing radiation input I_i with its diurnal and seasonal variation. Therefore, assuming average (or equivalent) radiation input I_i during daylight hours, C is based on the assumption of $8760/2$ daylight hours per year ($C = 2.39$).

During the model simulation, situations may occur where the crown layers are filled only partially (this is the normal case). Since photoproduction is proportional to leaf area, PS_i in this case has to be multiplied with the current crown fill ratio AT_i [$ha\ ha^{-1}$] to obtain the actual gross photoproduction rate PT_i [$t_{ODM}\ ha^{-1}\ a^{-1}$]:

$$PT_i = AT_i * PS_i$$

where

$$AT_i = AC_i * N_i / 10\,000 \quad \text{if } AC_i * N_i / 10\,000 < 1$$

and

$$AT_i = 1 \quad \text{else}$$

AC_i is the actual crown projection area [m^2] of a single tree of that class,

and the factor 10000 refers this area to 1 ha (10000 m²) in order to normalize AT_i .

The solar radiation I_i [W m⁻²] received by layer i is calculated from the cumulative leaf area index of the canopy layer above it (index $i + 1$) and the radiation I_{i+1} received by that layer (or the radiation above the canopy is for the uppermost layer). According to Lambert–Beer's law, for the five canopy layers:

$$I_i = I_{i+1} * \exp(-K_{i+1} * LAI_{i+1}) \quad \text{if } i < 5$$

and

$$I = I_5 \quad \text{if } i = 5$$

Energy losses for respiration and renewal

Over a given time period (i.e. year), the assimilated energy must balance exactly the energy lost to respiration, litter losses, and biomass increment.

The losses can be grouped into two categories. A certain amount of respiration is proportional to leaf photoproduction and hence leaf area, and the remainder is (roughly) proportional to the current amount of woody biomass.

The following energy losses are (approximately) proportional to leaf area: leaf respiration (maintenance and photorespiration); construction respiration; leaf litter and leaf renewal; fine root respiration, renewal, and litter; small branch and small root respiration, renewal, and litter; and fruit production. The remaining energy losses are (approximately) proportional to woody biomass: stem respiration and litter; coarse branch respiration and litter; coarse root respiration and litter.

According to estimates for mature tropical forest (Pasoh forest; Kira, 1978), approximately 50% of the gross photoproduction goes to leaf-area-proportional energy losses. Losses proportional to biomass occur at an annual rate of approximately 6.5% of the current woody biomass. This leaves some 7% of the gross photoproduction for net woody biomass increment.

In the FORMIX model, the state variable 'tree biomass' comprises only the woody parts of stems, branches, twigs, and coarse roots. It is calculated by solving the appropriate differential equation for the variable B_i . Assimilate demand for maintaining the woody parts of the tree R_i [t_{ODM} ha⁻¹ a⁻¹] is calculated in proportion to the wood biomass B_i :

$$R_i = SR_i * B_i$$

where SR_i [a⁻¹] is the specific respiration rate of this layer.

The respiration demands for leaves and fine roots as well as the assimilate needed for renewal of these biomass fractions are calculated from the actual gross photoproduction PT_i . This is done by multiplying the gross production rate with the leaf-proportional energy use efficiency PR_i [-] to yield the supply rate of remaining assimilate PB_i [$t_{ODM} \text{ ha}^{-1} \text{ a}^{-1}$]:

$$PB_i = PR_i * PT_i$$

The residue ($PT_i - PB_i$) can then be interpreted as the leaf-proportional part of the respiration and renewal demands.

Transition from one crown layer to another

As trees in one canopy layer reach a given maximum diameter, they also attain a corresponding height. Correspondingly, their canopy eventually grows into that of the next layer, and into better light conditions. The photoproduction changes accordingly. In the simulation model the corresponding tree numbers and the appropriate amounts of biomass must be moved to the next canopy layer, in adherence to the principle of mass and energy conservation.

Transition TN_i [$\text{trees ha}^{-1} \text{ a}^{-1}$] is activated if the diameter difference

$$DD_i = MD_i - D_i$$

between the maximum diameter of that class MD_i [m] and the actual diameter D_i [m] becomes zero (or less) (i.e. if trees exceed the maximum height of their canopy class, they must be counted as members of the next class). Thus:

$$TN_i = 0 \quad \text{if } DD_i > 0$$

and

$$TN_i = XT_i \quad \text{else}$$

where XT_i is the number of trees per hectare and year which move to the next class. Using specific transition rates TS_i [a^{-1}], the XT_i [$\text{trees ha}^{-1} \text{ a}^{-1}$] may be derived from the actual tree numbers N_i as follows:

$$XT_i = N_i * TS_i$$

Similarly to the determination of biomass losses due to mortality, the biomass transferred to the next layer TB_i [$t_{ODM} \text{ ha}^{-1} \text{ a}^{-1}$] can be derived directly by using the tree-specific biomass BT_i :

$$TB_i = BT_i * TN_i$$

Tree mortality

The mortality rates of trees in the different layers M_i [trees ha⁻¹ a⁻¹] are computed by multiplying the number of living trees by a specific mortality rate ms_i :

$$M_i = ms_i * N_i$$

The specific mortality depends on the canopy density in that class (as a measure of crowding), and hence on the number of trees of that class and their specific crown projection area. Both determine a crown closure deficit AR_i [-] which will switch the mortality rate from its normal value MN_i [a⁻¹] to a higher level MC_i [a⁻¹] if the canopy within that layer is overcrowded (a more continuous formulation will not affect the results):

$$ms_i = MN_i \quad \text{if } AR_i > 0$$

and

$$ms_i = MC_i \quad \text{else}$$

If, due to M_i , trees are dying, we have to subtract an appropriate biomass portion from the wood biomass pool. This biomass mortality rate MB_i [t_{ODM} ha⁻¹ a⁻¹] can be derived from M_i simply by introducing the specific biomass per tree BT_i [t_{ODM} tree⁻¹]:

$$MB_i = BT_i * M_i$$

Tree geometric relationships

In computing energy assimilation and dissipation rates in the forest, some basic physical relationships of tree geometry and photoproduction must be considered. For example, the photoactive surface of trees is restricted by a maximum crown diameter for a given stem diameter, and by a limited leaf area index: the LAI will only be increased as long as the net rate of energy assimilation of lower leaf layers is still positive (gross production minus leaf respiration). Also, the average height of the canopy of a given tree class determines its relative competitive position in the stand. In addition, the respiration balance of trees shifts as they grow. A stand of young trees has a lower total biomass than a stand of old trees, while total leaf mass will be about the same in both cases. Energy losses due to stem respiration will therefore be higher in a stand of older trees, reducing the net increment.

It is therefore not possible to restrict forest growth computations to calculations of biomass growth; rather, the characteristic geometric proportions in each canopy layer must also be available. This is best achieved by

keeping track not only of biomass, but also of the number of trees in each canopy layer. This allows the calculation of biomass per tree, and hence of volume, diameter, height, basal area, crown area, leaf area etc. using well-known parameters such as wood density, form factor (F), height-to-diameter ratio (h/d), crown-to-diameter ratio (CD), and leaf area index (LAI).

A simple division of the total wood biomass per hectare B_i by the appropriate actual stem number N_i yields the wood biomass (stem, branches, and coarse roots) per tree BT_i [t_{ODM} tree $^{-1}$]. It is set to zero if there is less than one individual left within a certain class (to exclude survival of fractional trees):

$$BT_i = B_i/N_i \quad \text{if } N_i > 1$$

and

$$BT_i = 0 \quad \text{else}$$

Using form factors F_i [–] and height-to-diameter ratios HD_i [m m^{-1}] for each crown layer given as table functions depending on biomass per tree BT_i (cf. Table 1), we can derive tree diameters D_i [m] as follows:

$$D_i = ((4 * BT_i * TR_i) / (\pi GF_i * HD_i))^{1/3}$$

Here TR_i [–] is the stemwood fraction of the total wood biomass and G [t_{ODM} m^{-3}] denotes the specific weight of wood expressed in organic dry matter. Via HD_i , D_i also determines tree height H_i [m]:

$$H_i = D_i * HD_i$$

For each layer, a constant crown diameter-to-stem diameter ratio CD_i [m m^{-1}] determines the crown diameter $CD_i * D_i$. Thus, the crown projection area AC_i [m^2] of a tree within layer i is:

$$AC_i = \pi/4 * (CD_i * D_i)^2$$

The (maximum) relative crown area xAT_i [ha ha^{-1}] of crown layer i is given by:

$$xAT_i = AC_i * N_i / 10\,000$$

from which the relative crown closure deficits AR_i [–] are determined via

$$AR_i = 1 - xAT_i$$

If AR_i becomes negative, which means a totally filled crown, we restrict xAT_i to values below or equal to unity to yield the total relative crown area AT_i [ha ha^{-1}]:

$$AT_i = xAT_i \quad \text{if } AR_i > 0$$

$$AT_i = 1 \quad \text{else}$$

Thus, the total (absolute) leaf area L_i [ha ha^{-1}] finally can be derived by multiplying the total relative crown projection area AT_i by the leaf area index LAI_i [ha ha^{-1}]:

$$L_i = AT_i * LAI_i$$

Seed production

To represent observations by Ashton et al. (1988) that seed production within dipterocarp forests occurs at time intervals of 5 years, we implemented the table function *sp* determining the number of seeds produced per tree as a function of time. Additionally, bad weather conditions during fruiting may damage a great fraction of the seeds produced. This is also accounted for in the shape of the table function *sp*.

The seed production rates S_i (number of seeds per hectare and year [$\text{ha}^{-1} \text{a}^{-1}$]) apply only to trees having reached maturity: for emergents and main canopy trees (indices $i = 4, 5$) they can then be calculated by:

$$S_i = N_i * SP \quad i = 4, 5$$

The total seed production rate S [$\text{ha}^{-1} \text{a}^{-1}$] of the stand is simply the sum of S_i ($i = 4, 5$):

$$S = S_4 + S_5$$

Assuming a specific seed survival fraction *ss* [–] accounting for seed mortality and grazing, the annual seedling input TN_0 [$\text{ha}^{-1} \text{a}^{-1}$] is then determined as:

$$TN_0 = SS * S$$

from which the biomass gain of the seedlings by seed production TB_0 [$t_{ODM} \text{ha}^{-1} \text{a}^{-1}$] can be derived using the specific initial seedling biomass *BS* [$t_{ODM} \text{seedling}^{-1}$]:

$$TB_0 = BS * TN_0$$

Logging according to the Selective Management System (SMS)

Under the Selective Management System (SMS), a certain number of main canopy trees remains after logging, while the emergents are logged 100%. Certain fractions of the remaining classes ($i = 1, 2, 3$) are destroyed, depending on the severity of the logging operations. The time of the first logging, the logging cycle, and the logging damage fractions F_i ($i = 1, 2, 3$) to poles, saplings, and seedlings per logging event are user-defined. Additionally, the user will be asked to define the number of main canopy trees remaining after logging.

A logging operation now constitutes a discrete event during simulation: biomass and number of emergents and main canopy trees are set to zero or to the new values determined by the logging conditions.

The remaining tree numbers and biomass in the seedling, sapling, and pole layers are determined as:

$$N_i(\text{new}) = (1 - F_i) * N_i(\text{old})$$

and $(i = 1, 2, 3)$

$$B_i(\text{new}) = (1 - F_i) * B_i(\text{old})$$

Parameter choice and sensitivity analysis

The parameters used for the sample simulations represent Malaysian lowland dipterocarp forest. They are listed in Table 1.

Some of the parameter values incorporated in the FORMIX model lack a solid empirical basis as in the past only little work has been done to determine light response curves, respiration rates, assimilate distribution patterns, and other important growth parameters for tropical rain-forest species. Therefore, an extensive sensitivity analysis investigating the influences of changes in the parameter set on the simulation results has been carried out. The results of the sensitivity analysis can be summarized as follows (see Bossel and Krieger, 1990a, for details):

- Over the full range of meaningful parameter choices, the FORMIX model exhibits only gradual response changes. Parameter changes do not result in unexpected reactions.
- The specific choice of the normal specific mortality rates MN_i , the specific mortality rates due to crowding MC_i , the specific transition rates TS_i and the threshold diameters DM_i has only a minor influence on model behavior and final results.
- The choice of parameters associated with the energy balance (P_{\max} , PR_i , SR_i) will affect the total biomass gain. These parameters should be determined accurately to represent concrete site conditions.
- The choice of the crown-to-stem diameter ratio CD_i has no significant effect on the biomass maximum in the range $20 < CD_i < 30$, but the gap regeneration rate (speed) is significantly increased for larger CD_i .

SIMULATION OF SINGLE GAP REGENERATION DYNAMICS

In the present section, we apply the FORMIX model to the simulation of regeneration dynamics in a single homogeneous forest gap under the conditions of (1) clearcut and single planting, and (2) logging according to

the Selective Management System (SMS) currently being practised in Malaysia (Thang, 1987).

Single gap simulations can represent natural forest growth only as long as mature tree mortalities (and/or numbers) are low, and gap formation is therefore not yet significant. In particular, this means that the single gap model will provide valid results for assessing forest dynamics for cutting cycles up to periods of approximately 200 years.

We found in all simulations that the effects of constant, or periodic, or irregular seed events on the overall dynamics of forest development and regeneration are insignificant. Even under adverse conditions, the presence of some main canopy or emergent trees ensures an abundance of surviving seedlings, and a corresponding regeneration of the forest. We therefore apply the same seedling scenario in all simulations, which follows the observations of Ashton et al. (1988).

Clearcut and single planting

The simulation starts with the planting of 10 000 seedlings per hectare on bare soil. No further seedlings are introduced until some of the trees have reached the main canopy and can start producing seeds. As trees grow into the emergent class, additional seeds are produced. The number of seedlings varies accordingly – after the maturing of the first trees, it is always sufficient to ensure regeneration.

The number of saplings follows that of the seedlings with a phase delay of about a decade. Approximately two decades later, the poles reach a maximum number per hectare and then start growing into the main canopy at approximately age 60. Emergents start appearing at about age 100.

The biomass plot (Fig. 4) shows the development of (cumulative) biomass for the five tree layers: The seedling biomass has a maximum at 15 years and becomes small thereafter. The sapling biomass has a maximum at 25 years, almost disappears at 70 years, and then again builds up to a substantial and continuous value for the rest of the simulation period of 500 years; during the whole period, saplings are present in abundance.

The pole biomass shows a very different behaviour: it has a maximum approximately at year 50, and then almost disappears entirely, only to reappear in year 320, with another maximum at year 390, and almost complete disappearance thereafter: the pole population appears in pulses. The main canopy trees show similar behaviour.

The reason for this ‘pumping’ of the poles and of the main canopy trees is identified by reference to the main canopy and emergent tree biomass: As poles grow into the main canopy, the latter becomes denser and drastically reduces the light availability for the pole class. Recruitment into

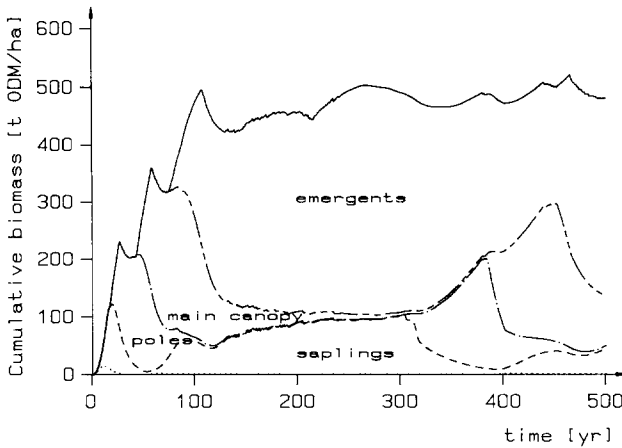


Fig. 4. Cumulative biomass as simulated by the FORMIX model (standard run).

the pole class stops completely; while remaining poles stagnate and eventually die. This process is repeated for the main canopy class, as emergents fill up the top canopy layer. Later, due to its mortality, the emergent crown opens up, providing better light conditions for the always-present sapling layer, and causing the sapling population to grow again into poles, hence repeating the forest growth cycle after year 320. This 'pumping' of the poles is a phenomenon commonly observed in natural tropical forests (Appanah, 1990, personal communication).

The energy balance of the forest is reflected in the diagram of gains and losses (see Fig. 5). After the initial growth stage, the gross production settles between 65 and 75 $t_{ODM}/(ha\ yr)$, in accordance with the observa-

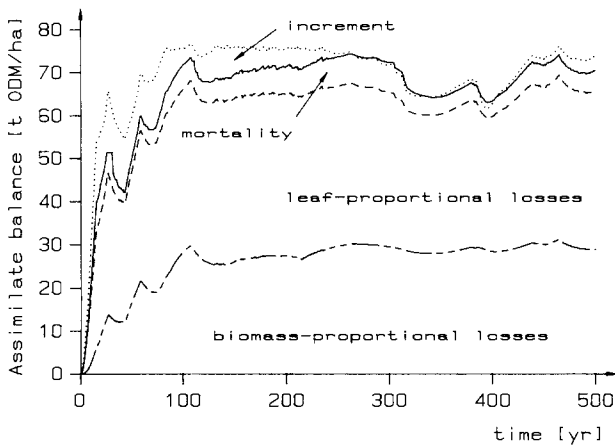


Fig. 5. Assimilate balance as a result of the FORMIX standard run.

tions reported by Kira (1978). Approximately 40% of the gross production goes into biomass-proportional respiration and litter losses (bottom curve), while 50% is used up by leaf-proportional respiration and litter losses (second curve from bottom). Tree mortality accounts for an increasing loss of up to 10% of gross production. The remainder (a maximum of 10% of gross production) goes into increment. Increment is highest in the growth stage (0 to 200 years, and after 450 years). The maximum increment attained is around $10 \text{ t}_{\text{ODM}}/(\text{ha yr})$.

The major result of this simulation (and of a large number of supporting simulations not discussed here) is the replication of the observed cyclical nature of forest growth *in the gap*. We (naively) expected the model to approach an equilibrium condition at some stable characteristic mix of tree biomass and tree numbers in each class, which could then be maintained indefinitely. This is definitely not the case. It could only be achieved by constant and well-defined thinning operations in the different layers. If such a steady state were to be achieved, a dynamic model such as FORMIX could certainly help in designing the proper-management strategy.

Logging according to the Selective Management System (SMS)

Logging operations according to the Selective Management System (SMS) currently being practised in Peninsular Malaysia remove all emergent trees, but leave a certain number of main canopy trees (32, per hectare; Thang, 1987). During logging operations damage and destruction to the pole, sapling, and seedling layers is unavoidable. The period of the logging cycle is 35 years. Underlying the SMS concept is the assumption that the remaining main canopy trees will grow into emergents during the 35 years, while poles will grow into main canopy trees, and that this cycle is sustainable. In the following, we compare results for different logging periods. This comparison is preliminary and has to be judged on the basis of the chosen model parameters.

It was stated in the previous section that because of the cyclical growth in gaps, the model of a single gap cannot produce an equilibrium composition of a natural forest, which could be used as the initial condition for unlogged forest. In order to approximate such a condition for the logging simulation runs, we use the same initial development of the forest as in the previous run, and introduce the first logging at year 125. At this time, the (woody) biomass distribution is approximately: seedlings (1%), saplings (15%), poles (2%), main canopy trees (51%), and emergent trees (31%).

The use of the single-gap model to simulate the development of logged or planted forest *before* significant gaps develop due to individual old tree mortality therefore appears to be legitimate. Logging in effect produces a

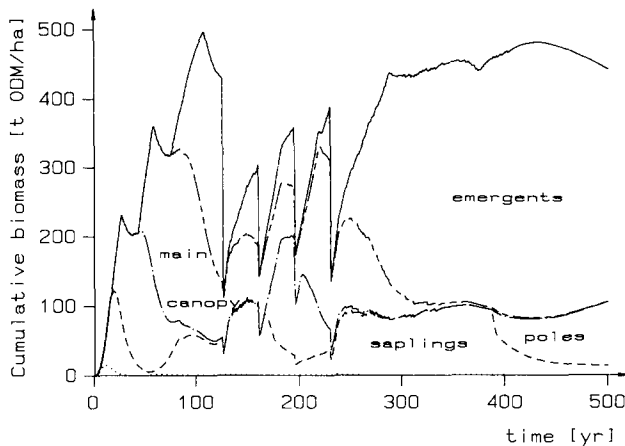


Fig. 6. Cumulative biomass predicted for a 35-year cutting cycle under SMS (Selective Management System).

synchronization of the gap dynamics in a natural forest, and this synchronization can be expected to persist for some time.

The biomass development for the 35-year SMS cycle is shown in Fig. 6. It is immediately obvious that this harvesting schedule produces neither a uniform timber assortment, nor a reliable and uniform harvest volume. The reason is that the cutting cycle is completely out of phase with any natural frequency of the (synchronized) forest system. A change (lengthening) of the logging period could lead to a better matching of logging and natural cycles, and would permit harvesting of a more or less constant assortment composition on a sustainable basis. Investigations indicate that a 100-year cycle would be in better agreement with the natural frequency of the system.

The biomass development for a 100 year SMS cycle is shown in Fig. 7. In this case we observe a repetition of the results every 200 years; i.e. the logging results are more or less identical at every second logging. At the 2nd, 4th, 6th etc. cuts, most of the trees harvested are emergents (approximately 230 t_{ODM}/ha of stem biomass). A similar volume can be harvested at the 1st, 3rd, 5th etc. cut; however, at these intervals the fraction of main canopy trees is somewhat larger. The agreement of the logging cycle with the natural frequency of the system is even more evident from a phase plot of poles and saplings: the state variables cycle in a 200-year loop.

These results are only minimally affected by parameter changes within permissible ranges. It must therefore be concluded that the currently envisioned 35 year SMS cutting cycle cannot be achieved on energy

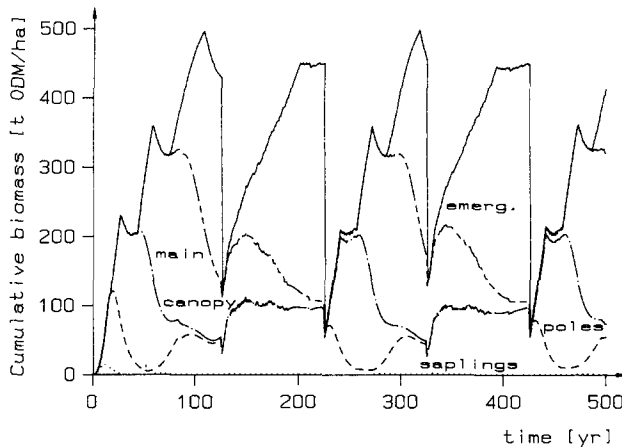


Fig. 7. Cumulative biomass predicted for a 100-year cutting cycle under SMS (Selective Management System).

grounds alone. If it should be continued, the cutting practice would be unsustainable.

SIMULATION OF FOREST MOSAIC DYNAMICS

In mature natural forests, the random formation of gaps causes the growth cycle to begin anew at different times in different locations. For this reason, the simulation results for a homogeneous patch cannot be expected to represent (planted) forest dynamics correctly after the onset of significant natural gap formation. For a more accurate description, a spatial adaptation of FORMIX is required.

After formulating and testing the model for one single gap, the model was expanded to represent a given heterogeneous spatial forest pattern. The user now defines a spatial forest structure given by a rectangle-shaped patchwork. (Other, also irregular shapes, could in principle be used.) Each patch is characterized by its coordinates in an appropriate coordinate grid. This allows a distinction between different site conditions by choosing different parameter sets for the specified parts of a given forest. The model is evaluated in parallel for all defined patches of this grid. Mutual influences of single gaps via falling dead trees and via seed dispersal are accounted for by random mortality rates and random seed events. A falling tree produces a new gap corresponding to its height and falling direction. Fructification appears simultaneously for all patches (Ashton et al., 1988) and produces a seedling input not only for patches containing mature trees themselves, but – depending on a randomly chosen wind direction – also

for the neighbouring plots. The auto-rotating two-winged dipterocarp seeds in particular easily reach neighbouring gaps.

After the simulation, a graphical user surface allows the display of the results as time-dependent maps showing the current developmental stage of the different plots as artificial aerial maps as well as vertical profiles. Additionally, a time-dependent stem diameter distribution can be produced on decimal or logarithmic scales.

Random mortality of mature trees

The single-gap version of the FORMIX model calculates tree mortality for all canopy layers in proportion to the current standing tree biomass. The proportionality constants are defined by parameters specifying the normal specific mortality MN_i and the specific mortality due to crowding MC_i . For mature trees in a forest grid, this principle is not applicable for two reasons:

(1) For older trees, crowding situations do not appear very often, and they are not capable of reacting quickly to crowding because the physiological parameters for mature trees (like crown shape, stem form, etc.) are more or less fixed.

(2) Apart from the biomass losses caused by the mortality of mature trees (main canopy and emergents) in the specific plot, dying trees normally damage the canopy of other plots while falling. Vice versa, the plot currently being evaluated is influenced by other trees falling into it and increasing the mortality rates within the plot.

Therefore, the mortality of main canopy and emergent trees (layers 4 and 5) is determined by a random process. Nevertheless, the previous normal specific mortality rates MN_4 and MN_5 are used to adjust the random number generator to guarantee an average mortality rate equal to that of the single-gap model.

If the random mortality process determines death of main canopy or emergent trees, we assume a 50% chance for the dead trees to fall. The remaining trees die standing-up. The falling trees undergo an additional random process to determine the falling direction. According to the tree height and the falling direction, the FORMIX simulator determines the plot which is hit by the falling canopy. Within this plot, a given percentage of all canopy layers will be damaged. If available, the falling direction can be modified by parameters representing the slope of the given plot or prevailing wind directions. Height, stem diameter and falling direction, as well as crown size of each dying tree, will be recorded in a special result file. After the simulation this information can be used to superimpose on the forest spatial pattern the location and shape of fallen trees.

Random seed production

At the beginning of each year, another random process determines whether this is a seed year or not. If so, an additional random generator is used to decide if the conditions for seeds during that period were good or not. Good conditions result in a survival of 500 seeds per mature tree, and for bad conditions only 20 seeds per mature tree survive. Again, the stochastic process is adjusted in order to gain the same mean seed input as for the single-gap model. Additionally, we exclude seed years following each other directly, which represents natural conditions more properly. In case of a seed year, a procedure (similar to that determining the plot hit by a falling tree) is used to model seed dispersal. Seventy percent of the seeds remain in the plot of their origin, 30% move to the determined target plot.

Simulation results from the spatial FORMIX model

The spatial version of the FORMIX model has been applied to a hypothetical tropical natural rain forest stand consisting of 25 quadratic plots of 400 m² each, i.e. 1 ha composed of 25 gaps of size 20 m by 20 m. All plots use the same parameter set except for the specific plot location parameters. Thus, the results shown below represent the temporal development of a forest with uniform site conditions and uniform species composition. Diversification of the different patches resulted entirely from the random tree mortality and the random seed dispersal.

After a period of 500 years, the simulated forest has matured and has developed into a heterogeneous forest mosaic (Fig. 8). In some plots, the uppermost layer is now the main canopy or even the pole layer. Since the last recorded simulation step (here: 10 years ago, time = 490 [a]) one emergent tree has died and fallen into another plot.

The total number of emergents and main canopy trees is in good agreement with empirically determined figures from mature tropical rain forest stands. The small number of seedlings gives reason for the assumption that there was no major seed event during the last 2 or 3 years.

To get a better picture of the vertical structure of the simulated forest, one can also display the canopy layer structure of the different plots (Fig. 9).

In order to compare the simulation results with empirically derived data, the user can combine the stem counts within the different plots and different layers to produce a diameter distribution curve. Proportional, logarithmic, and double-logarithmic representations can be chosen. On a double-logarithmic scale, the diameter distribution for the mature forest appears as a straight line with negative slope (Fig. 10). Some of the

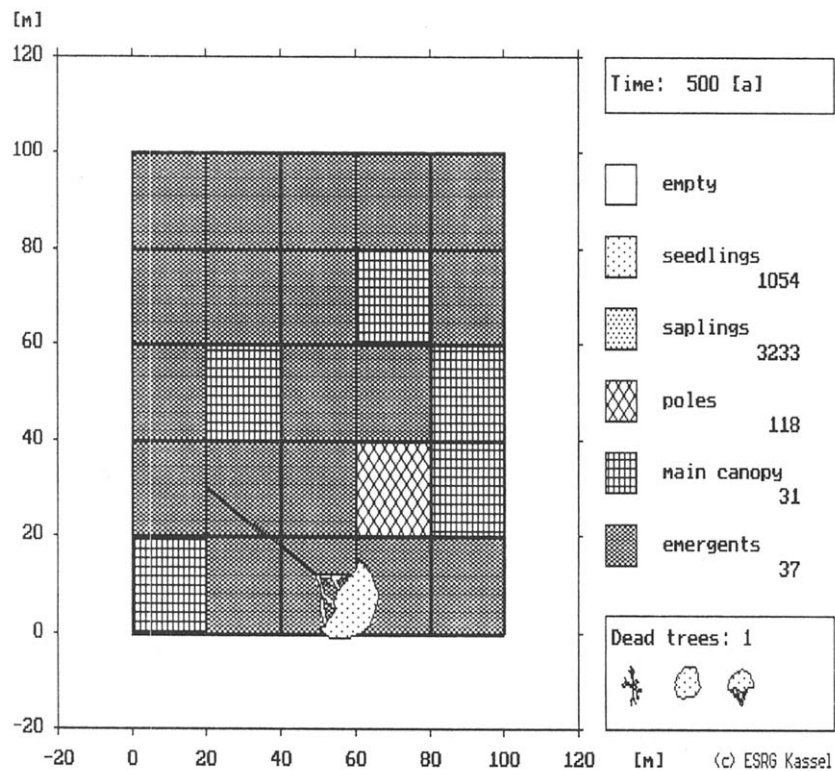


Fig. 8. Top view of the 1-ha test stand after 500 years of development.

diameter classes are not represented in this particular simulation run. On the one hand, this is due to the small number of only 25 simulated plots. On the other hand, empirically derived distributions also very often show gaps in the diameter distribution (Kato et al., 1978).

In contrast to the single-gap model, the stem diameter distributions of the forest mosaic model do not exhibit the pumping dynamics of the single gap. This is because the (simulated) forest consists of a large number of gaps (25) whose individual dynamics are determined by random effects, producing (approximate) equilibrium distributions in the aggregate.

Finally, a good overview over the structure of the simulated forests can be achieved by displaying the temporal development of a vertical intersect through the stand. Any profile of the stand can be chosen. Figure 11 shows the structure of the first five patches (20 * 100 m) after 500 years of development. The right-hand side of this intersection exhibits a dense upper tree layer with only few trees below, whereas at the left edge, emergents are missing and most of the trees are at the transition point between poles stage and main canopy.

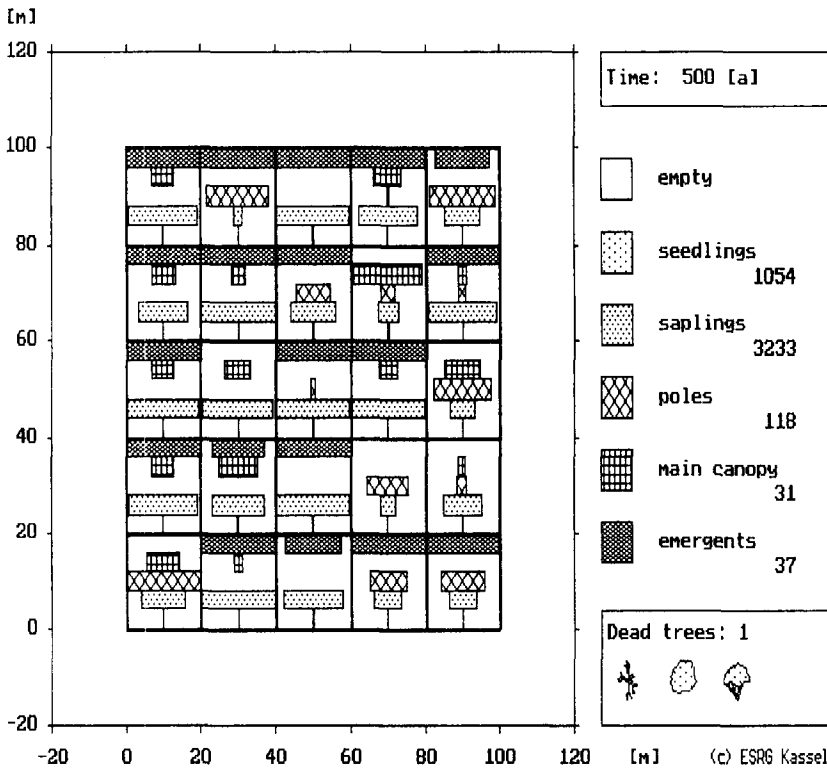


Fig. 9. Canopy layering of the 1-ha test stand after 500 years of development.

The overall diversity of the stand is illustrated in Fig. 12. Here, all the trees of the test stand are displayed and the user gets a good impression of the layer structure, of dense and open areas, and of the maximum height of the crowns.

DISCUSSION

In order to assess the general validity of the FORMIX model, its structural, behavioural, empirical, and application validity must be discussed, both on the gap level and on the level of the forest mosaic. In its present form the model cannot account for water or nutrient limitations.

The FORMIX forest dynamics model explicitly integrates relevant tree geometric relationships, light attenuation in a multilayer forest canopy, empirical photosynthesis data, energy accounting based on the law of energy conservation, conservation of mass, and empirical data from tropical natural forests. Although each of five canopy layers in a forest gap is described by only the two state variables biomass and tree number, the

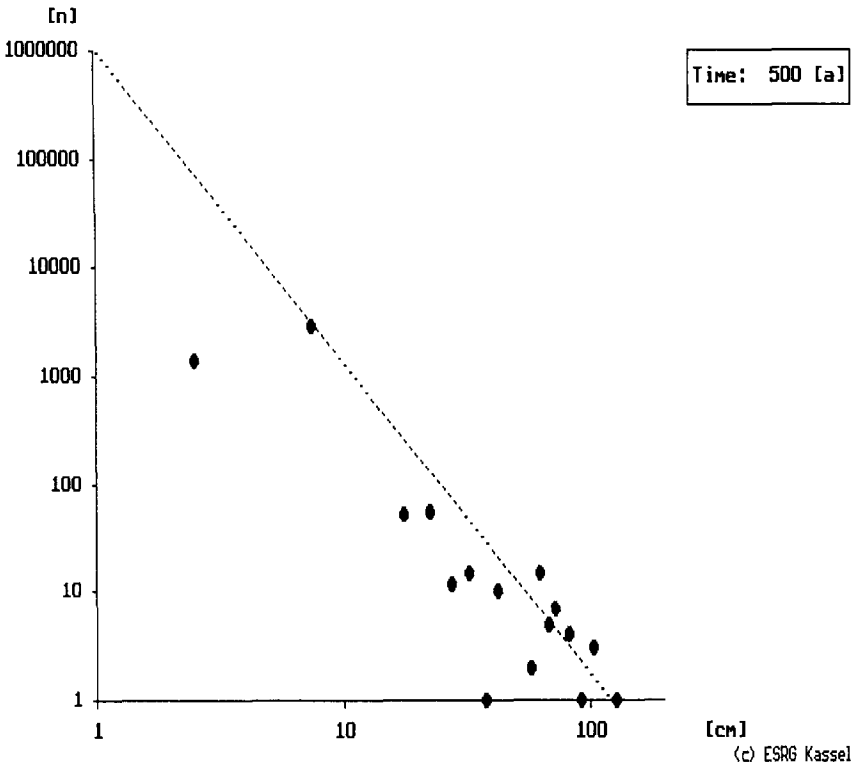


Fig. 10. Diameter distribution of the 1-ha test stand after 500 years (double-logarithmic scale). Straight line corresponds to diameter distribution in natural forest ($\ln(N) = 6.01927 - 0.28827 \ln(D)$, for Pasoh, Malaysia, after Appanah et al., 1990).

model contains the essential processes of forest growth and is therefore judged to amount to a structurally valid description of the natural forest on the gap level as well as on the forest mosaic level.

Comparisons of simulation results with empirical data for Southeast Asian forests (Appanah et al., 1991) as well as numerous plausibility and sensitivity tests (Bossel and Krieger, 1990a) have shown consistently that the FORMIX model in both the gap and the forest mosaic version produces forest response dynamics which are in good agreement with empirical observations, including the ‘pumping’ observations in single gaps and logged forest, and the ‘equilibrium’ observations in natural unlogged forest. The model is therefore judged to be behaviorally valid.

Key variables computed in the FORMIX simulations are generally in agreement with empirical observations (gross production, basal areas, tree numbers, diameters, heights, biomasses, crowding density, etc.) (Appanah et al., 1991; Bossel and Krieger, 1990b). Therefore, the model is judged to

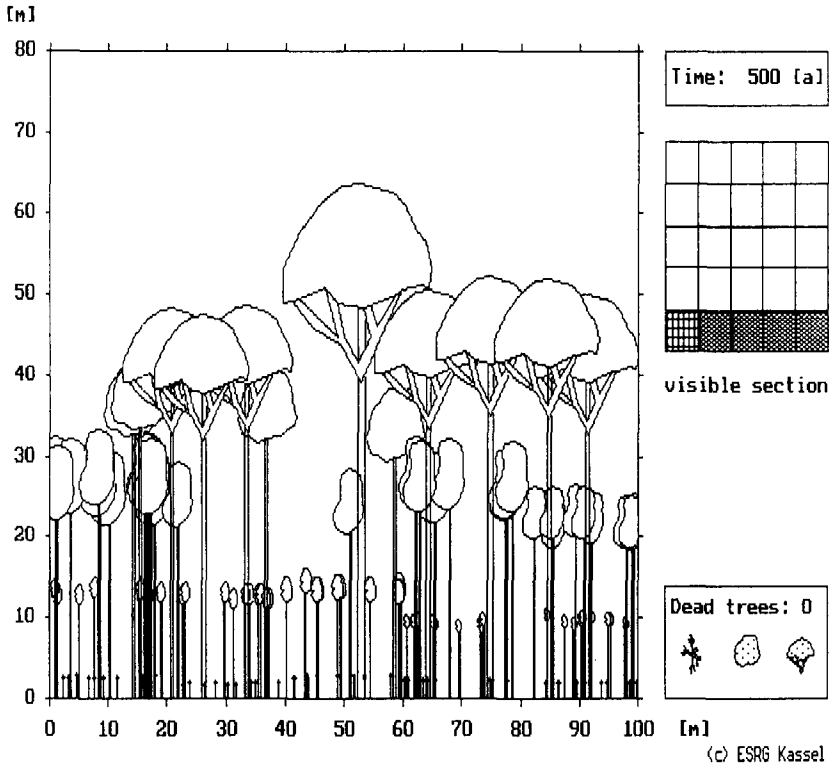


Fig. 11. Vertical profile (20 * 100 m) of the 1-ha test stand. Each tree symbol represents a certain number of actual trees: seedlings (10), saplings (10), poles (5), main canopy trees (1), emergents (1).

have a reasonable degree of empirical validity. Some differences occur in particular with respect to the emergent layer and are due to the current lack of differentiation between species with and without emergence potential (dipterocarps, non-dipterocarps): all trees are now potential emergents. (This deficiency has been remedied in a more recent version, Bossel and Krieger, 1990b).

The FORMIX model employs physically meaningful parameters, most of which can be determined relatively easily from empirical observations. Moreover, the number of parameters is surprisingly small. The model is somewhat sensitive to only a few of these parameters (CD_i , SR_i , PR_i). Uncertainties in these parameters produce differences in the natural frequencies of the system, but not in the response type. The model is therefore judged to have application validity.

Despite these encouraging results, we recognize that the model can and should be improved in a number of aspects.

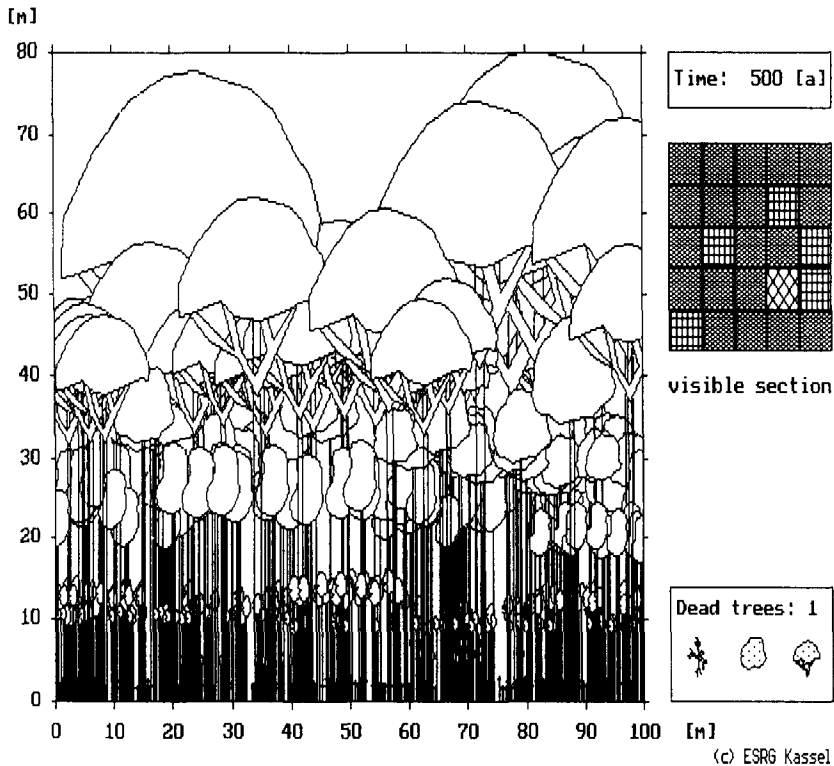


Fig. 12. Vertical profile of the whole 1-ha test stand.

The model should be expanded to include different physiognomic groups of tree species (pioneers, main canopy trees, emergents, shade-tolerant species, etc.) with their specific parameters, in order to approximate real forest species composition and development more closely. (This has in the meantime been achieved by Bossel and Krieger, 1990b, by introducing five different species groups with different photoproduction and respiration parameters. These determine their relative competitive advantage in each layer, and also which canopy layer they can ultimately reach). The model should also be supplemented by a soil-water model in order to simulate drought stress. Since regeneration dynamics are influenced by gap microclimate (temperature, evaporation, shading etc.), corresponding model additions might be useful. In order to test its generic applicability, the FORMIX model should also be modified and parametrized for application to temperate mixed forests.

Of particular interest to forest preservation and management would be the integration of the FORMIX model with a geographic information system (GIS) in order to provide long-term spatial simulations of the

development of actual forests under different logging methods, cutting cycles, and silvicultural treatments.

The data required for the parametrization and validation of the FORMIX model correspond only partially to data routinely collected in forest science. The modelling effort suggests that empirical data collection efforts in the following areas would significantly contribute to a better understanding of the forest system: light response curves for different physiognomic groups of forest trees ('guilds'); light attenuation for different canopy layers; crown diameter and tree geometry data for different guilds; carrying capacity of different sites in terms of basal area; structure of different natural forests; mortality and transition patterns of different canopy layers and guilds; assimilate allocation (partitioning) as a function of development stage; specific respiration rates of tree components as a function of temperature, etc.

SUMMARY AND CONCLUSIONS

Since the FORMIX model differs substantially from other forest growth models, we summarize again the major features:

The natural forest is visualized as being composed of five vertical canopy layers (tree classes) for the five development stages: seedlings, saplings, poles, main canopy, emergent trees.

Tree geometry is explicitly introduced in each tree class by using both biomass and stem number as state variables. From these, tree height and diameter, crown height and diameter, leaf area and its vertical distribution, stem volume, basal area, crowding competition, respiration fractions, etc. can be determined.

Energy accounting, based on the laws of energy and mass conservation, serves as the basic structural framework of the model. This ensures adherence to physical principles and consistency of results by constant balancing of all gains and losses.

The physical features of photosynthetic production in the leaf canopy are fully included by employing the actual light response curve of leaves, and accounting for the light attenuation of each leaf layer.

Assimilate losses (energy losses) are considered in two categories: one is proportional to leaf area, the other is proportional to biomass. The net difference between gross production and total losses goes into increment. Increment decreases as trees mature and their biomass-proportional losses consume an increasing relative amount of assimilate.

Transitions to other development stages as well as mortality losses are accounted for according to the principle of mass and energy conservation.

A distinction between different tree species (species-dependent light response curves etc.) has not been made in the present model since it would require a corresponding multiplication of state variables and would not significantly change the overall forest dynamics (but see Bossel and Krieger, 1990b).

Extensive simulations and sensitivity tests using the FORMIX model suggest the following conclusions:

The single gap model provides a (structurally and behaviorally) valid description of forest gap regeneration through the seedling, sapling, pole, main canopy, and emergent stage.

The single gap model can be used to simulate development of a forest after clearcut and planting up to the point where a significant mortality of mature trees begins (about 200 years). It may therefore be useful for forest planning.

The development of a natural forest mosaic and its long-term spatial dynamics can be simulated by a spatial distribution of FORMIX gap models with random mortalities and seed dispersal.

The single-gap simulations demonstrate very clearly that the (logged or planted) forest system has its inherent natural frequencies (eigendynamics). In the application to Malaysian lowland dipterocarp forest, those frequencies important to sustainable forest use have a period of approximately 100 and 200 years for main canopy and emergent trees, respectively.

In order to provide a sustainable timber harvest with a reasonably uniform assortment composition, cutting cycles must be in step with the natural growth frequencies of the system.

Neither the (now abandoned) 70 year Malayan Uniform System logging cycle, nor the (presently used) 35 year Selective Management System cycle are in any way near the natural frequency of naturally regenerating tropical forests in Peninsular Malaysia. They cannot be the basis for sustainable timber production.

These conclusions apply as well to similar forest management schemes in other (subtropical and tropical) parts of the world.

ACKNOWLEDGMENTS

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