INSTITUTE OF TERRESTRIAL ECOLOGY

NATURAL ENVIRONMENT RESEARCH COUNCIL

DFID FORESTRY RESEARCH PROGRAMME R6915

ITE PROJECT T01067B5

Functional Classifications, Physiological Ecology and Options for Parameterising and Modifying the Hybrid Forest Model for Application to Indonesian TMF

A component of the FRP Growth & Yield Frameworks Project, Co-ordinated by the University of Edinburgh

First Report, July 97 - Dec 98

GJ Lawson, AD Friend, RI Smith, J McP Dick

Institute of Terrestrial Ecology

Bush Estate, Penicuik

Midlothian EH 26 0QB

08/26/02

Contents

Summary

The DFID-FRP Growth & Yield Modelling Project (R6915) aims to develop a modelling framework to predict forest growth and yield following management interventions at the level of the forest management unit. This framework will be used to examine criteria and indicators of sustainable production in selected Indonesian Tropical Moist Forests ITE's contribution to the overall goal is: a) to work with IERM to acquire and undertake quality control on long-term datasets of permanent sample plots (PSPs), b) to develop methods to cluster tree species into 'functional groups' for use in statistical analyses of PSP growth data, and to parameterise model simulations; and c) to provide a modular-version of ITE's 'Hybrid' vegetation model to represent the biophysical processes in tree growth and competition in a form which can be incorporated IERM's SymFor[97] modelling framework.

Forest classifications can be physiognomic, structural or functional. Tropical forests are so complex, difficult to measure, and species rich, that growth models are only likely to be parameterised for a small number of functional classes which group species which are as similar as possible in their environmental responses and growth potential.

This report summarises previous attempts to classify tropical forests; introduces a range of 'gap' and process-based models of forest growth, including the Hybrid forest model; describes the variation in physiology of tropical trees and the degree to which this variability can be represented in process-based models; summarises the current efforts to simplify and modularise the Hybrid model, and develops a work programme for future work in the ITE areas of this project.

Physiological factors which are relevant to functional groups are based groupings of tropical trees are already partially represented in the Hybrid model:

Bud break is controlled by thermal time and soil moisture. However it may be necessary to introduce a photoperiod factor to control leaf initiation in deciduous or leaf-exchanging tropical species where this is not obviously related to soil moisture.

Stem elongation - is driven by photosynthesis, carbon allocation and allometric constants linking height with stem diameter, however these constants are likely to vary with age as well as species.

Bud dormancy - is driven by degree-days and interaction with frost in cold-deciduous species. Shortening day length and decreasing night temperatures may induce dormancy, but are not currently considered for dry-deciduous species.

Leaf loss in cold-deciduous species is controlled by empirical relations between latitude and daylength; and in dry-deciduous species it is triggered by soil moisture. All deciduous and evergreen tree types have a single annual leaf-turnover parameter (with partial nitrogen re-translocation). An improved representation of seasonal peaks in leaf loss may be required in tropical semi-deciduous forests.

Cambial growth is assumed by Hybrid to take place only at the end of each year, although carbon stores and maintenance respiration are derived daily. Carbon is allocated by a 'pipe-model' which holds leaf mass in proportion to cross-sectional area of living sapwood by progressively allocating available carbon to leaves, wood, roots and storage carbon. At least 10 parameters are involved in Hybrids carbon allocation algorithms, and several will be key in distinguishing functional tree types.

Root growth and death is a great unknown for trees in natural systems, and assumptions greatly affect predicted above-ground yields. Hybrid assumes different turnover rates for coarse and fine roots, with fine-root growth proportional to foliage increment, and only 2 soil layers represented. In reality, trees change their relative allocation of photosynthate between below and above-ground growth depending on which environmental resources are limiting, and this ratio varies considerably seasonally. Such considerations are important in modelling crop-tree competition, but will be less important in predicting tropical forest growth.

Ageing - is partially represented in Hybrid through its optimisation of nitrogen in canopy layers with respect to light, and the fact that photosynthetic efficiency, transpiration and respiration are partially related to nitrogen. Lower layers with a negative carbon balance are assumed to fall off.

Flowering and Fruiting are not represented in Hybrid. Biomass in heavily flowering trees can occasionally represent 20-30% of biomass-increment, but flowers often photosynthise themselves, and the overall significance of carbon losses to flowers and fruits is unlikely to be significant for this project.

Seedling growth and death is controlled by the same carbon-balance considerations as with mature trees. An input parameter sets the maximum number of trees in a plot and new saplings are introduced from all available tree-types to replace mortality. The initial dbh and variability of these saplings is set with input parameters. There is scope to parameterise seedling environmental responses differently to mature trees, since this is a frequent observation in tropical forests.

Modularisation The original Hybrid model has now been modularised and carbon and nitrogen exchanges calculated at sub-daily 'physiological timesteps'. This introduces better representation of day and night processes. Carbon and nitrogen allocation takes place on a daily timestep. The module has been provided to IERM for inclusion in SymFor[97.]

Analysis of PSP data - entence from Ron/Jan…………….

1. Introduction

This report discusses literature relating to the physiognomic, structural and functional classification of trees and forests. It also introduces a detailed physologically-based forest model, which sets the growth characteristics of a given species (or 'generalised plant types'), and calculates the degree to which a species' latent growth capacity is constrained by competition for light, water and nutrients. It assumed that tree species can be classified into groups which display similar responses to the environment, and to disturbance, and that these environmental responses can be translated into the parameter values which are required by the growth model.

All plant growth models use mathematical constructions to the represent processes real world. There are two challenges associated with these constructions. Firstly, the algorithms contained in the model should try to represent the bio-physical **processes** involved in tree growth and interactions. Secondly, the parameters used in the model, whether for particular species or for 'generalised plant types', should be capable of estimation from field measurements or literature knowledge. The model described in this report has around 70 vegetation, soil

This report will adopt the following structure:

- *Section 2 will summarise the rationale for the FRP Growth and Yield Project;*

- *Section 3 will introduce forest classification techniques and problems, focusing on whether it is feasible to classify trees into a small number of 'functional types', to assist in model parameterisation;*

- *Section 4 will consider process orientated models of forest growth with emphasis on carbon allocation and tropical applications;*

- *Section 5 will describe the structure of the Hybrid (v3.0) forest model, indicating the methods used to represent different physiological processes, highlighting areas where modifications are required for the purposes of the current project, and commenting on the current soil, climate and tree-growth parameters;*

- *Section 6 will examine existing literature on the physiology of tropical trees and comment on the degree to which parameterisation information required by Hybrid is available;*

- *Section 7 will explain current efforts to 'modularise' the Hybrid model in the sense of providing Fortran computer code for individual tree objects which can be incorporated more easily in the SYMFOR (Phillips et al 1998) modelling framework.*

- *Section 8 will present a preliminary analysis of Indonesian Permanent Sample Plot datasets available to the current project, and comment on tests being used to assess their internal consistency, species v size distributions, species spatial distribution and possible consequences of disturbance.*

2. Rationale for the Indonesia 'Growth and Yield Project'

Conventional growth and yield models range from simple statistical stand regressions of average diameter or height with stand age, through to models which use a knowledge of inter-tree distances, site indices and stand basal areas to empirically simulate the inter-tree competition for resources of light, water and nutrients (Adlard 1995, Alder 1995). The emphasis is frequently on developing models of sustainable silvicultural systems (Yarie *et al*. 1990, Howard & Valerio 1992, Vanclay 1996, Anderson & Bare 1994, Jobstl 1995).

In plantation monocultures of known age, the future development of stand timber volume can be predicted simply from repeated measurements which derive statistical diameter-age or height-age relationships. Given a large network of Permanent Sample Plots (PSPs), these predictions of future yields can be extremely reliable. Semi-subjective modifications can be made to the yield tables if trees at a particular site have been managed with sub-optimal thinning, or if height to diameter ratios depart exceptionally from the average. Over the years, whole-stand models, diameter-distribution models, distance-independent individual tree models and, finally, distance-dependant individual tree models have been developed (Wan Razail 1989, Vanclay 1994, Mohren & Burkhart 1994). Increasing detail on crown structure and branching characteristics has also been included (Chen *et al.* 1994, Koop & Sterck 1994).

Complex tropical forests have 3 characteristics which make yield modelling difficult: a) several hundred tree species may be present, b) the forest covers a wide range of growth habitats and c) tree age is often unrelated to size and may not restrict growth capacity. One approach to this complexity is to group species into classes of similar growth type and volume relationships based on factors like tree diameter (dbh) rather than age. Simple dbh-based stand growth or yield tables have been used in the tropics, but, in addition to the problems of species categorisation, they tend to ignore the great differences in future growth depending on tree density.

Techniques like the North Queensland Rainforest Management (NORM) Model have therefore been devised to express the likelihood of a tree of a given species increasing its diameter by 1cm in terms of: a) its starting diameter, b) the basal area of trees larger than the subject tree, c) the overall stand basal area, and d) an index of site quality. Similarly, the probability of tree death can be expressed in terms stand basal area, relative basal area, time since logging and site quality (Vanclay 1991)

In mixed-aged mixed-species stands, provided that ample information is available on the habitat preferences of different species it is sometimes possible to derive useful distance-dependent and species-specific growth functions for many different tree-classes within the stand (e.g. Vanclay 1991). However, there are clearly logistical and logical limits to the meaning of this exercise. Conventional growth and yield models predict the future growth of stands based on past statistical evidence from similar stands. If a new stand is growing in different climatic or edaphic conditions to those that were used to derive the original regression equations, then the predictions will fail. Similarly, unconventional spacings such as those involved in agroforestry or shelterbelts are unlikely to be well predicted.

Furthermore, the effects of systematic changes in growing conditions caused by desertification, global warming, CO_2 enrichment, atmospheric N-deposition, fertiliser application, improved genotypes, soil erosion, or changes in water-tables can be included in process-based models, but not in conventional extrapolations from past measurements. In recent decades, for example, tree yields in Central Europe have increased by 20-50% (exceptionally up to 100%), compared with those projected in older studies, and atmospheric-N deposition is thought to be at least partly responsible (Kreutzer 1993).

This project recognises the limitations of simple statistical extrapolations from permanent sample data, but seeks to use this data as an aid to parameterising a the Hybrid model, and to provide modular tree models to use within the SymFor modelling framework (Phillips *et al* 1998) . Based on reliable data, it is the aim of the overall project (DFID-R6915) to extend these models to provide a management tool

for a) planning sustainable extraction of timber from natural forests, b) making timber and cash-flow forecasts, c) allowing silvicultural and harvesting options to be investigated, d) identifying research requirements, and e) predicting the future structure and composition of the forest. There could also be a link to those groups who are attempting to assess the socio-economic (Howard 1993, Basiago 1995, Tan 1996) or biodiversity (Stork & Watt 1996) impacts of different land management options. Bio-economic modelling expansions of conventional growth and yield techniques therefore have the long-term potential to *quantify* the environmental and economic impacts of alternative management systems for natural forests (Gane 1992) and plantations (Adlard 1993).

3. Forest Classification

Plant taxonomy offers little guide to growth characteristics necessary for the parameterisation of models. In looking for alternative approaches it is useful initially to consider three types of classification: physiognomic, structural and functional.

3.1. Physiognomic Classifications

Physiognomy is the external appearance of the vegetation, and comprises such obvious features as colour, luxuriance, seasonality and overall species compositional determined by an initial visual assessment (Fosberg 1967). However, others (e.g. Kuchler 1967) tend to use definitions with include structural or functional components. Most regional classifications of tropical forest vegetation are based on physiognomic characteristics. Good examples are Robbins & Wyatt-Smith (1964), who classified the lowland dipterocarp forest of Malaya into 11 types, or Hall & Swaine (1981), who identified 7 types and 4 further subtypes in Ghanian high forest.

3.2. Structural Classifications

Structure can be defined by two components: vertical structure, or the arrangement of species into layers or strata and horizontal structure, where the spatial distribution of individuals confers a pattern to species distribution and the forest as a whole

3.2.1. Vertical stratification

Descriptions of vertical stratification require four basic measurements:

- *maximum height achieved by the canopy and emergent trees;*
- *above-ground layering of shoots and dependent lifeforms;*
- *underground layering of roots and rhizomes;*
- *maximum depth reached by roots*

Maximum main-canopy height in the tropics seldom exceeds 50m, and is influenced by the amount and periodicity of rainfall, temperature, soil drainage and nutrient levels. Emergent trees may extend to 70m. The tallest structures are found where there is an alternation of dry and wet seasons, a rainfall of around 2,000mm and freely drained soils, and particularly in the upper areas of fertile flood-plains. In the Indonesia-Malaysia region *Dryobalanops aromatica* and other dipterocarps can reach 60m (the tallest tree recorded in tropical forests was found in this region (84m, *Koompassia excelsa* - Foxworthy 1927). Increasing altitude clearly reduces canopy height (Table 1).

Table 1 Relationship between altitude and height in the forest canopy in W Malaysia (Robbins & Wyatt-Smith 1964)

Forest Formation	Altitude	Height (m)
Lowland dipterocarp forest	150	42
Upper dipterocarp forest	800	30
Lower montane oak-laurel forest	1,500	21
Montane ericaceous forest	1,800	15

Usually there are clearly distinguishable 'emergent' species rising at intervals above the main canopy. Beneath the main-canopy there are two classes of smaller trees: seedlings and saplings which have the potential to become canopy or emergent trees, and shrubs which stay permanently in the undergrowth (Jones 1956). There has been considerable debate about whether vertical stratification is characteristic of tropical forests, but the argument is more over degree more than substance, although tropical canopies dominated by a single-species tend to produce more pronounced layering of the sub-canopy than multi-species multi-aged forests (Richards 1983). The maximum values for species height, stem diameter, crown width, height to first branch, rooting type and depth (where known?) are all valuable structural classification criteria, capable of being tested in models.

The above-ground structural complexity of tropical forests is greatly complicated by the presence of epiphytes and climbers, which in some tropical forests comprise more than 10% of the species, can intercept up to 20% of the available light (Zotz & Winter 1994), and in certain circumstances will 'strangle' the host tree (Richards 1952).

Hallé *et al.* (1978) used the architectural qualities of tree branching to classify tropical trees into 23 different 'models', ranging from simple monoaxial trees through the main group of models with differentiated trunk and branch axes, to a small number of examples where the a single meristem can initiate both horizontal (orthotropic) and vertical (plagiotropic) growth (Figure 4). This architectural approach has been combined with fractal rules for branching patterns to develop programmes which will reproduce the appearance of almost any tree (de Reffye *et al.* 1995), and to examine light interception patterns of poplar (Chen *et al.* 1994) and walnut (Sinoquet *et al.* 1997). The required field measurements of parameters like branch and leaf angle are somewhat time consuming however. There is scope to develop single tree growth-models which combine fractal branching rules with algorithms to allocate assimilate between different tree components, based on pipe model theory (Shinozaki 1965, Rennolls 1994). Hybrid uses a pipe model to annually allocate photosynthate between leaves, roots, wood increment, and sapwood storage, but it has no formal representation of branching (Section 5.10).

3.2.2.   Horizontal structure

Horizontal structure can be considered at several scales. Firstly there is a distinction between closed-canopy forest and open forest. Then there is the pattern imposed by mosaics of natural or man-made gaps, and subsequent regeneration. And finally, the heterogeneity caused by the irregular distribution of tree species. Horizontal pattern is linked to temporal changes which have been classified (Whitmore 1975) into 'mature', 'gap' and 'building' phases.

The mature phase is the most extensive and stable part of the forest mosaic. Under the unbroken canopy only a low density of sciphilous herbs, seedlings and shrubs survive. When interspersed by numerous moribund trees this phase may be termed 'over-mature', and is characterised by breakage of limbs and tops and luxuriant growth of epiphytes.

The gap phase is created by natural or man-made removal of large trees, and the increase in light at the forest floor generates a rapid growth of seedlings, coppice shoots and climbers. Gaps usually represent less than a twentieth of the forest area, although this area may be greater in swamp forest where trees tend to have shorter lifespans (Longman & Jenik 1987).

The building phase is a successional stage when the undergrowth and young trees fill the gap. Productivity is high during this period, and the gaps will often be dominated by pioneer species like *Musanga crepropioides* and *Trema* spp. (Africa), *Cecropia* spp (America) and *Macaranga* spp. (Asia). Sometimes, particularly in open forest, the building phase can be retarded by the expansion of vegetatively-spreading bamboo thickets, tree-ferns, palms or climbers. This may be an important consideration for modelling.
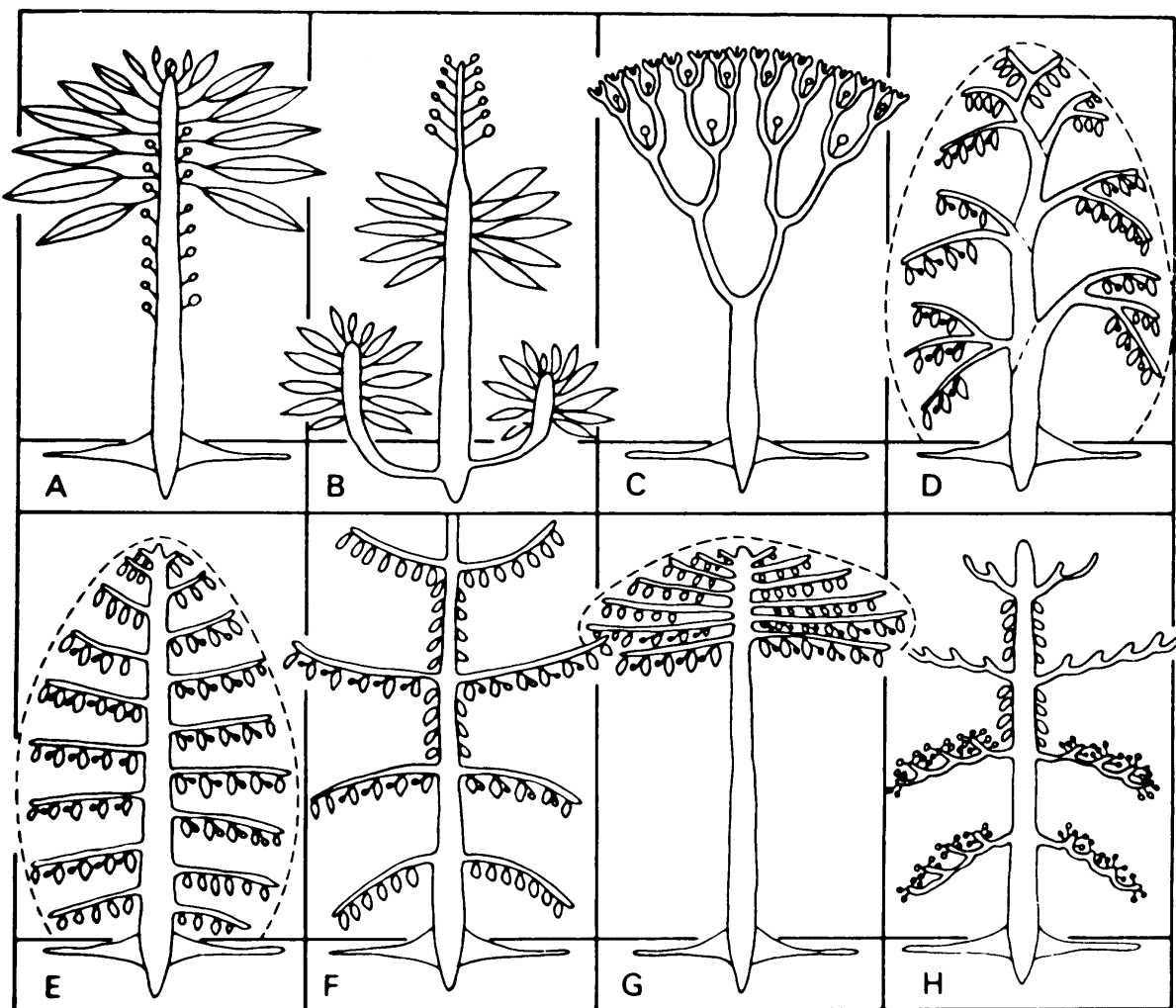
Figure 4. Architectural models of shoot systems in tropical trees (Halle et al. 1978). A. Corner's model; B. Tomlinson's model; C. Leeuwenberg's model; D. Troll's model; E. Rauh's model; F. Massart's model; G. Cook's model; H. Aubreville's model.

3.3. Functional Classifications

Mixed tropical forests are one of the most extraordinarily complex and species rich vegetation types in the world. It is not unusual for more than 200 species of tree to be represented in a single hectare, and it is often impossible to estimate the age of a tree from its size - particularly since growth rings are usually absent or unreliable (Philip 1987). The remainder of this section will therefore examine the **functional tree characteristics** which have potential to classify tropical tree species into different groups. Can these characteristics be used to simplify taxonomic or phylogenetic variation sufficiently to identify a small number of groups which share common niches and functional behaviour, and which can be parameterised identically in growth models?

Syntheses of the use of functional types for regional vegetation classification have appeared in recent literature on global change models (Smith *et al.* 1997) and ecosystem systematics (Simberloff & Dayan 1991). In this report the phrase 'functional groups' is used in a similar sense to 'functional attributes'

(Gillison, 1997, Gillison & Carpenter 1995), 'vital characteristics' (Noble & Gitay 1996, Roberts 1996), 'vital attributes' (Noble & Slatyer 1980) and possibly 'ecological guilds' (Silva *et al.* 1994, Brzeziecki & Kienast 1994). The term has been defined as 'those biotic components of ecosystems that perform the same function or set of functions within the ecosystem' (Smith *et al*. 1997). Species with similar physiological, life history and reproductive characteristics may not necessarily belong to the same 'functional type', since the true test is whether they respond in the same manner to ecosystem perturbations such as canopy opening (Friedel *et al.* 1988, Noble & Gitay 1989).

One set of functional characteristics are associated with environmental adaptation and periodicity. Examples are: the form in which a plant passes an unfavourable season, its time of flowering and fruiting, or its type of bud protection. Functional classifications date from the work of Raunkier (1907, 1934), in which he identified six main life forms based largely on the position of the perenniating bud (Figure 1).
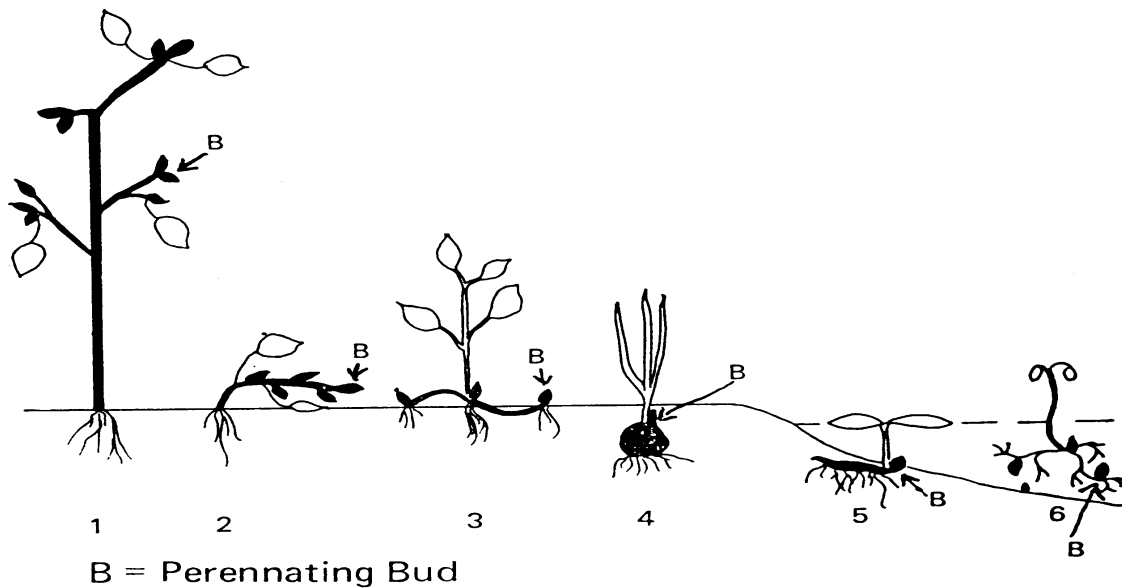
Figure 1 - Examples of the six main Raunkiaerian life forms. 1. Phanerophyte; 2. Chamaephyte; 3. Hemicryptophyte; 4. Geophyte; 5. Helophyte; 6. Hydrophyte. (Shimwell 1971)

The first of these life forms, phanerophytes, bear their buds or shoot apices in an exposed aerial position, and therefore occur more commonly in climates where prolonged periods of cold, drought and wind are infrequent. In moist tropical regions they comprise the bulk of the vegetation, and are main type relevant to this review. Phanerophytes are often further classified according to the height of buds above the ground ('megaphanerophytes' 30m>; 'mesophanerophytes' 8-30m; 'micro-phanerophytes' 2-8m; 'nanophanerophytes' <2m), although different authors chose different height categories. A second classification depends on the form of covering and protection of the buds, usually as a reflection of climatic adaptation, and a third criteria is often evergreen or deciduous growth habit. Based on these classifications, Raunkiaer (1934) originally identified 15 sub-types of phanerophytes (Table 2).

Table 2 Types of Phanerophytes recognised by Raunkiaer (1934).

No	Phanerophyte Sub-type	Example

1	Herbaceous ph	*Begonia* sp
2	Evergreen megaph. without bud covering	*Sequoia wellingtonia*
3	Evergreen mesoph. without bud covering	*Cupressus macrocarpa*
4	Evergreen microph. without bud covering	*Veronica salicifolia*
5	Evergreen microph. without bud covering	*Veronica salicofilia*
6	Epiphytic ph.	*Viscum album, Hedera helix*
7	Evergreen megaph. with bud covering	*Notofagus cunninghamii*
8	Evergreen mesoph. with bud covering	*Pinus sylvestris*
9	Evergreen microph. with bud covering	*Buxus sempervirens*
10	Evergreen nanoph with bud covering	*Ruscus aculeatus*
11	Semi-succulent ph.	Many cactaceae
12	Deciduous megaph. with bud covering	*Fagus sylvatica*
13	Deciduous mesoph. with bud covering	*Fraxinus excelsior*
14	Deciduous microph. with bud covering	*Salix capraea*
15	Deciduous nanoph. with bud covering	*Salix repens, Salix lapponum*

Raunkier's classification has been widely used, and extended, by plant sociologists to show a strong relationship between plant life form and climate, both on regional and localised scales, and functional classifications are increasingly used indicatators of environmental and ecological specialisation (Shimwell 1971).

Of more direct application to this study is the frequent 'binary classification' of tropical trees. Examples are 'pioneer' or 'climax' species, 'light-demanding' or 'shade-tolerant' species, 'secondary' or 'primary' species, 'r-selected' or K-selected' species (MacArthur & Wilson 1967). Swaine & Whitmore (1988) discusssed the lack of precision in these definitions and proposed a classification of 'pioneer species' based on seed germination and seedling establishment:

- *seeds only germinate in canopy gaps open to the sky and which receive some full sunlight;*

- *plants cannot survive in shade and young plants and never found under a closed forest canopy;*

- *seeds are small, produced copiously, and more or less continuously;*

- *seeds are produced from early in life;*

- *seeds are dispersed by animals or wind;*

- *dormant seeds are usually abundant in forest soils (especially fleshy-fruited species), seeds are orthodox (Roberts 1973);*

- *seedling carbon-fixation rates and compensation point are high;*

- *height growth is rapid;*

- *growth is indeterminate with no resting buds (e.g. syllepsis);*

- *leaves are short lived;*

- *rooting is superficial;*

- *woods are usually pale, low density, not silaceous;*

- *leaves are susceptible to herbivory, sometimes with little chemical defence;*

- *wide ecological range and phenotypic plasticity;*

- *often short-lived.*

Swaine & Whitmore (1988) also provided examples of pioneer and climax species groups, further classified according to tree height at maturity (Table 3).This careful clarification of the meaning of 'pioneer' and 'climax' species is useful in qualitative terms, but species clearly fall into a continuum between these extremes, and can indeed change position in the continuum as they age.

Table 3 - Examples of the pioneer and climax tree species groups from Africa (AF), the Eastern Tropics (ET) and tropical America (AM), subdivided into height class sub-groups (Swaine & Whitmore 1988).

Tree stature	Pioneers (germinate in full sun and require full sun for survival and growth)	Climax (germinate in shade, or rarely in full sun, and seedlings can survive and grow in shade)
Pygmy (Nanophamerophytes) <2 m tall	Probably none, class occupied by shrubs e.g. *Solanum* spp. (pantropical)	*Pycnocoma macrophylla* (AF) Many arecoid palms *Caussarea* spp. (AM) *Psychotria deflexa* DC. (AM)
Small (Microphanerophytes) 2-7.9 m tall	*Rauvolfia vomitoria* (AF) Most *Trema* (pantropical) Many *Macarange* spp. (AF,ET) *Pipturus* (ET) Some *Piper* spp. (ASM)	*Microdesmis puberula* (AF) Most Melastomataceae (ET,AM) *Drypetes ivorensis* (AF) *Diospyros buxifolia* (ET)
Medium (Mesophanerophytes) 8-29 m tall	*Musanga cecropioides* (AF) *Anthocephalus* (ET) *Macaranga hypoleuca* (ET) *Cecropia* spp. (AM) Most *Sloanea* spp. (AM)	*Turreanthus africanus* (AF) A few Dipterocarpaceae (ET) Fagaceae (ET) Most Myristicaceae (ET,AM) *Minquartia guianensis A*ubl.(AM)
Large (Megaphanerophytes) > 30 m tall	*Chlorophora excelsa* (AF) *Terminalia ivorensis* (AF) *Terminalia superba* (AF) *Lophira alata* (AF) *Pericopsis elata* (AF) *Paraserianthes falcataria* (ET) *Eucalyptus deglupta* (ET) *Goupia glabra* Aubl. (AM) *Laetia procera* Eichl. (AM) *Cedrela odorata* L. (AM) *Swierenia mahagoni* (L.) Jacq. (AM)	*Khaya ivorensis* (AF) *Entandrophragma* spp. (AF) *Funtumia elastica* (AF) *Aningeria robusta* (AF) Nearly all Dipterocarpaceae (ET) *Virola surinamensis* Warb. (AM) *Penthaclethra macroloba* (Willd.) Kuntze (AM) *Couratari* spp. (AM) *Vochysia maxima* Ducke (AM) *Eschweilera* spp. (AM)

Oldeman & van Dijk (1991) classified trees into six 'temperaments' based on a combination of two responses to light intensity as trees move through three age classes. Thus 'gamblers' have fast initial growth rates and intolerance of shading, and 'strugglers' have slower growth rates and relatively greater shade tolerance. Changes can take place between the temperaments during the seedling and juvenile stages (Figure 2).
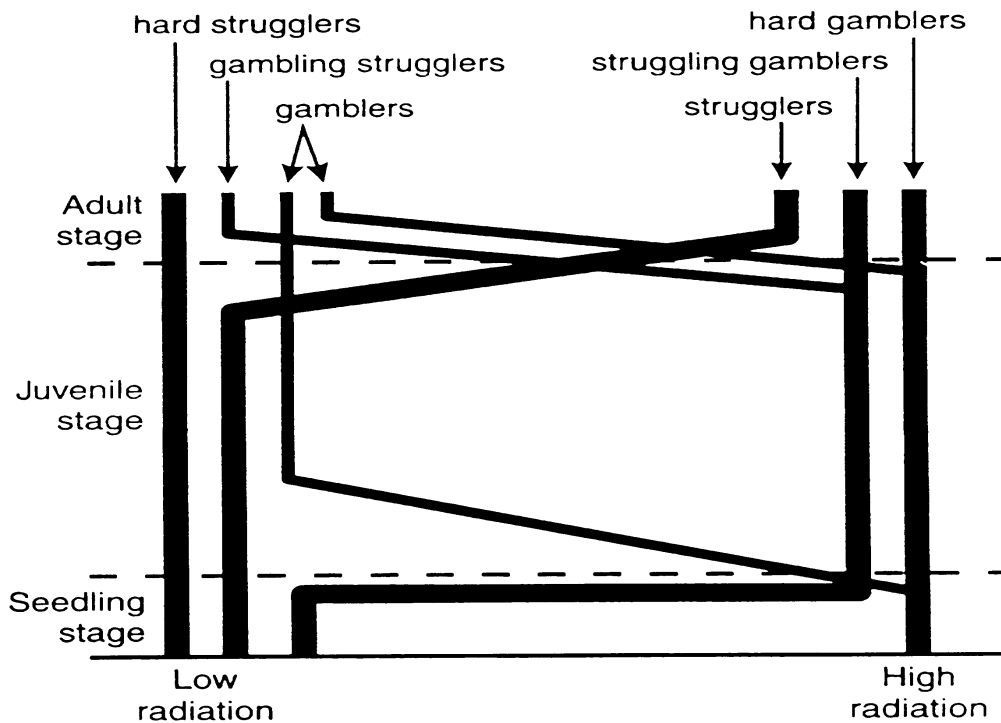

Figure 2 Six tree 'temperaments' according to Oldeman & van Dijk (1991). 'Hard gamblers' and 'hard strugglers' remain constant in shade tolerance through their entire lives. Other 'temperaments' change in their shade tolerance at some stage in the life cycle. Strugglers correspond to classic 'shade-tolerant trees' or 'climax species'. Hard gamblers are the classic 'light-demanding trees' or 'pioneer species'. The relative frequency of a temperament in tropical rainforest is indicated by the thickness of the bar.

Shugart (1984) produced a 2x2 matrix dividing species into (a) those requiring a canopy gap for successful regeneration, or otherwise; and (b) those typically generating a gap with the death of a mature individual of typical size, or otherwise. Shugart (1997) suggests that this simple classification could be expanded to consider a larger number of regeneration niches (Grubb 1977) or disturbance categories (Brokaw 1985). He also explores the relationships between the 4 categories: with role 1 species creating the gaps they need to regenerate; role 4 species regenerating in the shade and not drastically opening the canopy when they die. Some combinations of roles can replace each other reciprocally, e.g. role 1 species taking over a gap created by role 2 species or role 3 species giving away their space after they die to role 2 or 3 saplings.

Shugart's four functional roles have been used to replace species in a 'patch transition' model (Acevedo *et al.* 1966). A gap-size plot can be assigned to each of a set of states defined according to dominance of one of the roles. Transition probabilities among these states and mean holding times in

each transition lead to semi-Markovian analytical calculations of the stationary state probabilities. Forest dynamics, as the proportions of total canopy space occupied by each role in a collection of gap-size plots, is analysed using a chain of first-order differential equations to simulate the distributed time delays. Additional fixed time delays in the transition of every pair of states is also included to account for long time-lags.

Favrichon (1994) has also attempted a classification of rainforest species in Guyana as a precursor to growth modelling. He characterised species based on their maximum potential sizes and their diameter growth in response to light in a natural stand. Five 'functional categories' were identified: shade-tolerant understorey species, shade-tolerant canopy species, half-tolerant dominant species light-demanding species in the understorey and light-demanding canopy species.

In this project we will focus on more fundamental, and hopefully quantifiable, functional characteristics like photosynthetic response to different light intensities (Figure 3), specific leaf area, leaf nitrogen content, leaf geometry, carbon storage strategies.
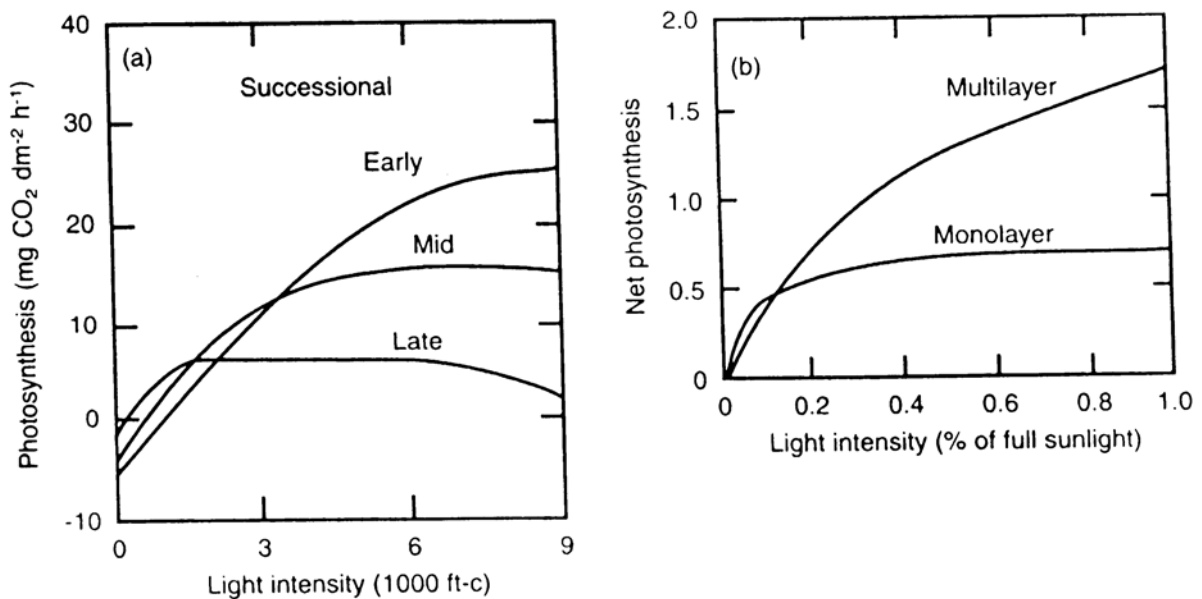
Figure 3 Typical responses of net photosynthesis in plants as a function of light intensity. Note that at the tissue and canopy levels, there is a reversal of photosynthetic efficiency at high vs low light intensities. (a) Idealized light saturation curves for early-, mid- and late-successional plants (from Bazzaz 1979). (b) The effect of light on net photosynthesis in multi-layered and mono-layered trees (Horn 1971). Both papers date from the 1970's so non-SI units are used.

4. Representation of Carbon Allocation in Tree and Forest Models

As indicated in Section 2, whole-stand models, diameter-distribution models, distance-independent individual tree models and, finally, distance-dependant individual tree models have been developed. Increasing detail on crown structure and branching characteristics has also been included, but it is now recognised that physiologically based growth models are required to represent complex mixtures of competing individuals and species, and to extrapolate predictions to different conditions, or degrees of disturbance, than would not be possible with conventional statistical models.

There are two categories of growth models which are suitable for mixed-species stands: 'gap models' and 'physiological models'. The latter are now increasingly including elements of competition between individual trees or generalised functional types. The Hybrid and HyPAR models (Section 5) are examples of this latter approach.

4.1. Forest Gap-Based Models

Shugart & Smith (1996) list 37 individual-tree 'gap models' which stemmed from the original JABOWA model of Botkin *et al.* (1972). These simulate the establishment, diameter growth and mortality of each tree in a given area (often the area dominated by the largest canopy tree). However, most have relatively simple protocols for estimating model parameters, and for describing the interactions between individuals. More recent gap models have included improved simple physiological approximations to the relationship between yield and light, water and nutrients; but none has yet included a satisfactory approach to carbon allocation within individual trees. The following two gap models are typical.

4.1.1. FORCLIM

FORCLIM (Bugman 1996, Bugman & Fishlin 1996, Bugman & Cramer 1998) is a gap model developed for central European conditions. It has three modules: *environment* - which generates monthly weather data and uses them to calculate bio-climatic output variables like day-degree sums and minimum winter temperature; *plants* - which calculates establishment, growth, mortality and litter production of trees on a forest patch on an annual time-step; *soil* - which tracks the decay of plant litter and humus in the soil as a function of bio-climatic variables and calculates annually the amount of nitrogen available for plant growth.

Diameter increment is a function of tree height, maximum tree height, allometric parameters and a growth function which is constrained by environmental constraints (light, growing season temperature, drought and nitrogen availability). Two light response curves are provided for shade-intolerant and -tolerant species. Growth is linked to degree day sum using a parabolic function. A square-root function relates drought stress to tree growth based on a species-specific drought tolerance. Growth is related to nitrogen availability according to one of three species-specific asymptotic growth curves. These four environmental constraint factors are multiplied together to provide an integrated reduction in overall growth.

Seedling cohorts are established if winter minimum temperature, available light and degree-days are above species-specific minima. Seedling numbers are generated randomly between 1 and maximum seedling density parameter. Tree mortality is calculated for individual trees (rather than cohorts) assuming a constant mortality fraction , supplemented by a stress-induced mortality which operates when an individual has increased by less than 10% of maximum or 0.3mm for more than two years.

Litter decomposition and nitrogen cycling largely follow Pastor & Post (1985), with organic matter and nitrogen fluxes simulated in two pools ('litter' and 'humus'). Generated monthly weather data are used to generate bio-climatic indices used elsewhere in the model: i.e. minimum winter temperature, day-degrees, evaporation and drought index.

4.1.2. FORMIX

FORMIX (Bossel & Krieger 1994) is the base model for FORMIND (Kohler & Huth 1998) It represents lowland dipterocarp as five storeys (seedlings, saplings, understorey, main canopy and emergents). Horizontal structure is represented as 25 subplots ('gaps') per hectare. Five species groups are introduced corresponding to each of the 5 storeys, with wood density, energy assimilation and respiration balance automatically resulting in a maximum height of each species groups corresponding to the respective canopy storey. The model therefore consists of a total of 5+4+3+2+1 tree classes. Over a year assimilated energy must balance respiration losses, litter loss and biomass increment. Species-specific leaf-proportional and biomass proportional loss parameters are estimated from energy balances for SE Asian tropical Forests. Allocation to roots and branches is assumed to be a fixed fraction (0.7) of net photosynthesis.

4.2.   Forest Physiology-Based Models

A number of physiology based models exist (e.g. FORGRO - Mohren & Vandeeven 1995) and DYNAMITE - Eikelboom & Janssen 1994) which model stand-level fluxes of carbon, nutrients (N,P & K) and moisture in temperate and tropical forests; but do not distinguish competitive effects between individual trees. The following physiological models do represent individual trees, although often as cohorts of trees of the same size and species, and attempt to understand vegetation dynamics through the competitive interactions of individuals or cohorts.

4.2.1. EXE

EXE (Martin 1992, 1996) is a combined model of energy, water, and momentum exchange, nutrient cycling and ecological dynamics based on the LINKAGES model (Pastor & Post 1985, Post & Pastor 1996). Neither of which are well described in the open literature. C and N cycling are treated explicitly. Seedlings are planted from a pool of 72 North-American tree species. Actual evaporation is calculated using a bucket model. Leaf decomposition is proportional to evaporation and lignin: nitrogen ratio. Wood decomposition occurs a fixed rates. When critical nitrogen levels are reached, cohort organic matter and nitrogen content are transferred to humus and nitrogen pools. Growth is constrained by drought days, defined as days during which the soil moisture is below wilting point in all soil layers to which the roots are found. Stomatal resistance is a function of light, temperature and humidity. EXE was a first attempt to couple a physiologically based water budget and an explicit treatment of ecological dynamics, but has not been further developed.

4.2.2. TREEDYN3

TREEDYN3 (Bossel 1996) computes the flows of carbon and nitrogen into and out of the wood, leaves, fine roots, fruit, litter, humus and plant-available nitrogen in tree-soil systems. Essentially it consists of 14 ordinary differential equations for 9 state variables describing tree growth and 5 state variables describing processes in the soil. It has a reasonably sophisticated representation of carbon and nitrogen cycling, including novel aspects in its approach to carbon-allocation, but surprisingly does not consider water as a variable. Diurnal, seasonal and annual dynamics are modelled for a forest stand consisting of identical species and identical age.

Photosynthesis is calculated from latitude, seasonal time and time-of-day rather than by using real or generated weather. Assimilate is allocated to leaves, fine roots, fruit or wood-increment depending on crown competition status. The order of allocation is: maintenance respiration, leaf and fine-root renewal (including growth respiration), leaf and fine root growth, fruit growth, wood increment. Leaf mass grows up to the point when the light fraction received by the lowest leaf layer falls to below a small (e.g. 5%) of above-canopy light. This together with the species- and stand- specific light extinction coefficient defines the maximum LAI of the stand (and also the fine-root mass through the functional balance q.v.). Leaf flush, leaf fall and root growth are functions of seasonal temperature.

Wood increment is invested in height and diameter growth, with the proportion depending on current light competition in the canopy. Competition exists when the crown area per tree is less than that which would be required on account of the current stem diameter and CD ratio. Competition causes tree mortality and diameter increment is the remaining trees increases till height/diameter has been reached. Trees are also subject to constant, low, background mortality.

Photosynthate is dynamically allocated between leaves, fine roots, fruit and wood increment. Leaf and root *demand* for photosynthate in a given time period are functions of their turnover rates, how far their masses are removed from a set goal for leaf/shoot ratio, and the maximum growth rate. The leaf growth rate corresponds to leaf *demand* modified by renewable nitrogen availability and the assimilate availability. Fine root growth rate, on the other hand, is affected only by assimilate availability. This accounts for the fact that the tree responds to nitrogen shortage by attempting to maintain and increase nitrogen uptake and hence fine root growth. Second priority is assigned to fruit growth, which is limited by both assimilate and nitrogen supply, as is wood increment.

Growth is limited by plant-available nitrogen stock and the rate at which it can be utilised by the available find root mass. Re-translocation of C and N before litterfall is temperature dependent. Decomposition and humification, and atmospheric N deposition are all accounted for, although not yet adequately since soil water content is not included.

Despite the lack of a hydrological component in TREEDYN there are four aspects which are worth considering for inclusion in single-tree versions of the Hybrid model. The first is the recognition that intense shading can cause suppressed saplings to divert resources into height rather than diameter growth. The second is an explicit representation of fruit biomass. The third is a separation of wood biomass into branchwood, stemwood and below-ground components, with the branchwood fraction is assumed to increase exponentially with increasing tree diameter. The fourth is the dynamic allocation of photosynthate described above.

4.2.3.   TREE-BGC

Forest-BCG (Running & Coughlan 1988) is a stand-level forest ecosystem model that calculates the carbon, water and nitrogen cycles through a forest ecosystem. TREE-BCG (Korol *et al.* 1991, 1995) allocates these stand-level estimates of photosynthesis to individual trees using a competition algorithm that incorporates tree height, relative radiation-use efficiency and absorbed photosynthetic active radiation. It has a mixed time resolution, with hydrology processes, photosynthesis and maintenance respiration calculated daily. Net photosynthesis is calculated daily, diminished by a temperature dependent maintenance calculation, and accumulated in a pool which is partitioned at the end of each year into leaf, stem and root compartments, after accounting for growth respiration. Initially the allocation to leaf, stem and root pools was parameterised to be in the proportions 0.25, 0.35 and 0.4, but Running and Gower (1991) introduced a mechanism to control the leaf/root partitioning ratio depending on whether light, water or nutrients were limiting. The preliminary partitioning ratio (C_{LC}) is modified ($C_{L\Psi}$) to allow more leaves to be produced the following year if the highest pre-dawn leaf water stress (Ψ_L) has not exceeded a defined maximum level (Ψ_{max}) usually 1.8-2.0 MPa). If this maximum level has been exceeded then the 'potential' partitioning to leaves is reduced in the following year:

$$C_{L\Psi} = C_{LC}(\Psi_{max} / \Psi_L)$$

Similarly leaf growth in the following year can be modified by nitrogen availability, in which case the current available nitrogen (N_{avail}, kg ha^{-1}) divided by the leaf N concentration (N_L, kg N kg^{-1} C) defines the carbon available for leaf growth (C_{LN}, kg C ha^{-1} yr^{-1}):

$$C_{LN} = C_{LC} (N_{avail} / N_L)$$

The model then takes the smallest of C_{LC}, $C_{L\Psi}$ and C_{LN} as the carbon actually allocated to leaf growth.

Finally, the leaf/root allocation ratio is defined by summing a soil water index (I_{sw}) and a nitrogen availability index (I_n). For the soil water index, the logic of Grier and Running (1977) and Nemani and Running (1989), relating site water balance to a carrying capacity of LAI is represented, where the water balance is defined as the average soil water deficit (i.e. fraction of field capacity). Calculation of this root/shoot partitioning ratio, together with the carbon allocated to leaf growth calculated above, allows the residual photosynthate to be allocated to stem growth. This method therefore allocates carbon according to the priorities: maintenance respiration, growth respiration, leaf growth, root growth, stem growth. This model predicts well the observed increase in allocation to leaves in fertilised tree plots, and the increase in root growth at the expense of stem growth in nutrient or water stressed situations.

4.2.4.　　　FORMIND

FORMIND (Kohler & Huth 1998) is based on the FORMIX2 model of Bossel & Krieger (1994). The forest area is divided into subplots (400-800m^2) which correspond to the maximum crown size of a dominant tree. One tree is chosen to represent a cohort of trees of the same functional group (FG) and size class. Mortality is simulated by reducing the number of trees represented by each cohort. Recruitment is accommodated by initiating new cohorts from time to time. There are 5 submodels: tree geometry, carbon-cycling, competition for light, mortality and recruitment of seedlings.

The *tree geometry module* uses FG-specific allometric relations between height and diameter, wood density, stem taper and crown diameter to describe the changing dimensions of individual trees. The *carbon-cycle module* assumed a familiar exponential light distribution within crows as a function of cumulative leaf area, with photosynthesis expressed as a saturation-type cure with parameters (α) for the initial slope of the light-response curve and the maximum rate of net photosynthesis per leaf area (P_m). Photosynthesis is calculated *annually* according to the distribution of individual tree (i.e. cohort) crowns. Total respiration depends on annual production and a diameter-dependent term which ensures that trees do not grow beyond a specified maximum diameter. The *light-competition module* assumes that leaves in the crown are homogeneously distributed, and the canopy is divided into layers. Average leaf area is calculated for each layer, and crown closure is based on the contribution of individual trees, reduced to 1 if trees overlap. Trees in one plot (usually 20x20m) only shade neighbouring plots in the case of emergents: in which case equal shading on the four neighbouring plots is assumed. The *mortality module* uses empirical multipliers for different functional types, and includes damage induced mortality caused by large falling trees. The *seedling recruitment* module assumes a constant input of seedlings from the seed bank, provided that light levels in the sub-plot are sufficient for germination.

The model has been applied dipterocarp evergreen tropical moist forest in Sabah for between 5 and 22 functional groups parameterised according to differences stem geometry, wood density, potential height, seedling production, light intensity for germination, maximum net photosynthesis, slope of light response curve, tree mortality weighting. Similar parameterisations of 5 functional groups (based on maximum height and pioneer-climax classification) were used to compare predicted and observed regrowth after a variety of logging regimes in Sabah (Huth *et al.* 1996).

FORMIND's carbon allocation routines are rather simple: a) a leaf-proportional respiration (0.5 - representing the annual sum of leaf and fine-root respiration and turnover); b) a biomass related energy loss (0.06 - representing the annual loss of biomass due to the respiration and loss of wood, branches and coarse roots); and c) allocation of photosynthate to stemwood using a single 'stemwood fraction' parameter (usually 0.7). It also assumes a constant air temperature and non-limiting water and nutrient conditions.

5. The Hybrid Model v3.0

This model is a 'hybrid' of the 'gap model' approach (Leemans 1991) which describes the irradiance environment of a forest canopy, an individual tree growth model (PGEN, Friend 1995), and a model of vegetation succession (ZELIG - Urban 1990). Hybrid fully describes the daily cycling of carbon, nitrogen and water within a unit of vegetation, and combines a mass-balance approach to these growth resources with the capacity to predict the relative dominance of different plant types (such as evergreen needle-leaved trees, cold deciduous broadleaved trees and C3 or C4 grasses). Individual trees and the grass layer compete with each other for light, water and nitrogen within a 'plot' of any size. In the standard Hybrid model (V3.0 - Friend *et al* 1996) the height distribution of the leaf canopy is calculated separately for 1m-layers of individual trees (for carbon flux) or for the aggregated forest canopy (for radiation interception and water flux). A 'horizontally disaggregated' treatment of radiation interception does exist as an option in a related combined tree and crop model termed 'HyPAR' (Lawson *et al.* 1995).

The following sections summarise the major processes in Hybrid. Friend *et al* (1996) give fuller details and equations, and Chapter 5 compares the tree characteristics of potential value in identifying 'functional groups' and the processes represented in Hybrid.

5.1. Irradiance calculations

Hybrid assumes the foliage area of each crown to be spread in 1m depth layers across the area of the modelled plot. Radiation absorption per individual per layer is the negative exponential (Beer-Lambert law) of the leaf area index of that species, with species-specific extinction coefficients $(K_{PAR,SW})$ required for both shortwave (SW) (400-3000nm) and photosynthetically active (400-700nm) radiation (PAR). SW and PAR reflectance are also calculated for each individual and each layer based on species-specific albedos ($\forall_{PAR,SW}$). The fraction of radiation absorbed by each entire layer is therefore based on the sums of absorbtions by all individual trees reaching that layer, having accounted for their species-specific extinction and reflection coefficients, and their relative leaf areas. The overall plot foliage distribution is recalculated each time an individual's tree's store of photosynthate is reallocated to its growth and storage compartments. This is normally annually.

The quantities of SW and PAR absorbed by the top layer of each individual are used as inputs to the photosynthesis and stomatal conductance routines

Species specific extinction coefficients ($K_{PAR,SW}$) and albedos $\forall_{(PAR,SW)}$ are scarce for tropical rainforest trees. Jarvis and Leverenz (1983) gives K_{PAR} values of 0.5 to 0.8 for broadleaved forests and 0.4 to 0.6 for coniferous forests. Foliage absorbs a higher proportion of PAR than SW, thus K_{PAR} tends to be higher thanK_{SW}. Albedo is dependent on leaf angle and surface characteristics. Average values are available for closed vegetation types (e.g. Jones 1992), but investigation is required to find appropriate values for different classes of tropical trees.

5.2. Net Photosynthesis

Hybrid calculates each day, and for each individual, the mean rate of total crown net photosynthesis, and the mean rate in the lowest crown layer. The model also assumes that foliage physiological properties (such as nitrogen content) decrease down through each tree crown, and total crown photosynthesis and transpiration are linearly related to values calculated for the top layer at all values of incident PAR (Sellers *et al.* 1992). Thus, for a given set of environmental conditions and crown total nitrogen content, only one calculation of photosynthesis is necessary to obtain the rate for the entire crown.

The total net photosynthesis per square meter is therefore product of mean daytime net photosynthesis in the upper layer of an individual and the fraction of incident PAR that is absorbed by the total crown, divided by the extinction coefficient for PAR. Thus, the net photosynthesis routine (PGEN - Friend 1995) need be called only once per day for each individual. Furthermore the carboxylation-limited calculation in this routine, which is a linear function of foliar nitrogen, only requires to be called once per day per species rather than per individual.

A consequence of the assumption that foliage nitrogen is allocated optimally within each crown, and that photosynthetic capacity is a linear function of foliage nitrogen is that the nitrogen content of each leaf must be directly proportional to the time-averaged PAR absorbed by that leaf relative to the whole crown.

5.3.   Maintenance Respiration

Mean night-time foliage maintenance respiration is assumed to be a linear function of total foliage nitrogen content and an exponential function of air temperature. The coefficient of proportionality to nitrogen is not currently assumed to vary between species. Mean daily fine root maintenance respiration is calculated in a similar manner.

Sapwood maintenance respiration rates are assumed to be linear functions of living carbon mass, and exponential functions of air temperature. Again, the constant of proportionality to carbon mass is unlikely to vary from species to species. Daytime and night-time sapwood maintenance respiration are calculated separately using mean temperatures for the appropriate periods.

5.4.   Carbon Balance

Individual tree carbon stores are incremented daily by their net carbon balance after accounting for net photosynthesis and growth respiration If, at the end of the year, after accounting for maintenance respiration, this balance is positive then carbon is allocated to storage and the growth of roots, leaves and stem (Section 5.10). If the carbon balance for a layer of an individual tree is negative then that layer will die, and a proportion of the carbon and nitrogen is reallocated within the tree. This simulates the process of tree growth and canopy lifting. If the whole tree is in negative carbon balance at the end of the year, and there is insufficient storage carbon to compensate, it will die.

5.5.   Stomatal Conductance

Stomatal conductance controls the flux of CO_2 into, and water out of, the leaves of higher plants. CO_2 is required for photosynthesis and transpiration depletes soil water. Transpiration is also an important determinant of leaf temperature. The mean daytime stomatal conductance of the uppermost layer of each tree is calculated each day using empirical relationships with irradiance (PAR), soil water potential, above-canopy air temperature, above-canopy water vapour pressure deficit and above-canopy CO_2 concentration. Conductance in lower layers is scaled to match net photosynthesis. The parameters are the same as used by Stewart (1988) with the exception of soil water response which now has linear closing between -0.2 MPa and -1.5 Mpa.   Literature measurements of stomatal conductance in tropical forests will be sought as alternatives to the existing parameterisation.

The effect of tree height on leaf water potential is included by reducing water potential by 0.015 MPa for each 1m of mean crown height on an individual tree basis (Friend *et al.* 1993).

5.6.   Foliage Energy Balance & Transpiration

Daytime energy balance is solved each day in order to calculate the foliage temperature and rate of transpiration of each plot. Transpiration influences soil water content, and foliage temperature influences net photosynthesis and dark respiration. Calculations follow Friend (1995), with individual tree conductances added to plot boundary layer conductance. Isothermal net radiation of the entire

canopy is calculated by summing absorbed shortwave radiation across individuals and accounting for long-wave radiation absorptance and emittance. Plot transpiration is calculated from the canopy-to-air vapour density deficit and total resistance to water flux, calculating the saturation density of water at leaf temperature.

5.7.   Nitrogen Uptake

Uptake of mineral N by each tree occurs each day and is held in a store ready for allocation at the end of the year. Daily uptake is positively related to fine root mass, soil mineral N content and the C/N ratio of the entire plant (excluding C and N bound in heartwood). It is assumed that the tree does not take up nitrogen if the carbon/nitrogen mass ratio is lower than 10 kg C/kg N or if nitrogen in the top crown layer is greater than .004kg/m^2

5.8.   Phenology

The ability to sense when foliage display will yield carbon gains without undue risk of frost damage is an important feature of all cold deciduous plant species. There is good evidence for a progressive loss of dormancy with increased chilling, and this is modelled as a chilling induced decrease in the heat sum required to reach a given stage of budburst (Cannell & Smith 1983).

5.9.   Litter Production

A parameter sets the annual fraction of grass fine root carbon and nitrogen pools which will enter the soil each day. Tree litter production takes place annually, but has three components: (a) a fixed turnover of foliage and root carbon controlled by appropriate parameter, (b) a proportion of the carbon and nitrogen contained in tree canopy layers which drop off (Section 4.10), and (c) any tree that dies in the year, either through long-term negative carbon balance, or through a stochastic factor. As a crown layer drops off the sapwood which supported it is assumed to be converted to heartwood, and diameter and height increments take place accordingly. A proportion of nitrogen is currently parameterised to be translocated from dying leaves, but not roots (Nambiar & Fife 1991).

5.10.   Carbon Allocation

Carbon allocation to grass allocation assumes a 1:10 ratio for support: and photosynthetic foliage carbon and a 1:1 ratio for above- to below-ground growth. Grass metabolic respiration is assumed to be 25% of new allocation, and sufficient nitrogen is assumed to be taken up to maintain plant C:N ratios within acceptable limits.

Carbon allocation in trees is calculated following litter production, and if, for example, the annual proportion of roots dying (turnover) is greater than one, then carbon is taken directly from the plant carbon pool to the soil. Three constraints are used to calculate carbon allocation. First it is assumed that there is a fixed relationship between diameter at breast height and woody carbon mass. Secondly, it is assumed that foliage area is linearly proportional to the sapwood area at breast height - derived from pipe stem theory - Shinozaki *et al.*1965). Thirdly, it is assumed that there is a fixed ratio between foliage and fine root carbon masses. These constraints are parameterised differently for each species. Following carbon allocation, nitrogen is partitioned to maintain constant relative C:N rations between sapwood plus bark, foliage, and fine root compartments. As heartwood grows, sapwood carbon and nitrogen become locked up until released by soil decomposition. Stem respiration is predicted from foliage mass if the fraction of sapwood that is alive is known. There are few measurements of foliage area/sapwood area ratios in the tropics, and fewer where living sapwood fractions are measured. Collation of studies on the wood anatomy of different tropical species will allow better parameterisation of these ratios.

Hybrid v3.0 assumes annual growth increments (for planned changes see Section 7). At the end of each year the annual net, positive, carbon balance of each tree is available for growth. If carbon balance is negative, carbon for maintenance requirements is withdrawn from sapwood storage. If this is insufficient then the tree dies. It is assumed that a minimum fraction of any available carbon is always used for new wood plus bark growth. The remaining annual carbon pool (after accounting for respiration) is then partitioned between foliage, wood plus bark, storage, and fine root carbon compartments. The cross sectional areas of total wood, non-storage inside-bark , sapwood and heartwood are calculated and volumes calculated using species-specific allometric constants, form-factors, bark thickness, and above:below ground wood mass ratio.

Hybrid has a rather sophisticated representation of above-ground carbon storage, and explicitly represents the trade-offs associated with sapwood: its role as a water transport medium, its role as a storage compartment and its contribution to maintenance respiration. If storage is low, trees are more susceptible to death in a fluctuating environment, and storage also aids trees survive the effects of herbivory (Waring & Pitman 1985). In Hybrid 3.0, if sufficient carbon is available following allocation to foliage and fine roots, the sapwood storage volume of each tree is completely filled at the end of each year. This takes priority over any stem growth above the minimum. Stored carbon is then available for allocation at the end of the next year. Any carbon remaining after storage is filled is used to increment the overbark diameter, increasing in turn the sapwood area. The amount of living sapwood so calculated is an important factor in calculating stem respiration. Living sapwood ratios, and foliage to sapwood ratios, may well turn out to be important 'functional characteristics' determining a tree species strategic balance between high stress tolerance and high growth rate.

5.11. Nitrogen Allocation

As mentioned previously, if the annual carbon balance of the lowest crown layer in an individual tree is negative, a proportion of the sapwood is turned into heartwood. Heartwood is also formed if insufficient carbon is available to produce the foliage and fine roots that could have been supported by the sapwood area at the end of the year. If there is an increase in heartwood area, the corresponding increase in hartwoood carbon is matched by a mass of nitrogen which is made unavailable for subsequent re-translocation during the life of the tree.

After subtraction of losses in litterfall and fixing in heartwood, the available nitrogen pool is allocated between foliage, sapwood plus bark, and fine roots, on the basis of fixed relative C:N rations between the three compartments. Thus the C:N ration of any one tissue will vary as a function of nitrogen uptake and loss, but the relative ratios between tissues will not change.

Foliage nitrogen is further divided into three compartments: rubisco-bound, chlorophyll-bound and 'other'. This partitioning is important for calculating photosynthesis rates. The 'other' fraction (structural, nuclear and cytoplasmic material) does not increase unless leaf structure increases, and the first two components are given priority if foliar nitrogen concentration increases. Foliage longevity and photosynthetic efficiency is related to the 'other' N fraction and Hybrid includes a species specific parameter to influence the relationship between this 'other' nitrogen fraction and total foliar nitrogen content. The ratio of rubisco-N to chlorophyll-N represents the relative investment in light harvesting and dark reaction machinery, so can be considered as an adaptation to different levels of irradiance. Information is available from temperate crops to suggest initial values for these parameters (Evans 1989), and will be sought in literature on photosynthesis of tropical trees.

5.12.   Soil Nitrogen and Carbon

Carbon and nitrogen flows are based on the Century model (Parton *et al.* 1993) with additional wood litter inputs, fixed foliage and fine root lignin fractions, limits to the N:C ratios of surface and root metabolic litter, soil moisture decomposition rate as function of % water filed pore-space, site-independent clay and sand fractions, and no separate ammonium and nitrate pools (i.e. no volatisation, denitrification and nitrification). The Century model was chosen for incorporation because only it gave

reasonable predictions of both soil carbon storage and nitrogen mineralisation rate, for a wide range of litter input rates and climate conditions without requiring detailed parameterisation of microbial kinetics.

5.13. Plot Hydrology

Rain intercepted by the canopy is calculated as a linear function of total Lear Area Index (Running & Coughlan 1988), and the same value is currently used for all species. Maximum evaporation of intercepted rain is calculated using the Penman-Monteith equation, and any excess of intercepted rain enters the soil as throughfall. In the interest of generality, snowfall and snowpack accumulation are also included. One half of soil water above field capacity, following any inputs from rain and throughfall, and losses through evapotranspiration, is routed to outflow. This creates the possibility of the soil containing water above field capacity for short periods. Bulk soil water on a given day is calculated from the amount of water remaining in the soil at the end of the previous day, and soil water field capacity (Campbell 1985). More sophisticated soil models which use pedotransfer functions to derive soil hydraulic parameters from simpler measurements of sand:silt:clay and bulk density, and macro-pore flow, have been used in versions of Hybrid (Arah & Hodnett 1977). Bulk soil water potential is used to calculate stomatal conductance. Species-specific Parameters

Hybrid v4.3 uses 32 species-specific parameters (Table 4), and around 20 more related to the levels and variability of initial starting conditions of soil, hydrology and nutrients, and controlling the type of simulation to be run (Appendix I). There are some additional parameters, such as several related to stomatal conductance (Section 3.5 - Stewart 1988), which are currently hard-wired into the code, but these do not vary between species. The existence of literature to help determine appropriate values for these 32 parameters is considered in Section 5.

Table 4 - The 32 species-specific parameters used in Hybrid, V4.3 and typical values for 8 Generalised Plant Types. C3GR=C3 grass; C4GR=C4 grass;BREV=broad-leaf evergreen; BRCD=broadleaf cold deciduous;BRDD=broadleaf dry deciduous; NLEV=needleleaf evergreen; NLCD=needleleaf cold deciduous; NLDD=needleleaf dry deciduous.

Parameter	C3GR	C4GR	BREV	BRCD	BRDD	NLEV	NLCD	NLDD
kpar - PAR extinction coefficient	0.65	0.65	0.65	0.65	0.65	0.5	0.5	0.5
ksw - SW extinction coefficient	0.48	0.48	0.48	0.48	0.48	0.37	0.37	0.37
rhop - PAR reflection coefficient	0.05	0.05	0.05	0.05	0.05	0.03	0.03	0.03
rhos - SW reflection coefficient	0.2	0.2	0.2	0.2	0.2	0.11	0.11	0.11
fturn - turnover rate of foliage (proportion yr-1)	0.0031	0.0031	0.33	0.33	0.33	0.33	0.33	0.33
wturn - turnover rate of wood (proportion yr-1)	0.0031	0.0031	0.01	0.01	0.01	0.01	0.01	0.01
rturn - turnover rate of fine roots (proportion yr-1)	0.0031	0.0031	2	2	2	2	2	2
sla - specific leaf area (m2 kg C-1)	36	36	36	36	36	12	12	12
bark - bark thickness as fraction of total diameter (trees)			0.033	0.033	0.033	0.01	0.01	0.01
crratio - ratio of stem to foliage biomass (grass)	1	1						
lasa - ratio between leaf area and sapwood area (m2 m-2)	0	0	4167	4167	4167	3333	3333	3333
ah - Allometry a parameter for dbh (m) to height (m)	0	0	28.51	28.51	28.51	32.95	32.95	32.95
bh - Allometry b parameter for dbh (m) to height (m)	0	0	0.4667	0.4667	0.4667	0.5882	0.5882	0.5882
stf - proportion of woody biomass below ground (proportion)	0	0	0.22	0.22	0.22	0.222	0.222	0.222
rlratio - biomass ratio between fine roots and foliage (kg C kg C-1)	1	1	1	1	1	1	1	1
frcoeff - foliage nitrogen retention coefficient (proportion)	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
rrcoeff - fine root nitrogen retention coefficient (proportion)	1	1	1	1	1	1	1	1
woodd - mean wood and bark specific gravity (kg C m-3)	0	0	305	305	305	205	205	205
formf - tree form factor (dimensionless)	0	0	0.6	0.6	0.6	0.56	0.56	0.56
Fsr - ratio between C:N ratios of foliage and sapwood	0.145	0.145	0.145	0.145	0.145	0.145	0.145	0.145
frr - ratio between C:N ratios of foliage and fine roots	0.86	0.86	0.86	0.86	0.86	0.86	0.86	0.86
live - proportion of sapwood alive (proportion)	0	0	0.17	0.17	0.17	0.0708	0.0708	0.0708
storef - maximum proportion of live sapwood used as C storage	0	0	0.67	0.67	0.67	0.67	0.67	0.67
Nupc - N uptake parameter (m2 kg C-1 d-1)	0.036	0.036	0.036	0.036	0.036	0.036	0.036	0.036
ngr - maximum leaf conductance to CO2 (m s-1)	1359	1359	1672	1672	1672	2223	2223	2223
Gmin - cuticular conductance to CO2 (m s-1)	4.81E-05	4.8E-05	4.8E-05	4.8E-05	4.8E-05	4.8E-05	4.8E-05	4.8E-05
pruba - proportion of foliage nitrogen bound in Rubisco (p	0.67	0.67	0.67	0.67	0.67	0.83	0.67	0.83
Nrc - proportion of foliage nitrogen bound in chlorophyl	9.13	9.13	9.13	9.13	9.13	9.13	9.13	9.13
d_leaf - leaf characteristic dimension (m)	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
weff - factor for effect of water-filled pore-space on N uptake	2	2	2	2	2	2	2	2
ptype - Phenology type (controls leaf loss 1=grass;2=EV;3=CD;4=DD)	1	1	2	3	4	2	3	4
rgf - factor to allow for growth respiration (proportion)	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75
wmf - factor for calculating minimum wood mass increment	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1

6. Tree growth physiology and current representation in Hybrid

6.1. Introduction

As emphasised in Section 3, Hybrid V3.0 has been mainly parameterised for generalised plant types, but it has also adequately predicted the distribution of tree species in part of North America. It represents trees as individuals for carbon and nitrogen cycling, but light interception is partially calculated by aggregating the canopy into 1m depth layers with no horizontal variation. Hybrid also operates at a global scale over very long time-steps. Thus, there is not necessarily a match between the physiological parameters necessary to drive Hybrid as the physiological characteristics which are important for characterising differences between different tropical trees into meaningful functional groups. The following section discusses various aspects of the growth physiology of tropical trees, comments on whether they are currently represented in Hybrid, and suggests likely improvements or data requirements during the coming year.

6.2. Bud break

Information is contained in papers and regional flora on the time of bud-break for different tropical tree species. Simon (1914) concluded that there was probably no month without leaf-flushing in the tropical forests of West Java, but it is normally has seasonal peaks, particularly in forests with periodic dry-seasons (Medway 1971, Frankie 1974). Peak bud-break often occurs just before the onset of rains, though it may occur after the main rains (Whitmore 1975). The trigger for flushing is therefore not solely soil water content, and many species appear to demonstrate a period of dormancy when even heavy rains cannot stimulate bud-break. Additional factors like temperature and photoperiod are likely to be involved (Longman 1969). Buds are often maintained in a 'pre-dormant' state by inhibition from mature leaves (Wareing 1969), and out-of-season flushing can be stimulated by defoliation caused by caterpillars (Germain and Evrard 1956).

Hybrid includes a degree-day parameter which sets the thermal time necessary for bud-burst in deciduous temperate tree types. It may be necessary to introduce a photoperiod parameter to control bud-burst in certain tropical deciduous trees.

6.3. Rate of stem elongation

Two processes are involved in the production of new stems: the formation of additional nodes, and the elongation of internodes between them. Certain species of bamboos and vines can elongate pre-formed tissue at almost 1m per day. Rainforest species are extremely variable in their initial rates of height growth, with a marked difference between pioneer species (4, 5 and 6 in Figure 5) and climax species (1, 2 and 3 in Figure 5). Note also that the climax species tend to increase height growth as they age, whereas the reverse is true with pioneer species. In Ghana, Swaine and Hall (1983) observed that, during the first 5 years of growth, the majority of climax trees had grew at less than 0.5m per year, whereas 8 species of pioneers that exceeded an average rate of 2m per year. In favourable conditions even more rapid growth is possible, and Nicholson (1965), for example, recorded a growth of 8m in the first year after stump-planting *of Albizia falcataria*. Water, nutrient, light and temperature clearly effect the rate of stem elongation, in a manner which varies from species to species and may be difficult to predict.

Hybrid calculates the height growth of individual trees based on the net amount of photosynthate produced during a growing season, which is allocated to new leaf, roots and sapwood according to calculations in a pipe stem model and the calculated height to the base of crown (derived from cabon-

balance in the lowest layer). Height (H) is increased to match the increase in stem breast-height diameter (D) according to an allometric equation of the form :

$$H = aD^b$$

The parameters a and b are empirically derived for individual species or species groups, but these values (and the proportional bark thickness) are not assumed to change through the life of the tree. Other species specific parameters relevant to stem elongation are stem form factor, ratio of bark thickness to diameter, fraction of wood below ground, and fraction of sapwood alive (Table 4).
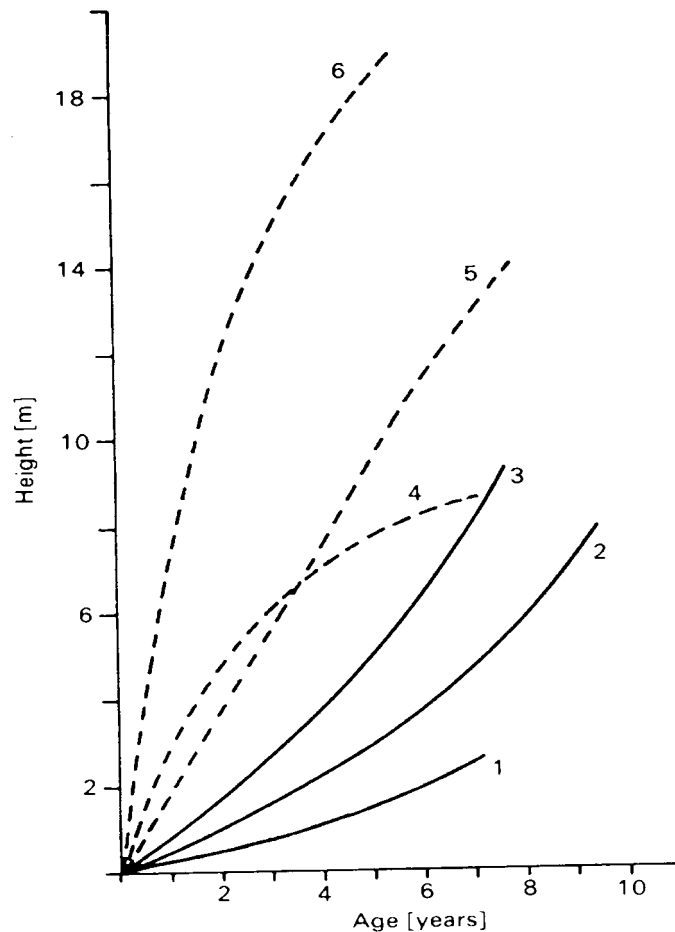

Figure 5. Height growth of young trees under natural conditions in Zaire. Full line = canopy species: (1) Soorodophloeus senkeri, (2) Oystigma oxyphyllum; (3) Gilbertiodendron dewevrei. Dotted line = secondary species in clearings: (4) Calancoba welwitschii; (5) Terminalia superba; (6) Musanga cecropioides (Lebrun & Gilbert 1954)

It is a priority in the coming year to collate information on allometric relationships between height and diameter for the widest possible range of Indonesian TMF trees, including separate relationships for juvenile stages where appropriate. Bark thicknesses, and maximum heights and diameters should also be collated from tree floras and other sources. It may also be necessary to introduce species-specific maximum heights and diameters.

6.4. Onset of bud dormancy

The height of a tree depends on the factors influencing the rate of node production and internode elongation, as discussed in the previous section, but it is also controlled by the duration of the period of shoot elongation, the number of preformed nodes within resting buds, and the period of bud dormancy. Bud dormancy and growth-flushes are normal growth patterns for tropical tress, even in fairly constant climates, and many species have dormant buds for 9-10 months in a year. Very fast growing species show little dormancy (Coombe and Hadfield 1962), whereas other pioneers show marked dormancy, especially as they age (Njoku 1963). Some species may even regularly abort living shoot tips (Addicott 1982).

The physiological factors that induce a change from active shoot growth to terminal bud dormancy appear to include both external and internal factors. Shortening day-length and cooler nights appears to induce dormancy in a range of species (Njoku 1964, Longman 1969, Longman 1978, Singh and Nanda 1981), but other factors like the red/far-red ratio of light, water stress and nutrient shortage may also be important.

Internal conditions within the tree also control the onset of dormancy, with each shoot flush potentially confined to those leaves and stem units pre-formed in the bud, in a form of 'programmed dormancy'. With rapidly growing young stems leaf production may deprive the growing tip of sufficient photosynthate, and in many cases stems can be induced to continue extension growth if young expanding leaves are removed (Hallé & Martin 1968).

Hybrid incorporates the interaction of chilling and bud dormancy in cold-deciduous species but effectively assumes that buds are formed at the same time as leaf abscision in dry-deciduous species. Height growth is calculated annually, driven by allometric relationships to dbh, and there is no explicit representation of episodic growth and dry-deciduous dormancy.

6.5. Growth of leaves

Many tropical tree leaves can change orientation in response to sunflecks, and may close to protect buds from cooler temperatures in high-altitude species (Smith 1974), or to minimise water-stress (Ernst 1971). The growth rates of tropical tree leaves can be exceptionally rapid, often being completed in less than two weeks, long before full rigidity and pigmentation is achieved. Early leaf flushing and maturation provides a protection mechanism from herbivory since herbivorous insects emerge with the rains and attain a peak biomass during the wet months (Murali & Sukumar 1993).

Leaf growth is usually determinate, so the duration of its period of expansion is limited. Temperature and photoperiod have major effects on leaf size, although this varies from species to species, with some evidence that climax species produce larger leaves in long-days, whilst the reverse may be true of pioneers (Longman & Jenik 1987).   Upper canopy leaves tend to be vertically inclined whereas those in deep shade are frequently horizontal. Shading commonly increases rates of leaf growth and final size. Leaves expanding in full sunlight are often smaller, thinker and yellowish-green.

Hybrid includes parameters for specific leaf area (*sla*), and the 'leaf characteristic dimension' (*d_leaf*), both of which are affected by leaf size and thickness. The value used for species-specific PAR- and SW- reflection coefficients (*rhop, rhos*) also incorporate leaf characteristics such as angle and reflectivity. Information on the size and shape of mature leaves has been used for classification purposes and should be collated for target Indonesian trees.

6.6. Leaf senescence and abscision

Leaves reach peak photosynthetic capacity around the time that expansion ceases. At senescence a change of colour takes place marking the wholesale breakdown of chlorophyll, ribonucleac acid and protein and the rapid translocation of some, but not all, of its organic and inorganic nutrients.

Abscission usually follows quickly. A wide range of factors induce leaf-fall in trees, including lowered light intensity, changed temperature and photoperiod, mineral nutrient deficiency and water stress. Older leaves are much more likely to be abscised in times of stress.

In seasonal tropical climates, leaf fall tends to peak in the first half of the dry season (Bray & Gorham 1964). However there is comparatively little information on the leaf longevity of tropical trees (Bentley 1979, Chabot & Hicks 1982). Minimum life-span for undamaged leaves is likely to be around 3 months (Swaine *et al* 1984), and whilst the majority of leaves do not last more than around 15-months, there are some well-documented cases in which life-span is at least 2-3 years (Swaine *et al* 1984, Grubb 1977).

It is often difficult to tell whether a tropical species is deciduous or evergreen, since leaves are seldom totally shed at the same time. Longman and Jenik (1987) recognised 4 categories:

 • *periodic deciduous growth, where leaf-fall occurs well before bud-break with a life-span of about 4-11 months;*

 • *periodic leaf-exchanging growth, where leaf-fall is associated with bud-break and life-span is often about 12 (or 6) months;*

 • *periodic evergreen growth, where leaf-fall is completed well after bud-break and life-span is 7-15 months or more;*

 • *continuous evergreen growth, where there is a continuous formation of leaves with variable life-spans from 3 to 15 months.*

Periodic deciduous growth is common, even in the moist uniformly moist rain forests (Taylor 1960, Janzen 1975). The chief adaptive advantage of deciduous leaves is to avoid severe water stress, but there is a considerable 'cost' attached to being leafless in the tropics since respiratory losses of carbon from branches and twigs are considerable at high temperatures (Janzen & Wilson 1974). Deciduous habit may be apparent in mature individuals of a given species, experiencing exposure to radiation in the canopy, whilst younger trees retain their leaves. Despite the range of behaviour represented by the above 4 categories, it is true that leaf-shedding may be one of the 'vital characteristics' to be used in classifying tropical trees. A useful distinction has been made, for example, between facultatively deciduous trees, such as *Ochroma pyramidalis* and *Tectona grandis*, and obligately deciduous species, such as *Ceiba pentandra*, *Cordia alliadora* and *Enterolobium cyclocapum* (Medina 1983).

Nutrient availability affects the structure and longevity of leaves of forest trees, with small leathery leaves tending to be produced on infertile soils due to N- ,or more usually, P- deficiency (Medina & Cuevas 1989). Such leaves are more durable and better protected from herbivory than large leaves (Choong *et al*. 1992). Evergreen species tend to have a lower nitrogen use efficiency. However, the longer residence time of N is favourable in nutrient poor environment (Sobrado 1991). This is largely the reason why evergreen habits dominate on the heavily-leached soils of high-rainfall zones. Reserves of nitrogen are maintained in the twigs of drought-deciduous species and in the older leaves of evergreen species, providing some nitrogen for the reconstruction of new leaves following drought and during leaf exchange respectively (Sobrado 1995).

Hybrid parameterises trees as either evergreen, cold-deciduous or dry-deciduous (*ptype*) . For cold-deciduous species, the day on which foliage ceases to be a net exporter of carbon due to senescence is calculated from empirical relations based on latitude and daylength. Leaf fall in dry-deciduous species is triggered when average soil water potential in the rooting zone falls below -1.5 MPa. All plant-types have a species-specific constant for leaf turnover/year (*fturn*), and a proportion of foliar nitrogen that is retained in the dying leaves rather than being retranslocated (*frcoeff*). More realistic simulation of the gradual leaf-shedding of many moist tropical forest species will depend on a the derivation of empirical constants in algorithms containing both soil water potential and daylength.

6.7. Cambial activity

The wood and bark produced by the activity of vascular cambium in trees obviously creates the bulk of forest biomass, with the exception of palms and bamboos. Yearly increases in stem diameter vary greatly between species and individuals, and naturally decrease as trees become larger. An analysis of 120,000 trees in Amazonia predicted that the average tree in diameter class 25-35cm would be growing at about 8mm a year; for larger trees the increment would decline below 4mm (Heinsdijk and de Miranda Bastos 1963). In a wet tropical forest in Costa Rica, analysis of 13-year increments of 45 tree and one liane species showed a range of median annual diameter increases between 0.3mm and 13.4mm (Lieberman *et al.* 1985). In plantations, and exceptional dominant individuals in forest clearings, annual diameter increments of 20-60mm can occur.

Increase in diameter is the result of activity by two different lateral meristems: the vascular cambium and the phellogen (cork) cambium, both of which may be cutting off cells towards the outside and inside. Repeated measurements of tree diameters are the main observed variables available to this project to test model calibrations and predictions, despite an array of measurement and methodological problems (Section 8 and Whitmore 1989).

Many deciduous or leaf-exchanging species exist in the humid tropics, include *Homalium tomentosum*, *Pterocarpus indicus* and *Tectona grandis* in SE Asia, *Bursera sinarouba, Geothalsia meiantha, Swietenia mahogani* and *Taxodium disticum* in Central America; and *Ceiba pentandra, Chlorophora excelsa, Entandrophragma* spp. and *Terminalia* spp in West Africa (Borman & Berlyn 1981). These potentially possess annual growth rings, to aid in ageing trees, but such rings are generally difficult to rely on. Cambial activity ceases at the beginning of the leafless period, and resumes following a trigger from auxin exported by expanding leaf buds (Longman 1987). Species which flower during this leafless period may, however, induce an export of auxin resulting in a resumption of cambial activity and possible 'false rings'. Cambial activity may in some cases be most rapid while shoots are extending, but in cocoa (Alvim 1964) and other species (Hopkins 1970) it was slow while flushing proceeded, and reached a peak during the rainy season.

In addition to internal plant hormone triggers on cambial growth are likely to be external influences like temperature (Kwakwa 1964), moisture stress Murray (1966) and solar radiation (Breitsprecher & Bethel 1990).

Recent success with dendrochronological techniques in SE Asian trees has been reported by (Worbed 1995), and periodicity of growth in Dipterocarpacea is reviewed by Killman and Thong (1995).

Hybrid currently assumes that cambial expansion takes place once per year when the year's accumulated carbon, after accounting for litterfall, respiration, and replenishment of sapwood storage, is allocated between cambial, root and shoot growth. The allocation routine in Hybrid contains several species-specific parameters controlling this partitioning (Section 4.10): including allometric height constants (*ah, bh*), form factor (*formf*), bark-thickness fraction (*bark*), ratio between leaf area and sapwood area (*lasa*), biomass ratio between fine roots and foliage (*rlratio*), mean wood and bark specific gravity (*woodd*), proportion of sapwood which is alive (*live*), maximum proportion of live sapwood used as C storage (*storef*), and the minumum wood mass increment factor (*wmf*).

6.8. Root formation and turnover

Root characteristics across species vary largely independently of shoot characteristics, but there tends to be a 'functional equilibrium' (Brouwer 1983) between shoot and root growth. Maximum root biomass is generally obtained at a lower level of resource supply than maximum shoot biomass (Figure 6). This illustrates that root response to fertiliser additions depends greatly on the concentration range studied. Root response to nutrients also depends on whether one examines the whole root-system, or the response of some part of it. Root-system averages based on root-cores generally show significantly lower shoot : root ratios at low soil phosphorus levels (Gower 1987, Vitousek & Sanford 1986);

whereas detailed 3-dimensional studies shown that both the number and total length of individual roots increases close to patches of high- phosphorus concentrations in heterogeneous soils (Mou *et al.* 1995, Tardieu *et al.*1992).
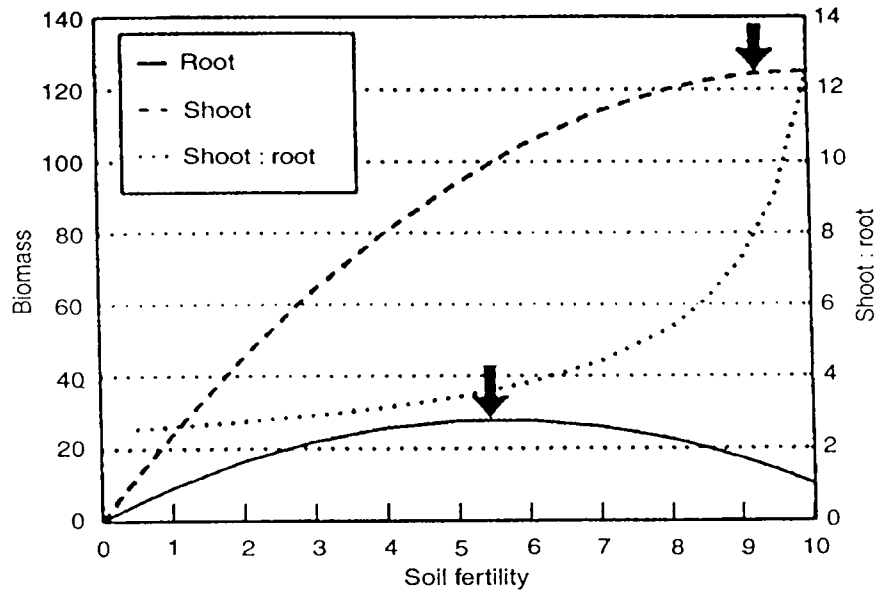

Figure 6 - Schematic relationship between shoot and root biomasss production and soil fertility. The maximum root size is often obtained at intermediate shoot biomass, and between the optimum conditions ofr root and those for shoot growth the uptake rate per unit root increases rapidly (van Noordwijk et al 1995).

Dhyani *et al.* (1990) found that root weight ranged from 27% (*Leucaena leucocephala*) to 72% (*Eucalyptus tereticornis*) of total tree biomass in a comparison of five tree species at 2 years of age. Toky & Bisht (1992) found for 6-year-old trees of 12 species, that fine-root biomass ranged from 9% (*Acacia catechu*) to 27% (*Morus alba*) of total biomass with a median value of 20.3%. These figures probably do not reflect the relative importance of roots in annual carbon allocation in trees, as roots may have a higher turnover rate than above-ground tissues. Sanford (1985) estimated fine root turnover in Venezuela in the top 10 cm at 25% per month

Brouwer's 'functional equilibrium' concept assumes that the allocation of growth resources in the plant to root and shoot meristems is modified by current environmental conditions: if water or nutrients are in short supply the root system gains a larger proportion of available carbon, and when light is limiting the shoot increases in size relative to the root systems. Feedbacks between above-ground and below-ground parts of a tree are therefore so important that there is little point developing a complex above-ground processes in a tree unless below-ground processes are considered in similar detail.

Lawson (1994), reviewed existing literature on tropical tree root distribution growth rates. The main conclusions were:

• *Reasonable data exist on the fine-root biomass of natural tropical forests, but there is less on plantations or trees on farms. Even less data exists on tree fine-root length or surface area from any habitat, and it is these data, rather than biomass, which are needed for the modelling of nutrient or water uptake.*

• *Tree root turnover is very rapid in the tropics and may represent a greater nutrient input to the soil than litterfall. Fine root growth can be extremely rapid after forest clearance or coppicing. Older stands often have more fine-roots near the surface reflecting increased inputs of leaf litter.*

30

Tree fine roots grow most rapidly in the rainy season, and in seasonally dry climates use stored carbohydrates to respond extremely rapidly to the first rains.

• *The vertical distribution of fine-roots is mainly influenced by the supply of nutrients, soil moisture, and considerations of oxygen supply or soil-resistance to growth. Tree fine-roots generally show the same exponential decline in rooting density with depth as shown by crop roots, although the few reported exceptions need to be investigated. Competition, drought and nutrient supply at depth cause trees to root more deeply, but it is not yet certain whether tree species or clones can be found with a genetic disposition to deep rooting. A negative exponential distribution is currently the best approximation to describe the change in root length density with depth.*

• *Horizontal distribution of tree roots can be several times tree height, and trees usually compete below-ground long before canopies touch. Limited evidence suggests that some trees have a tendency to spread more widely than others in identical conditions.*

• *The death of tree fine-roots is controlled by the carbon supply from above-ground, the carbon requirement for root growth and maintenance, and the micro-environment around individual roots. Fine-root growth is highly responsive to changes in above-ground photosynthesis and the patchy distribution of nutrients in the soil. Root and stem carbohydrate reserves are necessary for the tree to survive the regular pruning sustained by agroforestry trees.*

• *Nutrient uptake consists of both mass-flow in the soil solution, and active uptake driven by concentration gradients in the root. Fine roots are more efficient than coarse roots, but the latter may have their absorbing surface increased several hundred fold by mycorrhizas. Trees in poor soils often have a high root:shoot ratio, and finer roots than those well supplied with nutrients. Fine roots from different species differ considerably in their nutrient uptake rates per unit length.*

• *Compartment models of root growth and resource uptake exist, and can describe flows of carbon, nitrogen and phosphorus between the atmosphere, tree and the soil. These models should be developed to include the implications of changes in above-ground photosynthesis.*

• *Topological models of root growth are being developed using fractal branching rules and pipe-stem-theory to predict the branching behaviour of tree root systems. In the long-term, predicted distributions of fine roots, in at least 2-dimensions, could be used together with leaching and nutrient-flow models , to predict possible nutrient uptake in different soil physical conditions.*

Van Noordwijk *et al.* (1996) provide a review of root processes and opportunities for fractal modelling. Van Noordwijk and van de Geijn (1996) also collate the root, shoot and soil parameters required for process-orientated models of plant growth.

One factor with potential to considerably complicate models is the direct transfer of photosynthate between mother trees and seedlings through mycorrhizal connections (Allen 1992, Simard *et al 1997*) or through direct root-anastomoses, which may allow dominant trees to exploit the carbon stores of neighbouring supressed trees (Leroy Duval 1974).

Hybrid has a simple approach to root growth and distribution. Species-specific parameters set the proportion of woody-biomass below-ground (*stf*) and the overall wood-turnover rate (*wturn*) controls the annual loss of coarse-roots and branches. Turnover of fine roots is set separately (*rturn*), as is the proportion of carbon that is retained in the fine-roots rather than being retranslocated (*rrcoeff*). The annual allocation of carbon is determined by a fixed ratio of foliage biomass to fine-root biomass (*rlratio*), and is currently not responsive to environmental conditions. Hybrid has been modified in the HyPAR programme to explicitly represent the competition between tree and crop rooting systems based on their relative root length and water or nitrogen uptake demands (Crout 1997). However the current version of Hybrid assumes that all water and nitrogen in the surface layer is available to both

tree and grass roots, with the rate of maximum nitrogen uptake set by a species-specific parameter (*nupc* - with units of kgN kgC roots^{-1}). Water and nitrogen uptake in a deeper layer is accessible only to tree roots. Water is allocated between grass and trees on the basis of their stomatal conductance.

6.9. Physiological changes with age

Long-lived perennial plants usually show variation in structure and function as they grow older. Leaves in the upper canopies seldom resemble closely those produced by seedlings of the same species. Thus the leaf of *Celtis mildbraedii* from the canopy is a quarter of the length and only 9% of the area of that taken from the undergrowth (Roth 1984).. These differences may be due to the effect of environment, genotype, and gradual ageing or more rapid phase-changing from a 'juvenile' to a 'mature' stage. As trees mature they frequently change their branching and leafing patterns. In the canopy leaves are generally smaller, drip points are often absent, compound leaves have fewer leaflets, leaf shape may alter, and leaf-production becomes more spasmodic (Longman & Jenik 1987).

Hybrid assumes that species morphological and growth characteristics do not change with age, although it optimises the distribution of nitrogen to the canopy layers with respect to light. Photosynthetic efficiency and transpiration are partially related to nitrogen content so this is an indirect, and probably sufficient, representation of leaf ageing. Lower canopy layers with a sustained negative energy balance are assumed to be shed, with some recycling of nitrogen.

6.10. Flowering

Precocious and excessive flowering in a timber species is a disbenefit, since it can divert significant quantities of carbon, and arrest stem growth. Pioneer species like *Anthopcephalus chinensis*, *Dipterocarpus oblongifolius*, Citrus spp, *Funtumia africana, Hildegardia barteri, Monodora tenufolia, Finus caribaea, Trema guineensis*, and *Tectona grandis* have been observed to flower as early as two years of age, especially in the nursery or in rapidly growing plantations. Maturation times are much longer in the natural forest, and it is often 60 years before the majority of dipterocarps in the upper canopy of Malaysian forests start to flower (Ashton 1969).

Some species exhibit more or less continuous flowering in mature trees (e.g. *Harungana madagascariensis, Dillenia suffruticosa* and *Trema orientalis*), but the great majority of species flower periodically. Individual trees may show variation within the crown with some parts in flower, whilst others are in fruit. Synchronised flowering can occur over many hectares of forest, and some species are so reliable in their flowering that villagers use them to time crop planting (Longman & Jenik 1987).

Flowering frequency varies from 3-4 months for *Ficus sumatrana* to 10-15 years in *Homalium grandiflorum* (Medway 1972). Regular annual flowering occurs in a number of common forestry plantation species, including *Cedrela odorata, Gmelina arborea, Tectona grandis, Terminalia ivorensis* and *Pinus kesiya*. Biannual tendencies appear to be characteristic of most canopy trees in Surinam (Schulz 1960)

Although dipterocarps may occasionally flower again after 1-3 years the interval is more commonly about 3-8 years (Wycherley 1973). In these irregularly spaces 'mast' flowering and fruiting seasons the majority of dipterocarps in a region will flower profusely over a period of months, although the peak flowering times for related species may not overlap (Chan & Appanah 1980). It is thought that periods of prolonged drought or larger diurnal fluctuations of temperature may stimulate floral initiation, but the links with climate are poorly understood (Longman 1985). Certainly, considering the forest as a whole, flowering very often peaks during the dry season, particularly for deciduous species, and the early part of the rains.

Hybrid does not represent flowering. This contrasts with other forest models like Formix (Huth *et al* 1994) and Treedyn (Bossel 1996), which although they ignore some physiological processes contained in Hybrid, do include flowers as a potential carbon sink. Other authors conclude, however, that

flowering can stimulate photosynthic efficiency, and is very unlikely to represent a significant net sink for photosynthate (Dick *et al.* 1990).

6.11. Fruit development

The variability of flower development is compounded with fruit development. High proportions of flower abscision in some species mean that several thousand flowers may be reduced to a handful of fruit (Grison 1978, Chan 1977). Fruit maturation periods in West Malaysia varied from 3 weeks to 9 months (Ng and Loh 1975).

Hybrid does not represent fruiting. The climatic triggers and interactions are clearly so complex that there is little hope of modelling this mechanistically. Empirical functions could be included to simulate observed monthly variations in fruit maturation, but there is little information on how flowering and fruiting may be affected by the stand management which the Growth and Yield Project is attempting to model.

6.12. Seed germination and dormancy

A number of different types of seed germination can be recognised based on structure and function. There are variations in whether the hypocotly elongates and carries the cotyledons well above the ground surface, the rate of cotyledon abscision, whether they stay within the seed coat, whether the embryo has already developed into a viviparous seedling before becoming detached from the parent plant (prior germination), or whether the radicle emerges within a few days or weeks of dispersal (prompt germination) - which tends to be common with large seeds, or if the seeds are maintained in the seedbank, or in dried fruits (delayed germination). These classifications of seed germination and dormancy (Table 5) may be of functional significance, and could be an aid to identifying 'functional types'.

Table 5. Classifications of seed germination and dormancy (Longman & Jenik 1987)

Timing	Class	Requirement	Examples
PRIOR	**Viviparous**	None	*Ceriops* *Dryobalanops aromatica* *Magonia pubescens* *Pithecellobium racemosum* *Pouteria ramiflora* *Rhisophora*
PROMPT	**Direct**	None	Cocoa Many dipterocarps *Montezuma speciosissima* *Mora excelsa*
	Indirect	Passage through gut may remove some dormancy	*Azadirachta indica* *Nauclea latifolia* *Securinega virosa*
DELAYED	**Dormant (dry seeds)**	Water Damage to testa/pericarp, and entry of water ('hard' seeds)	*Delonix regio* *Enterolobium cyclocarpum* *Hymenaea courbaril* *Leucaena leucocephala* *Ochroma lagopus* *Parkia javanica*
	Dormant (imbibed seeds)	After-ripening at relatively high temperatures Specific amounts and wavelengths of light	*Elais guineensis* Rice *Cecropia* *Chlorophora excelsa* *Macaranga* *Musanga* *Piper* *Trema*

			Harungana madagascariensis
		Specific temperature regime	Didymopanax Ochroma lagopus Heliocarpus donnellsmithii Phytolacca icosandra
		Leaching of water-soluble inhibitors Entry of oxygen Altered hormonal balance Time for embryo to develop	Tomato

The ecological significance of dormancy is to spread out to months, or even years the supply of seedlings, and increase the probability of seedling surviving.

Hybrid does not model seed germination directly. Forest management often selectively removes certain species, and will have consequent implications for the species composition of seed reaching the forest floor. Management may also change environmental conditions which control dormancy and germination. Thus, whilst it will prove impossible to introduce a fully mechanistic explanation of the many factors controlling flowering, fruiting, seed-dormancy and germination in different tropical tree species, it will be necessary to introduce a link between the numbers and 'fecundity' of mature trees of different species present in a plot and the species composition of the newly germinated seedlings. The G&Y Project, in conjunction with RBGE, should also tabulate seed size and type (e.g. winged or not) for target Indonesian species.

6.13. Seedling growth

Seedlings compete for resources of water, light and nutrients in a similar manner to mature trees, but with the difference that their initial carbohydrate reserves enable significant growth before they require to become self-sufficient. Likelihood of seedling death in forests is exceedingly high, but can be predicted through the same processes as with larger trees: continuing negative carbon balances associated with deep shade, possible desiccation of seedlings growing on bare ground, possible nutrient shortages if root systems cannot access sufficient resources. Major differences between seedling and mature growth are largely explained by the former's lack of reserves. Species differences in susceptibility to pest attack on stems (Ladipo 1986), or leaf browsing (Molofsky & Fisher 1993), or fungal infection (Augsburger *et al.* 1990) may make a crucial difference between survival or death. Small differences in tolerance of deep shade (influenced by leaf dimension, orientation, nitrogen content, rubiso levels, photo-inhibition etc. - Kwesiga 1986, Anten *et al* 1996, Castro *et al.* 1995, Scholes *et al.*1997, Zipperlen & Press 1996) are crucial in determining whether a seedling can grow away from neighbouring competitors. Mycorrhizal associations may be important in providing the high levels of nutrients necessary for efficient photosynthesis in the shade (Cooperband *et al.*1994, Bowman & Panton 1993, Becker 1983), or possibly for direct carbon subsidies from parent trees. The ability of certain species to alter leaf orientation in response to response to sunflecks (Ackerly & Bazzaz 1995) , or to adapt their photosynthetic mechanisms quickly in response to the saturating levels of light present in sunflecks (Pearcy 1990, Chazdon 1992, Chazdon & Kaufmann 1993, Claussen 1996) are indicators of effective survival strategies. Recovery of seedlings from periods of drought is often a major difference between species (Veendaal *et al.*1996, Fisher et al.1991, Blain & Kellman 1991, Reekie & Wayne 1992, Gerhardt 1993, Holmes & Cowling 1993, Medina and Francisco 1994).

Hybrid uses a general input parameter (*imax*) to set the maximum density of trees/ha, and the number of 1.5 m tall saplings to be introduced into a plot is simply calculated by subtracting the number of trees surviving the previous year (or time period) from this density. The species composition of these saplings is currently equally divided between all species deemed to exist in the locality, whether they

currently exist in the plot or not. Initial dbh for these saplings is set with a general input parameter (*idbh*), as is the degree of variability around this mean (*idbhv*). Usually this initial size is parameterised between 1mm and 2mm. There is no attempt to make the growth and survival of seedlings of different species responsive to environmental conditions in a different way to that of mature trees.

This section has touched briefly on the processes controlling growth and survival of seedlings. Much more information exists on the physiology of tropical tree seedlings than for mature trees, and excellent recent compilations are available (e.g. Swaine 1996). Developing a useful model of seeding growth and survival is complex, but could be based on the modular tree object code (Section 6), parameterised for seedlings rather than for mature trees, and run for small sample sub-plots, with manageably small numbers of seedlings, at grid intersections throughout the main plots used for Hybrid.

7. Modularising the Hybrid Model

For the purposes of R6951 AD Friend has significantly simplified and modularised the original Hybrid model (Friend et al 1997 These modules have been supplied to the University of Edinburgh (P Phillips) for inclusion in the SymFor toghether with a working paper explaining the algorithms (Appendix II)

The main program loops through 10ths of a day, with an equal division between the day and night periods. In order to test the physiological parameterisations the environmental forcing is kept constant apart from a day/night difference in radiation. No soil hydrology is calculated in order to isolate the physiological behavour of the component processes from uncertainties in environmental modelling.

On each physiological timestep the model calls subroutines that calculate environmental variables, N uptake, vegetation C balance, and litter production. At a longer timestep, prescribed here as 1 day, the model calls the allocation subroutine which allocates stored C and N to the various plant parts.

The model is implemented using a single-leaf approach, with no treatment of horizontal heterogenity. The canopy is treated as one big leaf, and all calculations are made on a ground area basis. The processes calculated are N uptake, vegetation C balance, litter production, and C and N allocation. N uptake is calculated as a linear function of fine root carbon mass and soil mineral nitrogen content. Any N taken up is added to the vegetation N store.

Vegetation C balance is calculated as the difference between canopy net photosynthesis and maintenance respiration. Canopy net photosynthes is calculated by linearly scaling the rate of net photosynthesis at the top of the canopy with the fraction of incident photosynthetically active radiation that is absorbed by the canopy (fPAR). The rate of net photosynthesis at the top of the canopy is calculated using a biochemical model based on Farquhar et al., and requires stomatal conductance and the amount of N at the top of the canopy (topN) to be known. Stomatal conductance is calculated only from topN in the current implementation. topN is calculated from total canopy N and fPAR. The use of fPAR in this manner is consistent with the idea that the distribution of physiological capacity within the canopy is optimal with respect to absorbed PAR. The net vegetation C balance is added to a C store pool.

Foliage maintenance respiration is calculated for the nightime as a linear function of foliage C and an exponential function of temperature. Foliage maintenance respiration is not calculated during the day as this flux is accounted for by so-called 'dark' respiration. Stem and fine root maintenance respiration is also calculated as a linear function of their respective C contents and an exponential function of temperature.

If total maintenance respiration is greater than the size of the C store, then it is assumed that respiration is only as big as the labile pool size, with priority given to foliage respiration. This concept is not in itself entirely satisfactory, and will be subject of further development.

C and N litter production is calculated as simple fractions of the C and N contents of the vegetation pools (i.e. store, foliage, sapwood, heartwood, and fine root), with different (fixed) rates for each pool.

C and N allocation is calculated using an approach based on the pipe model, with leaf area optimisation and allometry. 50 % of the C and N in the vegetation stores is assumed to be available for allocation on each timestep.

8. Statistical analysis of Indonesian Sample Plot Data

9. Workplan

To be completed

9.1. Data Collation

- Information on dates and seasonality of leaf budburst for target species (Section 5.2).

- Information on allometric relationships between height and diameter, and form factors, for Indonesian TMF trees, including separate relationships for juvenile stages where appropriate. Bark thicknesses, and maximum heights and diameters should also be collated from tree floras and other sources (Section 5.3).

- Information on triggers for episodic growth and dry-deciduous dormancy (Section 5.4).

- Information on the size and shape of mature leaves has been used for classification purposes and should be collated for target Indonesian trees (Section 5.5).

- Information on seasonal leaf-fall patterns, for monthly (?) leaf turnover rates, estimates on nitrogen retranslocation, possible linkages between rainfall , soil moisture or day-length and leaf-fall (Section 5.6)

- Parameterisation information for bark-thickness fraction (bark), ratio between leaf area and sapwood area (lasa), biomass ratio between fine roots and foliage (rlratio), mean wood and bark specific gravity (woodd), proportion of sapwood which is alive (live), maximum proportion of live sapwood used as C storage (storef), and the minumum wood mass increment factor (wmf) (Section 5.7)

- Parameterisation information on species-specific proportion of woody-biomass stored below-ground (stf) and the overall wood-turnover rate (wturn), turnover of fine roots (rturn), proportion of nitrogen that is retained in the fine-roots rather than being retranslocated (rrcoeff, and foliage biomass to fine-root biomass (rlratio) (Section 5.8).

- Information on major parameterisation changes with age or position in canopy (Section 5.9)

- Information on whether flowering is ever a sufficiently important sink for photosynthate or block on main-stem growth to include in Hybrid (Section 5.10)

- Review of whether sufficient information exists on the pattern and rates of flowering and fruiting in target Indonesian species for this to be included more explicitly in Hybrid (Section 5.11).

- Tabulation of seed size and type (e.g. winged or not) for target Indonesian species to add to a database of tree species physiognomy which can be used for functional classification. This would be created in conjunction with the taxonomic computing unit at the RGBE. Attributes might be max height, max dbh, crown size, bark thickness, mature leaf dimensions, leaf thickness, rooting-type, seed size, seed type, sapwood proportion, wood density. (Section 5.12).

9.2. Statistical Analysis

Ron to complete this. Includes analysis of existing growth & Yield data and data and extra species specific physiognomic (see above).

Also could include the strategy for constraining Hybrid parameters to sensible ranges, and running sensitivity tests. Then the main task - back calibrating key parameters (which are they?) using observed diameter increases from PSPs

9.3. *Model Development*

Andrew to complete giving details of the modularisation, thoughts on how to handle seeds, numbers of mother trees, seedling growth etc. And how the individual tree objects could be integrated within a SYMFOR type competition model.

- It may be necessary to introduce a photoperiod parameter to control bud-burst in certain tropical deciduous trees (Section 5.2)

- It may also be necessary to introduce species-specific maximum heights and diameters (Section 5.3)

- Consider whether episodic growth and dry-deciduous bud dormancy should be introduced (Section 5.4)

- More realistic simulation of the gradual leaf-shedding of many moist tropical forest species will depend on a the derivation of empirical constants in algorithms containing both soil water potential and daylength.(Section 5.6).

- Determine whether it may be feasible to change some key parameters (e.g. specific leaf area or photosynthetic response) when trees move from juvenile to canopy to emergent stages. (Section 5.9).

- Introduce a link between the numbers and 'fecundity' of mature trees of different species present in a plot and the species composition of the newly germinated seedlings, and tabulate seed size and type (e.g. winged or not) for target Indonesian species (Section 5.12).

- Develop a model of seeding growth and survival based on the modular tree object code, and parameterised for seedlings rather than for mature trees; run this for sub-plots, with manageably small numbers of seedlings, at grid intersections throughout the main plots used for Hybrid (Section 5.13)

10.References

Acevedo, M.F., Urban, D.L. & Shugart, H.H. 1996. Models of forest dynamics based on roles of tree species. *Ecological Modelling*, **87**, 267-84.

Ackerly, D.D. & Bazzaz, F.A. 1995. Seedling crown orientation and interception of diffuse-radiation in tropical forest gaps. *Ecology*, **76**, 1134-46.

Addicott, F.T. 1982. *Abscission*. Berkeley: University Press.

Adlard, P.G. 1993. *Sustainability*. Vol. Study 5. Shell/WWF Tree Plantation Review ed. Godalming, Surrey: Shell/ WWF.

Adlard, P.G. 1995. Myth and reality in growth estimations. *Forest ecology and management*, **71**, 171-6.

Alder, D. (1995). Growth modelling for mixed tropical forests. ODA; Tropical Forestry Papers

Allen, M.J. 1992. *Mycorrhizal functioning - an integrative plant-fungal process*. New York: Chapman & Hall.

Alvim, PdeT. 1964. Tree growth periodicity in tropical climates. In: *Formation of Wood in Forest Trees*, edited by M.H. Zimmermann, 479-495. New York: Academic Press.

Anderson, D.J. & Bare, B.B. 1994. A dynamic programming algorithm for optimisation of uneven-aged forest stands. *Canadian Journal of Forest Research*, **24**, 1759-65.

Anten, N.P.R., Hernandez, R. & Medina, E.M. 1996. The photosynthetic capacity and leaf nitrogen concentration as related to light regime in shade leaves of a montane tropical forest tree, tetrorchidium-rubrivenium. *Functional Ecology*, **10**, 491-500.

Arah, J. & Hodnett, M. 1997. Approximating soil hydrology in agroforestry models. *Agroforestry Forum*, **8**, 17-20.

Ashton, P.S. 1969. Speciation among tropical forest trees - some deductions in the light of evidence. *Biological Journal of the Linnean Society*, **1**, 155-96.

Augspurger, C.K., Burdon, J.J. & Leather, S.R. 1990. *Spatial patterns of damping-off disease during seedling recruitment in tropical forests*. Uk: Blackwell Scientific Publications; Oxford.

Basiago, A.D. 1995. Sustainable development in Indonesia: a case study of an indigeneous regime of environmental lay and policy. *Int J of sustainable Development and World Ecology*, **2**, 199-211.

Bazzaz, F.A. 1979. The physiological ecology of plant succession. *Annual Review of Ecology and Systematics*, **10**, 351-71.

Becker, P. 1983. Ectomycorrhizae on Shorea (Dipterocarpaceae) seedlings in a lowland Malaysian rainforest. *Malaysian Forester*, **46**, 146-70.

Bentley, B.L. 1979. Longevity of individual leaves in a tropical rain-forest understorey. *Ann Bot*, **43**, 119-21.

Blain, D. & Kellman, M. 1991. The effect of water-supply on tree seed-germination and seedling survival in a tropical seasonal forest in veracruz, mexico. *Journal of Tropical Ecology*, **7**, 69-83.

Borman, F.H. & Berlyn, G. 1981. Age and growth rate of tropical trees: new directions for research. *Bull Yale Univ School of Forestry and Env Studies*, **94**, 1-137.

Bossel, H. 1996. TREEDYN3 forest simulation model. *Ecological Modelling*, **90**, 187-227.

Bossel, H. & Krieger, H. (1994). Simulation of multi-species tropical forest dynamics using a vertically and horizontally structured model. Contrasts between biologically-based process models and management-oriented growth and yield models. Papers presented at the IUFRO S4.01 conference, held Wageningen, Netherlands, 2-6 September 1991. Forest-Ecology-and-Management

Botkin, D.B. 1993. *Forest dynamics: and ecological model*. Oxford: University Press.

Botkin, D.B., Janak, J.F. & Wallis, J.F. 1972. Some ecological consequences of a computer model of forest growth. *J.Ecol.*, **60**, 849-72.

Bowman, D.M.J.S. & Panton, W.J. 1993. Factors that control monsoon-rain-forest seedling establishment and growth in north australian eucalyptus savanna. *Journal of Ecology*, **81**, 297-304.

Bray, J.R. & Gorham, E. 1964. Litter production in forests of the world. *Advances in Ecological Research*, **2**, 101-57.

Breitspecher, A. & Bethel, J.S.A.D. 1990. Stem-growth periodicity of trees in a tropical wet forest of Costa Rica. *Ecology*, **71**, 1156-64.

Brokaw, N.V.L. 1985. Gap-phase regeneration in a tropical forest. *Ecology*, **66**, 682-7.

Brouwer, R. 1983. Functional equilibrium: sense or non-sense? *Netherlands Journal of Agricultural Science*, **31**, 335-48.

Brzeziecki, B. & Kienast, F. 1994. Classifying the life-history strategies of trees on the basis of the Grimian model. *Forest ecology and management*, **69**, 167-87.

Bugmann, H.K.M. 1996. A simplified forest model to study species composition along climate gradients. *Ecology*, **77**, 2055-74.

Bugmann, H. & Cramer, W. 1998. Improving the behaviour of forest gap models along drought gradients. *Forest ecology and management*, **103**, 247-63.

Bugmann, H. & Fischlin, A. 1996. Simulating forest dynamics in a complex topography using gridded climatic data. *Climatic Change*, **34**, 201-11.

Burton, P.J. & Bazzaz, F.A. 1995. Ecophysiological responses to tree seedlings invading different patches of old-field vegetation. *Journal of Ecology*, **83**, 99-112.

Campbell, G.S. 1985. *Soil Physics with Basic*. New York: Elsevier.

Cannell, M.G.R. & Smith, R.I. 1983. Thermal time, chill days and prediction of budburst in Picea sitchensis. *J.appl.ecol.*, **20**, 351-63.

Castro, Y., Fetcher, N. & Fernandez, D.S. 1995. Chronic photoinhibition in seedlings of tropical trees. *Physiologia Plantarum*, **94**, 560-5.

Chabot, B.F. & Hicks, D.J. 1982. The ecology of leaf life-spans. *Ann. Rev. Ecol. Syst.*, **13**, 229-59.

Chan, H.T. 1977. *Reproductive biology of some Malaysian dipterocarps*. Ph.D. Dissertation. Aberdeen.

Chan, H.T. & Appanah, S. 1980. Reproductive biology of some Malaysian dipterocarps 1. flowering biology. *Malaysian Forester*, **43**, 132-43.

Chazdon, R.L. 1992. Photosynthetic plasticity of two rain forest shrubs across natural gap transects. *Oecologia*, **92**, 586-95.

Chazdon, R.L. & Kaufmann, S. 1993. Plasticity of leaf anatomy of two rain forest shrubs in relation to photosynthetic light acclimation. *Functional Ecology*, **7**, 385-94.

Chen, S.G., Ceulemans, R. & Impens, I. 1994. A fractal-based populus canopy structure model for the calculation of light interception. *For Ecol & Manage.*, **69**, 97-110.

Choong, M.F., Lucas, P.W., Ong, J.S.Y., Pereira, B., Tan, H.T.W. & Turner, I.M. 1992. Leaf fracture-toughness and sclerophylly - their correlations and ecological implications. *New Phytologist*, **121**, 597-610.

Claussen, J.W. 1996. Acclimation abilities of 3 tropical rain-forest seedlings to an increase in light-intensity. *Forest ecology and management*, **80**, 245-55.

Coombe, D.E. & Hadfield, W. 1962. An analysis of the growth of Musanga cecropioides. *J.Ecol.*, **50**, 221-34.

Cooperband, L.R., Boerner, R.E.J. & Logan, T.J. 1994. Humid tropical leguminous tree and pasture grass responsiveness to vesicular-arbuscular mycorrhizal infection. *Mycorrhiza*, **4**, 233-9.

Coster, C. 1923. Lauberneuerung und andere periodische Lebensprozesse in dem trocenen Monsungebiet Ost-Javas. *Annls jard bot Buitenz*, **33**, 117-9.

Crout, N.M.J. 1997. Nutrient relationships in the HyPAR model. In: *Agroforestry Modelling and Research Coordination - Annual Report July 96 - June 97*, edited by G.J.et al. Lawson, 43-50. Edinburgh: Institute of Terrestrial Ecology.

de Reffye, P., Houllier, F., Blaise, F., Barthelemy, D., Dauzat, J. & Auclair, D. 1995. A model simulating above- and below-ground tree architecture with agroforestry applications. *Agroforestry Systems*, **30**, 175-97.

Dhyani, S.K., Narain, P. & Singh, R.K. 1990. Studies on root distribution of five multipurpose tree species in Doon Valley, India. *Agroforestry Systems*, **12**, 149-61.

Dick, J.McP., Jarvis, G. & Barton, C.V.M. 1990. Influence of male and female cones on assimilate repdouction of Pinus controta trees within a forest stand. *Tree Physiology*, **7**, 49-63.

Eikelboom, K.G. & Janssen, B.H. 1994. *The program of the model DYNAMITE (DYnamics of Nutrients And Moisture in Tropical Ecosystems)*. Wageningen: The Tropenbos Foundation.

Ernst, W. 1971. Zur okologie der Miombo-Walder. *Flora*, **162**, 317-31.

Evans, J.R. 1989. Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia*, **78**, 9-19.

Favrichon, V. 1994. Classification des sspeces arborees en groupes fonctionnels en vue de la realisation d'un modele de dynamique de peuplement en foret Guyanaise. *Rev. Ecol.(Terre vie)*, **49**, 379-403.

Fisher, B.L., Howe, H.F. & Wright, S.J. 1991. Survival and growth of virola-surinamensis yearlings - water augmentation in gap and understory. *Oecologia*, **86**, 292-7.

Fosberg, F.R. 1967. A classification of vegetation for general purposes. In: *Guide to the checklist for IBP areas*, edited by G.F. Peterken, Cambridge: University Press.

Foxworthy, F.W. (1927). Commercial trees of the Malay Peninsula. Malay Forest Record 3

Frankie, G.W. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology*, **62**, 881-919.

Friedel, M.H., Bastin, G.N. & Griffin, G.F. 1988. Range assessment and monitoring of arid lands: the derivation of functional groups to simplify vegetation data. *Journal of Environmental Management*, **27**, 85-97.

Friend, A.D. 1995. PGEN: an integrated model of leaf photosynthesis, transpiration and conductance. *Ecological Modelling*, **77**, 233-55.

Friend, A.D., Schugart, H.H. & Running, S.W. 1993. A physiology - based gap model of forest dynamics. *Ecology*, **74**, 792-7.

Friend, A.D., Stevens, A.K., Knox, R.G. & Cannell, M.G.R. 1997. A process-based terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0). *Ecological Modelling* **95**, 249-287.

Gane, M. 1992. Sustainable forestry. *Comm For Rev*, **71**, 83-90.

Gerhardt, K. 1993. Tree seedling development in tropical dry abandoned pasture and secondary forest in Costa Rica. *Journal of Vegetation Science*, **4**, 95-102.

Germain, R. & Evrard, C. (1956). Etude ecologique et phytosociologique de la foret a Brachystegia laurentii. INEAC Brussels No 67: 10105

Gillison, A.N. 1997. The modus line: an equilibrium model for plant species and plant functional types. , .

Gillison, A.N. & Carpenter, G. 1995. A generic plant functional attribute set and grammar for vegetation description and analysis. *Unpublished study*, .

Gower, S.T. 1987. Relations between mineral nutrient availability and fine root biomass in two Costa Rican tropical wet forests : A hypothesis. *Biotropica*, **19**, 171-5.

Grier, C.C. & Running, S.W. 1977. Leaf area of mature northwestern coniferous forests: relation to site water balance. *Ecology*, **58**, 893-9.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review*, **52**, 107-45.

Grubb, P.J. 1977. Control of forest growth and distribution on set tropical mountains: with special reference to mineral nutrition. *Ann. Rev. Ecol. Syst.*, **8**, 83-107.

Hall, J.B. & Swaine, M.D. 1981. *Distribution and ecology of vascular plants in a tropical rain forest: forest vegetation in Ghana*. The Hague: Junk.

Halle, F. & Martin, R. 1968. Etude de la croissance rythmique chez l'Hevea. *Adansonia*, **8**, 475-503.

Halle, F., Oldeman, R.A.A. & Tomlinson, P.B. 1978. *Tropical trees and forests: an architectural analysis*. Berlin: Springer Verlag.

Heinsdijk, D. & de Miranda Bastos, A. 1963. Inventarios florestais na Amazonia. *Biol Setor Inventarios Florestais (Brazilia)*, **6**, 1-100.

Holmes, P.M. & Cowling, R.M. 1993. Effects of shade on seedling growth, morphology and leaf photosynthesis in 6 subtropical thicket species from the eastern cape, south-africa. *Forest ecology and management*, **61**, 199-220.

Hopkins, B. 1970. Vegetation of Olokemeju forest reserve Nigeria VI The plants on the forest site with special reference to their seasonal growth. *J Ecology*, **58**, 765-93.

Horn, H.S. 1991. *The Adaptive Geometry of Trees*. Princetown: University Press.

Howard, A.F. 1993. A linear programming model for predicting the sustainable yield of timber from a community forest on the Osa Peninsula of Costa Rica. *Forest ecology and management*, **61**, 29-43.

Howard, A.F. & Valerio, J. 1992. A diameter class growth model for assessing the sustainability of silvicultural prescriptions in natural tropical forests. *Comm For Rev*, **71**, 171-7.

Hubbell, S.P. & Foster, R.B. 1986. Biology, chance and history in the structure of rainforest tree communities. In: *Community Ecology*, edited by R.J. Diamond & T. Case, 314-329. New York: Harper and Row.

Huth, A., Ditzer, T. & Bossel, H. 1996. *Simulation of the growth of tropical rain forests (final report for GTZ)*. University of Kassel: Centre for Environmental Systems Research.

Huth, A., Hahn-Schilling, B. & Bossel, H. 1994. Effects of various logging strategies on the growth of peat swamp forest - simulations using FORMIX. OT: Untersuchung der Auswirkungen von

verschiedenen Nutzungsstrategien auf das Wachstum von Moorregenwald - Simulationen mit FORMIX. *Zeitschrift fur Okologie und Naturschutz*, **3**, 217-25.

Janzen, D.H. 1975. *Ecology of plants in the tropics*. London: Edward Arnold.

Janzen, D.H. & Wilson, D.E. 1974. The cost of being dormant in the tropics. *Biotropica*, **6**, 260-2.

Jarvis, P.G. & LEvrenz, J.W. 1983. Productivity of deciduous and evergreen forest. In: *Encylopedia of Pland Physiology*, edited by O.L. Lang, P.S. Nobel, C.B. Osmond & H. Ziegler, Vol. 12D, 233-280. Berlin: Springer-Verlag.

Jobstl, H.A. 1995. Models for sustainability in forestry. *Centralblatt fur das Gesamte Forstwesen.*, **112**, 19-31.

Jones, E.W. 1956. Ecological studies in rainforest of S.Nigeria: Okumu Forest Reserve. *J.Ecol.*, **44**, 83-117.

Killman, W. & Thong, H.L.A.S. 1995. The periodicity of growth in tropical trees with special reference to Dipterocarpacea - a review. *Iawa Journal*, **16**, 329-35.

Kohler, P. & Huth, A. 1998. The effects of tree species grouping in tropical rainforest modelling: simulations with the individual based model FORMIND. *Ecological Modelling*, **109**, 301-21.

Koop, H. & Sterck, F.J. 1994. Light penetration through structurally complex forest canopies: an example of a lowland tropical rainforest. *Forest ecology and management*, **69**, 111-22.

Korol, R.L., Running, S.W. & Milner, K.S. 1995. Incorporating intertree competition into an ecosystem model. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **25**, 413-24.

Korol, R.L., Running, S.W., Milner, K.S. & Hunt, E.R., Jr. 1991. Testing a mechanistic carbon balance model against observed tree growth. *Canadian Journal of Forest Research*, **21**, 1098-105.

Kreutzer, K. 1993. Changes in the role of nitrogen in Central European forests. In: *Forest decline in the Atlantic and Pacific Region*, edited by R.F.and M.-D. Huettle. D, 82-96. Berlin: Springer-Verlag.

Kuchler, A.W. 1967. *Vegetation Mapping*. New York: Ronald Press.

Kwakwa, R.S. (1964). The effects of temperature and day-length on growth and flowering in woody plants. MSc Thesis, University of Ghana

Kwesiga, F.R. 1986. Some Photosynthetic Characteristics of Tropical Timber Trees as Affected by the Light Regime During Growth. *Annals of Botany*, **58**, 23-32.

Ladipo, D.O. 1986. Screening of indigenous forest species for genetic resistance to insect pests in Nigeria. *IUFRO 18th World Congress*, **1**, 228-35.

Lawson, G.J. 1994. Roots in Tropical Agroforestry Systems. In: *Agroforestry Modelling and Research Coordination*, edited by M.G.R. Cannell, N.M.J. Crout, R.C. Dewar, G.J. Lawson, P.E. Levy, D.C. Mobbs & W.H. Robertson, 22. Edinburgh: Institute of Terrestrial Ecology.

Lawson, G.J., Crout, N.M.J., Levy, P.E., Mobbs, D.C., Wallace, J.S., Cannell, M.G.R. & Bradley, R.G. 1995. The tree-crop interface - representation by coupling of forest and crop process-models. *Agroforestry Systems*, **30**, 199-221.

Lebrun, J. & Gilbert, G. 1954. Une classification ecologique des forets du Congo. *INEAC Brussels Pub*, **63**, 1-89.

Leemans, R. 1991. Sensitivity analysis of a forest sucession model. *Ecological Modelling*, **53**, 247-62.

Leroy Duval, J. (1974). Structure dynamique de la rhizosphere de l'okoume dans ses rapports avec la sylviculture. Centre Tech Forestier Trop, Nogent-sur-Marne

Lieberman, D., Lieberman, M., Hartshorn, G. & Peralta, R. 1985. Growth rates and age-size relationships in tropical wet forest trees in Costa Rica. *Journal of Tropical Ecology*, **1**, 97-109.

Longman, K.A. 1969. The dormancy and survival of plants in the humid tropics. *Symp Soc Exp Biol*, **23**, 471-88.

Longman, K.A. 1978. Control of shoot extension and dormancy - external and internal factors. In: *Tropical Trees as Living Systems*, edited by P.B. TRomlinson & M.H. Zimmerman, 465-495. Cambridge: University Press.

Longman, K.A. & Jenik, J. 1987. *Tropical forest and its environment*. Harlow,Essex: Longman.

MacArthur, R.H. & Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princetown: University Press.

Martin, C.E., Loeschen, V.S. & Borchert, R. 1994. Photosynthesis and leaf longevity in trees of a tropical deciduous forest in Costa Rica. *Photosynthetica*, **30**, 341-51.

Martin, P. 1992. Exe - a climatically sensitive model to study climate change and co2 enhancement effects on forests. *Australian Journal of Botany*, **40**, 717-35.

Martin, P.H. 1996. Climate-change, water-stress, and fast forest response - a sensitivity study. *Climatic Change*, **34**, 223-30.

Medina, E. 1983. Adaptations of tropical trees to moisture stress. In: *Ecosystems of the world (14A) Tropical Rainforest Ecosystems*, edited by F.B. Golley, 225-237. Amsterdam: Elsevier.

Medina, E. & Cuevas, E. 1989. Patterns of nutrient accumulation and release in Amazonian forests of the upper Rio Negro basin. In: *Mineral Nutrients in Tropical Forest and Savanna Ecosystems*, edited by J. Proctor, 217-240. Oxford: Blackwell.

Medina, E. & Francisco, M. 1994. Photosynthesis and water relations of savanna tree species differing in leaf phenology. *Tree Physiology*, **14**, 1367-81.

Medway, L. 1972. Phenology of a tropical rainforest in Malaya. *Biological Journal of the Linnean Society*, **4**, 117-46.

Mohren, G.M.J. & Burkhart, H.E. 1994. Contrasts between biologically-based process models and management-orientated growth and yield models. *Forest ecology and management*, **69**, 1-6.

Mohren, G.M.J. & Vandeveen, J.R. 1995. Forest growth in relation to site conditions application of the model forgro to the solling spruce site. *Ecological Modelling*, **83**, 173-83.

Molofsky, J. & Fisher, B.L. 1993. Habitat and predation effects on seedling survival and growth in shade-tolerant tropical trees. *Ecology*, **74**, 261-5.

Mou, P., Jones, R.H., Mitchell, R.J. & Zutter, B. 1995. Spatial distribution of roots in Sweetgum and Loblolly pine monocultures and relations with above-ground biomass and soil nutrients. *Functional Ecology*, **9**, 689-99.

Murali, K.S. & Sukumar, R. 1993. Leaf flushing phenology and herbivory in a tropicad dry deciduous forest, southern India. *Oecologia*, **94**, 114-9.

Murray, D.B. (1966). Soil moisture regimes. Cacao Res, Trinidad, Ann Rep 1965, pp34-39

Nambiar, E.K.S. & Fife, D.N. 1991. Nutrient retranslocation in temperate conifers. *Tree Physiology*, **9**, 185-207.

Nemani, R.R. & Running, S.W. 1989. Testing a theoretical climate-soil-leaf area hydrologic equilibrium of forests using satellite data and ecosystem simulation. *Agric For Meteorology*, **44**, 245-60.

Ng, F.S.P. & Loh, H.S. 1975. Flowering to fruiting periods. *Malaysian Forester*, **37**, 127-32.

Nicholson, D. 1965. A plot of Albizia falcata. *The Malayan Forester*, **28**, 240-2.

Njoku, E. 1963. Seasonal periodicity in the growth and development of some forest trees in Nigeria. *J.Ecol.*, **51**, 617-24.

Njoku, E. 1964. Seasonal periodicity in the growth and development of some forest trees in Nigeria. *J.Ecol.*, **52**, 19-26.

Noble, I.R. & Gitay, H. 1996. A functional classification for predicting the dynamics of landscapes. *Journal of Vegetation Science*, **7**, 329-36.

Noble, I.R. & Slatyer, R.O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio*, **43**, 5-21.

Oldemann, R.A.A. & van Dijk, J. 1991. Diagnosis of the temperament of tropical forest trees. In: *Rainforest Regeneration and Management*, edited by A. Gomez-Pompa, T.C. Whimore & M. Hadley, 21-66. (Man and Biosphere Series no 6). Paris: UNESCO.

Parton, W.J., Scurlock, J.M.O., Ojima, D.S., Glimanov, T.G., Scholes, R.H., Schimel, D.S., Kirchner, T., Menaut, J.C., Seastedt, T. & Garcia, M. 1993. Observations and modelling of biomass and soil organic matter dynamics for the brassland biome worldwide. *Global Biogeochemical Cycles*, **7**, 785-809.

Pastor, J. & Post, W.M. 1985. *Development of a linked forest productivity - soil process model*. ONRL/TM-9519: US Department of Energy.

Pearcy, R.W. 1990. Sunflecks and photosynthesis in plant canopies. *Annual Review of Plant Physiology and Plant Molecular Biology*, **41**, 421-53.

Philip, M.S. 1987. Obstacles to measuring growth and yield in tropical rain forests. In: *Natural management of tropical moist forests*, edited by Vincent & Mergen, 135-148. Yale: University Press.

Phillips, P. 1998. *User Manual for SymFor 97*. (Available on http://meranti.ierm.ed.ac.uk/g&y/) ed. University of Edinburgh: Institute for Ecology and Resource Management.

Post, W.M. & Pastor, J. 1996. Linkages - an individual-based forest ecosystem model. *Climatic Change*, **34**, 253-61.

Raunkier, C. 1934. *Life forms of plants and statistical plant geography*. Oxford: Clarendon Press.

Reekie, E.G. & Wayne, P. 1992. Leaf canopy display, stomatal conductance, and photosynthesis in seedlings of 3 tropical pioneer tree species subjected to drought. *Canadian Journal of Botany-Revue Canadienne De Botanique*, **70**, 2334-8.

Reich, P.B., Uhl, C., Walters, M.B. & Ellsworth, D.S. 1991. Leaf life-span as a determinant of leaf structure and function among 23 amazonian tree species. *Oecologia*, **86**, 16-24.

Rennolls, K. 1994. Pipe-model theory of stem-profile development. *For Ecol & Manage.*, **69**, 41-55.

Richards, P.W. 1952. *The Tropical Rain Forest: An Ecological Study*. .

Richards, P.W. 1983. The three-dimensional structure of tropical rain forest. In: *Tropical Rainforest: ecology and management*, edited by S.L. Sutton, T.C. Whitmore & A.C. Chadwick, 3-10. Oxford: Blackwell.

Robbins, R.G. & Wyatt-Smith, J. 1964. Dryland forest formations and forest types in the Malayan peninsula. *Malayan Forester*, **27**, 188-216.

Roberts, D.W. 1996. Landscape vegetation modeling with vital attributes and fuzzy-systems theory. *Ecological Modelling*, **90**, 175-84.

Roth, I. 1984. *Stratification of tropical forests as seen in leaf structure*. The Hague: Junk.

Running, S.W. & Coughlan, J.C. 1988. A general model of forest ecosystem processes for regional applications. 1' Hydrological balance, canopy gas exchange and primary production processes. *Ecol Modelling*, **42**, 125-54.

Running, S.W. & Gower, S.T. 1991. FOREST-BCG, as a general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiology*, **9**, 147-60.

Sanford, R.L. 1985. *Root ecology of mature and successional Amazonian forests*. Ph.D. Dissertation. University of California, Berkley.

Scholes, J.D., Press, M.C. & Zipperlen, S.W. 1997. Differences in light energy utilisation and dissipation between dipterocarp rain forest tree seedlings. *Oecologia*, **109**, 41-8.

Schulz, J.P. 1960. *Ecological studies on the rainforest in northern Suriname*. Amsterdam: North-Holland.

Sellers, P.J., Berry, J.A., Collatz, G.J., Field, C.B. & Hall, F.G. 1992. Canopy reflectance, photosynthesis and transpiration III. A reanalysis using improved leaf models and a new canopy integration scheme. *Remote Sensing of Environment*, **42**, 187-216.

Shimwell, D.W. 1971. *Description and classification of vegetation*. London: Sidgewick and Jackson.

Shinozaki. 1965. A quantitative analysis of plant form - the pipe model theory. 1. basic analysis. *Japanese Journal of Ecology*, **14**, 97-105.

Shugart, H.H. 1984. *A theory of forest dynamics*. Berlin: Springer-Verlag.

Shugart, H.H. 1997. Plant and ecosystem functional types. In: *Plant Functional Types*, edited by T.M. Smith, H.H. Shugart & F.I. Woodward, 20-43. Cambridge: University Press.

Shugart, H.H. & Smith, T.M. 1996. A review of forest patch models and their application to global change research. *Climatic Change*, **34**, 131-53.

Silva, J.N.A., de Carvalho, J.O.P., do Lopes, C.A.J., de Oliveira, R.P. & de Oliveira, L.C. 1994. Growth and yield studies in the Tapajos Region, Central Brazilian Amazon. In: *Growth and Yield of Tropical Forests*, edited by IUFRO, 19-29. Toyko: IUFRO.

Simard, S.W., Perry, D.A., jones, M.D., Myold, D.D., Durall, D.M. & Milina, R. 1997. Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature*, **388**, 579-82.

Simberloff, D. & Dayan, T. 1991. The guild concept and the structure of ecological communities. *Ann. Rev. Ecol. Syst.*, **22**, 115-43.

Simon, S.V. 1914. Studien uber die Periodizitat der Lebensprozesse der in dauernd fechten Tropengebieten heimishen Baume. *Jahrb viss Bot*, **54**, 71-187.

Singh, K. & Nanda, K.K. 1981. Effect of photoperiod on extension growth, rest period and flowering of Bauhinea acuminata seedlings. I. Analysis of the first year growth. *Indian J Exp Biol*, **19**, 337-40.

Sinoquet, H., Adam, B., Rivet, P. & Godin, C. 1997. Interactions between light and plant architecture in an agroforestry walnut tree. *Agroforestry Forum*, **8**, 37-41.

Smith, A.P. 1974. Bud temperature in relation to nyctinastic leaf movement in an Andean giant rosette plant. *Biotropica*, **106**, 32-46.

Smith, T.H., Shugart, H.H. & Woodward, F.I. 1997. *Plant Functional Types: their relevance to dcosystem properties and global change*. International geosphere-bioshpere programme book series ed. Cambridge: Cambridge University Press.

Sobrado, M.A. 1991. Cost-benefit relationships in deciduous and evergreen leaves of tropical dry forest species. *Functional Ecology*, **5**, 608-16.

Sobrado, M.A. 1995. Seasonal differences in nitrogen storage in deciduous and evergreen species of a tropical dry forest. *Biol. Plant.*, **37: 291-295**, 291-5.

Stewart, J.B. 1988. Modelling surface conductance of a pine forest. *Agricultural Meteorology*, **43**, 19-35.

Stork, N. & Watt, A.D. (1996). Rapid Ecological Assessment of the forested buffer zones around the Kerinci Seblat National Park, Sumatra,. Report to CIFOR from the Institute of Terrestrial Ecology

Swaine, M.D. 1996. *The ecology of tropical forest tree seedlings*. Carnforth: Parthenon Press.

Swaine, M.D. & Hall, J.B. 1983. Early succession on cleared forest land in Ghana. *J.Ecol.*, **71**, 601-27.

Swaine, M.D., Hallm, J.B. & Lieberman, D. 1984. Leaf dynamics in tropical forest trees. In: *Tropical Rain Forests - the Leeds Symposium*, edited by A.C. Chadwick & S.O. Sutton, 321-322. Leeds: Philosophic and Literary Society.

Swaine, M.D. & Whitmore, T.C. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio*, **75**, 81-6.

Tan, L.C. (1996). Initiatives on assessing sustainability: status and future directions. Summmary of the thrid international project advisory panel meeting on testing criteria and indicators for sustaibable managemen of forests, Turrialba, Costa Rica, CIFOR/CATIE Special Publication

Tardieu, F., Bruckler, L. & Lafolie, F. 1992. Root clumping may affect the root water potential and the resistance to soil-root water transport. *Plant & Soil*, **140**, 291-301.

Taylor, C.J. 1960. *Synecology and silviculture in Ghana*. Edinburgh: Nelson.

Toky, O.P. & Bisht, R.P. 1992. Observations on the rooting pattern of some agroforestry trees in an arid region of north-western India. *Agroforestry Systems*, **18**, 245-63.

Urban, D.L. 1990. *A versatile model to simulate forest pattern: a users guide to ZELIG version 1.0*. Virginia: University of Virginia.

Vanclay, J.K. 1991. Review of data requirements for developing growth models for tropical moist forests. *Comm For Rev*, **70**, 248-71.

Vanclay, J.K. 1994. Sustainable timber harvesting: simulation studies in the tropical rainforests of north Queensland. *Forest ecology and management*, **69**, 229-320.

Vanclay, J.K. 1994. *Modelling forest growth and yield: applications to mixed tropical forests*. Uk: CAB INTERNATIONAL; Wallingford.

Vanclay, J.K. 1996. Assessing the sustainability of timber harvests from natural forests: limitations of indices based on successive harvests. *Journal of Sustainable Forestry*, **3**, 47-58.

van Noordwijk, M. & van de Geijn, S.C. 1996. Root, shoot and soil parameters required for process-orientated models of crop growth limited by water or nutrients. *Plant and Soil*, **183**, 1-25.

van Noordwijk, M., Lawson, G.J., Soumare, A., Groot, J.J.R. & Hairiah, K. 1996. Root distribution of trees and crops: competition and/or complementarity. In: *Tree-crop interactions - a physiological approach*, edited by C.K. Ong & P. Huxley, 319-364. Wallingford: CABI International.

Veenedaal, E.M., Swaine, M.D., Agyeman, V.K., Blay, D., Abebrese, I.K. & Mullins, C.E. 1996. Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. *Journal of Ecology Oxford*, **84**, 83-90.

Veenendaal, E.M., Swaine, M.D., Agyeman, V.K., Blay, D., Abebrese, I.K. & Mullins, C.E. 1996. Differences in plant and soil-water relations in and around a forest gap in west-africa during the dry season may influence seedling establishment and survival. *Journal of Ecology*, **84**, 83-90.

Vitousek, P.M. & Sanford, R.L. 1986. Nutrient cycling in moist tropical forests. *Ann. Rev. Ecol. Syst.*, **17**, 137-67.

Wan Razali, W.M. (1989). Summary of growth and yield studies in tropical mixed forests of Malaysia. FRIM-Reports. 1989, No. 51, 16-38; 60 ref

Wareing, F.P. 1969. The control of dormancy in seed plants. *Symp Soc Exp Biology*, **23**, 242-62.

Waring, R.H. & Pitman, G.B. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology*, **66**, 889-97.

Whitmore, T.C. 1975. *Tropical Rainforests of the Far East*. Oxford: University Press.

Whitmore, T.C. 1984. *Tropical rain forests of the far east*. Oxford: University Press.

Whitmore, T.C. 1989. Guidelines to Avoid Remeasurement Problems in Permanent Sample Plots in Tropical Rain Forests. *Biotropica*, **21**, 282-3.

Worbed, M.A.D. 1995. How to measure growth dynamics in tropical trees: a review. *Iawa Journal*, **16**, 337-51.

Wycherley, P.R. 1982. The phenology of some fruit tree species in a lowland dipterocarp forest. *The Malayan Forester*, **45**, 21-32.

Yarie, J., Dyck, W.J. & Mees, C.A. 1990. Role of computer models in predicting the consequences of management on forest productivity. In: *Inmpact of intensive harvesting on forest site productivity*, edited by J. Yarie, W.J. Dyck & C.A. Mees, Furneaux Lodge, Marlborough: International Energy Agency.

Zipperlen, S.W. & Press, M.C. 1996. Photosynthesis in relation to growth and seedling ecology of two dipterocarp rain forest tree species. *Journal of Ecology Oxford*, **84**, 863-76.

Zotz, G. & Winter, K. 1994. Photosynthesis of a tropical canopy tree, ceiba-pentandra, in a lowland forest in panama. *Tree Physiology*, **14**, 1291-301.

Appendix I

Hybrid 4.3 Non-species-specific input variables
Version 1.2.97

Value	Name	Comment
'SITES/test'	siten	name of site (20 characters or fewer)
0	ind	set to 1 if read in initial plot values from indata.in.
0	trans	0 for default, 1 for trans spin-up, 2 for trans trans
2	nsteps	number of timesteps per day
500	nyrs	number of years in simulation
10	nmyrs	number of years for *_mo.out averaging.
1	rep	reporting frequency (0 = annual, 1 = once per site).
1	dyn	ann and biom reporting frequency (0 = once per site, 1 = each year, 2= 10 year means).
0	mid	mid-year screen output (0=off, 1=0n).
1	ran_s	random soil flag (0 = non-random, 1 = random).
14.34	isc	initial soil C (kg/m2).
0.1	iscv	variation in initial soil C (fraction).
0.001	idbh	initial tree dbhs (m).
0.9	idbhv	variation in initial dbhs (fraction).
1490	syear	start year (for atmospheric CO2 partial pressure)
1	co2f	type of atmospheric CO2 simulation (0 = no change; 1 = inc.)
0	dtf	type of temperature simulation (0 = no change; 1 = inc.)
0	ndepf	type of Ndep simulation (0 = no change; 1 = inc.; 2 = ppt effect; 3 = inc. and ppt effect)
28	caoi	pre-ind CO2 partial pressure if co2t = 0 (Pa)
0	dti	current divergence of temperature from norm (K)
20	ndepi	pre-ind mineral N deposition rate at 0 m ppt (kg N ha-2 year-1)
10	nplots	number of plots in simulation (N.B. indata.d must be set accordingly)
200	area	plot area (M2)
2000	imax	max. density of trees (trees/ha).
10	ireg	no. trees of each GPT or spp. to be planted each year.
0.00001	acc	accuracy of pipe model solution (m)
0.13	prubal	Lower limit of pruba for no frost damage to foliage.
0.0005	intc	canopy rain interception coefficient (0.0005 m LAI-1 d-1)
0.0007	smeltc	snowmelt coefficient (m oC-1 d-1))

0.2	d_one	maximum water holding capacity of top soil layer (m)
-0.033	swpmax	maximum soil water potential (MPa)
5	bsoil	soil parameter (dimensionless)
0.9	fout	resistance to drainage (proportion of outflow allowed each day)
0.581	ssr	soil field capacity as proportion of saturation (proportion)