9 SYMFOR Technical Note Series

An ecological model for the management of natural forests derived from the Tropenbos permanent sample plots at Pibiri, Guyana

June 2002

P.D. Phillips
P. van der Hout
E.J.M.M. Arets
R.J. Zagt
P.R. van Gardingen

Centre for the Study of Environmental Change and Sustainability (CECS)
The University of Edinburgh
John Muir Building
Mayfield Road
Edinburgh EH9 3JK
United Kingdom
Tel: +44 131 650 7860
Fax: +44 131 650 7863
Email: info@symfor.org
http://www.symfor.org/technial

DFID Department for International Development This publication is an output from a project funded through the Forestry Research Programme of the UK Department for International Development (DFID) for the benefit of developing countries. The views expressed are not necessarily those of DFID. R6915 Forestry Research Programme.

Summary

An ecological model describing the processes of growth, recruitment and mortality was developed using a dataset from permanent sample plots established at Demerara Timbers Limited at Pibiri, in central Guyana by the Tropenbos-Guyana Programme. The model was implemented in the SYMFOR framework and calibrated and tested with simulations of primary forest dynamics.

This document describes the data and development of the model, including species groups and the sub models for growth, recruitment and mortality. These were integrated within the SYMFOR framework for evaluation and application. Results of typical simulations are presented as to enable assessment of the performance of the model.

This document is intended to document the process of model development in such a way that would facilitate the development of similar models for other areas, forest types or applications.

The full text of this document is available from http://www.symfor.org/technical/pibiri.pdf.

Contents

1 Introduction

Sustainable forest management requires knowledge of the impacts of management on future forest structure and composition. Acquisition of such knowledge often requires the application of a detailed, flexible modelling system calibrated for the local region. Prediction by experience gained in-situ or in comparable conditions elsewhere, or by yield projection methods, is often not possible because of the novelty of management systems and the differences between different areas of tropical forest.

SYMFOR is a software framework for ecological and management models relating to mixed tropical forests (Phillips and van Gardingen, 2001a). It uses Permanent Sample Plot (PSP) data to simulate processes in the forest at the level of individual trees. This enables predictions to be made regarding the future of the forest under scenarios for which field data do not necessarily exist. Models within SYMFOR have been applied in Indonesia to establish the sustainability of alternative management scenarios (van Gardingen *et al*., 2001), and to test criteria and indicators of sustainability (van Gardingen and Phillips, 1998). Before this study, models such as this did not exist for Guyana, although suitable PSP data were available.

The demand for an individual-based growth and yield model for Guyana implemented within the SYMFOR framework was documented in previous reports for the DFID project R6915 (van Gardingen, 2001b, Phillips and van Gardingen, 2001b).

Two datasets were identified as being suitable for this analysis: the permanent sample plots (PSP) from Pibiri in the DTL concession in Central Guyana which are managed by the Tropenbos-Guyana Programme, and the PSP from the Barama Company Limited (BCL) concession in North-west Guyana. Previous studies (Alder, 2000; ter Steege, 2000) demonstrated that the two forests were distinct in terms of species composition, which led to the decision to model the two areas separately.

This report describes the models developed for the first area to be studied: the Tropenbos plots. The approach used was a similar sequence to that used for Indonesia (Phillips *et al*., 2002):

- Collation and assessment of data quality;
- Production of ecological species groups;
- Calibration of the diameter growth model component;
- Development and calibration the mortality and recruitment model components;
- Integrate the model components to form an ecological model for Pibiri in the SYMFOR framework; and
- Test the Pibiri ecological model against the assumption that primary forest doesn't change statistically with time.

The SYMFOR framework requires data describing the position of all trees above the minimum diameter at breast height (DBH) threshold. The Pibiri data could provide this for all trees above 20 cm DBH, whilst sub-samples were used for trees between 5 and 20 cm DBH. For this reason it was decided to develop a data generation process for trees of DBH between 5 and 20 cm so that these individuals could also be represented in the model.

2 Model description

2.1 Introduction

The ecological model was developed to be implemented in the SYMFOR framework (Phillips and van Gardingen, 2001a; 2001b). The model was developed to represent the processes of *diameter increment* (growth); *recruitment* (new trees appearing in the stand at the minimum diameter threshold of 5 cm); and *mortality* (death from natural causes). In addition, the model was required to produce initial data for trees with DBH from 5 to 20 cm based on statistical analysis of data from the Pibiri plots. The model was designed to run with an annual timestep. A summary of the model parameters and their implementation within SYMFOR is given in Appendix A.

2.2 Growth model

The form of the growth model was based on the ecological concept of competition for resources between trees. Growth was defined as a function of diameter (*D*) and a competition index. No further ecological criteria were applied in terms of the functional form of the growth equation.

The model used for the Pibiri data is a simplification of the version developed for Indonesia. The stochastic growth model implemented previously was shown to have no significant effect on the value or variance of predictions of yield or species composition of the forest, and has been omitted. The deterministic growth model has been simplified by the introduction of a diameter independent competition index.

The growth of individual trees *I* was described as the predicted diameter increment for a tree in a given year described by the equation (1):

$$I = D(a_0 + a_1 e^{-a_2 D}) + a_3 C + a_4 \tag{1}$$

where a_0, a_1, a_2, a_3, a_4 and a_5 are model parameters, *D* is the DBH of the tree. The diameter-independent competition index (*C,* eqn. 6) was devised to describe the competition environment for each individual tree in the plot.

An overtopping shade index was calculated for all trees with DBH greater than 20 cm for neighbours within a 30 m radius of the tree that have larger DBH (eqn. 2).

The over-topping shade-index *S* was defined, for tree *i*, as:

$$S = \sum_{j=1}^{n} \frac{D_j}{D_i d_{\mathrm{ij}}} \text{ where} (D_j > D_i) \text{and} (D_j > 20cm) \tag{2}$$

where there are *n* trees that have a DBH (D_{j}) larger than tree *i* within a radius of 30 m that tree (D_{j}) and d_{ij} is the distance in metres between the trees.

For small trees (*D* < 20 cm), this was combined with an index based on the number of over-topping small trees. This was defined, for tree *i*, as:

$$O = \text{count}\left[\text{if } (D_{\mathrm{k}} > D_i)\right] \text{ for } k = 1 \text{to } l; \text{where} D_i, D_k \le 20\,\text{cm} \tag{3}$$

where there are *l* trees within the same 10x10 m grid-square as tree *i* that have a diameter, D_{k}, larger than D_{i} for tree *i*.

These indices were combined to produce a diameter-dependent index (eqn. 4). This combined index had the properties of being a continuous function of diameter.

$$C_d = \begin{cases} S + O & \text{if } D_{\mathrm{i}} < 20 \\ S & \text{if } D_i \ge 20 \end{cases} \tag{4}$$

A diameter-independent competition index (C, eqn. 6) was derived by modelling the relationship between C_d and D (eqn. 5) and subtracting equation 5 from equation 4:

$$\hat{C}_\mathrm{d} = \frac{b_0}{b_1 + D} + b_2 \qquad (5)$$

$$C = C_\mathrm{d} - \hat{C}_\mathrm{d} \qquad (6)$$

2.3 Recruitment model

Models of recruitment describe the appearance of new trees in the simulation at or just above the minimum diameter threshold used in the model. The SYMFOR framework does not represent small individuals (seedlings and saplings) and for this reason the ecological processes of germination, growth and mortality of seedlings cannot currently be described. An alternative approach has been implemented where the probability of a new tree becoming established is described as a function of the environment within small gridsquares within the plot. The annual probability of recruitment (F) occurring in that grid-square was modelled as a function of the mean growth rate using equation 7:

$$F = r_1 e^{-r_2 I'} + r_3 I' + r_4 \qquad (7)$$

where r_1, r_2, r_3 and r_4 are parameters and I' is the predicted growth rate of a tree at a randomly selected location within the grid-square. The growth rate is predicted using the growth model described above (eqn. 1), for a tree with the same diameter as the minimum DBH threshold of 5 cm.

A model parameter, T_I, represents the time required for ingrowth as the number of years required for a tree to grow from seed to a DBH of 5 cm. It is used in the simulation when an area of ground is cleared of seedlings, for example when the soil surface is damaged during log extraction.

2.4 Mortality model

Natural mortality (M) was described as a stochastic process dependent on diameter. For trees with diameter less than 12.5 cm the mortality probability used is a constant value given by the parameter m_0. For trees with diameter greater than 12.5 cm the equation used calculate natural mortality probability, P, was:

$$M = \begin{cases} m_0 & \text{if} \quad D < 12.5 \\ m_1 e^{m_2 (D-12.5)} + m_3 (D - 12.5) + m_4 & \text{if} \quad 12.5 \le D < D_{95} \\ m_1 e^{m_2 (D_{95}-12.5)} + m_3 (D_{95} - 12.5) + m_4 + m_5 (D - D_{95}) & \text{if} \quad D_{95} \le D \end{cases} \qquad (8)$$

where m_1, m_2, m_3, m_4 and m_5 are parameters, D_{95} is the 95-percentile value of the diameter probability distribution and D is the diameter of the tree in cm. The basis for this approach is discussed later (see section 3.6).

Simulated falling trees cause simulated damage and mortality to the surrounding trees as in other SYMFOR models (Phillips *et al.*, 2002). This involves the stochastic determination of the direction of fall, leading to an area in which trees may be subject to damage, and the application of a stochastic model to determine whether damage (and mortality) actually occur in a given instance.

2.5 Small tree data generation

The parameter n_t represents the number of trees per ha with in the range $5 \le D < 20$ cm. At the start of each simulation, n_t trees are created at random locations within the plot. The location of each tree is checked so that its stem does not overlap with adjacent trees, and if it does a new position is selected. The diameter, D of the new tree is estimated to fit the probability distribution, Q, given by:

$$Q = e^{g(D-5)} \tag{9}$$

where g is the parameter describing the probability function.

2.6 Other functions

The SYMFOR framework required estimates of the dimensions of individual trees to simulate processes such as damage during harvesting. These are, total tree height H, crown-point height C_P and crown-radius C_R. The basal area, B and volume, V of individual trees is required for the management model and analysis of results from simulations. All of these attributes are derived for each tree from estimates of DBH D using auxiliary functions.

Tree height, H, is calculated by an inverse linear relationship with DBH, D:

$$H = \frac{sDH_{\mathrm{m}}}{sD + H_{\mathrm{m}}} \tag{10}$$

where s has a value 200 and H_{M} represents maximum tree height with a value of 45 m.

The "crown-point", C_P (m), of a tree was defined to be the height at which the tree has maximum crown width, calculated using a simple linear relationship with tree height, H (m):

$$C_{\mathrm{P}} = f_{\mathrm{C}} H \tag{11}$$

where the parameter f_{C} has the value 0.55.

The calculation of tree stem basal area, B, assumes that the stem cross-section is circular. Thus:

$$B = \frac{\pi}{4} D^2 \tag{12}$$

The coefficients and assumptions made in equations 10 – 12 are derived from anecdotal experience since data are not available for rigorous calibration.

Stem volume, V, is calculated as a function of basal area, B, using the equation:

$$V = f_{\mathrm{V}} B \tag{13}$$

where f_{V} is a parameter with the value 12.8 for Guyana (Alder 2001).

3 Calibration

3.1 Introduction

Calibration is the process of calculating or estimating values for the parameters used in the model for a particular region or type of forest. Data from the Pibiri permanent sample plots were used to calibrate the model.

The species described in the data were grouped into ten ecological species groups for three reasons:

1. To enable calibration of the model by reducing the number of taxa for which models were produced;
2. To enable calibration of the model by increasing the amount of data per taxa;
3. To enable the description of the forest in terms of ecological functional types.

One set of model parameters (Section 2) were produced for each of the species groups.

3.2 Data

The plot layout and data collection are described elsewhere (van der Hout, 2000), and only a summary is presented here. The Tropenbos data comprise 15 plots, each 140 m by 140 m located at Pibiri in the Demarara Timbers Limited forest concession in Central Guyana, South America. The soils in this area are principally brown sands with some white sands and pegasse/alluvium. The plots are located within 2 km of each other, in three groups. Four experimental treatments were applied plus one control. The 15 plots were established in three blocks of five, with each experiment treatment applied to one plot per block.

All trees with a Diameter at Breast Height (DBH) greater than 20 cm were recorded in each sample plot. For these trees, the tree number, DBH, position (x and y co-ordinates) and species (local name and scientific name) were recorded. Other data, regarding specific details of the tree (such as crown shape, damage, etc) were also recorded. The plots were divided into 20 m by 20 m sub-plots. Data for trees with DBH between 5 and 20 cm were recorded in the sub-plots in the south-west 10 m by 10 m quadrant. The same data were recorded as for larger trees, with the exception of tree position.

3.3 Species groups

In order to group the species, it was necessary to assess the population density for each taxon recorded in the data set. Table 1 shows that only 21 taxa were represented by more than 100 trees. This number progressively increased as the minimum number of trees decreased.

Minimum number of trees	Number of taxa	Number of trees	% of sample
100	21	7124	74
50	38	8235	86
10	102	9315	97
1	181	9634	100

Table 1 Minimum number of trees in a taxon for the Pibiri permanent sample plots.

The process for grouping species involved three stages: (1) a clustering analysis to make the groups using the most populous species; (2) discriminant analysis to add the less populous species to the existing groups; and (3) a subjective stage where species with little or no data were assigned to the groups.

Clustering analysis of populous species

For each species, a set of variables was produced:

- Average growth rate at low competition;
- Average growth rate at medium competition;
- Average growth rate at high competition;
- Average growth rate of new recruits (DBH of 5-6 cm);
- D_{95}, the 95-percentile point in the DBH frequency distribution (as an index of mortality behaviour).

Growth rates were evaluated for each of the measurement intervals: 1993-1995, 1995-1997, 1997-2000. The measurement interval was calculated from the survey date contained in the data. Negative diameter increment observations, and thus negative growth rates, were not rejected or altered except where an obvious error was observed as detailed in the section "analysis of growth".

Low and high competition levels were specified using the diameter-independent competition index C (eqn. 6) The parameters b_0, b_1 and b_2 were evaluated by regression, and found to be 176 ± 2, -0.01 ± 0.05 and –3.1 ± 0.1 respectively. Values of C above 1.0 were classed as being *high competition*, and values below –1.0 were classed as being *low competition*, with *medium competition* being defined between these values ($-1<C\leq1$).

The 21 data points arising from the taxa with more than 100 observations were insufficient to form groups as many groups would have contained just one species. The grouping process thus used taxa with at least 50 trees, giving 38 species (Table 1). Data were evaluated for these species, and normalised so that the range of each variable was from 0.0 to 1.0. A clustering procedure was then used to group the species according to the normalised variable values. There were 22179 growth measurements in the data following cleaning. The 38 taxa that had at least 50 trees recorded in the data that were used for making groups accounted for 19240 growth measurements.

The clustering process requires the user to decide how many groups there should be in advance. Ten groups were used to define the initial grouping to be consistent with previous studies (Phillips *et al.*, 2001). The groups and their normalised variables were then examined. The production of 10 groups was able to separate species with extreme ecological characteristics, and discriminated between the species at opposite ends of the range of characteristic values. The number of groups was retained for the next step of the species grouping process.

The discriminant analysis: for less populous species

Remaining ungrouped species with a minimum of 20 observations were added to the existing groups using discriminant analysis. The data from the existing groups were used as training data to initialise this process. The characteristics used to define groups were the 95 percentile point on the cumulative DBH distribution and the mean growth rate.

The 24 taxa that had at least 20 and less than 50 trees in the data, account for 1403 growth measurements. After this process, 20643 growth observations could be assigned to one of 10 species groups (62 taxa).

Two taxa (Kaditiri and Burada) were not assigned to groups by the discriminant analysis:

- Kaditiri has a mean growth rate of 1.17 +- 0.13 cm yr^{-1} (31 observations) and a 95 percentile point of DBH of 57 (21 observations);
- Burada has a mean growth rate of 0.45 +- 0.03 cm yr^{-1} (80 observations), and a 95 percentile point of DBH of 78 (36 observations).

It was not practical to create new groups for these taxa because they represented only 57 trees in the entire dataset, which would not be enough to calibrate the model. It was decided to manually add these taxa to the nearest groups for the given mean growth rate and 95 percentile point on the DBH distribution. This resulted in Kaditiri being added to the Crabwood group (group 10), and Burada being added to the Swamp Baromalli / Morabukea /Yaruru group (group 7),.

Adding the remaining taxa to groups

The remaining taxa were grouped using a second discriminant analysis. The lack of data for these groups resulted in the 95 percentile point of DBH and mean growth rate being associated with large uncertainties. These data were used in the absence of alternative published sources of information.

Eight taxa were represented by only one measurement survey and could not be grouped by the second discriminant analysis. “Devil's ear” had large individuals and was added to group 7 (with Swamp Baromalli). The other seven taxa were added to group 1.

There were 22179 growth measurements in data. The 119 taxa with less than 20 trees in the data that were added to existing groups, accounted for 1536 growth measurements and 725 trees. After this process, 22179 (all) growth observations were assigned to one of 10 species groups (181 taxa).

A summary of the species group characteristics is given as

Group	Name (reference)	D_{95}	$\bar{I}$	Light Preference	Dominant taxa	%
1	Small pioneers	35	0.24	Gaps	Warakosa, Trysil, Aiomorakushi	5.6
2	Medium-sized trees slow growing	45	0.18	Indifferent	Wirimiri, Sand Baromalli, Black Kakaralli	31.3
3	Small trees very slow growing	35	0.08	Indifferent	Adebero, Fine leaf Arara, Kakirio	6.4
4	Small trees slow growing	30	0.13	Indifferent	Waiaballi, Karishiri, Marishiballi, Kairiballi	23.4
5	Large slower growing trees	70	0.21	Indifferent	Greenheart, Soft Wallaba	16.1
6	Small trees faster growing	40	0.30	Gaps	Kereti, Silverballi, Moraballi	2.3
7	Large faster growing trees	70	0.32	Average	Morabukea, Yaruru	7.8
8	Very large fast growing shade loving trees	110	0.70	Shade	Parakusan, Purpleheart	1.7
9	Large very light intolerant trees	85	0.22	Shade	Kabukalli, Manyokinaballi	1.2
10	Medium-sized pioneers	50	0.47	Gaps	Crabwood, Kaditiri	4.2

Table 2 Description of the ten species groups derived from the Pibiri dataset._ D_{95} is the 95-percentile of the frequency distribution for diameter at breast height D, $\bar{I}$ is the mean diameter increment and % is the percentage of individuals in the dataset.

Vernacular	Group	Family	Species
Warakosa	1	Leguminosae/Mimosa.	*Inga spp.*
Trysil	1	Leguminosae/Mimosa.	*Pentaclethra macroloba (Willd.) Kuntze*
Aiomorakushi	1	Sapotaceae	*Pouteria cladantha Sandw. cf*
Wirimiri	2	Lecythidaceae	*Lecythis confertiflora (A.C. Smith) Mori*

Baromalli, sand	2	Bombacaceae	*Catostemma fragrans Benth.*
Kakaralli, black	2	Lecythidaceae	*Eschweilera sagotiana Miers*
Adebero	3	Violaceae	*Paypayrola guianensis Aubl. / P. longifolia Tul.*
Arara, fine leaf	3	Annonaceae	*Bocageopsis multiflora (Mart.) R.E. Fries*
Kakirio	3	Myrtaceae	*Calyptranthes forsteri O. Berg*
Waiaballi	4	Dichapetalacea	*Tapura guianensis Aubl.*
Karishiri	4	Annonaceae	*Oxandra asbeckii (Pulle) R.E. Fries*
Marishiballi	4	Chrysobalanaceae	*Licania cf. canescens Benoist*
Kairiballi	4	Chrysobalanaceae	*Licania heteromorpha Benth. var. perplexans Sandw.*
Greenheart	5	Lauraceae	*Chlorocardium rodiei (Schomb.) Rohwer, Richter & van der Werff*
Soft Wallaba	5	Leguminosae/Caesalp.	*Eperua falcata Aubl.*
Silverballi, Kereti	6	Lauraceae	*Ocotea puberula (Rich.) Nees*
Moraballi	6	Sapotaceae	*Pouteria coriacea (Pierre) Pierre*
Morabukea	7	Leguminosae/Caesalp.	*Mora gongrijpii (Kleinh.) Sandw.*
Yaruru	7	Apocynaceae	*Aspidosperma exselsum Benth.*
Parakusan	8	Leguminosae/Papillion.	*Swartzia jenmanii Sandw.*
Purpleheart	8	Leguminosae/Caesalp.	*Peltogyne venosa (Vahl) Benth. subsp. densiflora (Spruce ex Benth.) M.F. da Silva*
Kabukalli	9	Celastraceae	*Goupia glabra Aubl.*
Manyokinaballi	9	Apocynaceae	*Geissospermum sericeum (Sagot) Benth. & J.D. Hook.*
Crabwood	10	Meliaceae	*Carapa guianensis Aubl.*
Kaditiri	10	Leguminosae/Caesalp.	*Sclerolobium guianense Benth. var. guianense*

Table 3 The scientific names of the dominant species in each group, corresponding to the local (vernacular) names used elsewhere.

3.4 Growth model

The purpose of the growth model was to explain some of the variation of growth rate within each species group. The model was calibrated separately for each species group using multivariate regression. The amount of variation in the dataset that is explained by the model is described by the R^2 statistic (Table 4). When combined, the species grouping and the growth model together explained 22.3 % of the observed variation in the dataset. This value is similar to that obtained for most growth models in tropical forests. The residual variation in growth rates (77.6 %) was analysed to establish if any casual effects could be ascertained from the data. It appeared that the residuals were randomly distributed and it is assumed that this variation results from effects including measurement error, genetic effect and site specific effects and events such as pests, diseases and weather.

Group	a_0	a_1	a_2	a_3	a_4	R^2 (%)
1	-0.0081	0.0267	0.0169	-0.0293	0.024	7.0
2	0.0030	0.0297	0.0601	-0.0188	-0.058	3.5
3	-0.0014	-0.0524	0.1259	-0.0074	0.214	7.0
4	0.0031	0.0277	0.0814	-0.0130	-0.027	5.9
5	0.0021	0.0402	0.0522	-0.0189	-0.078	6.5
6	0.0054	0.0137	0.0224	-0.0351	-0.033	8.4
7	0.0017	0.0471	0.0310	-0.0272	-0.213	14.0
8	0.0064	0.0630	0.0312	-0.0400	-0.197	5.4
9	0.0019	0.0267	0.0309	-0.0212	-0.123	7.6
10	-0.0115	0.0390	0.0124	-0.0552	0.021	10.3

Table 4 Parameters for the Pibiri growth model (eqn. 1) and the associated goodness of fit R^2 (%).

3.5 Recruitment model

The probability of ingrowth was estimated at the scale of individual 10x10m gridsquares as a function of competition index *C*. The competition index was calculated for a "virtual" tree with *D* of 5 cm at the centre of each gridsquare. This was used to create a frequency distribution of the competition index for all gridsquares. The frequency distribution was generated using seven bins for competition index

Data from the permanent sample plots were analysed for each species group to record the number of gridsquares in which ingrowth was observed and its associated competition index. If more than one individual of a species group was observed, the gridsquare was recorded once for each individual. The probability of ingrowth *F* was calculated for observed data was calculated:

$$F = \frac{N_\mathrm{F}}{N_G} \tag{15}$$

where N_F is the number of gridsquares with recruitment and N_G is the total number of gridsquares within the stated competition index range. The probability of recruitment was modelled using equation 7 as a function of predicted growth rate *I'* calculated for each species group within a specified competition index bin. These data were then used to calibrate equation 7 using regression.

The data points used for regression (one for each combination of species group and competition index bin) were weighted by the total number of sub-plots in each growth rate bin giving the correct arithmetic mean.

The resulting regressions produced value for R^2 ranging from 8 to 92 % with the exception of group 9 which recorded no ingrowth. The parameters for group 9 were derived from those for species group 5 adjusted during the tuning of the model (Section 0).

No data were available to estimate T_I, the ingrowth time parameter. This was estimated for each species group from the mean observed diameter increment for trees in the 5-6 cm size class. The distribution of observed increments were not normally distributed and the value of the 75-percentile of I was used to calculate T_I:

$$T_I = \frac{5}{I_{75}} \tag{16}$$

The estimate is subject to a significant uncertainty since it is not based on data. Alternative methods of calculation, such as the mode or geometric mean would be equally applicable.

Group	r_1	r_2	r_3	r_4	R^2	T_I
1	5.728	0.240	1.361	-5.720	69.4	17
2	-11.680	0.379	-4.128	11.700	58.5	28
3	-0.573	-3.005	2.225	0.582	8.4	49
4	-15.130	0.307	-4.102	15.170	30.9	30
5	-1.367	0.665	-0.774	1.362	58.2	23
6	-2.956	0.165	-0.440	2.955	27.3	16
7	0.305	0.000	0.152	-0.295	76.7	27
8	-0.524	0.000	0.018	0.523	25.1	13
9	-0.548	0.665	-0.310	0.544	-	40
10	0.123	-1.042	-0.160	-0.120	91.5	7

Table 5 Parameter values for the recruitment model (eqn. 7)

3.6 Mortality model

The mortality probability was modelled as a function of diameter. The calibration was derived using the assumption that the diameter distribution for each species group in primary forest does not change with time.

Diameter frequency distributions were generated for each species using data from all plots from the 1993 survey. The distribution was grouped using a bin width of 7.5 cm. This approach fulfilled the requirement of having equal bin widths starting at 5 cm and having a boundary at 20 cm, in order to use all the data and correctly handle the reduced sampling area for trees with DBH < 20 cm. The mean value of D was used to describe each bin rather than the mid-point as the distribution was not linear. The contents of the first two bins ($D < 20$ cm) were multiplied by 7.84 to compensate for the smaller sampling area (0.25 ha compared to 1.96 ha for the larger trees).

The shape of the size class distribution was modelled for each species group as a function of mean DBH $\overline{D}$:

$$N_L = p_0 e^{-p_1(\overline{D}-5)} + p_2 e^{-p_3(\overline{D}-5)} \tag{17}$$

where N_L is the number of live trees in a size class and p_0, p_1, p_2 and p_3 are constants evaluated by regression.

A typical DBH frequency distribution is classically referred to as an “inverse-J” distribution which can be modelled by a negative exponential functional. Several of the species groups in the Pibiri dataset exhibited more complex distributions (e.g., groups 5, 7 and 8), and a combination of two negative exponentials was required to model these groups.

The probability of mortality was calculated for each combination of species group and diameter size class. The assumption was made that the mortality probability is the same as the fractional decrease in numbers of live trees within a size-class, when that size-class experiences one year's growth, required to maintain the diameter distribution. The growth equation (1) was applied to the mean DBH ($\overline{D}$) using a value of zero for the competition index C to predict the mean diameter of the size class after one years' growth ($\overline{D'}_{t+1}$). The probability of mortality, M, was then calculated, for each species group and diameter size class, as:

$$M = \frac{\overline{D} - \overline{D'}_{t+1}}{\overline{D}} \tag{18}$$

The probability distribution of natural mortality with diameter for each species group was modelled using equation 8 and the values of parameters evaluated by regression. Parameter m_0 represents the probability calculated for the smallest diameter class. Parameter D_{95} represents the 95-percentile point in the DBH distribution. Parameter m_5 was evaluated by tuning the model to meet the requirement of dynamic equilibrium in unlogged primary forest.

Group	m_0	m_1	m_2	m_3	m_4	m_5	D_{95}	R^2 (%)
1	1.23	-8.95	0.028	-0.157	11.06	0.15	26.0	100.0
2	2.00	22.71	0.003	0.065	-21.2	0.10	39.0	49.1
3	2.50	2.15	0.139	0.010	0.0	0.02	16.0	99.0
4	3.00	24.44	0.006	0.134	-21.76	0.05	20.0	67.6
5	0.90	23.89	0.004	0.067	-22.72	0.05	62.0	98.7
6	1.90	-0.90	0.000	0.043	1.7	0.30	36.0	99.4
7	5.63	-1.37	0.090	-0.017	2.13	0.02	57.0	99.6
8	3.23	6.88	0.054	0.008	-0.2	0.20	96.0	97.2
9	0.98	1.74	0.317	-0.003	0.82	0.15	66.0	99.8
10	5.00	-10.50	0.021	-0.121	12.24	0.15	39.0	100.0

Table 6 Parameters for the mortality model, equation 8.

Removing damaged trees

The death of trees damaged by other trees dying and falling in the SYMFOR framework is simulated independently from natural mortality. The analysis of mortality data from the permanent sample plots indicated that 632 trees died from natural mortality and an additional 86 died from being damaged by other falling trees. There was, however, some ambiguity relating to the interpretation of the codes in the dataset.

The method of representing damage in the SYMFOR framework for the Pibiri data was the same as had been developed for Indonesia. The damage probabilities were scaled so that only 1/3 as much damage was simulated. This decision was supported by the PSP data and also by anecdotal evidence from field visits following logging (Bird, 2001).

3.7 Small tree data generation

Data representing small trees (5-20 cm) were generated for the model using equation 9. This equation was calibrated by generating a diameter frequency distribution for each species group for the sub-plots containing trees in the 5-20 cm size class. A frequency distribution of DBH was generated using data from 10 of the 15 plots. The other five plots were retained for validation of the procedure. The frequency distribution was generated using 3 cm size classes to generate 5 bins in the 5 to 20 cm range for each species group. The analysis utilised data from the 1993 survey as these data represented unlogged primary forest. The parameter

g was determined by regression. The total number of trees per hectare of each species group (n_t) in the size class of 5 to 20 cm was determined as the average from the 10 plots used in the size class distribution.

Group	g	n_t
1	0.117	42
2	0.125	145
3	0.352	133
4	0.227	326
5	0.07	37
6	0.287	16
7	0.388	56
8	0.086	5
9	0.418	6
10	0.267	14

Table 7 Parameters used in the generation of small trees ($5 \leq D < 20$ cm) using equation 9.

3.8 Evaluating and tuning the model

The Pibiri model described above was implemented in SYMFOR framework. The model was tested using data from primary forest using the hypothesis that such forest should remain in dynamic equilibrium. This hypothesis was used as a basis to evaluate and tune the parameters of the model.

Initial evaluation

The parameters that were varied as a result of this process were those considered to have the largest uncertainty resulting from the process of calibration:

- Mortality probability slope parameter for trees with large DBH values (m_5);
- Mortality probability for small trees (m_0);
- Mortality probability constant component (m_4); and
- The overall recruitment probability (r_1, r_3 and r_4: scaled together by the same amount).

Changes to these parameters were made incrementally over many repeated simulations. The parameters of the model demonstrated significant interactions often resulting from the underlying ecological nature of the model.

The performance of the model was evaluated using descriptive data output by the model at intervals during an extended simulation of 350 years. The basal area and number of stems within a species group were used to evaluate the model. It was expected that whilst these values would vary with time in individual simulations, but that the mean of many simulations over time would be expected to remain unchanged.

Initial analysis of the model demonstrated that some of the parameters needed to be altered in order to achieve adequate performance. Selected model parameters were modified (tuned) to improve performance in order to demonstrate a dynamic equilibrium in primary forest.

It was necessary to generate recruitment parameters for species group 9 because there were no data available for the initial calibration. In addition the rates of mortality of small trees had to be increased.

Tuning parameters.

There were no data describing the ingrowth of species group 9. The initial evaluation of the recruitment model component used the same parameter values as group 5 as these groups have similar ecological characteristics representing slow-growing, large trees. The values of parameters r_1, r_2, r_3, and r_4 were adjusted for group 9 during the tuning process until satisfactory performance was obtained with the values shown in Table 5.

The mortality sub-models needed to be adjusted to maintain the observed species composition over time. Small trees dominate the number of individuals in each species group. The mortality rate for small trees m_0 in equation 8 was adjusted for each species group. The parameters m_1, m_3 and m_4 also had to be adjusted to balance the changes in m_0.

The model parameters shown in Tables 4 and 5 show the values after these modifications.

4 Discussion

The characteristics of the Pibiri model are discussed in terms of the characteristics of the species groups derived from the data and a series of figures demonstrating the performance of the resulting model in primary forest and after simulated logging.

4.1 Species analysis.

The derivation of species groups (Table 2) used taxa based on local species names. Some of the more significant taxa are discussed here.

- Greenheart was the largest taxon with 1190 trees representing 14.4 % of the population. This taxa showed no light preference for recruitment and formed species group 5 representing large slow growing trees and comprised 16.1 % of the population. Greenheart dominated this species group.
- Wirimiri (951 trees, 11.5 % of the population) and Sand Baromalli (682 trees, 8.3 % of the population) formed the basis of group 2 characterised by medium sized, slow growing trees. The resulting group was the most populous in the data comprising 31.3 % of the population.
- Group 4 was the second largest species group representing 23.4 % of the population and was characterised by small slow growing trees. This group was dominated by Adebero, Waiaballi and Karishiri.
- The largest trees in the forest were described by species group 8 which was dominated by Purpleheart (53 trees, 0.6 % of the population) and Parakusan (57 trees, 0.7 % of the population). Small trees of these taxa were found mainly under dense canopy, although that may not be representative of the habitat where germination, establishment and early growth usually take place.
- The shade demanding species (Group 9) grew very slowly in gaps but much better under dense canopy. This group contained smaller trees than group 8 and was dominated by Kabukalli with 52 trees or 0.6 % of the population. Interestingly, field experts have observed Kabukalli to exhibit pioneer characteristics when young, although the growth data suggest that it grows faster in shaded conditions when larger.
- Crabwood with 317 trees or 3.8 % of the population were the fastest growing species found in canopy gaps and dominated species group 10 for medium sized pioneers.
- Small pioneers were in group 1 which was dominated by the taxa, Warakosa, Trysil and Aiomorakushi.
- Species groups 3 and 6 contained a variety of small sub-canopy trees, with the faster growing species in group 6.
- Species group 7 contained the remaining large trees.

The ecological characteristics of the species and resulting species groups could be interpreted as representing the ecological characteristics of various ecological functional types, including pioneer, canopy emergent, sub-canopy, light demanding, and shade tolerant species.

4.2 Simulations of primary (unlogged) and logged forest.

The Pibiri model was tested in the SYMFOR framework. These applications are illustrated here.

The predicted growth rates for each species group are shown as Figure 1. Groups 1-5 and 9 are slow growing species. The highest growth rates were predicted for group 8 which is dominated by Purpleheart. Maximum growth rates for most species were observed at stem diameters of less than 40 cm.

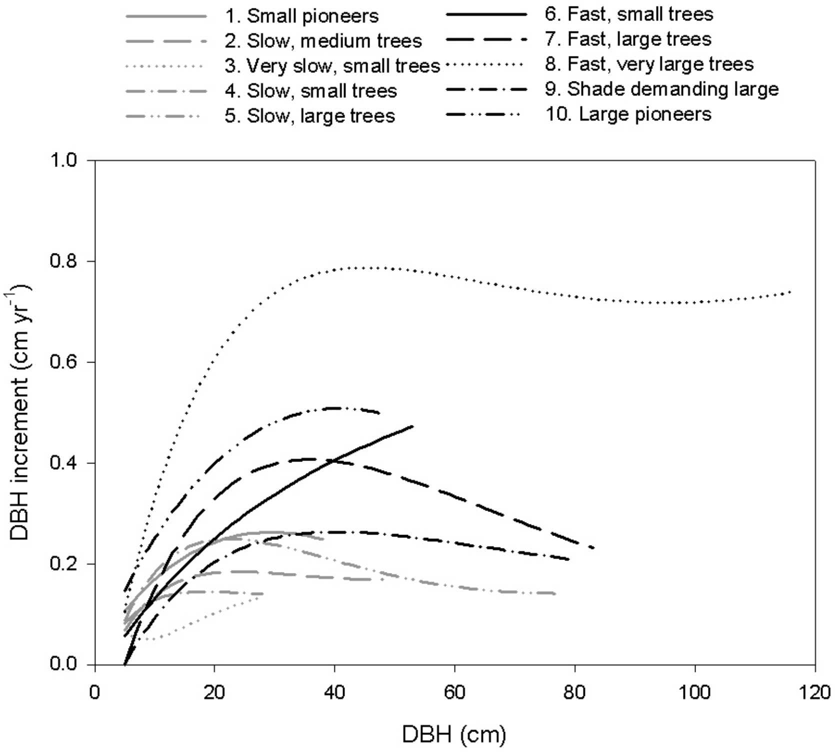

Figure 1 Predicted growth rates as a function of DBH. These rates were calculated for average competition (C = 0). The values are shown for the range from the minimum diameter of 5 cm up to the 99 percentile of the diameter frequency distribution for each species group.

The performance of the model was assessed by examining changes in the basal area and number of stems in each species group over time for unlogged primary forest. Figure 2 shows one example simulation reporting the total basal area of the plot (all species groups,). The total basal area shows some interannual variability, but the trend is that total basal area remains relatively constant.

Ecological models interact with management models in the SYMFOR framework. The purpose of the framework is to provide a tool to support analysis of management and policy options for tropical forests. A simple logging treatment was simulated in the SYMFOR framework by simulating logging of the twenty largest trees in the one hectare plot, with the associated damage to the residual stand. It should be noted that this level of extraction is more severe than current management practice in Guyana and was chosen to demonstrate the ecological response to a severe disturbance. Management practice, the effect of markets and yield regulation are not the subjects of this report, and have not been addressed. The simulation was performed 10 times on each of 6 plots from the 1993 survey of the Pibiri site: 2, 3, 7, 8, 12 and 13. 500 years of forest development following a single logging operation in the first year.

Figure 2 Variation in total basal area with time for 1 ha of unlogged primary forest, in a single simulation. No management interventions were simulated. This figure was taken directly from the time-series plotter in SYMFOR.

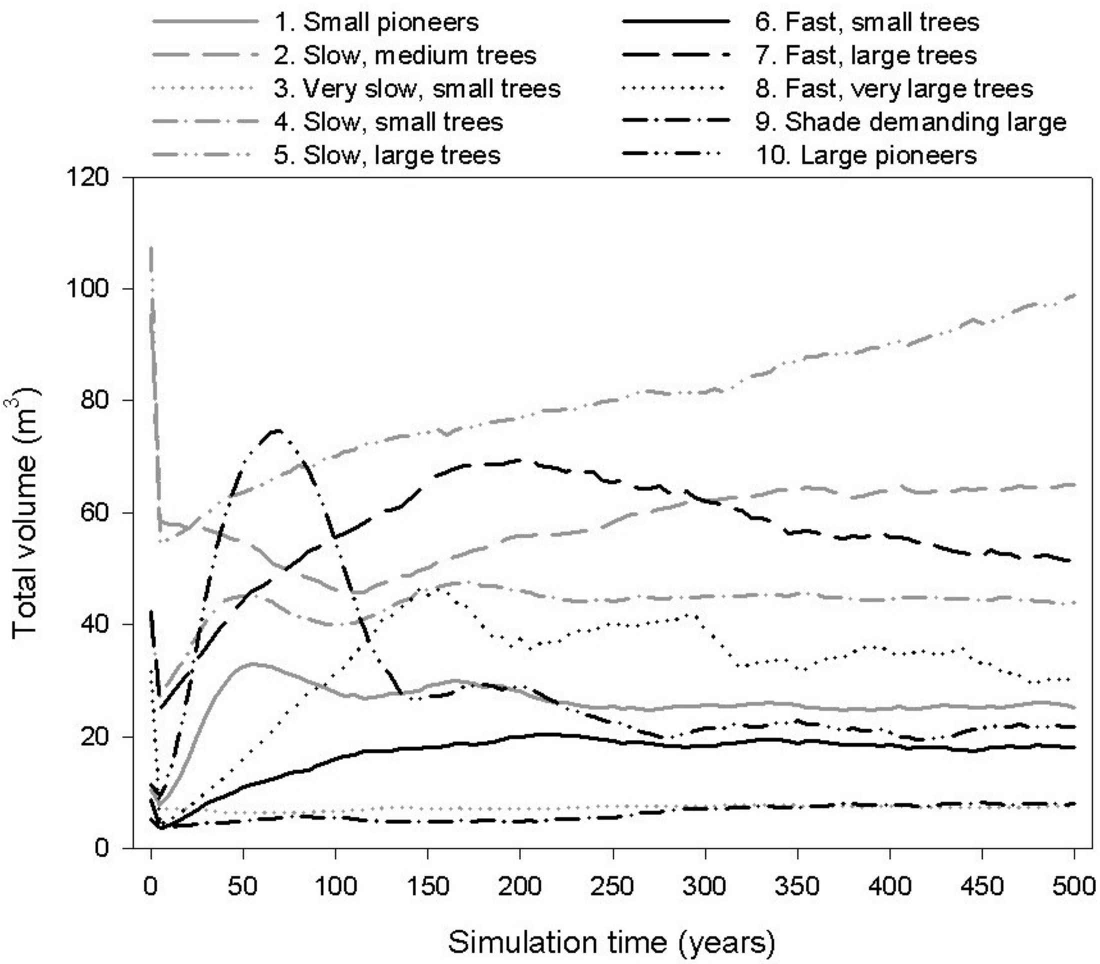

Figure 3 The sum of volume over all trees of each species group against time, showing forest development after logging. The figure shows the mean results over all 10 repetitions of simulations on each of 6 plots. A dynamic equilibrium, in terms of species composition and size distributions, has almost been established, albeit after 500 years.

The simulation predicted that very significant changes in species composition can be expected following heavy logging of this forest type. The total volume (Figure 3) and number of stems (Figure 4) of each species group and balance between groups changed significantly following logging. The time required to reach a new equilibrium between the groups is predicted to exceed 500 years, although the total number of trees of each species group stabilises after less than 250 years. This is more than twice the length of time compared to forests in Southeast Asia using similar analysis with the East Kalimantan model in the SYMFOR framework. The reason for this difference is related to the complex interactions between recruitment, growth, mortality and competition, but is likely to be dominated by the much lower annual growth rates observed in Guyana.

During these simulations and their subsequent analysis, it was noted that there exists significant differences between the plots in terms of species composition. For this reason all simulation studies should be based on multiple simulations using a range of plots.

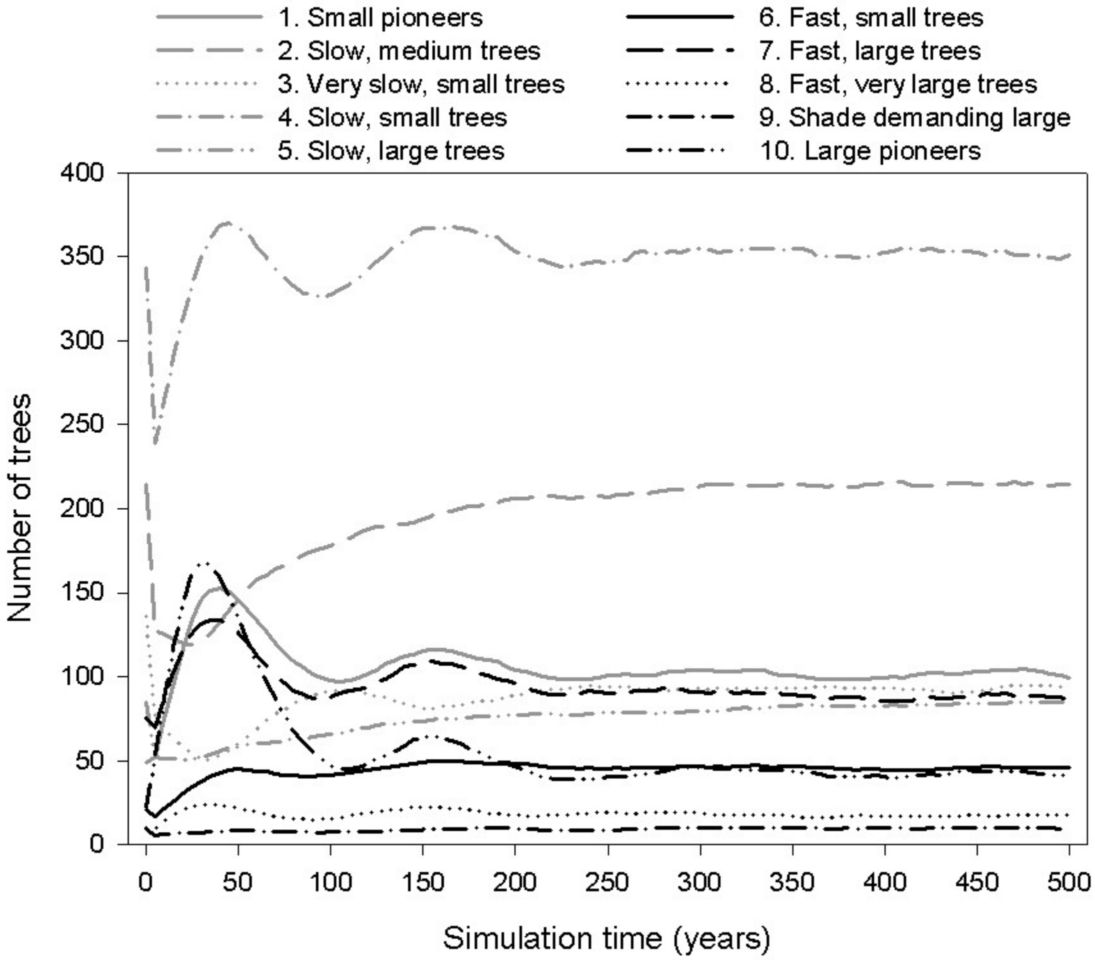

Figure 4 The number of trees of each species group against time, showing forest development after logging. The figure shows the mean results over all 10 repetitions of simulations on each of 6 plots.

5 Assumptions and limitations

5.1 Assumptions

This section describes the assumptions required for the development and implementation of the Pibiri ecological model described in this document. Other models within the SYMFOR framework, including management models, that have their own associated assumptions that are not described here.

For many of the assumptions, their accuracy is not quantifiable, or even meangingful. Even if it were, quantifying it would not quantify the impact of making the assumption on model results (the relationship is not often linear or simple). Their effect on model results contributes to the systematic uncertainty associated with the results, but can be extremely difficult to quantify; while parameter values may be altered to test their effect, this is not usually possible for model assumptions (Phillips *et al.*, 2002).

Extremely few modellers present their assumptions, because it opens up a very large and messy can of worms. It invites critics to hit at the weak spots of the model, and discredit results. The correct approach is a balance between the two, by estimating the systematic error associated with the assumptions. This is very difficult, and must be done for each application of the model separately, because it depends on the starting conditions and management model scenarios used, as well as the results that are quoted. Approaches may be used to minimise the effect of such systematic errors, for example by comparisons of two alternative scenarios; the systematic errors will be very similar for the two scenarios, and will largely cancel out. Otherwise, qualitative statements may be used to account for the effects of the assumptions on model results.

Data generation

1. The number of small trees in each species group with DBH in the range of 5 to 20 cm is the same in every plot at the start of a simulation;
2. The small trees with DBH from 5 cm to 20 cm are established at random locations within the plot at the start of each simulation;

Growth model

3. Trees grow deterministically as a function of their species group, diameter and competition environment;
4. Trees cannot decrease in stem diameter;
5. Competition is only caused by larger neighbouring trees within a 30 m radius of the tree;
6. No competition is experienced by a tree from neighbouring trees that are more than 30 m away;
7. Competition does not increase as a function of distance to a neighbouring tree for distances less than 3 m;
8. Small trees with diameters of less than 20 cm only produce competition for other trees in the same 10x10m grid square. This competition is density dependant and not related to distance;

Recruitment model

9. The probability of recruitment is a function of predicted growth rate;
10. The probability of recruitment may be non-zero even when the predicted growth rate is zero;
11. Seedlings and saplings with a diameter between 0 cm and 5 cm grow with the same diameter increment as trees with a DBH between 5 cm and 6 cm;
12. A constant supply of seedlings exists for all species groups, except shortly after an area has been cleared (as part of a management process);

Mortality model

13. Mortality is stochastic (a random event), and is described as a function of species group and diameter;
14. The probability of a tree falling immediately after natural death is 50 %. All other trees are assumed to rot whilst standing and cause no additional damage to the residual stand;
15. The area under which damage may occur resulting from a falling tree is described by a kite-shape;
16. There are no catastrophic mortality events (drought, flood, hurricane, etc) described in the model, and the effects of such processes are captured in the mean rates of mortality;
17. Any mortality due to damage from falling trees or silvicultural activity occurs at the same time as the damage itself, with no time delay;

Other assumptions

18. The behaviour of all trees within a species group is specified in the same way;
19. Trees at the edge of the simulated plot interact with trees on the other side of the plot, through plot-wrapping;
20. All sites are equivalent, in terms of their ability to support tree species compositions and diameter distributions;
21. All sites are equivalent, in terms of their suitability and access for logging and other management activities;
22. Non-modelled phenomena (such as climate, the presence of climbers, pests, disease, watercourses, slope, soil-types, etc.) are constant over time and are the same as for the data used for calibration;
23. The calculations of stem basal area and volume assume that all trees are circular in cross-section;
24. The calculation of stem volume assumes that all trees have the same taper and volume to basal area ratios;

In a given simulated year, the forest processes are simulated in the following order: management, growth, mortality, recruitment.

5.2 Limitations

The model should only be applied to areas of forest with similar soils, species composition and tree density as the plots used to calibrate the Pibiri model. The rates of growth, recruitment and mortality should be similar to those observed in the Pibiri sample plots. In practice, this means primary or managed natural forests in the Guyana shield in north-eastern South America on the same soils as Pibiri.

The suitability of the model should be evaluated before it applied to new areas or forest types. Data from the new area should be compared with those used for calibration of the Pibiri model. The nature of the comparison will depend on whether repeated diameter measurements are available to estimate growth rates.

In all cases the user should compare:

- Stand basal area and volume
- Stand density
- Species composition by individual species and ecological species groups. This comparison should consider the number of stems in each taxa and their total basal area.

If repeated measurements are available from permanent sample plots, these should be used to calculate mean diameter increments for each species groups. These should be compared with the values reported in Table 4.

The method of comparison will need to be subjective and result in an assessment of how similar the new area is to the Pibiri plots used for calibration. In the absence of sufficient information for the above analysis, a more simple comparison should be made with whatever data is available, and suitable provisos appended to the description of any simulation results.

6 Conclusions

The Pibiri ecological model has been developed, calibrated and implemented within the SYMFOR framework. This implementation was then tested and tuned against the criteria that the structure of an unlogged primary forest should not change significantly with time.

The ecological species groupings and initial simulations with the model describe ecologically relevant characteristics and processes in the forest. The results indicate that this forest is characterised by relatively slow growing species and that this forest type requires very long periods to recover after major disturbance.

The model is suitable for use with data from Pibiri, Guyana, or other areas of similar forest. Subsequent distributions of SYMFOR will include this ecological model, which is called “Guyana-Pibiri”.

Applications of the model will be published separately.

7 Acknowledgement

The authors would like to acknowledge the staff of Guyana Forestry Commission, the DFID GFC-support project and Tropenbos-Guyana Programme for the provision of the data necessary for this work, assistance in data processing and their comments on the model.

8 References

Alder, D., 2000. Development of growth models for applications in Guyana. Technical report for the Guyana Forestry Commission Support Project, 47 pgs.

Bird, N., 2001. On: The low levels of natural damage observed in forests in Guyana. Pers. Comm.

Phillips, P.D., Brash, T.E., Yasman, I., Subagyo, P., van Gardingen, P.R., 2002. An individual-based spatially explicit tree growth model for forests in East Kalimantan (Indonesian Borneo). Ecol. Model. (in press).

Phillips, P.D., van Gardingen, P.R., 2001a. The SYMFOR Framework for Modelling the Effects of Silviculture on the Growth and Yield of Tropical Forests. In the proceedings of IUFRO 4.11 Conference: 'Forest Biometry, Modelling and Information Science', (Editor; K.Rennolls), University of Greenwich, 25-29 June 2001. 12 pages. http://cms1.gre.ac.uk/conferences/iufro/proceedings/

Phillips, P.D. and van Gardingen, P.R., 2001b. The SYMFOR framework for individual-based spatial ecological and silvicultural forest models. SYMFOR Technical Notes Series No. 8, The University of Edinburgh. http://www.symfor.org/technical/framework.pdf

Phillips, P.D., 2001. Development of Modelling Objectives, Guyana: Back to Office Report. The University of Edinburgh, Edinburgh, 30 pgs. http://www.symfor.org/btor/Guyana_jun01.pdf

ter Steege, H., 2000. Plant diversity in Guyana: with recommendations for a protected areas strategy. Tropenbos Series 18, Tropenbos Foundation, Wageningen, Netherlands.

van Gardingen, P.R., 2001a. Project Memorandum (Exit Strategy) FRP project R6915. The University of Edinburgh, Edinburgh, 89 pgs.

van Gardingen, P.R., 2001b. Partnership Building FRP Projects R6915, R7278, ZF0151: Back to Office Report. The University of Edinburgh. 90 pgs. http://www.symfor.org/btor/partnership_mar01.pdf

van Gardingen, P.R., McLeish, M.J., Phillips, P.D., Dadang Fadilah, Tyrie, G., Yasman, I., 2001. Timber yield, financial and ecological analysis of the sustainable management of logged-over Dipterocarp forests in Indonesian Borneo. For. Ecol. Man. (submitted).

van Gardingen, P.R. and Phillips, P.D., 1998. SYMFOR: a tool for sustainable forest management. In: Laumonier, Y., Proceedings of the EU_FIMP/INTAG international conference on data management and modelling using remote sensing and GIS for tropical forest land inventory, Jakarta, Indonesia, 473-490.

van der Hout, P., 2000. Pibiri Permanent Plots. Objectives, Design and Database Management. Tropenbos-Guyana Reports 2000-2, Georgetown, Guyana.

9 Appendix A – The model parameters

The following table shows the model parameters as described in the text, a summary of their usage, and the corresponding variable name in the SYMFOR computer program code.

Parameter	Name in SYMFOR	Usage
$a_0 – a_4$	p0 – p4 (species group)	Growth model coefficients
$b_0 – b_2$	dicomp1, dicomp2, dicomp3	Diameter-independent competition model coefficients
$r_1 – r_4$	i1 – i4 (species group)	Recruitment model coefficients
$m_0 – m_5$	b0 – b5 (species group)	Mortality model coefficients
D_{95}	p95 (species group)	An effective maximum tree DBH
7.5 cm	mbinwidth	The width of the smallest DBH bin for mortality modelling
T_I	ingrowthtime (species group)	The minimum time for a seed to reach a DBH of 5 cm
G	gendist (species group)	Coefficient in the model of DBH distribution for small trees
n_t	ntreesph (species group)	The number of trees per ha to be created at model initialisation
5 cm	dbhmin	The minimum DBH of trees to be created at model initialisation
20 cm	dbhfill	The maximum DBH of trees to be created at model initialisation
f_C	a (species group)	The fraction of tree height at which the crown begins
H_m	maxheight (species group)	The maximum height of a tree of any diameter
s	startslope (species group)	A coefficient in the equation relating height to DBH
f_V	formheight (species group)	The ratio of basal area to modelled timber volume