



An individual-based spatially explicit simulation model for strategic forest management planning in the eastern Amazon

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Abstract

A model to simulate the ecological processes of tree growth, mortality and recruitment, and the processes of forest management, in the *terra firme* forests of the eastern Amazon is described. It is implemented within the SYMFOR (<http://www.symfor.org>) framework. It is based on measurements of all trees that have a diameter greater than 5 cm from experimental plots in the Jarí Cellulose and Tapajós National Forest areas over a 16-year period. Ten species groups are used to describe the natural processes affecting tree behaviour. Growth rates are calculated for each species group using the tree diameter and a competition index. Mortality and recruitment are simulated as stochastic processes. Recruitment probability is based on the predicted growth rate of a hypothetical tree. Options exist to vary the human interaction with the forest reflecting forest management decisions, as for other SYMFOR models. Model evaluation compares the performance of the model with data describing forest recovery for 16 years following logging.

The model was applied to simulate current forest management practice in the Brazilian Amazon, with 40 m³ ha⁻¹ of timber extracted with a cutting cycle of 30 years. Results show that yields are sustained for three harvests following the first logging of primary forest, but that the composition of timber moves towards lightwooded species rather than hardwooded. The predicted size of extracted trees decreases and the number of trees extracted increases with successive harvests, leading to a prediction of increased costs and lower profits for the logging company despite constant yields. The standing volume of all trees just before harvest is reduced by 15% over 150 years, with pioneer species becoming increasingly prevalent in the stand.

The model, in the SYMFOR framework, can be used to help understand the differences between alternative forest management strategies in the Brazilian Amazon. Such knowledge is required to improve forest management, regulation and certification, and help to conserve the worlds largest remaining tropical forest.

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1. Introduction

The people, economy and ecology of forested areas are affected enormously by the management of their forests. As such, tropical forests play a crucial role in the livelihoods of millions of forest-dependent poor people worldwide. Timber yield from the forest gives short-term financial returns to those with the rights to harvest, but this must be balanced against long-term social, economic and environmental sustainability of all products and services from the forest, both now and in the future. It is necessary to have information describing the likely future state of forests given alternative management interventions, in order to make better-informed decisions and policy for sustainable and equitable forest management.

Natural tropical forests are complex ecosystems for which data often do not exist to adequately describe the long-term effects of alternative forest management strategies. Simulation tools that can represent the ecosystem, including the underlying processes involved in forest growth, regeneration and management that are required to predict attributes of managed tropical forests. These tools should be accessible to forest managers and policy makers, allowing them to evaluate aspects of simulated management relating to the forest. The tools should be capable of simulating currently implemented management scenarios as well as new practices that have no direct precedent.

Brazilian Amazonia represents the largest and most biologically diverse area of remaining natural tropical forest. Brazil's 544 million ha of forest is decreasing by 2.3 million ha per year (FAO, 2001), increasing the need for conservation or sustainable management. Increasingly, forest management in Brazil is becoming regulated and certified. The processes of regulation and certification use current knowledge and estimates to define limits and requirements for forest management strategies. Current knowledge is based on individual experience and field measurements, such as those of Silva et al. (1995, 1996), and while these have been extensive and valuable, they have not been able to establish the likely long-term effects of a given management strategy on the forest (FAO, 1997). There is a requirement for a simulation tool that can help to fill the knowledge gap to inform assessments of long-term sustainability.

1.1. Existing approaches

Few simulation models have been produced that describe dynamics of primary or selectively managed forests in Amazonian Brazil. Kammesheidt et al. (2002) and Finegan (1992) built models of secondary forest growth on agricultural land. Stone (1998) simulated timber extraction over a 10-year period for economic evaluation, but did not include tree growth models. Dale et al. (1994) model land-use practices, focusing on deforestation for agriculture. Only the CAFOGROM model (Alder, 1995; Alder and Silva, 2000) attempts to simulate tree growth for selectively managed forests in Eastern Amazonia.

CAFOGROM uses a cohort approach. These cohort models are not spatially explicit and do not account for the changes in growth environment caused by management intervention. They are able to make predictions of yield, but will have little sensitivity to the detail of alternative silviculture or management strategies, particularly in terms of levels of logging damage, spatial structures created in the forest and species composition change.

Vanclay (1994) introduces the range of model types produced for tropical forests. Phillips et al. (2003) describe other models that have been used to describe the growth, ecology and yield for tropical forests, and explain their reasons for choosing an individual-based spatially-explicit model form such as that of Gourlet-Fleury and Houllier (2000). Similar reasons apply in this study:

- the model is to be initialised with real data and applied to forest management scenarios, rather than for testing ecological hypotheses, so should be empirical and avoid complexity that does not improve the model (such as representations of tree physiology);
- the model must capture the differences between forest management strategies in terms of their effect on tree behaviour, so should be individual-based and spatially-explicit;
- the model must be capable of simulating effects over time periods longer than the life of a tree (which may be 10 years or less), so the species groups should be the same for all sub-models and the number of species groups should be limited (Phillips et al., 2001);

- the model form must be such that it can be calibrated from the data available (discussed later, in respect to competition index).

SYMFOR (Phillips and van Gardingen, 2001a,b) is a framework that combines models of forest ecology with models describing important elements of management treatments commonly recommended in selective logging of tropical forests. The SYMFOR framework uses a description of natural forest ecology in the form of an ecological model describing tree growth, mortality and seedling recruitment for each tree above a minimum diameter. The models are individual-based, meaning that each tree is considered separately on the basis of the unique conditions it experiences, and may be spatially explicit.

Such models are able to simulate with validity many forest management scenarios that were not described in the data used for calibration because the system simulates the conditions leading to forest state, rather than forest state itself. As long as the model is used within the range of conditions described by the calibration data, the model is valid. This is an advantage over more simplistic models such as CAFOGROM, although a compromise must be made over applicability of the models: they are too data-demanding to be directly applied at the scale of forest management operations because of the intensive data requirements and computational processing required, so are necessarily strategic planning tools for yield regulation and harvesting techniques.

This paper describes a model that is built in the SYMFOR framework using data from managed natural forests of the eastern Amazon and that has been applied to explore the effects of typical logging operations repeated every 30 years. It may be viewed as a companion to the paper describing the SYMFOR models developed using data from Indonesia (Phillips et al., 2003) and Guyana (Phillips et al., 2002). This paper is distinct in that it describes a model built using data from the eastern Amazon, with different ecology to Indonesia and Guyana, and applied to management scenarios currently typical of Brazil. The model is capable of significantly more advanced examinations of alternative management scenarios, and this paper presents the model as a tool, giving an example of its application.

2. Model description

2.1. Introduction

The ecological model described here was developed to be implemented in the SYMFOR framework (Phillips and van Gardingen, 2001a,b). The model was developed to represent the processes of *diameter increment* (tree growth), *recruitment* (new trees appearing in the stand at the minimum diameter threshold of 5 cm), and *mortality* (tree death from natural causes). These processes use a representation of competition in the form of a competition index, derived explicitly for each tree from the data describing the other trees. The model was designed to run with an annual timestep. The choice of form of the particular models was based on the data from which the models were developed. Detail was included only where it was justified by the data or by a well-documented process. In the following text, all probabilities and random numbers used in the model are within the range 0.0–1.0 unless otherwise stated.

2.2. Competition index

The competition index, C_t , for tree t , is calculated based on the grid-square location of the trees:

$$C_t = z_1 \sum_{i=1}^{n_1} \frac{D_i}{D_t} + z_2 \sum_{j=1}^{n_2} \frac{D_j}{D_t} + z_3 \sum_{k=1}^{n_3} \frac{D_k}{D_t} \quad (1)$$

where z_1 , z_2 and z_3 are the coefficients for the relative competition importance of zones 1, 2 and 3, respectively, i , j and k are the over-topping trees in the three zones, n_1 , n_2 and n_3 are the total number of over-topping trees in the three zones, and D is diameter of tree i , j , etc. Zone 1 is a 10 m × 10 m grid-square containing tree t , and zones 2 and 3 are defined relative to zone 1 as shown in Fig. 1. This approach allows the calculation of a spatial competition index for data where tree positions are known only to within a sub-plot, rather than with precise x and y coordinates.

Competition was modelled as a function of diameter (Eq. (2)), and the modelled value was then subtracted from the absolute value (Eq. (3)). This leads to a competition index symmetric about zero, and, on average, independent of tree diameter.

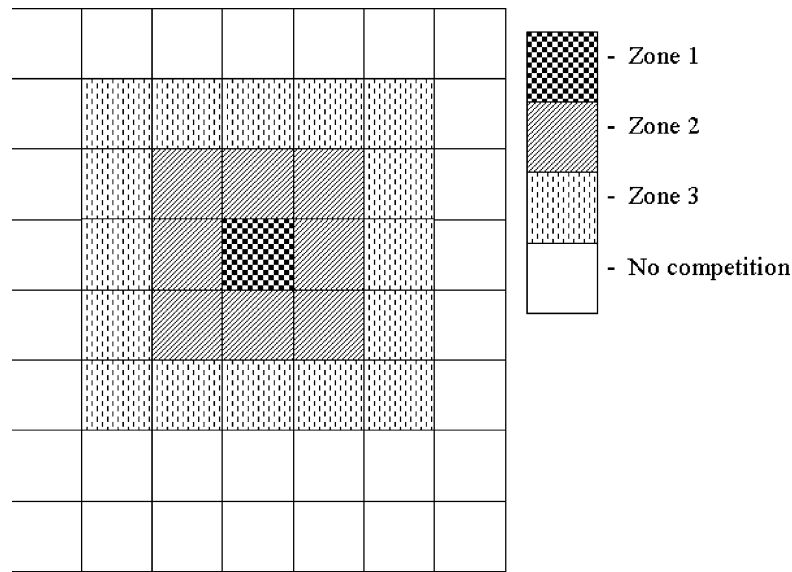


Fig. 1. The different zones of competition, for a tree in zone 1, using 10 m × 10 m grid-squares. The competition indices from these different zones may be combined in different ratios, leading to competition indices that depend differently on distance from the object tree.

The diameter-independent competition index, C , is calculated by the equations:

$$\hat{C}_t = \frac{b_0}{b_1 + D} + b_2 \quad (2)$$

$$C = C_t - \hat{C}_t \quad (3)$$

where \hat{C}_t is the predicted value of the competition index, C_t is calculated from the tree diameter, D , and b_0 , b_1 and b_2 , are parameters. The diameter-independent competition index, C , is the competition index used in the subsequent models.

2.3. 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 to define the form of the growth equation.

The model used for the Brazilian data is the same as that used for Guyana (Phillips et al., 2002), and a simplification of the version developed for Indonesia (Phillips et al., 2003).

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

$$I = D(a_0 + a_1 e^{-a_2 D}) + a_3 C + a_4 \quad (4)$$

where a_0 , a_1 , a_2 , a_3 , a_4 and a_5 are model parameters and D is the diameter at breast height (1.3 m, DBH) of the tree. The diameter-independent competition index, C (Eq. (3)), was devised to describe the competition environment for each individual tree in the plot.

2.4. 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) hence 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 grid-squares 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 the equation:

$$F = r_1 e^{-r_2 I} + r_3 \quad (5)$$

where r_1 , r_2 and r_3 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 (Eq. (4)), for a tree with the same diameter as the minimum DBH threshold of 5 cm.

A model parameter, T_1 , 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 mechanically scarified and compacted during log extraction.

2.5. Natural mortality model

Natural mortality (M) is modelled as a stochastic process dependent on diameter only, reflecting more limited data availability than for growth (see “data and model calibration”). The probability function, or its derivative, has discontinuities at two diameters above the minimum modelled diameter: b_d plus 5 cm (to represent increased mortality for smaller trees), and D_{95} , the 95-percentile value of the diameter probability distribution, to represent increased mortality for trees reaching their biophysical limit. The equation used calculate natural mortality probability, M , for a tree of diameter D (cm), was

$$M = \begin{cases} m_0 & \text{if } D < b_d + 5 \\ m_1 & \text{if } b_d + 5 \leq D < D_{95} \\ m_1 + m_2(D - D_{95}) & \text{if } D_{95} \leq D \end{cases} \quad (6)$$

where m_0 , m_1 and m_2 are parameters.

2.6. Damage mortality model

Simulated naturally falling trees cause simulated damage and associated mortality to the surrounding trees. This is not as in other SYMFOR models (Phillips et al., 2002, 2003), however, due to the abundance of lianas in Amazonian forests: the stochastic determination of the direction of a tree’s fall leads to an enlarged area in which all, rather than a proportion of, trees are

killed by damage. This increased damage represents the tangling effect of lianas in tree crowns.

The model only represents large trees falling, but, when they do, they create a large area of damage in which all trees are killed. The size and shape of the gaps would vary, in practice, but for modelling purposes a simplification is required. The basis for the resulting model was developed from data, and is described later. The area of damage represented by a rectangle is defined relative to the dimensions of the falling tree. The dimensions and shape are shown in Fig. 2 where the length of the area of damage is the tree height plus three times the crown radius and the width is four times the crown radius.

Damage resulting from trees being felled during harvesting is simulated in the same way as for trees

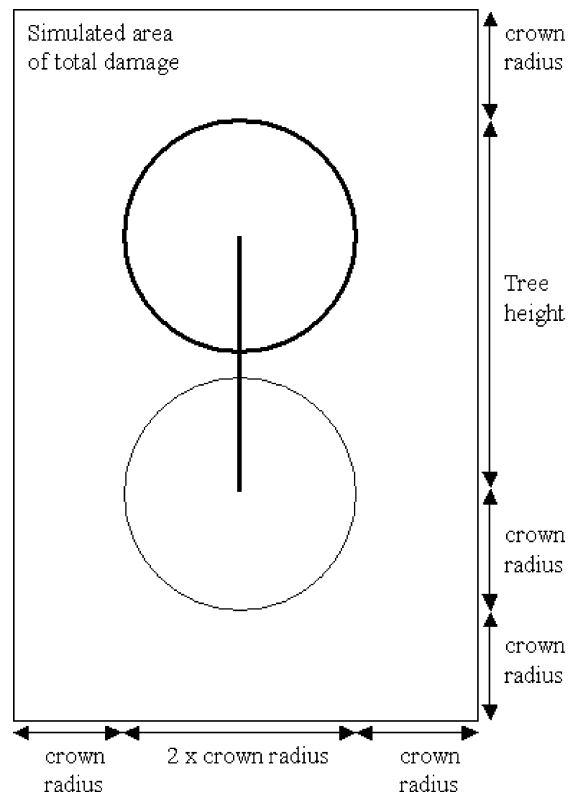


Fig. 2. The shape and dimensions of the rectangular area of damage created by the fall of a large tree: a rectangle with dimensions four times crown radius by three times crown radius plus tree height. The heavy lines represent the stem and crown of the tree in their positions after tree-fall, with the lighter circle representing the original position of the crown before tree fall.

with natural mortality if the user elects to simulate no liana cutting before logging. In contrast, if liana cutting before logging is selected, a smaller area of damage is created as a trapezium-shaped area using the same approach as defined in other SYMFOR models (Phillips et al., 2002, 2003). The trapezium has length equal to the height of the tree, and maximum width at the crown point, equal to the crown diameter.

2.7. Other functions

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

Total tree height, H , is calculated by an inverse linear relationship with DBH:

$$H = \frac{sDH_m}{sD + H_m} \quad (7)$$

where s has a value 200 and H_m represents maximum tree height with a value of 50 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):

$$C_P = f_C H \quad (8)$$

where the parameter f_C has the value 0.55.

The “crown-radius”, C_R (m), of a tree was defined to be the radius of the tree crown, which is assumed to be circular in cross-section, calculated using a relationship with DBH:

$$C_R = \left(\frac{10}{D} + \frac{1}{15} \right)^{-1} \quad (9)$$

The coefficients and assumptions made in Eqs. (7)–(9) are derived from anecdotal experience because data are not available for rigorous calibration.

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

$$B = \frac{\pi}{4} D^2 \quad (10)$$

Stem volume, V , is calculated as a function of diameter, D (cm), and crown-height, C_P , after Queiroz (1984) as

$$V = 0.5179 \times \left(\frac{D}{100} \right)^2 C_P + 0.0775 \quad (11)$$

3. Data and model calibration

3.1. Methodology

Calibration is the process of calculating or estimating values for the parameters used in the model for a particular region or type of forest. Empirical models are calibrated using regressions of real data. Data from the “Sistema de Inventario Continuo” (SFC) database, owned and designed by Embrapa, were used to calibrate the model.

3.2. Data

Details of the data are described by Silva et al. (1995). The environment is described by Silva et al. (1996). The plot layout and data collection information are held by Embrapa Amazonia Oriental.

PSP datasets have been recorded from forests in the Tapajós and Jari Cellulose lands in the State of Pará. Data have already been used to analyse the impact of logging on species composition, growth and forest structure (Silva et al., 1995), and for growth and yield studies (Silva et al., 1996). They were also used for the definition of species groups and growth functions of the growth model CAFOGROM (Alder, 1995; Alder and Silva, 2000).

The series of plots at Tapajós km 114 comprise 60 PSP, each of 0.25 ha. All trees with DBH greater than 5 cm were measured and the species and DBH recorded. The tree data includes information about which 10 m × 10 m sub-plot they are in, but no finer spatial resolution was recorded. Sub-samples were made for seedlings (taller than 30 cm) and saplings (DBH greater than 2.5 cm), but growth information is not available since individuals of these sizes were not marked. 48 of the plots were located in forest that

was logged-over in 1981, with five measurements made over the period 1981–1995. 12 of the plots are in unlogged forest, with four inventories made over the period 1983–1995.

The series of plots at Tapajós km 67 comprise 36 plots, each of 0.25 ha. They have the same design and inventories as the plots described above. The forest containing the plots was logged in 1979, with seven inventories made over the period 1981–1997. An analysis of these plots was made in 1994 by Silva et al. (1995).

The series of plots in Jari comprise 40 plots, each of 1 ha. All trees with a DBH greater than 20 cm DBH were inventoried, with DBH and species information recorded. The tree data includes information about which 10 m × 10 m sub-plot they are in, but no finer spatial resolution is held. 5% sub-samples were made for trees with DBH between 5 and 20 cm. 36 plots were logged in 1985, and 4 plots have not been logged. They were all measured six times over the period 1984–1996.

3.3. Competition model

The values used for the parameters z_1 , z_2 and z_3 (in Eq. (1)), calculating the absolute competition index for each tree, were 9, 4 and 1, respectively. These values were selected arbitrarily to represent the decrease in competition with increasing distance between trees.

The parameters in Eq. (2), the model of absolute competition index as a function of tree diameter, were evaluated by regression and are given in Table 1.

3.4. Species groups

The species described in the data were grouped into 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 were produced for each of the 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 2 shows that 85 taxa were represented by more than 100 trees.

The process for grouping species involved three stages, as performed by Phillips et al. (2001, 2002): (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.

For each species, a set of variables was produced:

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

Low and high competition levels were specified using the diameter-independent competition index C (Eq. (6)). Values of C above 40.0 were classed as being *high competition*, and values below -40.0 were classed as being *low competition*, with *medium competition* being defined between these values ($-40 < C \leq 40$).

Table 2 shows the number of taxa meeting different data thresholds. The grouping process used taxa with at least 50 trees, giving 103 species (40 species had

Table 1
The values of the parameters in the equation modelling absolute competition index as a function of diameter

Parameter	Value
b_0	6004
b_1	-1.580
b_2	-130.8

Table 2
Minimum number of trees in a taxon for the permanent sample plots

Minimum number of trees	Number of taxa	Number of trees	Percentage of sample
100	85	38848	81.6
50	143	43064	90.5
20	235	46107	96.9
1	485	47581	100.0

missing data for at least one of the six characteristic variables, and could not be included in the clustering analysis). Data were evaluated for these species, and normalised so that the range of values of each variable was from 0.0 to 1.0. A clustering procedure was then used to group the species according to the normalised values of variables 1–5 (above).

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, 2002). The groups and their normalised variables were then examined. The production of 10 groups was able to separate species with extreme ecological characteristics, and to discriminate between the species at opposite ends of the range of characteristic values. Varying the number of groups between 9 and 12 did not significantly affect the ability of the model to describe species behaviour, so the 10 groups were retained.

An alternative clustering process was applied using the values of variables 5 and 6 only, as used by Alder (1995). This process led to a similar result as for variables 1–5, and was adopted. It was not, and is not in general, necessarily the case that the simpler method used here would lead to equivalent results to the more rigorous approach, and thus the more rigorous approach is important.

Remaining ungrouped species 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 the groups and the species were the 95 percentile point on the cumulative DBH distribution and the mean growth rate (as for the clustering process). Group formation using the high-frequency species ensures that the distinction between species groups reflects real differences, by minimising the influence of anomalous data.

The species grouping process grouped 485 taxa into 10 groups, with average characteristics as given in Table 3.

3.5. 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 33.7% of the observed variation in the dataset.

The residual variation in growth rates (66.3%) was analysed to establish if any casual effects could be ascertained from the data. An estimate of the measurement uncertainty on any growth observation was made (using data from Indonesia: see Phillips et al., 2003), and found to be 0.3 cm. The variation that could be

Table 3
A summary of the characteristics of the species groups

Group name (reference)	P95	G	Dominant members	N_t	N_s
Slow growing mid-canopy	41.8	0.21	Sapotaceae, Lauraceae, <i>Guatteria poeppigiana</i>	8978	87
Slow growing understorey	15.9	0.09	<i>Rinorea flavescens</i> , <i>Duguetia echinophora</i> , <i>Talisia longifolia</i>	5964	48
Medium growing mid-canopy	57.2	0.29	<i>Geissospermum sericeum</i> , <i>Carapa guianensis</i> , <i>Pouteria</i> spp.	4851	76
Slow growing lower canopy	27.7	0.18	<i>Protium apiculatum</i> , <i>R. guianensis</i> , <i>Neea</i> spp.	11016	101
Medium growing upper canopy	72.5	0.26	<i>Couratari oblongifolia</i> , <i>Minuartia guianensis</i>	2732	34
Fast growing upper canopy	76	0.54	<i>Sclerolobium chrysophyllum</i> , <i>Trattinickia rhoifolia</i> , <i>Didymopanax morototoni</i>	1356	29
Fast growing pioneers	35.8	0.54	<i>Inga</i> spp., <i>Sloanea froesii</i> , <i>Bixa arborea</i> , <i>J. copaia</i>	8606	49
Emergents—climax	104	0.37	<i>Manilkara huberi</i> , <i>Goupia glabra</i> , <i>Hymenaea courbaril</i> , <i>Dipteryx odorata</i>	1409	36
Very fast growing pioneers	38.7	1.26	<i>Cecropia sciadophylla</i> , <i>J. leucoma</i> , <i>J. spinosa</i>	2007	9
Very fast growing upper canopy	78.2	0.94	<i>Tachigalia myrmecophylla</i> , <i>S. tinctorium</i>	662	16

P95 is the 95 percentile on the cumulative diameter frequency distribution (cm), G is the growth rate (cm per year), N_t is the number of trees, and N_s is the number of species in each group. It should be noted that the data that were used to produce include data from recently logged-over forest.

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

Group	a_0	a_1	a_2	a_3	a_4	R^2 (%)
1	0.0025	0.0077	0.0452	-0.0005	0.1174	4.9
2	0.0054	-0.0111	0.0504	-0.0002	0.1136	5.7
3	0.7447	-0.7389	-0.0001	-0.0007	0.1953	3.3
4	0.0041	0.0211	0.1590	-0.0005	0.1030	5.5
5	0.0014	0.0221	0.0291	-0.0004	0.0023	8.0
6	-0.0506	0.0811	0.0046	-0.0009	0.1523	14.4
7	2.2632	-2.2464	-0.0001	-0.0016	0.3680	13.0
8	-0.0029	-0.1747	0.1634	-0.0008	0.6001	9.2
9	0.0093	0.3329	0.0776	-0.0050	-0.4276	18.3
10	0.0065	0.0805	0.0287	-0.0011	-0.1354	15.9

explained by the measurement uncertainty was highly correlated to the mean growth rate of a species group: all of the remaining variation in growth rates of trees in slow growing species groups could be explained by measurement uncertainty, but not for species groups typified by high growth rates.

Lianas can be a dominant feature of Amazonian forests, sometimes with several on a single tree. They can grow to large diameters (10–20 cm). They grow up one tree, but then spread through the canopy.

The way that lianas affect tree growth and the process of gap formation and regeneration was tested. The data contained an index of infestation by lianas for each tree, with integer values 1–4. A simple model of the effect of lianas on growth rate was constructed, and could explain only 1% of the variation in growth rates. It was decided not to include a representation of liana infestation for the purposes of growth modelling, though other studies, with more detailed data, may find significant effects.

It appeared that the residuals from the growth model were randomly distributed and it is assumed that this variation results from effects including measurement error, the effect of lianas, genetic effect and site specific effects and events such as pests, diseases and weather.

3.6. Recruitment model

The probability of ingrowth was estimated at the scale of individual 10 m × 10 m grid-squares as a function of the diameter-independent competition index, C . The competition index was calculated for a hypothetical tree with D of 5 cm at the centre of each grid-square. This was used to calculate the pre-

dicted growth rate associated with a particular species group and grid-square, using the model calibrated for growth (Eq. (4), Section 3.5). The growth rate for all grid-squares was binned into a histogram (or frequency plot of growth rate classes) for each species group.

Data from the permanent sample plots from Tapajós (for which data about trees with DBH above 5 cm were recorded) were analysed for each species group to record the number of observations of ingrowth by grid-square, and hence the number of observations of ingrowth for each growth-rate class. The probability of ingrowth, F , was then calculated for each growth rate class for each species group:

$$F = \frac{N_F}{N_G} \quad (12)$$

where N_F is the number of observations of ingrowth and N_G is the number of grid-squares. The probability of recruitment was modelled for each species group by regression as a function of predicted growth rate, I , using Eq. (5). The data points used for regression (one for each combination of species group and growth rate bin) were weighted by the total number of grid-squares in each class to give the correct arithmetic mean.

The resulting regressions produced value for R^2 ranging from 0%, for species exhibiting no ingrowth probability response to growth rate, to 86%, for the pioneer-type species.

No data were available to estimate T_1 , the ingrowth time parameter. The predicted diameter increments, I , of trees with DBH of 5 cm and a diameter-independent competition index of -250 (very low competition in unlogged forests) were used in an estimation of the

“ingrowth time” parameter T_1 :

$$T_1 = \frac{5}{I} \quad (13)$$

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

3.7. Mortality model

The mortality probability was modelled as a function of diameter. To obtain the mortality probability as a function of diameter, it was necessary to split the data into diameter classes, and to count the number of mortality observations and the number of live-tree observations for each class. This was performed for each species group. Diameter class widths were allowed to vary, within some limitations. A class boundary was forced at a diameter of 20 cm, since the Jari data had a minimum DBH of 20 cm. The smallest diameter class had a lower bound at 5 cm. The largest diameter class had an upper bound 150% of the largest mortality observation, for each species group. The mean value of tree diameter, D , was used to describe each class rather than the mid-point because the diameter distribution was not linear.

Mortality observations were made over intervals not equal to 1 year. To convert these observations into annual mortality observations, an annual-equivalent variable was used:

$$A = \frac{1}{Y} \quad (14)$$

where Y is the number of years in the interval over which the mortality observation was observed. For each plot, interval and species group, A was summed and expressed as a proportion of the number of live trees, obtaining a probability.

For all the groups, the probability of mortality was approximately constant over all diameters, with the exception of the first diameter class. The mortality was thus modelled with three parameters: the width of the first diameter class, the probability of mortality in that diameter class, and the probability of mortality in all other diameter classes.

The representation of mortality of large trees was found to be poor. This had been found for previous

SYMFOR models (Phillips et al., 2002, 2003). This is unsurprising, since little data were available to estimate mortality of large trees. Consequently, in the current model the probability of mortality is increased by a percentage per centimeter DBH, m_2 for all trees with DBH above a specified threshold (the D_{95} variable in Eq. (6)). The resulting values of the parameters are shown in Table 6.

3.8. Model tuning

When the calibrated model had been implemented in the SYMFOR framework, initial simulations showed that the simulated dynamic equilibrium was not as observed in the data, assuming the unlogged forest data represented the dynamic equilibrium. This was a result of slight imbalances between the growth, mortality and recruitment sub-models; an almost inevitable consequence of the uncertainty in parameter values calibrated from a limited dataset. Selected model parameters were modified (tuned) to improve performance in order to demonstrate a dynamic equilibrium in primary forest.

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_2);
- Mortality probability for small trees (m_0);
- Mortality probability constant component (m_1);
- The recruitment probability (r_1 and r_3);
- The recruitment as a function of growth rate, for pioneer species (r_1).

The latter change was required because, for the same value of competition index, the pioneer species groups showed strong recruitment in logged-over forest compared to unlogged forest. This suggests that the competition index did not fully represent the conditions that affect trees growth following logging. It is suggested that the lack of absolute spatial resolution, necessitated by the lack of absolute tree-position data, may be the cause of this, since the effect has not been seen in other SYMFOR models (Phillips et al., 2002, 2003). Another possible influence is the lack of data from unlogged forest. Of the PSP, only 7 out of a total of 64 ha of data represent unlogged forest dynamics. The model was thus primarily calibrated from logged-over

Table 5
Parameter values for the recruitment model (Eq. (7), Section 2.4)

Group	r_1	r_2	r_3	R^2	T_1
1	0.029	-3.05	0.0065	68	18
2	0.045	0.0	0.022	0	33
3	1.22	-0.036	-1.214	48	12
4	0.30	-0.82	-0.238	75	17
5	0.70	-0.02	-0.692	24	25
6	0.0079	-2.81	-7.5E-3	51	9
7	0.148	-2.29	-0.304	74	6
8	2.6E-04	-6.91	0.0045	29	13
9	0.118	-0.79	-0.275	86	3
10	0.20	-0.013	-0.197	12	10

forest, but then the performance was tuned to be able to represent unlogged forest.

Changes to these parameters were made incrementally over many repeated simulations. The parameters of the model demonstrated significant interactions resulting from the underlying ecological nature and structure of the model. The model parameters given in Tables 4, 5 and 6 show the values after these modifications.

3.9. Damage mortality model

Model simulations with very few tree-falls (not calibrated from data) showed that gap formation led to the ingrowth of more pioneers (trees of species group 7 and 9) than were observed in the PSP data. This led to the conclusion that the PSP were perhaps (deliberately, or by chance) located in forest without areas with low competition (gaps) and were not entirely representative of a larger area, since tree-fall is known to

occur in primary forest. This was possible because the plots are small, and field experience showed the gaps, and the space between gaps, to be relatively large.

An analysis of the data from the intensively studied plots (ISP) of the Dendrogene project (<http://www.cpatu.embrapa.br/dendro/index.htm>) was undertaken in an attempt to establish the frequency and size of gaps. The ISP block 6 comprises a square 100 ha of forest, in which the positions of all trees with a DBH greater than 20 cm were recorded. One enumeration of this plot was made in 2001.

For analysis, the area was divided into 10 m × 10 m grid-squares, and those with zero tree records were selected. A clustering algorithm was used to group the grid-squares together using the position variables (x and y). For each cluster, the area of the gap was calculated using the minimum and maximum x and y values. This gave a maximum value for the area, assuming the area was rectangular. The proportion of the area of each cluster made up by zero-tree grid-squares was then calculated. Some clusters had a significantly higher proportion of gap than others. Those with over 50% were selected.

This process selected 10 clusters, with an average area of 0.4 ha, that had more than 50% of their grid-squares without trees. This leads to the conclusion that 5% of the total area had regions (of average size 0.4 ha) in which 50% or more of the 10 m × 10 m grid-squares had no trees above 20 cm. Gaps have no trees above 20 cm, however, and the area of the cluster was known to be a maximum. Thus, it is reasonable to refine the previous conclusion to the statement that, “about 2% of the total area has gaps with an average size of 0.2 ha”. Field experience of the Tapajos forest area suggests this is a reasonable conclusion. The assumed cause of the large gap size is lianas tying smaller trees to large trees that, when they fall, create a gap the size of many trees.

Although the number and size of gaps were estimated, the dynamics of the gaps were not known and no data were available to evaluate this. If a gap exists for 5 years, that means over a period of 5 years 10 gaps of 0.2 ha appear in 100 ha, which corresponds to 2 large gaps per year, or 1 per 50 years per ha. Similarly, if a gap exists for 10 years that means 1 per 100 years per ha, and were a gap to exist for 2 years, that means 1 per 20 years per ha. Since these gaps are defined as being the absence of trees of diameter 20 cm

Table 6
Parameters for the mortality model (Eq. (6), Section 2.5)

Group	m_0	m_1	m_2	D_{95}	b_d
1	2.3	1.8	0.0	41	7.5
2	2.9	2.9	0.5	15	3.8
3	1.85	1.1	0.2	57	15.0
4	2.9	2.4	0.5	27	5.0
5	1.9	0.5	0.25	72	7.5
6	4.0	2.1	0.5	76	7.5
7	6.7	5.0	0.0	35	7.5
8	3.0	0.85	0.0	104	15.0
9	8.9	4.5	0.5	38	5.0
10	4.3	4.0	0.5	78	15.0

or more, the time for a gap to disappear is the time until a tree within the gap reaches 20 cm. For the pioneer species this was calculated as a minimum of 11 years. This suggests 1 gap per 110 years per ha, which was used to tune the model.

The area of damage, in this model, for a tree of diameter 80 cm, is 0.13 ha (see Fig. 1). This is taken as a minimum diameter for a tree to fall and create a gap, leading to an average gap size of around 0.2 ha every 110 years. This was used as the basis for development of the relatively crude damage model described earlier (Section 2.6).

To avoid the edge effects from gaps dominating simulations, the minimum recommended plot size for simulations using this model is 1 ha.

4. Results and discussion

4.1. Model evaluation and validation

The performance of the model was evaluated using a sequence of 16 years' data from the plots at Tapajós km 67 (a subset of the data used for model calibration, as described earlier). These plots are described briefly earlier in this paper and by Silva et al. (1995). There are 36 plots, each 0.25 ha. Data from the first measurement were used to initialise simulations that were then run for 16 years. These simulated data were compared with the real data from the most recent enumeration of the plots. Results are shown for all species groups in Fig. 3 and for each species group individually in Figs. 4 and 5.

The model was tuned to the situation of unlogged forest, but validated against a sequence of data recorded immediately following heavy logging. This is a tough test of a model; the conditions in the logged-over forest vary considerably from the unlogged forest state, and these conditions are represented in the model by a simple competition index.

The time period of 16 years was sufficient to cover much of the complex forest dynamics following the initial heavy logging event, although it would cover only the beginning of the succession process. The general trends of the model reflected those of the data well (see Fig. 3). For most species groups, the simulated behaviour, in terms of the number of trees and sum of basal area, agreed well with the real data (see Fig. 4).

The number of trees after year 8 for many species differed between the data and the simulation results (Fig. 4a, c, e and Fig. 5c, g, i). Following logging, reduced competition in many areas led to increased recruitment of most species groups. Perhaps, in the real forest, there was over-crowding of the gaps by small trees, leading to increased mortality of the small trees in the following years. The model does not simulate density dependent mortality (although this relationship was tested during model development), and increased mortality in the small trees was not observed in the data available for calibration. The growth of these small trees will be inhibited by competition, however, so that, even while the number of trees was over-estimated, the basal area is well modelled at the end of the validation period.

Limitations of the model should be considered when examining the results. (1) During and after simulated

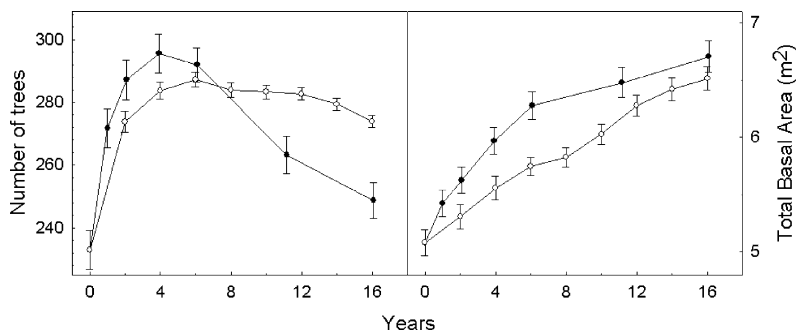


Fig. 3. Variation in the mean number of trees and the mean sum of basal area per plot for the Tapajós km 67 plots (starting 2 years after logging) for the real data (black) and the simulation model (white). The error bars represent the standard error on the mean over all plots for each point, and therefore arise from the variation between plots.

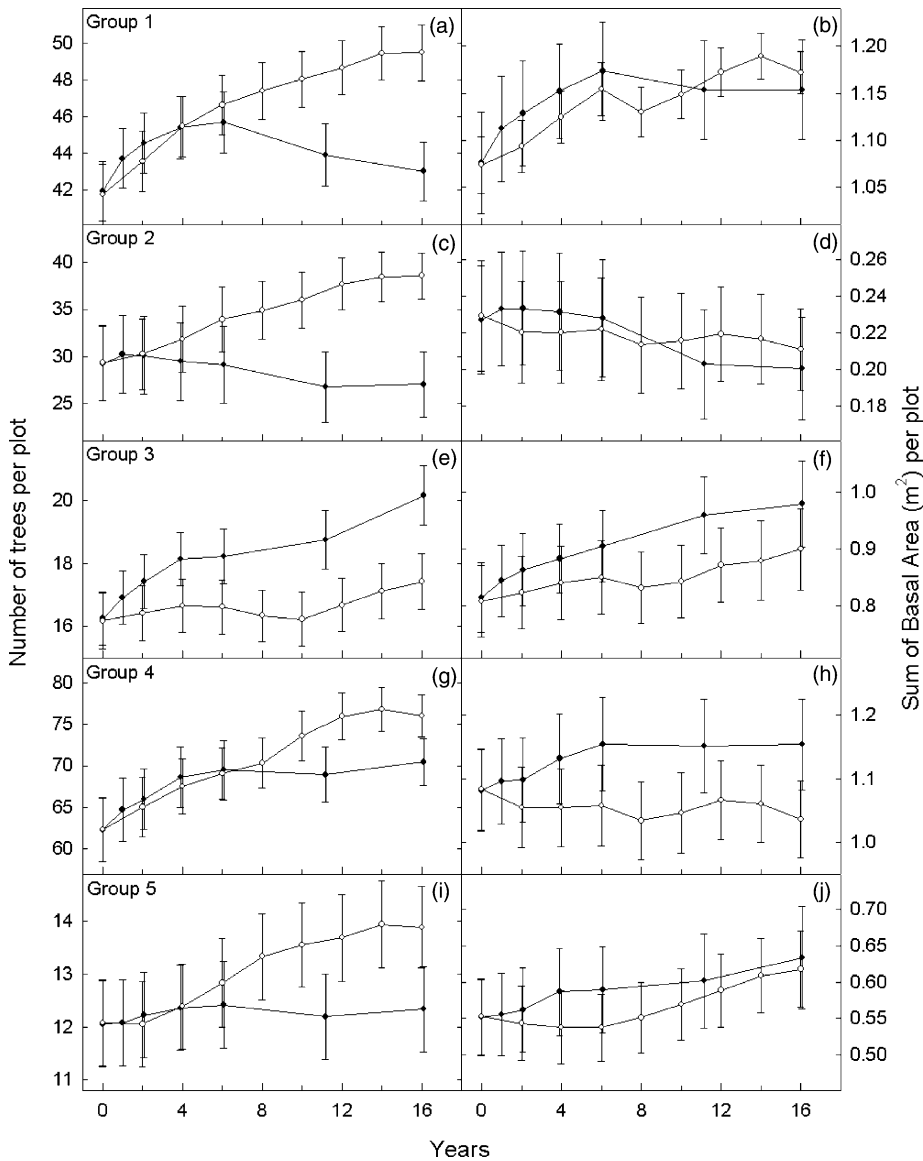


Fig. 4. Variation in the mean number of trees and the mean sum of basal area per plot for the Tapajós km 67 plots (starting 2 years after logging) for the real data (black) and the simulation model (white), shown for species groups 1–5 separately. The error bars represent the standard error on the mean over all plots for each point and therefore arise from the variation between plots.

logging, SYMFOR simulates scarified areas of forest where seedlings and saplings have been cleared and will take some time to regenerate. The simulation here was initialised with data from forest that was already logged, and thus the areas of damage were not modelled in SYMFOR. In practice, the gaps will exist

for longer than simulated here, because SYMFOR assumes that seedlings exist before the opening of gaps. (2) The plots used in this study were 0.25 ha, which is the same size as the field of influence used in competition modelling (see Fig. 1). Since plot-wrapping is used to avoid edge effects, the competition is likely to

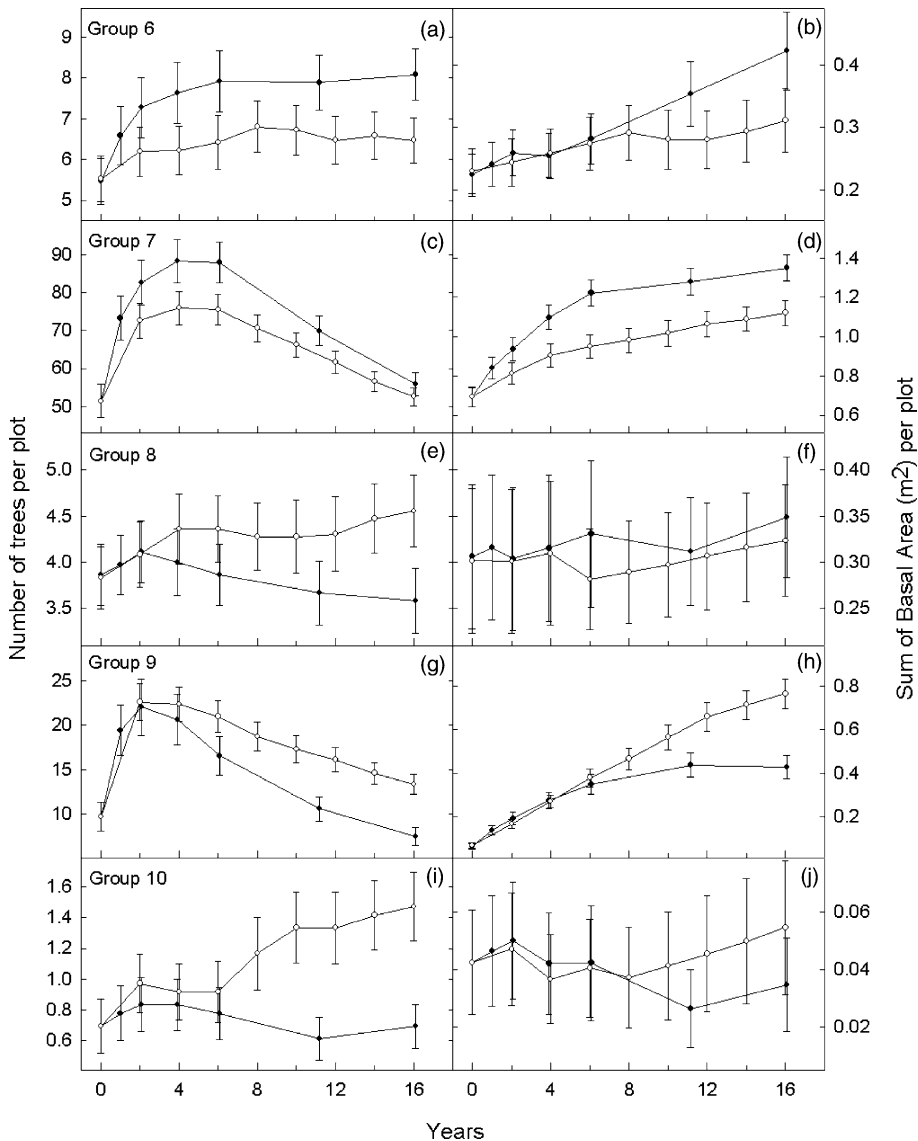


Fig. 5. Variation in the mean number of trees and the mean sum of basal area per plot for the Tapajós km 67 plots (starting 2 years after logging) for the real data (black) and the simulation model (white), shown for species groups 6–10 separately. The error bars represent the standard error on the mean over all plots for each point, and therefore arise from the variation between plots.

be almost homogeneous across each plot, and much spatial variation of competition would not be simulated adequately.

There may be concern over the use of the same data for model development as for model validation. The situation is not as simple as this, given that:

- The data used for validation were a sub-set of the data used for model calibration from one particular region. The model may be expected to represent the average behaviour of all regions used for calibration, and not to represent a single region, although data from a single region were used for validation and

would normally be used in subsequent simulations such as scenario analysis.

- The sub-models of growth, recruitment, mortality and logging were developed separately, tuned to work together for unlogged forest, and validated together on logged-over forest.
- The balance between growth, recruitment and mortality for each species group is delicate and the dynamic equilibrium observed in data was achieved by tuning to unlogged forest data. The model was validated against data from logged forest, however. The similarity between the data and simulation results show that the model form, balanced by tuning, represents well the forest dynamics.

Given these considerations, the validation is the most rigorous test of the model currently possible. Leaving out plots during model construction would have rendered the weakest sub-models (recruitment and mortality) substantially weaker still, and was not considered to be a realistic option.

4.2. Simulation of a management strategy

Forest management plans in the Brazilian Amazon are typically approved if they propose a logging intensity of no more than $40 \text{ m}^3 \text{ ha}^{-1}$ and a cutting cycle of at least 30 years, as documented in Brazilian legislation (*Portaria* 48/95). The minimum diameter for harvested trees is 45 cm.

The effects of this strategy on standing stock, harvest and species composition, were examined by applying the ecological model described in this paper over several cutting cycles starting with primary forest.

The management model in SYMFOR uses utilisation group data for each tree in the input file. For ingrowth trees, the utilisation group value is assigned stochastically according to the proportions observed in the input file for a given ecological species group. In these simulations two utilisation groups were used, representing either commercial or non-commercial status. This status was allocated on the basis of records of species that were logged in the PSP data (described in Section 3.2). In practice, some large trees of commercial species are left in the forest because of poor form or because they are hollow. A stem quality value between 0 and 1 is assigned to each tree stochastically when it first enters the model.

An arbitrary stem quality limit was used to prevent harvest of all trees with a stem quality lower than 0.3. Cutting of lianas prior to logging was simulated (with 100% success assumed) to reduce simulated damage from tree-fall. The skid-trail pattern and damage associated with extracting the log from the forest was calibrated according to damage levels observed in the PSP data described above (Section 3.2). Tree selection for logging was made in a two-step process, first identifying the trees that passed all logging requirements, then selection of the qualifying trees at random until the maximum volume had been reached, or until there were no more qualifying trees.

Ten plots were simulated for 160 years, with logging in year 4 and subsequently at 30-year intervals. The plots were square 1 ha plots formed by joining four 0.25 ha PSP records from the Tapajós region. The 0.25 ha plots used were from unlogged forest and located as close as possible to each other. Ten repeated simulations were made for each 1 ha composite plot, and mean results calculated for each plot over all repetitions. Final results were then calculated as the mean and standard error over all plots.

Results of the simulations are given in Figs. 6–10, and Table 7. Fig. 6 shows the standing volume (for all trees with a diameter greater than 5 cm) as a function of simulation time. The standing volume falls over the period, although this effect becomes less with each successive harvest as the forest approaches a periodic equilibrium.

Fig. 7 shows the harvested volume for each logging operation, and Fig. 8 shows the standing commercial volume (trees that pass all harvesting requirements) as a function of simulation time. It may seem that if the average harvest is less than $40 \text{ m}^3 \text{ ha}^{-1}$ then there should be no residual standing commercial volume. The simulation limited the possible harvest to 40 m^3 per plot, however, rather than as an average over all plots: some plots had residual commercial volume while others did not attain their target 40 m^3 . The average concession-wide harvest would be expected to be equivalent to the average commercial volume before the harvest. The logging strategy limited the yield for the first three harvests in some individual 1 ha plots, although a yield of 40 m^3 was available for the first four harvests if all plots were taken together. After that time, the availability of commercial timber limited the harvest.

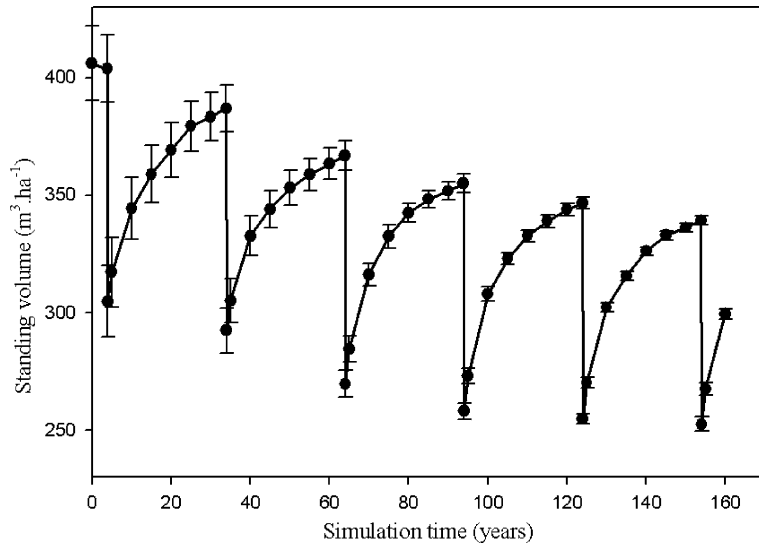


Fig. 6. Simulated standing volume ($\text{m}^3 \text{ha}^{-1}$) of all trees with diameter greater than 5 cm for the period covering six logging cycles, beginning with primary forest.

Fig. 7 shows the harvested volume broken into constituent hardwood and lightwood components. This was possible by using the ecological species grouping (see Section 3.4) data for the harvested trees. The commercial species within species group 7 (fast growing pioneers) were assumed to be lightwoods. These

are dominated by *Jacaranda copaia* (Bignoniaceae). Harvested trees from other species groups were assumed to be hardwoods. It is clear that the harvested volume decreases with each subsequent harvest and fails to reach the target $40 \text{m}^3 \text{ha}^{-1}$ on average in the fourth harvest. At the same time the proportion of the

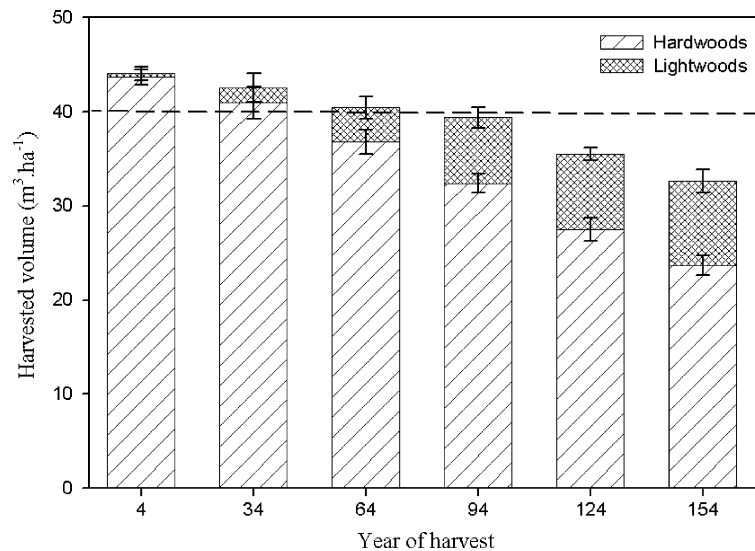


Fig. 7. Harvested timber volume per hectare for each simulated harvest. The total harvest is comprised of lightwoods (mostly *J. copaia*), and the hardwoods.

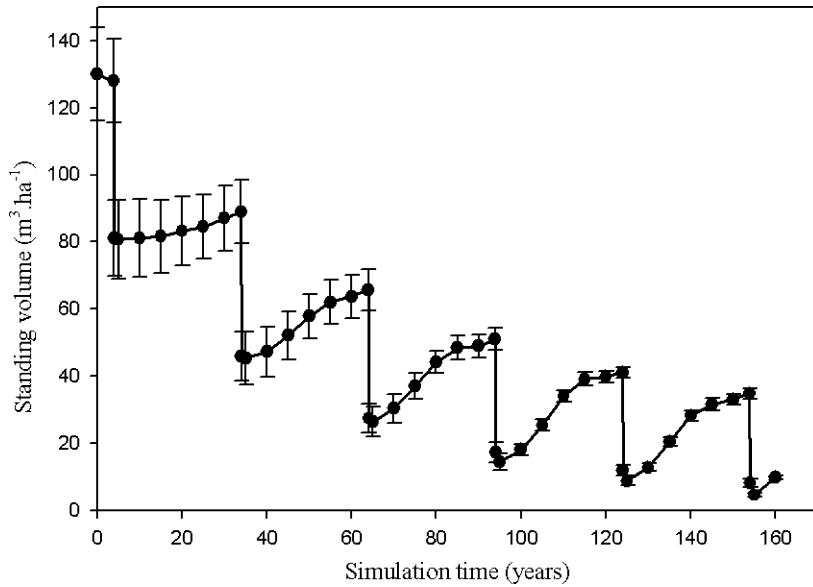


Fig. 8. Simulated standing volume ($\text{m}^3 \text{ha}^{-1}$) of all commercial trees for the period covering six logging cycles, beginning with primary forest.

harvest made up of hardwoods also decreases, which may have a significant effect on the financial viability of future harvests.

Figs. 9 and 10 suggest that although the target harvested volume was attained for the first three cycles,

the cost of the logging operation may have gone up. An increase in the number of stems felled and extracted means more work for the logging team and equipment, and associated costs. A decrease in mean stem volume is also likely to lead to increased wastage at

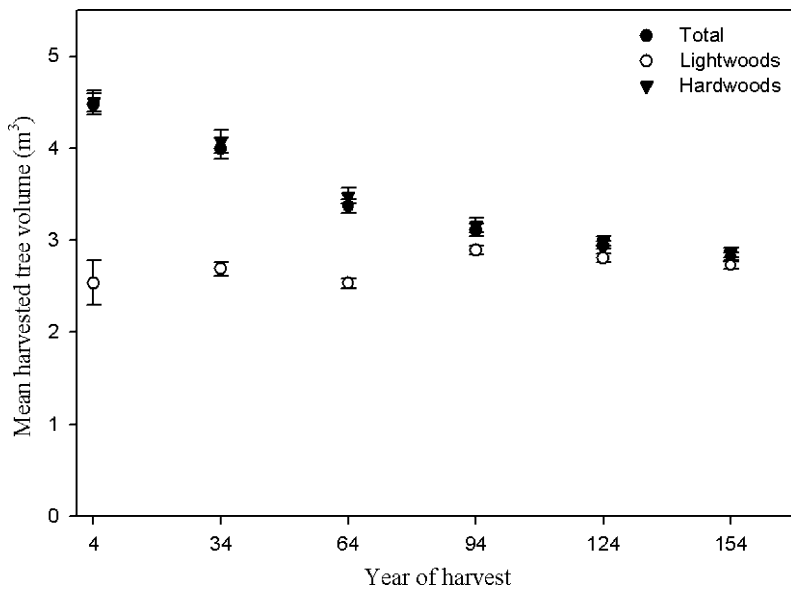


Fig. 9. The mean volume of harvested trees, shown for the total (all harvested trees) and its constituent hardwood and softwood components.

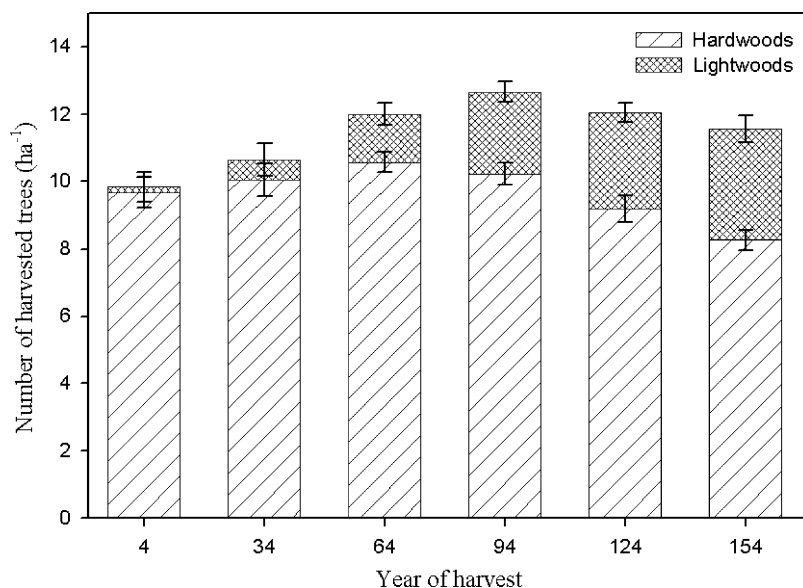


Fig. 10. The number of trees harvested per hectare, shown for the total (all trees) and its constituent hardwood and softwood components.

the sawmill. These factors suggest that profits from the first harvest of primary forest will not be sustained even if timber yield is.

The species composition of the forest in terms of ecological function changes as a result of logging. Table 7 compares the composition of the forest before the first harvest (year 4) with that before the last simulated harvest (year 154). The notable differences are the increase in the proportion of trees and standing volume made up by pioneer species, and the decrease in the proportion of the standing volume made

up by climax and upper canopy species, especially hardwood species. As may be expected, this suggests that the forest would take significantly longer than 30 years to recover, in terms of volume and composition, from the removal of $40 \text{ m}^3 \text{ ha}^{-1}$ of some species.

4.3. Discussion of the model

The spatial aspect of SYMFOR allows a spatial representation of the processes of logging activity. The individual-based, spatially explicit nature of the

Table 7

The percentage of the total number of trees, N , and the percentage of the total standing volume, V , made up of each species group

Species group	N	ΔN	V	ΔV
Medium-growing mid-canopy	21.5 ± 0.6	-4.0 ± 0.6	17.8 ± 1.7	-4.8 ± 1.7
Slow growing understorey	18.8 ± 0.8	-1.3 ± 0.8	5.8 ± 0.3	$+0.0 \pm 0.3$
Medium growing mid-canopy	7.8 ± 0.4	-1.9 ± 0.4	16.2 ± 1.3	-8.5 ± 1.3
Slow growing lower canopy	31.2 ± 1.6	-2.4 ± 1.6	15.5 ± 1.0	-1.6 ± 1.0
Medium growing upper canopy	5.4 ± 0.2	-1.3 ± 0.2	14.4 ± 1.2	-7.0 ± 1.3
Fast growing upper canopy	2.5 ± 0.2	$+0.3 \pm 0.2$	6.1 ± 0.9	$+0.0 \pm 0.9$
Fast growing pioneers	9.4 ± 0.6	$+7.5 \pm 0.6$	5.5 ± 0.4	$+15.7 \pm 0.5$
Emergents—climax	2.2 ± 0.1	-0.3 ± 0.1	16.6 ± 2.8	-10.4 ± 2.8
Very fast growing pioneers	0.7 ± 0.1	$+3.5 \pm 0.2$	0.5 ± 0.1	$+17.1 \pm 0.6$
Very fast growing upper canopy	0.7 ± 0.1	0.0 ± 0.1	1.4 ± 0.3	-0.4 ± 0.3

The difference (ΔN and ΔV) between the primary forest situation (N and V), and the situation immediately preceding the sixth logging operation shows the simulated species composition change as a result of repeated logging operations. Large changes are shown in italics. The uncertainties are calculated as standard errors from the mean value over all simulated plots.

ecological model described here leads to the implicit simulation of gap dynamics and succession through a distance-dependent competition index. Application of the ecological model remains valid for describing the response of the forest to a disturbance as long as the competition index values in the simulation are within the range encompassed by the calibration data. This allows the simulation of management strategies that were not represented by the calibration data.

The application of the model demonstrated quantitatively many of the trends that may be expected and are observed in the field to result from the specified forest management strategy. It showed the expected change in overall species composition and changes in the quantity, size and composition of harvested timber. Linkage of these results to a suitable financial model of concession operations (van Gardingen et al., 2003) would enable quantitative estimations of the financial viability of repeated harvesting of forest that was initially primary forest.

The effects of the stochastic components of the model are accounted for in simulation results by the calculation of mean values with an associated standard error. Other sources of uncertainty in simulation result are the systematic errors arising from the assumptions made in the model and from parameter value uncertainties. These were quantified for an ecological model developed for Indonesia (Phillips et al., 2003), where they were found to generally increase with simulation time. The effects of such systematic errors on simulation results are likely to be very similar for two different management models, however. This means that the systematic error on the difference between the results from two management strategies would be close to zero. In general, therefore, more accurate simulation results can be expected for comparisons between management scenarios (van Gardingen et al., 2003) than for absolute predictions.

Comparisons between the results of different models is difficult, since different models are made to simulate different effects, and are reported in different ways. The model described here is individual-based and spatial, representing every tree above a minimum diameter. In comparison, the model CAFOGROM (Alder and Silva, 2000) is cohort-based and cannot represent the ecological processes of succession following disturbances that are not represented in the data used for calibration. The models of Gourlet-Fleury

and Houllier (2000) and Gourlet-Fleury and Montpied (1995) are individual-based but are inappropriate to apply for more than one generation in a changing forest system, since the species groups used are different for the growth, recruitment and mortality models, so reference to the original data must be made to assign group numbers to new tree recruits.

5. Conclusions

The ecological model described, implemented in the SYMFOR framework, forms a tool for producing information describing the likely future state of forests given alternative management interventions for *Terra Firme* forests in the Eastern Amazon. It has been used to examine the effects of a current management practice in Brazil, applied over several cutting cycles, and suggests that financial benefits from logging may decrease with successive harvests, even before the target timber volume yield cannot be sustained. The ecological implications of the management scenario are that the proportion of pioneer species will increase significantly while that of the large climax and canopy species will decrease. This can be expected to have secondary effects in terms of the conditions in the forest experienced by other flora and fauna. Application of this model in the Brazilian Amazon would enable the generation of knowledge regarding the effects of alternative management scenarios, and increased ability to manage the forests more sustainably.

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