

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

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6

7 **Abstract**

8 A model to simulate the forest processes of growth, mortality and recruitment, and the  
9 human process of forest management, in the *Terra Firme* forests of the eastern Amazon is  
10 described. It is implemented within the SYMFOR (<http://www.symfor.org>) framework. It  
11 is based on measurements from experimental plots in the Jarí and Tapajós national forest  
12 areas over a 16 year period. All trees within the plot that have a diameter greater than 5  
13 cm are simulated. 10 species groups are used to describe the natural processes affecting  
14 tree behaviour. Growth rates are calculated for each species group using the tree diameter  
15 and a competition index. Mortality and recruitment are stochastic, and recruitment  
16 probability is based on the predicted growth rate of a hypothetical tree. Options exist to  
17 vary the human interaction with the forest reflecting forest management decisions, as for  
18 other SYMFOR models. Model evaluation compares model performance with data  
19 describing forest recovery for 16 years following logging.

20

21 The model is applied to current forest management practice in the Brazilian Amazon,  
22 with  $40 \text{ m}^3 \cdot \text{ha}^{-1}$  of timber extracted on a cutting cycle of 30 years. Results show that the  
23 yield can be sustained for 3 harvests following the first logging of primary forest, but that

1 the yield is increasingly lightwoods rather than hardwoods. The size of trees extracted  
2 decreases and the number of trees extracted increases with successive harvests, leading to  
3 increased costs and lower profits for the logging company despite constant yields. The  
4 standing volume of all trees just before harvest is reduced by 15 % over 150 years, with  
5 pioneer species increasingly prevalent relative to climax or canopy hardwood species.

6

7 The model, in the SYMFOR framework, constitutes a tool that can be used to generate  
8 knowledge to understand the differences between alternative forest management  
9 strategies in the Brazilian Amazon. The new knowledge can then be used to improve  
10 forest management, regulation and certification, and help to conserve the worlds largest  
11 remaining tropical forest.

12

13 **Keywords:** model, individual, forest, tree, spatial, Brazil, Amazon, competition, species  
14 grouping, management, certification, regulation.

## 1 1 Introduction

2 The people, economy and ecology of forested areas are affected by the management of  
3 their forests. Timber yield from the forest gives instant revenue to the harvesting  
4 organisation, but this must be balanced against detriment to other products and services  
5 from the forest, both now and in the future, through regulation. In order to make better-  
6 informed decisions for enhanced sustainable forest management, it is necessary to have  
7 information describing the likely future state of forests given alternative management  
8 interventions.

9

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

18

19 Brazilian Amazonia represents the largest and most biologically diverse area of  
20 remaining natural tropical forest. Brazil's 544 million ha of forest is decreasing by 2.4  
21 million ha per year (FAO, 1999), increasing the need for conservation or sustainable  
22 management. Increasingly, forest management in Brazil is becoming regulated and  
23 certified. The process of regulation and certification use current knowledge and estimates

1 to define limits and requirements for forest management strategies. Current knowledge is  
2 based on individual experience and field measurements, and while these have been  
3 extensive and valuable (Silva *et al.* 1995; 1996), they have not been able to establish the  
4 likely long-term effects of a given management strategy on the forest. A need exists for a  
5 simulation tool that can help to fill the knowledge gap to inform assessments of long-term  
6 sustainability.

### 7 **1.1 Existing approaches**

8 Few simulation models have been produced that describe forest dynamics in Amazonian  
9 Brazil. Alder (1995) and Alder and Silva (2000) developed models for forests in Eastern  
10 Amazonia using a cohort approach. The models are distance-independent and do not  
11 account for the changes in growth environment caused by management intervention.  
12 They are able to make predictions of yield, but will have little sensitivity to alternative  
13 silviculture or management strategy detail, particularly in terms of levels of logging  
14 damage and species composition change.

15

16 SYMFOR (Phillips and van Gardingen 2001a; 2001b) is a framework that combines  
17 models of forest ecology with models describing important elements of management  
18 treatments typically applied in selective logging of tropical forests. The SYMFOR  
19 framework uses a description of natural forest ecology in the form of an ecological model  
20 describing tree growth, mortality and seedling recruitment, and thus the forest as a whole.  
21 The models are individual-based, meaning that each tree is considered separately on the  
22 basis of the unique conditions it experiences, and may be spatially explicit.

23

1 Such models are able to simulate with validity many forest management scenarios that  
2 were not described in the data used for calibration because the system simulates the  
3 conditions leading to forest state, rather than forest state itself. As long as the model is  
4 used within the range of conditions described by the calibration data, the model is valid.  
5 This is an advantage over more simplistic models, although a compromise must be made  
6 over applicability of the models: they are too complex to be directly applied at the scale  
7 of forest management operations, so are necessarily strategic planning tools.

8

9 This paper describes a model that is built in the SYMFOR framework using data from the  
10 eastern Amazon managed natural forests and applied to explore the effects of heavy  
11 logging repeated every 30 years. The model is capable of significantly more advanced  
12 examinations of alternative management scenarios, and this paper presents the model as a  
13 tool, giving an example of its application.

## 1 2 Model description

### 2 2.1 Introduction

3 The ecological model was developed to be implemented in the SYMFOR framework  
4 (Phillips and van Gardingen, 2001a; 2001b). The model was developed to represent the  
5 processes of *diameter increment* (tree growth); *recruitment* (new trees appearing in the  
6 stand at the minimum diameter threshold of 5 cm); and *mortality* (tree death from natural  
7 causes). These processes use a representation of competition in the form of a competition  
8 index, derived explicitly for each tree from the data describing the other trees. The model  
9 was designed to run with an annual timestep. In the following text, all probabilities and  
10 random numbers used in the model are within the range 0.0 to 1.0 unless otherwise  
11 stated.

### 12 2.2 Competition index

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

$$15 \quad C_t = z_1 \cdot \sum_{i=1}^{n_1} \frac{D_i}{D_t} + z_2 \cdot \sum_{j=1}^{n_2} \frac{D_j}{D_t} + z_3 \cdot \sum_{k=1}^{n_3} \frac{D_k}{D_t} \quad (1)$$

16 where:  $z_1$ ,  $z_2$  and  $z_3$  are the coefficients for the relative competition importance of zones 1,  
17 2 and 3, respectively;  $i$ ,  $j$  and  $k$  are the over-topping trees in the three zones;  $n_1$ ,  $n_2$  and  $n_3$   
18 are the total number of over-topping trees in the three zones; and  $D$  is the tree diameter.  
19 Zone 1 is the 10 by 10 m grid-square containing tree  $t$ , and zones 2 and 3 are defined  
20 relative to zone 1 as shown in Figure 1.

21

1 To help understand the influence of competition on growth and other dynamic tree  
2 attributes, the competition was modelled as a function of diameter, and the modelled  
3 value was then subtracted from the absolute value. This leads to a competition index  
4 symmetric about zero, and, on average, independent of tree diameter.

5

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

$$7 \quad \hat{C}_t = \frac{b_0}{b_1 + D} + b_2 \quad (2)$$

$$8 \quad C = C_t - \hat{C}_t \quad (3)$$

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

### 12 **2.3 Growth model**

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

17

18 The model used for the Brazilian data is the same as that used for Guyana (Phillips *et al.*,  
19 2002a), and a simplification of the version developed for Indonesia (Phillips *et al.*,  
20 2002b).

21



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

$$3 \quad I = D(a_0 + a_1 e^{-a_2 D}) + a_3 C + a_4 \quad (4)$$

4 where  $a_0$ ,  $a_1$ ,  $a_2$ ,  $a_3$ ,  $a_4$  and  $a_5$  are model parameters and  $D$  is the DBH of the tree. The  
5 diameter-independent competition index,  $C$  (eqn. 3), was devised to describe the  
6 competition environment for each individual tree in the plot.

## 7 **2.4 Recruitment model**

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

$$16 \quad F = r_1 \cdot \exp(-r_2 \cdot I) + r_3 \quad (5)$$

17 where  $r_1$ ,  $r_2$  and  $r_3$  are parameters and  $I$  is the predicted growth rate of a tree at a  
18 randomly selected location within the grid-square. The growth rate is predicted using the  
19 growth model described above (eqn. 4), for a tree with the same diameter as the minimum  
20 DBH threshold of 5 cm.

21

22 A model parameter,  $T_1$ , represents the time required for ingrowth as the number of years  
23 required for a tree to grow from seed to a DBH of 5 cm. It is used in the simulation when

1 an area of ground is cleared of seedlings, for example when the soil surface is damaged  
2 during log extraction.

### 3 **2.5 Natural mortality model**

4 Natural mortality ( $M$ ) is modelled as a stochastic process dependent on diameter. The  
5 probability function, or its derivative, has discontinuities at two diameters:  $b_d$  plus 5 cm  
6 (to represent increase mortality for smaller trees), and  $D_{95}$ , the 95-percentile value of the  
7 diameter probability distribution, to represent increased mortality for trees reaching their  
8 biophysical limit. The equation used calculate natural mortality probability,  $M$ , for a tree  
9 of diameter  $D$  (cm), was:

$$10 \quad M = \begin{cases} m_0 & \text{if } D < b_d + 5 \\ m_1 & \text{if } b_d + 5 \leq D < D_{95} \\ m_1 + m_2(D - D_{95}) & \text{if } D_{95} \leq D \end{cases} \quad (6)$$

11 where  $m_0$ ,  $m_1$  and  $m_2$  are parameters.

### 12 **2.6 Damage mortality model**

13 Simulated falling trees cause simulated damage and associated mortality to the  
14 surrounding trees. This is not as in other SYMFOR models (Phillips *et al.*, 2002a;  
15 Phillips *et al.*, 2002b), however, due to the presence of lianas in Amazonian forests. The  
16 stochastic determination of the direction of a tree's fall leads to an area in which all trees  
17 are killed by damage.

18

19 The basis of the model is that only large trees fall, but, when they do, they create a large  
20 area of damage in which all trees are killed. The size and shape of the gaps would vary, in  
21 practice, but for modelling purposes a simplification is required. The size and shape of

1 the area of damage is based around the dimensions of the falling tree, converted to a  
2 rectangular shape. The dimensions and shape are shown in figure Figure 2. The length of  
3 the area of damage is the tree height plus 3 times the crown radius. The width of the area  
4 of damage is 4 times the crown radius.

5

6 Damage due to the fall of trees felled in a logging operation is simulated in the same way,  
7 if the user elects to simulate no liana cutting before logging. If liana cutting is selected,  
8 however, the simulation of damage created is the same as for falling trees in other  
9 SYMFOR models (Phillips *et al.*, 2002a; Phillips *et al.*, 2002b) for forests where lianas  
10 are not present. Trees above a minimum diameter,  $D_m$ , that die, fall with an probability of  
11  $P_f$ .

## 12 **2.7 Other functions**

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

19

20 Total tree **height**,  $H$ , is calculated by an inverse linear relationship with DBH,  $D$ :

$$21 \quad H = \frac{sDH_m}{sD + H_m} \quad (7)$$

22 where  $s$  has a value 200 and  $H_M$  represents maximum tree height with a value of 50 m.

1

2 The “**crown-point**”,  $C_P$  (m), of a tree was defined to be the height at which the tree has  
3 maximum crown width, calculated using a simple linear relationship with tree height,  $H$   
4 (m):

$$5 \quad C_P = f_C H \quad (8)$$

6 where the parameter  $f_C$  has the value 0.55.

7

8 The “**crown-radius**”,  $C_R$  (m), of a tree was defined to be the radius of the tree crown,  
9 which is assumed to be circular in cross-section, calculated using a relationship with tree  
10 diameter,  $D$  (cm):

$$11 \quad C_R = \left( \frac{10}{D} + \frac{1}{15} \right)^{-1} \quad (9)$$

12 The coefficients and assumptions made in equations 7, 8 and 9 are derived from  
13 anecdotal experience since data are not available for rigorous calibration.

14

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

$$17 \quad B = \frac{\pi}{4} D^2 \quad (10)$$

18 Stem **volume**,  $V$ , is calculated as a function of diameter,  $D$  (cm), and crown-height,  $C_P$ ,  
19 as:

$$20 \quad V = 0.5179 \cdot \left( \frac{D}{100} \right)^2 C_P + 0.0775 \quad (11)$$

- 1 which was calibrated by Queiroz (1984). For this equation to be valid, the coefficient
- 2 values used in equations 7 and 8 are required to be as stated.

## 1 3 Data and model calibration

### 2 3.1 Methodology

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

7

8 When the calibrated model had been implemented in the SYMFOR framework, initial  
9 simulations demonstrated that some parameter values needed alteration in order to  
10 achieve adequate performance. Selected model parameters were modified (tuned) to  
11 improve performance in order to demonstrate a dynamic equilibrium in primary forest.

12

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

- 15 • Mortality probability slope parameter for trees with large DBH values ( $m_2$ );
- 16 • Mortality probability for small trees ( $m_0$ );
- 17 • Mortality probability constant component ( $m_1$ );
- 18 • The recruitment probability ( $r_1$  and  $r_3$ );
- 19 • The recruitment as a function of growth rate, for pioneer species ( $r_1$ ).

20 The latter change was required since, for the same value of competition index, the  
21 pioneer species groups showed strong recruitment in logged-over forest compared to  
22 unlogged forest. This suggests that the competition index does not perfectly represent the

1 conditions that affect trees growth following logging. It is suggested that the lack of  
2 absolute spatial resolution, necessitated by the lack of absolute tree-position data, may be  
3 the cause of this, since the effect has not been seen in other models (Phillips *et al.*, 2002a;  
4 2002b). Another possible influence is the lack of data from unlogged forest. Of the PSP,  
5 only 7 ha represent unlogged forest dynamics out of a total of 64 ha of data. The model  
6 was thus primarily calibrated from logged-over forest, but then tuned to the unlogged  
7 forest scenario.

8  
9 Changes to these parameters were made incrementally over many repeated simulations.  
10 The parameters of the model demonstrated significant interactions often resulting from  
11 the underlying ecological nature of the model. The model parameters given in the tables  
12 below show the values after these modifications.

### 13 **3.2 Data**

14 Details of the data are described by Phillips (2002b; 2002c) and Silva *et al.* (1995). The  
15 environment is described by Silva *et al.* (1996). The plot layout and data collection  
16 information are held by Embrapa Amazonia Oriental.

17  
18 PSP datasets have been recorded from forests in the Tapajos and Jari Florestal lands in  
19 the state of Para. They have already been used to analyse the impact of logging on species  
20 composition, growth and forest structure (Silva *et al.*, 1995), and for growth and yield  
21 studies (Silva *et al.*, 1996). They were also used for the definition of species groups and  
22 growth functions of the growth model CAFOGROM and its successor (Alder, 1995;  
23 Alder and Silva, 2000).

1

2 The series of plots at Tapajos km 114 comprise 60 PSP of 0.25 ha each. All trees with  
3 DBH greater than 5cm have species and DBH recorded. The tree data includes  
4 information about which 10 x 10 m sub-plot they are in, but no finer spatial resolution is  
5 held. Sub-samples are made for seedlings (taller than 30 cm) and saplings (DBH greater  
6 than 2.5 cm), but growth information is not available since individuals of these sizes are  
7 not marked. 48 of the plots are located in forest that was logged-over in 1981, with 5  
8 inventories made over the period 1981 to 1995. 12 of the plots are in unlogged forest,  
9 with 4 inventories made over the period 1983 to 1995.

10

11 The series of plots at Tapajos km 67 comprise 36 plots of 0.25 ha each. They have the  
12 same design and inventories as the plots described above. The forest containing the plots  
13 was logged in 1979, with 7 inventories made over the period 1981 to 1997. An analysis  
14 of these plots was made in 1994 by Silva *et al.* (1995).

15

16 The series of plots in Jari comprise 40 plots of 1 ha each. All trees with a DBH greater  
17 than 20 cm DBH were inventoried, with DBH and species information recorded. The tree  
18 data includes information about which 10 x 10 m sub-plot they are in, but no finer spatial  
19 resolution is held. 5 % sub-samples were made for trees with DBH between 5 and 20 cm.  
20 36 plots were logged in 1985, and 4 plots have not been logged. They were all  
21 inventoried 6 times over the period 1984 to 1996.



### 1 **3.3 Data cleaning and intermediate processing**

2 The data were cleaned based on studies of the DBH observations, the taxonomic  
3 identification records, and the mortality codes. This led to some taxonomic and mortality  
4 code data being changed, and some data being rejected, usually because of erroneous  
5 DBH observations.

6

7 The survey information was changed into time-interval-based growth. Typically  
8 measurement intervals were 2 years, which is usually long enough for the growth  
9 observation to dominate its uncertainty, and thus give meaningful data. Each interval was  
10 used to calculate a separate growth observation for each tree, where suitable diameter  
11 data were available (i.e., non-zero or non-missing diameter observations). Growth  
12 observations were accepted if they passed a set of rules derived from extreme (erroneous)  
13 growth observations: this left some observations of negative diameter increment in the  
14 dataset and so did not produce a positive bias by their exclusion.

15

16 Ingrowth (recruitment) past a diameter threshold of 5 cm was identified by a missing  
17 diameter in one survey followed by a non-missing diameter in the next survey. Only data  
18 from the Tapajos regions were used in this analysis, since these were the only datasets for  
19 which trees with a diameter of 5 cm were recorded.

20

21 Tree mortality was identified by trees with a non-missing DBH observation in one  
22 survey, followed by a missing DBH observation. Mortality from logging or logging

1 damage was separated from natural mortality using mortality codes. It was assumed that  
2 the trees that were not found had died from natural causes.

### 3 **3.4 Competition model**

4 The values used for the parameters  $z_1$ ,  $z_2$  and  $z_3$  (in eqn. 1), calculating the absolute  
5 competition index for each tree, were 9, 4 and 1, respectively, giving highest competition  
6 from trees close to the subject tree.

7

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

### 10 **3.5 Species groups**

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

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

17 One set of model parameters were produced for each of the species groups.

18

19 In order to group the species, it was necessary to assess the population density for each  
20 taxon recorded in the data set. Table 2 shows that 85 taxa were represented by more than  
21 100 trees.

22

1 The process for grouping species involved three stages, as performed by Phillips *et al.*  
2 (2001; 2002a): (1) a clustering analysis to make the groups using the most populous  
3 species; (2) discriminant analysis to add the less populous species to the existing groups;  
4 and (3) a subjective stage where species with little or no data were assigned to the groups.

5

6 For each species, a set of variables was produced:

7 1. Mean growth rate;

8 2. Average growth rate at low competition;

9 3. Average growth rate at medium competition;

10 4. Average growth rate at high competition;

11 5. Average growth rate of new recruits (DBH of 5-6 cm);

12 6.  $D_{95}$ , the 95-percentile point in the DBH frequency distribution (as an index of  
13 mortality behaviour).

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

18

19 The grouping process used taxa with at least 50 trees, giving 143 species (Table 2). 40  
20 species had missing data for at least one of the 6 characteristic variables, and could not be  
21 included in the clustering analysis. Thus only 103 species were used at this stage. Data  
22 were evaluated for these species, and normalised so that the range of values of each

1 variable was from 0.0 to 1.0. A clustering procedure was then used to group the species  
2 according to the normalised values of variables 2 – 6 (above).

3

4 The clustering process requires the user to decide how many groups there should be in  
5 advance. Ten groups were used to define the initial grouping to be consistent with  
6 previous studies (Phillips *et al.*, 2001; 2002a). The groups and their normalised variables  
7 were then examined. The production of 10 groups was able to separate species with  
8 extreme ecological characteristics, and discriminated between the species at opposite  
9 ends of the range of characteristic values. Variation in the number of groups between 9  
10 and 12 did not significantly affect the ability of the model to describe species behaviour,  
11 so the 10 groups were used. An alternative clustering process was applied using the  
12 values of variables 1 and 6 (above) only, as used by Alder (1995). This process led to a  
13 similar result as for variables 2 – 6, and was adopted since it was simpler.

14

15 Remaining ungrouped species were added to the existing groups using discriminant  
16 analysis. The data from the existing groups were used as training data to initialise this  
17 process. The characteristics used to define the groups and the species were the 95  
18 percentile point on the cumulative DBH distribution and the mean growth rate (as for the  
19 clustering process).

20

21 The species with less observations are generally less important to forest structure and  
22 dynamics, less important from a commercial point of view, and were more likely to be  
23 assigned to an inappropriate group due to being mis-represented by the variable values

1 calculated from the dataset. In order to correct this, it is necessary to apply expert  
2 knowledge of the species formed from a general accumulation of experience over years  
3 of forestry. This was not done since suitable expertise was not available at the time of  
4 model development, but can be carried out in the future for less common species without  
5 losing model validity. It should be noted that model results would not be expected to  
6 change significantly as a result of this, since the taxa most likely to be incorrectly  
7 represented are infrequent taxa exhibiting non-extreme behaviour.

8

9 The species grouping process grouped 485 taxa into 10 groups, whose average  
10 characteristics are given in Table 3.

### 11 **3.6 Growth model**

12 The purpose of the growth model was to explain some of the variation of growth rate  
13 within each species group. The model was calibrated separately for each species group  
14 using multivariate regression. The amount of variation in the dataset that is explained by  
15 the model is described by the  $R^2$  statistic (Table 4). When combined, the species  
16 grouping and the growth model together explained 33.7 % of the observed variation in  
17 the dataset. This value is slightly larger than that obtained for most growth models in  
18 tropical forests.

19

20 The residual variation in growth rates (66.3 %) was analysed to establish if any casual  
21 effects could be ascertained from the data. An estimate of the measurement uncertainty  
22 on any growth observation was made (using data from Indonesia: see Phillips *et al.*,  
23 2002b), and found to be 0.3 cm. The variation that could be explained by the

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

5

6 Lianas can be a dominant feature of Amazonian forests, with up to several on a single  
7 tree. They can grow to significant diameters, although diameter is not a useful measure of  
8 their size or effect, quite often. They grow up one tree, but then spread through the  
9 canopy. The extent and effect of their interaction with tree crowns is not well known. It  
10 was hypothesized that they may have some effect on tree growth, as well as the process  
11 of gap formation and regeneration. The data contained a simple index of infestation by  
12 lianas for each tree. A simple model of the effect of lianas on growth rate was  
13 constructed, and could explain 1 % of the variation in growth rates. It may be suggested  
14 that the effect of lianas is significant and should therefore be modelled. There were  
15 difficulties with this, however:

- 16 • Half of the growth observations do not have usable records of liana presence;
- 17 • The data about lianas are simply assignments of one of three codes, and it is  
18 unclear exactly what these mean;
- 19 • Serial records for individual trees show the liana index changing without apparent  
20 consistency, or perhaps the timescale for their change is short;
- 21 • Within the data there are no records that could be used to infer liana dynamics,  
22 and thus it could be applied only as a random factor contributing to the simulated  
23 variation in growth rates.

1 With these difficulties, and the relatively small effect on growth rates, it was decided not  
2 to include a representation of liana infestation for the purposes of growth modelling.

3

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

### 8 **3.7 Recruitment model**

9 The probability of ingrowth was estimated at the scale of individual 10 by 10 m  
10 gridsquares as a function of diameter independent competition index  $C$ . The competition  
11 index was calculated for a hypothetical tree with  $D$  of 5 cm at the centre of each  
12 gridsquare. This was used to calculate the predicted growth rate associated with a  
13 particular species group and grid-square, using the model calibrated for growth (eqn. 4,  
14 section 3.6). The growth rate for all gridsquares was binned into a histogram for each  
15 species group.

16

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

$$22 \quad F = \frac{N_F}{N_G} \quad (12)$$

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

6

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

9

10 No data were available to estimate  $T_I$ , the ingrowth time parameter. The predicted  
11 diameter increments,  $I$ , of trees with DBH of 5 cm and a diameter-independent  
12 competition index of -250 (very low competition in unlogged forests) were used in an  
13 estimation of the “ingrowthtime” parameter  $T_I$ :

$$14 \quad T_I = \frac{5}{I} \quad (13)$$

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

### 18 **3.8 Mortality model**

19 The mortality probability was modelled as a function of diameter. To obtain the mortality  
20 probability as a function of diameter, it was necessary to split the data into diameter  
21 classes, and to count the number of mortality observations and the number of live-tree  
22 observations for each class. This was performed for each species group. Diameter class



1 widths were allowed to vary, within some limitations. Class boundary were forced at a  
2 diameter of 20 cm, since the Jari data had a minimum DBH of 20 cm. The smallest  
3 diameter class had a lower bound at 5 cm. The upper bound of the largest diameter class  
4 was 1.5 times the size of the largest mortality observation, for each species group. The  
5 mean value of tree diameter,  $D$ , was used to describe each bin rather than the mid-point  
6 as the diameter distribution was not linear.

7

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

$$10 \quad A = \frac{1}{Y} \quad (14)$$

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

14

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

19

20 During model tuning for this model, as for other models (Phillips *et al.*, 2002a; 2002b),  
21 the performance relating to large trees was found to be poor. This is unsurprising, since  
22 little data were available to describe the behaviour of mortality of large trees.  
23 Consequently, mortality probability is increased in the model for trees with DBH above a

1 specified threshold (the  $D_{95}$  variable in eqn. 6) by a percentage per cm DBH,  $m_2$ . The  
2 resulting values of the parameters are shown in Table 6.

### 3 **3.9 Damage mortality model**

4 Model simulations with some, un-calibrated, tree fall showed that any gap formation due  
5 to tree fall led to the ingrowth of more pioneers (trees of species group 7 and 9) than were  
6 observed in the PSP, even in the PSP with the most pioneers. This led to the conclusion  
7 that the PSP were perhaps (deliberately, or by chance) located in forest without  
8 significant gaps. This is possible, because the plots are small, and field experience shows  
9 the space between the gaps to be relatively large.

10

11 An analysis of the data from the Intensively Studied Plots (ISP) of the Dendrogene  
12 project (<http://www.cpatu.embrapa.br/dendro/index.htm>) was undertaken in an attempt to  
13 establish the frequency and size of gaps. The ISP block 6 comprises a square 100 ha of  
14 forest, in which the positions of all trees with a DBH greater than 20 cm are recorded.  
15 One enumeration of this plot has been made.

16

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

1

2 This process selected 10 clusters, with an average area of 0.4 ha, that were more than 50  
3 % made up of zero-tree grid-squares. The conclusion is that 5 % of the area is in 0.4 ha  
4 areas in which 50 % or more of the 10 m by 10 m grid-squares have no trees above 20  
5 cm. Gaps have no trees above 20 cm, however, and the area of the cluster was known to  
6 be a maximum. Thus it is reasonable to refine the previous conclusion to the statement  
7 that, “about 2 % of the area is in 0.2 ha areas with 100 % of the grid-squares having no  
8 trees with diameter above 20 cm”.

9

10 The possibility of observing this from a random distribution of trees was tested. The  
11 positions of the 16,111 trees observed in the ISP were regenerated according to a flat  
12 random distribution throughout the ISP, and the analysis was repeated. This process was  
13 repeated 10 times. The mean “proportion of cluster area made up by zero-tree grid-  
14 squares for the cluster with the largest value” was  $0.52 \pm 0.01$ , and the mean “number of  
15 clusters with that proportion greater than 0.5” was  $1.0 \pm 0.2$ . Since 10 such clusters were  
16 observed in the ISP, it is concluded that the trees are not distributed among the grid-  
17 squares randomly, and that gaps were observed.

18

19 Although the number-density and size of gaps was estimated, the dynamics of the gaps  
20 were not known and no data were available to evaluate this. If a gap exists for 5 years,  
21 that means over a period of 5 years 10 gaps of 0.2 ha appear in 100 ha, which  
22 corresponds to 2 gaps per year, or 1 per 50 years per ha. Similarly, if a gap exists for 10  
23 years that means 1 per 100 years per ha, and if a gap exists for 2 years, that means 1 per

1 20 years per ha. Since these gaps are defined as being the absence of trees of diameter 20  
2 cm or more, the time for a gap to disappear is the time until a tree within the gap reaches  
3 20 cm. For the pioneer species this was calculated as a minimum of 11 years, using the  
4 SAS program, "GrowthTimeTo20cm.sas". This suggests 1 gap per 110 years per ha,  
5 which was used to tune the model.

6

7 The area of damage, in this model, for a tree of diameter 80 cm, is 0.13 ha. This is taken  
8 as a minimum diameter for a tree to fall and create a gap, leading to an average gap size  
9 of around 0.2 ha every 110 years.

10

11 It should be noted that the average area of damage observed in the ISP plot, and  
12 simulated by this model, was 0.2 ha. To avoid the edge effects dominating simulations,  
13 the minimum recommended plot size would be 1 ha for simulations using this model.

## 1 4 Results and discussion

### 2 4.1 Model evaluation and validation

3 The performance of the model was evaluated using a long time-sequence of real data. The  
4 longest time sequence available is 16 years, for the plots from Tapajos km 67. These plots  
5 are described by Silva *et al.* (1995). They were logged in 1979, and the plots were set up  
6 in 1981. The most recent enumeration of the plots was made in 1997. There are 36 plots,  
7 each 0.25 ha. The data from 1981 were used to initialise simulations that were run for 16  
8 years, after which the simulated forest data were output to be compared with the real data  
9 from the most recent enumeration of the plots. Results are shown for all species groups in  
10 Figure 3 and for each species group in turn in Figure 4.

11

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

16

17 The time period of 16 years was sufficient to cover much of the complex forest dynamics  
18 following a heavy logging event. The general trends of the model reflected those of the  
19 data well (see Figure 3). For many species groups, the simulated behaviour, in terms of  
20 the number of trees and sum of basal area, agreed well with the real data (see Figure 4).

21

1 A notable exception to this was the number of trees after year 8 for many species.  
2 Following logging, the reduced competition in many areas led to increased recruitment of  
3 most species groups. Perhaps, in the real forest, there was over-crowding of the gaps by  
4 small trees, leading to increased mortality of the small trees in the following years. The  
5 model does not include dependence of competition on the probability of mortality  
6 (although this relationship was tested during model development), and increased  
7 mortality in the small trees is not observed. The growth of these small trees will be  
8 inhibited by the competition, however, so that, even while the number of trees was over-  
9 estimated, the basal area is well modelled at the end of the validation period.

10

11 Other limitations in the ability of the model in this particular case should be born in mind  
12 when considering the results. (1) During and after simulated logging, SYMFOR models  
13 damaged areas of forest where even seedlings and saplings have been cleared and will  
14 take some time to regenerate. The simulation here was initialised with data from forest  
15 that was already logged over, and thus the areas of damage were not modelled in  
16 SYMFOR. In practice the gaps will exist for longer than simulated here, because  
17 SYMFOR assumes that seedlings exist in the absence of cleared gaps. (2) The plots used  
18 in this study were 0.25 ha, which is the same size as the field of influence used in  
19 competition modelling (see Figure 1). Since plot-wrapping is used to avoid edge effects,  
20 the comepetition is likely to be almost homogeneous across each plot, and a lot of the  
21 spatial elements of the competition cannot be used.

22

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

3 • Tuning has a strong effect on the final model balance between growth,  
4 recruitment and mortality for the different species groups. The model was tuned to  
5 the situation of unlogged forest, but validated for logged over forest. The  
6 similarity between the data and simulation results show that the basic model form,  
7 balanced by tuning, represents well the forest dynamics.

8 • The sub-models of growth, recruitment, mortality and logging were developed  
9 separately, tuned to work together for unlogged forest, and validated together on  
10 logged-over forest.

11 • The data used for validation were a sub-set of the data used for model calibration,  
12 from one particular region. The model may be expected to represent the average  
13 behaviour of all regions used for calibration, and not to represent a single region,  
14 although this was the case for validation and would normally be the case in a later  
15 analysis.

16 Given these considerations, the validation is expected to be a rigorous test of the model.

## 17 **4.2 Simulation of a management strategy**

18 Forest management plans in the Brazilian Amazon are generally approved at present if  
19 they demonstrate a strategy of harvesting a target timber volume of 40 m<sup>3</sup> per hectare on  
20 a cutting cycle of 30 years (ref, Ian?). The minimum diameter for harvested trees is 45  
21 cm. The effects of this strategy on standing stock, harvest and species composition,  
22 applied over several cycles to initially primary forest, was examined using the ecological  
23 model described in this paper.

1

2 The management model in SYMFOR uses utilisation group data for each tree in the input  
3 file. For ingrowth trees, the utilisation group value is assigned stochastically according to  
4 the proportions observed in the input file for a given ecological species group. In these  
5 simulations two utilisation groups were used, representing either commercial or non-  
6 commercial status. This status was allocated on the basis of records of species that were  
7 logged in the PSP data (described in section 3.2). In practice, some large trees of  
8 commercial species are left in the forest because of poor form or because they are hollow.  
9 A stem quality value between 0 and 1 is assigned to each tree stochastically when it first  
10 enters the model. A stem quality limit was used to prevent harvest of all trees with a stem  
11 quality lower than 0.3. Cutting of lianas prior to logging means that when simulated  
12 felled trees fall, they do not create as much damage (tree mortality) as for natural  
13 mortality. Instead, damage was simulated as if lianas were not present in the forest (see  
14 Phillips *et al.*, 2002b). The skid-trail pattern and damage associated with extracting the  
15 log from the forest was calibrated according to damage levels observed in the PSP data  
16 described above (section 3.2). Tree selection for logging was made in a two-step process,  
17 first identifying the trees that passed all logging requirements, then selection of the  
18 qualifying trees at random until the required volume had been reached, or until there were  
19 no more qualifying trees.

20

21 10 plots were simulated for 160 years, with logging in year 4 and at 30 year intervals  
22 subsequently. The plots were square 1 ha plots formed by joining four 0.25 ha PSP  
23 records from the Tapajos region. The 0.25 ha plots used were from unlogged forest, and



1 located as close as possible to each other. Since the model contains stochastic elements,  
2 10 repeated simulations were made for each 1 ha plot, and mean results calculated for  
3 each plot over all repetitions. Final results were then calculated as the mean and standard  
4 error over all plots.

5

6 Results of the simulations are given in Figures 5-9, and Table 7. Figure 5 shows the  
7 standing volume (for all trees with a diameter greater than 5 cm) as a function of  
8 simulation time. The standing volume decreases over the period, although the decrease  
9 slows with each successive harvest as the forest approaches a periodic equilibrium.

10

11 Figure 6 shows the harvested volume for each logging operation, and Figure 7 shows the  
12 standing commercial volume (trees that pass all harvesting requirements) as a function of  
13 simulation time. It may seem that if the average harvest is less than  $40 \text{ m}^3 \cdot \text{ha}^{-1}$  then there  
14 should be no residual standing commercial volume. The simulation limited the possible  
15 harvest to  $40 \text{ m}^3$  *per plot*, however, rather than as an average over all plots. Some plots  
16 had residual commercial volume while others did not attain their target  $40 \text{ m}^3$ . The  
17 possible average concession-wide harvest would be equivalent to the average commercial  
18 volume before the harvest. The logging strategy limited the harvest for the first three  
19 harvests for any given plot, or the first four harvests for a larger scale area. After that  
20 time, the availability of commercial timber limited the harvest.

21

22 Figure 6 shows the harvested volume broken into constituent hardwood and lightwood  
23 components. This was possible by using the ecological species grouping (see section 3.5)

1 data for the harvested trees. The commercial species within species group 7 (fast growing  
2 pioneers) were assumed to be lightwoods. These are dominated by *Jacaranda copaia*  
3 (Bignoniaceae). Harvested trees from other species groups were assumed to be  
4 hardwoods. It is clear that the harvested volume decreases with each subsequent harvest  
5 and fails to reach the target  $40 \text{ m}^3 \cdot \text{ha}^{-1}$  on average in the fourth harvest. At the same time  
6 the proportion of the harvest made up of hardwoods also decreases, which may have a  
7 significant effect on the financial viability of future harvests.

8

9 Figure 8 and Figure 9 show that although the target harvested volume was attained for the  
10 first three cycles, the cost of the logging operation went up. An increase in the number of  
11 stems felled and extracted means more work for the logging team and equipment, and  
12 associated costs. A decrease in mean stem volume is likely to lead to increased wastage at  
13 the sawmill. These factors suggest that profits from the first harvest of primary forest will  
14 not be sustained even if timber yield is.

15

16 The species composition of the forest in terms of ecological function changes as a result  
17 of logging activity. Table 7 compares the composition of the forest before the first harvest  
18 (year 4) with that before the last simulated harvest (year 154). The notable differences are  
19 the increase in the proportion of the number of trees and standing volume made up by  
20 pioneer species, and the decrease in the proportion of the standing volume made up by  
21 climax and upper canopy species. As may be expected, this suggests that the forest would  
22 take significantly longer than 30 years to recover from the removal of  $40 \text{ m}^3 \cdot \text{ha}^{-1}$  of some  
23 species.

### 1 4.3 Discussion

2 The spatial aspect of SYMFOR allows a process-based spatial representation of the  
3 effects of logging activity. The individual-based, spatially explicit nature of the  
4 ecological model described here leads to the implicit simulation of gap dynamics and  
5 succession through a distance-dependent competition index. While competition index  
6 values in the simulation are within the range encompassed by the calibration data, usage  
7 of the ecological model remains valid for describing the response of the forest to a  
8 disturbance. This allows the simulation of management strategies that were not  
9 represented by the calibration data.

10

11 The application of the model demonstrated quantitatively many of the trends that may be  
12 expected resulting from the logging strategy. It showed the change in species  
13 composition, the change in composition of harvested timber, the changes in quantities of  
14 harvested timber and the size and number of trees harvested. Linkage of these results to a  
15 suitable financial model of concession operations would enable quantitative estimations  
16 of the financial viability of repeated harvesting of primary forest.

17

18 The effects of the stochastic components of the model are accounted for in simulation  
19 results by the calculation of mean values with an associated standard error. Other sources  
20 of uncertainty in simulation result are the systematic errors arising from the assumptions  
21 made in the model and from parameter value uncertainties. These were quantified for an  
22 ecological model developed for Indonesia (Phillips *et al.*, 2002b), and were found to  
23 generally increase with simulation time. The effects of such systematic errors on

1 simulation results are likely to be very similar for two different management models,  
2 however. This means that the systematic error on the difference between the results from  
3 two management strategies would be close to zero. In general, therefore, more accurate  
4 simulation results can be expected for comparisons between management scenarios than  
5 for absolute predictions.

1 5 Conclusions.

2 The ecological model described, implemented in the SYMFOR framework, forms a tool  
3 for producing information describing the likely future state of forests given alternative  
4 management interventions. It has been used to examine the effects of current  
5 management practice in Brazil, if continued for several cutting cycles, and shows that  
6 financial benefits from logging will decrease with successive harvests, even before the  
7 target yield cannot be sustained. The ecological implications of the management scenario  
8 are that the proportion of pioneer species will increase significantly while the large  
9 climax and canopy species will decrease. This can be expected to have knock-on effects  
10 in terms of the conditions in the forest experienced by other flora and fauna.

11

12 Application of this model in the Brazilian Amazon would enable the generation of  
13 knowledge regarding the effects of alternative management scenarios, and increased  
14 ability to manage the forests more sustainably.

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5

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10

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20

21





- 1 **Table 1: The values of the parameters in the equation modelling absolute**
- 2 **competition index as a function of diameter.**

Parameter	Value
$b_0$	6004
$b_1$	-1.580
$b_2$	-130.8

1 **Table 2: Minimum number of trees in a taxon for the permanent sample plots.**

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

1 **Table 3: A summary of the characteristics of the species groups. P95 is the 95**  
 2 **percentile on the cumulative diameter frequency distribution (cm), G is the growth**  
 3 **rate (cm.yr<sup>-1</sup>), N<sub>t</sub> is the number of trees, and N<sub>s</sub> is the number of species in each**  
 4 **group. It should be noted that the data that were used to produce this table include**  
 5 **data from recently logged-over forest.**

Group Name (reference)	P95	G	Dominant members	N <sub>t</sub>	N <sub>s</sub>
1 Medium-growing mid-canopy	41.8	0.21	Sapotaceae, Lauraceae, <i>Guatteria poeppigiana</i>	8978	87
2 Slow growing understorey	15.9	0.09	<i>Rinorea flavescens</i> , <i>Duguetia</i> <i>echinophora</i> , <i>Talisia longifolia</i>	5964	48
3 Medium growing mid-canopy	57.2	0.29	<i>Geissospermum sericeum</i> , <i>Carapa guianensis</i> , <i>Pouteria</i> <i>spp.</i>	4851	76
4 Slow growing lower canopy	27.7	0.18	<i>Protium apiculatum</i> , <i>Rinorea</i> <i>guianensis</i> , <i>Neea spp</i>	11016	101
5 Medium growing upper canopy	72.5	0.26	<i>Couratari oblongifolia</i> , <i>Minguartia guianensis</i>	2732	34
6 Fast growing upper canopy	76	0.54	<i>Sclerolobium chrysophyllum</i> , <i>Trattinickia rhoifolia</i> , <i>Didymopanax morototoni</i>	1356	29
7 Fast growing pioneers	35.8	0.54	<i>Inga spp.</i> , <i>Sloanea froesii</i> , <i>Bixa arborea</i> , <i>Jacaranda</i> <i>copaia</i>	8606	49

---

8	Emergents - climax	104	0.37	<i>Manilkara huberi</i> , <i>Goupia</i> <i>glabra</i> , <i>Hymenaea courbaril</i> , <i>Dipteryx odorata</i>	1409	36
9	Very fast growing pioneers	38.7	1.26	<i>Cecropia sciadophylla</i> , <i>Jacaratia leucoma</i> , <i>Jacaratia</i> <i>spinosa</i>	2007	9
10	Very fast growing upper canopy	78.2	0.94	<i>Tachigalia myrmecophylla</i> , <i>Sclerolobium tinctorium</i>	662	16

---

1

1 **Table 4: Parameters for the Pibiri growth model (eqn. 4) and the associated**  
 2 **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

3

1 **Table 5: Parameter values for the recruitment model (eqn. 7, section 2.4).**

Group	$r_1$	$r_2$	$r_3$	$R^2$	$T_I$
1	0.029	-3.05	0.0065	68	18
2	0.045	2.4E-11	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

2

1 **Table 6: Parameters for the mortality model, equation 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	3.75
3	1.85	1.1	0.2	57	15
4	2.9	2.4	0.5	27	5
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
9	8.9	4.5	0.5	38	5
10	4.3	4.0	0.5	78	15

2

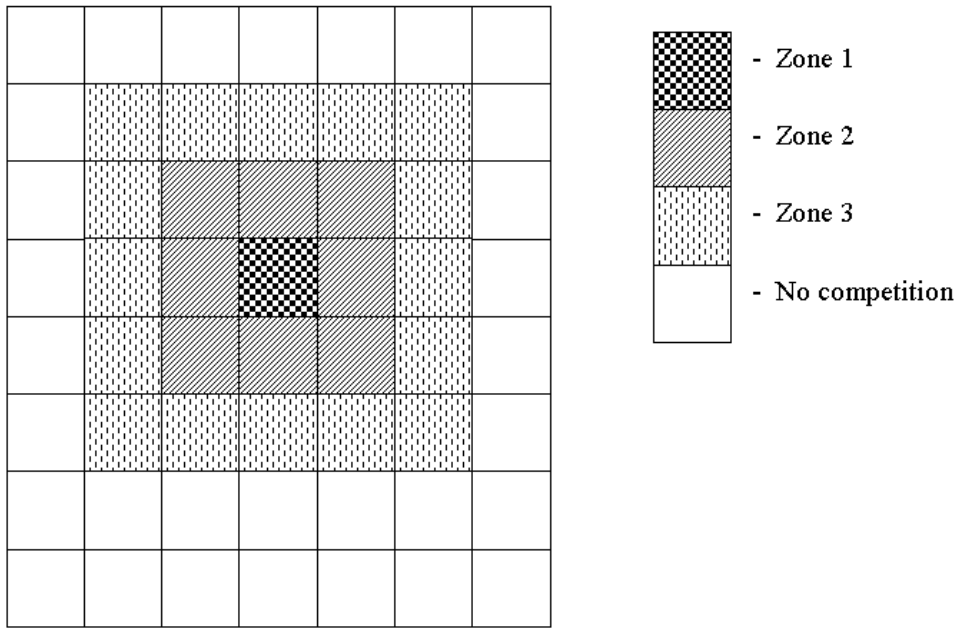


1 **Table 7: The percentage of the total number of trees, N, and the percentage of the**  
2 **total standing volume, V, made up of each species group. The difference ( $\Delta N$  and**  
3  **$\Delta V$ ) between the primary forest situation (N and V), and the situation immediately**  
4 **preceding the sixth logging operation shows the simulated species composition**  
5 **change as a result of repeated logging operations. Large changes are shown in bold.**  
6 **The uncertainties are calculated as standard errors from the mean value over all**  
7 **simulated plots.**

Species group	N	$\Delta N$	V	$\Delta V$
1. Medium-growing mid-canopy	21.5 ± 0.6	<b>-4.0 ± 0.6</b>	17.8 ± 1.7	-4.8 ± 1.7
2. Slow growing understory	18.8 ± 0.8	-1.3 ± 0.8	5.8 ± 0.3	+0.0 ± 0.3
3. Medium growing mid-canopy	7.8 ± 0.4	-1.9 ± 0.4	16.2 ± 1.3	<b>-8.5 ± 1.3</b>
4. Slow growing lower canopy	31.2 ± 1.6	-2.4 ± 1.6	15.5 ± 1.0	-1.6 ± 1.0
5. Medium growing upper canopy	5.4 ± 0.2	-1.3 ± 0.2	14.4 ± 1.2	-7.0 ± 1.3
6. Fast growing upper canopy	2.5 ± 0.2	+0.3 ± 0.2	6.1 ± 0.9	+0.0 ± 0.9
7. Fast growing pioneers	9.4 ± 0.6	<b>+7.5 ± 0.6</b>	5.5 ± 0.4	<b>+15.7 ± 0.5</b>
8. Emergents - climax	2.2 ± 0.1	-0.3 ± 0.1	16.6 ± 2.8	<b>-10.4 ± 2.8</b>
9. Very fast growing pioneers	0.7 ± 0.1	<b>+3.5 ± 0.2</b>	0.5 ± 0.1	<b>+17.1 ± 0.6</b>
10. Very fast growing upper canopy	0.7 ± 0.1	0.0 ± 0.1	1.4 ± 0.3	-0.4 ± 0.3

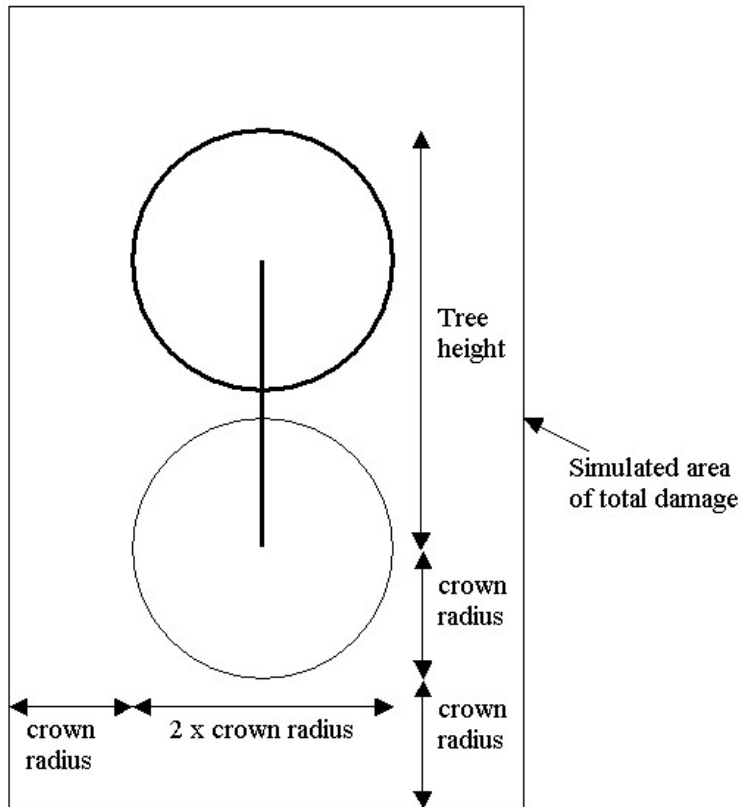
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- 1 **Figure 1: The different zones of competition, for a tree in zone 1. The competition**
- 2 **indices from these different zones may be combined in different ratios, leading to**
- 3 **competition indices that depend differently on distance from the object tree.**



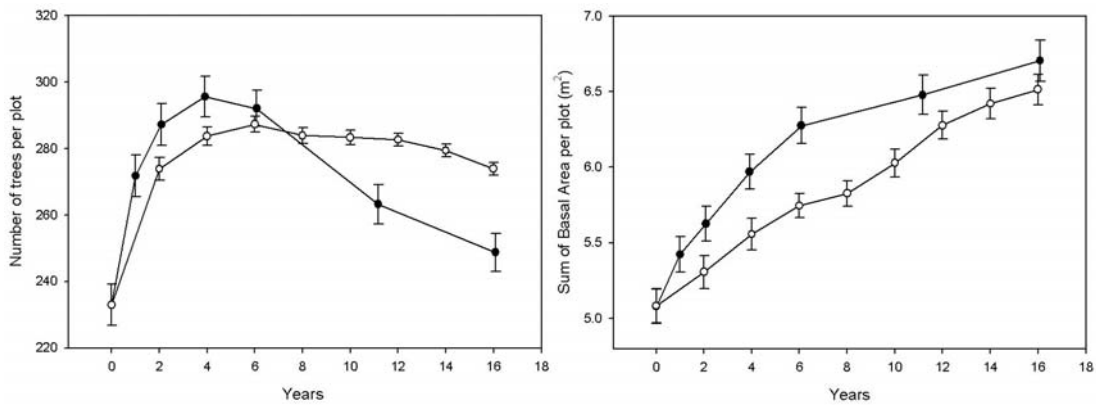
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- 1 **Figure 2: The shape and dimensions of the rectangular area of damage created by**  
2 **the fall of a large tree. The heavy lines represent the stem and crown of the tree in**  
3 **their positions after tree-fall, with the lighter circle representing the original**  
4 **position of the crown before tree fall.**



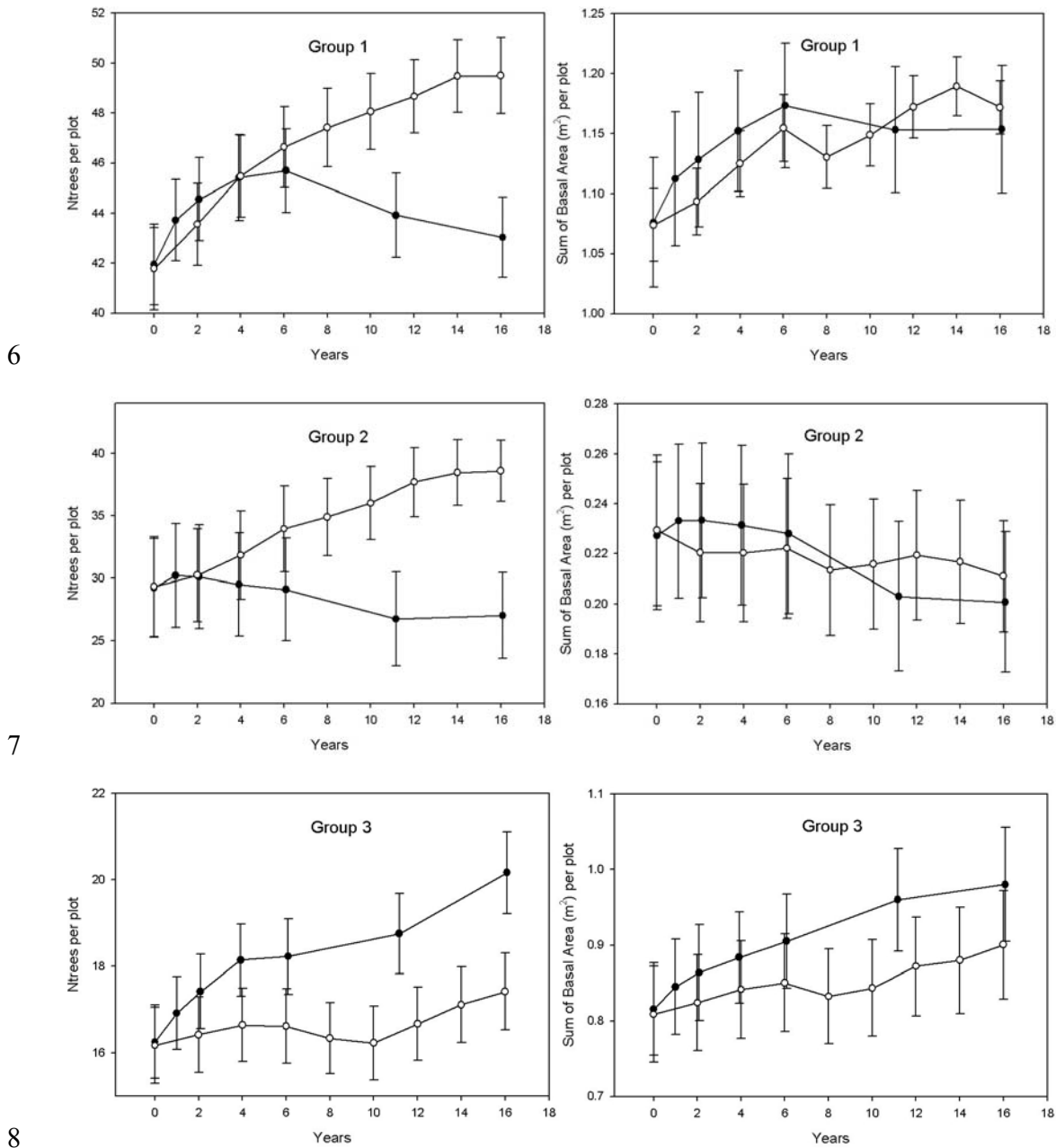
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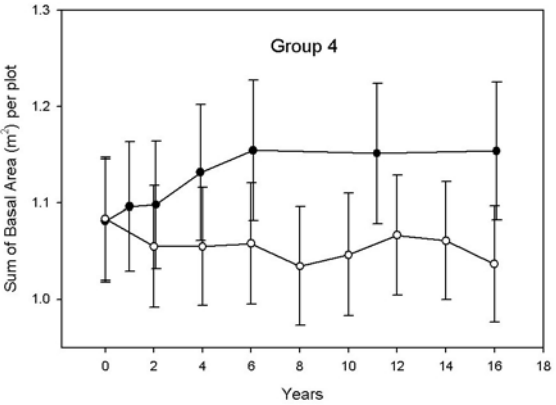
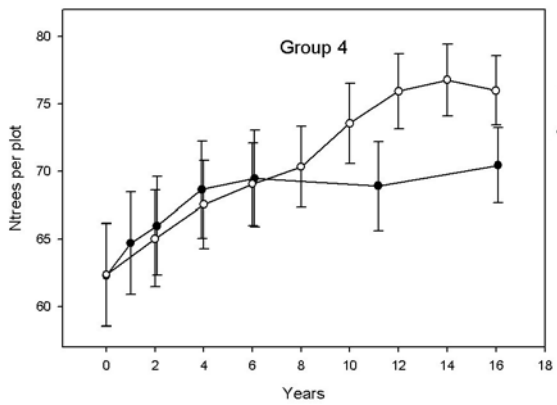
1 **Figure 3: The variation in the mean number of trees, and the mean sum of basal**  
2 **area, per plot for the Tapajos km 67 plots (starting two years after logging) for the**  
3 **real data (black) and the simulation model (white). The error bars are the standard**  
4 **error on the mean over all plots, and therefore arise from the variation between**  
5 **plots.**



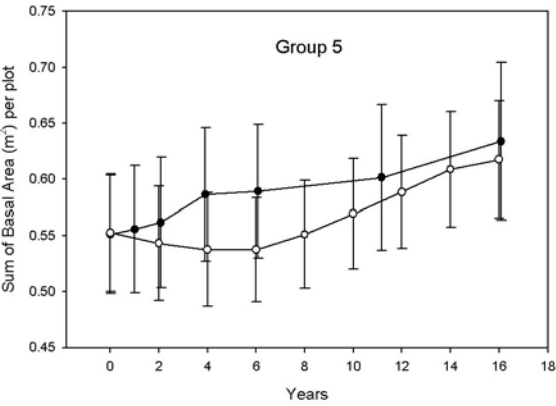
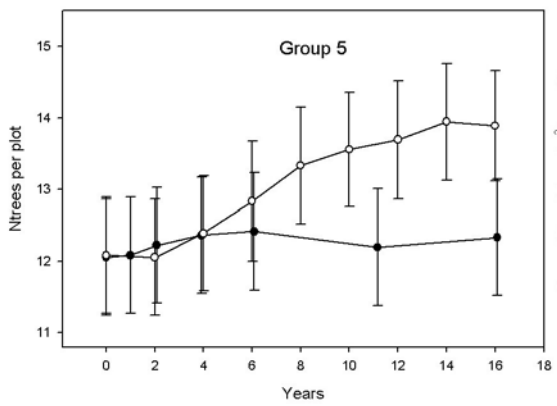
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1 **Figure 4: The variation in the mean number of trees, and the mean sum of basal**  
 2 **area, per plot for the Tapajos km 67 plots (starting two years after logging) for the**  
 3 **real data (black) and the simulation model (white), shown for each species group**  
 4 **separately. The error bars are the standard error on the mean over all plots, and**  
 5 **therefore arise from the variation between plots.**

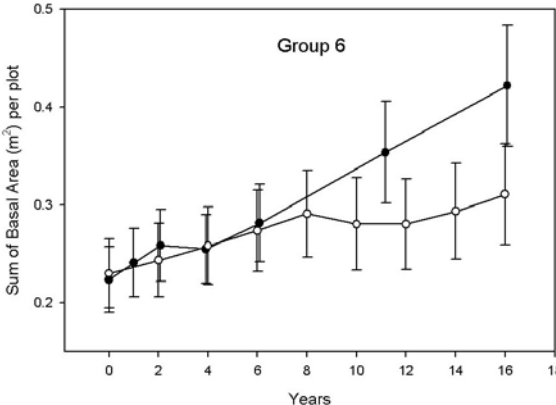
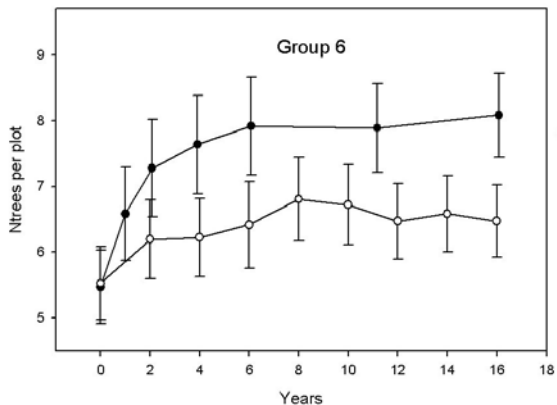




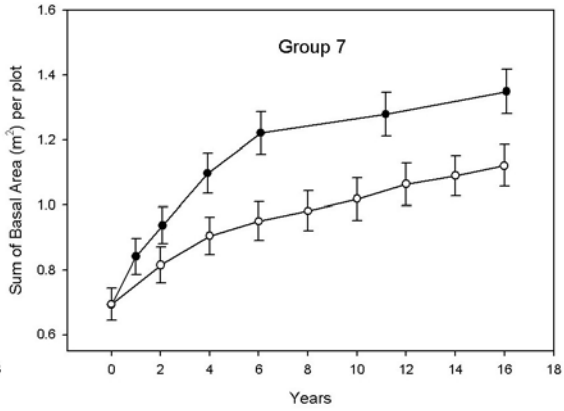
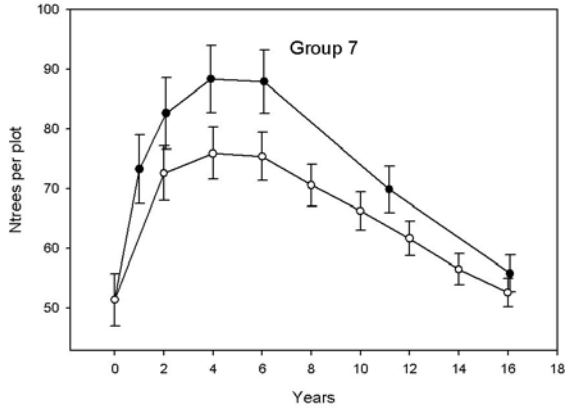
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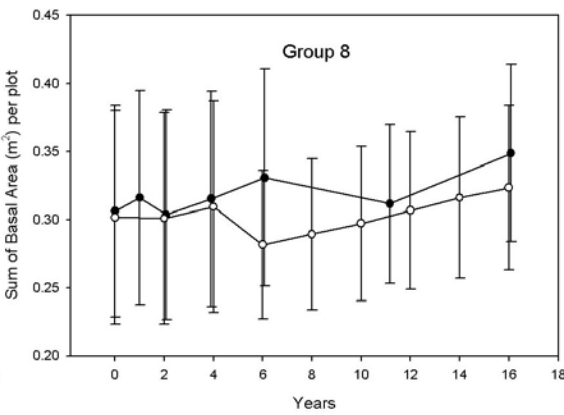
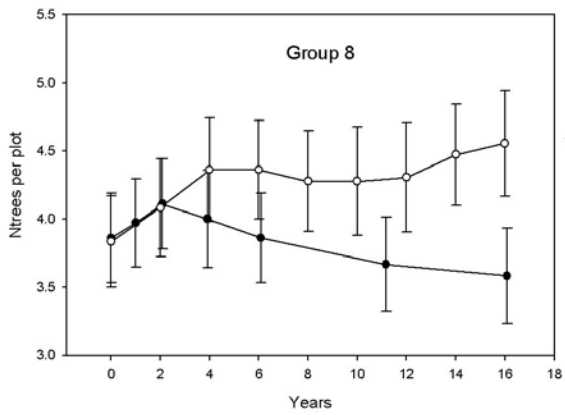
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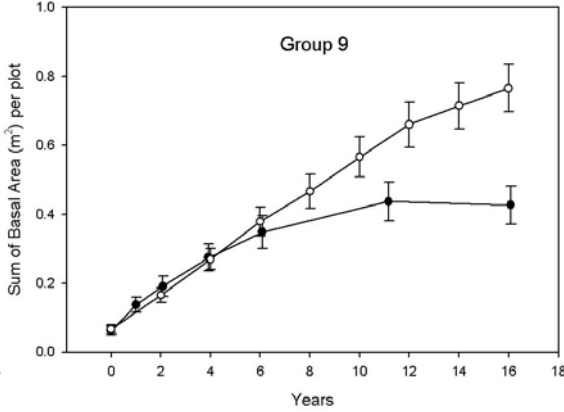
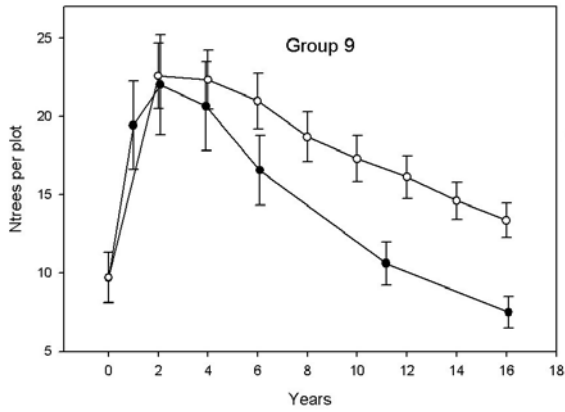
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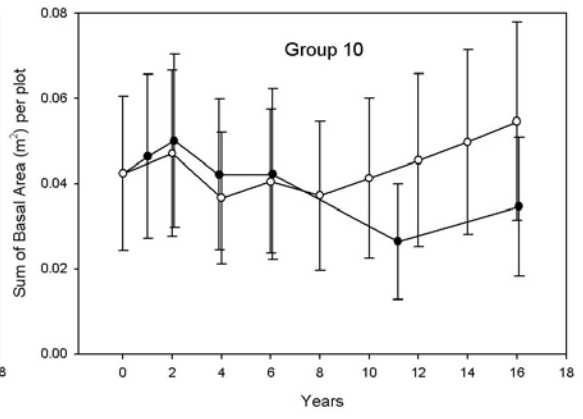
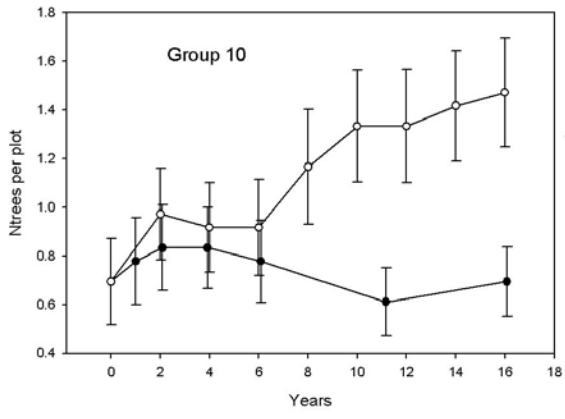
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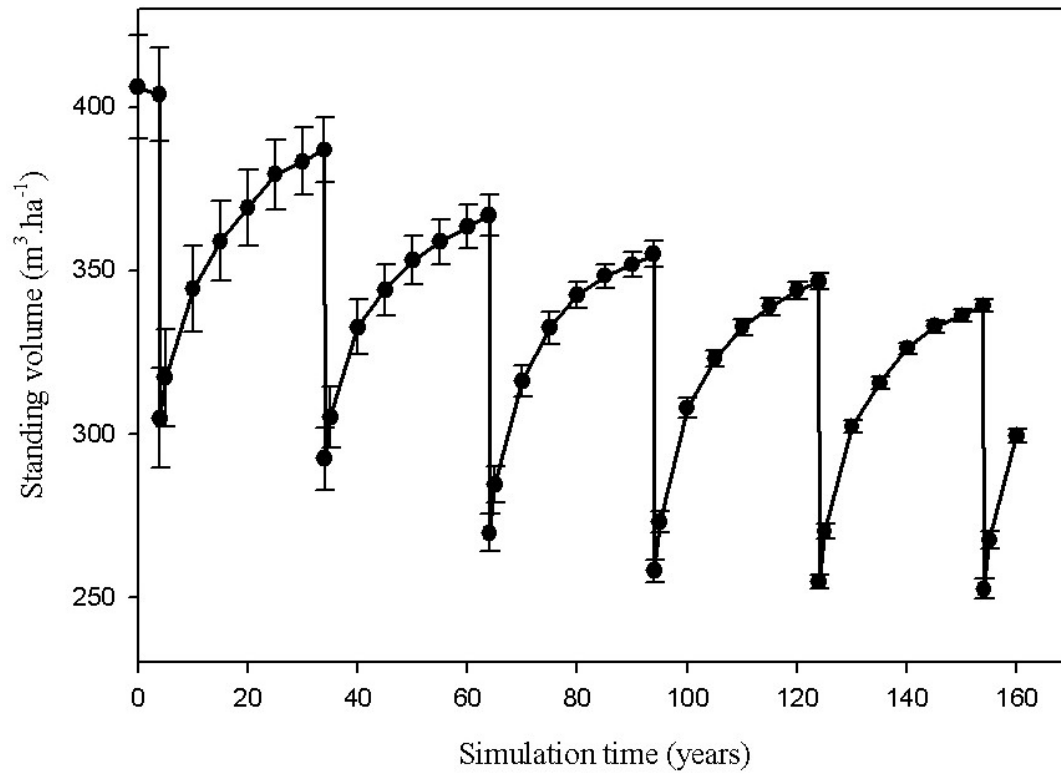
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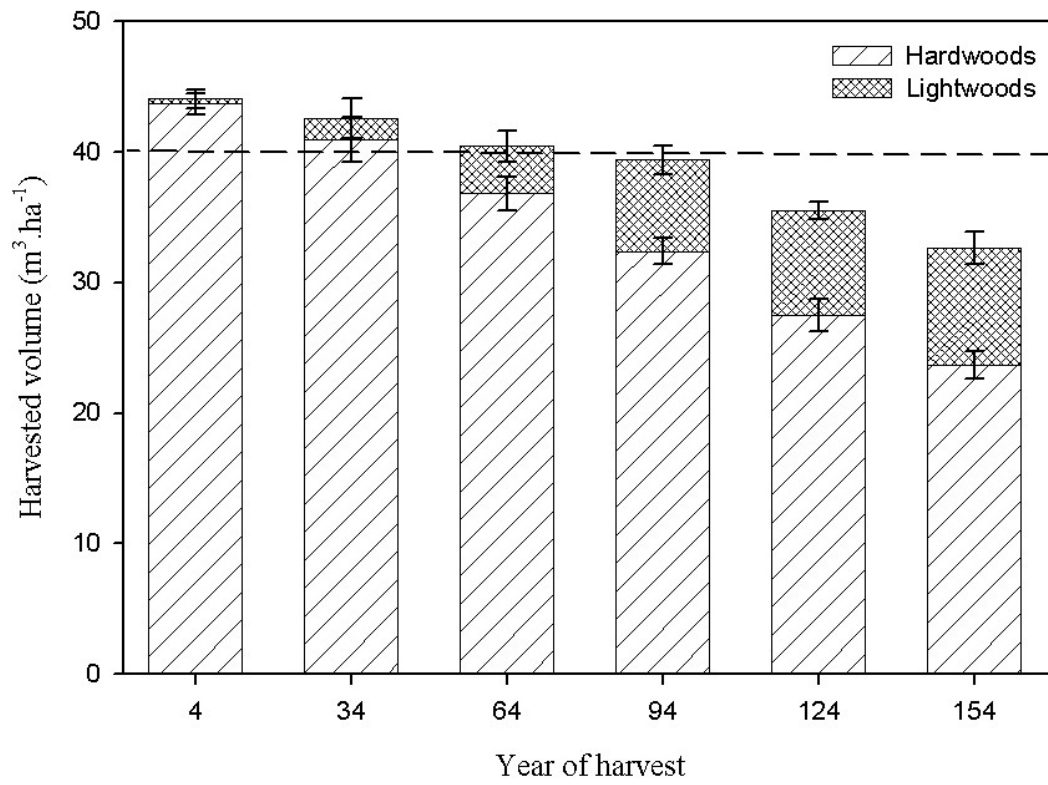


- 1 **Figure 5: The simulated standing volume ( $\text{m}^3 \cdot \text{ha}^{-1}$ ) of all trees with diameter greater than 5 cm for the period covering 6 logging cycles, beginning with primary forest.**
- 2

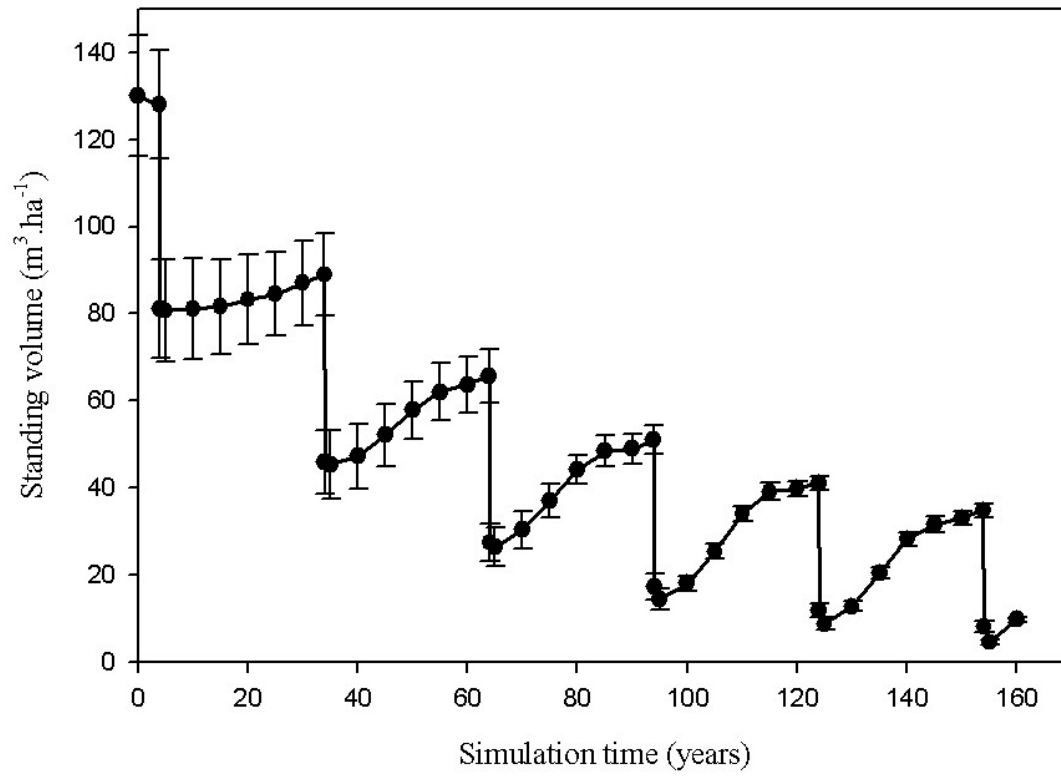


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1 **Figure 6: The harvested timber volume per hectare, for each simulated harvest. The**  
2 **total harvest is comprised of the lightwoods (mostly *Jacaranda copaia*), and the**  
3 **hardwoods.**

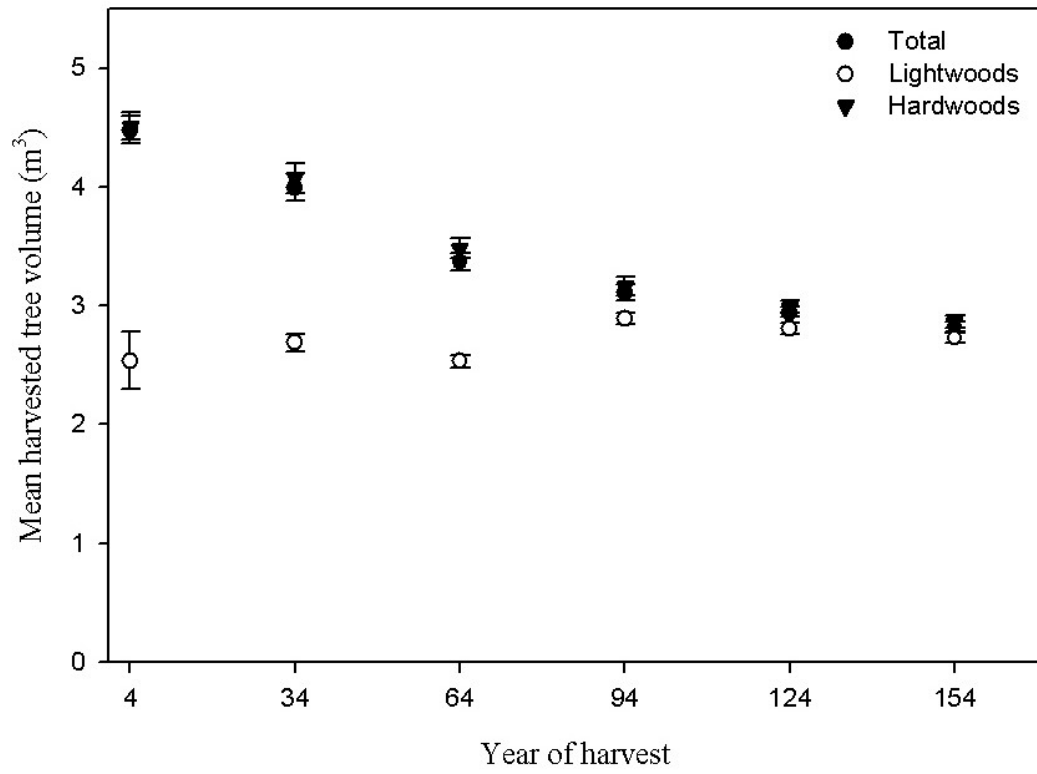


- 1 **Figure 7: The simulated standing volume ( $\text{m}^3 \cdot \text{ha}^{-1}$ ) of all commercial trees for the**
- 2 **period covering 6 logging cycles, beginning with primary forest.**



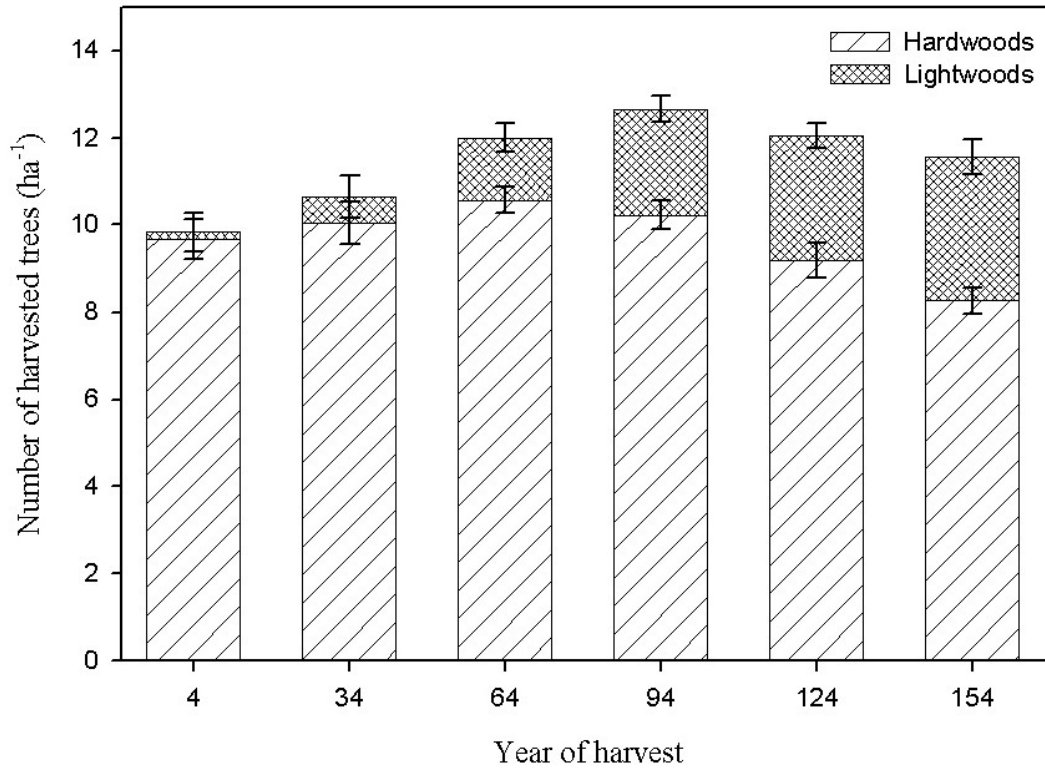
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- 1 **Figure 8: The mean volume of harvested trees, shown for the total (all harvested**
- 2 **trees) and its constituent hardwood and softwood parts.**



3

- 1 **Figure 9: The number of trees harvested per hectare, shown for the total (all trees)**
- 2 **and its constituent hardwood and softwood parts.**



- 3
- 4