ELSEVIER

Forest Ecology and Management 130 (2000) 141–157

Forest Ecology
and
Management

www.elsevier.com/locate/foreco

An empirical cohort model for management of *Terra Firme* forests in the Brazilian Amazon

Denis Alder[a,*], J.N.M. Silva[b]

[a] *9 Stansfield Close, Headington, Oxford OX3 8TH, UK*
[b] *EMPRAPA Amazônia Oriental, PO Box 48, 66095-100, Belem, Pará, Brazil*

Received 15 April 1999; accepted 15 June 1999

Abstract

A model to project forest growth in the *Terra Firme* forests of the eastern Amazon is described. It is based on 12–17 years measurements from experimental plots at Jarí and Tapajós. Forest stands are represented by cohorts of species group, diameter, and defect. There are 54 species groups, with a robust diameter increment function fitted to each, tables of mortality by crown and defect status, and recruit lists by disturbance level and locality. Stand level functions partition trees by crown status, and modify growth for stand density. Recruitment is a function of basal-area losses. Evaluation compares model performance with two experiments involving heavy felling in Tapajos State Forest. At one site, total bole volume growth of all species over 45 cm DBH was 2.56 m^3 ha^{-1} $year^{-1}$ over 17 years, whereas the model projected 3.13 m^3 ha^{-1} $year^{-1}$. At the other site, actual growth over 12 years was 0.39 m^3 ha^{-1} $year^{-1}$, with the model giving an identical result. Both felled and control plots are compared in the study and accurately simulated. Some weaknesses in the model are discussed. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Growth modelling; Species groups; Increment; Mortality; Logging damage; Natural tropical forest; *Terra Firme* forest; Tapajos; Amazonia

1. Introduction

The sustainable management of natural tropical forests for timber production requires effective systems for predicting future forest growth and yield in response to various human interventions. Because of the complexity of the forest, computer simulation methods have dominated this field. Reviews of the methodology are provided by Vanclay (Vanclay, 1994, 1995) and Alder (1995). Methods are generally divided into empirical models, based on extrapolation of data from permanent sample plots; and process-based models which attempt to simulate eco-physiological processes using a limited number of experimentally derived parameters.

The classical approach to empirical modelling of natural forest is the method of stand projection by diameter classes. Before the advent of computers, such models were calculated by hand using broad diameter classes and few species groups. There was no interaction between stand density and growth rates. Such approaches probably date back to the 1860s (Brasnett, 1953). Few of the publications relating to this type of model attempt any assessment of accuracy,

---

[*] Corresponding author.
E-mail addresses: d-alder@eurobell.co.uk (D. Alder), natalino@captu.embrapa.br (J.N.M. Silva)

0378-1127/00/$ – see front matter © 2000 Elsevier Science B.V. All rights reserved.
PII: S0378-1127(99)00196-6

and projections have often been presented uncritically (e.g. Alder, 1990; Howard and Valerio, 1992). Silva (1989) evaluated the STANDPRO stand projection model (Kofod, 1982; Korsgaard, 1988) using data from Tapajós National Forest in eastern Amazonia, and found it generally accurate for short periods, but requiring modification for longer term projections.

In recent times, the inherent computational inefficiencies of diameter class projection when dealing with many species and small diameter classes have lead to the adoption of an alternative empirical approach for natural tropical forests. This is the cohort model, proposed by Vanclay (1989) for his model of the North Queensland rainforests. The cohort method is an empirical method closely related to classical stand projection. Trees are grouped into narrow classes (typically 1 cm wide) of similar species, and possibly other characteristics such as competitive or defect status, which are known as cohorts. Growth is simulated by changing cohort parameters in response to tree and stand functions, whereas in diameter class models trees are 'moved' between classes using various often unsupported statistical assumptions (Alder, 1995, 1977). The forest stand is represented in the model as a list of cohorts, rather than as a table of species by size classes as in classical stand projection methods. Empty classes are not represented in the list, while new cohorts can be created and added to the list by processes such as the splitting of existing cohorts (to emulate competition or defect), or the addition of new cohorts as recruits. The approach is efficient and flexible, and allows a variety of tree and stand dynamic functions to be introduced into the model without difficulty. Alder (Alder, 1995, 1997, 1998a) has adopted this method for simulation models of natural forest in Eastern Amazonia (CAFOGROM), remnant forests in northern Costa Rica (SIRENA), and lowland tropical forest in Papua New Guinea (PINFORM). Several variant models have also been derived from this work. Burslem et al. (1996) produced a version called COSSI adapted to data sets from plots on Kolombangara, Solomon Islands (Whitmore, 1989). Chandrasarker (1997) adapted CAFOGROM to coastal forests in the Sundarabans, Bangladesh.

A common feature of these various models is the limited evaluation to test their accuracy. SIRENA (Alder, 1997) and CAFOGROM (Alder, 1995) have been tested by comparing the general behaviour of the model with expected and known characteristics of natural forest growth and yield. The PINFORM model was subject to more rigorous testing for bias in short-term projections (Alder, 1998b). The general problem is that long-term data does not exist in the localities involved which can be used for comparisons.

The present study discusses improvements that have been made to the original CAFOGROM model for the eastern Amazon *Terra Firme* forests in order to obtain more accurate responses than earlier versions, and presents results from comparisons of the model simulations with two series of experimental plots in Tapajos National Forest.

2. Data sources

The data that provides the empirical basis for the CAFOGROM model is taken from 136 sample plots at two localities: Tapajós National Forest, and on the Jarí Florestal lands in the state of Pará, Brazil. The environment is described in Silva et al. (1996), and comprises a climate with mean monthly temperatures from 24° to 26°C, and average annual rainfall of 1900 mm. Table 1 shows the numbers and measurement periods of the plots, according to the research

Table 1
EMBRAPA research plots included in the CAFOGROM analysis

Location	RP code	Plots	Sample area (ha)	First year	Last year	Measurements
Tapajós	11	48	12	1981	1995	5
	12	36	9	1981	1997	7
	14	12	3	1983	1995	4
Jarí	21	36	36	1984	1994	5
	25	4	4	1984	1994	5
Total		136	64			

Table 2
Numbers of trees, species, and related information in the permanent sample plot database used to develop CAFOGROM

Total (trees × measurements)	217991
Individual trees	52320
Valid increment measurements	168480
Mortality observations	13407
Recruitment observations	16405
Harvested trees	379
Total species	486
Species with 500 + trees	18
Species with 100 + trees	98
Species with 10 + trees	316
Trees of unknown species	5080

plot (RP) codes. Table 2 gives information about the database of measurements from these plots. There are a number of other plots in secondary forests at these sites which have not been included in this study.

The plots at Tapajós are all of 0.25 ha (50 m × 50 m), and are measured completely down to 5 cm DBH. The plots at Jarí are of 1 ha. They are measured down to 20 cm DBH. A sub-sample of 0.1 ha on these plots is measured down to 5 cm DBH. In this article, all references to basal area and recruitment, unless otherwise qualified, relate to this minimum 5 cm limit. Table 2 shows some statistics from the database. It comprises some 217 000 records on 52 000 trees and 486 species. In some cases species identification is only down to the genus level, while ca. 10% of all observations relate to unknown or unconfirmed species. These are mostly smaller trees of rare occurrence. Of these 486 species, some 98 have more than 100 tree records, which represents an approximate minimum for reliable mortality information.

The plots have been subject to various treatments. Silva et al. (1988, 1994a, 1995) describe in detail the layout and execution of the experiment at RP12. It was logged in 1979, removing some 70 m^3 ha^{-1}, and the plots then established in 1981. At that time the mean basal area was ca. 20.1 m^2 ha^{-1}. The RP14 plots are a control series of 12 $\frac{1}{4}$-ha plots which have not been previously logged, and might be characterised as virgin forest. RP 11 comprises an adjacent site of 36 $\frac{1}{4}$-ha plots which were established prior to logging in 1981, logged in 1982, and then re-measured thereafter. These plots were also subject to thinning treatments in 1995, but this is too recent for the growth response to be included in the current analysis. RP11 is designed as a randomised block experiment, but this has not influenced the method of analysis for the growth model, where they are simply treated as discrete permanent plots.

At Jarí, the 1-ha plots are also laid out as a control series of four plots (RP25) which have not been felled or treated, and a randomised block felling and thinning experiment (RP21). Again, the experimental design has not influenced the analysis for the growth model except to the extent that it provides a well-distributed range of felling intensities and stand densities for regression analysis. These plots were also established prior to felling in 1984, and re-measured immediately afterwards. They were also thinned in 1995, but results from this have not been included in the analysis.

3. Formation of species groups

Formation of species groups is a key process in development of models for natural tropical forests. The large number of species (486 in the present data) is not a fundamental problem in the model design. However, many of them are represented by only a few observations. There were 170 species with <10 observations each, which is too few to obtain reasonable estimates of diameter increment in relation to tree size and competitive status. There were 388 species with fewer than 100 trees, which is probably the minimum to obtain estimates of mortality that can be partitioned by factors such as crown position, damage, size, and so on. Different authors have approached the question of forming species groups in various ways. Vanclay (1989) classified species by volume group, logging rule, and growth attributes. Vanclay (1991) used an *F*-test to group growth functions that were not statistically different. Vanclay et al. (1997) propose the use of groups based on morphological attributes. Silva (1989) used groups based on ecological guild (shade-bearers, light-demanders, extreme pioneers) and on commercial attributes. Palms and unidentified trees were assigned distinct groups. Alder (Alder, 1995, 1997) used an ordination method based on two axes: Mean diameter increment, and largest observed tree. He also experimented with the *F*-test method (Vanclay, 1991), but found that for poorly represented species, it resulted in an arbitrary classification that respected neither botanical nor ecological affinities. The large majority of observations entered one or two groups, resulting in a classification of little practical value.

For the present model, an extension of the two-axes ordination method used by Alder (1995) was adopted, designed to give greater ecological coherence within groups. Groups were formed by a mathematical ordination using five species attributes. These were commercial/non-commercial, percentage of trees observed as dominants or emergents, mean diameter increment, mean annual mortality rate, and maximum observed diameter. These variables were transformed in order to achieve a more normal distribution, and somewhat similar scaling, as shown below.

Attribute	Transformation
Commercial of non-commercial	Coded + 8 or -8
Diameter increment, i_d (cm year^{-1})	$\ln(i_d)$
Annual mortality rate, r_m	$\ln(r_m/[1-r_m])$
Proportion of dominant trees, p_d	$\ln(p_d/[1-p_d])$
Largest diameter, d_{max}	$\ln(d_{max})$

These transformations were selected from among several alternatives examined in order to give symmetric, approximately normal data distributions. In summary, diameter increment and maximum diameter were transformed by taking the natural logarithm. The two percentage values were transformed using the logistic function, and the commercial/non–commercial values scaled on the range +8 to −8. Subsequently, all values were re-normalized by the transformation:

$$v_k = (x_k - \mu)/\sigma$$

where x_k is the original variate for species k, μ the mean for all species, σ the standard deviation and v_k the re-normalized variate for species k.

The ordination was carried out on the transformed, re-normalised variates, in order to minimise scaling and distribution effects on the groups formed (Green and Carroll, 1978; Collett, 1991). Initial group centroids were first established using species which were common, using an integer grid in the five-dimensional ordination space to avoid group centroids with too great a proximity. Other species were then compared with all possible centroids on the basis of Euclidean distance in the transformed and re-normalized space, and assigned to the most nearest group. The group centroid was not adjusted during this process, but remained identified with the initial value. At the end of the classification, centroids for each group were re-calculated from the assigned grouping, and could be used as initial values for a new iteration. Two or three iterations resulted in stable group centroids.

This method ensures a robust classification that brings together species with similar ecology, maximum size, growth rates, and mortality. Although the commercial attribute enters the classification as a continuous variate for reasons of algorithmic simplicity, it is scaled so that it complete divides the groups between commercial and non-commercial categories.

The resultant groups are shown in Table 3 with some associated statistics. The column headed *Cat.* gives the species category. This is used within CAFOGROM to define treatment and harvesting regimes, and to group species for presentation on output graphs and tables. Within the model, these letters can be changed interactively to give desired groupings. The *Group* column designates a unique three-letter group code. This is the same as the species mnemonic for the most typical species of the group (i.e. both common and near the group centroid). The *principal species* are three most common species within the group. For several groups, there are three or fewer species, in which case, the group is entirely comprised of the listed species. The column headed *Com.* designates fully commercial species with a tick mark. The number of species and the total number of records (trees × measurements) contributing to each group are shown in the next two columns. The *Dom.%* column gives the percentage of observations relating to dominant or emergent trees. This implies trees which are receiving full overhead illumination over the entire upper surface of the crown. Mean diameter increments in cm year^{-1} are given for impeded trees and for dominants. *Impeded* is here simply defined as all trees which are either sub-dominant or understorey trees. The column *AMR%* gives annual mortality rate as a percentage. This is the average percentage of trees which die over a one-year period. The last four columns show the typical size distribution for trees in the species group, using cm diameter classes of 5.00–24.99, 25.00–44.99, 45.00–64.99, and 65.00 cm plus classes. The distribution is shown as the percen-

Table 3
Species groups in the CAFOGROM model and related statistics. See text for explanation of abbreviated column headings

Cat.	Group	Principal species in group	Com.	No. spp.	No. obs.	Dom. %	Diam increment		AMR %	Frequency % by diameter class			
							Imp.	*Dom.*		*5–24*	*25–44*	*45–64*	*65+*
A	CAG	*Carapa guianensis, Brosimum parinarioides, Copaifera multijuga*	✓	8	3138	22.13	0.31	0.60	1.74	65	26	6	3
A	CUO	*Couratari oblongifolia, Manilkara huberi, Caryocar villosum*	✓	7	4111	18.35	0.18	0.47	2.27	69	17	6	8
A	DDM	*Didymopanax morototoni, Macoubea guianensis*	✓	2	444	9.31	0.53	0.97	1.81	90	7	1	2
A	EDU	*Endopleura uchi, Astronium gracile, Trattinickia rhoifolia*	✓	8	1992	10.99	0.25	0.67	1.69	76	15	4	5
A	GOG	*Goupia glabra, Pouteria bilocularis, Hymenaea courbaril*	✓	9	2927	21.90	0.23	0.47	1.19	48	27	11	14
A	LIC	*Licaria canella, Nectandra myriantha, Gustavia hexapetala*	✓	7	2776	5.70	0.24	0.63	3.88	83	13	2	1
A	MEL	*Holopyxidium jarana, Mezilaurus lindaviana, Parkia pendula*	✓	14	3040	10.37	0.16	0.34	0.94	73	20	5	2
A	MNG	*Minquartia guianensis, Iryanthera juruensis, Manilkara bidentada*	✓	3	2955	6.82	0.21	0.25	2.36	61	25	7	6
A	TAM	*Tachigalia myrmecophylla, Erisma uncinatum*	✓	2	1094	13.19	0.42	1.20	4.56	77	13	4	5
A	VIM	*Virola melinonii, Micropholis venulosa, Eperua schomburgkiana*	✓	13	3060	19.37	0.26	0.51	2.00	75	21	3	1
B	BRG	*Brosimum guianensis, Virola cuspidata, Parinari excelsa*	✓	5	1583	3.54	0.19	0.51	2.63	94	6		
B	GUK	*Guarea kunthiana, Cordia scabrifolia, Trymotococus paraensis*	✓	17	2421	1.11	0.09	0.21	4.02	96	4		
B	IRS	*Iryanthera sagotiana, Ocotea spp, Brosimum sp*	✓	17	1947	1.04	0.18	0.11	3.64	83	16	1	
B	JAC	*Jacaranda copaia*	✓	1	2845	14.02	0.44	0.92	2.31	94	5	1	
B	VII	*Cordia bicolor, Virola michelli, Vochysia maxima*	✓	4	2428	7.50	0.31	0.41	2.39	86	11	3	
C	GES	*Geissospermum sericeum, Eschweilera amara, Corytophora rimosa*		9	5772	6.64	0.18	0.34	1.17	64	29	4	2
C	HV*	*Hevea spp, Maytenus pruinosa, Swartzia corrugata*		17	1487	29.85	0.24	0.42	1.42	53	33	8	7
C	MIS	*Miconia surinamensis, Phyllanthus nobilis, Inga rubiginosa*		11	936	0.04	0.21	0.66	8.30	89	8	2	1
C	MOC	*Dendrobangia boliviana, Mouriri callocarpa, Stryphnodendron barbatimam*		4	1870	3.61	0.21	0.27	4.34	79	18	2	1
C	OCU	*Ocotea douradensis*		1	765	1.54	0.26	0.41	2.87	87	10	2	1
C	SCC	*Sclerolobium chrysophyllum, Piptadenia suaveolens, Parkia multijuga*		10	3464	20.33	0.44	1.24	3.23	76	14	5	5
C	SCT	*Sclerolobium tinctorium, Sclerolobium guianensis, Parkia ulei*		3	945	8.35	0.43	1.01	3.24	76	15	5	4
C	SPG	*Tapirira guianensis, Apeiba albiflora, Brosimum lactescens*		7	3152	10.05	0.32	0.62	2.96	76	19	4	1
C	STP	*Eschweilera blanchetiana, Eschweilera jurunensis, Sterculia pilosum*		12	7429	5.26	0.18	0.31	2.43	80	16	2	1
C	SYO	*Chimarrhis turbinata, Syzygiopsis oppositifolia, Enterolobium maximum*		10	3067	10.53	0.23	0.51	2.24	71	16	6	8
D	???	*Unidentified or unknown species*		1	21833	5.14	0.16	0.35	2.86	90	9	1	
D	AND	*Anaxagorea dolichocarpa, Protium opacum, Paraprotium amazonicum*		10	3100	1.49	0.24	0.30	3.37	99	1		
D	CN*	*Simaba cedron, Connarus sp., Cupania cf. hirsuta*		41	1670		0.16		1.64	83	15	2	
D	CRJ	*Casearia javitensis, Annona montana, Vismia cavennensis*		60	2450	0.01	0.12	0.02	2.81	100			
D	CSP	*Coussarea paniculata, Sagotia racemosa, Casearia favitensis*		7	6021	1.14	0.09	0.10	3.48	100			
D	DUE	*Duguetia echinophora, Duroia sprucei, Conceveiba guianensis*		3	3813	1.03	0.09	0.23	4.11	97	3		
D	ESC	*Eschweilera coriacea, Sloanea obtusa, Pouteria laurifolia*		9	1631	1.52	0.15	0.18	0.71	88	11	1	
D	EUL	*Eugenia lambertiana, Myrciaria floribunda, Duguetia surinamensis*		4	2366	0.32	0.12	0.18	3.06	98	2		
D	LAJ	*Guarea sp, Lacunaria jenmanii, Ampelocera edentula*		5	1808	1.33	0.13	0.20	5.34	96	4		
D	MI*	*Guatteria poeppigiana, Miconia sp, Perebea guianensis*		13	9427	3.66	0.19	0.43	4.86	94	6		
D	MYF	*Myrcia falax, Bocageopsis multiflora, Rollinia fendleri*		3	1875	0.13	0.12	0.09	3.10	99	1		
D	NE*	*Eschweilera odora, Neea sp, Eperua bifuga*		10	12000	3.49	0.13	0.28	2.60	92	8		
D	NEC	*Neea constricta, Eschweilera spp, Diospyros praetermissa*		5	1721	0.47	0.14	0.18	2.13	94	6		

Table 3 (*Continued*)

Cat.	Group	Principal species in group	Com.	No. spp.	No. obs.	Dom. %	Diam increment		AMR %	Frequency % by diameter class			
							Imp.	*Dom.*		*5–24*	*25–44*	*45–64*	*65+*
D	PO*	*Rinorea guianensis, Pouteria sp, Lecythis poitequi*		4	11243	5.07	0.14	0.17	2.60	83	15	2	
D	PRA	*Protium apiculatum*		1	9022	2.91	0.22	0.49	2.99	93	7		
D	PRS	*Protium sagatianum, Sloanea spp*		2	1087	1.37	0.17	0.13	3.76	88	12	1	
D	RIF	*Rinorea flavescens, Miconia guianensis, Trema micrantha*		28	7588	0.41	0.07	0.09	4.45	100			
D	RIL	*Cordia alliodora, Quararibea guianensis, Rinorea lindeniana*		20	5290	3.30	0.14	0.19	2.00	98	2		
D	STE	*Drypetes variabilis, Sterculia excelsa var. pilosa, Pithecelobium race*		10	2813	1.10	0.20	0.20	1.68	92	8		
D	TA*	*Tachigalia sp, Ormosia sp, Swartzia brachyrachis*		14	3821	10.84	0.22	0.34	3.30	92	8	1	
D	THS	*Theobroma speciosum, Toulicia bulata, Xylopia benthamiana*		3	1497	2.47	0.07	0.07	2.13	100			
D	TLL	*Talisia longifolia, Mouriria plasschaerti, Terminalia spp*		3	2000	1.92	0.06	0.47	2.55	96	4		
E	BIA	*Bixa arborea, Inga alba*		2	4953	5.32	0.61	1.16	2.51	84	15	1	
E	CEL	*Cecropia leucoma, Cecropia sp, Xylopia nitida*		6	2972	13.39	0.66	1.12	8.60	95	5		
E	CES	*Cecropia sciadophylla, Cassia spruceana*		2	4310	18.59	1.14	1.60	3.92	88	12		
E	HEP	*Maquira sclerophylla, Helicostylis pedunculata, Ormosia flava*		12	2171	11.36	0.25	0.52	2.10	78	21	2	
E	IN*	*Inga spp, Diospyros santaremnensis*		2	13329	3.46	0.46	1.08	4.25	96	4		
E	JCS	*Porouma longipendula, Jacaratia spinosa, Beilschwiedia sp*		4	1926	4.39	0.57	1.08	3.98	93	7		
E	SLF	*Sloanea froesii, Sclerolobium sp*		2	8606	0.86	0.31	0.58	6.10	99	1		

tage of tree numbers. This is a useful indicator of species ecology and typical size.

4. Diameter and mortality models

Increment data for each species group are summarized using diameter classes whose width increases by $\sqrt{2}$, with separate classes for the dominant and impeded trees. Within CAFOGROM, a regression is fitted to this summary data for each group with the form:

$$i_d/d = \alpha + \beta_1 C + \beta_2 \ln(d) \qquad (1)$$

where i_d is diameter increment in cm year^{-1}, d the tree diameter at breast height in cm, C the zero for dominant trees, and one for impeded trees. The terms α, β_1, and β_2 are coefficients estimated by linear regression. Vanclay (1994) has reviewed many different types of increment model that have been chosen by various authors. The above model was devised after some experimentation as it was found to have robust properties for automatic application, giving a suitable shape of function even when the data was sparse and not well-distributed.

Two examples are shown in Figs. 1 and 2. The first is for a faster growing, more light demanding species, *Jacaranda copaia*, which is the sole species in its group. In this case, the function fits well, although lack of fit is apparent for the impeded trees. The robust properties of the model are clear in this diagram. Increment tends to zero as diameter does, there is a single maximum increment, and growth then declines to a zero increment that defines a maximum size for the species. There are several other functions which show these properties, but the authors found that they either fitted the data less well, or produced inappropriate forms with the data given. The authors also experimented with different systems of weighting, to test the best approach. Weighting by inverse of variance, by number of trees (*N*), *ln*(*N*), and $\sqrt{N}$ were all tested, but generally gave less suitable shapes than this simple unweighted regression fitted to the class mean.

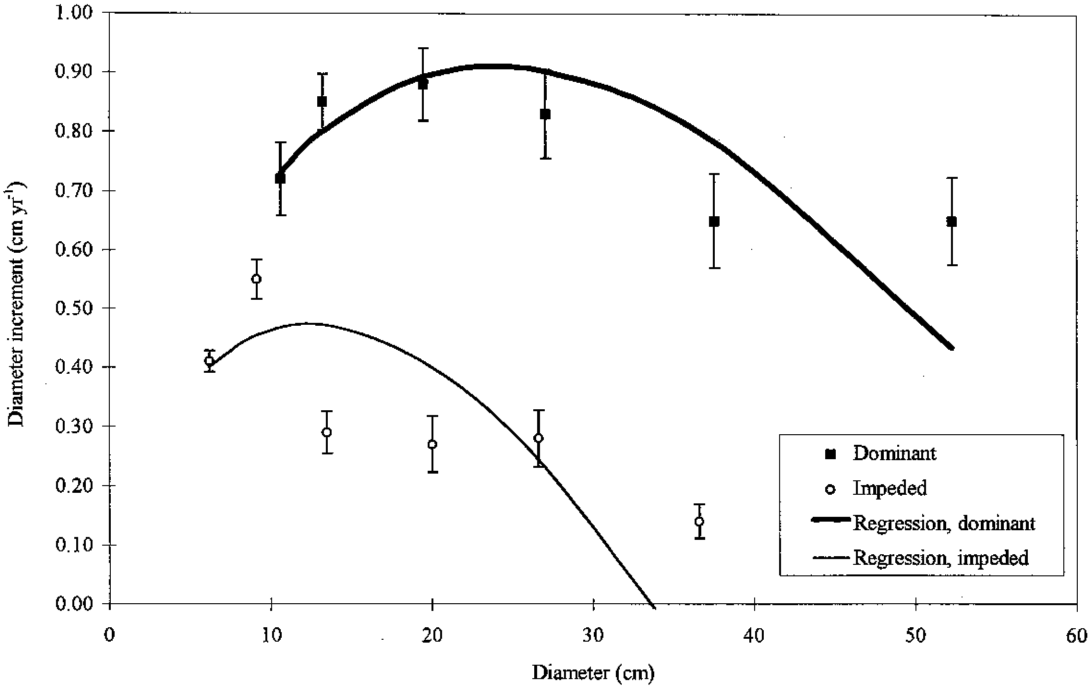

Fig. 1. Diameter increment function for *Jacaranda copaia*. Data points are class means; error bars are ±1 SE.

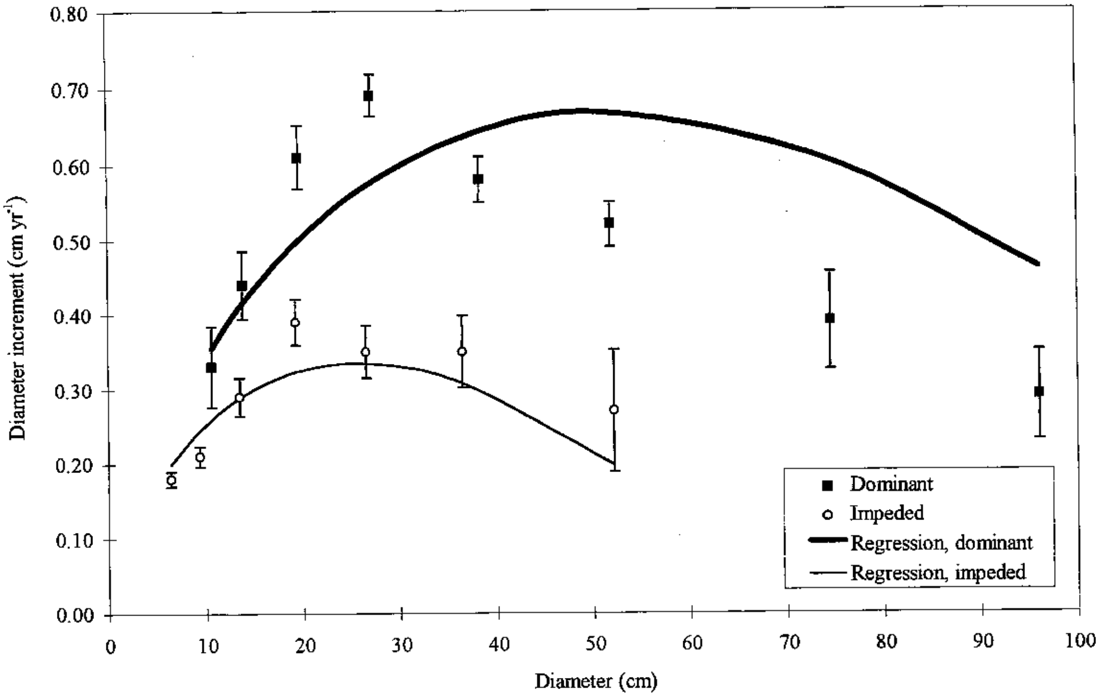

Fig. 2. Diameter increment function for group CAG, including *Carapa guianensis* and similar species. Data points are class means; error bars are ±1 SE.

Fig. 2 shows another example, for the somewhat slower growing and more shade tolerant group of species similar to *Carapa guanensis*. In this case, a common weakness of the function is clear. It tends to underestimate growth in the important size classes from 20 to 30 cm DBH, and overestimate growth on the larger dominant trees. Although the model as a whole does not appear to be especially sensitive to these weaknesses, they probably account for some inadequacies in the representation of stand structure over long-term projections, as will be discussed.

Mortality was calculated for each species group for three categories of tree: Dominants, impeded trees, and defective trees. Defective trees were those scored on the plots as either damaged, leaning, or showing signs of decay or crown dieback. It did not included trees of bad form, but otherwise undamaged and healthy, since this is considered to be primarily a species attribute, and does not especially relate to growth. Mortality was calculated as annual mortality rate (Sheil et al., 1995), and estimated with varying measurement periods using a linear approximation:

$$\mathrm{AMR} \approx \frac{\Sigma t_k^{-1}}{N} \quad (2)$$

where t_k is the measurement interval in years for a plot and period during which tree k dies, and N the total number of observations (trees × number of measurement intervals) including live and dead trees. For example, given five trees measured over say 2, 2, 3, 3, and 4 years, and assuming the last tree dies, then Eq. (2) gives t_k as $\frac{1}{4}$ and N as 5. The estimated AMR is 0.05 or 5%. The equation is derived assuming mortality is a linear function of time and is approximately correct for typically low mortality rates of 1–5% applicable to trees in natural forest.

Mortality varies substantially between species groups, but did not vary greatly with size. It is however quite sensitive to competitive status, especially for more light demanding species. It also tended to be clearly higher for the defective trees. For this reason, a look-up table of mortality rates, by species group, crown and defect status, was adopted for the model. Mortality also increases substantially following log-

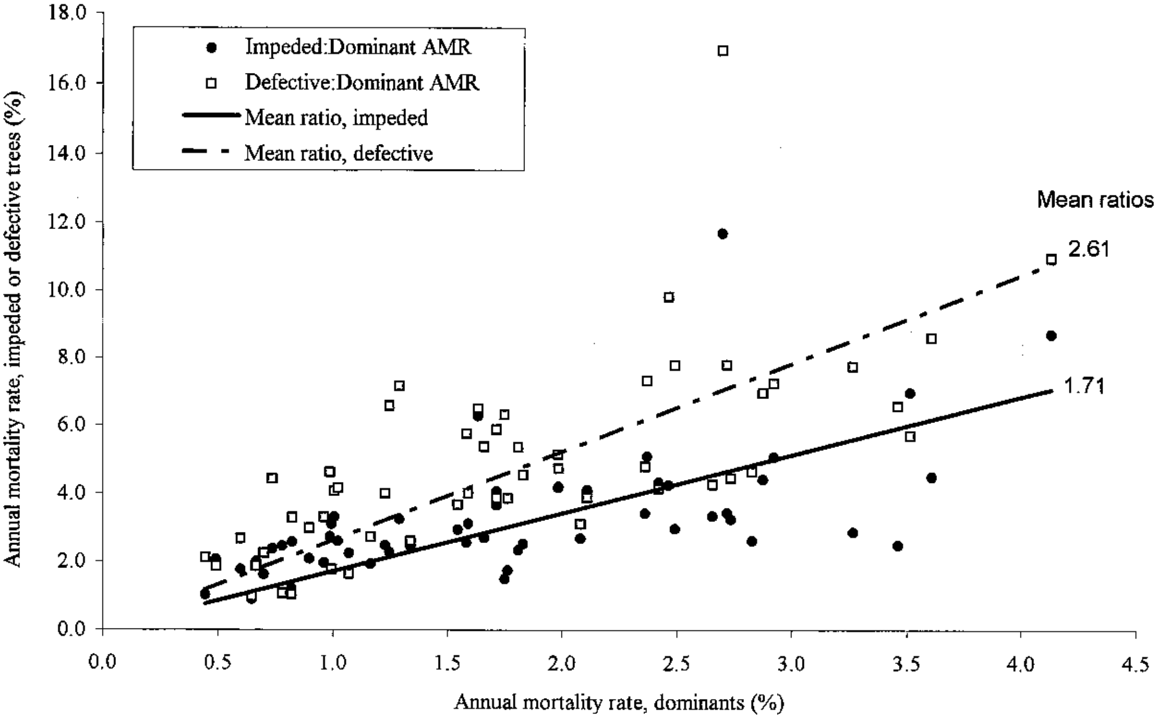

Fig. 3. Comparison of dominant, impeded and defective mortality rates for species groups. Each point represents a species group mean.

ging, but this is treated in the model as part of the logging damage module, and is discussed separately. Fig. 3 shows the ratios between dominant and impeded or defective mortality. Each point on the graph gives the mean values for one species group. On average, impeded trees have mortalities 1.71 times higher than dominants. Defective trees show a mortality 2.61 times higher. For no species group is dominant mortality higher than impeded mortality. For dominant trees, mortality rates range from 0.5% to 4.1% per annum. Higher mortality rates are associated with species which tend to have an extreme light-demanding niche. Average mortality rates for species groups can be seen in Table 3.

Both the diameter increment and mortality functions are modified within CAFOGROM by functions determined by aggregate stand parameters. In the case of increment, this is a competition effect, and is performed in the simulation by a crown classification function. Fig. 4 shows data from the sample plots, summarised by treatment means (blocks). The basal area of impeded trees (subdominant and understorey trees) is plotted against the total standing basal area. CAFOGROM fits a linear regression to this data (dotted line) and also allows the program's user to modify this via interaction with the mouse (solid line) for sensitivity analysis and calibration. The regression model has the coefficient values:

$$G_\mathrm{i} = 1.272G - 14.55 \tag{3}$$

where G_i is basal area of impeded trees, and G the total basal area. This equation implies that at a stand basal area of 11.4 $\mathrm{m}^2\,\mathrm{ha}^{-1}$, the impeded basal area will be zero. In the simulation model, this regression (or more precisely, the user-adjustable line, which may or may not be coincident with it) is used to assign canopy status to cohorts. The cohorts belonging to smaller trees are assigned to the impeded class until the G_i value from the model is reached. Remaining cohorts are assigned to the dominant fraction.

Experimentation showed that this crown classification scheme was not sufficient on its own to explain the influence of competition on growth, and a second factor was introduced into the model, which is a general increment multiplier. For each plot, an increment multiplier is calculated as the plot basal-area

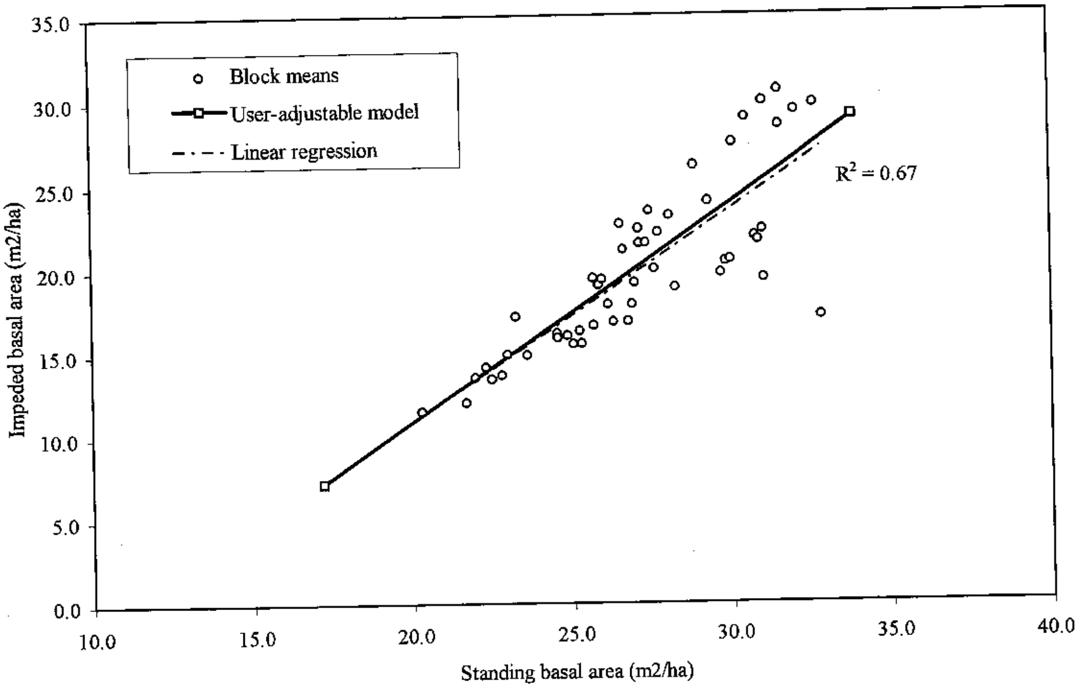

Fig. 4. Model for proportion of impeded basal area.

increment divided by the overall average basal-area increment. This shows a declining trend with an R^2 of 33%. This is modelled by the equation:

$$F_i = 3.02 - 0.076G \quad (4)$$

where F_i is a multiplier to adjust tree increments for stand density, and G the stand basal area. CAFOGROM presents this model graphically superimposed on the data points, and allows the user to adjust the regression line interactively for local calibration or sensitivity analysis. The coefficient values shown in Eq. (4) are those used for the model evaluations in this paper. With these, the multiplier takes a value of one at a stand basal area of 26.6 $m^2\,ha^{-1}$. At the higher observed densities of around 35 $m^2\,ha^{-1}$, the multiplier is 0.36, implying that stand basal-area increment tends to be 36% of average values. Conversely, at the lower observed densities around 20 $m^2\,ha^{-1}$, the multiplier is 1.5, with increments 50% above the average. These refer to the gross basal-area increment on standing trees, excluding the effects of mortality and recruitment.

Mortality in basal-area terms does not show a density dependent trend, but on the contrary, seems to be relatively constant in terms of basal area apart from periods of stand disturbance, when it increases markedly. A simple percentage basal-area factor will tend to result in increasing mortality with stand density. To compensate for this, the model provides a fixed mortality limit, which can be adjusted by the user when calibrating the model. For the trials discussed here, it was set to a value of 0.5 $m^2\,ha^{-1}\,year^{-1}$. To constrain mortality estimated by species group, crown status, and defect status to this limit, the model calculates mortality in two steps. It first uses the lookup values (by group, crown status, and defect status), and works out the overall basal-area mortality that would occur were these applied. If this violates the constraining value (0.5 $m^2\,ha^{-1}\,year^{-1}$ or as otherwise set by the user), then the provisional values are adjusted proportionately downwards. However, catastrophic mortality associated with logging is not subject to this constraining process.

5. Recruitment

Recruitment is defined as ingrowth into the smallest measurement diameter, which for this model is 5 cm

DBH. It is modelled firstly at the stand level, to determine the total amount of recruitment. This is then partitioned up into species groups using different lists which depend on general locality (Tapajós or Jarí) and degree of disturbance. Total recruitment levels themselves are determined by one of two different functions:

1. Following logging or thinning treatment, recruitment depends on the amount of basal area removed, including losses from damage. This relation is quite strong, with an R^2 of 59.6% for the combined data from Tapajós and Jarí. Trends over time for individual experiments show that recruitment approximately halves with each year after disturbance. As with other models in CAFOGROM, the fitted regression is displayed with the data, and can be adjusted interactively by the user for calibration and sensitivity analysis. The actual function used for the evaluations in this paper was:

   $$I_g = 0.019\, L_g^{1.86} \tag{5}$$

   where I_g is recruitment basal area, in $m^2\,ha^{-1}\,year^{-1}$, and L_g the basal area lost in harvesting or thinning and associated mortality, in $m^2\,ha^{-1}$.
2. For undisturbed stands, or for those several years after disturbance, the recruitment rate is determined by a baseline figure which is weakly conditioned by stand density, which is again user adjustable. This gives recruitment basal areas of from 0.7 to 0.5 $m^2\,ha^{-1}\,year^{-1}$ for stand basal areas from 20 to 30 $m^2\,ha^{-1}$.

The transition from the post-disturbance recruitment to the baseline function depends on the time interval used in the model and the annual exponential halving of recruitment rates. When recruitment after disturbance drops below the level predicted by the baseline function, then the baseline function is adopted.

Lists are used to partition the total recruitment into species groups. Different lists are compiled for the post-disturbance and baseline recruitment situations. The lists are expressed as percentages of total recruitment occurring in each group. In the cohort model, new cohorts are added for each species group that occurs in the recruitment. The list includes the mean recruit diameter, as it has been found from earlier work that model results are sensitive to this figure (Alder, 1995).

6. Post-logging mortality and damage

Jonkers (1987) describes clearly some of the processes that cause mortality and damage during logging. These have distinctively different effects on trees of different sizes. The opening of skid trails tends to impact mainly smaller trees, as the tractor will avoid larger ones. Trees in the trail are of course destroyed outright. As a harvested tree falls, its crown will tend to crush or break in half smaller trees, which will be killed outright. Larger trees will survive with more or less damage. The experiments at Tapajós and Jarí score damage with a variety of codes. For the purposes of CAFOGROM, the data was simply re-classified on a binary scale to distinguish trees with moderate to severe damage, which are treated as defective. This included also crown die-back and stem breakage from natural decay, so that there is no direct distinction between artificially induced and naturally occurring defect. However, for the logging damage analysis, a tree was treated as damaged only if it was non-defective before logging, and defective after logging. For mortality, there is no distinction as to cause, but purely on the basis of timing. Mortality following harvest was analysed via the logging damage function; before harvest or for later re-measurements, it was treated as non-catastrophic mortality.

In CAFOGROM, the logging damage data is read as a file summarising damage (ie. trees which become defective following logging) and mortality by plots and size classes. The number of harvested trees is used to indicate the intensity of felling. For general mortality levels, the model re-summarises this file using logging intensities in classes of 0, 1–4, 5–8, 9–12, 13–16, and 17+ trees per ha removed. This is presented as the graph shown in Fig. 5 with linear regressions which predict average mortality or damage as a percentage of standing basal area before felling. The fitted equations are shown on the graph. The R^2 values are not directly meaningful as no error information is given. Each plotted point is in fact the summary of a number of sample plots.

CAFOGROM also re-summarises the logging damage data in another way, which is shown in Fig. 6. In this, the level of damage within each 10-cm

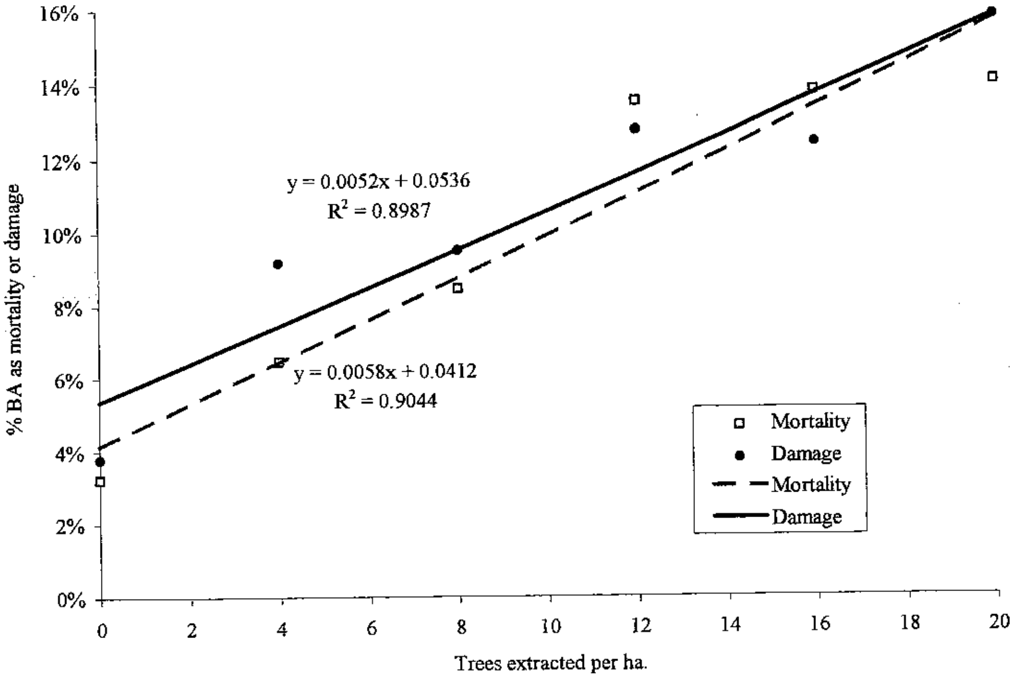

Fig. 5. Models of logging mortality and residual damage. Each point summarises several plots in the same logging intensity class.

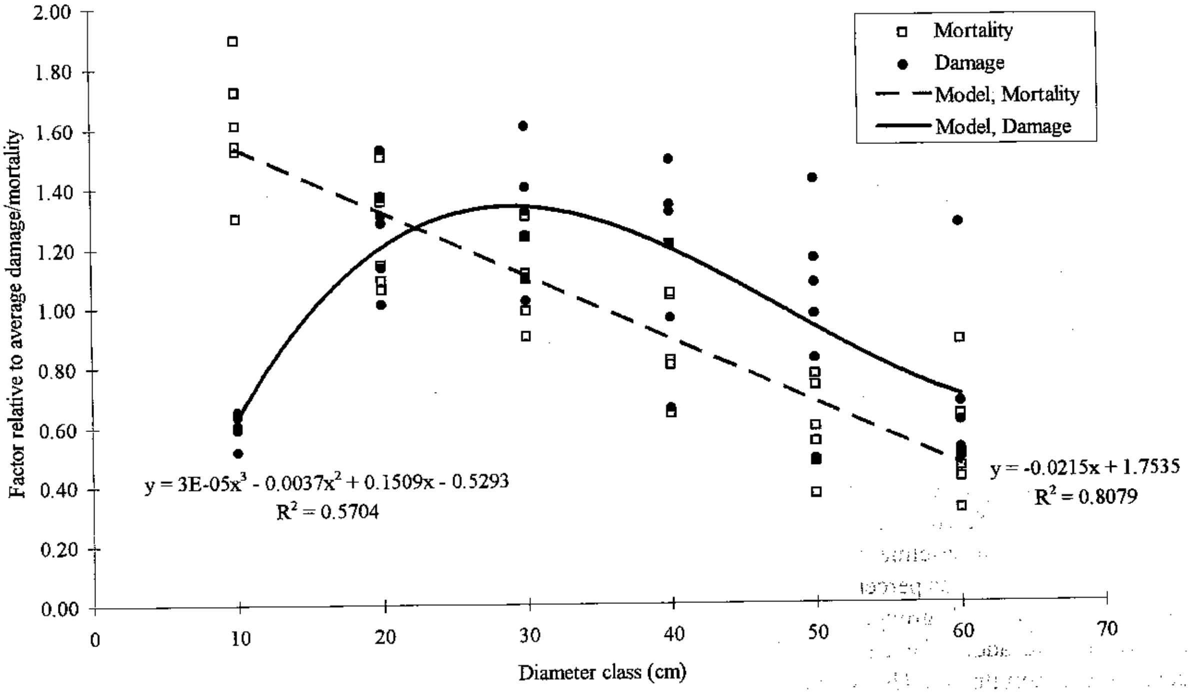

Fig. 6. Relative logging damage and mortality by size classes. Each point summarises several plots in the same logging intensity class.

diameter class is calculated relative to the plot average, and then graphed against size class. This gives an indication of how damage is distributed by size. CAFOGROM uses a linear regression for mortality, or complete loss of trees. For trees which are damaged but remain alive, the function shape is more complex, and is approximated by a cubic polynomial. For trees above 60 cm DBH, the damage and mortality levels calculated for the 60 cm class are applied.

The marked reduction in damage for small trees is interesting, and can be understood in terms of the definitions used. Trees which are completely destroyed are not considered part of the damage function. For small trees, impacts tend to be on an all-or-nothing basis, where the tree is either completely lost or not effected. Hence, these sizes are not common in the category of partially damaged trees. Larger trees are not generally destroyed on skid trails or completely flattened or broken during felling, and hence figure more prominently among the partially damaged fraction.

In the model, these functions are applied in the following way. Harvesting is simulated by selecting eligible trees, according to the logging rules given. The count of trees removed gives the harvesting intensity. From the regressions on Fig. 5, the direct mortality and damage due to logging are calculated. Using the functions on Fig. 6, these are calculated for each cohort as a function of its DBH. Mortality is applied by reducing the residual stock of the cohort. Damage is applied by splitting the cohort into proportionate damaged and undamaged fractions, which will thereafter follow their own distinct growth patterns.

7. Evaluation of model performance

CAFOGROM was evaluated for accuracy by comparing projections of the experimental plots with the observed values. The first example illustrated is the experiment RP12 at Tapajós km 67. This experiment, as has been noted, was logged quite heavily some 2 years prior to plot establishment in 1981. Subsequently, no further treatments have been applied. Fig. 7 shows simulation results. For commercial species, actual volumes of trees over 45 cm DBH grew from 32 to 44 $m^3 ha^{-1}$ over the period 1981

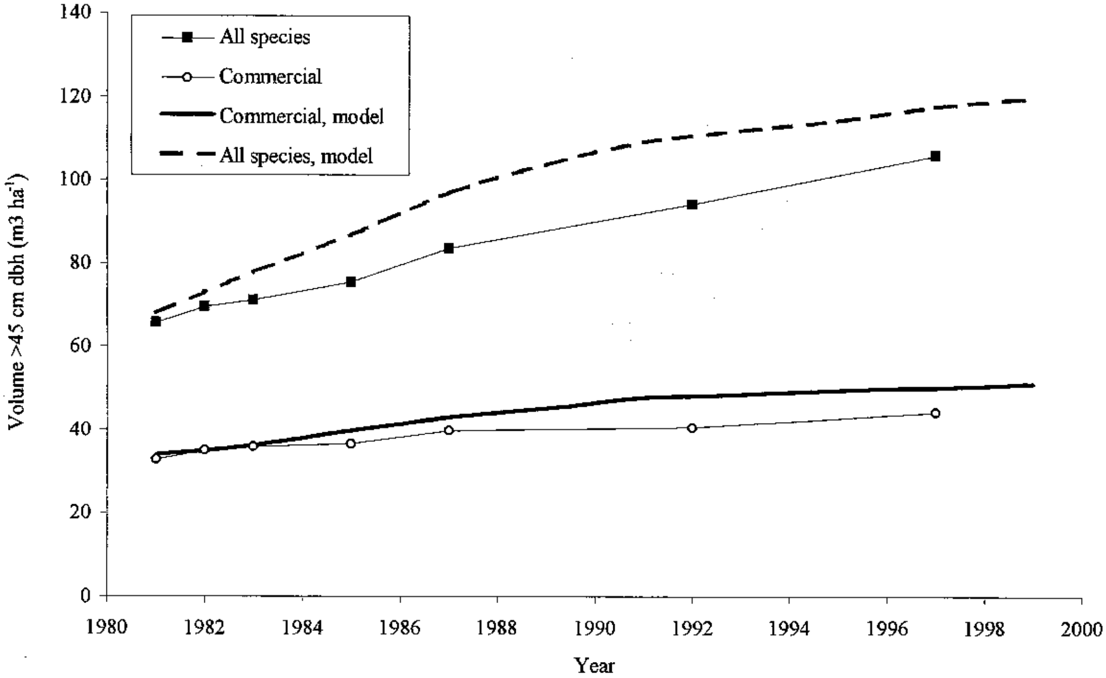

Fig. 7. Simulated and actual volume development, RP12, Tapajos. Data points are means of 36 PSPs.

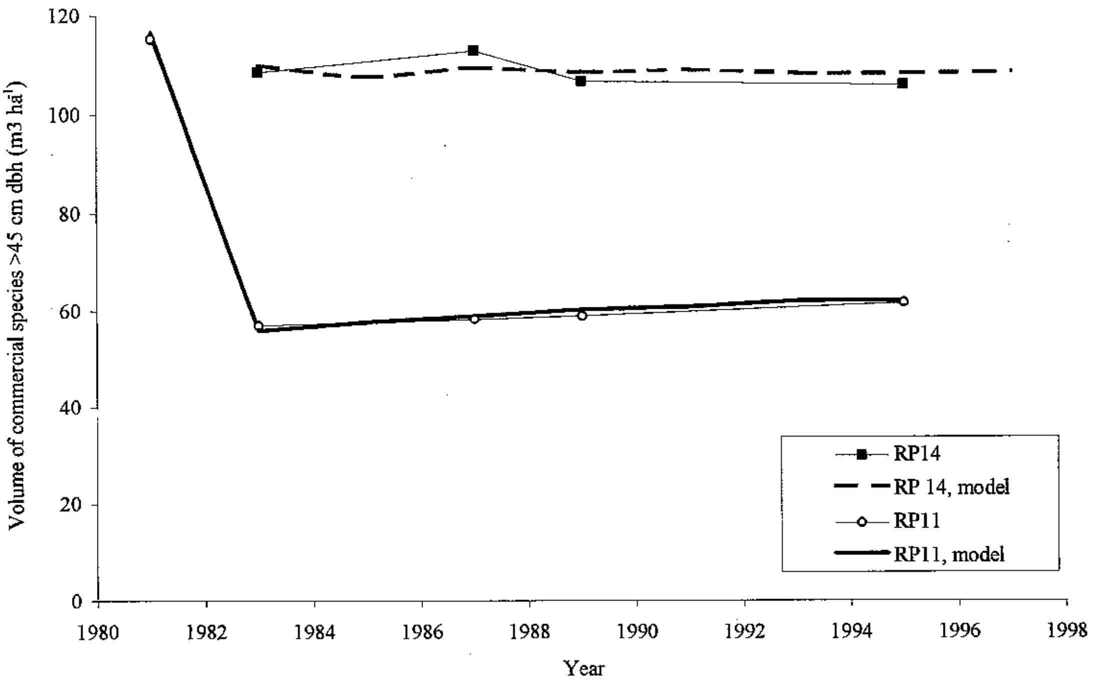

Fig. 8. Simulated and actual volume development on research plots RP11 and RP14, Tapajos. Data points are means of all PSPs on each experiment.

to 1997 (16 years), or a mean annual increment of 0.75 m^3 ha^{-1} $year^{-1}$. The simulator shows an MAI of 1.0 m^3 ha^{-1} $year^{-1}$ over the same period, somewhat overestimating growth. A similar overestimation occurs for the volume of all species over 45 cm DBH. The actual MAI over the 16-year period is 2.56 m^3 ha^{-1} $year^{-1}$. The model projects a growth of 3.13 m^3 ha^{-1} $year^{-1}$over the same period.

For experiments RP11 and RP14 at Tapajós km 114, commercial volume projections are quite accurate, as shown in Fig. 8. Volumes on the control plots (RP14) decline slightly over the period, from 108 to 105 m^3 ha^{-1} on the actual plots, or from 110 to 108 m^3 ha^{-1} in the model. The treated stands (RP11) were harvested in 1983. The simulation of this treatment appears to be very effective, tracking exactly both the combined effect of removals and damage, and the subsequent development of the stand. The rather flat line that is seen in fact belies a complex combination of post-felling mortality, recruitment, and growth, whose net effect over the 12-year period from 1983 to 1995 is to result in an actual MAI of 0.39 m^3 ha^{-1} $year^{-1}$for commercial volume over 45 cm DBH. As the graph indicates, the model over this period projects an almost identical result.

The differences in growth and response between RP11 and RP12 are associated with differences in species composition, especially in the advance growth. There may also be site effects, but these have not been studied to date. The species effects are, however, clear. The RP12 site is richer in *Jacaranda* and *Didymopanax* in the advance growth sizes of 20–30 cm DBH. It is clear from the model that these faster growing species account for much of the difference in the dynamism of the RP12 plots, versus the relatively static growth at RP11. As Alder (1998b) found in Papua New Guinea, species composition alone can account for much of the variation in growth rates between different natural forest sites.

The overestimation of growth by the model at RP12 appears to be associated with the weakness of the diameter increment function. As has been discussed relative to Figs. 1 and 2, this function tends to overestimate growth on larger trees. Generally, detailed comparisons between CAFOGROM and the various experiments show that the model replicates the main features of stand growth and dynamics, including:

- An increase in increment following felling. Generally, the model is less dynamic than actual stands with current calibrations, but adjusting the increment multiplier relative to the fitted regression (Eq. (4)) can compensate for this.
- A sharp increase in mortality following felling. CAFOGROM reflects this fairly well.
- Increased but exponentially declining recruitment after felling. This is modelled very accurately for RP12 data, and reasonably well for Jarí plots (RP 21, RP 25). The plots at RP 11 have higher recruitment in the baseline state, and somewhat lower recruitment after disturbance. The reasons for these differences are not known.
- Tendency of basal area to an equilibrium at about 32–33 $m^2\ ha^{-1}$ within 30–40 years after felling. At this level, recruitment, mortality and increment balance. The equilibrium level is very sensitive to mortality rates, and less sensitive small adjustments to either the increment function or recruitment rates. Small changes to the mortality limit, of the order of 0.1 $m^2\ ha^{-1}\ year^{-1}$ can produce changes of the order of 2–3 $m^2\ ha^{-1}$ in the equilibrium basal area.
- The conventional features of stand structure, in the form of the reverse *J*-shaped diameter distribution, and the distribution of basal area by size classes (Korsgaard, 1992). CAFOGROM reflects these well in long-term simulations, although there are indications that trees tend to remain in the smaller size classes a little to long. This may also reflect inadequate mortality in these components.

8. Discussion

Calibration of the version of CAFOGROM described here shows that the model is sensitive to several parameters which may need to be refined or improved in future. The shape of the diameter increment function sensitively influences the transition rate of trees from the smaller to larger size classes, and effects the size class distribution. With long-term projections, too few trees tend to grow into the largest sizes. This effect is not apparent with the evaluations made here, over 15–17 years, but is seen in the shape of the diameter class distribution in very long projections. Different species groups may require different functional forms for an optimum result. The use of a standard, automatically-fitted regression for all species groups may not be the best approach. A decision-tree method will be considered in future to select from among alternative functional forms when fitting the diameter increment model.

As has been noted, mortality is a sensitive parameter which effects net stand growth rates and equilibrium basal area. Mortality is difficult to measure and relate functionally to other parameters, due to the large sample sizes required. Also, as several studies show, it can be influenced over quite long periods by past stand disturbance (e.g. Whitmore, 1989).

Recruitment is also a sensitive parameter, with a distinctive pattern of lags relative to the timing of stand disturbance (reflecting the time needed for seedlings to reach the defined recruit size, which is 5 cm DBH for CAFOGROM). It is a very stochastic phenomena, as many random factors extraneous to the model influence the occurrence of heavy seed falls (e.g. weather patterns, phenological rhythms, inundation, forest fires). The growth characteristics of recruits and small trees strongly and sensitively influences longer term projections from the model. The currently available evaluation data (12–17 years) is too short a series to fully test how successful the model is in emulating these processes. This sensitivity to small-sized tree distribution also means that conventional commercial forest inventories according to current standards in the Brazilian Amazon are almost useless as a starting point for model simulations. These tend not to measure trees below 30 cm diameter. For simulation purposes, a sub-sample of trees down to at least 10 cm DBH is essential for projections over 30–40 years or more.

The version of the model described here does not consider site variation. The means by which a site factor can be incorporated in this type of model has been explored for the related PINFORM model in Papua New Guinea (Alder, 1998b). The experience there suggested that site variation could account for growth variation over a range from ±30% of the mean stand basal-area growth rate within the lowland tropical forest type. It can therefore substantially influence estimates of annual allowable cuts and appropriate felling cycles, and is an important factor to be considered in future. The available data sets for CAFOGROM, which are concentrated on experimental plots at three localities, are not ideal for this purpose. It is however likely that in future other permanent sample plots established within the Amazonian region may be included within the analysis.

In spite of these limitations, CAFOGROM can provide some useful insights into the management of *Terra Firme* forests in Amazonia. The short-term projections shown in Figs. 7 and 8 indicate commercial volume growth (DBH 45 cm and above) ranging from 0.39 to 1.0 m^3 ha^{-1} $year^{-1}$. In this the model and the actual data are in close agreement. Longer projections with the model suggest that these divergent rates will tend to converge to a rate of about 0.6–0.7 m^3 ha^{-1} $year^{-1}$ at both sites as stand structures normalise and species composition diversifies. The current differences relate to substantial differences in the stand structure, species composition, and recruitment after felling. The model is quite successful in emulating these differences over the period studied. The accuracy of longer term projections remains to be seen.

It is beyond the scope of this paper to present in detail the implications of CAFOGROM for forest management. The model provides a flexible tool allowing many parameters of forest management to be varied and tested in their effects. However, like any model, the results of such simulations are only as good as the model itself. The present paper has concentrated on describing the empirical basis of the model and the results of its evaluation against two series of sample plots measured over 12–17 years. The further implications for forest management will be considered in other publications.

Acknowledgements

The development of the CAFOGROM model was financially supported by the United Kingdom Department for International Development. The experimental sites at Tapajós and Jarí are supported by EMBRAPA Amazonia Oriental. Additional financial and logistic support has been given by at various times by IBAMA (Brazilian Institute for the Environment) and the World Wide Fund for Nature (WWF).

References

Alder, D., 1990. GHAFOSIM: A projection system for natural forest growth and yield in Ghana. Consultancy report to Ministry of Lands and Natural Resources, Ghana, pp. 114.

Alder, D., 1995. Growth Modelling for Mixed Tropical Forests. Department of Plant Sciences, University of Oxford, Tropical Forestry Paper 30, p. 231.

Alder, D., 1997. User's Guide for SIRENA II - A simulation model for the management of natural tropical forests. CODEFORSA/DFID Integrated Forest Management Project, Internal Report, p. 45.

Alder, D., 1998a. PINFORM: A growth model for lowland tropical forest in Papua New Guinea. International Tropical Timber Organisation, Yokohama. Project PD 162/91 Internal Report. pp. 49.

Alder, D., 1998b. The ITTO permanent sample plots in Papua New Guinea: Some results of analysis. Paper presented to ITTO workshop on Permanent sample plots and growth models for natural forest management in Papua New Guinea, held at the Forest Research Institute, Lae 10th–13th Nov 1998, pp. 16.

Brasnett, N.V., 1953. Planned Management of Forests. George, Allen and Unwin Ltd., London. pp 128–135.

Burslem, D.F.R.P., Alder, D., Whitmore, T.C., 1996. COSSI: A cohort simulation model of forest growth and yield in the Solomon Islands. Department of Plant Sciences, University of Oxford,Oxford Forestry Institute Occasional Papers 50, pp. 64.

Chandrasarker, B., 1997. Growth and yield modelling for the Sundarbans Reserved Forest in Bangladesh. M.Sc. Thesis, Durrell Institute of Conservation and Ecology, University of Kent, Canterbury.

Collett, D., 1991. Modelling Binary Data. Chapman and hall, London. pp. 369.

Green, P.E., Carroll, J.D., 1978. Mathematical tools for applied multivariate analysis. Academic Press, London. Student Edition, pp. 376.

Howard, A.F., Valerio, J., 1992. A diameter class growth model for assessing the sustainability of silvicultural prescriptions in natural tropical forests. Commonwealth Forestry Review. 71 (3), 171–177.

Jonkers, W.B.J., 1987. Vegetation structure, logging damage and silviculture in a tropical rainforest in Surinam. Wageningen Agricultural University, pp. 172.

Kofod, E.O., 1982. Stand table projections for the mixed dipterocarp forests of Sarawak. Forest Department, Kuching, Sarawak. FAO report FAO/MAL/76/008 Field Document. 9, pp. 107.

Korsgaard, S., 1988. A manual for the stand table projection simulation model. The Council for Development Research, Copenhagen, pp. 75.

Korsgaard, S., 1992. An analysis of growth parameters and timber yield prediction. The Council for Development Research, Copenhagen, pp. 120.

Sheil, D., Burslem, D.F.R.P., Alder, D., 1995. The interpretation and mis-interpretation of mortality rate measure. Journal of Ecology. 83, 331–333.

Silva, J.N.M., 1989. The behaviour of the tropical rainforest of the Brazilian Amazon after logging. D.Phil. thesis, Department of Plant Sciences, Oxford University, pp. 302.

Silva, J.N.M., de Carvalho, J.O.P., Lopes, C.A., De Oliveira, R.P., De Oliveira, L.C., 1996. Growth and yield studies in the Tapajós region, Central Brazilian Amazon. Commonwealth Forestry Review 75 (4), 325–329.

Silva, J.N.M., de Carvalho, J.O.P., Lopes, J do C.A., 1988. Growth of a logged over tropical rainforest of the Brazilian Amazon. In: Wan Razali, M., Chan, H.T., Appanah, S. (Eds.), Proceedings of the seminar on Growth and Yield in tropical Mixed/Moist Forests, 20–24 June 1988, Kuala Lumpur, pp 117–136.

Silva, J.N.M., de Carvalho, J.O.P., Lopes, J do C.A., de Oliveira, R.P., de Oliveira, L.C., 1994a. Growth and yield studies in the Tapajós region, central Brazilian Amazon. In: Konohira, Y. (Ed.), Proceedings from the IUFRO international symposium Growth and Yield of Tropical Forests, Tokyo University of Agriculture and Technology, pp 19–29.

Silva, J.N.M., de Carvalho, J.O.P., Lopes, J.C.A., Almeida, B.F., Costa, D.H.M., de Oliveira, J.C., Vanclay, J.K., Skovsgaard, J.P., 1995. Growth and yield of a tropical rainforest in the Brazilian Amazon 13 years after logging. Forest Ecology and Management. 71, 267–274.

Vanclay, J.K., 1989. A growth model for North Queensland rainforests. Forest Ecology and Management. 27, 245–271.

Vanclay, J.K., 1991. Aggregating tree species to develop diameter increment equations for topical rainforests. Forest Ecology and Management 42, 143–168.

Vanclay, J.K., 1994. Modelling of Growth and Yield of Tropical Moist Forests, CAB International, Wallingford, pp. 312.

Vanclay, J.K., 1995. Growth models for tropical forests: A synthesis of models and methods. Forest Science. 41, 7–42.

Vanclay, J.K., Gillison, A.N., Keenan, R.J., 1997. Using plant functional attributes to quantify site productivity and growth patterns in mixed forests. Forest Ecology and Management. 94, 149–163.

Whitmore, T.C., 1989. Changes over twenty-one years in the Kolombangara rain forests. Journal of Ecology 77, 469–483.