

Using models to predict recovery and assess tree species vulnerability in logged tropical forests: A case study from French Guiana

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Abstract

A major challenge for forest managers is to define the optimal cutting cycle to ensure that the resource is sustained in the long term. Matrix models of forest dynamics allow time-projection of diameter-class distributions and thus assessment of the time needed, after logging, to recover a given part of the exploitable stock. They are easy to build and they only require, as input variables, the diameter structure of the population(s) under scope. However, such models are based on a coarse description of tree population dynamics and must be used with caution. In particular, as trees are only described from a diameter threshold (usually 10 cm dbh), recruitment of a new tree cannot be linked with the preceding generation since too much time elapsed between seed dispersal and the installation of a 10-cm recruit. This causes predictions of matrix models to be highly questionable in the long term when ingrowth to larger dbh classes greatly depends on the way recruitment has been modelled.

We used a case study from French Guiana to test whether or not a simple matrix model is reliable enough to help forest managers choose between management alternatives. We focused on the major timber species *Dicorynia guianensis* Amshoff (Caesalpiniaceae) harvested under a selective cutting regime. We compared predictions of *D. guianensis* stock recovery in the short and long term provided by two models: StoMat, a non-regulated matrix model, and SELVA, a single-tree distance dependent model explicitly simulating the entire species life cycle. Both models were independently calibrated on data from Paracou permanent sample plots.

We showed that: (i) the short-term recovery of the exploitable stock predicted by StoMat is reliable for a large range of disturbance conditions; (ii) recruitment implementation in StoMat does not influence projections until the third felling cycle; (iii) for shared initial stand conditions SELVA and StoMat give consistent mid- and long-term predictions: the simple recruitment model used into StoMat could efficiently summarise the regeneration processes of the species under low felling intensity. Our results indicate that the current felling regime used in French Guiana may not be sustainable on a long-term basis. In any case, no more than 60% of the initial stock would be recovered after logging.

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We conclude that simple models can provide as reliable predictions as more complicated ones. They may be sufficient to assess the recovery of a species' exploitable stock even in the long term, or at least assess the (un)sustainability of particular harvesting regimes.

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1. Introduction

In tropical forests managed for timber production using selective harvesting systems, sound assessment of management parameters such as species minimum diameter cutting limits (DCL) and the length of felling cycles remains a crucial issue for forest managers. Sustainable forest management must ensure, at least, that recommended felling regimes are compatible with the regeneration capacities of the species logged, on a short-, mid- and long-term basis. To project long-term demographic and growth response of exploited populations of trees, modelling is required.

Various types of models of population dynamics have been developed for tropical forests (Alder, 1995; Vanclay, 1995). They differ from each other according to the level of stand description, the way tree interactions are considered and the degree to which physiological processes are described. Some models are thus highly detailed, such as single-tree distance dependent models (Moravie et al., 1997; Chave, 1999; Gourlet-Fleury, 1999; Gourlet-Fleury and Houllier, 2000; Phillips et al., 2003, 2004). Gap models (Shugart et al., 1980; Doyle, 1981; Bossel, 1991; Huth and Ditzer, 2000, 2001) and single-tree process based models (Kohler and Huth, 1998; Huth and Ditzer, 2000; Kohler et al., 2000; Huth and Ditzer, 2001; Kammesheidt et al., 2001; Kohler et al., 2001) propose less explicit description of the forest. Finally, cohort models (Alder and Silva, 2000) and matrix models rely on the coarsest description of the forest. Nevertheless, matrix models have been widely used in tropical rainforests to deal with economic (Boscolo et al., 2001), carbon sequestration (Boscolo et al., 1997), or management issues (Osho, 1991; Ingram and Buongiorno, 1996; Boscolo and Buongiorno, 1997; Favrichon, 1998; Favrichon and Young Cheol, 1998; Boscolo and Vincent, 2000; Spathelf and Durlo, 2001).

Matrix models of forest dynamics allow time projections of diameter class distributions, useful to estimate the time needed after logging to recover a given part of the stock of valuable trees above the DCL and assess felling cycles (Mengin-Lecreux, 1990; Vanclay, 1994; Debroux, 1998; Favrichon, 1998; Alder et al., 2002; Sist et al., 2003). Once calibrated on permanent sample plots, these models can easily be used by managers as they only require, as input variables, the diameter structure of the population(s) under consideration, data that are usually available from classical forest inventories (Durrieu de Madron and Forni, 1997; Alder, 2002).

However, matrix models are highly questionable when used to predict the long-term behaviour of exploited species population(s), i.e. after two or three felling cycles. At that point, ingrowth into upper classes becomes highly dependent on the way the recruitment into the first diameter class has been modelled. The lower limit of the first class usually is 10 cm dbh, the threshold considered in most permanent sample plots. On an individual species basis, recruitment into the ≥ 10 cm dbh classes is generally too infrequent an event to be correctly assessed and, moreover, newly recruited trees cannot be linked to the presence of mother trees because too much time elapsed since seed dispersal; repeated felling of those trees has uncertain consequences on recruitment.

The question that we address in this paper is the following: can a simple model, in this case an Usher matrix model, be reliable enough to help forest managers choose between management alternatives? Implicitly, if the answer is no, a more complicated model should be preferred, and the question becomes whether or not a simple model yields the same predictions as a more realistic model.

The present case study from French Guiana involves two models of population dynamics: a non-regulated matrix model, StoMat (Gourlet-Fleury

et al., 2004b) and a single-tree distance dependent model, SELVA (Gourlet-Fleury, 1999). These two models were independently calibrated on data derived since 1984 from permanent sample plots of the Paracou field station (Forest Department of CIRAD). To evaluate the reliability of long-term predictions of both models, we focused on the recovery dynamics of a major Guianan timber species, *Dicorynia guianensis* Amshoff (Caesalpinaceae). After evaluating the respective performance of the two models, we compared long-term simulation outputs provided by StoMat and SELVA under a selective cutting regime.

2. Material and methods

2.1. Species and site

D. guianensis Amshoff (Caesalpinaceae) is a large canopy tree species endemic to the Guiana shield, and the most important timber species in French Guiana (Hammond et al., 1996). Because of its relative abundance and favorable wood properties, 20,000 m³ of logs of this species are felled each year in the managed forests of French Guiana, i.e. about 30% of the total wood production. *D. guianensis* trees are usually felled above a DCL of 60 cm dbh and natural populations are exploited with a 40-year felling cycle. In the Sinnamary region, where the study site is located, the density of exploitable trees varies between 0.2 and 2 trees/ha (Schmitt, 1985).

D. guianensis is found on all types of soils and shows spatial aggregation at the scale of 50–100 m (Kokou, 1994; Collinet, 1997). Trees are able to produce seeds after reaching ca. 25 cm dbh (Caron et al., 1998). The seeds are wind-dispersed in indehiscent flat pods, the majority of which fall within 30 m from the mother tree (Loubry, 1993).

Regeneration from seed by this species is characteristic of shade-tolerant species *sensu* (Canham, 1989): seeds are able to germinate and establish as seedlings in the shade, and seedlings and saplings require moderate openings to reach the canopy (Baraloto, 2001). Analysis of potential growth and sensitivity to canopy disturbance of adult trees has ranked *D. guianensis* in the emergent mid-tolerant species category (Favrichon, 1994).

This study was conducted in the Paracou field station (5°18'N; 52°53'W), near Sinnamary (Gourlet-Fleury et al., 2004a). The station's experimental design is composed of three blocks of four permanent plots (9 ha, 300 m × 300 m each) established in 1984 in a previously undisturbed lowland rainforest. Treatments of increasing silvicultural intensity, involving selective harvesting for timber or fuelwood and thinning, were applied on plots in 1986–1987 according to a random block design (see Fig. 1 for illustration and details). In each block, three plots received a different treatment while one plot was kept protected to serve as control. High harvesting intensities experimentally applied to the plots did not reflect current logging practices in French Guiana (typically, 1–3 trees from 20 commercial species felled/ha) but rather possible logging scenarios.

On each plot, all trees above 10 cm dbh were identified, mapped and periodically measured for girth on a 250 m × 250 m central subplot since 1984 (Schmitt and Bariteau, 1990). Moreover, extensive censuses of the plots allowed recording of trees recruited to a 10-cm threshold and of dead trees (standing or fallen). Measurements and censuses were conducted annually in 1984–1995 and since then in alternate years.

Growth, mortality and recruitment data from these plots were analysed by Gourlet-Fleury (1997) for development of specific growth and mortality models for *D. guianensis* populations over 10 cm dbh. As part of a multidisciplinary research program launched in 1999, field experiments and inventories were conducted at Paracou on the early stages of *D. guianensis* (Gourlet-Fleury, 2002). Population studies of reproductive phenology, seed production, seedling survival and growth allowed characterization of life history and demography of the species' early regeneration (Jésel, 2005). In addition, juveniles of *D. guianensis* from 1 to 10 cm dbh were extensively surveyed and mapped in 1999 on a 36.36-ha study area, the Southern Block (Fig. 1). Growth and mortality rates for the 1–10 cm dbh population were calculated from a re-census in 2002.

2.2. Models overview

2.2.1. Stochastic matrix models (StoMat)

StoMat (Gourlet-Fleury et al., 2004b) is a management-oriented software running density independent

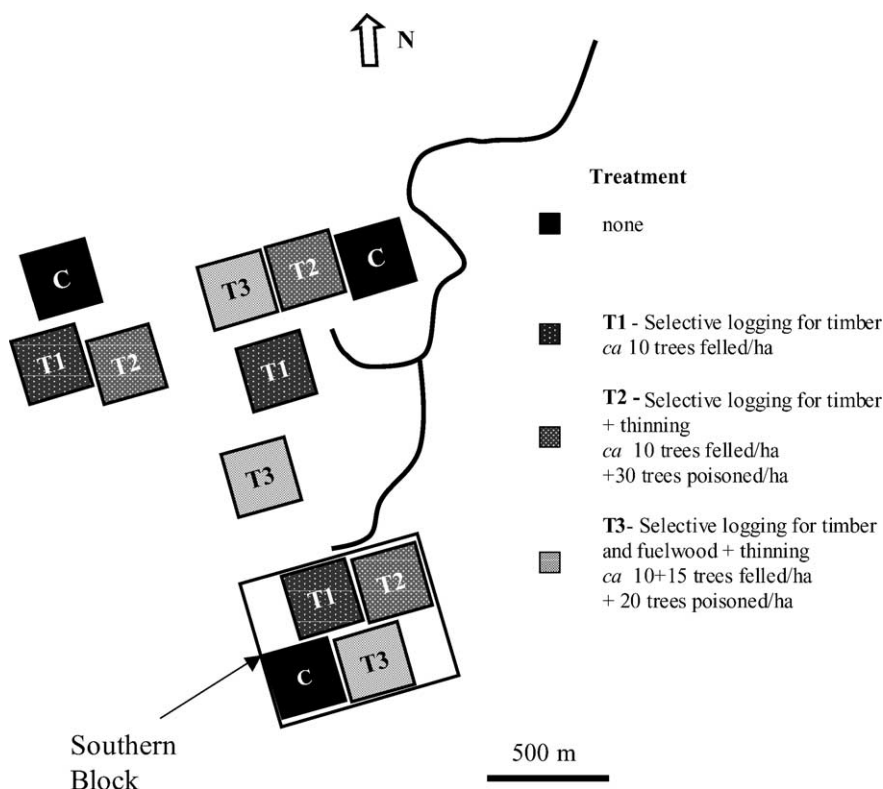


Fig. 1. Map of Paracou permanent plots. T-labeled plots were logged in 1986–1987 according to three silvicultural treatments of increasing intensity. T1: selective harvesting of timber from 58 commercial species (diameter cutting limit: 50 or 60 cm dbh according to species). T2: selective harvesting of timber followed by stand thinning involving the poisoning of all non-commercial species ≥ 40 cm dbh. T3: selective harvesting of timber and non-commercial species for fuelwood (diameter cutting limit 40–50 cm dbh) followed by stand thinning of all non-commercial species ≥ 50 cm dbh. (T1–T3: three repetitions per treatment in a random block design.) C-labeled plots were undisturbed and conserved as control in each block.

stochastic matrix models, designed to be calibrated with minimum data sets from permanent sample plots. It was specifically parameterised for *D. guianensis* to assess the recovery of the exploitable stock of trees in forests managed in the Sinnamary region.

In the model, trees (≥ 10 cm dbh) were distributed among 6 dbh classes (numbered 1–6) of 10 cm intervals, with the largest class including trees above

DCL (≥ 60 cm). The population is characterized, at a given time, by a vector y that records the number of individuals in each dbh class. The temporal evolution of y is calculated using an Usher matrix A with a 1-year time-step. Thus,

$$y(t+1) = A \times y(t)$$

where

$$A = \begin{bmatrix} (1 - b_1 - m_1) + f_1 & \cdots & f_i & \cdots & \cdots & f_6 \\ b_1 & \cdots & 0 & 0 & 0 & 0 \\ 0 & \cdots & 1 - b_i - m_i & 0 & 0 & 0 \\ 0 & 0 & b_i & \cdots & 0 & 0 \\ 0 & 0 & 0 & \cdots & \cdots & 0 \\ 0 & 0 & 0 & 0 & b_5 & 1 - b_6 - m_6 \end{bmatrix}$$

Contrary to standard Usher models, the parameters b_i , m_i and f_i are not fixed but are variables randomly drawn at each initialisation. As a consequence, the model is stochastic.

The transition parameter b_i is the probability of a tree in dbh class i to survive and move up to the next diameter class between time step t and $t + 1$. The b_i parameters were computed from annual dbh increments measured in Paracou permanent plots in 1984–1986, before any treatment was applied. They thus reflect potential growth under undisturbed conditions. To account for within-class variability, dbh increments were sampled according to the observed frequency distribution of increments. To avoid extreme values, only part of the distribution bounded by the 5th and the 95th percentile was considered (Appendix A (1)).

The mortality parameter m_i is the probability of a tree in dbh class i to die between t and $t + 1$. The m_i parameters were estimated using all available data on natural mortality (i.e. excluding damage caused by logging). Plots were pooled by treatment and dbh classes grouped (10–40, 40–60 and ≥ 60 cm) to obtain enough observations by group. To account for within-group variability, mortality rates were randomly drawn between the minimum and maximum values observed among treatments (Appendix A (2)).

The fecundity parameter f_i is the number of new trees potentially produced by a tree of dbh i between t and $t + 1$. The f_i parameters determine the number of trees recruited in the first dbh class at each step. In the field, *D. guianensis* trees are able to produce seeds once they attain ca. 25 cm dbh. To take into account the time needed for a seed to reach the first 10–20 cm dbh class, we considered in the model that only trees ≥ 40 cm dbh feed into the first class; therefore f_1 , f_2 and f_3 were set at 0 in the model. Fecundity parameters were calculated for each year at the beginning of the year. Estimates of f_i were found to be constant in the control plots while varying with time since treatment in the logged plots: recruitment is enhanced immediately after logging with the opening of the canopy, then slows down with the increase of competition. Two different sets of fecundity parameters were thus considered for the implementation of StoMat: StoMat(1) uses the parameters estimated on the control plots and StoMat(2) uses the parameters estimated in the T1-treated plots (Appendix A (3)).

Logging damage was taken into account by subtracting a damage vector to y at the first year of each felling cycle. This damage vector contains estimates of the fraction of *D. guianensis* trees killed in each dbh class, computed from the T1-treated plots (Appendix A (4)).

Each simulation provided by StoMat was the mean result of 10,000 repetitions run with a different sampling of the parameters b_i and m_i . For this study, the f_i values were kept constant.

2.2.2. SELVA

SELVA (Gourlet-Fleury, 1999) is a single-tree distance-dependent model designed to explicitly simulate forest stand dynamics in the most realistic way. SELVA is set up on the CAPSIS 4.0 Java platform (Coligny et al., 2003, and see <http://capsis.free.fr>). In this model, the position of each tree ≥ 10 cm dbh in the stand is known and described by individual growth, mortality and recruitment sub-models on a 3-year time step.

Standard sub-models were developed to simulate the mean behaviour of trees of any species, and specific sub-models were developed for some valuable species. In the version used in our study, SELVA ran a specific set of sub-models designed for *D. guianensis*, while all surrounding trees were grown according to the standard implementation of the model. In addition, original sub-models governing *D. guianensis* regeneration were added to simulate the entire life cycle of the species (Fig. 2).

Standard implementation of SELVA can be summarized as follows (see Gourlet-Fleury, 1999 and Gourlet-Fleury and Houllier, 2000 for extensive description and justification):

Individual diameter increment is modelled by a “ $\Delta D = \text{average} \times \text{modifier}$ ” type model, an adaptation of the “ $\Delta D = \text{potential} \times \text{reducer}$ ” form proposed by Hahn and Leary (1979) and Leary and Holdaway (1979). “Average” is a Korf model (Zeide, 1993) utilizing tree diameter only as the independent variable. “Modifier” is an exponential function of two indices describing the local competition exerted upon a tree by neighbours within a ≤ 30 m radius.

Tree mortality is governed by logistic models dependent on tree size, past growth and local competition. When falling, trees inflict damage on

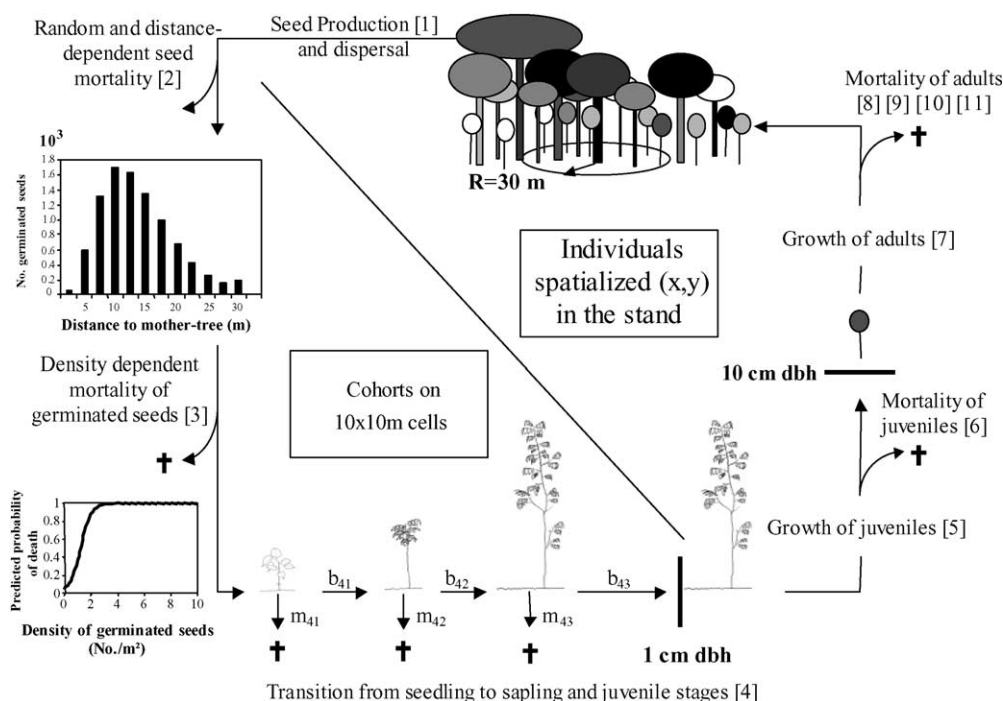


Fig. 2. Outlines of the multi-stages demographic model of *D. guianensis* population implemented into SELVA. Over the entire tree life cycle, main developmental stages and ecological processes taken into account in the model are shown. Numbers in brackets refer to equations clarified in Appendix B.

their neighbours according to the relative size and relative position of the trees involved.

Recruitment above 10 cm dbh is modelled by a general logistic function dependent on local basal area. This function gives, for any 10 m × 10 m cell in the stand, the probability of recruitment of a given number of new trees.

The implementation of *D. guianensis* population dynamics using SELVA specifically adapted the standard implementation of the model for trees ≥ 10 cm dbh. It included an original multi-stage sub-model of recruitment based on the main ecological processes governing seed production and early regeneration (Fig. 2). All relationships considered in the analysis were calibrated from field data (Appendix B). Some relationships based on fewer data were empirically adjusted to correctly render and stabilize *D. guianensis* population structures in the long term: (i) the density-dependent mortality of germinated seeds was adjusted to emulate observed spatial patterns of juvenile and adult distributions; (ii)

the model of standing mortality of juveniles was extrapolated from the adult model and adapted to account for the juveniles' light demands; (iii) the model of adult standing mortality was also modified from the SELVA standard model. Parameters of the last two models were tuned to render observed diameter structure of juveniles and achieve the long-term stabilization of the population.

In the course of a simulation using SELVA, *D. guianensis* trees interact spatially with the other trees through variations in competition with local neighbors and direct damage caused by tree-fall. Logging influences *D. guianensis* population dynamics through tree-falls and decreases in seed production resulting from the felling of mother-trees.

2.3. Evaluation of models performance

Evaluating forest growth models is a complex procedure involving several interrelated steps (Vanclay and Skovsgaard, 1997). We examined in

detail the logical and biological consistency, statistical properties and characteristics of errors of SELVA components in Gourlet-Fleury (1997) and Gourlet-Fleury and Houllier (2000). We did the same for *D. guianensis* sub-models that could be calibrated using data sets (results not detailed here, but see Appendix B for growth). We further evaluated the global performance of StoMat and Selva, regarding the prediction of *D. guianensis* population dynamics, as explained in the next paragraphs.

2.3.1. StoMat

We expected StoMat to correctly predict the recovery of the exploitable stock in the short-term but to show increasing uncertainty of predictions in the long-term. To evaluate the reliability of StoMat on the first felling cycle period (40 years), we ran simulations with StoMat(1) and StoMat(2) from two stand situations encountered at Paracou: (i) the three T1-treated plots and (ii) the Southern Block. Initial conditions were those of the plots in 1987 immediately after logging.

We compared StoMat outputs with available field data of *D. guianensis* stock recovery over the 17-year period following logging in the Paracou plots. We focused on two variables: the number of trees ≥ 60 cm dbh (potentially exploitable stock, hereafter N_{60}) and the number of trees ≥ 10 cm dbh, (hereafter N_{10}). N_{60} and N_{10} were computed from the 12 growth measurement surveys conducted at Paracou between 1986 and 2003.

2.3.2. SELVA

We expected SELVA to correctly render the structure, demography and spatial pattern of *D. guianensis* population ≥ 1 cm dbh, on a mid- and long-term basis. The data on initial stand conditions used in SELVA were those of the Southern Block, where data on juveniles were available. We observed that, in every simulation, an initial period of about 450 years elapsed before the variables of the population stabilized. This represents the time necessary for the *D. guianensis* population as a whole (seeds to senescent adults) to be generated by the interacting sub-models. Comparison of the short-term evolution of population structure predicted by SELVA with the observed chronosequence at Paracou was therefore not relevant.

To evaluate the reliability of SELVA, we ran 900-year simulations (300 cycles of 3 years) starting from the initial conditions of the Southern Block in 1999 without simulating any disturbance. We repeated the simulations 20 times to account for the variability generated by the stochastic components of the sub-models. A confidence interval was computed for the mean outputs using Student $t_{\alpha=0.05}$. We then compared the mean stabilised output (450–900-year period) and the mean *D. guianensis* population behaviour observed in Paracou undisturbed plots. As for StoMat, we examined population and stock recovery through variation of N_{60} and N_{10} . In addition, we examined the turnover (mortality and recruitment rates) of adult trees and the diameter structure of the whole population.

2.4. Comparison between models

To perform a relevant comparison between models predictions, we considered as shared initial stand conditions the mean projection of the Southern Block generated by SELVA for year 1999 + 450. Mean diameter structure of the *D. guianensis* population simulated by SELVA for this year was thus computed and loaded into StoMat. The logging regime simulated was 10 felling cycles of 42 years (instead of 40 years, to match with the 3-year time step of SELVA), cutting all *D. guianensis* trees above DCL (60 cm dbh) at the end of each cycle. StoMat(1) and StoMat(2) implementations were run to evaluate the influence of fecundity parameters on predictions. Output variables examined were N_{10} and N_{60} .

3. Results

3.1. Performance of StoMat

StoMat correctly simulated short-term recovery of the exploitable stock (N_{60}) in both stand situations studied (Fig. 3). Regardless of the implementation used for fecundity parameters, short-term predictions of N_{60} were well-correlated with field observations in the T1-treated plots and the Southern Block ($r^2 = 0.99$, with no significant bias in either case).

Short-term recovery of N_{10} was better predicted by StoMat(2) than by StoMat(1) (Fig. 3). The predictions

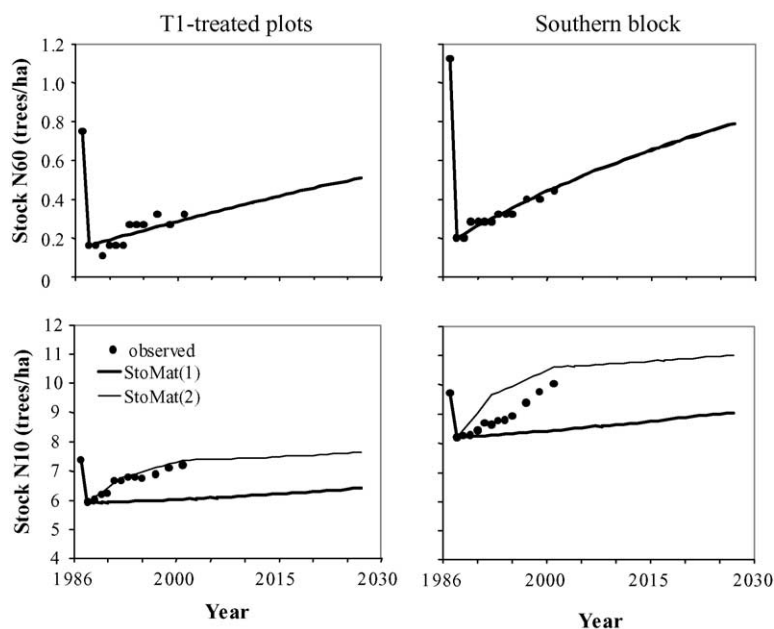


Fig. 3. Observed and StoMat-predicted stock recovery of *D. guianensis* in Paracou permanent plots after logging in 1986. Data are separately presented for two sets of plots differing in past logging treatment: the T1-treated plots ($N = 3$) and the Southern Block (extended area around $N = 4$ plots) (see Fig. 1). N_{60} = number of trees ≥ 60 cm dbh (exploitable stock) and N_{10} = number of trees ≥ 10 cm dbh (total stock).

made by StoMat(2) correlated well with the observed N_{10} recovery in T1-treated plots ($r^2 = 0.98$, with no significant bias) but overestimated the observed N_{10} recovery in the Southern Block.

3.2. Performance of SELVA

Long-term simulations of N_{60} and N_{10} made by SELVA in the Southern Block both stabilized after an initial period of ca. 450 years (Fig. 4). From year 1999 + 450 to year 1999 + 900, mean simulated N_{60} was 0.91 trees/ha with the largest confidence interval being [0.74–1.06]. In comparison, actual mean N_{60} observed in the Southern Block in 1984–1986 before treatment was 1.12 trees/ha. Mean simulated N_{10} over the stabilized period was 11.15 trees/ha with the largest confidence interval being [10.17–11.87]. In comparison, actual mean N_{10} observed in the Southern Block in 1984–1986 was 9.68 trees/ha. Actual values of *D. guianensis* stock were close but not included into the confidence interval of the mean simulation generated by SELVA. Thus, SELVA tended to slightly underestimate N_{60} and slightly overestimate N_{10} with

respect to the actual, undisturbed, situation of the Southern Block.

The recruitment and mortality rates of adult trees (≥ 10 cm dbh) generated by SELVA over the stabilized period were stable and counteracted each other (Fig. 5). The mean value for both mortality and recruitment rates was 0.14 trees/ha/year (1.3% of the living trees). In comparison, mean field values derived from control plots between 1984 and 2001 were 0.05 trees recruited/ha/year and 0.03 trees dead/ha/year (0.8 and 0.5% of the living trees, respectively). Thus SELVA simulated an adult-tree turnover rate that was 4–5-times greater than that observed in the field.

The mean diameter structure of the population generated by SELVA over the stabilized period was similar to that observed in the Southern Block both for the juveniles and adults (Fig. 6). However, trees grown by SELVA tended to over-accumulate in the 10–15-cm class whereas intermediate and larger classes (from 30 cm dbh) tended to be depleted. The deficit of trees above DCL was already pointed out above while examining SELVA-simulated N_{60} .

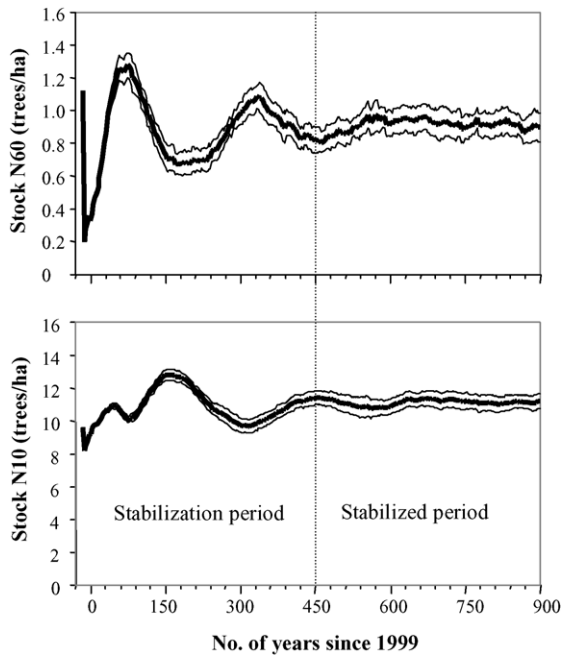


Fig. 4. SELVA-simulated stock recovery of *D. guianensis* in Paracou Southern Block. Data are mean (thick line) and bounds of the 95% confidence interval (light lines) computed from a set of 20 repetitions of 900-year simulation. Initial stand conditions loaded were 1999 field conditions for any simulation. On the x-axis, the real evolution of the plots observed between 1984 and 1999 is represented by years—15 to 0.

3.3. Comparative study of StoMat and SELVA predictions on *D. guianensis* stock recovery

According to SELVA predictions, the logging regime considered would allow a 57–67% recovery of the *D. guianensis* exploitable stock over the five first felling cycles before a clear decrease of the exploitable stock would occur (Fig. 7a). This coincided with a predicted regular and severe decrease of the whole adult-tree population that began as soon as the first felling cycle (Fig. 7b).

StoMat(1) and StoMat(2) yielded the same predictions for N_{60} recovery after the first felling, slightly differed on the recovery after the second cycle (difference = 7%) then subsequently clearly diverged (Fig. 7a and Table 1). StoMat(2) behaviour became nonsensical after the second cycle by predicting a constant increase of N_{60} and a demographic explosion of the whole population ≥ 10 cm dbh under repeated felling (Fig. 7b). Thus, StoMat(2) showed complete

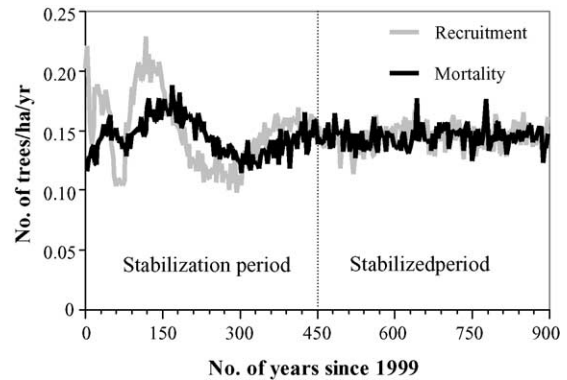


Fig. 5. SELVA-simulated long-term evolution of recruitment and mortality rates of *D. guianensis* adult trees. Data are mean annual numbers of trees recruited over 10 cm dbh and mean annual numbers of dead adult trees estimated from 20 repetitions of 900-year simulation. The 95% confidence interval around mean values is not represented to keep the figure legible. Extreme values of the confidence interval bounds ranged 0.08–0.25 trees/ha, and 0.09–0.20 trees/ha for recruitment and mortality rates, respectively.

discordance with SELVA-generated predictions in the long-term. In contrast, StoMat(1) and SELVA gave concordant long-term predictions for both N_{60} and N_{10} . StoMat-predicted recovery was lower than values predicted by SELVA but showed a very similar trend. After the first three felling cycles, StoMat-predicted N_{60} and N_{10} values were often within the SELVA-predicted confidence interval (Table 1).

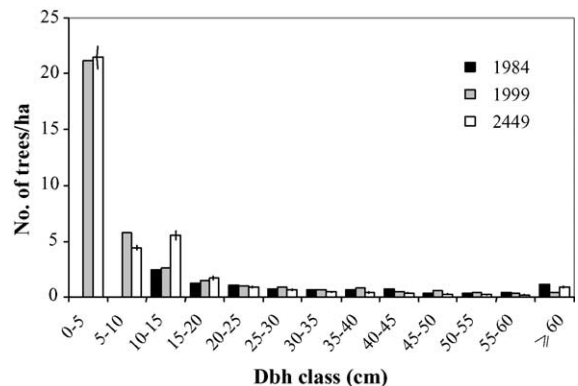


Fig. 6. Observed and SELVA-predicted diameter structure of *D. guianensis* population in the Southern Block. Bars represent structures observed in 1984 (before any perturbation) and in 1999 (13 year after logging treatment), as well as the mean structure ($\pm 95\%$ confidence interval) generated by SELVA for year 1999 + 450 ($N = 20$ repetitions). Data on trees under 10 cm dbh are not available for 1984.

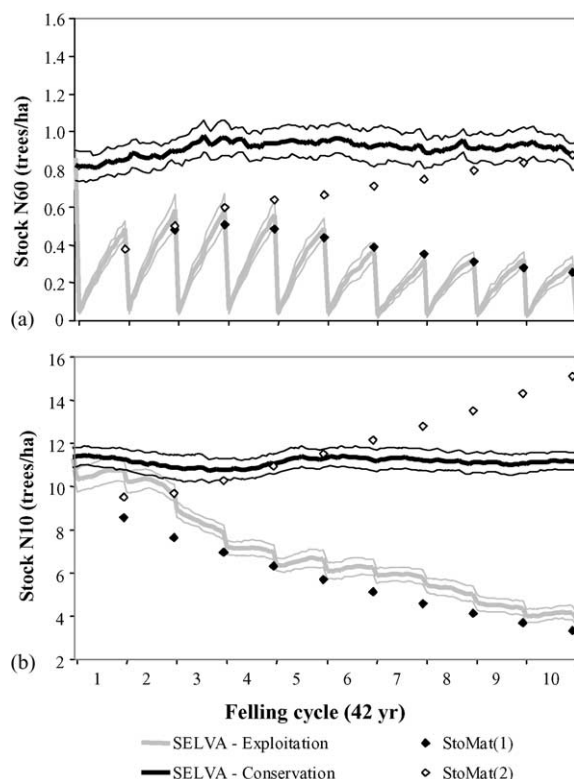


Fig. 7. StoMat and SELVA predictions upon the long-term evolution of an exploited population of *D. guianensis* trees. Stabilized conditions at year 1999 + 450 generated by SELVA were used as shared initial stand situation for both models. Logging regime considered is 42-year felling cycles cutting all exploitable trees at the end of each cycle.

Table 1

StoMat and SELVA predictions upon the long-term evolution of an exploited population of *D. guianensis* trees. Stabilized conditions at year 1999 + 450 generated by SELVA were used as shared initial situation for both models

	Stock N_{60} (trees/ha)			Stock N_{10} (trees/ha)		
	SELVA	StoMat (1)	StoMat (2)	SELVA	StoMat (1)	StoMat (2)
Reference (1999 + 450 year)	0.86 (0.80–0.92)	0.86	0.86	11.30 (10.72–11.87)	11.30	11.30
1st felling (+492 year)	0.49 (0.45–0.53)	0.38	0.38	10.73 (10.23–11.24)	8.58	9.51
2nd felling (+534 year)	0.58 (0.50–0.67)	0.48	0.50	9.71 (9.35–10.08)	7.62	9.67
3rd felling (+576 year)	0.58 (0.50–0.67)	0.51	0.60	7.87 (7.53–8.20)	6.95	10.31
4th felling (+618 year)	0.56 (0.49–0.63)	0.48	0.64	6.98 (6.63–7.33)	6.31	10.92
5th felling (+660 year)	0.49 (0.43–0.54)	0.44	0.66	6.65 (6.26–7.05)	5.68	11.52
6th felling (+702 year)	0.36 (0.31–0.41)	0.39	0.71	6.26 (5.90–6.62)	5.11	12.16
7th felling (+744 year)	0.32 (0.28–0.36)	0.35	0.75	5.81 (5.48–6.14)	4.59	12.82
8th felling (+786 year)	0.32 (0.28–0.36)	0.31	0.80	5.00 (4.64–5.36)	4.11	13.54
9th felling (+828 year)	0.32 (0.28–0.36)	0.28	0.84	4.37 (4.05–4.69)	3.69	14.30
10th felling (+870 year)	0.29 (0.25–0.34)	0.26	0.88	4.16 (3.84–4.49)	3.33	15.09

Logging regime considered is a 42-year felling cycle, cutting all exploitable trees at the end of each cycle. Simulated values are means (95% confidence interval bounds).

4. Discussion

4.1. Using StoMat for predicting *D. guianensis* recovery

Our study showed that StoMat gave reliable short-term predictions of N_{60} after the first felling, regardless of the implementation used (StoMat(1) or StoMat(2)). This implies that the short-term recovery of the exploitable stock above DCL is independent of recruitment but rather is dependent on the growth of trees remaining after logging. It is important to notice that the parameters of StoMat calibrated on undisturbed stands (growth and mortality) were useful predictors of the behaviour of the trees after logging. In fact, analyses of post-logging dynamics of *D. guianensis* at Paracou have shown that the stimulating effect of logging disturbance on diameter increment is compensated by negative effects on mortality (increase after logging in intermediate dbh classes).

On the contrary, only StoMat(2) short-term predictions of N_{10} appeared reliable. The use of StoMat(1) in logged plots led to significant underestimates of this variable. This was expected as logging had a positive effect on recruitment in the first classes, due to the enhancement of survival and growth of juveniles by logging gaps. The logging effect on recruitment implemented in StoMat(2) perfectly rendered T1-treated plots post-logging recovery of N_{10} as expected since fecundity parameters were

calibrated on those plots. When applied to the Southern Block stand situation, StoMat(2) predictions overestimated N_{10} values. Actually, the Southern Block area recorded higher level of logging disturbance than in T1-treated plots (mean of 20 trees felled/ha versus 10 trees felled/ha). Higher extraction and damage levels in plots T2 and T3 in the Southern Block (see Fig. 1) caused the young *D. guianensis* trees to suffer heavier losses than in T1, resulting in a decreased post-logging recovery of N_{10} .

Usher matrices, like those used in StoMat, have several constraints related to the classical hypotheses underlying their use (Caswell, 2000). Among them, the stationarity hypothesis, which states that the transition parameters b_i and m_i must be constant, is the most limiting: in real stands, population dynamics are influenced by environmental conditions such as variation in stand density (Cushing, 1988; Caswell, 2000). In addition, Usher matrices impose an exponential population growth (negative or positive) depending on the first eigen-value of the matrix (except when this value is 1, which is rarely the case). Several solutions can be proposed to overcome those constraints:

- (i) Make all the parameters dependent of the state of the stand at each time step (see Cushing, 1988; Favrichon and Young Cheol, 1998; Boscolo and Vincent, 2000; Sist et al., 2003). This necessitates large data sets to calibrate the matrix regulation and to define the complete actual and undisturbed stand conditions.
- (ii) Change the parameters in the course of simulations. This requires having a good idea of the time schedule and the effect of a given disturbance.
- (iii) Limit the use of these models to cases involving low stand disturbance and short periods of time.

The third option is the most practical for models, designed to be used in forests where only limited datasets are available. In tropical forests of Africa and South America, including managed forests of French Guiana, selective logging is predominant with extraction levels typically not exceeding 1–5 trees/ha and felling cycles usually short (Sist, 2000). This study showed that a non-regulated matrix model implemented with transition parameters calibrated in undis-

turbed stands can correctly predict the short-term evolution of a species exploitable stock even in heavily disturbed stands. As simulated harvesting systems usually involve short felling cycles, we may consider long-term simulations to have some reliability since the frequent cutting of the larger trees may act as a regulating factor for population growth.

However, reliable simulations require correct assessment of the fecundity parameters as was shown for StoMat in this study. In particular:

- (i) The average time required for a seed to reach the first diameter class must be estimated to correctly link one generation of trees to the next. For example, in our study, we considered that new *D. guianensis* recruits to 10 cm dbh were derived from trees ≥ 40 cm dbh. This threshold was determined using SELVA simulations of the entire species life cycle. On average, 60 years were found to elapse between the dispersal of a seed crop and the recruitment of a new tree from this seeding event. Since the minimum seeding dbh of *D. guianensis* trees is 25 cm dbh, mother trees must have attained 40 cm dbh when a seed they produced yields a new recruit (given a mean diameter increment of 0.25 cm/year). When no details are available on the early regeneration stages, this generation time-lag must be roughly assessed based on ecological knowledge of the species.
- (ii) The impact of stand disturbance on juvenile survival and growth, and thus on recruitment, must be taken into account. For example, in our study we considered that fecundity parameters change with time following logging intervention. This necessitates long-term data from permanent experimental plots logged according to current practices.

4.2. Using SELVA for predicting *D. guianensis* recovery

Some processes implemented in SELVA were empirically described and tuned to yield patterns of observed demography and spatial distribution under the hypothesis of a stable evolution of the *D. guianensis* population in the long term. In particular, mortality models were tuned to counteract recruitment. However, this hypothesis of mortality-recruitment parity is debatable. Indeed, field observations in

Paracou control plots over the last 18 years show a continuous trend toward the expansion of the *D. guianensis* population in the stand with a mean recruitment rate exceeding the mean mortality rate by 60%. This tendency may indicate either a progressive colonization of the site by the species or a temporal fluctuation of population growth. In comparison, the fluctuations of population growth generated by SELVA, once stabilized, never exceeded 10% over 6 cycles (18 years).

As a consequence of the above hypothesis, the turnover of adult trees simulated by SELVA is too high when compared to observed data. This is due to a higher than observed recruitment rate, mechanistically compensated by a higher mortality rate. In addition, the switch between the juvenile and adult models of diameter increment (independently calibrated) in SELVA is responsible of some differences between simulated and observed diameter structure. From 1 to 10 cm dbh, juveniles are grown according to their diameter only. When they reach 10 cm dbh their simulated average growth rate is 0.3 cm/year, which is in agreement with field measurements at Paracou. From 10 cm dbh trees are then grown according to their diameter and their neighbouring environment. The field data used to calibrate growth in the 10–15 cm dbh class included trees, which had recently recruited and old suppressed trees giving an average growth rate of 0.17 cm/year. As a result, during simulations, juveniles grown by SELVA have their growth rate suddenly reduced when switching to the adult model of growth.

4.3. Is a simple model enough to assess *D. guianensis* vulnerability?

We showed that StoMat(1) and SELVA gave similar long-term predictions of *D. guianensis* recovery with the exception of the first three felling cycles during which StoMat underestimated N_{60} and N_{10} . This may be explained by the initial stand conditions loaded into StoMat(1). Indeed, initial diameter structure considered was SELVA-generated and showed a deficit in the intermediate tree size classes (Fig. 6). This resulted in less ingrowth to the class ≥ 60 cm dbh and consequently in a deficit of recruitment in the 10–20 cm class. StoMat fecundity parameters did not counteract this effect until the fourth felling cycle (Table 1). At the same time, the

repeated felling began to negatively impact *D. guianensis* regeneration in the SELVA model that caused the evolution curves generated by StoMat(1) and SELVA to converge after the fourth felling cycle.

It should be noted that the harvesting regime simulated in SELVA, involving harvest of only *D. guianensis* trees, resulted in a low level of stand disturbance (0.6 trees/ha, on average). This explains why StoMat(1) implemented with parameters calibrated on undisturbed plots yielded the most similar predictions to SELVA. The stimulating effect of stand opening on recruitment implemented in StoMat(2) and calibrated on heavily logged plots (10 trees/ha) appeared to be inappropriate in this context. Long-term predictions of StoMat(2) need to be compared with SELVA predictions for higher-intensity disturbance regimes. However, despite the positive reaction of *D. guianensis* to stand opening, the rapid population increase predicted by StoMat(2) in the long term appeared quite unrealistic; this underlines the limitations of matrix models, which do not take into account competitive interactions between neighbouring trees.

Finally, we note that, under certain conditions of use, StoMat can provide predictions as reliable as those obtained using SELVA, a more complicated model, and may be sufficient to assess the recovery of *D. guianensis* exploitable stock even in the long term.

5. Conclusion

Matrix models are powerful tools for forest managers, as they are easy to build, simple to use, and can provide reliable predictions of the long-term recovery of a species exploitable resource when correctly used. The case studied in this paper yielded the following observations:

- (i) In the short term (i.e. the duration of a felling cycle), recovery of a species exploitable stock predicted by a matrix model appear to be robust, even when parameters calibrated on undisturbed stands are used to simulate species recovery in highly disturbed stands (10–20 trees felled/ha).
- (ii) Predictions of a matrix model up to the second felling cycle can be regarded as adequate without

paying much attention to the way recruitment is modelled.

- (iii) Long-term behaviour can be assessed through a simple recruitment model linking the larger dbh classes to the smallest, calibrated from undisturbed plots. This conclusion is not suitable, however, when felling intensity exceeds 1–2 trees/ha, as greater opening of the stand can significantly influence recruitment, particularly for light-demanding species. We, however, argue that in the absence of available data on the regeneration behaviour of tropical timber tree species, the use of matrix models calibrated on undisturbed stands can at least serve to demonstrate the unsustainability of particular harvesting regimes.

Despite the fact that some model components still require improvement, SELVA has already proved its reliability as a simulator of the long-term dynamics of *D. guianensis*, and consistency observed between its predictions and those of StoMat increase our confidence in its performance.

Finally, the consistent predictions of StoMat and SELVA presented in this study should be considered

by French Guiana forest managers, since they indicate that a harvesting regime involving cutting all *D. guianensis* trees above the DCL of 60 cm dbh every 42 years (let say 40 years) may not be sustainable over the long term (10 cutting cycles). In any case, no more than 60% of the initial stock will recover after logging. This should be balanced with the predicted recovery of the other logged species, and might necessitate the modification of the logging rules currently in use.

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Appendix A

Parameters derived from Paracou sample plots implementing *D. guianensis* population dynamics in StoMat. (1) Dbh growth: the interval of variation defined by the 5th and the 95th percentiles of the distribution of observed dbh increments was split into five equal intervals. The observed frequency of each interval is given in below table. (2) Mortality: natural mortality was estimated for three groups of dbh classes by treatment. The minimum and maximum values of annual mortality rates over treatments are given in the below table. (3) Recruitment: fecundity parameters (f_i) are the ratios between the number of trees recruited above 10 cm dbh and the number of trees ≥ 40 cm dbh. f_i were computed for each year of data. Average estimates separately computed on control and T1-treated plots are given in the below table. (4) Logging damage: the average fraction of *D. guianensis* trees killed by logging was assessed in T1-treated plots. The value for the last class includes tree fell.

(1) Dbh growth

Dbh class	N trees	Dbh increment (cm/year)			Observed frequency distribution (fraction by class)				
		Mean	Min	Max	Int.1	Int.2	Int.3	Int.4	Int.5
10–20 cm	207	0.16	0.00	0.48	0.436	0.240	0.151	0.089	0.084
20–30 cm	93	0.31	0.00	0.56	0.158	0.158	0.341	0.221	0.122
30–40 cm	68	0.35	0.08	0.72	0.121	0.242	0.152	0.303	0.182
40–50 cm	55	0.35	0.00	0.80	0.269	0.250	0.308	0.154	0.019

Appendix A (Continued)

(1) Dbh growth									
Dbh class	N trees	Dbh increment (cm/year)			Observed frequency distribution (fraction by class)				
		Mean	Min	Max	Int.1	Int.2	Int.3	Int.4	Int.5
50–60 cm	33	0.33	0.00	0.87	0.290	0.355	0.161	0.129	0.065
≥60 cm	48	0.23	0.00	0.64	0.350	0.275	0.200	0.125	0.050

(2) Mortality

Dbh class	Mortality rate (%)	
	Min	Max
10–40 cm	0.19	0.64
40–60 cm	0.90	2.09
≥60 cm	0	1.79

(3) Recruitment

Dbh class	Fecundity parameter estimate			
	Control plots (StoMat (1))		T1-treated plots (StoMat (2))	
	Year 1–5 after treatment		Year 6–14 after treatment	Year 15- to next felling
10–20 cm	0	0	0	0
20–30 cm				
30–40 cm				
40–50 cm	0.033	0.176	0.076	0.033
50–60 cm				
≥60 cm				

(4) Logging damage

Dbh class	Proportion of trees killed (%)
10–20 cm	22.4
20–30 cm	0
30–40 cm	4.5
40–50 cm	0
50–60 cm	0
≥60 cm	80 (real) – 100 (used in simulation)

Appendix B

Explicit parameterisation of the single-tree distance dependent model of population dynamics implemented for *D. guianensis* in SELVA. Main ecological processes driving *D. guianensis* regeneration from seeds (see Fig. 2 for a simplified overview of the species life cycle) are described and modelled according to field observational and experimental data.

Process	Description	Models and variables	Parameters*
Seed production	Trees set seeds when reaching 25 cm dbh. The number of seeds produced depends on tree crown area and the frequency of seeding events which varies with tree dbh class	$N_{\text{seed}} = \text{frequency} \times n_{\text{seed}}$ $n_{\text{seed}} = a_1 \times s_{\text{crown}} - b_1 \quad (1)$ $s_{\text{crown}} = c_1 \times D^{d_1}$ $N_{\text{seed}} = \text{number of seeds produced by a tree during a 3-year cycle}$	$a_1 = 136.33$ $b_1 = 11691$ $c_1 = 0.1699$ $d_1 = 1.7082$ estimated from observed data

Appendix B (Continued)

Process	Description	Models and variables	Parameters*
		n_{seed} = number of seeds produced during a seeding event frequency = average number of seeding events per cycle. Frequency varies with tree dbh class s_{crown} = tree crown area (m^2) D = diameter at breast height (cm)	
Mortality of seeds	Seeds are dispersed around mother trees and suffer (i) random mortality due to fungal rotting and insect predation and (ii) distance-dependent mortality due to predation by granivorous mammal	$m_{\text{seed}} = a_2$ (2) m_{seed} = global mortality rate of dispersed seeds; Surviving seeds are germinating. They are dispersed around the mother-tree according to a density probability function (gamma law), calibrated on observed data, and split on 10×10 m cells: $\Gamma_{b_2, c_2}(\text{dist}) = \frac{c_2^{b_2} \text{dist}^{b_2-1} e^{-\text{dist}/c_2}}{\Gamma(b_2)}$ dist = distance to mother tree (m)	$a_2 = 0.97$ $b_2 = 4.28$ $c_2 = 2.91$ estimated from observed data
Mortality of germinated seeds	The overlap of the seed shadows of neighboring trees creates crowding places where germinated seeds experiment increased mortality	$m_{\text{gseed}} = \frac{1}{1 + e^{(a_3 \times \text{dens} + b_3)}} \quad (3)$ m_{gseed} = mortality rate of the germinated seeds; dens = number of germinated seeds per 10×10 m cell	$a_3 = 0.025$ $b_3 = 3$ adjusted empirically (see Section 2)
Seedling to juvenile transition	Survivors from previous step are grown by a simple matrix model considering three stages: seedlings, saplings (0.5–1 cm dbh) and pre-recruited juveniles (1 cm dbh). The matrix operates on each 10×10 m cell	$N_{c+1} = A \times N_c + R_c$ (4) with $A = \begin{bmatrix} 1 - b_{41} & 0 & 0 \\ m_{41} & 1 - b_{42} - m_{42} & 0 \\ 0 & m_{42} & 1 - b_{43} - m_{43} \end{bmatrix}$ N_c = vector of the numbers of individuals in each stage at simulation cycle c ; A = matrix of transition parameters; R_c = vector of recruited seedlings (one non null value, equal to the number of survivors to step (3))	$b_{41} = 0.44$ $b_{42} = 0.008$ $b_{43} = 1$ $m_{41} = 0.56$ $m_{42} = 0.56$ $m_{43} = 0.14$ estimated from observed data
Juvenile growth	Surviving 1 cm dbh juveniles are given coordinates (x , y) according to the original seed dispersion pattern. Diameter increment is individually modeled	$\log(\Delta D + 1) = a_5 + b_5 + \varepsilon_5$ (5) ΔD = mean annual diameter increment (cm/year) over a cycle (3 years); D = diameter at breast height (cm) at the beginning of the cycle; this model explains 39% of the variance observed	$a_5 = 0.0214$ $b_5 = 0.0233$ $\varepsilon_5 \sim N(0; 0.067)$ estimated from observed data
Juvenile mortality	Juveniles die standing when they either do not grow enough or the local stand basal area becomes too high. They can also be broken by falling neighbors	$m_{\text{juv}} = \frac{1}{1 + e^{(a_6 + b_6 \Delta D + c_6 G_{30})}} \quad (6)$ m_{juv} = probability for a juvenile to die standing; ΔD = mean annual diameter increment (cm/year) during previous simulation cycle; G_{30} = total basal area (m^2/ha) of trees ≥ 10 cm dbh located ≤ 30 m from the juvenile	$a_6 = 2.55$ $b_6 = 12.0$ $c_6 = 0.1$ adjusted empirically (see Section 2)

Appendix B (Continued)

Process	Description	Models and variables	Parameters*
Adult tree growth	The diameter increment of trees ≥ 10 cm dbh is depending on individual diameter and local competition exerted by neighboring trees	$\log(\Delta D + 0.2) = \log(D) + \log[\log(K) - \log(D)]$ $+ a_7 \text{NBD} + b_7 \Delta \text{NBD} + c_7 + \varepsilon_7$ (7) This is a “ ΔD = average \times modifier” type model, with average = Gompertz model, depending on the diameter of the tree and modifier = linear model depending on two competition indices; ΔD = mean annual diameter increment (cm/year) over previous cycle; D = diameter at breast height (cm) at the beginning of the simulation cycle; K = asymptotic size (cm), parameter of the Gompertz model; NBD = number of trees, located ≤ 30 m, larger in dbh than the focal tree; ΔNBD = variation of NBD during previous simulation cycle; this model explains 35% of the variance observed	$a_7 = -0.0033$ $b_7 = -0.0150$ $c_7 = -4.37$ $K = 135.2$ $\varepsilon_7 \sim N(0; 0.375)$
Adult tree mortality	Four death scenarios are implemented into SELVA to manage mortality of adult trees of any species. Adult trees can die standing or can fall (in this case primary, secondary and complex tree-fall are distinguished). For <i>D. guianensis</i> trees, standing death was specifically modeled while tree-fall death was standard	$m_{\text{Dgstanding}} = \frac{1}{1 + e^{(a_8 + b_8 \Delta D + c_8 + D d_8)}} \quad (8)$ $m_{\text{fall1}} = \frac{1}{1 + e^{(a_9 + b_9 D + c_9 G_{30})}} \quad (9)$ $m_{\text{fall2}} \quad (10)$ $m_{\text{fall3}} = \frac{1}{1 + e^{(a_{11} + b_{11} G_{30})}} \quad (11)$ $m_{\text{Dgstanding}}$ = specific probability of a <i>D. guianensis</i> adult tree to die standing; m_{fall1} = standard probability of any tree (comprising <i>D. guianensis</i> trees) to fall alone; m_{fall2} = standard probability of any tree to be broken or up-rooted by the fall of a neighboring tree. Secondary tree-falls are mechanistically created by the simulator depending on their relative position and diameter according to primary tree-fall tree; m_{fall3} = standard probability of any tree, at the margin of newly-created gaps, to overbalance and fall (complex tree-fall); ΔD = mean annual diameter increment (cm/year) over previous cycle; D = diameter at breast height (cm) at the beginning of the simulation cycle; G_{30} = total basal area (m^2/ha) of trees ≥ 10 cm dbh located ≤ 30 m from the focal tree	$a_8 = 3.42$ $b_8 = 4.96$ $c_8 = -0.0034$ $d_8 = 1.43$ $a_9 = 2.884$ $b_9 = -0.01$ $c_9 = 0.182$ $a_{11} = 2.884$ $b_{11} = 0.182$ $a_8 - d_8$ and $a_{11} - b_{11}$ adjusted empirically (see Section 2); $a_9 - c_9$ estimated from observed data

*Parameters derived from linear and non linear regression analyses were assessed using least squares estimation. Parameters derived from logistic regression analyses (mortality models) were assessed using maximum likelihood estimation. Appropriate transformations of the explained variable was performed if needed.

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