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Impact of selective logging on the dynamics of a low elevation dense moist evergreen forest in the Western Ghats (South India)

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Abstract

Within the framework of a programme on the functioning of dense moist evergreen forests of the Western Ghats, the French Institute of Pondicherry, in collaboration with the Karnataka Forest Department, installed permanent plots to monitor the dynamics of a low elevation forest. The preliminary results of the comparison of the demographic processes in two compartments are presented: one compartment had never been harvested, while the other was selectively felled in 1979–1980. They are compared in terms of species composition, recruitment, mortality and individual growth, in order to describe the natural forest dynamics and evaluate the impact of selective felling. In both compartments, the mortality rate, around 0.9% yr^{-1}, is lower than in other tropical moist evergreen forests, while the average diameter increment, at 2.1 (unlogged stand) and 2.9 mm yr^{-1} (logged stand), is higher. The impact of selective felling, 10 to 15 years after the harvest, is mainly noticeable: (i) on mortality of trees with dbh $>$ 40 cm belonging to lower canopy and intermediate stratum species which died about four times more in the logged compartment; and (ii) on diameter increment of emergent and upper canopy tree species whose growth is still stimulated by about 50%. Despite the general trend of a reduction in the difference between the density and the basal area of the two compartments, medium-term modification of the demographic processes among the various structural ensembles in the logged compartment, indicates that selective felling may not be sustainable in the long-term without consequences on the forest structure and composition. © 1998 Elsevier Science B.V.

Keywords: India; Dense moist evergreen forest; Growth; Mortality; Recruitment; Forest dynamics; Selective logging

1. Introduction

In the context of the ongoing debates on conservation of biodiversity, forest degradation and sustainable forestry in the tropics, there is a pressing need to assess the consequences of different management techniques on forest structure and dynamics, not only the immediate damages resulting from felling (e.g., Bertault and Sist, 1995), but also the short- and long-term reaction of the forest in terms of growth, regeneration and mortality (e.g., Maitre, 1986; Bariteau and Geoffroy, 1989; Schmitt and Bariteau, 1990; Durrieu de Madron, 1994). Although several silvicultural systems—polycyclic and monocyclic, selective or not, with or without thinnings, etc. (see

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Durrieu de Madron, 1993)—have been proposed and applied in the tropical 'natural' forests all over the world, there is still a lack of reliable information on their long-term sustainability (i.e., long-term maintenance of forest structure and diversity). Several experiments have thus been set up in order to provide such comparative information on forest dynamics in natural and disturbed forests, with an emphasis on the changes, both immediate and delayed, in the forest structure, composition and demographic processes (growth, mortality and recruitment) due to silvicultural operations (Maitre, 1986; Schmitt and Bariteau, 1990).

Although no such experimental site has been so far installed in the Western Ghats of India, this paper aims at contributing to these empirical investigations by comparing the dynamics of a logged and an unlogged compartment in a low elevation dense moist evergreen forest. This type of forest once occupied vast areas along the southwestern coast of India, extending from the coastal plain to the crest of the Ghats (Pascal, 1984, 1988). Large-scale harvesting operations began in the 19th century and were continued throughout the colonial and post-Independence period according to various silvicultural systems: selective fellings, regeneration fellings, irregular shelterwood system (Loffeier, 1989). Thus, pushed back by exploitation and extension of agriculture and plantations (Buchy, 1996), these endangered forests are now only found in steep and not easily accessible zones.

After classifying and mapping the forests of South India (Pascal et al., 1982a,b, 1984; Pascal, 1986, 1992), the French Institute of Pondicherry (IFP) launched a collaborative research programme with the Karnataka Forest Department on the functioning and dynamics of one of the rare well preserved moist evergreen forests: the Kadamakal Reserve Forest (Kodagu District, Karnataka). The first stage of this programme was the study of the reconstitution of the forest after selective felling by monitoring the dynamics of a logged compartment for a few years (Loffeier, 1988, 1989). The IFP then installed permanent plots and transects in another compartment which had never been harvested: their monitoring provided the basis for studies on stand development, growth and yield (Pélissier, 1995; Pascal and Pélissier, 1996; Elouard et al., 1997; Pascal et al., in press), primary productivity, phenology (Aravajy, 1995), seed dispersal (Sinha and Davidar, 1992) and tree architecture (Durand, 1997; Houllier et al., 1997).

As a continuation of the work of Loffeier (1989), the objective of this paper is to present and compare the results of the diachronic study of the demographic processes carried out in the two (logged and unlogged) compartments, in order: (i) to provide a global assessment of the forest dynamics; and (ii) to evaluate the effects of moderate selective felling, though the monitoring plots were not designed as in statistical experimental sites devoted to that purpose.

2. Materials and methods

2.1. Study site

The data are from two compartments near the village of Uppangala in the Kadamakal Reserve Forest (12°30′N; 75°39′W). The zone has a wet tropical climate with a monsoon regime: the average rainfall is 5100 mm yr^{-1}, interrupted by a dry season (sensu Bagnouls and Gaussen, 1953) of 4 to 5 months, from November to April. The soils belong to the category of ferrallitic soils which can be further classified into two types: evolved soils on thick alterites in the interfluves, and younger soils on scree-covered slopes (Loffeier, 1989; Pascal and Pélissier, 1996). In both cases, the soils are acidic and their mineral richness, although limited (Ferry, 1994), is still higher than that observed in other intertropical forest soils (Bourgeon, 1992; Swamy and Proctor, 1994).

2.2. Sampling design

The two compartments, each measuring 28 ha, are about 5 km apart. The logged compartment (A) is at an elevation of 300–400 m with gentle slopes, while the unlogged compartment (B) is at a slightly higher elevation (500–600 m) in a steeper area. However, they belong to the same *Dipterocarpus indicus-Kingiodendron pinnatum-Humboldtia brunonis* (authority names not cited in the text are given in Table 1) type of the low elevation dense moist evergreen forests (Pascal, 1984, 1988). The main difference between these compartments lies mostly in their recent history and management.

Table 1
Floristic composition of the two compartments at the first survey (1986 in A; 1990 in B): relative frequency and basal area of (i) the 10 most common species in compartment B, (ii) the group of light-demanding species and (iii) the three structural ensembles

	Rank	Relative density		Relative basal area	
		A %	B %	A %	B %
Vateria indica L.	1	28.82	17.13	36.43	29.50
Myristica dactyloïdes Gaertn.	7	3.17	13.53	1.16	11.28
Humboldtia brunonis Wall.	3	9.22	13.48	1.96	2.45
Knema attenuata (J. Hk. and Thw.) Warb.	8	2.88	6.18	1.47	4.91
Palaquium ellipticum (Dalz.) Baillon	14	0.86	4.91	0.65	3.42
Drypetes elata (Bedd.) Pax and Hoffm.	13	1.15	4.12	0.64	4.35
Dipterocarpus indicus Bedd.	2	10.37	3.44	10.02	11.71
Reinwardtiodendron anaimalaiense (Bedd.) Mabb.	14	0.86	3.27	0.18	1.53
Mesua ferrea L.	6	4.32	2.85	4.90	3.71
Garcinia morella (Gaertn.) Desr.	16	0.29	2.27	0.10	0.61
Light-demanding species[a]	–	2.59	1.27	3.11	0.75
Emergent and upper canopy species (SE I)[b]	–	54.47	36.22	73.70	62.07
Lower canopy and intermediate stratum species (SE II)	–	29.97	41.83	19.80	32.82
Understorey species (SE III)	–	15.56	21.95	6.50	5.11

Minimum dbh = 10 cm.

[a] List of light-demanding species (from Pascal, 1984, 1988): *Antidesma menasu* Miq. ex Tul., *Archidendron monadelphum* (Roxb.) Nielson, *Callicarpa tomentosa* (L.) Murray, *Caryota urens* L., *Clerodendron viscosum* Vent., *Croton malabaricus* Bedd., *Glochidion malabaricum* Bedd., *Macaranga peltata* (Roxb.) Mueller, *Mallotus philippensis* (Lam.) Mueller, *M. tetracoccus* (Roxb.) Kurz, *Memecylon* sp., *Pajanelia longifolia* (Willd.) Schum., *Pterospermum diversifolium* Bl., *Sterculia guttata* Roxb., *Vitex altissima* L.

[b] Grouping of species in the different structural ensembles is based on the tables of Pascal, 1984, 1988 and Pélissier, 1995.

Compartment A had once been moderately and selectively felled: in 1979–80, about 8.5 large trees (diameter > 60 cm) per ha were felled then hauled using elephants, a method that causes much less damage than mechanized skidding (Loffeier, 1989). The sampling design set up in 1985 (Loffeier, 1988) consists in 14 plots of 600 m^2 (20×30 m) spread over an 100×150 m systematic grid (Fig. 1a). As one part of the zone was burned down shortly after felling, only the measurements recorded in the ten southern plots (totalling 0.6 ha) that were not burned, have been taken into consideration.

Compartment B is in an area that was planned to be harvested, but was spared due to a ban on felling that was imposed in 1988 in Karnataka State. If the site was ever affected by human disturbance, it was limited to minor forest products collected by villagers (Salaün, 1995): Uppangala is the nearest village, about 10 km away, and the compartment, which has been strictly protected since 1990, was only accessible by foot before opening of the logging track in the 1980s. This compartment was first surveyed in 1990. The monitoring system contains five 20 m wide transects, 180 to 370 m long, oriented in a north–south direction and 100 m apart, thus constituting a systematic sampling of 3.12 ha (Fig. 1b).

2.3. Measurements and data

In each sampling unit of A and B compartments, all the trees with dbh (diameter at breast height, or above the buttresses) ≥ 10 cm were numbered, located and identified. The botanical identification was most often made in the field with the help of the key of Pascal and Ramesh (1987) based on vegetative characters. In doubtful cases, the specimens were collected and identified at the French Institute herbarium.

Different techniques were used to measure tree girth in the two compartments: flexible measuring tape in compartment A and fixed metal dendrometers in B. The accuracy of the measurement varies according to the method: ± 2 mm in A and ± 0.2 mm in B. In A, measurements were made during the dry season in 1985–86, 1987–88 and 1992–93 (designated as the 1986, 1988 and 1993 measurements in

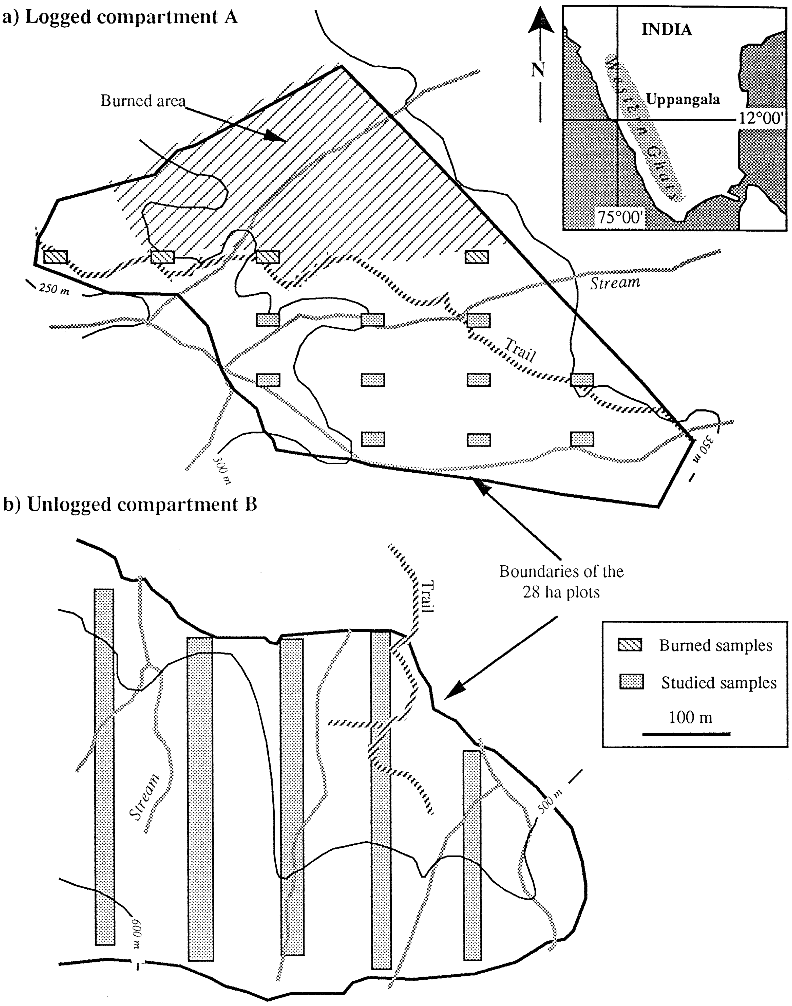

Fig. 1. Location map and sampling design of the two compartments.

the following), while in B the trees were measured twice a year between 1990 and 1994, once at the end of the dry season and again at the end of the rainy season. Recruitment was observed in 1992–93 in compartment A (Cousin and Voyez, 1993) and in 1994 in B (Laborde, 1994). As the monitoring periods were different and only partially overlapping, it was not possible to completely exclude the bias that may result from possible climatic effects (see Phillips and Gentry, 1994).

For some analyses, the species were grouped either into three structural ensembles (sensu Oldeman, 1974)—by distinguishing emergent and upper canopy species (SE I), lower canopy and intermediate stratum species (SE II) and understorey species (SE III)—or according to their ecological behaviour—light-demanding vs. shade-tolerant species—(for a definition of these groups see the tables in Pascal, 1984, 1988 and Pélissier, 1995).

3. Results

3.1. Initial structure and species composition

As the structure and floristic composition of both compartments have already been presented (Loffeier, 1988, 1989 for A; Pélissier, 1995; Pascal and Pélissier, 1996 for B), the emphasis here is on the comparison between the two compartments.

Initial stand density and basal area of trees with dbh $\geq$ 10 cm were slightly lower in compartment A in 1986 (578 stems ha^{-1}; 34.8 m^2 ha^{-1}) than in the unlogged compartment B in 1990 (606 stems ha^{-1}; 39.3 m^2 ha^{-1}). The difference in density is higher than the 8.5 trees ha^{-1} felled in A in 1979–80, while in basal area it is lower than the loss due to felling and estimated about 7 m^2 ha^{-1} by Loffeier (1989), the difference having probably decreased over the period since harvest. But the comparison of the initial mean density and basal area per 20 × 30 m quadrats in the two compartments, revealed no significant difference (t-tests, $P > 0.25$): six years after felling, A and B can be considered as equivalent in terms of stand density and basal area.

The floristic richness was quite different in the two compartments, but this is probably due to the difference in the sample area (0.6 ha and 347 trees for A vs. 3.12 ha and 1891 trees for B) and the large number of rare species: of the 111 species identified in the Kadamakal Reserve Forest (compartments A and B and their immediate surroundings), 54 species were found in A at the first survey in 1986, compared to 88 in B in 1990, of which 58 were represented by less than two individuals per ha and 47 were also present in A.

As the estimates of species richness are affected by the number of sampled individuals (especially when there are numerous rare species), the two compartments were adjusted to a common size using the rarefaction method (Hurlbert, 1971) which provides the expected number of species, $E(S_n)$, in a sample of n individuals selected at random from each compartment. In B, for $n = 606$, 1212 and 1818 (i.e., the mean number of trees per 1, 2 and 3 ha), $E(S_n)$ was equal to 64.4, 80.1 and 89.3 species respectively. Moreover, the predicted species richness curves, $E(S_n)$ vs. n, of the two compartments were quite similar upto $n = 347$, the total number of individuals recorded in A (Fig. 2).

In both compartments, *Vateria indica* was the most common species (Table 1), whereas differences in relative frequency were found for other species. Light-demanding species were also more common in the logged compartment. In terms of basal area, the dipterocarps, *V. indica* and *Dipterocarpus indicus*, dominated in both compartments, representing 46.4% of the basal area in A in 1986 and 41.2% in B in 1990. In compartment B, they were followed by a lower canopy species, *Myristica dactyloïdes*, which was much less frequent in A.

The analysis of the two-way contingency table describing the frequency of structural ensembles in both compartments revealed a significant compart-

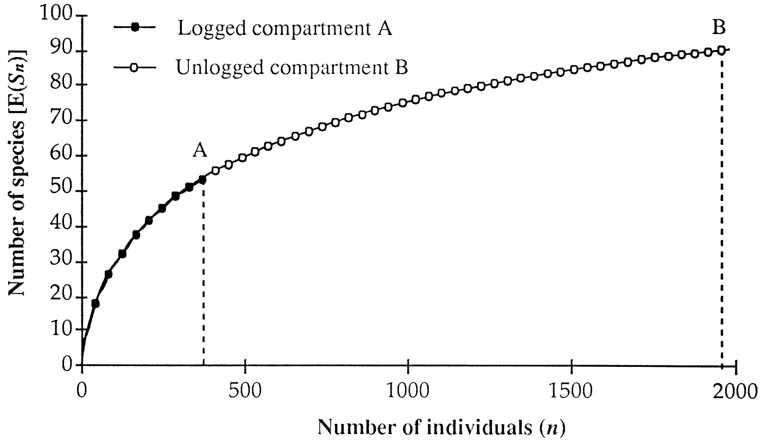

Fig. 2. Species richness curves for the two compartments. $E(S_n)$ is the expected number of species in a sample of n individuals randomly selected from a collection containing N_r individuals and S species: $E(S_n) = \sum_{i=1}^{S} \left[1 - C^{n}_{N_r - N_i}/C^{n}_{N_r}\right]$ with, $\sum_{i=1}^{S} N_i = N_t$ and $n < N_t$ (Hurlbert, 1971).

ment effect on the initial stand structure ($P < 0.0001$). The relative contributions of the various cells to total Chi-square indicated that the observed frequencies that differed most from the expected values were A* SE I (55.0%) and A* SE II (19.7%): emergent and upper canopy species were much more abundant in A (especially *D. indicus* and *V. indica*), while lower canopy and intermediate stratum species were less frequent than in B (Table 1). The fact that *D. indicus* represented a smaller proportion of the basal area in A than in B results probably from the selective felling. However, many more stems in the logged compartment, but smaller than in the unlogged compartment, could also mean that regeneration of this species has been stimulated after the harvest.

3.2. Changes in floristic composition

In compartment A, four poorly represented species (*Antiaris toxicaria* Lesch., *Aphanamixis polystachya* (Wall.) Parker, *Beilschmiedia wightii* (Bl.) Kosterm. and *Caryota urens* L.) disappeared between 1986 and 1993, while five other species (*Cinnamomum* sp., *Holigarna arnottiana* J. Hk., *Microtropis stocksii* Gamble, *Sterculia guttata* Roxb. and *Vitex altissima* L.) appeared. As each of these species was represented by only one individual and although two of them (*S. guttata* and *V. altissima*) were light-demanding species (see Table 1), it was considered that the floristic composition remained unchanged.

In compartment B, while there was no disappearance of species between 1990 and 1994, three new species, *Agrostistachys meeboldii* Pax and K. Hoffm., *Clerodendron viscosum* Vent. and *Syzygium hemisphericum* (Walp.) Alston were found, so that the number of species listed went up from 88 to 91 in the 3.12 ha.

3.3. Mortality

Assuming the loss of a constant fraction of the population each year, the annual mortality rate was estimated using the negative exponential decay model by the formula: $m = 100 \cdot (\mathrm{Ln}\, N_o\text{-}\mathrm{Ln}\, N_s)/t$ (Condit et al., 1995; Sheil et al., 1995), where N_o is the initial number of trees and N_s is the number of trees still alive in year t (recruitment being omitted).

All the species pooled together, the estimates of annual mortality rate (Table 2) did not appear significantly different in both compartments (t-test, $P = 0.98$). Analysing the distribution of dead trees according to compartments and structural ensembles in a two-way contingency table revealed no interaction ($P = 0.97$), and annual mortality rates were not significantly different in A and B compartments for each of the three structural ensembles (t-tests, $P > 0.6$). However, the loss in basal area due to mortality, averaging 0.40 $\mathrm{m}^2\ \mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$ in A against 0.26 $\mathrm{m}^2\ \mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$ in B, suggested an influence of tree size.

To test how compartment (Comp), tree dbh (d) and structural ensemble (SE) influenced mortality, a logistic regression model was fitted on the probability of mortality during t years (p_t). To take into account the different observation periods in both compartments, the model was expressed as follow: let $s_t = (1 + \exp[f(\mathrm{Comp, SE}, d)])^{-1}$ be the probability of survival over t years; if we assume that mortality rate is constant over time and that $\exp[f(\mathrm{Comp, SE}, d)] \ll 1$ (which was actually the case for our data), then the annual survival probabil-

Table 2
Comparison of mortality in compartments A and B according to structural ensemble

	Initial number of trees		Number of dead trees		Mortality rate (% yr^{-1})	
	A	B	A	B	A	B
All species pooled together	347	1891	21	65	0.89	0.87
Emergent and upper canopy species (SE I)	189	685	7	22	0.54	0.82
Lower canopy and intermediate stratum species (SE II)	104	791	9	25	1.29	0.80
Understorey species (SE III)	54	415	5	18	1.39	1.11

Minimum dbh = 10 cm.
Period of study: 1986–1993 in A; 1990–1994 in B.

Table 3

Parameter estimates of the logistic regression for probability of mortality according to: tree dbh in cm (d); compartment with two classes, Comp A (logged) and Comp B (unlogged); and structural ensemble with three classes, SE I (emergent and upper canopy species), SE II (lower canopy and intermediate stratum species) and SE III (understorey species)

Parameter (associated variable)	Parameter estimate	Standard error	Wald Chi-square	P-Value
β_0 (Intercept)	−3.146	0.456	47.50	0.0001
β_B (*Comp B*)[a]	−0.909	0.311	8.53	0.0035
β_d $(1/d_{30})$	11.311	5.120	4.88	0.0272
$\beta_{A*SE\ I}$ (Comp A $*$ SE I)	−1.401	0.535	6.86	0.0088
$\beta_{A*d>40}$ (Comp A $*$ $d_{>40}$)	1.657	0.6157	7.24	0.0071

Residual Chi-square of the model = 0.0014; $P = 0.97$.

[a] Compartment effects were corrected in order to account for time lap between the two successive inventories (see text): $\beta_B - \log(4) = -2.295$ and $\beta_A - \log(7) = -1.946$.

ity $s = (1 + \exp[f(\text{Comp, SE}, d)])^{-1/t}$ can be approximated by:

$$s \approx 1 - \frac{1}{t} \cdot \exp[f(\text{Comp,SE},d)]$$

$$= 1 - \exp[f(\text{Comp,SE},d) - \log(t)].$$

In order to compare the two compartments, each estimated compartment effect must thus be corrected by the term $-\log(t)$, which accounts for the length of the monitoring period.

After preliminary analyses using the LOGISTIC procedure in SAS (Statistical Analysis Systems Institute, 1989), the final estimated model was (Table 3):

$$p_t = 1 - 5_t = \frac{\exp(\beta_0 + \beta_B 1_B + \beta_{A*SE\ I} 1_A 1_{SE}\ I + \beta_{A*d>40} 1_A 1_{d>40} + \beta_d/d_{30})}{1 + \exp(\beta_0 + \beta_B 1_B + \beta_{A*SE\ I} 1_A 1_{SE\ I} + \beta_{A*d>40} 1_A 1_{d>40} + \beta_d/d_{30})}$$

where the β_is are parameters; 1_A, 1_B, $1_{SE\ I}$ and $1_{d>40}$ are indicator variables taking value 1 when associated to compartment A, compartment B, structural ensemble I and trees with dbh > 40 cm, respectively, and 0 otherwise; and d_{30} equals d when tree dbh < 30 cm and 30 when tree dbh ≥ 30 cm.

The model, corrected for the different period, is illustrated in Fig. 3. It reveals: (i) a clear tendency of a decreasing mortality with increasing diameter for small trees up to 30 cm dbh in both compartments; (ii) a lower average mortality in the unlogged compartment B than in the logged compartment A, the

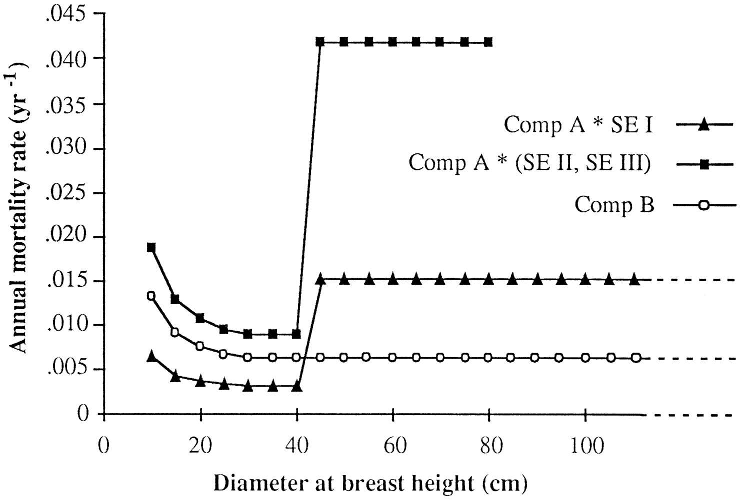

Fig. 3. Estimated annual mortality rate according to dbh, compartment, logged (A) or unlogged (B), and structural ensemble (SE I, II and III) using a logistic regression model.

Table 4
Comparison of recruitment in compartments A and B according to structural ensemble and species behaviour

	Initial number of trees		Number of recruited trees		Recruitment rate	
	A	B	A	B	A	B
All species pooled together	347	1891	44	106	1.68	1.34
Emergent and upper canopy species (SE I)	189	685	14	34	0.98	1.19
Lower canopy and intermediate stratum species (SE II)	104	791	17	34	2.17	1.03
Understorey species (SE III)	54	415	13	38	3.19	2.19
Light-demanding species	9	24	9	6	13.26	5.98
Shade-tolerant species	338	1867	35	100	1.37	1.28

Minimum dbh = 10 cm.
Period of study: 1986–1993 in A; 1990–1994 in B.

mean effect of A being -1.95 while it is -2.30 for B (see Table 3); but (iii) a clear increasing mortality for trees > 40 cm dbh in compartment A, which was much more sensible in SE II and III than in SE I.

Since the type of mortality was observed in compartment B, it is possible to state that half died as chablis (natural treefall) while the other half died standing. Such data were not available for compartment A.

3.4. Recruitment

Considering that a constant number of stems was recruited each year, the annual recruitment rate was estimated in each compartment by: $r = 100 \cdot N_n / N_0 t$, where N_0 is the initial number of trees, N_n is the number of stems newly recruited including those subsequently dead before second inventory and given by $N_n = N_r e^{\lambda' t}$, with N_r the number of stems recruited which are still alive in year t, and λ' the annual mortality of recruited stems approximated by the rate into the 10–15 cm dbh class (0.0099 in A; 0.0106 in B).

All the species pooled together, the annual recruitment rate in A and B (Table 4) were not significantly different (t-test, $P = 0.62$). Comparison of the distribution of recruited trees according to compartments and structural ensembles in a two-way contin-

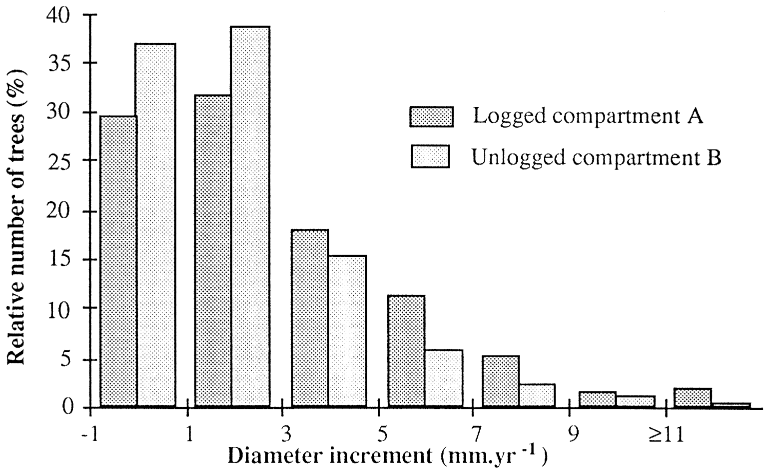

Fig. 4. Distribution of trees according to diameter increment classes in the two compartments (344 trees for A; 1918 trees for B).

gency table revealed no interaction effect ($P = 0.68$). There was no significant difference between the annual recruitment rates in A and B compartments for each of the three structural ensembles (t-tests, $P > 0.3$) as for the two species groups, light-demanders and shade-tolerants (t-tests, $P > 0.5$).

Table 5
Parameter estimates of the backward stepwise regression for annual diameter increment $\log(\Delta d + 1)$ (with Δd in mm yr^{-1}) according to: $\log(d)$ with d being the initial dbh in cm; compartment with two classes, Comp A (logged) and Comp B (unlogged); and structural ensemble with four classes, SE O (light-demanding species), SE I (emergent and upper canopy species), SE II (lower canopy and intermediate stratum species) and SE III (understorey species)

Variable	Parameter estimate	Standard error	F-Value	P-Value
Intercept	−0.601	0.082	54.22	0.0001
Comp A	−0.588	0.194	2.69	0.0025
SE O	3.315	0.659	25.27	0.0001
SE I	0.350	0.039	76.61	0.0001
SE II	1.171	0.150	60.93	0.0001
$\log(d)$	0.443	0.030	215.29	0.0001
Comp A* SE I	0.367	0.100	13.48	0.0002
Comp A* SE II	0.295	0.104	8.02	0.0047
Comp A* $\log(d)$	0.137	0.067	4.25	0.0395
$\log(d)^*$ SE O	−0.851	0.215	15.59	0.0001
$\log(d)^*$ SE II	−0.3031	0.051	35.68	0.0001

RMSE = 0.5426; adjusted-$R^2 = 0.264$; $P = 0.0001$.

3.5. Growth

All the species being pooled together, there was a significant difference (t-test, $P = 0.0001$) in the mean diameter increment of trees with initial dbh ≥ 10 cm and still alive at final inventory: 2.9 mm yr^{-1} (SD = 3.7) in A; 2.1 mm yr^{-1} (SD = 2.1) in B. This resulted in an increase in basal area that averaged 0.86 $\mathrm{m}^2\ \mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$ in the logged and 0.59 $\mathrm{m}^2\ \mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$ in the unlogged compartment. The comparison between the two compartments for each of the three structural ensembles revealed only a significant difference in SE I (t-test, $P = 0.0001$) which attained an increment of 3.9 mm yr^{-1} (SD = 4.4) in A against 2.8 mm yr^{-1} (SD = 2.5) in B. Regarding the distribution of diameter increment according to diameter class, Fig. 4 shows that most of the trees had low increments, while, especially in A, the growth was concentrated in a few trees. Moreover, there was a positive correlation between diameter increment and initial dbh in both compartments (Pearson's coefficients: $r^2 = 0.45$ in A; $r^2 = 0.36$ in B).

Effects of the different factors on annual diameter increment (Δd) were analyzed using the GLM and the Stepwise Regression procedures in SAS (Statistical Analysis Systems Institute, 1989). A covariance analysis was first estimated taking: because of heteroscedasticity of the data, $\log(\Delta d + 1)$ as dependent

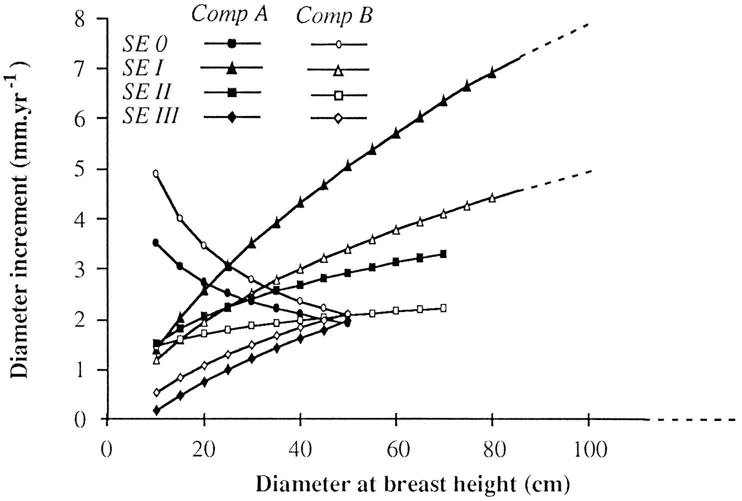

Fig. 5. Average predicted diameter increment as a function of the compartment, logged (A) or unlogged (B), structural ensemble (SE 0, I, II and III) and initial dbh using a general linear model.

variable (6 trees from the logged compartment which had highly negative diameter increments were thus removed) and $\log(d)$ as a covariate (d being initial tree dbh); and, compartment (Comp) and structural ensemble (SE) as categorial variables. For this analysis, a special class called SE 0 was created for the light-demanding species.

The complete model showed no significant interaction between the covariate and the two factors ($P = 0.336$). After elimination of this triple interaction term and taking a 0.05 significant level, the model fitted revealed a $\log(d) *$ Comp interaction ($P = 0.049$) but no Comp effect ($P = 0.067$). Testing a by structural ensemble model showed highly significant $\log(d)$ effect in SE I, II and III ($P \leq 0.0002$) and Comp effect in SE I and III ($P \leq 0.0005$). The final model was thus fitted using a backward elimination procedure of variables with significant levels less than 0.05 (Table 5).

As illustrated in Fig. 5, the structural ensembles had contrasting growth behaviour and reaction to logging: (i) in both compartments, initial dbh had a significant positive effect on annual diameter increment of shade-tolerant species (SE I, II and III) while this effect was negative for light-demanding species (SE O); (ii) emergent and upper canopy species (SE I) and lower canopy and intermediate stratum species (SE II) exhibited a strong positive reaction to logging which increased with tree size; while (iii) understorey (SE III) and light-demanding species (SE O) had a milder negative reaction which vanished with tree size.

4. Discussion

When compared to other tropical dense moist evergreen forests, the annual rate of recruitment (1.68% in A; 1.34% in B) is close to the values commonly encountered: Phillips and Gentry (1994) reported from 28 sites over all tropical regions, recruitment rates for trees ≥ 10 cm dbh averaging, with 95% confidence interval, $1.65 \pm 0.26\%\ \mathrm{yr}^{-1}$ and $1.75 \pm 0.44\%\ \mathrm{yr}^{-1}$ for nine of these sites located in South-East Asia. On the other hand, their mean mortality rates ($1.77 \pm 0.24\%\ \mathrm{yr}^{-1}$ for the 28 sites over all tropical regions; $1.72 \pm 0.44\%\ \mathrm{yr}^{-1}$ for the nine South-East Asian sites) are higher than that observed in Uppangala ($0.89\%\ \mathrm{yr}^{-1}$ in A; $0.87\%\ \mathrm{yr}^{-1}$ in B). We do not have sufficient data to make a more accurate analysis of such a result, but it seems from field observations that, in Uppangala (as in other evergreen forests of the Western Ghats), large treefall gaps involving many secondary broken trees are quite rare apart from catastrophic events like cyclones or landslides (Pascal, 1984, 1988; Pélissier, 1995), which could be the explanation for the low mortality rates.

The comparison of the two compartments in order to evaluate the impact of selective felling poses some methodological problems, which are linked to the nature of the design of the Uppangala forest monitoring site, and should be kept in mind: (i) although the two compartments belong to the same forest and do not exhibit any glaring differences in ecological conditions, it is not possible to guarantee that they had exactly the same structure before logging; (ii) the absence of replication, the relatively small area surveyed and the short monitoring periods render the estimations of mortality and recruitment a little imprecise—the situation is different in Fisherian experimental designs where replications provide some statistical safeguards against bias due to ecological heterogeneity (Maitre, 1986; Schmitt and Bariteau, 1990; Bertault and Sist, 1995); (iii) the non-conformity and relative brevity of the periods studied also pose a problem because short-term forest dynamics is influenced by climatic events; (iv) lastly, the accuracy of the increment measurements is not the same in the two compartments: it is about 10 times better in compartment B, a point which can partly explain the strong dispersion of the data from compartment A.

In spite of these methodological drawbacks, the comparison of the initial structures of the two compartments (1986 in A; 1990 in B) clearly shows that in the short-term (i.e., 6 years after felling), selective logging had no immediate drastic consequences (see also Loffeier, 1989) in terms of forest structure and composition. The only significant difference is the presence of many more small stems of *D. indicus* in the logged compartment that could indicate that regeneration of this species was stimulated after the harvest. However that may be, the growing stock has increased in both compartments during the period of study, in terms of density ($+0.79\%\ \mathrm{yr}^{-1}$ in A and

$+0.47\%$ yr^{-1} in B) as well as basal area ($+1.61\%$ yr^{-1} in A and $+1.02\%$ yr^{-1} in B in average) revealing that the two compartments are in a phase of accretion. This phenomenon is especially clear in the logged compartment A and the difference between the two compartments has narrowed, from 4.8% (initial) to 0.4% (final) in stand density and from 12.9% (initial) to 5.7% (final) in stand basal area.

Although no significant difference between the two compartments has been evidenced in annual mortality and recruitment rates, all the species pooled together as well as among structural ensembles, the predicted mortality of large trees (with dbh > 40 cm) was much higher in the logged compartment A than in the unlogged compartment B. This was observed for emergent and upper canopy species but appeared particularly true for the lowest structural ensembles (SE II and III) which died about four times more in A than in B. Though direct inferences suffer from possible differences in initial stand structures and ecological conditions of the compartments, it seems reasonable to relate such results to impact of felling: changes in microclimatic conditions due to felling of canopy trees or opening of hauling tracks (Loffeier, 1989) may be a cause of an increasing mortality that can extend for a long period after the harvest (Durrieu de Madron, 1994; Vanclay, 1994). Species of the lowest structural ensembles which cannot tolerate direct sunshine were indeed the most affected.

Another result concerns the tendency of mortality to be higher for trees of small diameter, whatever be the compartment, logged or unlogged. This phenomenon, well known in temperate forests, is badly documented for tropical forests. It is however in accordance with the results of Durrieu de Madron (1993)–who monitored 11,000 trees in 18.75 ha over a 7-year period in French Guiana–, but in opposition to many other studies reporting from tropical forests, a mortality that does not significantly differ with tree size (see Swaine et al., 1987; Sheil and May, 1996).

There was, in both compartments, a relationship between dbh and diameter increment which is actually interpreted as the result of several factors: (i) the interspecific variability; and (ii) social hierarchy among trees and unequal competition for light which favours bigger trees. This has also an important methodological consequence: modifying the census threshold gives rise to a sharp variation in the mean individual increment, but does not greatly modify the estimate of the increment in stand basal area. When the diameter census threshold is lowered from 10 to 3.18 cm dbh (i.e., circumference of 10 cm) in compartment A, the density goes up from 578 to 2023 stems ha^{-1}, the basal area increases from 34.8 to 42.7 m^2 ha^{-1}, whereas the relative basal area increment remains almost stable from 2.68 to 2.65% yr^{-1} (from 0.93 m^2 ha^{-1} yr^{-1} to 1.13 m^2 ha^{-1} yr^{-1}) and the mean individual diameter increment falls from 2.9 to 1.3 mm yr^{-1} (Cousin and Voyez, 1993; Laborde, 1994).

An important difference, which may also be considered as a possible response to selective logging, is seen in the diameter increment of big trees which is significantly higher in A than in B. Like in M'Passa (Gabon), where 15% of the individuals yield 70% of the stand basal area increment (Hladik, 1982), here the growth is also concentrated in a small number of trees. Taking into account the effect of initial dbh, emergent and upper canopy species were identified as the most boosted structural ensemble ($+50\%$ on diameter increment in average), while stimulation on lower canopy and intermediate stratum species was moderate ($+20\%$ in average) and even negative on understorey and light-demanding species.

Thus, harvesting as it was practised in compartment A (selective felling of a few big trees and limited mechanisation), did not greatly affect the floristic composition: the changes were limited to local disappearance and appearance of rare species in both compartments. However, the global dynamic balance was more favourable in A than in B in spite of no significant difference between their annual mortality and recruitment rates. In the short- to medium-term, the impact of selective felling may appear to be beneficial because the growth of the economically interesting species (mainly emergent and canopy species) is stimulated; but, in the long-term, the repetition of such operation—with a regular 30 years rotation as it had been planned for the Kadamakal Reserve Forest (Loffeier, 1989)—could augment the risk of an alteration of the ecosystem structure, because the demographic processes (of mortality in particular) were not uniformly modified among the various structural ensembles. However, the results obtained in Uppangala have to be confirmed by the study of bigger samples over longer periods covering, if possible, several logging rotations.

5. Conclusion and perspectives

These results complement those of Pascal et al. (in press), Pascal and Pélissier (1996) on the structure and composition of the low elevation moist evergreen forests of the Western Ghats, Pélissier (1995) on structure and dynamics, and Loffeier (1988, 1989) on reaction after the harvest. They also confirm the conclusions of these authors: if fire and its destructive impact are ignored, the immediate and medium-term (say 10–15 years after logging) impact of a single selective felling, as it was practised in the Western Ghats until its provisional ban in 1988, seems to be limited. The composition of the forest is not greatly altered, and the growing stock (i.e., stand density and basal area) gradually recovers and tends to become similar to that of unlogged forest within 20 years. However, the modification of the demographic processes which is not uniform among the various structural ensembles, seems to indicate that the repetition of selective felling might not be sustainable in terms of forest structure and composition.

Short-term forest recovery after selective felling is mainly due to the sharp stimulation of the growth of standing trees. However, it was observed that this stimulation concerns only few big trees, especially the tallest, belonging to certain species, a result which is consistent with observations in Western Africa (Maitre, 1986). This is why a more detailed analysis of the growth variations according to species, tree size (stem diameter and crown morphology), social status and local availability of light is now underway in compartment B.

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