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# Stand dynamics in a logged and silviculturally treated Costa Rican rain forest, 1988–1996

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# Stand dynamics in a logged and silviculturally treated Costa Rican rain forest, 1988–1996

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**Abstract**

The lowland rain forests of Central America are poorly known from the standpoint of management for timber production. We studied the stand dynamics of a logged Costa Rican rain forest under three different regimes of post-logging silvicultural treatment. The site was located on low hills with Ultisols in Holdridge's Tropical Wet Forest life zone. The *Pentaclethra macroloba*-dominated forest had been high graded before planned management began. Management of the 540 × 540 m (29.2 ha) experimental area began with a timber harvest in the whole area during 1989–1990, 4 trees $ha^{-1}$ being cut overall for 10.1 $m^3 ha^{-1}$. The experimental plots were 180 × 180 m (3.24 ha), comprising a 100 × 100 m (1.0 ha) central permanent sample plot (PSP) with a 40-m wide buffer strip. Two types of post-harvest silvicultural treatment: liberation/refinement (in 1991) and shelterwood (in 1992) were applied under a complete randomized block design with three replicates, using logged but untreated plots as controls. PSP data reported are for the 1988–1996 period for individuals with $\geq$10 cm DBH. The most marked changes in forest structure were caused by silvicultural treatment, basal area under the liberation/refinement treatment being reduced to ca. 65% of its probable mature forest value. Recruitment exceeded mortality in the years following intervention under all three treatments, but forest structural recovery was slowest under the liberation/refinement treatment. Post-intervention mortality rates appeared higher under the liberation/refinement treatment than under the control or shelterwood treatments, though differences were not statistically significant. In relation to tree attributes, mortality rates increased with decreasing DBH increment, crown illumination and quality of crown form. Commercial DBH increments were higher under the liberation/refinement treatment than in control plots during the 1993–1996 period. On the basis of its response to intervention during the first seven years of management, the forest appears resilient and productive; trends over time in mortality rates under the most intense silvicultural regime require close attention however. *Pentaclethra*-dominated forests are important components of the productive forest resources of Costa Rica and Nicaragua and, given current deforestation rates in areas such as southern Nicaragua, it is now urgent that the existing biophysical knowledge of these forests be applied to forest conservation and management. © 1999 Elsevier Science B.V. All rights reserved.

*Keywords:* Costa Rica; Nicaragua; Forest management; Silvicultural treatment; Mortality

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## 1. Introduction

The management of natural tropical forests for timber production has achieved widespread acceptance as a land-use alternative which may simultaneously contribute to social well-being, economic development and the conservation of biodiversity. In spite of a burgeoning of research and development activity related to such management over the last 20 years, a large part of the information base for its execution is derived either from sound general forestry practice (e.g. that related to the planning and control of harvesting) or, in specifically tropical aspects, from the European colonial period (e.g. techniques for silvicultural diagnosis, and the theory and practice of silvicultural treatment and silvicultural systems for the tropics, see Dawkins, 1958; Baur, 1968; Hutchinson, 1993). Although information on stand dynamics and growth and yield is a basic necessity for forest management planning, however, the colonial period yielded relatively little in this respect (Baur, 1968). The tentative generalisations on the likely commercial productivity of neotropical moist forests outlined by Wadsworth (1983) were derived, to a large extent, from knowledge existing three decades ago or more.

In the past several years, research results from the neotropics have contributed to filling this information gap for certain forest types and socioeconomic contexts, with particular emphasis on forests of the Guiana Shield and Amazonia (de Graaf, 1986; Jonkers, 1987; Poels, 1987; Hendrison, 1990; de Graaf et al., 1996; Suriname; Schmitt and Bariteau, 1990; Durrieu de Madron, 1994; Favrichon et al., in press, French Guiana; Silva et al., 1995, Brazilian Amazonia). This work, however, is orientated towards management operations on large scales in situations with relatively little pressure for land conversion. In other neotropical regions, such as Central America, the need for research and development work on management of smaller forest tracts by communities or individual landowners is more pressing (Comisión Centroamericana de Ambiente y Desarrollo, 1991). Furthermore, it appears clear that, in ecological and silvicultural terms, the response to management of forests of the Guiana Shield and Amazon basin may not necessarily be extrapolated to other neotropical forest regions. Stand dynamic patterns in many South American forests, for example, appear to be different from those of the Central American Atlantic Moist Forest ecoregion (the ecoregion concept is taken from Dinerstein et al. (1995)). This difference is illustrated by rates of natural mortality in forest free of human disturbance, which appear to be markedly lower in Guiana Shield forests (Durrieu de Madron, 1994; Favrichon et al., in press) and those of northern and central Amazonia (Uhl et al., 1988; Rankin-de-Merona et al., 1990; Favrichon et al., in press), than in lowland forests of northeastern Costa Rica (Lieberman et al., 1985). Additionally, Hammond and Brown (1995) have argued that, with respect to aspects of seed ecology, there are fundamental differences between the tree floras of areas of the Guiana Shield which have been free of drastic forest disturbance over long time periods, and those of areas subjected to greater levels of natural or human disturbance.

The aforementioned interregional differences – in the socioeconomic context in which forest management for timber is or could be carried out, in stand dynamic processes and in the autecology of canopy tree species – represent strong arguments in favour of greater emphasis on information gathering for forest management in hitherto little-studied areas such as Central America. A necessity for more generalised information gathering on forest growth and yield in any case remains due to the need to answer numerous outstanding questions related to the dynamics of managed stands (Palmer and Synnott, 1992; Alder and Synnott, 1992; Alder, 1995). An understanding of the medium-to-long-term effects of different silvicultural treatments (as opposed to just logging) on neotropical forests is a particular necessity, as published information on this subject is dominated by the work carried out in the development of the CELOS Management System for Suriname forests (de Graaf, 1986; Jonkers, 1987; Poels, 1987; de Graaf et al., 1996) and that at Paracou in French Guiana (Schmitt and Bariteau, 1990; Durrieu de Madron, 1994).

The present paper reports on biophysical aspects of forest response to timber harvesting and silvicultural treatment in a lowland rain forest of northeastern Costa Rica. The forest, dominated by the legume tree *Pentaclethra macroloba*, is similar to that at La Selva Biological Station (Hartshorn and Hammel, 1994), 7 km from our study site. In the context of the Central American Atlantic Moist Forest ecoregion, similar forests occupy infertile, well-drained lowland soils from southeastern Nicaragua through eastern Costa Rica to western Panama, up to ≈350 m asl. These forests represent important components of the forest resources of the three countries involved. For example, more than 60% of the timber currently harvested legally in Costa Rica comes from the Atlantic Moist Forests of that country (G. Chaves, personal communication, National System of Conservation Areas, Ministry of Environment and Energy, San José, Costa Rica, May 1998). The forests of southeastern Nicaragua represent one of the country's major remaining forest areas (e.g. Alves-Milho, 1996).

The study was carried out in the context of small-scale management by private landowners – the typical context of forest management in Costa Rica. We attempted to answer the following questions: what changes in stand structure occur under different silvicultural treatments? What are the rates of recruitment, growth and mortality during the first years of management and how are they related to silvicultural treatment? The relationships of diameter increments to the characteristics of individual trees (with emphasis on functional group and taxonomic identity) are examined in a separate paper (Finegan et al., in press).

## 2. Methods

### 2.1. Study site

The study was carried out at La Tirimbina Farm (now Tirimbina Rain Forest Centre), near La Virgen, Sarapiquí Canton, Heredia Province, Costa Rica (10° 24′N, 84° 06′W) (Fig. 1). The life zone is tropical wet forest (Holdridge's system; Tosi, 1969) with mean annual precipitation of 3864 mm and mean annual temperature 24.5°C. The site belongs to the Central American Atlantic Moist Forest ecoregion, whose conservation status is considered vulnerable by the criteria of Dinerstein et al. (1995). La Tirimbina farm is a mosaic of cultivated land (pepper, cocoa, rubber and ornamental plants), logged mature forest, and a secondary forest situated on the foothills of the Central Volcanic mountain range of the country at 160–220 m asl. The farm lies on highly weathered old lava flows in which the dominant material is andesitic basalt (Mata, 1997). Topography is of low hills dissected by streams, some of which rise within the property. Soils are Ultisols, relatively deep, well-drained clays of very low fertility, with pH ca. 4.0 and acid saturation usually >80% (Mata, 1997).

### 2.2. Silvicultural experiment

The forest in which the study was carried out was undisturbed mature vegetation until around 1960, after which it was lightly logged at irregular intervals until 1989 (J.R. Hunter, personal communication). The forest is dominated by *P. macroloba* (Fabaceae/Mim.) with abundant large palms (*Iriartea deltoidea*, *Socratea exorrhiza* and *Welfia regia* are common) and ca. 100 species $ha^{-1}$, ≥10 cm DBH (Natural Forest Management Unit, CATIE, unpublished data). The experimental area is a 540 × 540 m (29.16 ha) plot which was placed under management for the sustainable production of timber in 1989 (full details are given by Quirós and Finegan, 1994). Timber was harvested from the whole area under strict planning and control in 1989 and 1990, the overall mean number of trees cut being 4 $ha^{-1}$, for a mean volume of 10.1 $m^3\,ha^{-1}$ (Quirós and Finegan, 1994). The range of the number of trees cut in individual 1.0 ha permanent sample plots (see below) was 0–15; restrictions on harvesting on steep slopes and close to streams, as well as the long history of logging at this site, limited the overall mean volume harvested.

Three different regimes of post-harvest silvicultural intervention were applied to nine 180 × 180 m (3.24 ha) plots by a complete randomised block design (three replicate plots per silvicultural regime; hereafter, silvicultural regimes are referred to as 'treatments' and individual 3.24 ha plots as 'treatment plots') in 1991 and 1992. The first treatment was the timber harvest already described with no subsequent intervention, the option commonly described as 'log and leave' and referred to, hereafter, as the 'control' treatment. The second treatment was applied in 1991. It involved a refinement, consisting of the ring-barking of all non-commercial trees ≥40 DBH (diameter at breast height, 1.3 m) except for those identified as being of ecological importance (e.g., as providers of fruit or roosting sites to forest vertebrates) during the planning of the harvest, and a subsequent liberation of individuals determined to be potential crop trees. For the liberation, trees close to each potential crop tree were ring-barked if their DBH

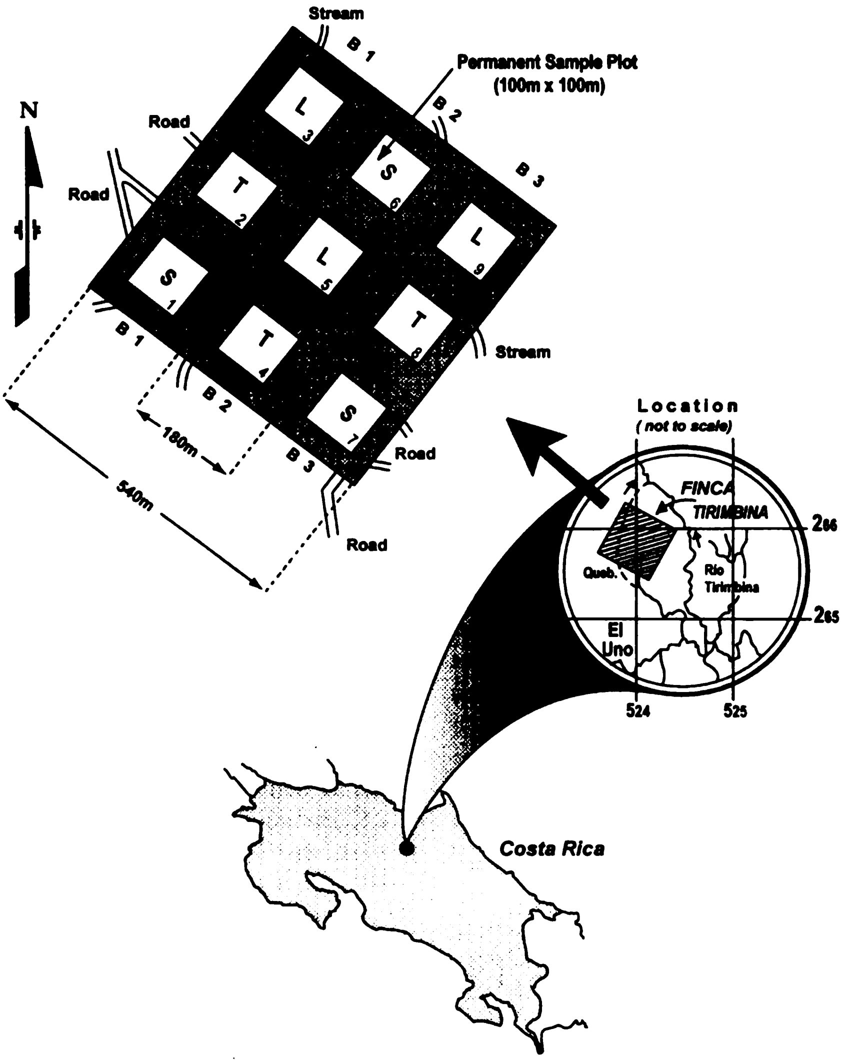

Fig. 1. Geographical location of La Tirimbina study site, northeastern Costa Rica, and diagram of silvicultural experiment. Explanation of symbols on experimental diagram: B1–B3, numbers of experimental blocks; T, control treatment (timber harvest with no post-harvest silvicultural treatment), L, timber harvest plus post-harvest liberation/refinement treatment, S, timber harvest plus post-harvest shelterwood treatment.

was equal to or greater than that of the potential crop tree and (a) their crowns overtopped or had lateral contact with that of the potential crop tree and (b) they did not meet the preceding condition, but were located within a 10 m radius of the potential crop tree. Potential crop trees were identified by criteria of species (current market value), crown form (perfect, good or tolerable according to Dawkins's scale (Alder and Synnott, 1992)) and stem form (stem offering at least one merchantable log, i.e. straight and 4 m in length). This treatment is, hereafter, referred to as the 'liberation/refinement' treatment. The third treatment was applied in 1992 and consisted of the formation of a shelterwood, with the aim of maintaining a continuous high canopy while creating, through the thinning of the middle stores of the forest, conditions for the regeneration of the more light-demanding commercial species (see Baur, 1968). For this treatment, non-commercial trees $\geq 10$ cm DBH and whose crowns were not part of the upper canopy of the forest were felled by chainsaw and cut into manageable size for manual removal. Pieces of diameter >10 cm were sold as industrial firewood and smaller-diameter material given away locally for domestic use. This treatment will, hereafter, be referred to as the 'shelterwood'.

Stand dynamic processes (all individuals $\geq$10 cm DBH, including palms but excluding lianas) were monitored in a square 1.0 ha permanent sample plot (PSP) in the centre of each 3.24 ha treatment plot. As silvicultural treatments were applied to each complete 3.24 ha plot, the PSPs were separated from neighbouring treatment plots, as well as adjacent unmanaged forest, by 40-m wide buffer strips. The width of the buffer strips is equivalent to the approximate maximum canopy height of the forest as recommended by Dawkins (1958); the limited area available for the execution of the experiment precluded the adoption of the wider buffer strips recommended by more recent authors (Alder and Synnott, 1992).

Each permanent sample plot was divided into square subplots of 20 × 20 m to facilitate the location of trees. Measurements were of all trees $\geq$10 cm DBH and were begun in 1988 in three PSPs with the intention of obtaining information on pre-intervention dynamic processes in the forest studied; these were PSP 3 (assigned to the liberation/refinement treatment), 4 and 8 (both designated as control plots). Enumeration of the complete set of nine PSPs was implemented in 1990; the six additional PSPs set up in this latter year were all enumerated before the timber harvest. The control and liberation treatments were subsequently measured annually to 1994 and again in 1996, while the shelterwood treatment was measured in the years 1990, 1991, 1993, 1994 and 1996. At the first enumeration, DBH of all trees and palms at or above the minimum diameter limit was measured to the nearest mm with a fibreglass diameter tape. The point of measurement was permanently marked on each tree with paint, as was a code identifying each individual.

In all subsequent enumerations, DBH of all trees was measured and their condition evaluated. Recruits into the $\geq$10 cm DBH class were identified and measured for DBH.

### 2.3. Analysis of data

As only three PSPs were measured over the full period 1988–1996, the bulk of our analysis concentrated on the 1990–1996 period, for which data from all nine PSPs were available. Data from the three plots enumerated from 1988 on were used, however, to back up conclusions derived from between-treatment comparisons for 1990–1996 with evidence of changes over time – with particular emphasis on comparison between pre- and post-intervention time periods – in single plots. Characterisations of the state of the forest were made for the years 1990, 1993 and 1996 and diameter increments and mortality rates were calculated for two time periods, 1990–1993 (the period during which the effects of silvicultural treatment on stand dynamic processes were not apparent) and 1993–1996 (the period during which such effects were apparent). Stand dynamics under the three treatments were characterised on the basis of changes in density (number of trees per hectare, $N\,\mathrm{ha}^{-1}$), basal area ($\mathrm{m}^2\,\mathrm{ha}^{-1}$) and distributions of trees and basal area in 10-cm diameter classes. Natural mortality was defined as all mortality not attributable to damage or destruction during timber harvesting, or destruction by silvicultural treatment, as established by observation during measurement of the plots. Rates of natural mortality were estimated using the logarithmic model (Lieberman et al., 1985), both for individual PSPs and for 3.0 ha per treatment. Stand half-lives were estimated on the basis of the logarithmic model (Lieberman et al., 1985). The use of equal census periods for these calculations (three years) avoided dependence of mortality rates on the length of the census period (Sheil and May, 1996).

For analysis of diameter increments we used data in the annual range – 2 mm (an arbitrary minimum which, nevertheless, recognizes that 'negative growth' may sometimes be genuine) – 50 mm. A total 4659 trees gave at least one increment within this range and were used in analyses. Between-treatment comparisons of absolute and relative increments of stand basal area, and median diameter increments per PSP, were carried out using the non-parametric Kruskal–Wallis analysis of variance.

## 3. Results

### 3.1. Stand dynamics

Timber extraction destroyed 5.0% of all trees in 8.0 ha and damaged an additional 2.7%; the respective

Table 1
Structural dynamics of a managed lowland rain forest at La Tirimbina, northeastern Costa Rica, 1990–1996, under three different regimes of silvicultural treatment. Data are means of numbers of trees ($N$ ha$^{-1}$) and basal area ($G$ m$^2$ ha$^{-1}$), figures in parentheses are standard deviations

| Treatment | Year of study | | |
|---|---|---|---|
| | 1990 | 1993 | 1996 |
| *Control* | | | |
| $N$ total | 504 (77) | 504 (97) | 533 (94) |
| $N$ commercial | 173 (16) | 178 (30) | 189 (36) |
| $G$ total | 21.9 (1.8) | 22.2 (0.7) | 23.7 (1.1) |
| $G$ commercial | 12.8 (2.4) | 12.9 (1.6) | 13.9 (1.7) |
| *Liberation* | | | |
| $N$ total | 483 (77) | 393 (54) | 418 (64) |
| $N$ commercial | 178 (55) | 133 (19) | 146 (26) |
| $G$ total | 25.1 (3.4) | 18.6 (1.7) | 18.8 (1.4) |
| $G$ commercial | 15.5 (1.4) | 11.7 (1.5) | 12.7 (1.3) |
| *Shelterwood* | | | |
| $N$ total | 495 (45) | 420 (85) | 428 (22) |
| $N$ commercial | 195 (8) | 165 (13) | 184 (11) |
| $G$ total | 22.2 (1.0) | 20.5 (1.4) | 21.4 (1.1) |
| $G$ commercial | 12.9 (1.5) | 12.6 (1.1) | 13.8 (1.3) |

ranges for individual PSPs (omitting PSP 8 in which no tree was harvested) were 2.0–14.7% for trees destroyed and 1.6–8.0% for trees damaged (Natural Forest Management Unit, CATIE, unpublished data). On account of these marked between-plot variations in the impact of the timber harvest, mean stand density and basal area in the control plots did not decline in the three years immediately following harvesting (1990–1993; Table 1). Recruitment exceeded mortality in both the study periods in these plots, and it was found that both stand density and basal area increased markedly in the 1993–1996 period (Table 1).

As is to be expected, stand dynamic patterns under the two regimes of post-harvest silvicultural treatment differed markedly from those of the control plots. The liberation/refinement treatment applied in 1991 reduced stand density $N$ by almost 20% compared to its value in 1990, and basal area dropped by 26% of the 1990 value to below 20 m$^2$ ha$^{-1}$ in 1993 (Table 1). Basal area of undisturbed mature lowland forest in northeastern Costa Rica is around 28 m$^2$ ha$^{-1}$, with $\geq$10 cm DBH (Finegan and Sabogal, 1988; Hartshorn and Hammel, 1994), so that the 1993 value in the liberation/refinement plots at La Tirimbina may be estimated at ca. 65% of that of the original mature forest of the site. It may be noted that Dawkins (1958) concluded that in order to obtain significant increases of commercial growth in tropical moist forest, basal area should be reduced to 40–60% of its original value, a rule of thumb verified independently by de Graaf (1986) working in Surinam. Recruitment exceeded mortality during the 1993–1996 period in the liberation/refinement plots and mean stand density increased markedly. There was little change in total stand basal area, however, as mortality during this period included larger trees, particularly those eliminated in the refinement stage of the treatment, while all recruits were by definition small.

The reduction of stand density by the shelterwood treatment was similar in proportional terms to that of the liberation, but basal area decline in the former was much lower than in the latter, as shelterwood formation is accomplished by the removal of medium-sized and small trees, while liberation and particularly refinement involve the removal of many larger trees (Table 1). As in the case of the other two treatments, recruitment exceeded mortality under the shelterwood in the second period of the study.

Mean commercial basal area increased by ca. 1 m$^2$ ha$^{-1}$ in all three treatments in the second period of the study. Percent commercial basal area was greater after silvicultural intervention, however, increasing from 63% in 1993 to 68% in 1996 in the liberation/refinement plots and from 62% to 65% under the shelterwood, while remaining relatively constant at ca. 59% in the control plots.

Estimated annual rates of natural mortality (logarithmic model) for the two three-year periods of the study varied markedly between PSPs (Table 2). Most of these whole-stand annual mortality rates (for 3.0 ha per treatment, as well as means for 1.0 ha) were nevertheless similar, at 1.6–2.3%, to those obtained for old-growth forests at nearby La Selva Biological Station (Lieberman et al., 1985). Mortality rates for the 1993–1996 period under the liberation/refinement treatment appeared higher than those in the other treatments, and higher than that for the 1990–1993 period in the same treatment. An analysis of variance for mortality rates during 1993–1996 showed no block effects but significant differences between treatments ($p < 0.05$); a subsequent Tukey test ($\alpha = 0.05$)

Table 2
Annual mortality rates (logarithmic model) $m$ and population half-lives $t_{0.5}$ for whole stands during two three-year periods in the managed lowland rain forest at La Tirimbina. Figures in parentheses are 95% confidence limits, see Table 1 for further details of forest structure

| Experimental treatment | | 1990–1993 | | | 1993–1996 | | |
|---|---|---|---|---|---|---|---|
| | | $N$ | $m$ | $t_{0.5}$ | $N$ | $m$ | $t_{0.5}$ |
| Control | x | 504 | 2.20 (0.85) | — | 504 | 1.97 (2.20) | — |
| | 3.0 ha | 1512 | 2.21 | 31.4 | 1508 | 2.08 | 33.4 |
| Liberation | x | 483 | 2.29 (2.35) | — | 393 | 3.60 (2.44) | — |
| | 3.0 ha | 1448 | 2.24 | 31.0 | 1173 | 3.65 | 19.8 |
| Shelterwood | x | 495 | 1.63 (2.21) | — | 420 | 1.69 (0.37) | — |
| | 3.0 ha | 1485 | 1.68 | 41.3 | 1256 | 1.88 | 41.1 |

showed, however, that the treatment effect was due to differences between the liberation/refinement and shelterwood treatments, neither silvicultural treatment differing from the control. All the observed annual mortality rates are within the range of 1–5% considered by Alder (1995) to represent normal expected values for tropical moist forest, with or without intervention. Nevertheless, as Swaine et al. (1987b) have emphasised, seemingly small differences of mortality rates may represent, as at La Tirimbina, twofold or greater differences in the numbers of trees dying. The possible significance of mortality rate variation is perhaps better brought home by the stand half-lives for 3.0 ha: these ranged from 41 year (shelterwood plots in both time periods) to only 19.8 year (liberation/refinement plots, 1993–1996).

The causes of mortality in the La Tirimbina plots are currently undergoing detailed investigation, but a preliminary assessment may be made here. The relationships between whole-stand annual mortality rates 1990–1996 and four attributes of individual trees are shown in Fig. 2, for each experimental treatment. In agreement with the conclusions of Swaine et al. (1987a), trees of zero or negative diameter increment had markedly greater mortality rates than those with mean annual diameter increments ≥1 mm (Fig. 2(b)). As other studies have shown for individuals ≥10 cm DBH (e.g. Lieberman et al., 1985; Durrieu de Madron, 1994 and reviews by Swaine et al., 1987b and Alder, 1995), however, there was no clear relationship of mortality rates to initial diameter (Fig. 2(d)). Notably, mortality increased with decreasing crown illumination (as found in a southeast Asian forest by Korsgaard, 1986, (cited by Swaine et al., 1987b) and increasingly poor crown form (Fig. 2(b) and (c)).

Overall changes in forest structure at La Tirimbina under different silvicultural regimes are summed up by the distributions in 10-cm DBH class of individual trees (Fig. 3(a)) and basal area (Fig. 3(b)). Distributions of both these structural parameters were similar across treatments in 1990, though the number of larger trees was slightly greater in the liberation plots, especially for individuals ≥70 cm DBH, so that total basal area in those plots was greater than in the others. By 1996, the number of individuals in the 10–19.9-cm DBH class had increased markedly in the control and liberation-refinement plots, as recruitment increased following canopy opening, and basal area in this diameter class had increased under all three treatments. However, developmental patterns differed strikingly between treatments among individuals ≥20 cm DBH. Basal area of control plots increased throughout the diameter range to 50 cm DBH, only declining above this limit, presumably as a consequence of the timber harvest. In contrast, both numbers of individuals and basal area were considerably lower in 1996 than in 1990 in the liberation/refinement plots.

### 3.2. *The effects of silvicultural treatment on diameter growth*

Overall, annual diameter increments varied between −2 mm (the arbitrary limit established for permissible negative increments) and 48 mm. Diameter increments were markedly influenced by silvi-

Erratum: Figure 2. The crown illumination scale should read from 5 (emergent) to 1 (no direct light). Crown illumination and crown form were determined as described by Finegan, B., Camacho, M. and Zamora, N. 1999. Diameter increment patterns among 106 tree species in a logged and silviculturally treated Costa Rican rain forest. Forest Ecology and Management 121, 159-176.

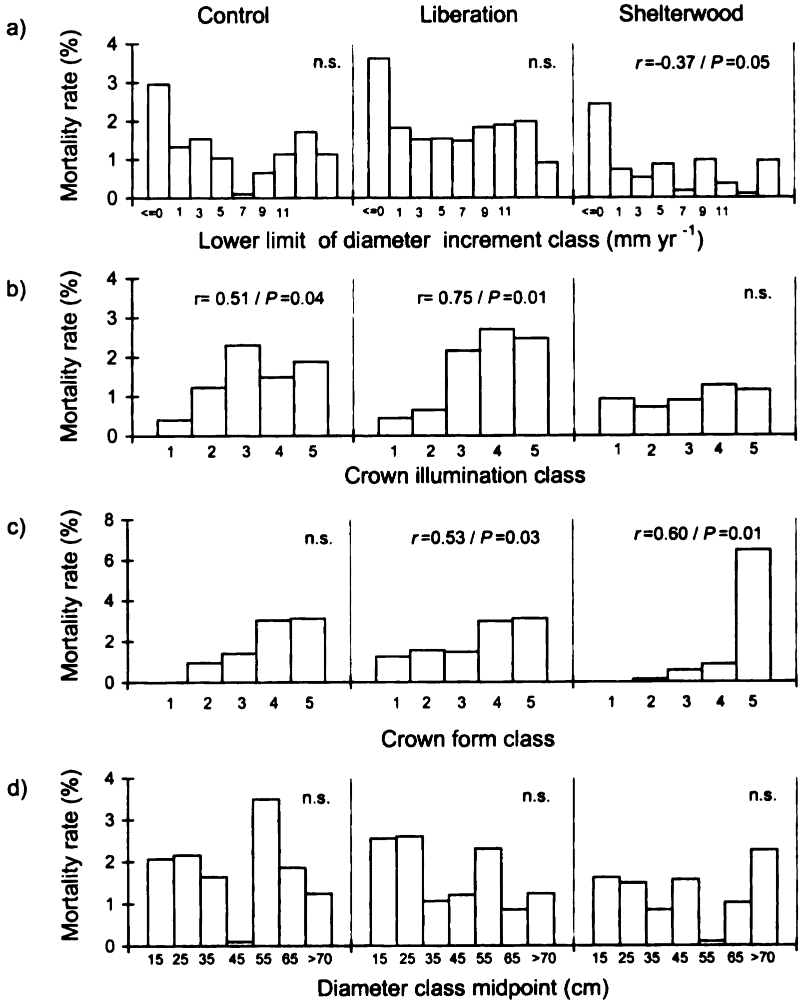

Fig. 2. Annual natural mortality rates (logarithmic model), 1993–1996, for trees in different categories of (a) annual DBH increment prior to death, (b) crown illumination, (c) crown form and (d) DBH class (cm) under three regimes of silvicultural treatment in a managed lowland rain forest at La Tirimbina, northeastern Costa Rica. Values of correlation (Spearman's r) between mortality rate and tree category are shown on each graphs; NS = not significant.

cultural treatments. This influence is evident on observation of the trends of diameter increment over time (pre- and post-intervention) in the three plots enumerated from 1988 on, as well as through formal statistical comparisons of treatments for given time periods, both before and after the application of the silvicultural treatments. Median diameter increments of commercial species varied relatively little over the period 1988–1996 in PSP 8 (control and with no tree harvested within the plot; Fig. 4(b)), and a period of higher increments during 1990–1993 in PSP 4 (also control) may have been a reaction to the relatively heavy timber harvest impact in this plot during 1989 (Fig. 4(a); 12 trees standing within this PSP were harvested, and the crowns of three trees cut in the buffer zone surrounding it fell within the PSP). Silva et al. (1995) noted that the stimulation of diameter growth by logging may last as little as three years, and indeed, increments in PSP 4 declined to their pre-intervention level by the 1994–1996 period. On the other hand, median increments of commercial species during the period 1993–1996 in PSP3, first enumer-

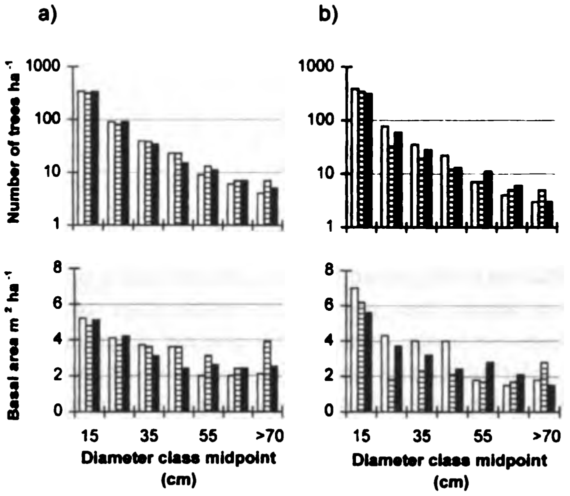

Fig. 3. Distributions in 10 cm DBH classes of the number of trees ha$^{-1}$ and stand basal area (m$^2$ ha$^{-1}$) (a) just before timber harvest and (b) in 1996, 6–7 years after timber harvest, under the three different silvicultural regimes applied in the La Tirimbina rain forest. Data are means ha$^{-1}$ ($N = 3$). Open bars, control plots (timber harvest but no post-harvest silvicultural treatments), cross-hatched bars, liberation/refinement treatment, closed bars, shelterwood treatment. See text for full description of silvicultural treatments.

ated in 1988 and subjected to the liberation/refinement treatment in 1991, were double those in the three annual periods up to the application of the treatment (Fig. 4(c)).

In terms of formal statistical comparisons, there were no significant differences between treatments in median diameter increments for the period 1990–1993, whether for all trees, trees of non-commercial species, all trees of commercial species, or potential crop tress ($n = 3$ per treatment; Table 3). For the period 1993–1996, however, median diameter increments in both, liberation/refinement and shelterwood treatments were greater than those in the control for the whole stand, all commercial trees and potential crop trees (Table 3; see also Fig. 5).

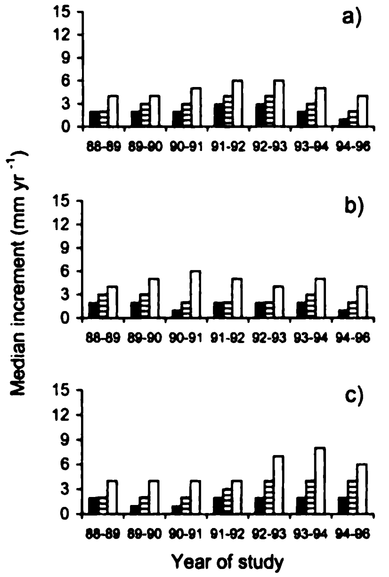

Fig. 4. Median annual diameter increments, 1988–1996, in the three 1.0 ha permanent sample plots (PSPs) enumerated before timber harvesting in 1989–1990. (a) PSP 4, control, timber harvested in 1989; (b) PSP 8, control, timber harvested in 1990 but no trees cut within PSP, only in buffer strip of experimental plot; (c) PSP 3, timber harvested in 1990 and liberation/refinement treatment applied in 1991. Open bars, commercial species, closed bars, non-commercial species, cross-hatched bars, all species.

Table 3
Periodic median annual DBH increments (mm) of different groups of trees ≥10 cm DBH in a managed lowland rain forest at La Tirimbina, northeastern Costa Rica, over two time periods, and results of statistical comparisons between treatments ($N = 3$ per treatment)

| | 1990–1993 | | | | | 1993–1996 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Control | Liberation | Shelterwood | $H$[a] | $P$[b] | Control | Liberation | Shelterwood | $H$ | $P$ |
| All trees | 3 | 3 | 3 | 0.603 | 0.739 | 2 | 4 | 3 | 6.742 | 0.034 |
| Non-commercial | 2 | 2 | 2 | 0.630 | 0.734 | 1 | 3 | 2 | 3.466 | 0.178 |
| Commercial | 5 | 5 | 6 | 2.111 | 0.348 | 4 | 7 | 6 | 6.764 | 0.033 |
| Potential crop trees | 5 | 5 | 6 | 1.332 | 0.513 | 5 | 7 | 6 | 6.054 | 0.048 |

[a] Parameter of Kruskal–Wallis non-parametric analysis of variance.
[b] Probability associated with value of $H$.

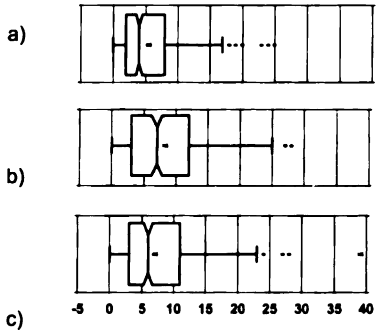

Fig. 5. Box-and-whisker plots of periodic annual increments of DBH of all trees ≥10 cm DBH under the three different silvicultural treatments (total area of PSPs 3.0 ha per treatment). (a) control; (b) liberation/refinement; (c) shelterwood. The extreme left-hand vertical line represents the 10th percentile and that at the extreme right, the 90th percentile. The box represents the range embraced by the first (left-hand side) and third (right-hand side) quartiles, while the notch and line dividing the box represent the median and the asterisk, the mean. See text for full description of silvicultural treatments.

## 4. Discussion

### 4.1. General aspects of forest response to intervention at La Tirimbina

During the first 6–7 years of the management process, the ways in which the La Tirimbina forest responded to intervention were similar, in general terms, to those shown by other tropical moist forests (Dawkins, 1958; Baur, 1968; de Graaf, 1986; Swaine et al., 1987b; Hendrison, 1990; Hutchinson, 1987, 1993; Durrieu de Madron, 1994; Alder, 1995; Silva et al., 1995; Favrichon et al., in press): even after the most drastic changes in forest structure (those imposed under the liberation/refinement treatment), post-intervention recruitment exceeded mortality, indicating the commencement of forest recovery; whole-stand annual mortality rates showed evidence of an increase after the liberation/refinement treatment, but were always below 5%; mortality was greater among trees with zero growth than in actively-growing trees, as also among trees with partially or completely shaded crowns than among those whose crowns were fully illuminated, and increased with decreasing quality of crown form; silvicultural treatments applied with the objective of increasing the growth of potential crop trees achieved this objective. Moreover, this broadly typical forest response was stimulated by a management process which simply adapted principles of tropical forest management for timber production to local conditions – we did not seek to be innovative with respect to basic principles, as the mere application of those principles was innovation enough in the national and regional context of the present study. As we have emphasised in the introduction to this paper, however, the preceding points do not imply that no further examination of forest response to the management process is required for La Tirimbina and the extensive area of similar forest. We believe there is particular scope for development of understanding of the relationship between different types of silvicultural treatment and rates of growth and mortality, factors which are discussed in Section 4.2.

### 4.2. Rates of growth and mortality, and the effects of silvicultural treatment

Lieberman and Lieberman (1987) showed that the *P. macroloba*-dominated forests of La Selva Biological Station are among the most dynamic tropical forests yet studied, in terms of rates of mortality, recruitment and tree diameter growth. The mortality and growth rates of the La Tirimbina control plots for the 1990–1996 period (annual mortality rates of 2.0–2.3% like those at La Selva, and median annual diameter increments of 5 mm for commercial species) appear to confirm that this dynamism is one of the outstanding characteristics of this forest type. Elevated growth rates and frequent recruitment may, at first sight, indicate a forest with characteristics favourable to management for timber production. It is suggested that indeed, post-logging stand recovery in the control plots, and the maintenance during the same period of mortality rates similar to those of undisturbed forest at La Selva, are good preliminary indicators that forest integrity may be maintained in the context of timber harvesting. The results of the present study, however, also suggest that options for silvicultural treatment of this type of forest require careful additional study.

Silvicultural treatments are typically the single forest management operation with the greatest effect on forest structure, but are also the least well-studied operation with respect to neotropical forests. The liberation/refinement treatment applied at La Tirimbina, in aspects such as percent basal area removed, was based on recommendations previously outlined by Dawkins (1958) and de Graaf (1986), while incorporating the liberation concept in order to direct treatment to the immediate neighbourhood of potential crop trees (Hutchinson, 1987; Jonkers, 1987). The proportional reduction in stand basal area brought about by the treatment applied at La Tirimbina was similar to that recorded in the other studies cited. Silvicultural treatments increase the growth rates of commercial trees, but where the necessary analyses have been carried out, indications are that they also increase natural mortality rates in comparison with untreated plots, especially in the first years after the application of treatments (de Graaf, 1986; Durrieu de Madron, 1994; Favrichon et al., in press). It is necessary to discuss both methodological aspects of the estimation of mortality rates and possible ecological causes of increased mortality following stand disturbance.

The importance of obtaining reliable estimations of mortality rates has often been underestimated in studies of the dynamics and productivity of tropical forests, and such reliable estimations may be difficult to obtain (Alder and Synnott, 1992; Alder, 1995). This latter difficulty arises, for example, because even though all the trees which survive a measurement period in a PSP provide data for the estimation of growth rates, only a small percentage of them die and provide data for the estimation of mortality rates. In addition, the distribution of mortality may be heterogeneous in space and time. At the scale of 1.0 ha PSPs, as used in the present study, occasional treefalls and other spatially and temporally localised factors may generate marked between-plot and between-measurement period variations in observed mortality rates (see Lieberman et al., 1985). Such factors undoubtedly represent one explanation for the marked between-plot variation in mortality rates observed at La Tirimbina, one particularly important consequence of which is to limit the capacity of the La Tirimbina experiment to detect between-treatment differences in these rates.

The statistically significant difference of mortality rates between liberation-refinement and shelterwood treatments during 1993–1996 is difficult to interpret. It seems possible that the difference was due to the markedly different effects the two treatments have with respect to canopy openness, as the liberation/refinement treatment, by its very nature, leaves the trees more exposed than those in the other treatments. Indeed, numerous precedents exist to support the interpretation that the La Tirimbina results indicate a tendency towards higher post-treatment mortality rates in the liberation/refinement plots. Post-canopy disturbance increases of mortality in tropical forests have been detected by several authors and ascribed to various ecological factors. 'Exposure shock' (de Graaf, 1986), the death of trees exposed by treatment to more open environments than those in which they have hitherto developed, is often commented upon anecdotally, as is the possible vulnerability of gap-edge trees to windthrow, which leads to the enlargement of gaps (Whitmore, 1984, his Fig. 2.3; de Graaf, 1986; Swaine et al., 1987b; Durrieu de Madron, 1994; H-F. Maitre, personal communication). Quantitative studies of these phenomena in tropical forests are few, but tend to back up the anecdotal evidence. In an undisturbed moist neotropical forest, trees adjacent to gaps suffered a greater risk of falling than those which were surrounded by trees as tall as, or taller than, themselves; gap-edge trees were significantly more likely to fall into gaps than away from them, possibly due to crown asymmetry (Hubbell and Foster, 1986; Young and Hubbell, 1991).

In managed forest, damage caused by the breaking up or falling of trees dying after the application of silvicultural treatment may be another factor (de Graaf, 1986) though Durrieu de Madron (1994) showed that the falling of poisoned trees caused much less damage to the surrounding stand than that of uprooted or broken live trees in control plots. This latter author also suggested that an increase in mortality in treatment plots four years after the application of treatment at Paracou, French Guiana, may have been caused by the senescence of cohorts of short-lived pioneer trees; he asserts that mortality rates in logged and treated plot should return to the values shown in control plots within 10 years after disturbance. Neither the present study at La Tirimbina, nor the others cited here, however, have yet demonstrated that mortality in silviculturally treated plots does in fact return to control levels after its early increase. The effects on stand yield of estimated half-lives as low as those at La Tirimbina require investigation.

As a final point, it is pertinent to ask why the natural *Pentaclethra*-dominated forests of the Atlantic slope of Central America are so dynamic as compared to other tropical wet forests, and whether the same factors that underlie the natural dynamism also contribute to high mortality in the first years following the application of silvicultural treatment. Answers to these questions are also currently unavailable, but further research in this field may yield key elements of understanding for sustainable forest management in this area of Central America.

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A journal concerned with conceptual, scientific and design approaches to land use. By emphasizing ecological understanding and a multi-disciplinary approach to analysis and planning and design, it attempts to draw attention to the interrelated nature of problems posed by nature and human use of land. In addition, papers dealing with ecological processes and interactions within urban areas, and between these areas and the surrounding natural systems which support them, will be considered. Papers in which specific problems are examined are welcome. Topics might include but are not limited to landscape ecology, landscape planning and landscape design. Landscape ecology examines how heterogeneous combinations of ecosystems are structured, how they function and how they change. Landscape planning examines the various ways humans structure their land use changes. Landscape design involves the physical strategies and forms by which land use change is actually directed. *Landscape and Urban Planning* is based on the premise that research linked to practice will ultimately improve the human made landscape.

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