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# Successional patterns of mortality and growth of large trees in a Panamanian lowland forest

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## Summary

**1** All trees ≥ 19.1 cm d.b.h. (diameter at breast height) in three 1-ha forest plots in Panama were tagged and measured in 1975 and recensused in 1980 and 1988 to examine mortality, growth and recruitment. Plots ranged in age from old second-growth (plot 1), to disturbed primary forest of intermediate age (plot 2) to undisturbed primary forest perhaps 500 years old (plot 3). Common species were classified into two regeneration classes – gap-positive recruitment (GPR) or gap-neutral recruitment (GNR) – on the basis of other studies.

**2** As plot age increased, tree density decreased slightly and forest composition changed from dominance of GPR to GNR trees. Species diversity was similar in plots 1 and 3 and lower in plot 2. Basal area per stem and total basal area increased with plot age.

**3** Overall mortality rate was 2.0% per year. The mortality rate was 58% greater in the second period (1980–88) than in the first (1975–80). When all trees were considered, no effects of plot age or size on mortality were detected. However, when common species were considered according to their regeneration class, mortality exhibited significant regeneration class by size and regeneration class by plot interaction. Mortality of GPR trees increased with girth size and decreased with plot age. The converse was true for GNR trees.

**4** Growth rate increased and relative growth rate decreased exponentially with tree size. After correction for the effects of size, GNR trees exhibited significantly faster growth than GPR trees (20 vs. 14 $\mathrm{cm}^2\,\mathrm{year}^{-1}$).

**5** We conclude that mortality patterns of large trees can vary with the age of the stand and are essentially uncorrelated with patterns exhibited by the same species at juvenile stages. Changes in mortality with size and stand age appeared dependent on regeneration class. A successional gradient is suggested from plots 1 to 3 whereby GNR species replace GPR species over time, though the number of large trees did not decrease significantly. Population studies confined only to stands of older or younger forest would probably fail to detect many successional effects noted in this study. The time scale at which mortality data are compiled can also affect results.

*Keywords*: demography, life history, mortality, old growth, Panama, secondary growth, spatial patterns, succession, trees, tropical forest ecology

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## Introduction

The effect of natural disturbances on the structure and dynamics of tropical forest communities is a topic of considerable current interest (Denslow 1987; Brandani *et al.* 1988; Schupp *et al.* 1989). In particular, the role of tree-fall gaps has been examined in terms of its potential influence on the diversity of forest communities as well as the distribution, abundance and life history traits of the component species (Hartshorn 1978, 1980; Whitmore 1978, 1989; Brokaw 1987; Denslow 1987; Brokaw & Scheiner 1989; Welden *et al.* 1991). Few estimates exist for gap creation rates and mortality, although growth and recruitment rates have been calculated for some size/age classes in tropical forest stands in both the Old and New World (Brokaw 1982; Putz & Milton 1982; Lang & Knight 1983; Swaine *et al.* 1987;

Lieberman & Lieberman 1987; Brandani *et al.* 1988; Hubbell & Foster 1990a,b; Welden *et al.* 1991; Clark & Clark 1992). Long-term data on the mortality rates of tropical forest trees, however, particularly on mortality rates of large trees, continue to be scant, leaving the most fundamental element of gap creation largely undocumented. This lack of information has been specifically remarked on in the literature (Hartshorn 1980; Hubbell & Foster 1986; Swaine *et al.* 1987; Swaine & Hall 1988; Clark & Clark 1992).

The demography of larger trees, particularly their mortality, is also a key factor governing the structure of tropical forest communities. Yet, to date, few studies have concentrated on patterns of mortality of larger individuals of particular species or species classes over the long term and in different successional stages. Attention is more often focused on the regeneration phase in tropical tree demography (Sork 1987; Schupp *et al.* 1989; Augspurger & Kitajima 1992). Our study examines changes in mortality, growth, recruitment and spatial patterns of a population of larger trees monitored over 13.6 years in three plots of different ages at a single lowland forest site in central Panama. The relations between mortality, tree size and age of the plots are discussed in the context of forest dynamics and succession to provide insight into the ecological processes that relate to the growth and mortality of larger members of the forest community.

## Methods

### STUDY SITE

The study site, Barro Colorado Island (BCI), is a 15-km$^2$ nature reserve located in Gatun Lake, Republic of Panama. The forest on BCI has been free from human intervention since at least 1923. Presently, the entire island is covered by moist tropical forest (Holdridge & Budowski 1956), estimated to range in age from 70 to as much as 500 years (Foster & Brokaw 1982; Lang & Knight 1983; Hubbell & Foster 1990b; Piperno 1990). Detailed information on the climate, soils, flora and fauna of BCI can be found in the literature (e.g. Croat 1978; Leigh *et al.* 1982).

### INITIAL LAYOUT OF PLOTS

In February 1975, all trees equal to or greater than 60 cm diameter at breast height (19.1 cm d.b.h.) in three noncontiguous 1-ha forest plots on BCI were tagged (Milton 1980). A girth size of 60 cm was chosen to conform to sample plots elsewhere on the island. Each plot was laid out in a 100-m × 100-m square. The three plots were located in the central or plateau area of the island (altitudinal range 120–155 m a.s.l., mean about 150 m; Hubbell & Foster 1983, 1990). Although there are some slopes on the plateau, all plots were located in essentially flat areas; plateau soils have been characterized as similar to Amazonian oxisols (Hubbell & Foster 1990b). Maps showing the location of each plot in relation to a series of clearly marked trails are found in Milton (1980) and Putz & Milton (1981).

Each tree was permanently marked with a numbered metal tag, its diameter at breast height was recorded to the nearest centimetre and its location was mapped using compass co-ordinates, marked trails and a series of key trees as reference points (Milton 1980). Species determinations were obtained for 93% of the tagged trees. A detailed analysis of the composition and spatial patterns of tagged trees are presented in Milton (1980).

### AGE ESTIMATES OF PLOTS

Prior to beginning work in 1975, the age of each plot was estimated using historical information as well as features such as plot location. Plot 1 was characterized as late secondary growth, estimated to be *c.* 70–100 years old (Foster & Brokaw 1982; Putz & Milton 1982; Hubbell & Foster 1983). It occurs in an area of the plateau known to have been cleared at some point in the fairly recent past. Its acknowledged younger age is one reason why this portion of the plateau forest was largely excluded from the more recent old-growth forest dynamics project of Hubbell and Foster on BCI (Hubbell & Foster 1983). Plots 2 and 3 were characterized as 'primary' or structurally mature sections of the Barro Colorado forest (Putz & Milton 1982; Foster & Brokaw 1982; Hubbell & Foster 1983, 1990a). Plot 3 (which is now in the central area of the 50-ha old-growth plot of Hubbell & Foster), was regarded as old primary forest, largely undisturbed for 300–500 or more years (Foster & Brokaw 1982; Hubbell & Foster 1990b; Piperno 1990). Plot 2, which is near the periphery of the area of second growth, was regarded as somewhat younger or more recently disturbed than plot 3 due to its location and the presence of a high number (27) of larger individuals of *Trichilia tuburculata*, suggesting the establishment of a cohort of this species in this area at some point in the past, perhaps as the result of a natural disturbance.

### RECENSUS WORK

In February 1980, 5 years after plot establishment, trees were recensused to document mortality (Putz & Milton 1982). In September 1988, 8.6 years after the 1980 census and 13.6 years after plot establishment, the three plots were censused again. This census was designed to study the fate of the original 1975 population with emphasis on mortality and growth patterns. Tag numbers of missing, fallen or dead trees were recorded and any remains were examined to try and determine cause of death. To examine growth, the diameter of each live tree was remeasured at breast height. Eleven of the largest trees, however, were not remeasured as their huge girth and buttressing made such an exercise largely meaningless. The lack of information on girth increment in such large trees is unfortunate but not unprecedented (e.g. Manokaran & Kochummen 1987; Swaine *et al.* 1987). Recruitment between 1975 and 1988 was estimated by counting the number of unmapped trees in each plot which were now large enough ( ≥ 19.1 cm d.b.h.) to be included in the sample. Most recruits were not identified as to species. Unless otherwise indicated, the analyses and results presented below do not include recruits.

### DATA ANALYSIS

Analyses were organized into three sections: (1) characteristics of the plots in 1975; (2) mortality; and (3) growth. In general we addressed the questions of whether there were differences in mortality or growth of trees of different size and ecological categories overall and within and between plots. The initial 1975 data set contained a total of 519 tagged trees. Characteristically, many species were represented by only one or a few individuals. For analytical purposes, we grouped the 519 trees into common and uncommon species. Common species were defined as those whose frequency was greater than six individuals in the 1975 census; 20 species fit this criterion (Table 1). In analyses, whenever appropriate, we first examined data for all trees and then carried out a more detailed examination of material from the common trees.

In analyses, we also utilized a quantitative data set from BCI provided by the work of Welden *et al.* (1991) that permitted us to classify 16 of our 20 common species into one of two regeneration classes: gap positive recruitment (GPR) species or gap neutral recruitment (GNR) species. Species designated as GPR were those identified by Welden *et al.* (1991) as showing significantly better recruitment in low-canopy as contrasted with high-canopy sites, whereas GNR species were those having a recruitment not significantly better than average in low-canopy sites. As Welden *et al.* (1991) pointed out, the sites they designated as *low-canopy* generally correspond to *gaps* as that term has been used by other authors (Welden *et al.* 1991, p. 36). Of the four common species not allocated to either GPR or GNR, one, *Guatteria dumetorum*, exhibited significantly better recruitment in low-canopy sites (Welden *et al.* 1991) but had previously been classified as a persistent species (Foster & Brokaw 1982, p. 120) and, as it did not seem to fit the concept of the GPR groups, we excluded it from analysis (15 trees). The other three species, *Guarea glabra*, *Hura crepitans* and *Virola surinamensis*, were not listed in Welden *et al.* (1991) and thus were not classified (8, 17 and 16 trees, respectively).

The 243 trees of the 16 common species classified as GPR or GNR were sorted according to d.b.h. in 1975 into three size groups, each containing 33% of the 243 trees: small ( ≥ 19.1 cm but < 25.6 cm d.b.h.), medium ( ≥ 25.6 cm but < 40.7 cm d.b.h.) and large

**Table 1** Mean (± SD) diameter at breast height (d.b.h.) and relative growth rate (*RGR*) of the 20 most common species in the three plots of tropical forest studied. Only trees with d.b.h. ≥ 19.1 cm were considered

| Species | Gap class* | d.b.h.(cm) | *RGR* † (% year$^{-1}$) | Mortality‡ (% year$^{-1}$) | *n* |
|---|---|---|---|---|---|
| *Alchornea costaricensis* | GPR | 35 ± 14.7 | 1.7 ± 1.09 | 3.0 | 12 |
| *Alseis blackiana* | GPR | 32 ± 16.3 | 2.0 ± 1.45 | 0.6 | 24 |
| *Beilschmiedia pendula* | GPR | 57 ± 16.6 | 1.7 ± 0.79 | 0.0 | 7 |
| *Cordia alliodora* | GPR | 38 ± 7.8 | 1.5 ± 1.00 | 4.5 | 11 |
| *Guatteria dumetorum* | – | 51 ± 22.4 | 3.0 ± 1.72 | 0.5 | 15 |
| *Guarea glabra* | – | 33 ± 22.4 | 1.6 ± 1.27 | 1.0 | 8 |
| *Gustavia superba* | GPR | 26 ± 5.0 | 0.8 ± 0.58 | 0.3 | 27 |
| *Hasseltia floribunda* | GNR | 25 ± 6.4 | 2.9 ± 3.12 | 2.5 | 7 |
| *Heisteria concinna* | GNR | 23 ± 4.1 | 1.4 ± 1.28 | 1.1 | 7 |
| *Hirtella triandra* | GNR | 24 ± 4.5 | 0.9 ± 0.82 | 1.1 | 7 |
| *Hura crepitans* | – | 56 ± 44.3 | 2.4 ± 1.25 | 0.5 | 17 |
| *Jacaranda copaia* | GPR | 63 ± 18.7 | 1.8 ± 1.88 | 5.9 | 20 |
| *Ormosia coccinea* | GNR | 34 ± 12.3 | 2.8 ± 2.79 | 4.3 | 9 |
| *Poulsenia armata* | GNR | 48 ± 33.5 | 2.7 ± 1.86 | 3.5 | 16 |
| *Pterocarpus rohrii* | GPR | 45 ± 23.8 | 1.5 ± 1.55 | 6.0 | 9 |
| *Quararibea asterolepis* | GNR | 70 ± 35.9 | 1.7 ± 1.61 | 0.6 | 25 |
| *Tetragastris panamensis* | GNR | 41 ± 18.0 | 1.7 ± 0.93 | 1.9 | 9 |
| *Trichilia tuberculata* | GNR | 32 ± 9.5 | 1.6 ± 1.20 | 1.7 | 38 |
| *Virola sebifera* | GNR | 28 ± 11.9 | 2.5 ± 1.93 | 3.8 | 15 |
| *Virola surinamensis* | – | 50 ± 42.7 | 4.0 ± 2.62 | 2.1 | 16 |

* GPR (gap-positive recruitment) and GNR (gap-neutral recruitment) indicate whether recruitment for the species is significantly better in forest gaps (see text).

† RGR is relative growth rate of the basal area at breast height and was calculated as the change in basal area between 1975 and 1988 divided by the average basal area.

‡ Mortality was calculated as ln (number of trees alive in 1975/number alive in 1988)/13.58.

( ≥ 40.7 cm d.b.h.). To analyse patterns of mortality of very large trees (VLT), which potentially create large gaps and may therefore have important effects on the dynamics of forest diversity, trees were also partitioned into two size classes: d.b.h. < 66.8 cm (not VLT) and d.b.h. ≥ 66.8 cm (VLT).

Plots were characterized in terms of composition, basal area of stems and total basal area per plot. The hypothesis that the proportion of trees in each species class did not differ across plots was tested by a $G^2$ test. Basal area of stems was calculated assuming a circular cross-sectional shape and it was log-transformed before performing an ANOVA. Plot, species type and the interaction were effects included in the model. Errors were tested for normality by a Shapiro–Wilkinson *W* test. If normality and homoscedasticity of errors were not met, the effects of plot and species type on the distribution of trees in the three size classes would be studied by a logit model. Total basal area was calculated as the sum of the basal area of each stem in each category.

A series of analyses were performed to look for patterns in mortality and to test specific hypotheses. First, a logit model was used to study the effects of plot, size group, species type and their interactions on the probability that trees ≥ 19.1 cm d.b.h. that were alive in 1975 were dead by 1988. Effects were tested by likelihood ratio with respect to the saturated model ($G^2$, SAS Institute, 1989). Model selection was based on Akaike's information criterion (Christensen 1990) and significance of effects.

Secondly, an identical analysis of mortality was performed, but instead of using three size classes, trees were classified as very large trees (VLTs) or not very large trees (not VLTs). Particular attention was paid to the mortality of very large trees since large trees are believed to open up correspondingly large gaps and play a particularly important role in maintaining species diversity in tropical forests (Hartshorn 1980; Brokaw 1982; Hubbell & Foster 1986; Schupp *et al.* 1989).

Thirdly, we tested the assumption that mortality rates did not change over time. The 1980 census allowed us to partition the study period in two sub-periods: 1975–80 and 1980–88. To compare mortality between these two periods, the number of dead trees in each plot in 1985 was interpolated by assuming a constant *per-capita* mortality rate within each plot between 1980 and 1988. Independence between death and period was tested by a $G^2$ statistic.

Growth rate was defined as the change in basal area ($BA$, cm$^2$) per year. Growth rate of each tree still alive in 1988 was analysed by covariance methods as a function of plot, species type and average size between 1975 and 1988 [covariate, $(BA_{75}/2) + (BA_{88}/2)$]. Homogeneity of slopes was tested among all combinations of plots and species types by including appropriate interaction terms in the model. Nonsignificant interactions involving the covariate were dropped out of the final model. Errors were tested for normality as indicated above.

## Results

### CHARACTERISTICS OF PLOTS IN 1975

#### *Number of trees and plot compositions*

Plot 1, the youngest plot, had the highest number of trees while the two older plots had lower and similar numbers of trees (Table 2). The proportion of trees of different species types (i.e. GPR and GNR, as defined above) was significantly different between plots ($G^2_2 = 52.75$, $P < 0.001$). Plots 2 and 3 had significantly greater proportions of GNR species and smaller proportions of GPR species than plot 1 (Table 2).

**Table 2** Number of stems, basal area per stem, and total basal area of stems in three 1-ha forest plots which differed in age. GPR (gap-positive recruitment) and GNR (gap-neutral recruitment) indicate whether recruitment for the species is significantly better in forest gaps (see text). Basal areas reported are least-square means calculated in log scale and transformed back to the original units. These values are more representative of the typical tree *BA* because of the strong skewness of the original data

| Species | Plot 1 | Plot 2 | Plot 3 | All | Mean |
|---|---|---|---|---|---|
| No. of stems | | | | | |
| GPR | 69 | 24 | 17 | 110 | |
| GNR | 24 | 59 | 50 | 133 | |
| GPR + GNR | 93 | 83 | 67 | 243 | |
| All trees | 195 | 156 | 168 | 519 | |
| Basal area (cm$^2$ stem$^{-1}$) | | | | | |
| GPR | 938 | 1046 | 1164 | | 1045 |
| GNR | 564 | 897 | 1270 | | 873 |
| Mean GPR & GNR | 728 | 969 | 1216 | | 963 |
| Mean all trees | 955 | 1154 | 1217 | | 1103 |
| Total *BA* (m$^2$) | | | | | |
| GPR | 9.4 | 7.1 | 3.2 | 19.7 | |
| GNR | 0.6 | 9.2 | 19.8 | 29.7 | |
| All trees | 39.9 | 49.5 | 52.7 | | |

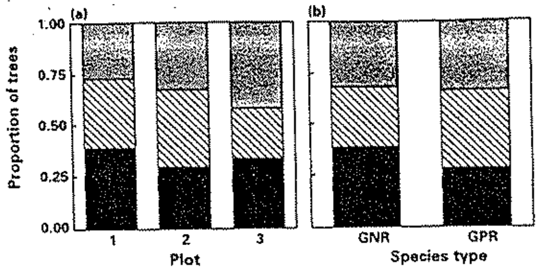

**Fig. 1** Distribution of trees in three size classes (■, ≥ 19.1, < 25.6 cm d.b.h.; ▧, ≥ 25.6, < 40.7 cm d.b.h.; ▨, ≥ 40.7 cm d.b.h.) as affected by (a) plot age and (b) regeneration class (GPR, gap-positive recruitment; GNR, gap-neutral recruitment).

### *Basal area*

When all trees are considered, mean basal area per stem in plots 2 and 3 was 50% greater than in plot 1 (Table 2). Because the distribution of tree size was very skewed, a better description of the trees is given by the analysis of the log-transformed data, which is less sensitive to the few extremely large trees in each plot. The means for each plot (transformed back to the original metric) indicated an increase in basal area per stem of 21% from plot 1 to 2, of 27% from plot 1 to 3 and of 5% from plot 2 to 3. None of these difference was significant by a Wilcoxon test ($P > 0.14$)

The log-transformation of basal area per stem of the 16 common species, as well as other transformations applied to achieve normality and homoscedasticity of errors were not successful. A Wilcoxon signed-rank test of *BA* in all combinations of plots and species types indicated that *BA* of GNR species was significantly smaller in plot 1 than in plot 3 ($P = 0.012$, Table 2). The pattern of size was further explored by a logit model with size class as the response variable, and plot and species type as the factors. Both plot and species type significantly affected the distribution of size of the trees ($G^2_6 = 12.5$, $P < 0.05$). In agreement with the effects indicated in Table 2, the proportion of large trees increased and that of small and medium trees decreased from plot 1 to plot 2 to plot 3 (Fig. 1a). While the proportion of large trees was similar in both the GPR and GNR classes, there was a significantly greater proportion of small trees and a significantly smaller proportion of medium trees in the GNR class than in the GPR class (Fig. 1b).

### *Total* BA *of all trees*

Total basal area of all trees with d.b.h. ≥ 19.1 cm increased from *c.* 40 m$^2$ (100%) in plot 1 to *c.* 50 m$^2$ (124%) in plot 2 to *c.* 52.7 m$^2$ (132%) in plot 3 (Table 2). While GPR trees represented 94% of the *BA* of common species in plot 1, they comprised only 44% of *BA* in plot 2 and 14% of *BA* in plot 3. These changes reflected the increase in number and size of GNR trees from the youngest to the oldest plot.

## MORTALITY

Between 1975 and 1988, a total of 123 trees (23.8% of the original population) died. Of the 519 trees measured alive in 1975, 37 were dead by 1980. The interpolation of numbers of trees alive, based on the mortality observed within plots between 1980 and 1988, yielded an estimate of 428 trees alive in 1985. Based on this estimate and the observed value before 1980, there was a 58% increase in mortality in the second period (2.4 vs. 1.5 year$^{-1}$, $G^2 = 5.033$, $P = 0.025$). The analysis of mortality of all trees indicated no significant effects ($P > 0.20$) of plot age, size class or interaction. However, logistic regression detected a tendency of mortality to decrease with size in plots 2 ($P = 0.10$) and 3 ($P = 0.069$).

The best model to describe the observed pattern of mortality of the 16 common species included plot (P), species type (G), size (S) and the interactions P x G and G x S ($G^2_9 = 14.15$, $P = 0.116$). The interaction G x S was significant at the 0.05 level (Table 3). Mortality of GNR species decreased with increasing tree size. In contrast, mortality of GPR species was low and similar for small and medium trees, but significantly greater in large trees. The interaction P x G was significant at the 0.08 level (Table 3). Mortality of GNR species increased uniformly from plot 1 to 2 to 3, whereas GPR species exhibited a contrasting response having a mortality of 0.03 year$^{-1}$ in plot 1 and of *c.* 0.01 year$^{-1}$ in plots 2 and 3.

Two GPR species, *Jacaranda copaia* and *Pterocarpus rohrii*, suffered the highest mortality (Table 1). In 1975, there was a total of 20 individuals of *J. copaia* in the three plots, 17 of which were in plot 1. Eleven of these 20 individuals died over the course of our study (10 in plot 1). Eight of the nine *P. rohrii* tagged in 1975 were in plot 1; by 1988, four of these had died as well as the single individual in plot 3.

The results of Welden *et al.* (1991) indicate that mortality in high and low canopy sites is highly correlated. We found no correlation across species between juvenile (d.b.h. < 4 cm) mortality in low

**Table 3** Average mortality rate (% year$^{-1}$) of gap-positive (GPR) and gap-neutral (GNR) trees of different sizes in three plots of tropical forest that differ in age. GPR and GNR indicate whether recruitment for the species is significantly better in forest gaps (see text). Species and number of individuals in each group are listed in Table 1

| Regeneration class | d.b.h.<br>19–26 (cm) | 26–41 (cm) | ≥ 41 (cm) |
|---|---|---|---|
| GPR | | | |
| Plot 1 | 2.0 | 2.4 | 4.9 |
| Plot 2 | 0.6 | 0.7 | 1.6 |
| Plot 3 | 0.5 | 0.7 | 1.6 |
| GNR | | | |
| Plot 1 | 2.0 | 1.5 | 1.0 |
| Plot 2 | 2.4 | 1.8 | 1.3 |
| Plot 3 | 3.3 | 2.5 | 1.8 |

**Table 4** Least-square means of growth rate (cm$^2$ year$^{-1}$) for the different species types in three 1-ha forest plots that differ in age. GPR (gap-positive recruitment) and GNR (gap-neutral recruitment) indicate whether recruitment for the species is significantly better in forest gaps (see text). Growth rate was measured over a period of 13.6 years

| Species | Plot 1 | Plot 2 | Plot 3 | Mean |
|---|---|---|---|---|
| GPR | 16 | 15 | 13 | 15$^a$ |
| GNR | 27 | 15 | 20 | 20$^b$ |
| Mean | 21$^a$ | 15$^b$ | 17$^{ab}$ | |

Means represent the corrected growth rate for a tree of approximately 36 cm d.b.h.
Means followed by no common superscript letter are significantly different by Tukey's HSD with $\alpha = 0.05$.

($P = 0.82$) or high ($P = 0.16$) canopy sites reported by Welden *et al.* (1991), and adult mortality measured in our study (Table 1).

### MORTALITY OF VERY LARGE TREES (VLTs)

Ninety-one of the initial 519 trees were VLTs. Overall (1975–88) mortality of VLTs was 33% greater than for the rest of the trees but not significantly so (0.027 vs. 0.020 year$^{-1}$, $P = 0.43$). Per capita mortality of VLTs was not significantly different between plots ($P = 0.31$) but it was 80% higher in plot 1 than plots 2 and 3 combined. In 1975, there were a total of 33 VLTs within the 16 common species. An analysis of VLT mortality in common species using plot and regeneration class (GPR/GNR) did not detect any significant effects or interactions.

### CAUSES OF MORTALITY

Examination of dead trees in 1988 indicated that 25 (20.3%) of the 123 dead trees had snapped either at the base or between 1 and 18 m above ground level, 14 trees (11.4%) had been uprooted, two (1.6%) had been fallen on (they lay under another dead tree), and at least 14 others (11.4%) apparently had been involved in multiple tree falls. These are all minimum estimates as many dead trees had decayed or consisted only of a portion of the bole on the ground.

### GROWTH RATE

When all trees with positive growth rate were considered, there was a significant positive effect of tree size [$x$, ln ($BA$ dm$^2$ – 1.3)] on growth rate [$y$, ln ($GR$ cm$^2$ year$^{-1}$ + 4)]: $y = 1.73 \pm 0.076 + (0.66 \pm 0.029)x$ ($R^2 = 0.58$, $P < 0.0001$). Neither the slope nor the intercept of this relationship changed across plots ($P > 0.60$).

When we considered the subset of trees classified as GPR or GNR, a similar relationship between growth rate and size was detected: $y = 1.63 \pm 0.106 + (0.65 \pm 0.043)x$ ($R^2 = 0.61$). The covariance analysis indicated that, after correction for size differences, GNR trees grew faster than GPR trees (Table 4). Additionally, there was a tendency for trees in plot 1 to grow faster than those in plot 2 (Table 4). No significant interactions or effects of regeneration class or plot on the slope of the relationship between growth rate and size were detected ($P > 0.20$). The relationship between growth rate and size (basal area) of the trees was such that the relative growth rate declined exponentially with basal area.

Of the 178 GPR and GNR trees for which measurements of d.b.h. were obtained in 1975 and 1988, 13 exhibited a growth rate lower than or equal to zero. These trees were outliers and precluded normality of errors in the relationship between growth rate and size. Therefore, trees which showed no detectable growth were not included in analyses. In some cases, this lack of growth may result from sampling error; in other cases, growth may not have occurred. It is not unprecedented to find no discernable growth in some trees after a sample interval of 13 or more years (e.g. Lieberman & Lieberman 1987, p. 355).

### RECRUITMENT

A total of 46 recruits ≥ 19.1 cm d.b.h. were found in the three plots in 1988. Plot 1, with 27 recruits showed higher recruitment than the two older plots, which had twelve and seven recruits, respectively. In terms of replacement of dead trees, in 1988, plot 1 had 49% replacement, plot 2 had 39% and plot 3 had 19%; in combined data, 37% of the total number of trees dead by 1988 were replaced (123 dead trees vs. 46 recruits). Even with recruitment factored in, density declined in all plots.

## Discussion

In this study, we examined changes in the population of individuals tagged in 1975, with emphasis on mortality and growth. Our study population was composed exclusively of large trees, all of whom were ≥ 19.1 cm d.b.h. at the study's inception. Though recruits were tabulated in 1988, calculations deal only with the original tagged population. As plots were not replicated, most statistics apply strictly as descriptions of the plots studied, not as parameters of the population of all trees in tropical forests.

We observed changes in tree mortality with size and stand age that were dependent on regeneration class. Mortality of GPR trees was lower than that of GNR trees in the small size class, but the converse was true in the large size class. In plot 1, mortality of GPR trees was higher than GNR trees, whereas in plot 3, GNR trees exhibited higher mortality than GPR trees. These results are contrary to the findings of Hubbell & Foster (1990) that mortality of shadetolerant species is low and independent of size, whereas mortality of shade-intolerant species decreases significantly with size. In contrast, Swaine *et al.* (1987) reported that the risk of mortality of trees in tropical forests was independent of age once a tree reached a d.b.h. greater than 10 cm. Manokaran & Kochummen (1987) found that mortality rates were independent of size class in a tropical forest in Malaysia though higher mortality rates were noted for some regeneration classes. In a study of emergent and canopy species in a tropical forest in Costa Rica, Clark & Clark (1992) found that mortality at first declined sharply and then slightly increased with increasing size.

The discrepancy between our results and those of previous studies can be explained in two ways. First, we only studied large trees (d.b.h. ≥ 19.1 cm). Secondly, our study dealt with plots of different ages and thus included notable numbers of individuals of some heliophilic species such as *Jacaranda copaia* as well as lesser numbers of individuals of other heliophilic species such as *Ficus insipida* and *F. yoponensis*. With few exceptions, individuals of such species occurred only in plot 1. Such GPR species can attain massive size but many appear very likely to die at around 100 years of age – their estimated age in plot 1. The mortality of one species in our study, *J. copaia* (GPR), had a great influence on the effects of regeneration class, plot age and size that we detected and significantly affected the mortality of large GPR trees in plot 1. Individuals of the two *Ficus* species occurred only in plot 1 and half (three trees) died during the study; likewise, four of the eight *Pterocarpus rohrii* in plot 1 died during the study. The dynamics of mortality in second growth may be significantly influenced by large senescent individuals of such species. It would be difficult to detect these effects in studies that focused only on areas of primary forest where such species are rare.

Similarly, Hubbell & Foster's (1990a,b) result showing improved survivorship for increasingly larger GPR trees may reflect the fact that in their 50 ha old-growth plot, most larger individuals of the GPR class are from unusually long-lived GPR species (Hubbell & Foster 1990a). For example, in 1975, in our study, *Hura crepitans*, a heliophilic species which can ultimately attain a massive girth, occurred in all three plots with nine individuals in plot 1, five in plot 2 and three in plot 3. Yet *H. crepitans* showed the lowest mortality rate of our 20 common species, losing only a single individual (in plot 1) over the total study period.

Much research on tropical forest dynamics has centred on the examination of growth and survivorship of seedlings and saplings (Sork 1987; De Steven 1988; Schupp *et al.* 1989; Welden *et al.* 1991; Augspurger & Kitajima 1992). Our data suggest that the other end of the life history continuum is also worthy of attention since the ability to outlast competitors should help ensure the continued representation of such species in particular locales. Large individuals of heliophilic species in stands of old growth should not necessarily be viewed as vestiges of secondary succession heading toward local extinction (e.g. Brokaw 1987; Hubbell & Foster 1990a). Rather, such trees may be able to persist sufficiently long to outlive many of the GNR trees that grow up around them as the stand ages. In such cases, these GPR species might well persist in particular locales not only for hundreds but thousands of years.

Causes of mortality in tropical forest trees are generally difficult to determine because of the interplay between exogenous and endogenous factors (White 1979). Wind is frequently singled out as an important exogenous factor (Brokaw 1982), but it is difficult to know whether trees damaged by wind suffer because of some previous endogenous condition or whether chance is the principal factor at work here.

In our study, the high number of snapped stems suggest that mortality in many apparently healthy trees may often be induced by the fall of a neighbour. Data presented above suggest that senescence may play a considerable role in tree falls and gap formation in late second growth stands since, for example, it is highly improbable that 10 of 17 *Jacaranda copaia* in plot 1 would die between 1975 and 1988 simply by chance. Because of the large size and high mortality rate of many GPR species in plot 1, our data also suggest that large gaps in stands of older second growth can be similar in frequency and size to those in old-growth stands.

Episodic climatic disturbances may have a profound effect on tropical tree mortality. Between 1982 and 1985, 8.8% of the total tagged stems and 12% of the stems > 32 cm d.b.h. in the 50-ha Hubbell & Foster plot on BCI died. The mean annual mortality rate for the larger stems was estimated at 4.3% (Hubbell & Foster, 1993). Further, during this 3-year interval, 15.5% of trees ≥ 64 cm d.b.h. died (Hubbell & Foster 1990a). Over our 13.6-year study, we lost only 17% of our trees ≥ 66.8 cm d.b.h. Hubbell & Foster's mortality rates tend to be somewhat high relative to mean annual mortality rates for our two recensuses (i.e. 1.4% year$^{-1}$ between 1975 and 1980 and 2.3% year$^{-1}$ between 1980 and 1988). Hubbell & Foster's rates are also high relative to other mortality rates suggested for BCI (Putz & Milton 1982; Lang & Knight 1983).

High mortality in the 50-ha plot is attributed in large part to a severe 1982–83 El Niño drought suggested to have had a disproportionate effect on the mortality of certain tree species (Hubbell & Foster 1990a,b). To a large extent, any effect of this drought is masked in our data due to the longer intercensus sample interval. Comparison of results of the two data sets suggests that the time scale at which mortality data are compiled can affect results obtained. Because Barro Colorado is an island, it has been suggested that tree mortality rates here may be somewhat higher than in comparable mainland forest areas due to damages from increased wind velocity over the open water of Lake Gatun (Foster & Brokaw 1982). Comparative data in Putz & Milton (1982) and Brokaw (1982), as well as data from this study suggest that mortality rates on BCI are similar to those of various mainland tropical forest stands in both the Old and New World.

In our study, both intra- and interspecific growth and mortality rates were highly variable. Intraspecific differences presumably relate in large part to differing environmental conditions of individual trees, particularly access to light and moisture. Interspecific differences, on the other hand, often appeared to reflect regeneration class and/or species-specific life-history traits. Although many tropical tree species may share a specific life history trait (e.g. either gap-positive or gap-neutral recruitment), this in no way implies that species so-classified will necessarily be similar for a wide variety of other important characteristics (Welden *et al.* 1991; Clark & Clark 1992).

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