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MORTALITY RATES OF 205 NEOTROPICAL TREE AND SHRUB SPECIES AND THE IMPACT OF A SEVERE DROUGHT[1]

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Abstract. Mortality rates of 205 tree and shrub species were estimated during two intervals, 1982–1985 and 1985–1990, in two size classes, 1–10 and ≥10 cm in diameter, in a 50-ha census plot in tropical moist forest on Barro Colorado Island in Panama. The severe dry season of 1983 was the focus of the study, since prior observations had demonstrated that it caused mortality in the forest. Here we document that forest-wide mortality was ≈3%/yr during the drought interval but only 2%/yr during the period afterwards, and that excess mortality during the first interval amounted to 2% of stems in the larger size class and 1% in the smaller. Overall, just under 70% of all species had higher mortality during the first census interval, but not all species were equally affected. Canopy trees had significantly higher mean mortality rates during 1982–1985 than during 1985–1990, but treelets and shrubs showed no or slight differences. This was counter to our prediction that species with short root systems would suffer more from a long drought. Shrubs did, however, have higher mortality rates than trees and treelets during both census intervals.

We also evaluated mortality rates for subgroups of species that specialized on different microhabitats in the forest. As we predicted, colonist species (those associated with light gaps) had higher mortality rates than generalist species, 7–10%/yr compared to 2–4%/yr, but only in the smaller size class. Unexpectedly, colonizers had similar mortality rates as non-colonizers in the larger size class. Gap colonizers and generalist species were similarly affected by the drought—both had elevated mortality during 1982–1985.

Species whose distributions were associated with moister soils (on the slopes around the island's plateau or in a swamp in the midst of the 50-ha plot) also had elevated mortality during the drought period, but no more so than generalist species. This was counter to our prediction that species from moist microhabitats would suffer more during an extended drought than generalists. Understory treelets that were slope specialists had higher mortality than generalists during both census intervals, but not large trees that were slope specialists.

Our conclusions emphasize diversity as well as pattern. Every trend we illustrated had well-documented exceptions: large trees with lower mortality during the drought period, for example. Clearly, accurate predictions about how tropical forests will respond to climatic perturbations will require much detailed information from many species.

Key words: demography; drought; El Niño; forest; mortality; neotropics; trees; tropical.

INTRODUCTION

Turnover rates of tropical forests are often said to be high, with mortality rates >1% and sometimes >2%/yr (Lieberman et al. 1985, Manokaran and Kochummen 1987, Swaine et al. 1987*a, b,* Proctor et al. 1989, Phillips et al. 1994). These are forest-wide mortality rates, however, and tropical forests are exceedingly diverse communities; we should be emphasizing diversity of mortality patterns and diversity in response to environmental perturbations, not uniform estimates for entire communities. Studies reporting demographic parameters of a wide variety of species from a single community are needed to properly evaluate life history paradigms of tropical trees (Hubbell and Foster 1986*a, b,* Swaine and Whitmore 1988, Whitmore 1989, Alvarez-Buylla and Martínez-Ramos 1992, Clark and Clark 1992, Zimmerman et al. 1994). Unfortunately, there have been few studies giving mortality rates for individual tree species in the tropics; indeed, rates based on reasonable sample sizes have been reported in no more than ≈50 cases (Lang and Knight 1983, Primack et al. 1985, Hay and Barreto 1988, Martínez-

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Ramos et al. 1988, Primack and Lee 1991, Alvarez-Buylla and Martínez-Ramos 1992, Bullock 1992, Clark and Clark 1992, Milton et al. 1994, Zimmerman et al. 1994).

The very reason that diversity has been ignored in mortality studies is diversity. Individual species are rare, and small plots have too few stems from any one species to provide a reliable mortality estimate. To overcome this problem, we began a study of 50 ha of forest on Barro Colorado Island (BCI) in Panama in 1980 (Hubbell and Foster 1983, Condit 1995). With three complete censuses of the plot finished over the last decade, we now have good estimates of mortality rate for >200 species—two-thirds of those in the plot—and here we present the first community-wide survey of species-specific mortality rates in tropical trees. Our data allow an evaluation of basic hypotheses about forest mortality patterns by examining individual species: how many fit predictions and how many do not.

Adding interest to this survey was an unusually severe dry season that struck Barro Colorado in 1983 (Leigh et al. 1990). In Central Panama, the dry season typically lasts from mid-December to mid-April, when ≈215 mm of rain falls, but in 1982–1983, just 88 mm of rain fell during this period (Leigh et al. 1990, Windsor 1990). During 12 wk from late January to late April, 1983, just 3 mm of rain fell, and during March and April, temperatures were 2°C higher than normal (Leigh et al. 1990). Unusual wilting was already evident on Barro Colorado as early as March, and became more severe during the next several weeks (Leigh et al. 1990). This unusually severe dry season was associated with the strong El Niño event of 1982–1983.

The El Niño drought fell in the midst of the first census interval in the 50-ha plot, and mortality rates during this period thus include any impact caused by the drought. As of 1990, when the third census of the BCI plot was completed, we at last had the opportunity to compare mortality during the drought period with the period afterwards, evaluating changes in mortality for a large number of species. Did shrubs suffer more from the drought than trees, as the shorter root systems of shrubs might lead one to believe (Wright 1992)? Did species associated with moist microhabitats suffer more from the drought than more generally distributed species? Did species restricted to the swamp suffer less because the swamp remained moist? Did gap-colonizing species, which ought to have fairly broad tolerances for drought, suffer less? Answers to these questions as well as an overall description of mortality patterns are presented here.

Materials and Methods

Study site

The study was carried out in tropical moist forest on Barro Colorado Island (BCI) in central Panama. Detailed descriptions of the climate, flora, and fauna of BCI can be found in Croat (1978) and Leigh et al. (1982). Censuses of 50 ha of forest were carried out in 1981–1983, 1985, and 1990 (Hubbell and Foster 1983, 1986*a, b, c,* 1990*a, b,* 1992, Condit et al. 1992*a, b*; we refer to the first census, which lasted two years, as the 1982 census). About 48 ha in the plot are in old-growth forest (>600 yr); the remaining two are in 90-yr-old forest. All free-standing, woody stems ≥10 mm diameter at breast height (dbh) were identified, tagged, and mapped. The diameter of each stem was measured at breast height (1.3 m) unless there were irregularities in the trunk there, in which case the measurement was taken at the nearest lower point where the stem was cylindrical. Diameter at breast height of buttressed trees were taken above the buttresses.

Species analyzed

We included species in the analysis only if there were ≥20 live stems of the species at the beginning of a census interval for the particular period under consideration. This was an arbitrary cutoff, but we wanted to remove very small samples in which mortality rate could be greatly altered by one or two unusual events. There was no indication that our major results were affected by one cutoff as opposed to another: we repeated analyses using only species with $N \geq 50$ stems and found identical patterns to those presented here. A total of 205 species qualified with $N \geq 20$ stems for both census intervals: 194 species for the 10–99 mm size class and 128 species for the ≥100 mm size.

Species names follow those given in D'Arcy (1987), except for eight cases where we use more recent names. Appendix 1 lists these eight species and their synonyms in D'Arcy (1987), plus an additional 20 species whose names have changed since our early publications (Hubbell and Foster 1983, 1986*a,* 1990*b,* Welden et al. 1991). Appendix 1 allows any species listed in this study to be matched with a species mentioned in our earlier publications, in D'Arcy (1987), or in Croat (1978).

Species characteristics

We considered mortality rate as a function of three species characteristics—growth form, moisture preference, and tendency to recruit into light gaps. Species were divided into four growth forms—large trees, mid-sized trees, treelets (or understory trees), and shrubs—based on the maximum size attained (the sizes are given in Hubbell and Foster 1986*c*). Moisture regime was defined using the slopes in the 50-ha plot, which have higher soil moisture content during the dry season than the flat regions (Becker et al. 1988), and the swamp, which is flooded throughout the wet season (Hubbell and Foster 1986*c*). The slopes are moist because of a perched water table below the plateau that drains around its edge onto the slopes. Many species have distributions clearly demarcated by the slopes and the swamp (Hubbell and Foster 1986*c*), and K. E. Harms

(*personal communication*) calculated the density of each species in the different habitats. We used the ratio of density on the slopes to density on the low-lying flat areas as an index of "slope-specialization," and the ratio of density in the swamp to density on the low-lying flat areas as an index for "swamp-specialization." We considered "slope specialists" and "swamp specialists" as those species with ratios ≥ 1.5 (Condit et al., *in press*). Finally, we used the fraction of recruits found in light gaps, given in Welden et al. (1991), as a "colonizing index" for each species (Hubbell and Foster 1986*b* used a similar but not identical "index of heliophily"). Colonizers were defined as those species with an index ≥ 30 (Condit et al., *in press*); colonizers by our definition probably correspond with "pioneers" as defined by Swaine and Whitmore (1988), although they emphasized seed germination characteristics, which we do not consider here. Species missing from Welden's or Harms' calculations were omitted from the corresponding analyses here, that is, a species was considered a "non-colonizer" in our study only if it had a recruit index and the index was <30 (likewise for slope and swamp indices).

Mortality rate

Mortality was defined as death or disappearance. We recorded four different states of death: a standing stem, a fallen or broken stem, no stem at all but with the tree's tag located, and finally, neither stem nor tag. Many trunks were never found, as even large trees often died and completely rotted away during five years. Stems that snapped but resprouted were considered alive (Condit et al. 1993*a*).

Mortality rate was calculated in two different census intervals, 1982–1985 and 1985–1990, and in two size classes, 10–99 mm dbh and ≥ 100 mm dbh (based on the dbh at the beginning of each interval). Thus, every species had four mortality rates—in two size classes and two census intervals. Mortality rate m was calculated as

$$m = \frac{\ln(N_0) - \ln(N_t)}{t}, \qquad (1)$$

where N_0 is the number of initial stems, N_t the number remaining alive at year t, and $\ln(N)$ is the natural logarithm of N. This m is an approximation of the instantaneous mortality rate, or the derivative of the population trajectory, but since t is small relative to the mortality rates, the approximation should be very good. Eq. 1 is the most commonly used formula for calculating mortality in tropical forests (Swaine et al. 1987*b*, Clark and Clark 1992, Phillips et al. 1994), but an alternative formulation that yields an estimate equal to $[1 - e^{-m}]$ is sometimes used (Primack et al. 1985, Gilbert et al. 1994). The two estimates are nearly identical when m is small.

The time interval, t, used in Eq. 1 required close consideration because the census intervals for different 20×20 m subquadrats in the 50-ha plot were different. (The census interval was defined as the time elapsed between censuses for each 20×20 m subquadrat, which was accurate to ≤ 2 wk, since individual subquadrats took <2 wk to complete). For all the subquadrats in the 50 ha, the first census interval (1982–1985) varied from 1.9 to 4.5 yr and the second (1985–1990) from 4.9 to 5.6 yr. For t, we used the arithmetic mean of the census intervals for individual stems of any one species. Using the arithmetic mean is not strictly accurate, and it yields only an approximation of the true instantaneous mortality; however, as we demonstrate in Appendix 2, the bias is slight. Given the actual variation in census intervals during 1982–1985, we calculated an upper bound of 0.5% for the bias given a true mortality rate <0.06/yr, and 5% for the highest mortality rate observed, or 0.50/yr. Thus, even with census intervals varying as widely as they did during 1982–1985, our estimates based on the arithmetic mean time interval are accurate.

Statistical tests for individual species

To assess statistical significance of differences in mortality rates for individual species, confidence limits for the mortality rate of each species in each size class and census interval were calculated using the normal approximation to the binomial variance, as long as there were more than five dead stems ($D > 5$). This is the recommendation given by Dixon and Massey (1969); Sokal and Rohlf (1973) give looser restrictions for use of the normal approximation. For $D \leq 5$ and $N_0 \leq 500$, we calculated exact confidence limits using binomial probabilities. We created a table of 95% confidence limits for every pair of D and N (stopping at 500 because no species with $N_0 > 500$ had $D \leq 5$) by searching for a population mean $\hat{D}$ for which the binomial probability of observing D or less would be <0.025; this was the upper 95% confidence limit (Dixon and Massey 1969, Sokal and Rohlf 1973). The lower confidence limit was found analogously. Confidence limits were converted into annual mortality rates using Eq. 1.

Statistical tests for groups of species

Analyses of mortality patterns across groups of species were designed to determine whether mortality varied between census intervals, between size classes, and between growth forms; and as a function of colonizing, slope, or swamp status. Because this was an analysis of individual species, we did all tests on unweighted mortality rates of individual species; that is, the mortality rate of a species with 40 stems counted just as much as that of a species with 40,000 stems. A standard analysis of variance did not work on this dataset because it was extremely unbalanced, with several empty cells. Therefore, we tested each of the various factors separately, as much as possible testing each in isolation from the others.

First, we tested for differences in mean mortality rate between census intervals, with all growth forms combined, then with the four growth forms separated, using the Wilcoxon paired-sample (signed rank) test. The two size classes were always tested separately. Second, we tested for differences between size classes using exactly the same approach and statistical test, always evaluating the two census intervals separately. Thirdly, we tested for differences in mortality rates among the four growth forms, using the Kruskal-Wallis test, separately testing the two census intervals and two size classes. In each statistical test, a species was included only if $N \geq 20$ in all intervals and size classes relevant to the test. This meant that different tests had slightly different numbers of species included. Just one shrub species, *Sorocea affinis,* had >20 stems in the large size class, and so shrubs of this size class were never included in statistical tests.

We also considered the effect of swamp, slope, and colonization status on mortality. To do so, we used the Mann-Whitney *U*-test, comparing slope versus non-slope, swamp versus non-swamp, and colonizer versus non-colonizer species. The two size classes and census intervals were always considered separately. Initially, all growth forms were combined, then each test was repeated with the growth forms separated. Since there was no association between swamp status and either colonizer or slope status, the swamp category was always tested by itself, ignoring the other two categories. But slope and colonizer status were associated: there were only four slope specialist/colonizer species in the plot (significantly fewer than expected by chance, based on a chi-square test with a 2×2 contingency table). Thus, we did all slope tests considering only non-colonizers, and all colonizer tests considering only non-slope species; in both cases, swamp status was ignored.

The only assumption about underlying distributions that must be met for use of these non-parametric statistics is that when multiple samples are compared, they have similar distributions (Siegel 1956, Ghent 1973). This assumption seems warranted here, since the samples being compared were always different sets of mortality rates calculated in the same way.

Results are illustrated as unweighted mean mortality rates of various species groups. In addition, we calculated forest-wide mortality rate, based on all stems combined, with species identity ignored. The latter was mainly for comparison with the many other studies which report just this statistic from a forest.

Earlier publications.—A number of earlier papers have given some mortality information based on the same dataset used here (Hubbell and Foster 1990*b,* Leigh et al. 1990, Welden et al. 1991, Condit et al. 1992*b,* 1993*b,* 1994, Gilbert et al. 1994). Discrepancies between figures in earlier papers and those given here should be minor, and are due to on-going corrections to the dataset.

Results

Distribution of mortality rates

The modal mortality rate was 0.5–2%/yr in all four growth forms (Figs. 1 and 2). Nearly all species had rates below 6–8%/yr, with only a few >10% (Figs. 1 and 2). Mortality rates for all 205 species in each size class and census interval are given in Appendix 3, including estimates of 95% confidence limits.

The highest mortality rate observed was 48%/yr, in *Cecropia obtusifolia* (Moraceae) in the small size class and the first census interval, during which 18 of 23 stems died. The lower confidence limit in this instance was 26%, which was the highest of all lower confidence limits calculated (Table 1); there were a number of other cases where lower confidence limits were >10% (Table 1). Species with the highest mortality rates were all colonizing species. The lowest mortality rate was zero, observed in a number of instances, the most extreme being *Chamguava schippii* (Myrtaceae), in which no stems died of 194 (small size class, first interval). The upper confidence limit in this case was 0.66%, but other upper limits were lower, reaching 0.35%/yr in *Malmea sp.* (Annonaceae) and *Swartzia simplex var. grandifolia* (Leguminosae). In all four growth forms, there were species with upper confidence limits <1%/yr (Table 1).

Comparison of census intervals

Mean mortality rates were higher during 1982–1985 than during 1985–1990 (Table 2). For all growth forms combined, the difference between means was statistically significant in both size classes ($P < 0.0001$; Wilcoxon test). For each growth form separately, the difference in mean mortality was much more pronounced in large and mid-sized tree species than in treelets; shrubs were intermediate (Table 2). Indeed, there was no statistically significant difference in treelets in either size class.

About 70% of all species had higher mortality in the early census interval, but the percentage was lower in treelets and shrubs than in larger trees (Table 3). Nineteen species had significantly higher mortality during the early interval, fifteen in the smaller size class, three in the larger size class, and one species, *Poulsenia armata* (Moraceae), in both size classes (Table 3). In contrast, only two species had significantly higher mortality during the later census interval, both in the smaller size class (Table 3).

Mortality rates for individual species were fairly consistent between census intervals. Regressions of mortality during the first interval against mortality during the second interval were highly significant with positive slopes (*data not shown*); r^2 values for different growth forms and size classes were between 0.46 and 0.83. There were, however, exceptional species with very different mortality rates in the two intervals. In small stems of the mid-sized tree, *Garcinia madruno*

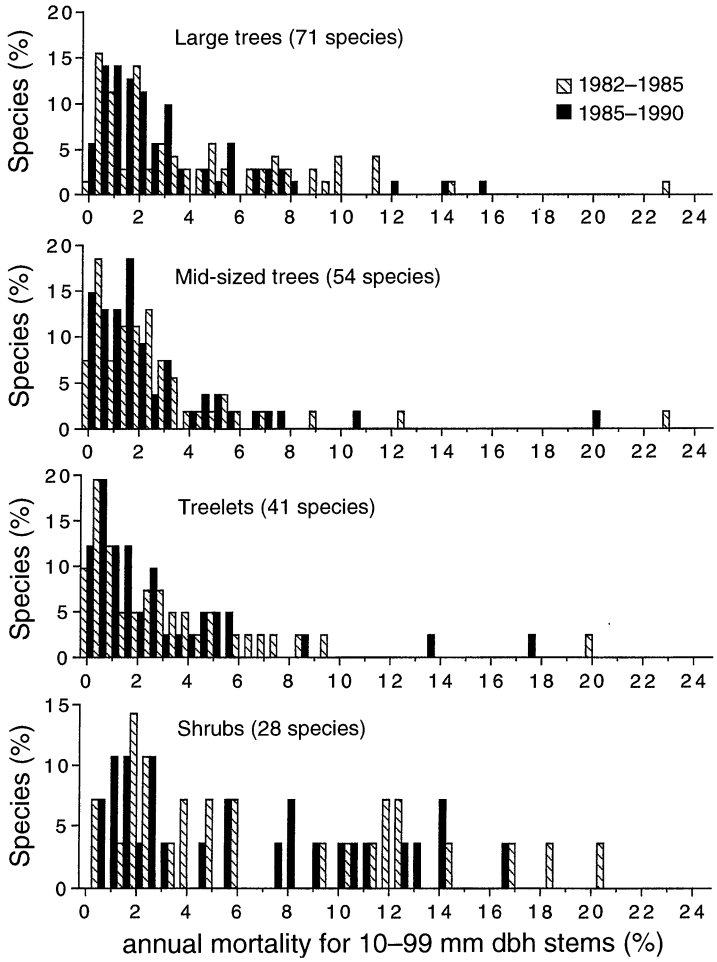

FIG. 1. Frequency distribution of mortality rates for 10–99 mm dbh stems in four growth forms and two census intervals. Annual percentage mortality is plotted in 0.5% intervals: 0.0%–0.499%, 0.5%–0.999%, 1.0–1.499%, etc. Only species with ≥20 stems in the 10–99 mm size class in both 1982 and 1985 are included. Two species of medium-sized trees had mortality estimates >25% (30.2% and 48.0%) in 1982–1985, based on >20 stems, but both had <20 stems in 1985 and so were omitted from the plot.

(Guttiferae), mortality was 0.7%/yr over the first interval and 6.6% over the second ($N > 600$); 15 stems died over the first three years, but 193 over the next five (Appendix 3). A reverse example was the shrub, *Anaxagorea panamensis,* with mortality of 5.3% during the first interval then only 1.2% during the second ($N > 400$). Condit et al. (1992*b*) gave other examples of extreme changes in mortality.

Comparison of size classes

With all growth forms combined, mean mortality rate was significantly higher in the smaller size class than in the larger ($P < 0.05$; Wilcoxon test) during both census intervals (Table 2). This overall trend, however, masked a sharp difference between growth forms. In large trees, the difference was highly significant ($P \sim 0.001$) during both intervals, but in mid-sized trees and treelets, there were no differences. In fact, in mid-sized trees, smaller stems had lower mortality than larger in 1985–1990. About 70% of large tree species had higher mortality in the small size class, but in mid-sized trees and treelets, species were equally divided (Table 4). A total of 40 species had significant differences in mortality between size classes; 15 of these species were significantly different during both census intervals. The significant differences were equally divided between higher mortality at the small size versus higher mortality at the large size class (Table 4). Most with higher mortality at smaller size were large trees, while most with higher mortality at the larger size were mid-sized trees (Table 4).

Two extremes illustrate the variation in how mortality changed with size. In 1982–1985, *Pterocarpus rohrii* (Leguminosae) had 2% mortality in the small size class but 8% in the large (with sample sizes >100); it also had higher mortality in the large size class in 1985–1990, but the difference was less extreme (Appendix 3). Conversely, *Ocotea whitei* (Lauraceae) in 1982–1985 had 7% mortality at the small size class but 2% at the large size (sample size > 100); again, the pattern was repeated in 1985–1990 (Appendix 3).

Comparison of growth forms

The mean mortality of shrub species was about double that of trees or treelets in the smaller size class (Table 2); this difference was statistically significant in both census intervals ($P < 0.001$; Kruskal-Wallis test). After removing shrubs from the analysis, there was no

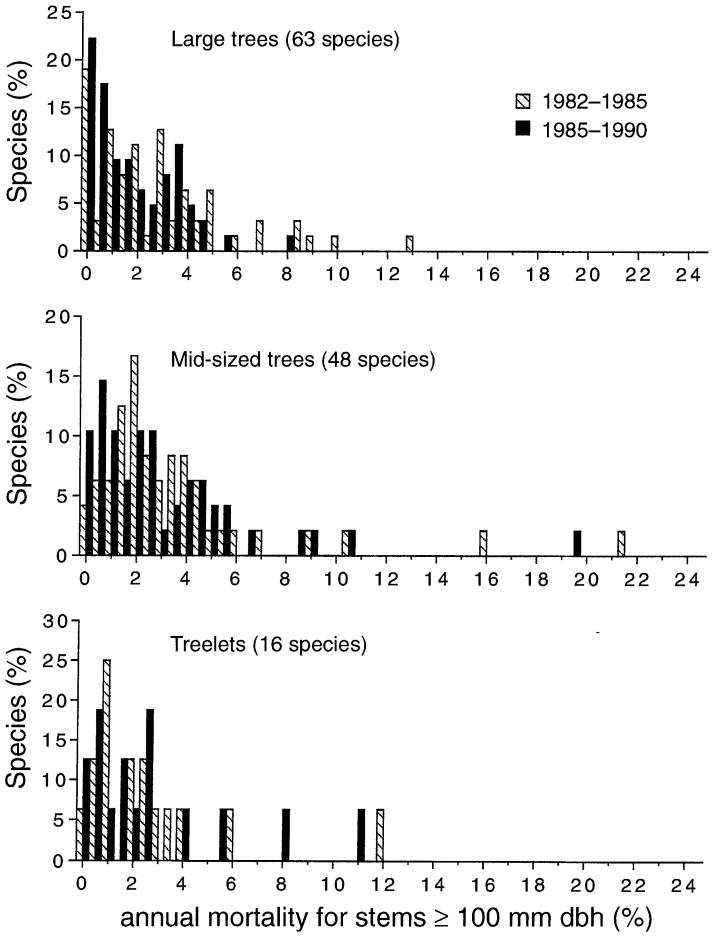

FIG. 2. Frequency distribution of mortality rates for stems ≥100 mm dbh in two different census intervals. Annual percentage mortality is plotted in 0.5% intervals: 0.0%–0.499%, 0.5%–0.999%, 1.0–1.499%, etc. Only species with at least 20 stems ≥100 mm dbh in both 1982 and 1985 are included.

significant variation among the remaining three groups. In the larger size class, there was no significant variation during 1982–1985, but in 1985–1990 large trees had significantly lower mortality than mid-sized trees and treelets ($P < 0.05$, Table 2).

Colonizers

Overall mortality.—Colonizers had higher mean mortality rates than non-colonizers in all growth forms and both census intervals (Fig. 3), but only in the small size class (for the small size class, $P < 0.01$ in seven tests and $P < 0.05$ in the eighth; Mann-Whitney test). The mean mortality rate of colonizers in various growth forms was two to three times higher than that of non-colonizers. In the large size class, there were no significant differences between colonizers and non-colonizers.

Colonizers and the inter-census comparison.—Col-

TABLE 1. Maximum lower and minimum upper confidence limits (CL) on mortality rates in annualized percentages, for each growth form and size class.

	1982–1985				1985–1990			
	Maximum lower CL		Minimum upper CL		Maximum lower CL		Minimum upper CL	
Growth form	Species*	Rate	Species	Rate	Species	Rate	Species	Rate
Small size class: 10–99 mm dbh stems								
Large trees	*Prioria*	0.71	*Cecropia i.*	19.3	*Brosimum*	0.71	*Cecropia i.*	12.9
Mid-sized trees	*Heisteria c.*	0.80	*Cecropia o.*	26.0	*Malmea*	0.35	*Solanum*	14.7
Treelets	*Swartzia s. g.*	0.38	*Croton*	17.8	*Swartzia s. g.*	0.35	*Croton*	16.0
Shrubs	*Ouratea*	1.05	*Piper cu.*	15.7	*Capparis*	0.96	*Miconia n.*	14.2
Large size class: ≥100 mm dbh stems								
Large trees	*Alseis*	0.63	*Ocotea o.*	3.9	*Drypetes*	0.74	*Inga m.*	8.7
Mid-sized trees	*Oenocarpus*	0.38	*Solanum*	11.5	*Oenocarpus*	0.88	*Solanum*	13.1
Treelets	*Swartzia s. g.*	0.97	*Croton*	16.0	*Swartzia s. o.*	1.71	*Croton*	7.6

* Species are designated by their genus, plus initials of the species name if necessary for locating in Appendix 3.

TABLE 2. Mean ± 1 SE of mortality rate for each growth form, with the number of species given in parentheses. Means are unweighted (see *Methods*). For each entry, all species in the appropriate category with ≥20 stems at the start of the census were included in the mean; however, different statistical tests used different subsets of these totals (see *Methods*).

Growth form	10–99 mm dbh			≥100 mm dbh		
	1982–1985		1985–1990	1982–1985		1985–1990
	Mortality rate					
Large trees	4.6 ± 0.5 (73)	**	3.2 ± 0.4 (71)	3.2 ± 0.4 (64)	**	1.9 ± 0.2 (63)
						*
Mid-sized trees	4.5 ± 1.0 (58)	**	2.7 ± 0.4 (54)	4.0 ± 0.6 (50)	*	3.3 ± 0.2 (49)
Treelets	3.3 ± 0.6 (41)		2.9 ± 0.6 (41)	2.9 ± 0.7 (16)		2.9 ± 0.8 (16)
	**		**			
Shrubs	7.3 ± 1.1 (28)	*	6.3 ± 0.9 (28)	6.8 ± 0.0 (1)		7.5 ± 0.0 (1)
Total	4.7 ± 0.4 (200)	**	3.5 ± 0.3 (194)	3.4 ± 0.3 (131)	**	2.6 ± 0.2 (129)

*,** Asterisks between the 1982–1985 and 1985–1990 data denote statistically significant differences between census intervals, with * for $P < 0.05$ and ** for $P < 0.01$ (Wilcoxon test). For the 10–99 mm dbh size class, the row of asterisks between shrubs and the other groups indicates a statistically significant difference (Kruskal-Wallis t test) among growth forms due to shrubs, and likewise for large trees ≥100 mm dbh in 1985–1990. Statistically significant differences between size classes are not indicated, but are given in the text.

onizers and non-colonizers had similar changes in mortality between census intervals, as can be seen by comparing 1982–1985 rates with 1985–1990 (Fig. 3). With all growth forms combined, mortality was higher during 1982–1985 than during 1985–1990 for both colonizers and non-colonizers in both size classes ($P < 0.01$ in three of four cases and $P < 0.05$ in the fourth; Wilcoxon test). When separating growth forms, there were no significant differences among treelets nor shrubs, but all comparisons were significant for large tree species, for both colonizers and non-colonizers ($P < 0.01$ for the small size class, $P < 0.05$ for the large). In mid-sized trees, there was one significant difference in mortality between intervals: non-colonizers in the small size class had higher mortality during the early period ($P < 0.01$).

Colonizers and the size comparison.—Colonizers behaved much differently from non-colonizers in terms of size differences in mortality. Colonizers had higher mean mortality rate in the small size class in both census intervals ($P < 0.01$; Wilcoxon test) when all growth forms were combined. With growth forms separated, only large colonizing trees had significantly higher mortality in the small size class compared to the large ($P < 0.01$, both census intervals; Fig. 3). In contrast, non-colonizers of all growth forms showed no significant differences in mortality between size classes (Fig. 3).

Colonizers and growth form.—In the small size class, shrubs had higher mean mortality than treelets and trees of both colonizer and non-colonizer species ($P < 0.05$ in both groups and both census intervals; Kruskal-Wallis test; Fig. 3). There were no significant effects of growth form on mortality for colonizers nor non-colonizers in the large size class.

Slope specialists

Overall mortality.—In the small size class, slope-specialists had higher mean mortality rate than generalist species (Fig. 3; with all growth forms combined, $P < 0.05$ for 1985–1990 and $P = 0.06$ for 1982–1985; Mann-Whitney test). With growth forms separated, treelets in the small size class showed a significant difference ($P < 0.01$) in both census intervals (Fig. 3). There were no significant differences between slope and non-slope species in the larger size class, whether growth forms were combined or separated. Recall that all comparisons between slope and non-slope species excluded colonizers.

Slope and the inter-census comparison.—Slope and

TABLE 3. Differences in mortality rate between census intervals. Entries in the table are the number of species with higher mortality rate in either the early or late census interval; numbers in parentheses are the number of species with significant differences. In the large size class, four species of large trees had equal mortality (all 0.00) in the two intervals and are not included in the tallies.

	Size class					
	10–99 mm dbh		≥100 mm dbh		Fraction higher in 1982–1985	
Growth form	Higher in 1982–1985	Higher in 1985–1990	Higher in 1982–1985	Higher in 1985–1990	10–99 mm dbh	≥100 mm dbh
	No. species		No. species			
Large trees	54 (6)	17 (0)	42 (2)	17 (0)	0.76	0.71
Mid-sized trees	38 (4)	16 (1)	31 (2)	17 (0)	0.70	0.65
Treelets	25 (2)	16 (0)	10 (0)	6 (0)	0.61	0.63
Shrubs	18 (4)	10 (1)	0 (0)	1 (0)	0.64	0.00
Total	135 (16)	59 (2)	83 (4)	41 (0)	0.70	0.67

TABLE 4. Differences in mortality rate between size classes. Entries in the table are the number of species with higher mortality rate in either the small size class or the large size class; numbers in parentheses are the number of species with significant differences. In 1985–1990, one large tree species had equal mortality (at 0.00%) in the two size classes and is not included in the tallies.

	Census interval					
	1982–1985		1985–1990		Fraction higher at small size	
Growth form	Higher at 10–99 mm dbh	Higher at ≥100 mm dbh	Higher at 10–99 mm	Higher at ≥100 mm	1982–1985	1985–1990
	No. species		No. species			
Large trees	44 (9)	18 (5)	39 (8)	19 (3)	0.71	0.67
Mid-sized trees	18 (5)	29 (7)	23 (3)	19 (7)	0.38	0.55
Treelets	8 (1)	8 (2)	8 (1)	8 (2)	0.50	0.50
Shrubs	0 (0)	1 (1)	0 (0)	1 (1)	0.00	0.00
Total	70 (15)	56 (15)	70 (12)	47 (13)	0.56	0.60

non-slope species had similar changes in mortality between census intervals (Fig. 3). With all growth forms combined, mortality was significantly higher in 1982–1985 than in 1985–1990 for slope and non-slope species alike, in both size classes ($P < 0.05$; Wilcoxon test). Separating growth forms, the effect held only for large trees ($P < 0.05$ for slope and non-slope in the small size class but just for non-slope in the large size class). None of the other three growth forms showed significant differences between census intervals: neither slope nor non-slope species and neither size class (Fig. 3).

Slope and the size comparison.—Both slope and non-slope specialists showed no differences in mortality between size classes (Fig. 3). Recall again that the slope comparison excluded colonizers, and only large colonizing tree species had a significant mortality difference between size classes.

Slope and growth form.—The higher mortality of shrubs in the smaller size class held in slope and non-slope species alike (Fig. 3; $P < 0.05$ in all comparisons in both census intervals; Kruskal-Wallis test). The effect of growth form on mortality in the larger size class (lower mortality among large trees, 1985–1990 only) did not hold in slope nor non-slope species. This did not appear to be just a sample size problem, but was instead due to the fact that the slope comparison was made only among non-colonizers, and it was colonizer

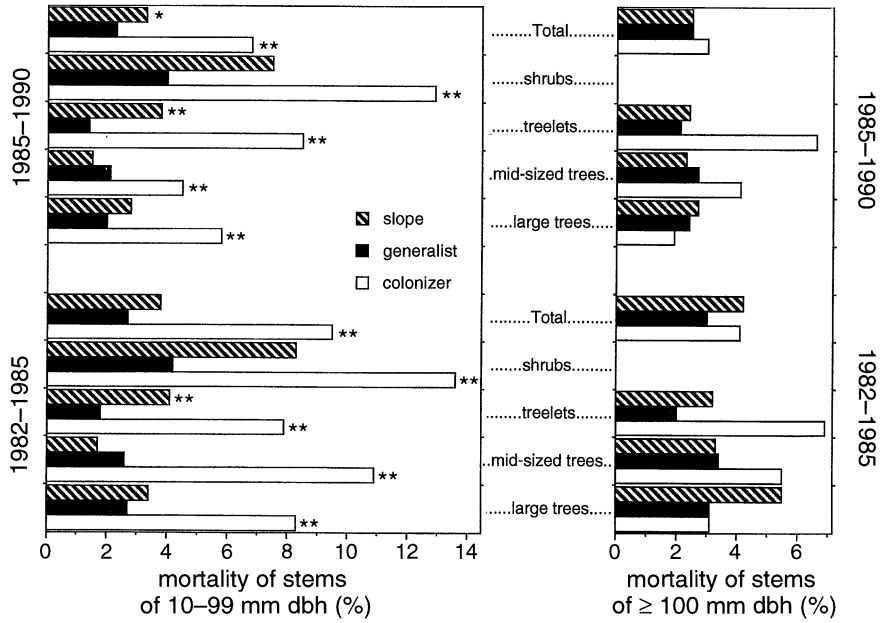

FIG. 3. Mean mortality rates for slope specialists and colonizing species compared to generalist species, of four growth forms and separated into two census intervals (above and below) and two size classes (left and right). The total category is the combination of the four growth forms that follow. Asterisks at the end of each bar indicate a statistically significant difference between the marked column and the generalist column (*, $P < 0.05$; **, $P < 0.01$; Mann-Whitney U-test). All the main results of this study—mortality comparisons between species groups—are summarized in this figure (except for swamp specialists).

TABLE 5. Unweighted mean mortality rates of swamp specialists. Entries in parentheses are the number of species on which the mean was based.

	1982–1985			1985–1990		
	Swamp		Non-swamp	Swamp		Non-swamp
Small size class: 10–99 mm dbh						
			Mortality rate			
Large trees	4.3 (14)		4.6 (59)	3.0 (13)		3.2 (58)
Mid-sized trees	8.0 (11)		3.7 (47)	3.2 (9)		2.6 (45)
Treelets	5.8 (9)		2.6 (32)	4.9 (9)		2.4 (32)
			**			**
Shrubs	10.3 (8)		6.4 (20)	7.6 (8)		5.8 (28)
Total	6.7 (42)	*	4.2 (158)	4.4 (39)		3.2 (155)
Large size class: ≥100 mm dbh						
			Mortality rate			
Large trees	1.6 (13)	**	3.6 (51)	0.9 (13)	**	2.2 (50)
				*		
Mid-sized trees	3.2 (12)	*	4.2 (38)	2.6 (12)		3.5 (37)
Treelets	12.4 (1)		2.3 (15)	11.4 (1)		2.4 (15)
Total	2.7 (26)	**	3.6 (104)	2.1 (26)	*	2.7 (102)

*,** Asterisks between two columns denote a statistically significant difference between the mortality rates given in the two columns, * for $P < 0.05$ and ** for $P < 0.01$ (Mann-Whitney test). Among non-swamp species, the row of asterisks between shrubs and the other groups indicates statistically significant differences among growth forms due to shrubs only, and likewise for large trees in 1985–1990.

species only that showed the contrast in mortality between large trees and mid-sized trees or treelets at the large size.

Swamp specialists

Overall mortality.—In the larger size class, swamp specialists had lower mortality rates than non-swamp (Table 5B). The difference was statistically significant (Mann-Whitney test) when all growth forms were combined, and for large tree species (both census intervals) and mid-sized tree species (1982–1985 only) separately (Table 5B). The trend did not hold in the smaller size class; here, swamp specialists had higher mortality than non-swamp, but the difference was significant only in 1982–1985 and only when all growth forms were combined (Table 5A).

Swamp and the inter-census comparison.—Swamp and non-swamp species had similar changes in mortality between census intervals (Table 5). The difference was significant in the small size class, with $P < 0.05$ in swamp species and $P < 0.01$ in non-swamp; in the larger size class, $P = 0.09$ among swamp species and $P < 0.01$ for non-swamp (Mann-Whitney test). The difference remained statistically significant in some cases when growth forms were separated—mid-sized and large trees, both size classes ($P < 0.05$)—but only for non-swamp species. The lack of significant results among swamp specialists when growth forms were isolated was probably due to small sample size, since even among swamp species, every growth form had higher mean mortality during the early census interval (Table 5).

Swamp and the size comparison.—The difference in mean mortality between size classes, seen only in large tree species (Table 2), was maintained even when swamp and non-swamp species were separated ($P < 0.05$ for both groups in both census periods; Wilcoxon test). This can be seen by comparing mortality rates in Table 5A with those in Table 5B, for swamp and non-swamp species separately. The other growth forms did not show significant differences.

Swamp and growth form.—Shrubs had higher mortality rates than trees among non-swamp species (Table 5; $P < 0.01$ for both intervals; Kruskal-Wallis test), but in swamp species, significance was not achieved. The lack of significance in the latter case appeared to be due to low sample size, since swamp species showed the same trend as non-swamp, and $P < 0.10$ in both census periods. The effect of growth form in the larger size class (lower mortality among large trees, 1985–1990 only) was upheld at $P < 0.05$ only among swamp specialists; in non-swamp species, patterns were similar but $0.05 < P < 0.10$ (Table 5).

Forest-wide mortality

With all stems in the forest combined, annual mortality was 2.66% in 1982–1985 and 2.26% in 1985–1990 in the small size class, 2.75% and 1.98% in the large size class. In the small size class, there were 214,530 total stems with 18,142 dead over 1982–1985; there were 221,284 total stems with 24,864 dead over 1985–1990. In the large size class, there were 20,891 total stems with 1843 dead over 1982–1985, and 20,727 total stems with 2069 dead over 1985–1990. The differences between census periods were highly significant for both sizes, whereas the differences between size classes were significant in 1985–1990 but not in 1982–1985. These rates are lower than the averages shown in Table 2, which are unweighted means of individual species' mortality rates.

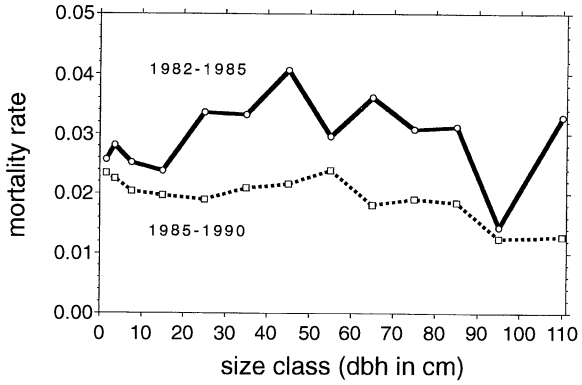

FIG. 4. Forest-wide annual mortality rates by size class. Points are plotted above the mid-point of each size class: 10–19, 20–49, 50–99, 100–199, 200–299, 300–399, etc., and finally, all stems ≥1000 mm dbh.

Mortality was higher during 1982–1985 in every size class (Fig. 4). The differences were significant in all size classes <500 mm dbh, in the 600–699 mm class, and in the ≥1000 mm class. The greatest differences in mortality between census intervals were in stems ≥200 mm dbh (Fig. 4) for which mortality was 3.37% over 1982–1985 and 1.99% over 1985–1990.

DISCUSSION

How long do tropical trees live? Mortality rates give the answer. *Prioria copaifera* had annual mortality rates of ≤0.6% in both saplings and large trees, and at this rate, a cohort of 1000 trees would last >1100 years (until the fraction alive fell to <0.001). *Swartzia simplex* var. *ochnacea* had mean mortality rates <0.35%/yr in 1982–1985, so a cohort of this species would last almost 2000 years. If large trees senesce, these would be over-estimates of life span, but our detailed study of mortality in *Prioria* (Condit et al. 1993*b*) did not show evidence for senescence: even larger trees had mortality no more than ≈1%/yr. Thus, it seems reasonable to conclude that some trees of the BCI forest are >1000 yr old.

On the other hand, a substantial number of species had annual mortality rates >2%/yr, including some abundant canopy dominants. *Trichilia tuberculata* (Meliaceae), the most abundant tree in the plot (Hubbell and Foster 1983, 1987), had mortality rates >2.25%/yr. At this rate, a cohort of 1000 trees would last only 300 years. More extreme, there were several colonizing species with annual mortality >10% (*Croton billbergianus*) or even 20% (*Solanum hayesii*), rates which would eliminate 1000 stems in 35–70 years.

The lowest mortality estimate, even using the upper end of 95% confidence limits, was 0.35%/yr in *Swartzia*. The highest value for the lower end of 95% limits was 26%/yr in *Cecropia*. This is almost a 100-fold range in mortality rates, quite a comment on the diversity of mortality rates in a tropical forest.

Our estimate of forest-wide mortality over 1982–1985 was 2.75%/yr in the large size class, which is high but not unprecedented for tropical forests (Swaine et al. 1987*b*)—Phillips et al. (1994) gave a figure of 2.8% for two plots in Peru. Our high figure represents the drought period, though, and the 1985–1990 rate of 1.98%/yr represents our best estimate of normal tree mortality at BCI. This is close to the annual rates of 2.2% (Lang and Knight 1983) and 2.0% (Milton et al. 1994) derived from smaller plots at BCI, and 2% for the La Selva forest in Costa Rica (Lieberman et al. 1985).

In a few species, we can compare mortality rates from the 50-ha plot with reports elsewhere. Lang and Knight (1983) and Milton et al. (1994) gave mortality data for 30 species on BCI, nearly all of which appear in Appendix 3 here; most species showed close matches in annualized mortality rates. Clark and Clark (1992) reported mortality estimates for *Dipteryx panamensis* and *Hyeronima alchornoides* in Costa Rica, and Alvarez-Buylla and Martínez-Ramos (1992) for *Cecropia obtusifolia* in Mexico; their figures corresponded closely to what we found at BCI.

Mortality rates in temperate forests appear to be similar. In old growth forest in Indiana, annual forest-wide mortality was 1.23% over 10 years (Abrell and Jackson 1977). For individual species, some hardwoods such as beech (*Fagus grandifolia*) and sugar maple (*Acer saccharam*) have very low mortality, often well below 1%/yr, but various species of *Betula, Quercus,* and *Ostrya* have rates of 3–10%/yr (Leak 1970, Monserud 1976, Harcombe and Marks 1983). Conifers tend to have fairly high mortality: 1.5–6%/yr (Yarranton and Yarranton 1975, Knowles and Grant 1983, Johnson and Fryer 1989). A consistent problem comparing studies of mortality in temperate and tropical forests is that temperate studies are often based on reconstruction of a population's history based on aging with tree rings, whereas all tropical studies have been based on permanent plots. Nevertheless, our overall conclusion would be that there are no obvious tropical–temperate differences in tree mortality.

The drought of 1983 led to general increases in mortality among BCI trees. If mortality in 10–99 mm stems had been the same in 1982–1985 as it was in 1985–1990, then 15,867 trees would have died over the 3.4-yr census interval instead of the 18,142 that did die. Thus, an additional 2275 trees died as a result of the drought, or 1.1% of the 10–99 mm stems. For stems ≥100 mm dbh, the drought killed an additional 483 trees, or 2.3% of the total, and for stems ≥200 mm dbh, an additional 338 stems, or 4.3% of the total, died. These calculations assume that mortality during 1985–1990 was not elevated by the earlier drought, so they are minimum estimates of excess mortality. The greater impact of the drought on larger stems was borne out by our observations of individual species: treelet and shrub species were less affected than larger trees. These patterns ran counter to our prediction that larger trees

with deeper roots would be buffered against long dry seasons compared to shrubs and small trees (Wright 1992).

The dry period afflicted colonizers, non-colonizers, slope, non-slope, swamp, and non-swamp species equally. We predicted that slope specialists would be affected more than non-slope specialists, but we could not demonstrate this. Nor was our prediction that colonizing species would be less affected than non-colonizers borne out. The drought had consistent effects on large and mid-sized tree species, whatever their soil or light gap preferences.

A few species ran counter to the overall trend and had much lower mortality during the drought than after. In one species, we know why: peccaries chewed the base of a large number of *Garcinia madruno* trees in 1989 and presumably were responsible for the greatly elevated mortality rate observed during 1985–1990. In addition, there were many species whose mortality rates were similar in the two periods, such as *Prioria copaifera.* Many species were apparently quite tolerant of the long drought.

Droughts have long been recognized as important disturbances in temperate forests, causing slight or substantial increases in tree mortality (Hursh and Haasis 1931, Yarranton and Yarranton 1975). In the tropics, the recognition of the importance of drought in forest dynamics is more recent, arising following the 1982–1983 El Niño, which affected forests on BCI, and in Borneo where large tracts of moist forest burned following a long dry period. Although the fires were partly the result of logging damage (Woods 1989), regular drought probably does play a role in structuring east Bornean forests (P. Ashton, *personal communication*).

Although the drought at BCI affected species of different microhabitats equally, there were consistent differences in baseline mortality among groups. Colonizing species of all growth forms had much higher mortality rates than non-colonizers, both during and after the drought. Although this is what everyone would expect (Swaine and Whitmore 1988), there were unanticipated results. The difference only showed up in the small size class, not the large: this is illustrated clearly by *Cecropia insignis,* with 15.8% mortality among saplings during 1985–1990 but only 3.2% mortality in the larger size class, and by *Zanthoxylum belizense,* which had 14.4% and 3.7% mortality in the small and large size classes, respectively. A thorough analysis of mortality in *Cecropia obtusifolia* in Mexico revealed the same pattern (Alvarez-Buylla and Martínez-Ramos 1992). Also contrary to the predicted pattern, some colonizers had low mortality even as saplings: *Gustavia superba* (Lecythidaceae) is an abundant roadside tree and a colonizer by Welden's index, yet its mortality in 1985–1990 was 1.9%/yr at the small size and 0.3%/yr at the large; *Macrocnemum glabrescens* (Rubiaceae) had a high colonizing index, but had mortality ≈1%/yr or less in the small size class; and *Jacaranda copaia* had the highest colonizing index in the plot and high growth rates (Condit et al. 1993*a*), yet had mortality <3.5%/yr in both size classes during 1985–1990.

Discussions of tropical tree life history have focused on the dichotomy between colonizers and non-colonizers (or pioneers and non-pioneers in some terminology): colonizers are species with small seeds that require high light levels to germinate, have high growth rates and mortality rates, and tend to recruit in light gaps. Shade-tolerant species possess the opposite suite of characters. In the current analysis, we evaluated just two of these features: the tendency to recruit in light gaps and mortality rate. Although we did find the expected correlation, there were many exceptions, and theories must account for the correlations as well as the exceptions. We must be wary that the dichotomy of life history traits is really a continuum (Whitmore 1989, Alvarez-Buylla and Martínez-Ramos 1992, Zimmerman et al. 1994), as illustrated by the range of mortality rates we found.

The other large difference among species groups was that shrubs had higher mortality than treelets and trees; this was consistent during and after the drought. The few non-colonizing species with very high mortality rates were shrubs, such as *Psychotria deflexa* (Rubiaceae), *Piper aequale* (Piperaceae), and *Conostegia cinnamomea* (Melastomataceae), which had mortality rates >10%/yr during both census periods. Mean mortality for shrubs was >6%/yr, and the four colonist shrub species had even higher mortality. Shrubs, however, had mortality rates less affected by the drought than larger trees, and treelets were like shrubs in this regard.

The excess mortality of slope specialists was less pronounced than that of colonizers or shrubs, but slope species did have higher mortality than generalists during both census intervals, although the difference was due solely to treelets and perhaps shrubs, not larger trees. Our prediction was that slope specialists would suffer more during the drought than generalists, because they are moisture-demanding species. Instead, we observed differences consistent across censuses: slope specialists of small stature had higher mortality rates during the drought and afterwards as well. Similar effects showed up in population trends: nearly all shrubs and treelets that are slope specialists in the plot declined in abundance over 1982–1985 and 1985–1990 (Condit et al., *in press*).

Our working hypothesis for these observations is that small-stature species (shrubs and treelets) that require moister soils (such as on the slopes) are uniformly suffering unusually high mortality rates and population declines on BCI because of the post-1966 drying trend, during which total rainfall has been 14% lower and severe dry seasons twice as frequent as before 1966 (Windsor 1990, Windsor et al. 1990, Condit et al., *in press*). Some larger trees of the moist microhabitats are also suffering high mortality and population declines—

Poulsenia armata and *Ocotea whitei* are examples—but other tree species affiliated with slopes, such as *Guatteria dumetorum* and *Calophyllum longifolium,* are doing just fine. We hypothesize that the division among large trees is caused by differences in seedling biology. Trees are associated with the moist slopes because their seedlings are drought-sensitive (Howe 1990), but some are also drought-sensitive as adults (*Poulsenia* and *Ocotea*) while others have longer roots and are drought tolerant as adults (*Guatteria* and *Calophyllum*). The latter group had normal mortality rates among the stems we measured, but the former had high mortality and appear to be dying back as a result of drought. On the other hand, we hypothesize that shrubs and treelets that are drought-intolerant as seedlings are also intolerant as adults, because their roots are short throughout development. (Among all groups, there are species with drought-resistance mechanisms not based on deep roots [see Mulkey et al. 1994], and these species are not restricted to the slopes.) These hypotheses lead to clear predictions about developmental changes in drought sensitivity that can be tested by evaluating physiological condition during drought (Wright and van Schaik 1994).

The most important aspect of our hypothesis from the perspective of forest dynamics is that the effects of climate change have not been caused solely by the 1983 El Niño, but are due to a longer term pattern of drought. This hypothesis leads to a clear prediction about future censuses of the 50-ha plot: the drought-sensitive species should continue to suffer very high mortality and population declines as long as the drier weather continues. If wetter conditions return, their populations should stabilize as mortality rates decline. Regardless, we see climatic shifts driving continuous shifts in demography and composition in the BCI forest, and we suggest that they probably always have and always will (Condit et al. 1992*b, in press*). Ongoing change is probably typical of tropical forests (Bush and Colinvaux 1990, Bush et al. 1990, Hart et al., *in press*).

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APPENDIX 1

The 28 species in this study that have been renamed since the 50-ha plot was initiated in 1981, or that do not appear in Croat (1978). The current name is the one appearing in Appendix 3 of this paper. Following it are synonyms from D'Arcy (1987) and from Croat (1978). The first publications from the 50-ha plot project used Croat's names, except for those species found in the plot but not listed in Croat (1978).

Current name	Name in D'Arcy	Name in Croat
Chamaedorea tepejilote	*Chamaedorea tepejilote*	*Chamaedorea wenlandiana*
Chamguava schippii	*Psidium anglohondurensis*	*Psidium anglohondurensis*
Chrysochlamys eclipes	*Tovomitopsis nicaraguensis*	*Tovomitopsis nicaraguensis*
Chrysophyllum argenteum	*Cynodendron panamense*	*Cynodendron panamense*
Garcinia intermedia	*Garcinia intermedia*	*Rheedia edulis*
Garcinia madruno	*Garcinia madruno*	*Rheedia acuminata*
Guarea sp. nov.	none	none
Guarea grandifolia	*Guarea grandifolia*	*Guarea multiflora*
Heisteria acuminata	*Heisteria acuminata*	*Heisteria longipes*
Hyeronima alcheornoides	*Hyeronima laxiflora*	*Hyeronima laxiflora*
Inga sp. nov.	none	none
Lonchocarpus latifolia	*Lonchocarpus latifolia*	*Lonchocarpus pentaphyllus*
Malmea sp. nov.	none	*Crematosperma* sp.
Nectandra purpurea	*Nectandra purpurea*	*Nectandra purpurescens*
Ocotea puberula	*Ocotea puberula*	*Ocotea pyramidata*
Ocotea whitei	*Ocotea whitei*	*Ocotea skutchii*
Oenocarpus mapoura	*Oenocarpus mapoura*	*Oenocarpus panamanus*
Ormosia croatii	*Ormosia coccinea*	*Ormosia coccinea*
Phoebe cinnamomifolia	*Phoebe cinnamomifolia*	*Phoebe mexicana*
Pourouma bicolor	*Pourouma guianensis*	*Pourouma guianensis*
Pouteria reticulata	*Pouteria unilocularis*	*Pouteria unilocularis*
Sapium aucuparium	*Sapium caudatum*	both (now considered synonyms)
Senna dariensis	*Senna dariensis*	*Cassia fruticosa*
Socratea exorrhiza	*Socratea exorrhiza*	*Socratea durissima*
Terminalia oblonga	*Terminalia oblonga*	*Terminalia chiriquensis*
Trichilia pallida	*Trichilia pallida*	*Trichilia montana*
Trichilia tuberculata	*Trichilia tuberculata*	*Trichilia cipo*
Virola sp. nov.	none	none

APPENDIX 2

The purpose here is to determine what m, the estimated mortality rate, would be if a population suffering idealized instantaneous mortality at a rate M were censused over a range of time intervals. Let N_0 be the initial population, with all individuals first censused at time 0. Each plant is re-censused again at time t, which varies for different plants. Let F_t be the fraction of the original population re-censused at time t. For example, consider 1000 plants censused on day 0, with 100 of the plants recensused after 0.5 years, 200 more after 1 year, 300 after 2 years, 200 after 3 years, and 200 after 4 years. Then $F_{0.5} = 0.1$ (100 out of 1000), $F_1 = 0.2$ (200 out of 1000), $F_2 = 0.3$, $F_3 = 0.2$, and $F_4 = 0.2$.

Under idealized mortality, the fraction of plants still alive at time t is e^{-Mt}, so the number of plants recorded alive at time t would be

$$N_t = N_0 F_t e^{-Mt}. \tag{A1}$$

In the example above, with $M = 0.02$/yr, at the 6-mo census there would be 99 of 100 plants still alive, at the 1-yr census there would be 196 of 200 alive, after 2 years, 288 of 300, after 3 years, 188 of 200, and after 4 years, 185 of 200. The total number of stems found alive throughout the survey, N, is the sum of N_t over all t, or

$$N = \int N_t dt = \int N_0 F_t e^{-Mt} dt. \tag{A2}$$

In the example, the total alive from all censuses would be 956 out of 1000. Since the mean time interval for the 1000 stems would be 2.25 years, our crude estimate of mortality (based on Eq. 1) would be $m = 0.019999$, only infinitesimally different from the true value of $M = 0.02$.

We consider more generally the case where the function F_t is constant between time t_1 and t_2, that is, where equal numbers of stems are censused at each time over the interval. We chose this case because it is mathematically simple, and because it is worse than the actual situation in our study, in which F_t was somewhat bell-shaped. Thus, $F_t = k$ over the specified interval, with $k = [1/(t_2 - t_1)]$ and $F_t = 0$ outside the interval. Substituting this for F_t in Eq. A2 and integrating from t_1 to t_2 yields:

$$N = N_0 \frac{e^{-Mt_2} - e^{-Mt_1}}{M(t_2 - t_1)}. \tag{A3}$$

Given M, Eq. A3 allowed us to calculate N and thus m (using Eq. 1). We calculated N and m for a set of values of M, using $t_1 = 4.6$ and $t_2 = 1.9$ (actual bounds for the 1982–1985 census interval) and found that the estimated $m < M$ in all cases, but the discrepancy was below $0.05 \cdot M$ for all $M < 0.5$ and below $0.01 \cdot M$ for all $M < 10\%$. The vast majority of species in the plot had mortality rates <6%/yr, where the bias was only $0.005 \cdot M$. Since we took a worst-case scenario (the uniform distribution for F_t), the actual bias would be even less.

APPENDIX 3

Mortality rates of 205 tree and shrub species in the BCI 50-ha plot that had ≥20 individuals in one size class for one census interval. A code for the growth form of each species is given immediately after its name (*T* = large tree, *M* = medium-sized tree, *U* = treelet, and *S* = shrub), followed by a dash, then zero to three codes indicating slope specialists (*S*), swamp specialists (*W*), and colonizers (*C*). For each species, the first row of data is for stems 10–99 mm in dbh and the second row for stems ≥100 mm dbh; if there is no second row, then $N < 20$ in both censuses for the larger size class.

	1982–1985					1985–1990				
Genus and species	*N**	*D**	Mortality rate*	95% confidence limits		*N*	*D*	Mortality rate	95% confidence limits	
Acalypha diversifolia S-WC	1566	449	9.65	10.57	8.77	1201	417	8.07	8.87	7.30
Acalypha macrostachya U-C	78	19	9.89	14.65	5.69	65	33	13.64	19.10	9.40
Adelia triloba U-C	230	33	4.38	5.92	2.93	199	52	5.71	7.34	4.22
	115	6	1.49	2.71	0.32	114	11	1.91	3.07	0.81
Aegiphila panamensis M-	111	22	7.32	10.54	4.39	103	32	7.08	9.72	4.76
	23	3	4.14	12.10	0.83	21	2	1.89	6.85	0.22
Alchornea costaricensis T-C	224	73	11.94	14.83	9.30	154	55	8.40	10.79	6.29
	160	10	1.89	3.08	0.74	158	19	2.39	3.50	1.34
Alibertia edulis U-W	303	11	1.13	1.80	0.47	340	19	1.10	1.59	0.61
Allophyllus psilospermus M-	145	26	5.81	8.13	3.65	139	23	3.42	4.88	2.07
	30	2	2.00	7.24	0.24	32	7	4.67	8.50	1.49
Alseis blackiana T-	6748	307	1.42	1.58	1.26	7194	453	1.23	1.35	1.12
	847	26	0.91	1.27	0.56	857	20	0.44	0.63	0.25
Amaioua corymbosa U-	29	1	0.88	4.91	0.02	29	0	0.00	2.41	0.00
Anacardium excelsum T-SW	5	1	5.54	31.30	0.13	3	1	7.63	44.45	0.15
	23	0	0.00	4.47	0.00	23	2	1.67	6.03	0.19
Anaxagorea panamensis S-SC	472	59	5.33	6.72	3.99	472	28	1.18	1.62	0.75
Andira inermis T-	276	9	0.94	1.56	0.33	270	7	0.50	0.87	0.13
	42	6	4.48	8.31	1.10	36	6	3.44	6.42	0.87
Annona acuminata S-W	509	42	2.65	3.46	1.86	525	47	1.78	2.30	1.28
Annona spraguei M-C	39	13	12.84	20.78	6.49	53	14	5.83	9.17	2.99
Apeiba membranacea T-	151	22	5.14	7.37	3.06	116	12	2.08	3.30	0.94
	238	23	3.06	4.34	1.83	226	14	1.19	1.83	0.58
Apeiba tibourbou M-	20	4	6.93	17.80	1.84	16	4	5.49	14.14	1.44
	26	3	3.88	11.36	0.80	23	9	9.36	16.85	4.02
Ardisia fendleri U-S	76	2	0.72	2.60	0.08	79	3	0.73	2.14	0.15
Aspidosperma cruenta T-S	403	14	0.97	1.48	0.47	418	15	0.69	1.04	0.34
	48	1	0.57	3.14	0.01	53	3	1.09	3.20	0.22
Astrocaryum standleyanum M-W	15	7	17.28	34.91	6.63	7	1	2.91	16.33	0.07
	233	12	1.55	2.44	0.69	225	20	1.76	2.54	1.00
Astronium graveolens T-	30	5	5.49	12.84	1.75	24	1	0.81	4.52	0.02
	35	0	0.00	3.32	0.00	35	1	0.54	3.02	0.01
Beilschmiedia pendula T-	2068	136	2.17	2.54	1.81	2366	171	1.43	1.64	1.22
	308	20	1.95	2.81	1.11	303	19	1.21	1.77	0.68
Brosimum alicastrum T-	682	13	0.57	0.88	0.26	717	18	0.48	0.71	0.26
	183	11	1.85	2.96	0.78	179	9	0.96	1.60	0.34
Calophyllum longifolium T-S	594	48	2.53	3.26	1.83	668	74	2.24	2.75	1.73
	55	5	2.88	6.74	0.93	54	8	3.05	5.29	1.04
Capparis frondosa S-	3536	109	0.89	1.06	0.73	3669	157	0.83	0.96	0.70
Casearia aculeata U-	443	41	2.82	3.70	1.97	449	44	1.95	2.54	1.38
	24	3	3.95	11.56	0.81	26	1	0.74	4.13	0.02
Casearia arborea T-C	120	29	9.09	12.59	5.93	98	31	7.24	9.99	4.83
	151	27	6.13	8.53	3.89	128	21	3.38	4.88	1.98
Casearia sylvestris M-	176	27	5.36	7.45	3.40	164	26	3.29	4.60	2.06
	72	10	4.31	7.12	1.75	67	9	2.73	4.60	1.02
Cassipourea elliptica M-W	698	17	0.80	1.18	0.42	778	31	0.77	1.05	0.50
	67	3	1.43	4.17	0.29	72	10	2.84	4.69	1.16
Cavanillesia platanifolia T-S	1	0	0.00	100.00	0.00	0	0			
	21	1	1.30	7.22	0.03	21	0	0.00	3.22	0.00
Cecropia insignis T-C	237	127	23.17	27.61	19.30	194	109	15.77	19.09	12.94
	280	43	5.28	6.90	3.74	249	40	3.22	4.24	2.25
Cecropia obtusifolia M-WC	23	18	48.01	81.78	26.04	13	7	14.66	31.44	5.90
	38	15	16.12	25.65	8.78	24	9	8.83	15.80	3.76
Ceiba pentandra T-	30	9	11.58	20.25	4.75	27	8	6.73	12.11	2.54
	42	3	2.27	6.65	0.46	40	6	2.90	5.39	0.72
Celtis schippii M-S	140	12	2.58	4.08	1.16	128	16	2.53	3.82	1.33
	42	5	3.75	8.75	1.19	38	9	5.13	8.83	2.03
Cestrum megalophyllum S-SW	309	95	10.69	12.94	8.61	236	105	11.18	13.48	9.12
Chamaedorea tepejilote S-S	32	14	17.40	28.42	9.33	22	11	13.21	23.52	6.55
Chamguava schippii U-	194	0	0.00	0.66	0.00	239	13	1.07	1.66	0.50
Chrysochlamys eclipes S-S	458	34	2.23	2.99	1.49	432	32	1.46	1.97	0.96

APPENDIX 3. Continued.

Genus and species	1982–1985					1985–1990				
	N*	D*	Mortality rate*	95% confidence limits		N	D	Mortality rate	95% confidence limits	
Chrysophyllum argenteum T-C	348	12	1.07	1.67	0.47	393	12	0.59	0.93	0.26
	75	1	0.41	2.29	0.01	84	4	0.92	2.37	0.25
Chrysophyllum cainito T-WC	49	2	1.27	4.58	0.15	57	3	1.02	3.00	0.21
	21	0	0.00	5.10	0.00	23	0	0.00	2.90	0.00
Coccoloba coronata M-	159	13	2.60	4.04	1.22	169	9	1.04	1.73	0.37
	22	0	0.00	5.38	0.00	21	1	0.92	5.10	0.02
Coccoloba manzanillensis U-	437	17	1.24	1.84	0.66	439	18	0.80	1.17	0.43
Conostegia cinnamomea S-SW	391	138	12.27	14.41	10.28	280	116	10.15	12.11	8.36
Cordia alliodora T-C	50	11	7.99	13.11	3.57	48	7	3.02	5.41	0.90
	61	6	3.16	5.79	0.73	60	7	2.35	4.18	0.68
Cordia bicolor M-C	460	52	4.11	5.25	3.01	500	112	4.87	5.79	3.98
	255	18	2.38	3.50	1.30	258	16	1.22	1.83	0.63
Cordia lasiocalyx M-S	1278	96	2.29	2.75	1.84	1222	122	2.00	2.36	1.65
	420	34	2.39	3.21	1.60	442	47	2.13	2.75	1.53
Coussarea curvigemmia U-	1462	38	0.86	1.13	0.59	1616	63	0.76	0.95	0.57
	40	1	0.82	4.53	0.01	46	6	2.66	4.92	0.64
Croton billbergianus U-WC	553	255	20.20	22.82	17.78	552	336	17.88	19.97	15.99
	67	22	12.35	18.03	7.55	67	30	11.37	16.01	7.63
Cupania latifolia T-S	46	6	4.14	7.66	1.00	39	4	2.06	5.27	0.55
Cupania rufescens T-W	50	1	0.61	3.38	0.01	65	2	0.60	2.16	0.07
Cupania sylvatica U-	934	20	0.66	0.95	0.37	1008	16	0.30	0.45	0.16
	28	1	1.11	6.16	0.02	30	0	0.00	2.36	0.00
Dendropanax stenodontus T-	63	11	6.87	11.19	3.02	51	9	3.73	6.34	1.43
	96	6	2.25	4.10	0.49	93	12	2.65	4.21	1.20
Desmopsis panamensis U-	11 718	1126	3.04	3.22	2.87	12 119	1639	2.76	2.89	2.62
Diospyros artanthifolia M-	39	3	2.61	7.65	0.52	42	0	0.00	1.70	0.00
Dipteryx panamensis T-	23	4	5.79	14.88	1.53	19	2	2.12	7.66	0.24
	33	0	0.00	3.40	0.00	33	0	0.00	2.00	0.00
Drypetes standleyi T-S	1977	51	0.70	0.89	0.51	2037	99	0.94	1.13	0.76
	196	1	0.13	0.74	0.01	227	7	0.59	1.03	0.16
Elaeis oleifera M-W	0	0				0	0			
	22	1	1.62	9.04	0.04	21	0	0.00	3.31	0.00
Erythrina costaricensis U-S	242	49	7.00	9.03	5.10	190	45	5.14	6.71	3.69
	47	5	3.31	7.71	1.06	46	12	5.73	9.31	2.73
Erythroxylum multiflorum M-	309	35	3.58	4.79	2.42	288	45	3.23	4.20	2.31
	18	1	1.66	9.23	0.04	20	5	5.41	12.71	1.70
Erythroxylum panamense U-W	104	7	2.19	3.86	0.61	105	10	1.91	3.13	0.76
Eugenia coloradensis T-	725	33	1.39	1.87	0.92	761	84	2.22	2.70	1.75
	78	9	3.47	5.83	1.29	79	14	3.69	5.73	1.85
Eugenia galalonensis U-	940	29	0.94	1.28	0.60	1131	53	0.91	1.16	0.67
	21	1	1.48	8.25	0.03	25	9	8.48	15.10	3.58
Eugenia nesiotica M-	461	14	0.91	1.39	0.44	481	9	0.36	0.59	0.13
	48	3	1.92	5.62	0.40	48	1	0.40	2.19	0.01
Eugenia oerstedeana M-	1955	138	2.23	2.61	1.86	2068	198	1.91	2.18	1.65
	133	15	3.44	5.24	1.75	140	25	3.71	5.23	2.31
Faramea occidentalis U-	22 232	743	1.05	1.12	0.97	23 742	1091	0.89	0.95	0.84
	1228	88	2.22	2.68	1.76	1402	146	2.08	2.42	1.75
Ficus tonduzii M-S	24	1	1.19	6.66	0.03	24	8	7.70	14.01	2.97
	42	5	3.85	9.00	1.22	37	8	4.61	8.12	1.65
Garcinia intermedia M-	3577	91	0.74	0.89	0.59	3948	164	0.80	0.93	0.68
	77	12	4.88	7.79	2.24	75	10	2.72	4.49	1.10
Garcinia madruno M-	629	15	0.73	1.11	0.36	655	193	6.61	7.57	5.70
	23	2	2.97	10.73	0.34	26	7	5.94	10.97	1.97
Genipa americana T-W	71	5	2.11	4.94	0.68	68	4	1.15	2.95	0.31
	20	0	0.00	5.19	0.00	20	0	0.00	3.52	0.00
Guapira standleyanum T-	140	21	4.94	7.14	2.90	117	15	2.61	3.98	1.33
	90	3	1.00	2.93	0.21	91	3	0.62	1.80	0.13
Guarea sp. nov. *M-*	1453	155	3.34	3.88	2.82	1397	200	2.93	3.35	2.53
	105	13	3.78	5.92	1.80	95	19	4.23	6.24	2.41
Guarea grandifolia T-	45	1	0.75	4.17	0.01	47	2	0.83	3.01	0.10
Guarea guidonia M-SW	1411	86	1.77	2.15	1.40	1465	99	1.32	1.59	1.07
	370	23	1.76	2.49	1.05	363	16	0.85	1.27	0.44
Guatteria dumetorum T-S	1302	122	3.05	3.59	2.51	1248	130	2.09	2.46	1.74
	285	31	3.46	4.70	2.26	280	34	2.43	3.26	1.63
Guazuma ulmifolia T-W	27	4	4.52	11.59	1.21	19	7	8.65	16.57	3.09
	28	0	0.00	3.83	0.00	30	1	0.62	3.48	0.01

APPENDIX 3. Continued.

Genus and species	1982–1985					1985–1990				
	*N**	*D**	Mortality rate*	95% confidence limits		*N*	*D*	Mortality rate	95% confidence limits	
Guettarda foliacea U-	304	12	1.20	1.89	0.53	299	26	1.72	2.40	1.07
	78	2	0.76	2.77	0.08	83	5	1.18	2.75	0.39
Gustavia superba M-C	244	31	3.94	5.36	2.58	179	17	1.87	2.78	1.00
	637	15	0.67	1.00	0.33	642	11	0.32	0.52	0.13
Hamelia axillaris S-W	113	38	12.20	16.39	8.53	92	36	9.43	12.82	6.55
Hampea appendiculata M-	35	22	30.21	47.40	19.28	16	9	15.79	31.28	7.35
	41	12	10.84	17.71	5.22	33	14	10.51	17.11	5.62
Hasseltia floribunda M-W	885	130	4.90	5.76	4.07	762	148	4.10	4.78	3.45
	262	25	3.06	4.28	1.88	255	33	2.63	3.55	1.75
Heisteria acuminata U-	100	8	2.44	4.18	0.80	101	2	0.38	1.38	0.04
Heisteria concinna M-	642	11	0.50	0.80	0.21	708	39	1.08	1.42	0.74
	246	6	0.72	1.30	0.15	256	13	0.99	1.53	0.46
Herrania purpurea U-C	522	31	1.87	2.53	1.22	531	30	1.11	1.51	0.72
Hirtella americana T-	42	2	1.26	4.55	0.14	39	3	1.52	4.44	0.30
Hirtella triandra M-S	3628	140	1.16	1.35	0.96	4102	189	0.90	1.02	0.77
	516	30	1.70	2.31	1.10	554	33	1.16	1.56	0.77
Hura crepitans T-W	27	3	3.11	9.09	0.64	22	0	0.00	3.17	0.00
	100	4	1.08	2.77	0.29	97	2	0.39	1.40	0.04
Hybanthus prunifolius S-	39 869	3648	2.92	3.01	2.83	41 107	4996	2.46	2.53	2.39
Hyeronima alcheornoides T-WC	57	7	3.98	7.08	1.16	58	15	5.70	8.83	3.00
	44	3	2.07	6.07	0.42	42	1	0.44	2.45	0.01
Inga cocleensis M-C	180	17	3.44	5.11	1.84	179	8	0.88	1.50	0.28
	39	6	5.70	10.61	1.42	39	9	5.07	8.71	2.00
Inga fagifolia T-W	50	1	0.65	3.63	0.01	53	4	1.50	3.84	0.40
Inga goldmanii T-	436	30	2.13	2.91	1.38	417	45	2.17	2.81	1.55
	62	16	8.78	13.44	4.75	51	13	5.57	8.89	2.75
Inga marginata T-S	832	194	7.56	8.65	6.52	734	222	6.82	7.75	5.94
	81	29	13.18	18.46	8.70	74	16	4.60	7.01	2.47
Inga pezizifera T-S	183	25	3.57	5.01	2.21	187	25	2.70	3.79	1.67
	25	9	10.56	18.80	4.46	15	7	11.84	23.93	4.54
Inga quaternata M-S	701	41	1.70	2.23	1.19	701	58	1.64	2.06	1.22
	34	5	4.38	10.23	1.40	40	5	2.53	5.91	0.80
Inga ruiziana T-	70	6	2.95	5.40	0.67	64	6	1.88	3.44	0.43
Inga sapindoides M-C	324	24	2.37	3.33	1.44	287	31	2.17	2.95	1.42
	67	9	4.32	7.28	1.62	67	7	2.08	3.69	0.60
Inga sp. nov. *U-*	196	5	0.75	1.74	0.24	236	14	1.16	1.78	0.56
Inga umbellifera M-	921	48	1.64	2.11	1.18	979	78	1.58	1.94	1.23
	21	6	10.01	19.40	2.89	17	5	6.59	15.53	2.06
Jacaranda copaia T-C	118	26	8.19	11.51	5.18	89	15	3.52	5.39	1.81
	224	7	1.02	1.78	0.27	230	18	1.55	2.28	0.85
Lacistema aggregatum U-	1514	142	3.15	3.67	2.63	1620	202	2.54	2.89	2.19
	43	8	6.29	11.01	2.21	40	5	2.54	5.93	0.81
Lacmellea panamensis M-W	55	0	0.00	2.10	0.00	54	1	0.36	1.99	0.01
	36	2	1.75	6.34	0.20	37	0	0.00	1.90	0.00
Laetia thamnia U-	499	39	2.58	3.40	1.78	502	64	2.60	3.25	1.97
Licania hypoleuca M-	101	3	0.92	2.69	0.18	105	4	0.73	1.87	0.20
Licania platypus T-S	244	11	1.20	1.93	0.50	284	26	1.82	2.53	1.13
Lindackeria laurina M-W	24	7	10.43	19.40	3.52	19	6	7.18	14.07	2.14
	85	4	1.44	3.70	0.39	78	9	2.30	3.86	0.85
Lonchocarpus latifolia T-C	695	46	2.20	2.84	1.57	707	62	1.75	2.20	1.32
	147	17	3.89	5.79	2.09	137	24	3.67	5.20	2.25
Luehea seemannii T-WC	101	27	10.13	14.21	6.50	97	32	7.63	10.50	5.14
	87	1	0.34	1.91	0.01	93	0	0.00	0.71	0.00
Macrocnemum glabrescens M-SC	72	0	0.00	1.33	0.00	76	4	1.02	2.60	0.27
	24	2	2.26	8.19	0.26	25	1	0.75	4.19	0.02
Malmea sp. nov. *M-*	262	5	0.59	1.37	0.20	304	1	0.06	0.35	0.01
Malpighia romeroana S-	54	3	1.81	5.28	0.37	63	8	2.58	4.46	0.87
Maquira costaricana M-	1195	62	1.58	1.97	1.19	1245	58	0.91	1.14	0.67
	223	35	5.18	6.95	3.51	200	39	4.13	5.47	2.87
Maytenus schippii M-	62	0	0.00	1.66	0.00	63	1	0.30	1.70	0.01
	20	3	4.73	13.86	0.94	19	2	2.12	7.65	0.24
Miconia affinis U-C	367	32	3.15	4.27	2.08	391	76	4.15	5.10	3.23
Miconia argentea M-WC	486	125	9.30	10.98	7.70	628	273	10.84	12.19	9.58
	45	4	2.80	7.17	0.75	50	15	6.71	10.47	3.57
Miconia elata U-	32	5	6.13	14.34	1.96	28	6	4.65	8.79	1.24
Miconia hondurensis U-W	23	4	6.71	17.25	1.78	24	. 4	3.48	8.92	0.92

APPENDIX 3. Continued.

Genus and species	1982–1985					1985–1990				
	*N**	*D**	Mortality rate*	95% confidence limits		*N*	*D*	Mortality rate	95% confidence limits	
Miconia nervosa S-C	359	146	18.55	21.73	15.63	293	170	16.60	19.37	14.19
Mouriri myrtilloides S-	6948	600	2.87	3.10	2.64	7707	1077	2.87	3.04	2.70
Myrcia gatunensis U-	38	2	1.74	6.26	0.20	47	3	1.26	3.70	0.26
Nectandra cissiflora T-	326	40	4.71	6.20	3.28	319	25	1.57	2.20	0.96
	23	2	3.05	11.02	0.35	20	0	0.00	3.54	0.00
Nectandra globosa M-SWC	105	19	5.54	8.16	3.15	103	16	3.20	4.83	1.69
Nectandra purpurea M-	76	7	3.03	5.37	0.86	75	6	1.60	2.92	0.36
Neea amplifolia S-	62	11	6.19	10.08	2.72	71	11	3.20	5.19	1.39
Ocotea cernua M-	322	33	3.31	4.46	2.20	309	24	1.54	2.16	0.93
	24	0	0.00	4.89	0.00	28	2	1.40	5.08	0.16
Ocotea oblonga T-	182	49	9.55	12.36	6.97	152	47	7.05	9.19	5.12
	33	5	4.53	10.61	1.45	31	11	8.22	13.89	3.87
Ocotea puberula T-	260	50	7.09	9.12	5.18	233	34	3.00	4.04	2.02
Ocotea whitei T-S	963	227	7.10	8.04	6.19	770	202	5.74	6.55	4.96
	167	14	2.47	3.80	1.20	170	14	1.60	2.45	0.78
Oenocarpus mapoura M-	1038	74	2.33	2.86	1.80	966	19	0.38	0.55	0.21
	752	14	0.57	0.88	0.27	746	9	0.23	0.38	0.08
Olmedia aspera U-S	392	71	5.35	6.62	4.13	334	82	5.35	6.54	4.22
	50	7	4.05	7.24	1.20	42	8	4.00	7.01	1.41
Ormosia croatii T-S	48	1	0.58	3.21	0.01	53	0	0.00	1.31	0.00
Ouratea lucens S-	1122	29	0.77	1.05	0.49	1240	60	0.94	1.18	0.71
Palicourea guianensis S-WC	377	113	11.79	14.05	9.67	659	322	12.82	14.30	11.44
Pentagonia macrophylla U-S	566	64	3.54	4.42	2.68	510	54	2.13	2.70	1.57
Perebea xanthochyma M-	255	23	3.53	5.01	2.12	255	25	1.98	2.77	1.22
Phoebe cinnamomifolia T-C	70	12	5.95	9.52	2.75	64	10	3.24	5.37	1.33
Picramnia latifolia U-S	1131	97	2.51	3.01	2.01	1137	145	2.58	3.00	2.16
	38	4	2.96	7.59	0.79	39	5	2.60	6.07	0.83
Piper aequale S-S	219	74	12.59	15.62	9.83	158	68	10.73	13.50	8.30
Piper arboreum U-S	107	24	7.98	11.35	4.93	82	22	5.97	8.66	3.62
Piper cordulatum S-	3147	400	4.48	4.92	4.04	3708	1273	8.05	8.50	7.61
Piper culebranum S-SW	120	56	20.87	26.95	15.73	65	17	5.81	8.81	3.22
Piper perlasense S-S	110	23	6.14	8.79	3.74	117	39	7.67	10.27	5.39
Piper reticulatum U-SW	171	19	3.55	5.19	1.99	160	28	3.66	5.06	2.35
Platymiscium pinnatum T-	185	18	3.16	4.66	1.73	179	28	3.24	4.48	2.07
	71	5	2.26	5.29	0.73	69	4	1.11	2.85	0.30
Platypodium elegans T-C	112	18	5.36	7.95	2.98	108	18	3.48	5.16	1.93
	58	9	5.22	8.83	1.98	49	5	1.96	4.59	0.63
Posoqueria latifolia M-	63	1	0.48	2.67	0.01	65	5	1.53	3.56	0.49
Poulsenia armata T-	2507	593	7.77	8.40	7.15	1822	418	4.95	5.43	4.48
	922	158	5.43	6.29	4.59	857	161	3.93	4.54	3.33
Pourouma bicolor T-S	29	1	1.24	6.88	0.03	31	3	1.97	5.77	0.41
Pouteria reticulata T-	1495	98	2.03	2.44	1.63	1548	117	1.49	1.76	1.22
	157	9	1.80	3.00	0.65	170	8	0.90	1.53	0.29
Pouteria stipitata M-	28	1	1.19	6.62	0.03	30	0	0.00	2.34	0.00
	33	3	2.93	8.58	0.58	31	2	1.26	4.56	0.15
Prioria copaifera T-	1077	15	0.47	0.71	0.23	1099	33	0.59	0.79	0.39
	279	3	0.36	1.07	0.08	309	8	0.50	0.85	0.16
Protium costaricense M-S	803	75	2.98	3.66	2.31	758	91	2.43	2.94	1.94
	110	24	7.42	10.56	4.58	101	20	4.18	6.10	2.43
Protium panamense M-	2650	149	1.87	2.17	1.57	2790	206	1.47	1.67	1.27
	65	17	9.00	13.64	4.99	51	6	2.37	4.37	0.56
Protium tenuifolium M-	2310	86	1.05	1.27	0.83	2552	169	1.30	1.50	1.10
	354	26	2.11	2.94	1.31	353	39	2.21	2.91	1.53
Psidium	35	0	0.00	2.83	0.00	37	1	0.52	2.88	0.01
Psychotria deflexa S-	88	27	12.75	17.95	8.22	77	40	14.13	19.23	10.11
Psychotria grandis U-SW	102	18	5.21	7.73	2.90	94	35	8.78	11.96	6.05
Psychotria horizontalis S-	6167	829	4.22	4.51	3.93	6437	1431	4.74	4.99	4.50
Psychotria marginata S-	582	92	5.47	6.61	4.37	691	183	5.84	6.71	5.01
Pterocarpus rohrii T-	1441	90	2.04	2.46	1.62	1521	138	1.81	2.12	1.51
	136	35	8.52	11.50	5.82	103	22	4.52	6.52	2.72
Quararibea asterolepis T-	1691	88	1.55	1.87	1.23	1684	109	1.26	1.50	1.03
	703	43	1.81	2.35	1.27	694	38	1.03	1.36	0.71
Quassia amara U-	148	5	0.92	2.14	0.29	143	7	0.95	1.67	0.26
Randia armata U-	900	43	1.49	1.94	1.05	920	73	1.57	1.93	1.21
	228	15	2.04	3.09	1.02	234	23	1.96	2.78	1.18
Rinorea sylvatica S-	2570	168	2.01	2.31	1.70	2612	201	1.52	1.73	1.31

APPENDIX 3. Continued.

Genus and species	1982–1985					1985–1990				
	*N**	*D**	Mortality rate*	95% confidence limits		*N*	*D*	Mortality rate	95% confidence limits	
Sapium aucuparium T-W	24	8	11.99	21.82	4.62	21	10	12.21	22.11	5.75
	23	5	7.16	16.80	2.26	20	4	4.07	10.46	1.08
Scheelea zonensis M-W	0	0				0	0			
	44	3	2.10	6.15	0.42	40	6	3.08	5.72	0.76
Senna dariensis S-C	204	79	14.53	17.96	11.46	136	71	14.02	17.68	10.94
Simarouba amara T-	993	165	5.92	6.83	5.02	995	241	5.31	5.99	4.65
	247	25	3.44	4.82	2.12	255	51	4.27	5.48	3.13
Siparuna pauciflora U-S	407	54	4.07	5.18	3.00	328	31	1.88	2.56	1.23
	24	2	2.61	9.43	0.30	26	1	0.74	4.15	0.02
Sloanea terniflora T-	516	20	1.16	1.68	0.66	505	17	0.65	0.97	0.35
	85	1	0.33	1.82	0.01	85	5	1.13	2.65	0.37
Socratea exorrhiza M-	438	74	6.39	7.88	4.96	380	92	5.33	6.46	4.27
	374	45	4.69	6.09	3.34	357	64	3.75	4.69	2.85
Solanum hayesii M-SC	85	43	23.25	31.23	16.82	64	42	20.24	28.07	14.71
	40	19	21.90	33.77	13.12	25	16	19.54	33.68	11.50
Sorocea affinis S-	3255	227	2.15	2.43	1.87	3326	267	1.59	1.78	1.40
	47	10	6.79	11.35	2.86	44	14	7.27	11.55	3.78
Spondias mombin T-WC	39	10	10.09	17.02	4.33	42	9	4.66	7.98	1.83
	24	3	4.36	12.78	0.89	23	1	0.84	4.67	0.02
Spondias radlkoferi T-C	137	36	9.49	12.77	6.52	108	28	5.71	7.97	3.70
	55	4	2.29	5.84	0.62	56	2	0.69	2.47	0.08
Sterculia apetala T-W	43	7	5.45	9.79	1.65	29	0	0.00	2.44	0.00
	25	0	0.00	4.39	0.00	24	0	0.00	2.79	0.00
Stylogyne standleyi S-W	712	51	2.26	2.89	1.65	732	54	1.45	1.85	1.07
Swartzia simplex var. grandifolia U-	2057	18	0.26	0.38	0.14	2219	30	0.26	0.35	0.17
	198	8	1.24	2.11	0.39	203	4	0.38	0.97	0.10
Swartzia simplex var. ochnacea U-	2597	28	0.32	0.44	0.20	2708	50	0.35	0.45	0.26
	104	1	0.31	1.71	0.01	112	4	0.69	1.77	0.19
Symphonia globulifera T-S	142	11	2.32	3.72	0.98	140	18	2.61	3.86	1.44
	46	14	10.39	16.46	5.38	38	8	4.45	7.83	1.59
Tabebuia guayacan T-	46	3	2.13	6.23	0.43	46	2	0.85	3.08	0.10
	30	2	2.08	7.54	0.25	28	0	0.00	2.45	0.00
Tabebuia rosea T-W	235	26	3.55	4.95	2.22	224	24	2.15	3.03	1.31
	81	9	3.28	5.52	1.22	75	9	2.38	4.01	0.89
Tabernaemontana arborea T-W	994	53	1.75	2.22	1.28	1026	66	1.27	1.57	0.96
	293	10	1.15	1.86	0.44	302	24	1.53	2.15	0.93
Tachigalia versicolor T-	2837	263	3.03	3.40	2.67	2895	442	3.16	3.46	2.87
	86	12	4.55	7.24	2.08	82	15	3.77	5.78	1.95
Talisia nervosa U-	813	23	0.75	1.06	0.45	819	35	0.83	1.10	0.55
Talisia princeps M-	616	19	0.87	1.27	0.48	629	14	0.42	0.65	0.20
Terminalia amazonica T-W	34	1	0.96	5.32	0.02	32	2	1.23	4.44	0.14
	28	1	1.18	6.57	0.03	28	0	0.00	2.43	0.00
Terminalia oblonga T-	49	1	0.58	3.25	0.01	48	3	1.22	3.58	0.25
	43	2	1.27	4.56	0.15	42	0	0.00	1.61	0.00
Tetragastris panamensis T-	2935	94	0.99	1.19	0.79	3375	201	1.17	1.33	1.01
	318	15	1.47	2.22	0.73	323	12	0.71	1.12	0.31
Thevetia ahouai U-SW	105	14	4.52	6.98	2.24	96	11	2.33	3.76	1.00
Trattinickinia aspera T-	62	12	6.71	10.76	3.12	49	8	3.38	5.88	1.17
	50	8	5.41	9.41	1.87	47	8	3.56	6.21	1.24
Trichilia pallida M-W	491	41	2.68	3.51	1.87	497	43	1.72	2.24	1.21
	76	5	2.16	5.03	0.70	75	5	1.31	3.06	0.42
Trichilia tuberculata T.	10 905	912	2.47	2.63	2.31	11 252	1268	2.26	2.38	2.13
	2022	205	3.25	3.70	2.81	1901	239	2.54	2.87	2.22
Triplaris cumingiana M-W	246	17	1.96	2.91	1.05	215	22	2.03	2.90	1.20
	125	9	2.11	3.53	0.76	127	5	0.75	1.75	0.24
Trophis racemosa M-S	258	8	0.89	1.51	0.28	275	17	1.21	1.80	0.64
	54	8	4.64	8.06	1.59	48	13	5.98	9.57	2.97
Turpinia occidentalis T-	84	23	10.04	14.46	6.17	57	19	7.72	11.58	4.51
	69	18	9.19	13.78	5.20	56	9	3.29	5.58	1.25
Unonopsis pittieri M-S	635	49	2.36	3.02	1.70	636	63	1.98	2.48	1.50
	136	11	2.56	4.11	1.08	147	6	0.79	1.43	0.17
Virola sp. nov. T-S	37	3	2.39	6.99	0.48	33	3	1.79	5.24	0.36
	21	3	4.40	12.90	0.88	20	0	0.00	3.40	0.00
Virola sebifera M-	1799	152	2.74	3.18	2.31	1688	188	2.25	2.57	1.93
	607	62	3.27	4.10	2.47	588	46	1.55	2.00	1.10

APPENDIX 3. Continued.

Genus and species	1982–1985					1985–1990				
	*N**	*D**	Mortality rate*	95% confidence limits		*N*	*D*	Mortality rate	95% confidence limits	
Virola surinamensis T-S	126	17	4.35	6.49	2.35	96	12	2.53	4.03	1.15
	174	20	3.50	5.08	2.01	163	13	1.53	2.38	0.72
Vismia baccifera U-W	74	17	8.72	13.16	4.80	74	16	4.64	7.06	2.49
Xylopia macrantha M-S	738	16	0.60	0.90	0.31	816	27	0.63	0.88	0.40
	79	4	1.44	3.69	0.39	99	4	0.78	1.99	0.21
Xylosma oligandrum S-	182	22	3.91	5.59	2.32	167	23	2.83	4.02	1.70
Zanthoxylum belizense T-C	117	42	14.86	19.73	10.61	144	76	14.39	18.03	11.34
	103	13	4.13	6.46	1.96	108	19	3.68	5.41	2.09
Zanthoxylum panamense T-C	214	51	8.37	10.76	6.15	168	45	5.94	7.76	4.27
	83	17	7.02	10.55	3.84	70	13	3.92	6.18	1.89
Zanthoxylum procerum M-C	181	16	2.88	4.33	1.50	184	45	5.33	6.96	3.83
	26	5	6.38	14.96	2.03	28	6	4.56	8.63	1.22
Zuelania guidonia M-W	27	2	2.13	7.68	0.25	27	6	4.75	9.00	1.28

* *N* is sample size, or the total number of stems alive at the start of a census interval, and *D* is the number of stems that died by the end of the interval. Mortality rates are given as annualized percentages along with upper and lower 95% confidence limits.