EFFECTS OF CLIMATE AND STAND AGE ON ANNUAL TREE DYNAMICS IN TROPICAL SECOND-GROWTH RAIN FORESTS

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Abstract. We monitored mortality and recruitment annually for six years for all trees ≥5 cm diameter at breast height in four 1-ha plots in second-growth, lowland rain forests in northeastern Costa Rica. Stands initially ranged in age from 12 to 25 years since abandonment of cattle pastures. In younger stands, abundance decreased 10–20% in the small size class (5–9.9 cm dbh), but increased 49–100% in the large size class (≥25 cm dbh). In the two youngest plots, 45.0% and 27.6% of the common tree species showed annual population increases of 3% or more, whereas 10% showed annual decreases of 4% or more. Annual rates of tree mortality for all size classes and recruitment into the 5-cm size class varied significantly among years, and mortality rates of trees 5–9.9 cm dbh were higher in younger than in older stands. Tree mortality was highest during the 1997–1998 El Niño Southern Oscillation (ENSO) year; on average, 5.6%, 3.5%, and 1.4% of trees died in the small, intermediate, and large size classes, respectively. Mortality rates during the ENSO year were 1.9 times higher for trees ≥10 cm dbh compared to non-ENSO years. Annual mortality rates for trees ≥10 cm dbh decreased significantly with increasing dry-season rainfall, but not with total annual rainfall during the census periods. Tree mortality (particularly for trees ≥25 cm dbh) in these secondary forests was highly sensitive to dry-season rainfall, even during non-ENSO years. Increased tree mortality during ENSO years is likely to accelerate forest dynamics and successional change in wet tropical second-growth forests.

Key words: dry-season drought; El Niño Southern Oscillation (ENSO); forest dynamics; mortality; rainfall; recruitment; succession.

INTRODUCTION

The world's tropical rain forests are undergoing major transformations due to deforestation, fragmentation, land use changes, and climate change. Throughout wet and dry tropical regions, second-growth forests are increasing in extent, economic importance, and conservation value (Brown and Lugo 1990, Corlett 1995, de Jong et al. 2001). Due to the transition from dominance by light-demanding pioneer tree species toward dominance by shade-tolerant species (Finegan 1996), second-growth forests are expected to exhibit more rapid changes in tree species composition than mature forests. These successional dynamics will be important in determining how tropical forests respond to global climate change and land use/land cover change. Demographic studies have documented effects of climatic variation on growth and mortality of tree species in moist and wet tropical old-growth forests (Condit et al. 1995, Clark et al. 2002, Potts 2003), and these effects can directly impact species composition (Slik 2004). Given the expectation that droughts related to

El Niño Southern Oscillation (ENSO) will increase in frequency in humid tropical zones (Hulme and Viner 1998, Timmerman et al. 1999), responses to climatic drivers in successional stands may be particularly important in shaping the role of tropical forests in global carbon and hydrological cycles.

Vegetation dynamics in young, second-growth tropical forests have been poorly studied. Quantitative data are lacking on rates of change in species abundance and size-class distributions within permanent sample plots. Our understanding of successional dynamics is largely based on chronosequence studies (Budowski 1965, Gomez-Pompa and Vázquez-Yánes 1981, Saldarriaga et al. 1988, Finegan 1996, Grau et al. 1996, Peña-Claros 2003), which limits our understanding of the effects of climate variation on successional dynamics. The few studies of tree dynamics in secondary tropical forests focus on older stands within the Panamanian isthmus (60 years or more since abandonment; Lang and Knight 1983, Milton et al. 1994, Condit et al. 2004) or examine forest dynamics following hurricanes (Whitmore 1989, Vandermeer et al. 2001, Pascarella et al. 2004, Vandermeer and Granzow-de la Cerda 2004).

Here, we summarize patterns of annual changes in tree populations and examine variation in mortality and

TABLE 1. Stand characteristics of four 1-ha second-growth monitoring plots.

Characteristic	Lindero Sur (LSUR)	Tirimbina (TIR)	Lindero El Peje (LEP)	Cuatro Rios (CR)
Stand age in 1997 (yr)	12	15	20	25
Density of trees ≥5 cm dbh (no. stems/ha)	1131	1067	1268	1138
Species density (no. species/ha)	64	99	106	121
Basal area (m²/ha)	17.13	18.11	25.49	30.32
Mean height of trees >10 cm dbh (m)	16.90	16.10	19.50	20.21
Mean soil [P] at 0–15 cm (mg/g)	1.30	0.45	0.90	0.46
Landscape matrix	forest	agricultural	forest	agricultural
Location	La Selva	La Virgen	La Selva	La Virgen

Notes: Measurements are for all trees ≥5 cm dbh in 1997, except for mean tree height, which was measured for trees ≥10 cm dbh in 1999. Soil phosphorus concentrations [P] were measured in 2000 based on 20 samples per plot.

recruitment of trees ≥5 cm dbh across six years, among stands, and among three size classes in four second-growth forests 12–25 years old in northeastern Costa Rica. Although it is known that the structure and vegetation composition of second-growth tropical forests differ substantially from old-growth forests (Lang and Knight 1983, Finegan 1992, 1996, Milton et al. 1994, Guariguata et al. 1997, Montgomery and Chazdon 2001, Sheil 2001; R. L. Chazdon, *in press*), our study is the first to provide replicated, plot-based rates of tree dynamics in young, second-growth forests based on annual census intervals. In mature tropical forests, mortality rates decrease with tree size within species (Clark and Clark 1992) as well as between size classes below and above 10 cm dbh (Condit et al. 1995, Lieberman et al. 1985). We therefore predicted that trees in the 5–9.9 cm dbh size class would exhibit higher rates of mortality than subcanopy (10–24.9 cm dbh) and canopy-sized trees (≥25 cm dbh).

Wet tropical climates show substantial annual variation in seasonal pattern of rainfall as well as in total annual rainfall (Walsh and Newbery 1999). Elevated tree mortality and decreased canopy tree recruitment during ENSO-related droughts have been documented in mature tropical rain forests in both Neo- and Paleotropical regions (Curran et al. 1999, Nakagawa et al. 2000, Williamson et al. 2000, Aiba and Kitayama 2002, Potts 2003, Slik 2004). Few studies, however, have examined mortality and recruitment rates in wet tropical forests with respect to variation in rainfall distribution within and across years (Condit et al. 2004), and these did not examine second-growth forests. A worldwide ENSO event during 1997–1998 (Potts 2003, Condit et al. 2004), our first year of monitoring, allowed direct assessment of the effects of a severe dry season on tree recruitment and mortality. Our study addressed three specific questions. (1) How does the annual rate of change in population size of common tree species vary among species and across stands of varying age? (2) How variable are rates of tree mortality and recruitment among plots, size classes, and years? (3) Do annual tree mortality and recruitment rates vary with climatic factors, such as annual rainfall, dry-season rainfall, or maximum annual temperature?

METHODS

The study was conducted in premontane wet forest at La Selva Biological Station and surrounding areas in the Atlantic lowlands of northeastern Costa Rica (Holdridge et al. 1975). Mean temperature in La Selva is 25.8°C with mean annual rainfall of 3962 mm (Sanford et al. 1994). Permanent sample plots of 1 ha were established at four sites in January–March 1997 (Table 1). Lindero El Peje and Tirimbina plots were 50 × 200 m, divided into 100 subplots of 10 × 10 m. At the other two sites, proximity to roads (Cuatro Rios) and broken topography (Lindero Sur), required use of two 0.5-ha subplots <200 m apart; each plot was 50 × 100 m, divided into 50 subplots of 10 × 10 m. Land use history and vegetation structure were similar within all sites.

All soils were on weathered ultisols on upland residual basalt (Sollins et al. 1994). Lindero El Peje and Lindero Sur plots at La Selva had higher levels of phosphorus in surface soils (Table 1).

Initial tree censuses were conducted from March to September 1997. All trees with a dbh of 5 cm or greater were tagged, mapped, identified to species, and measured for diameter at 1.3 m height if there were no buttresses, or above buttresses using a ladder. We measured diameter to the nearest 1 mm using an aluminum or nylon diameter tape. Location of diameter measurements was marked with paint to minimize measurement errors across years. Trees were identified by experienced field assistants (Marcos Molina and Orlando Vargas) and vouchers were collected routinely to compare with specimens identified at the La Selva Herbarium and at the Costa Rican Institute for Biodiversity. Annual censuses generally took place during July and August. Recruits into the 5-cm diameter class were tagged, mapped, and measured at each census. Stems were recorded as dead if no living tissues could be observed. In the case of trees with multiple stems, stems were considered independently if the branch point was below
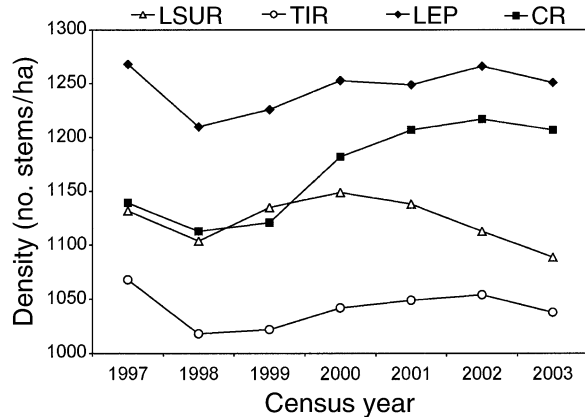
FIG. 1. Absolute changes in total tree density (trees ≥5 cm dbh) in four second-growth permanent sample plots from 1997 to 2003. Site names for sample plots are shown in Table 1.

1.3 m. Mortality and recruitment rates were calculated as percentages based on the previous year's abundance. All monitoring data were input into a specimen-based relational database (Biota; Colwell 1996). Annual mortality and recruitment rates accounted for the precise time interval between census periods using the number of days in interval/365 as a correction factor. Changes in tree abundance over all size classes were computed as annualized percent change in abundance ($r \times 100$) for species with 10 or more individuals recorded in either 1997 or 2003 using the equation $r = (\ln N_{2003} - \ln N_{1997})/6$. For species with 10 or more individuals in the 5–9.9 cm dbh or ≥10 cm dbh size class in 1997, we computed annualized mortality rates (m) using the equation $m = 1 - (M)^{1/6}$, where M is the proportion of individuals from the 1997 cohort that remained alive in 2003 (Sheil 1995). This equation, based on an exponential model of population growth, assumes a constant probability of mortality during the 6-yr interval.

Rainfall and temperature data were obtained from meteorological records of La Selva Biological Station (*available online*).[5] Monthly rainfall data were summed to obtain total dry-season rainfall (January–April) and total annual rainfall (August–July) for each census year. Temperature data were based on daily maximum values. To assess long-term patterns in annual and seasonal rainfall we computed coefficients of variation for calendar year and dry-season rainfall and correlations between these two variables for the period 1959–2003.

Statistical analyses were performed using Statistica for Macintosh (Release 4.1; StatSoft, Tulsa, Oklahoma, USA). All percentage variables were arcsine square-root transformations to normalize data. Single-factor ANOVA was used to compare differences among size classes, sites, and years. Since we did not have replicates of plots of different ages, separate two-factor AN-

[5] ⟨http://www.ots.ac.cr/rdmcnfs/datasets/meteoro/ls_met/⟩

OVAs were used to examine interactions between year and size class and between plot and size class. Linear regression analyses were used to examine effects of climatic variables (untransformed) on mortality and recruitment rates. In these regression analyses, the four plots were considered as replicates and mean values were used to assess overall effects of annual rainfall, dry-season rainfall, and annual mean maximum temperature.

RESULTS

Changes in abundance within size classes and species

In all four plots, tree density consistently decreased between 1997–1998 and 2002–2003 and increased from 1998 to 2000 (Fig. 1). Over the entire sampling period, tree density decreased in the two younger stands, Tirimbina and Lindero Sur, remained stable at Lindero El Peje, and increased at Cuatro Rios. In 2003, tree density was highest in the two older sites. All plots showed increasing density of trees ≥25 cm dbh, with the greatest increase (up to 100%) in the two younger plots, Lindero Sur and Tirimbina (Fig. 2). The oldest plot, Cuatro Rios, showed a net increase in density of small trees, whereas the youngest plot, Lindero Sur, showed a net increase in density of trees in the intermediate dbh class (Fig. 2).

Within plots, common tree species (at least 10 individuals present in 1997 or 2003) in the youngest stands showed large annual changes in population size (Appendix). In the two youngest plots, 45.0% and 27.6% of the common tree species showed annual population increases of 3% or more, whereas 10% showed annual decreases of 4% or more (Appendix). In contrast, the two older plots exhibited more stable popu-
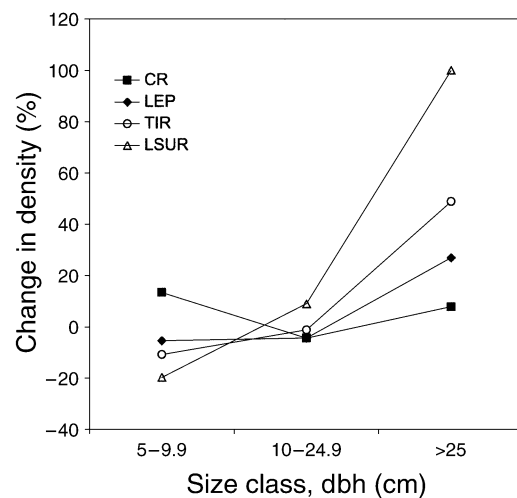

FIG. 2. Percentage change in density of three diameter size classes from 1997 to 2003 in four second-growth permanent sample plots. Site names for sample plots are shown in Table 1.

TABLE 2. Annual mortality rates for four size classes (dbh) for six years, and mean annual mortality rates during the five non-ENSO years (1999–2003).

Census year	Annual mortality rate, by size class (%)			
	5–9.9 cm	10–24.9 cm	≥25 cm	≥10 cm
1998	5.6 ± 3.5	3.5 ± 0.6	1.4 ± 1.1	3.1 ± 0.5
1999	2.9 ± 0.7	1.3 ± 0.6	0.5 ± 0.6	3.1 ± 0.5
2000	3.3 ± 1.9	1.5 ± 0.5	0.5 ± 0.6	1.1 ± 0.2
2001	3.9 ± 2.4	2.1 ± 0.6	0.9 ± 0.7	1.2 ± 0.4
2002	5.1 ± 2.9	2.9 ± 1.2	1.1 ± 0.8	1.9 ± 0.8
2003	3.7 ± 1.7	1.9 ± 0.6	0.9 ± 1.1	2.4 ± 0.6
Mean non-ENSO (1999–2003)	3.7 ± 1.8	1.9 ± 0.8	0.8 ± 0.7	1.6 ± 0.7
ENSO : non-ENSO ratio	1.51	1.81	1.78	1.90

Note: Data are reported as means ± 1 SD of four second-growth stands.

lations of common species, with 57% of common species showing modest or no changes in population size (<1% annual increase or decrease; Appendix). The most striking changes in population size were observed in the Lindero Sur plot, where abundance of the pioneer species *Cecropia insignis* and *Miconia affinis* decreased 5.0% and 4.2%/yr, respectively, and canopy species *Euterpe precatoria* and *Virola sebifera* increased 15.9% and 8.5%/yr, respectively. Common species that consistently increased in abundance across sites were the canopy tree species *Virola sebifera* and *Pentaclethra macroloba*, the subcanopy tree species *Warszewiczia coccinea* and *Guatteria aeruginosa*, and the canopy palms *Euterpe precatoria* and *Socratea exorrhiza* (Appendix).

Effects of year, size class, and plot on variation in mortality and recruitment

Annual mortality varied significantly across years ($P = 0.03$) and among size classes ($P < 0.0001$), with no significant year × size interaction ($P = 0.99$). For trees ≥10 cm dbh, annual mortality varied 2.8-fold over the six years, with the highest mortality rates occurring during the first census year, 1997–1998, the ENSO year (Table 2). In all years, mean annual tree mortality rates consistently decreased with size class (Table 2). This size-class difference was most pronounced in the two younger plots (Table 3). Plots did not differ significantly with respect to overall mortality rates ($P = 0.781$), but size class remained a highly significant fac-

tor ($P < 0.00001$), with a significant plot × size interaction ($P = 0.0026$, Table 3). Only trees in the 5–9.9 cm dbh class differed significantly in annual mortality among plots (one-way ANOVA, $P = 0.001$), with younger plots showing significantly higher mortality of small trees than older plots ($P < 0.02$, Table 3).

Recruitment of trees into the 5-cm size class also varied significantly across years (one-way ANOVA, $F_{5,18} = 10.69$, $P < 0.001$), reaching a peak of 4.9% in 2000 and another high value (4.0%) in 2002 (Fig. 3). Recruitment of trees into the 5-cm dbh class during 1997–1998 was reduced by a factor of 0.44 compared to mean recruitment rates between 1998 and 2003. Plots did not vary significantly in overall rates of tree recruitment into the 5-cm dbh class (one-way ANOVA, $P = 0.592$). Recruitment of trees into the 10-cm dbh class did not vary significantly among years ($P = 0.773$; Fig. 3), but did vary significantly among plots. The youngest plot, Lindero Sur, had significantly higher rates of recruitment into the 10-cm dbh class than the other three sites (Tukey's HSD, $P < 0.05$), which did not differ significantly from each other ($P > 0.10$). Overall, recruitment rates did not vary significantly between the two size classes (*t* test, $P = 0.675$).

For common species in the 5–9.9 cm dbh size class, annualized rates of mortality (%/yr) were highest for *Miconia affinis* (10.1–14.9%), *Vismia baccifera* (25.8% in Tirimbina), *Ossaea brenesii* (22.46% in Tirimbina), *Goethalsia meiantha* (18.8% in Lindero El Peje), and *Psychotria elata* (25.8% in Lindero El Peje; Appendix).

TABLE 3. Annual mortality rates (mean ± SD) for four dbh size classes in four second-growth plots.

Size class (dbh)	Annual mortality rate, by plot (%)			
	Lindero Sur (12 yr)	Tirimbina (15 yr)	Lindero El Peje (20 yr)	Cuatro Rios (25 yr)
5–9.9 cm	6.0[a] ± 1.9	5.2[a] ± 2.7	2.9[b] ± 1.1	2.1[b] ± 0.5
10–24.9 cm	2.0[a] ± 1.0	1.9[a] ± 1.1	2.2[a] ± 1.2	2.7[a] ± 0.9
≥25 cm	0.7[a] ± 0.9	0.5[a] ± 0.5	1.0[a] ± 0.9	1.3[a] ± 0.8
≥10 cm	1.7[a] ± 0.8	2.2[a] ± 0.8	1.9[a] ± 1.0	1.7[a] ± 0.9

Notes: Plot ages in 1997 are shown in parentheses under the plot name. Rates are averaged over all six years. Within size classes, significant differences between sites ($P < 0.05$) are indicated by different superscript letters.
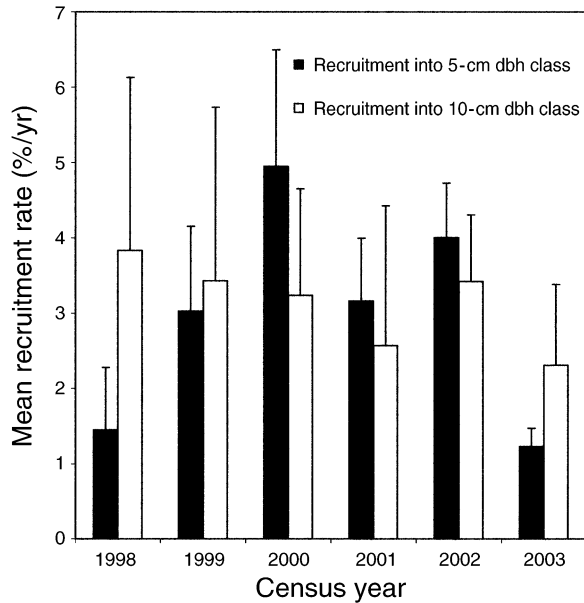
FIG. 3. Tree recruitment rates (mean ± SD) into the 5-cm and 10-cm dbh classes, averaged across four second-growth plots, over six years. Recruitment rate is calculated as the percentage of new recruits based on the number of stems present in the previous year.

Common species with high annualized mortality rates of trees ≥10 cm dbh included *Cecropia insignis* (9.6–20.6%), *Vismia baccifera* (7.0% in Tirimbina), *Stryphnodendron microstachyum* (7.5% in Tirimbina), and *Apeiba membranaceae* (5.8% in Cuatro Rios; Appendix).

Effects of climatic factors on tree mortality and recruitment

Annual rainfall and annual mean maximum temperature were not significant predictors of mean tree mortality or recruitment ($P > 0.05$ for all regressions). Dry-season rainfall (January–April), however, strongly and significantly predicted annual mortality for trees in the 10–24.9 cm and ≥25 cm size classes ($R^2 = 0.672$, $P = 0.046$ and $R^2 = 0.832$, $P = 0.011$, respectively), and was a marginally significant determinant for trees in the 5–9.9 cm class ($P = 0.055$). For all trees ≥10 cm dbh, dry-season rainfall explained 71.2% of the variation in annual mean mortality rates across the four plots ($F_{1,4} = 9.890$, $P = 0.034$; Fig. 4). Species varied considerably in their susceptibility to drought-induced mortality. In each plot, two to three of the common species ≥10 cm dbh showed higher mortality during 1997–1998 than in any other year of the study (Appendix). For one species, *Cecropia insignis*, the ENSO year yielded the highest mortality in two plots (Appendix).

Mean annual tree recruitment to 5 cm dbh, in contrast, was not significantly affected by dry-season rainfall ($F_{1,4} = 5.185$, $P = 0.085$), although data indicated

a trend toward increased recruitment in years with high dry-season rainfall (2000 and 2002). Annual rainfall and mean maximum temperature were not significant predictors of annual tree recruitment to 5 cm dbh ($P > 0.10$).

Annual and seasonal variation in rainfall

Over the six years of this study, annual rainfall (census year) was not significantly correlated with dry-season rainfall ($R = 0.207$, $P > 0.1$) or with mean maximum temperature ($R = 0.410$, $P > 0.1$). We found a marginally significant correlation between dry-season rainfall and mean maximum temperature ($R = 0.410$, $P = 0.054$), however. Dry-season rainfall was far more variable than annual rainfall; across the six years, annual rainfall varied 1.5-fold, compared to 3.3-fold variation in dry-season rainfall. Dry-season rainfall accounted for 10.6–30% of annual totals (calculated from August to July of each census year). Considering weather data over a 45-yr period from 1959 to 2003 at La Selva Biological Station, dry-season rainfall was significantly correlated with annual rainfall ($N = 45$, Spearman $R = 0.538$, $P = 0.0016$). Dry-season rainfall averaged 822 mm and was far more variable across years (CV = 39.9%) than annual rainfall (CV = 16.0%). On average, 19.1% (range 7.5–31.6%, CV = 32.9%) of annual rainfall occurred during the January–April dry season.

DISCUSSION

Tropical secondary forest stands demonstrated large changes in tree size distributions and population sizes of common species over only six years. Species composition in younger stands was more dynamic than in older stands, with over half of the common species increasing or decreasing population size by 2% or more per year (Appendix). Although older, second-growth, logged forests, and mature tropical forests show changes in tree abundance over time (Lang and Knight 1983,
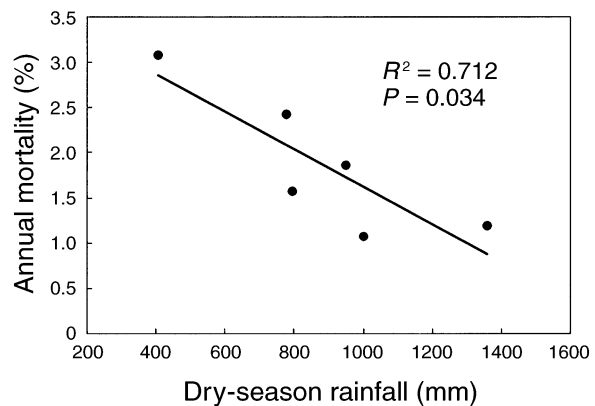

FIG. 4. Regression of mean annual mortality rate of trees ≥10 cm dbh on dry-season rainfall (total rainfall between January and April) across six years. Data are means for four second-growth plots.

Hubbell and Foster 1992, Milton et al. 1994, Swaine 1994, Condit et al. 1999, Sheil 2001, Laurance et al. 2004), these changes are less pronounced than those observed here for second-growth forests. Substantial changes in population sizes for stems ≥1 cm dbh were observed on Barro Colorado Island, Panama, where 10.5% of common species showed population changes of 5%/yr or more during a nondrought period (1985–1995) and 40% of species changed by 3%/yr or more during the 1982–1985 drought period (Hubbell and Foster 1992, Condit et al. 1999). In the more stable Pasoh forest in Malaysia, only 2% of species changed by 5% or more per year from 1987 to 1995 (Condit et al. 1999). These rates cannot be directly compared with those for larger size classes, however.

Despite these changes in composition and size distributions, annual tree mortality patterns for trees ≥10 cm dbh did not differ significantly from those observed in mature rain forests. During non-ENSO years, mortality for trees ≥10 cm dbh (Table 2) was similar to the median value of noncatastrophic tree mortality (1.6%/yr) among six tropical moist, wet, and rain forests (Lugo and Scatena 1996). Mortality rates for larger trees were lower than those for trees ≥19.1 cm dbh in old second-growth forest on Barro Colorado Island (Milton et al. 1994) and for trees ≥10 cm dbh in old second-growth at Fort Sherman, Panama (Condit et al. 2004). Canopy-sized trees in young secondary forests are young and generally vigorous, and many are long lived (Budowski 1965, Finegan 1996). The low rate of canopy tree mortality in these stands is reflected in the rarity of canopy gaps in second-growth forests in this region (Nicotra et. al. 1999, Montgomery and Chazdon 2001). Despite canopy closure and the absence of gaps in these stands, large numbers of trees are growing into the largest size class, particularly in younger stands (Fig. 2). Recruitment of canopy trees is therefore not linked with the formation of canopy gaps in these young, secondary forests. Further, we saw no evidence for thinning in larger tree size classes, as observed in 10–14-yr-old post-hurricane forests in Nicaragua (Vandermeer et al. 2001, Vandermeer and Granzow-de la Cerda 2004).

In the two youngest stands, trees 5–9.9 cm dbh exhibited higher mortality rates than trees in the same size class in older stands, reflecting a higher relative abundance of shade-intolerant species. In Lindero Sur for example, *Miconia affinis* composed 55.8% of the stems in this size class in 1997 and 47.4% of them died from 1997 to 2003. Although 50% of the *M. affinis* in the Lindero El Peje plot also died during the same interval, this species composed only 14% of the stems in this size class in 1997. Although photosynthetic light availability was higher in upper understory and subcanopy strata in these younger stands compared to older stands (M. B. Palomaki, *unpublished data*), light levels are probably still too low to support survival of shade-intolerant pioneer species that established early in suc-

cession. Trees ≥10 cm dbh did not differ in mortality rates across stands, however, suggesting that light levels in the subcanopy and canopy were adequate for survival of pioneer and early successional tree species.

Perhaps our most striking result was that annual variation in tree mortality in these wet, lowland, second-growth forests was strongly determined by the seasonal distribution of rainfall, but not by variation in total annual rainfall. In northeastern Costa Rica and in central Amazonia, years with low dry-season rainfall do not always correspond to years with low annual rainfall (Laurance et al. 2001). At La Selva Biological Station, the ENSO year 1997–1998 had the fourth lowest dry-season rainfall in the 46-yr record, but ranked 31st in annual rainfall. Tree mortality in this region therefore appears to be responding to the severity of the January–April dry season. Tree density declined over 1997–1998 and 2002–2003 at all sites (Fig. 1). During February 1998 and March 2003, La Selva received only 33.6 and 45 mm of rainfall, respectively, compared to the 100 mm that constitutes a ''dry month'' (Walsh and Newbery 1999). These results suggest that short-term water deficits can create hydraulic challenges for fast-growing evergreen tree species in tropical wet forests.

Other studies have demonstrated effects of ENSO-related droughts on tree mortality in tropical forests that receive lower annual rainfall or have more pronounced seasonality than La Selva. On Barro Colorado Island, Panama, 70% of the species ≥1 cm dbh that were examined had higher annualized mortality rates during 1982–1985 (1982–1983 ENSO) than during 1985–1995 (Condit et al. 1995). Mortality of trees ≥10 cm dbh in central Amazonian rain forests increased significantly from 1.1%/yr during the pre-ENSO period to 1.9%/yr during the 1997–1998 ENSO period (Williamson et al. 2000). Mortality of trees ≥10 cm dbh in a permanent sample plot in Sarawak, Malaysia, increased more than seven-fold, from 0.89%/yr during 1993–1997 to 6.37%/yr during 1997–1998 (Nakagawa et al. 2000). The ratio of mortality rates in the drought : nondrought intervals was higher for large trees (Potts 2003, Slik 2004), as we also found in our study (Table 2). During drought periods, competition for water and potentially other soil resources in older stands may become limiting to growth and survival for these species, increasing susceptibility to mortality during seasonally dry periods. Species appear to vary considerably in their susceptibility to drought-induced mortality. In our study, nine species showed their highest annual mortality rate during 1997–1998 in at least one plot (Appendix). In East Kalimantan, Borneo, early successional pioneer *Macaranga* trees in logged forests suffered 65% mortality in all size classes during the 1997–1998 ENSO (Slik 2004). All of these studies suggest the need for further examination of the effects of seasonal drought on tree mortality in tropical rain forests.

The stability of tree recruitment (in growth) into the 10-cm size class over time suggests that diameter increment growth of trees >5 cm dbh may be less affected by dry-season rainfall than for individuals <5 cm dbh. Annual mean diameter growth increments did not vary consistently across stands over the six-year time interval, and generally decreased from a peak value measured in 1997–1998, suggesting that tree diameter growth in these secondary forests may be less sensitive to climate variation than is tree mortality (Redondo et al. 2001; R. Chazdon, *unpublished data*). Higher rates of tree recruitment in the youngest site (Lindero Sur) reflect higher size-specific annual increment growth rates in this site (Redondo et al. 2001).

Although our study lacked replication of stands of different ages since abandonment, the temporal trends that we documented support robust conclusions based on successional dynamics (R. L. Chazdon, *in press*). Chronosequence approaches (space-for-time substitution), widely adopted in studies of forest succession, are based on one-time measurements of different stand ages, precluding assessments of tree dynamics during succession. If ENSO events occur more frequently, as some scenarios of global climate change predict (Timmermann et al. 1999), how will the dynamics of second-growth forests be affected? Based on the data presented here, ENSO-related droughts are likely to accelerate rates of species turnover during succession by increasing rates of canopy tree mortality and creating canopy gaps, particularly in older stands. These changes are not likely to lead to decreases in stand basal area or aboveground biomass, however. Canopy gaps will provide enhanced recruitment opportunities for both early and late successional species in the 10–24.9 cm dbh size class. Increased mortality of small trees is unlikely to have a strong effect on forest dynamics, since these changes do not create openings in the forest canopy. Rather, increases in diffuse light availability will enhance the growth and recruitment of shade-tolerant saplings and small trees in subsequent years. Our studies highlight the need for continuous, annual, long-term studies of tree dynamics in second-growth forests of a variety of ages and land use histories to project future changes in the composition and dynamics of tropical forests.

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APPENDIX

A table showing annualized changes in density and mortality rates of common tree species in four 1-ha second-growth monitoring plots from 1997 to 2003 is available in ESA's Electronic Data Archive: *Ecological Archives* E086-096-A1.