Journal of Tropical Ecology (2004) **20**:51–72. Copyright © 2004 Cambridge University Press
DOI: 1017/S0266467403001081 Printed in the United Kingdom

Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season

Richard Condit*[1], Salomon Aguilar*, Andres Hernandez*, Rolando Perez*, Suzanne Lao*, George Angehr*, Stephen P. Hubbell† and Robin B. Foster‡

* Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, USA
† Department of Botany, University of Georgia, Athens, GA 30602, USA
‡ Botany Department, The Field Museum, Roosevelt Rd. at Lake Shore Dr., Chicago, IL 60605, USA
(*Accepted 31 December 2002*)

Abstract: Tropical forest demography and dynamics were examined in three inventory plots across a precipitation gradient in central Panama. The harsh dry season of 1998 that accompanied the 1997–98 El Niño was spanned by censuses at all three sites. The wet and intermediate plots were similar in total species richness, the dry site somewhat lower in diversity; all three sites differed substantially from each other in species composition. Forest-wide growth of large trees was higher at the wet and intermediate sites than at the dry site, but sapling growth was highest at the dry site and lowest at the intermediate site. Forest-wide growth differences were reflected by individual species, for example, saplings of species at the dry site grew faster than saplings of the same species at the intermediate site. Forest-wide mortality was lowest at the dry site and highest at the wet, and this difference was also reflected by individual species. We suggest that low mortality and growth in the drier forest was due to the longer annual dry season and higher deciduousness, and that high sapling growth at the dry site was due to greater light penetration to the forest floor. Growth rates were elevated at all three sites during 1998, possibly due to reduced cloud-cover during the El Niño. Contrary to expectation, mortality during 1998 was not elevated at wet and intermediate sites during the El Niño drought, but was at the dry site. Finally, we found that some species performed poorly at one site and declined in abundance, while having stable or increasing populations at another site, demonstrating that the communities are not at equilibrium.

Key Words: Barro Colorado, climatic variation, El Niño, forest dynamics, Panama, precipitation gradient, tree species demography, tropical forest

INTRODUCTION

Tropical forests occur under a wide range of climates. The most conspicuous gradient is one of precipitation: tall, high-biomass tropical forest can be found where annual rainfall is as low as 1300 mm or as high as 12 000 mm. Forests across such a gradient vary greatly in species composition and structure, and moisture provides one of the major axes for classifying tropical forest (Beard 1944, Holdridge 1967). At the dry end, forests are less diverse, more deciduous, and frequently shorter in stature; wet forests are evergreen and far more diverse (Gentry 1982, 1988). Moreover, wet forests have higher growth and mortality (Murphy & Lugo 1986, Phillips *et al.* 1994). Few studies, though, have examined how the productivity and mortality of individual species varies with climate. To examine forest dynamics across a precipitation gradient, we set up medium and large-scale inventory plots within 55 km of each other near the Panama Canal, at sites differing in rainfall by more than 50%. We examined the hypothesis that dry conditions and deciduousness limit forest productivity and reduce diversity, and we tested whether demography of individual species were affected in the same way as the whole forest.

During the study, predictions began to surface for an unusually strong El Niño in 1997. Unusual droughts associated with El Niño events are known to elevate tree mortality in Latin America (Condit 1998*a*, Condit *et al.* 1992, 1995; Laurance *et al.* 2001, Leigh *et al.* 1990) and South-East Asia (Becker & Wong 1993, Becker *et al.* 1998, Cao 2000, Nakagawa *et al.* 2000, Walsh 1996, Woods 1989), but few studies have examined

[1] Corresponding author. E-mail: condit@ctfs.si.edu

individual species during a drought (Condit *et al.* 1992, 1995; Geldenhuys 1993, Newbery *et al.* 1999), and few have examined variation in the impact across a climate gradient (Aiba & Kitayama 2002). Given the plots already in place, we decided to assess the impact of the 1997 event with censuses before and after the anticipated drought of early 1998.

There are several hypotheses about how El Niño affects forest trees. First, based on observations during the 1983 El Niño, we predicted that a severe 1998 dry season would directly cause tree mortality (Condit *et al.* 1995, Leigh *et al.* 1990). Also based on the 1983 event, we predicted that growth rates would be elevated during the 1998 El Niño dry season (Condit *et al.* 1992), and we considered three alternative hypotheses to account for this: (1) that elevated mortality opens the canopy and increases light in the understorey; (2) that low cloud-cover during El Niño increases light levels (Wright *et al.* 1999); and (3) that temperature affects tree growth. The timing of the dry season in central Panama is consistent, so we could arrange censuses to span the severe dry conditions of March–April 1998. Unfortunately, light and temperature responses to El Niño conditions were not as easily predicted, and as it turned out, our censuses were not suited to test the third hypothesis. We report forest dynamics and climatic fluctuations before and during the 1998 dry period at all three sites, hoping to gain insight into hypotheses about forest dynamics and to provide a stronger basis for future studies of El Niño in Central America.

MATERIALS AND METHODS

Forests and climate

A near continuous corridor of tall, closed-canopy forest flanks the Panama Canal from the dry Pacific coast to the wet Caribbean (Condit *et al.* 2001), and we chose three study sites that span this climatic gradient. Two sites were on U.S. military land when the work started, but the military installations have since closed and the land is now owned by the government of Panama. The third site is the research reserve on Barro Colorado Island (BCI), operated by the Smithsonian Tropical Research Institute (Rubinoff & Leigh 1990).

The Pacific site is next to the Cocoli River, west of the Canal, near Panama City. On the Pacific slope, forests have been extensively disturbed in the past 200 y, and the vegetation is mostly young secondary forest (Condit *et al.* 2001). However, the Cocoli site has a small patch of forest with large *Anacardium excelsum* (to 1262 mm diameter) and *Cavanillesia platanifolia* (to 1650 mm). Nevertheless, these species are considerably smaller than they are at BCI (2234 and 2198 mm respectively), and we consider the Cocoli site mature secondary forest, probably 80–120 y since heavy disturbance.

The BCI site is near the centre of the isthmus and has old forest, >500 y since major disturbance (Piperno 1990); it has been described in detail elsewhere (Leigh 1999). The third site is near the Atlantic coast, 55 km north-west of the Cocoli site, near Fort Sherman, a former U.S. Army Base. The Sherman plot has apparently been free of severe disturbance for 200 y or more, since the largest trees are of slow-growing species (*Manilkara bidentata, Brosimum utile*). But there are signs of human impact in the area – the largest *Manilkara* in the plot has been slashed many times for latex, and the northern hectare of the plot was obviously cleared recently.

The sites differ in precipitation: mean annual rainfall at a gauge 6 km further from the Atlantic coast than the Sherman plot was 2892 mm (1960–2000); at BCI it was 2616 mm for the same period; at a gauge 4 km further from the Pacific Coast than the Cocoli plot, it was 2030 mm (1978–1998). We estimate that the Sherman site itself gets 3030 mm and Cocoli 1950 mm, based on the 23 mm km^{-1} change in rainfall observed between the station near Cocoli and the station near Sherman. In Condit *et al.* (2000), we used rainfall and potential evapotranspiration (PET) diagrams to estimate the duration of the dry season, or the mean interval during which PET exceeds rainfall. At Fort Sherman, the interval was 106 d; at BCI, 118 d; at Cocoli, 129 d.

Apart from rainfall, climate is similar at all three plots. All are below 200 m in elevation, and temperatures are typical of the lowland tropics. The forests never burn and are mostly evergreen, however there is a gradient of deciduousness following the climatic gradient: the leaf density of the Cocoli canopy declines by 19% in March relative to the wet season, by 10% at BCI and by 3% at Sherman (Condit *et al.* 2000). Forests differ a great deal in species composition across the isthmus of Panama, and much of the variation can be attributed to climate (Condit *et al.* 2002, Pyke *et al.* 2001).

We also measured fluctuations in rainfall and two other climatic variables during census intervals before, during, and after the 1997–98 El Niño, with census intervals defined as the time period between the average date of measurement of each tree (Table 1, Condit 1998*b*). The intensity of the dry season each year was measured as the total rainfall between 15 November and 15 April. El Niño dry seasons are distinguished by their early starting date (mid-November instead of mid-December in typical years) and their long duration, so this measure is the best we know for gauging the drought's severity. The impact of drought on trees is most pronounced at the end of the dry season in March and April, and so the droughtiness of each census interval was determined by the dry seasons which ended during the interval (Table 1).

Table 1. Census dates and climate during each census interval. Means ± 95% confidence limits; dry-season rainfall given for each year during a census interval (if census interval included second half of the dry season). NA, data not available for substantial parts of the given interval.

Site and climatic data	Census 1	Census 2	Census 3	Census 4
Sherman, mean census date	16 Mar 1996	25 Dec 1997	6 Feb 1999	
Sherman, range census date	Jan–Jun 1996	Dec 97–Jan 98	Jan–Mar 1999	
Mean daily min. temp. (°C)	NA	23.73 ± 0.10		
Mean daily max. temp. (°C)	NA	27.58 ± 0.12		
Dry season rain (mm)	1377, 554	226		
Mean daily PAR (mol m^{-2} d^{-1})	NA	30.7 ± 1.1		
Cocoli, mean census date	17 Nov 1994	19 Nov 1997	10 Dec 1998	
Cocoli, range census date	Nov–Dec 1994	Nov–Dec 1997	Nov–Dec 1998	
Mean daily min. temp. (°C)	24.19	NA		
Mean daily max. temp. (°C)	31.60	NA		
Dry season rain (mm)	333, 470, 267	196		
Mean daily PAR (mol m^{-2} d^{-1})	26.5 ± 0.6	30.2 ± 1.3		
BCI, mean census date	14 Jun 1995	25 Feb 1998	25 Mar 1999	6 Jun 2000
BCI, range census date	Jan–Oct 1995	Feb–Mar 1998	March 1999	Jan–Oct 2000
Mean daily min. temp. (°C)	23.91 ± 0.08	23.96 ± 0.12	23.37 ± 0.11	
Mean daily max. temp. (°C)	29.66 ± 0.09	30.10 ± 0.16	29.48 ± 0.13	
Dry season rain (mm)	927, 364	156	818	
Mean daily PAR (mol m^{-2} d^{-1})	30.9 ± 0.7	32.1 ± 1.1	30.4 ± 1.1	

We also considered temperature and photosynthetically active radiation (PAR) by averaging daily measurements during each census interval. PAR was measured by Licor LI-1905 sensors above the forest at a tower on BCI and at canopy cranes at Sherman and near Panama City (the latter is 7.9 km from the Cocoli plot). PAR, temperature and rainfall comparisons were based on complete daily records between every pair of censuses; data were missing for substantial periods during some intervals (Table 1). All climate data come from Panama Canal Authority and Smithsonian records (http://www.stri.org/tesp).

Forest inventory plots

Medium-sized forest census plots were established in 1994 at Cocoli and 1996 at Sherman. The former is a 4-ha L-shaped plot, a 300 × 100-m rectangle plus a 100 × 100-m square set to the side. The odd shape was chosen because either a 400 × 100-m or a 200 × 200-m plot would have included younger secondary forest. The Sherman plot is 5.96 ha, and has an even odder shape associated with its history (Figure 1). It started as a 400 × 100-m rectangle, but after the surveying was completed, we found that the northern 100 × 100-m section was in very young forest, probably cleared within the past 20 y for US Army training exercises. So another 100 × 100 m was added off the south side, matching the shape of the Cocoli plot. Then, when a canopy research crane was placed in this new hectare, additional strips 40 m wide were added so that the plot covered the entire reach of the crane.

The plots were censused following the methods described in Condit (1998*b*). All free-standing woody plants with stem diameter ≥10 mm were tagged, identified, measured and mapped. Taxonomy followed Croat (1978) and D'Arcy (1987), except where we specify recent revisions (see Appendices 1, 2); a complete species

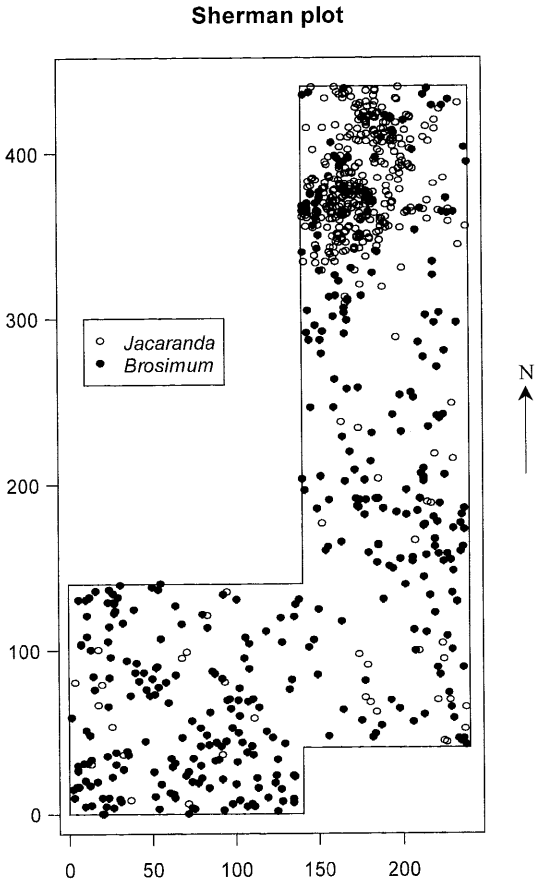

Figure 1. Locations of all individuals ≥10 mm dbh of *Jacaranda copaia* and *Brosimum utile* at the Sherman plot. *Jacaranda* was concentrated in the section of young forest. Distances in metres.

list, including synonyms, authorities and photographs, can be found on the web (http://ctfs.si.edu). Stem diameter was measured 1.3 m above the ground; if misshapen at that height, the measurement was taken below a swelling or above buttresses (Condit 1998*b*). Hereafter, stem diameter is abbreviated dbh whether it was precisely at breast height or not.

The single hectare of young forest at Sherman was very different from the mature forest: it was dominated by different species (*Jacaranda copaia, Miconia minutiflora, Schefflera morototoni*; Figure 1) and had high density and high mortality of trees between 100 and 300 mm dbh. The number of individuals 100–300 mm dbh declined by 10% in 3 y, suggesting that the hectare is self-thinning. Since the young forest greatly alters results for the Sherman plot, we consider only the 4.96 ha of mature forest for all comparisons.

The BCI plot is 50 ha, and has been censused five times between 1982 and 2000 (Condit 1998*b*, Hubbell & Foster 1983). Growth and mortality data have been reported elsewhere (Condit *et al.* 1992, 1993, 1995, 1999), but we reanalyse here using 1995 and 2000 data to provide the closest comparison possible with the other plots. In addition, random samples from 10 species were censused at BCI in 1997 and 1998 to assess the impact of the El Niño. All trees $\geq$300 mm dbh in the 1995 census were sampled in these 10 species, plus random draws of 220 individuals 100–299 mm dbh and 220 individuals 10–99 mm dbh per species. Half of the random samples were chosen from the slopes in the plot and half from the plateau, in order to include a range of soil moisture conditions (Becker *et al.* 1988, Harms *et al.* 2001). In species with fewer than 220 individuals in the 100–299 mm dbh range, we sampled all of those and increased the number < 100 mm to reach a total of 440 trees < 300 mm dbh; if there were insufficient individuals on either slope or plateau, the total sample was < 440 (but never < 340 in any of the species). The 10 species were chosen to span a range of responses to the previous drought in 1983: five had mortality rates greatly elevated during 1982–1985 relative to 1985–1990 (*Acalypha diversifolia, Beilschmiedia pendula, Guatteria dumetorum, Ocotea whitei, Poulsenia armata*) and five had mortality rates little altered over the same period (*Calophyllum longifolium, Desmopsis panamensis, Protium tenuifolium, Tachigali versicolor, Trichilia tuberculata*).

In the BCI subsample of 10 species, new recruits were not added to the census in 1997 nor 1998. This contrasts with the Cocoli and Sherman El Niño analyses, since the latter two were based on complete plots, and recruits from later censuses were incorporated into the analyses. We believe the latter method is better, since it includes all individuals of a given dbh category in every analysis, whereas the BCI subsample excluded a subset. Fortunately, any bias caused by the sampling difference is overcome by the fact that the BCI subsample spans census intervals prior, during and after the El Niño.

Census dates. The initial censuses considered here at all three sites were between late 1994 and early 1996 (Table 1). The pre-drought interval begins with this census, and it would have been ideal to have identical census dates everywhere, but this was before any El Niño forecast and we had to finish the 50-ha census of BCI (which takes nearly a year) at this time. Subsequent censuses were carried out at all three sites in early 1998 and then late 1998 or early 1999 (Table 1); these were designed so that the second census interval included the second half of the 1998 dry season, when the El Niño impact was predicted to be at its height. The BCI 1998 census was later than ideal because we had to census all three sites in a short period, however, climatic variables show that drought peaked during the second census at all three sites, and PAR peaked during the second census interval at BCI and Cocoli. Unfortunately, the period of high temperature associated with the El Niño was included by two census intervals at all three sites, and conclusions about temperature effects are thus impossible.

Analyses

Diversity. Since the three plots varied in size and tree density, total species richness may not convey diversity differences. We corrected for sample size using Fisher's α (Condit *et al.* 1998, Rosenzweig 1995). Using α, we estimated species richness for a fixed number of individuals, in order to compare different dbh categories at all three sites (Condit *et al.* 1998).

Mortality. Criteria for recording death in the field are described in Condit *et al.* (1995) and Condit (1998*b*). Trees recorded as standing dead may in fact not be dead, and a small number were recorded as alive in future censuses. For example, at Cocoli in 1997, 356 trees were recorded as dead. In 1998, 38 of those were found alive again, 19 because the main stem recovered and 19 that sprouted a new stem. When trees were found alive in future censuses, we corrected the prior census, so that the number we tallied as dead in 1997 at Cocoli was $356 - 38 = 318$. Since we have no correction after the final census at a site, mortality rate during the final interval is biased upward relative to previous intervals, but the difference is small.

Mortality was calculated as $[\ln(N) - \ln(S)]/t$, where N is the number alive at the start of a census period, S the number of survivors and t the mean time interval across all N (Condit *et al.* 1995, 1999). The interval for trees that died was based on the date on which their quadrats were visited during the second census (Condit *et al.* 1995). Confidence limits were found with binomial probabilities

(Condit *et al.* 1995, Gelman *et al.* 1995), but here we used exact binomial probabilities in all cases; in the earlier paper, we used normal approximations for large samples.

Growth. Growth was defined as the change in dbh divided by time, excluding cases where the diameter was taken at a different height or on a newly sprouted stem (Paciorek *et al.* 2000). Confidence limits were calculated with *t*-statistics. Growth rates were not normally distributed (closer to gamma-distributed), so we checked the accuracy of parametric confidence limits using bootstrap; in two species at BCI, 1000-replicate bootstrap limits were indistinguishable from limits based on the *t*-distribution. For both mortality and growth, statistically significant differences between estimates were assumed when 95% confidence limits did not overlap.

Errors in growth estimates. Estimates of mean growth can be sensitive to errors in dbh (Condit *et al.* 1993). Consider two sources of error: (1) small discrepancies in remeasurement of the same stem, and (2) large discrepancies because the wrong tree was measured or a digit was dropped. To estimate rates of error, we did a double-blind remeasurement of 1715 trees in 1995 and 2000 (Condit 1998*b*) and fitted the discrepancies with two normal distributions. The first describes small errors and has a standard deviation (SD_1) proportional to dbh; the second has a fixed larger standard deviation (SD_2). The 1715 errors were fitted best with $SD_1 = 0.0062 \times \text{dbh} + 0.904$, $SD_2 = 46.4$, (all units in mm), and 4.8% of the trees subject to the larger error (parameters fitted using the optim function with default settings, in the programming language R, version 1.5.1).

Before estimating growth, we discarded negative increments where the second dbh was 4 SD_1 below the first, since these were most likely due to the second type of error. The same correction cannot be applied to positive outliers, since trees grow. The fastest growing species at BCI, *Trema micrantha* and *Ochroma pyrimidale*, grew by as much as 30–50 mm y^{-1}, with a few valid records as high as 70 mm y^{-1} (valid because successive dbh measures from 1982 to 2000 showed consistently high growth). We thus exclude any record > 75 mm y^{-1} as an error.

If sample sizes are large, outliers should not be eliminated, since they produce overestimates as often as underestimates and will not bias estimates of the mean. We eliminated outliers because in small samples, in uncommon species or larger dbh classes, a single outlier can greatly alter the mean (Condit *et al.* 1993). Whether we eliminate outliers shrinking by 5 mm y^{-1} or 4 standard deviations, or those growing by 25 or 75 mm y^{-1}, has little impact on estimated means.

Bias caused by census interval differences. Since census intervals during the El Niño were only 1 y, while other intervals were 2–5 y, it was important to consider bias associated with time interval. Bias in mortality estimates are trivial for rates and intervals we use, but bias in growth estimates result from discarding outliers where growth was > 75 mm y^{-1}. To see why, consider a tree whose dbh appears to increase by 300 mm due to erroneous measurements. If the interval were 1 y, this tree would be discarded, but if it were 4 y, it would not be. Thus, by eliminating records where growth was >75 mm y^{-1}, we admit higher growth and bias growth estimates upward for longer time intervals. This bias runs counter to the growth trend we found, so our results are robust to it. If negative growth rates were dealt with similarly, for example by eliminating all growth rates less than −5 mm y^{-1} (as in Condit *et al.* 1993, 1999), the resulting bias would tend to overestimate growth in short intervals. This is why we did not discard negative outliers based on time-adjusted growth rates but rather on absolute dbh change.

Population trends. The rate of population change of a species was estimated as $[\ln(N_t) - \ln(N_0)]/t$, where N_0 and N_t are total populations ≥10 mm dbh at the beginning and end of a census interval. The time t was calculated as the arithmetic mean time interval for all N_0 individuals, as for mortality.

Comparison of individual species. Growth of a species was only considered when there were ≥5 individuals, and mortality when there were ≥20 individuals, in each census being compared; we also highlight growth in species with ≥20 individuals in each census, and mortality with ≥50. Ideally, we would have separately compared saplings and adults, but in the Sherman and Cocoli plots, there were very few species with big enough samples of large trees. So comparisons involving those plots were made only for saplings: 10–19 mm dbh for growth rates, 10–99 mm dbh for mortality rates.

RESULTS

Diversity

Fort Sherman had 215 species in the 1996 census in 4.96 ha of mature forest. BCI had 301 in 50 ha in 1995, and Cocoli had 169 species in 4 ha in 1994. The hectare of young forest at Sherman had 14 species not in the mature forest, bringing the total for 5.96 ha at Sherman to 229 species. A total of 443 species were recorded in all three plots during those censuses. Eighteen of these species remain unidentified, that is, they are identifiable morphospecies but we have not been able to match them

Table 2. Stem density, basal area and species richness at Cocoli, BCI and in Sherman old-forest (from the first census at Cocoli and Sherman and the 1995 census at BCI). The last three rows of the table give projected species richness (estimated with Fisher's α per ha) in the given numbers of individuals.

	dbh category	Cocoli 4 ha	Barro Colorado 50 ha	Sherman 4.96 ha
Total individuals (per ha)	≥ 10 mm	2045.8	4581.0	3660.9
	≥ 100 mm	271.0	429.1	511.9
	≥ 300 mm	81.0	82.4	95.4
Basal area (m^2 ha^{-1})	≥ 10 mm	33.1	31.0	30.8
	≥ 100 mm	31.5	27.1	27.2
	≥ 300 mm	26.8	19.6	18.2
Total species	≥ 10 mm	169	301	215
	≥ 100 mm	97	227	122
	≥ 300 mm	38	142	61
Fisher's α (from full plot)	≥ 10 mm	30.1	34.2	34.3
	≥ 100 mm	25.8	35.4	26.7
	≥ 300 mm	11.2	28.5	18.6
Species per ha	≥ 10 mm	114.5	168.8	156.0
(mean of non-overlapping	≥ 100 mm	53.0	90.9	78.0
100 × 100-m squares)	≥ 300 mm	21.0	35.3	30.3
Species per 5000 ind.	≥ 10 mm	138	172	167
Species per 500 ind.	≥ 100 mm	64	96	78
Species per 80 ind.	≥ 300 mm	21	35	28

to herbarium specimens. Just 9 of 255 386 individuals were not matched with one of the 443 morphospecies, all at Sherman. A full list of species and their abundances at Cocoli and Sherman is given in Appendix 1. Condit *et al.* (1996) gives the full list of BCI species.

Diversity was lowest at Cocoli, whether by total species counts or correcting for density with Fisher's α (Table 2). Sherman and BCI were very similar in diversity (Table 2).

Species composition

Of all species ≥ 10 mm dbh, Cocoli and Barro Colorado shared 111 species, Sherman and Barro Colorado shared 126 species, and Sherman and Cocoli shared 47 species. The plots differed more drastically in terms of abundance. For example, not a single one of the top 10 species in abundance at Sherman were among the top 10 at BCI nor at Cocoli, while BCI and Cocoli shared just one of their 10 dominant species (*Faramea occidentalis*). The pattern is similar for basal area dominance, with Cocoli and BCI sharing *Anacardium excelsum* among the 10 species with highest basal area, and neither sharing any species with the top 10 at Sherman. Correlations in log-abundance between sites, including all species present at each site, were very low: $r^2 < 0.01$ for Sherman vs. BCI and Sherman vs. Cocoli, and $r^2 = 0.12$ for BCI vs. Cocoli. If species present at one site but absent at the other were included (using log of abundance plus one), the correlations became negative in all cases.

Community-wide demographic rates

Mortality. Forest-wide mortality was lower at Cocoli than at Sherman or Barro Colorado in most dbh categories, with many differences statistically significant (Table 3, Figure 2a). Barro Colorado and Sherman were similar (Table 3, Figure 2a). All site comparisons were based on the longest intervals available at Cocoli (1994–1998) and Sherman (1996–1999), and the 1995–2000 interval of all 50 ha at BCI.

Growth. For trees with dbh ≥ 150 mm, forest-wide growth paralleled the trend showed by forest-wide mortality: Cocoli was slower growing than either Barro Colorado or Sherman, while the latter two did not differ (Table 4, Figure 2b). At smaller dbh, the trend was quite different, with Cocoli having the fastest growth rate, Sherman next, and Barro Colorado the slowest (Table 4, Figure 2b).

Impact of the 1998 dry season. Cocoli showed an increase in mortality during the 1998 census interval relative to the period just prior, and the change was statistically significant in saplings (Table 3). At Sherman, mortality was lower during 1998, but no difference was significant (Table 3). At BCI, data for 10 species pooled indicated no clear mortality increase during 1998 (Table 3).

The interval of 1998 was associated with high sapling growth (Figure 3): at Cocoli, Sherman and BCI (subsample of 10 species), growth rate was elevated significantly in

Table 3. Forest-wide mortality rates (% y^{-1}) at three sites, in two dbh classes, before and during the El Niño dry season (also after at BCI). At Cocoli, the 1997–98 interval included the El Niño, while at BCI and Sherman, it was the 1998–99 interval. Since the 1998 and 1999 censuses at BCI included just 10 species, mortality rates based on those censuses are for only a subset of the forest; for comparison, the 1995–2000 rates are given for the entire forest. CI are 95% confidence intervals, and N is the number of individuals alive at the start of a census interval.

	10–99 mm dbh			≥ 100 mm dbh		
Site	rate	CI	N	rate	CI	N
Cocoli, 1994–1997	1.34	1.18–1.51	6813	1.23	0.87–1.68	1075
Cocoli, 1997–1998	1.93	1.62–2.27	7055	1.70	1.02–2.66	1068
Cocoli, 1994–1998	1.59	1.44–1.75	6813	1.41	1.08–1.82	1075
BCI, 1995–1998 (10 spp.)	4.17	3.73–4.65	3033	2.51	2.10–2.98	1998
BCI, 1998–1999 (10 spp.)	4.25	3.52–5.10	2614	2.98	2.26–3.86	1807
BCI, 1999–2000 (10 spp.)	3.46	2.81–4.21	2434	3.02	2.34–3.84	1842
BCI, 1995–2000 (10 spp.)	4.31	3.96–4.67	3033	2.78	2.45–3.14	1998
BCI, 1995–2000 (all spp.)	2.81	2.78–2.84	200080	2.10	2.01–2.19	21056
Sherman, 1996–1998	2.72	2.52–2.92	15306	2.22	1.80–2.71	2490
Sherman, 1998–1999	2.31	2.09–2.56	14749	2.03	1.53–2.65	2450
Sherman, 1996–1999	2.69	2.54–2.85	15306	2.27	1.93–2.65	2490

all small dbh categories (Table 4 illustrates with data for 10–19 mm plants, but the significant differences held for dbh up to 50 mm at all sites). At larger dbh, the BCI subsample also showed a significant increase in growth during 1998, while Sherman showed an increase that did not reach significance (Table 4). In contrast, at Cocoli the trend reversed in larger trees, and 1998 growth was lower than growth in the prior interval (Figure 3a). Table 4 gives data for dbh 100–199 mm, where the difference was not quite significant, but for trees ≥ 500 mm at Cocoli, growth prior to 1998 was 8.8 mm y^{-1} while during 1998 it was 5.0 mm y^{-1}; this difference was statistically significant.

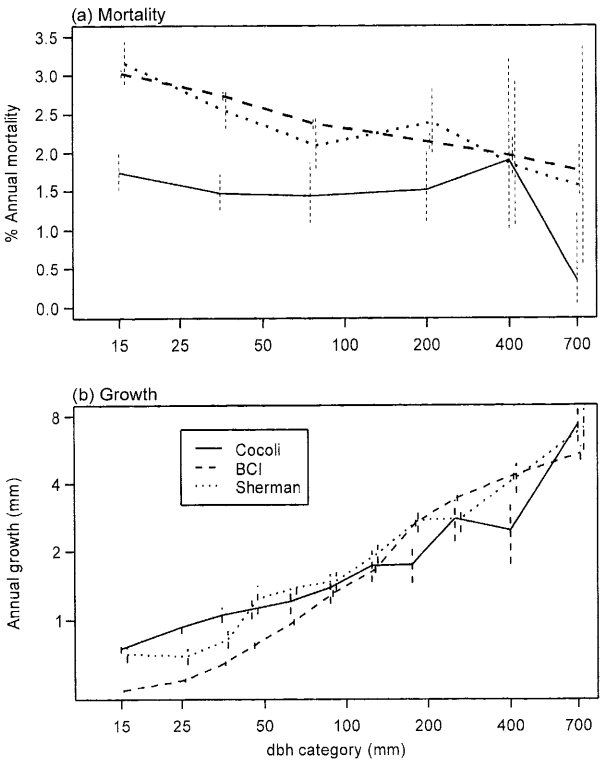

Figure 2. Forest-wide (a) mortality rate (% y^{-1}) and (b) growth rate (mm y^{-1}) at Sherman (1996–1999), Cocoli (1994–1998), and BCI (1995–2000). All species were combined and treated as a single large sample, divided into dbh categories; for mortality, categories are 10–19, 20–49, 50–99, 100–299, 300–499 and ≥ 500 mm; for growth, 10–19, 20–29, 30–39, 40–49, 50–74, 75–99, 100–149, 150–199, 200–299, 300–499 and ≥ 500 mm. Points are plotted above the midpoint of each interval (above 700 for the last). Vertical bars give 95% confidence intervals. The x-axis is log-transformed in both plots, but the y-axis is log-transformed only for growth (because our measure of mortality is already log-transformed).

Demographic rates of individual species

Mortality. Low mortality of saplings at Cocoli relative to BCI and Sherman is evident in rates for individual species (Figure 4a). Of 48 species at Cocoli with at least 20 individuals in the 10–99 mm dbh class, 32 (67% of the species) had mortality < 2% y^{-1}, compared with 48% of 101 Sherman species and 33% of 195 BCI species.

There were 27 species with at least 20 individuals at both Cocoli and BCI. Many had higher mortality at BCI, a few substantially higher (Figure 5a). But there were species whose mortality did not differ between the sites: of the 16 species with more than 50 individuals at both sites, several had very similar mortality at Cocoli and BCI (falling close to the line in Figure 5a). Striking, for instance, was *Swartzia simplex* var. *grandiflora*, which had nearly identical and exceedingly low mortality at both BCI and Cocoli (0.319% y^{-1} at BCI among 2281 individuals, and 0.322% y^{-1} at Cocoli among 154 individuals).

Comparing species common enough at Sherman and Barro Colorado, there was no trend for higher mortality at either site. As in the Cocoli–BCI comparison, there was a group of species clustered close to the line of equal mortality, but in the BCI–Sherman comparison, species far from the line were divided equally above and below (Figure 5b).

Table 4. Forest-wide growth rates (mm y^{-1}) at three sites, in two dbh classes, before, during, and (at BCI only) after the El Niño dry season (see Table 3). CI are 95% confidence intervals, and N is the number of individuals for which mean growth was calculated.

	10–19 mm dbh			100–199 mm dbh		
Site	rate	CI	N	rate	CI	N
Cocoli, 1994–1997	0.73	0.70–0.77	2803	2.09	1.79–2.39	498
Cocoli, 1997–1998	0.96	0.89–1.03	2932	1.70	1.37–1.03	523
Cocoli, 1994–1998	0.75	0.72–0.78	2682	1.74	1.56–1.96	484
BCI, 1995–1998 (10 spp.)	0.54	0.47–0.61	712	2.07	1.82–2.32	644
BCI, 1998–1999 (10 spp.)	0.78	0.69–0.87	589	2.75	2.44–3.05	616
BCI, 1999–2000 (10 spp.)	0.38	0.26–0.50	471	2.58	2.21–2.95	586
BCI, 1995–2000 (10 spp.)	0.67	0.59–0.75	623	2.33	2.09–2.57	589
BCI, 1995–2000 (all spp.)	0.49	0.48–0.49	70732	1.95	1.89–2.01	11864
Sherman, 1996–1998	0.62	0.56–0.68	5230	2.11	1.94–2.29	1405
Sherman, 1998–1999	0.81	0.77–0.84	5080	2.44	2.24–2.64	1369
Sherman, 1996–1999	0.70	0.65–0.76	4935	2.19	2.03–2.35	1307

Sapling mortality rates were significantly, and positively, correlated between sites, with $r^2 = 0.35$ for the Sherman–BCI comparison and $r^2 = 0.39$ for Cocoli–BCI ($P < 0.02$ at both sites). In both regressions, only species with ≥ 50 individuals at both sites were included (21 species for Sherman–BCI, 16 for Cocoli–BCI).

Growth. Site differences in sapling growth were evident in the distribution of rates for individual species, which were displaced slightly upward for Cocoli and downward for BCI (Figure 4b). These differences were also evident when comparing species that occurred at two sites: a majority of species found at both BCI and Cocoli had higher growth at Cocoli, and a majority of species found at BCI and Sherman had higher growth at Sherman (Figure 6). There were clear exceptions, however: individual species with statistically significant differences in growth rates opposite the forest-wide contrast (Figure 6).

Sapling growth rates (log-transformed) were significantly, and positively, correlated between Sherman and BCI, with $r^2 = 0.27$ ($P = 0.03$), but not between Cocoli and BCI (a positive correlation, but $r^2 = 0.14$

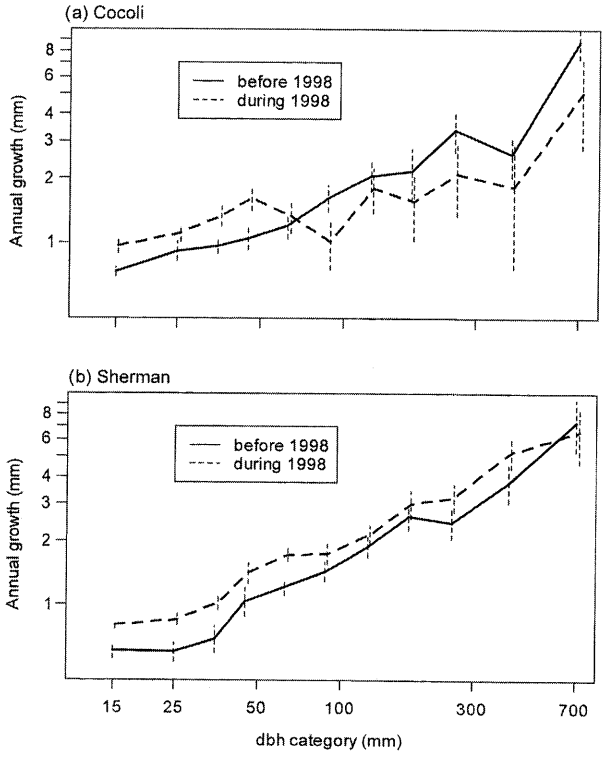

Figure 3. Forest-wide growth rate (mm y^{-1}) at (a) Cocoli and (b) Sherman during two census intervals, 1994–1997 and 1997–1998 at Cocoli, 1996–1997 and 1997–1999 at Sherman. Dbh categories were defined as in Figure 2. Vertical bars show 95% confidence intervals.

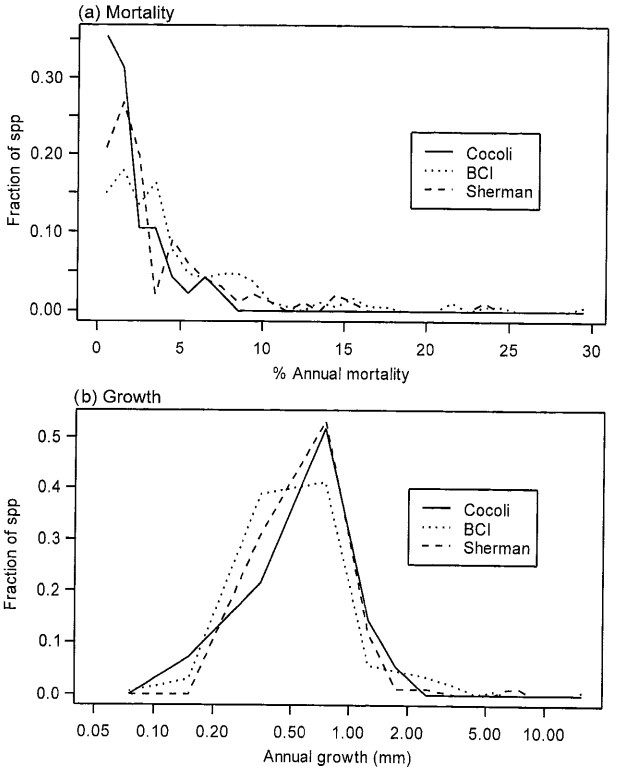

Figure 4. Distribution of (a) mortality (% y^{-1}) in the 10–99 mm dbh category and (b) growth (mm y^{-1}) in the 10–19 mm dbh category, including individual species with large enough samples (≥ 20 individuals for mortality; ≥ 5 individuals for growth).

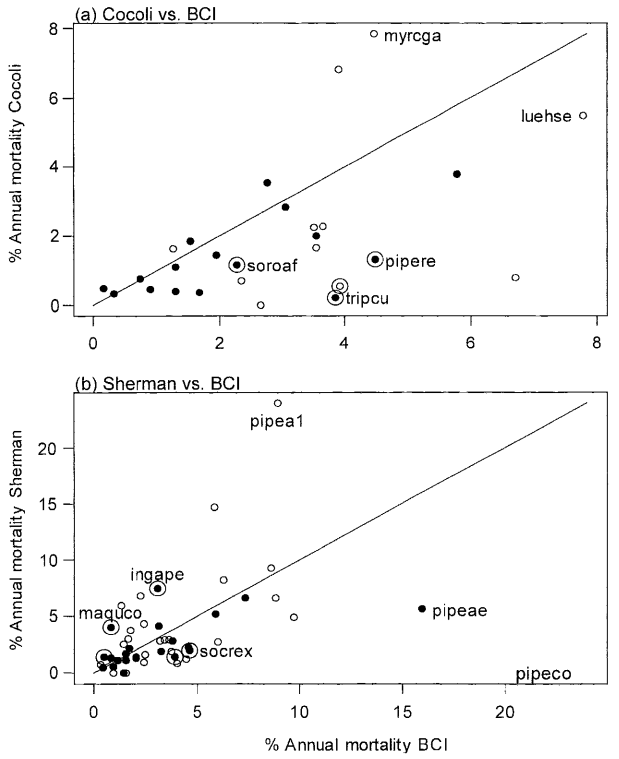

Figure 5. Comparison of sapling mortality (% y^{-1}) of individual species at two sites; (a) Cocoli vs. BCI and (b) Sherman vs. BCI. Each point represents a single species, showing the mortality rate among stems 10–99 mm dbh during 1994–1998 (Cocoli), 1995–2000 (BCI) or 1996–1999 (Sherman). Lines show equal mortality, so points below the line indicate higher BCI mortality. Only species with ≥ 20 individuals at both sites are included, and those with ≥ 50 individuals at both sites are shown with filled dots; circled dots had significant mortality differences. Some of the species are identified with six-letter codes: myrcga = *Myrcia gatunensis*, soroaf = *Sorocea affinis*, tripcu = *Triplaris cumingiani*, pipere = *Piper reticulatum*, luehse = *Luehea seemannii*, maquco = *Maquira guianensis*, ingape = *Inga pezizifera*, pipea1 = *Piper arboreum*, socrex = *Socratea exorrhizae*, pipeae = *Piper aequale* and pipeco = *Piper cordulatum*. There is no point for the latter because it had only 16 individuals at Sherman, but none died and this was significantly lower than mortality at BCI, where mortality was 26% y^{-1}. No other species with < 20 individuals showed a significant difference in mortality.

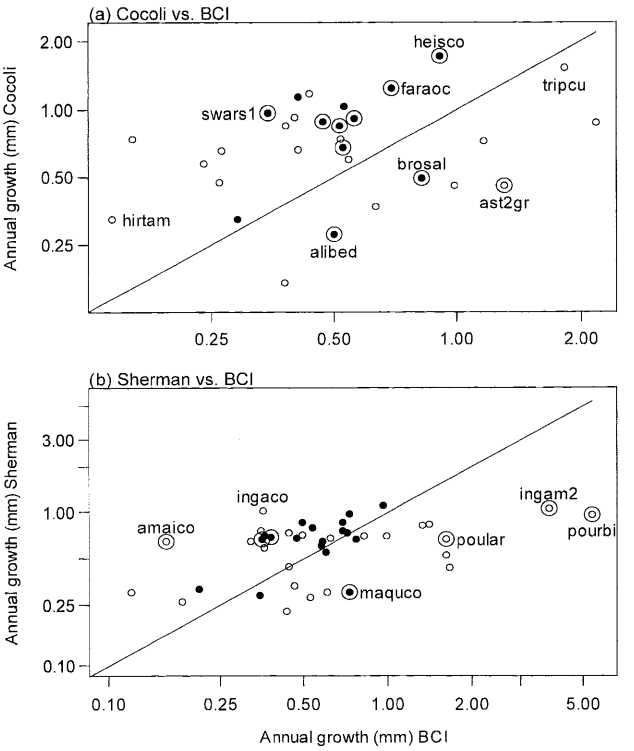

Figure 6. Comparison of sapling growth (mm y^{-1}) of individual species at two sites; (a) Cocoli vs. BCI and (b) Sherman vs. BCI. Each point represents a single species, giving the growth rate among stems 10–19 mm dbh during 1994–1998 (Cocoli), 1995–2000 (BCI) or 1996–1999 (Sherman). Lines show equal growth, so points below the line indicate higher BCI growth. Only species which had ≥ 5 individuals at both sites are included, and those with ≥ 20 individuals at both sites are shown with filled dots. Circled dots had significant growth differences between two plots. Species codes: hirtam = *Hirtella americana*, swars1 = *Swartzia simplex* var. *grandiflora*, faraoc = *Faramea occidentalis*, heisco = *Heisteria concinna*, alibed = *Alibertia edulis*, brosal = *Brosimum alicastrum*, ast2gr = *Astronium graveolens*, amaico = *Amaioua corymbosa*, ingaco = *Inga coclensis*, poular = *Poulsenia armata*, ingam2 = *Inga mucuna* and pourbi = *Pourouma bicolor*; other codes are given with Figure 5. No species with < 5 individuals had a significant difference in growth.

and P = 0.23). Only species with ≥ 20 individuals were included (18 for Sherman–BCI, 12 for Cocoli–BCI).

Population trends. Rates of population change of individual species were positively and significantly correlated ($r^2 = 0.20$ for BCI–Cocoli, $r^2 = 0.34$ for BCI–Sherman). But the BCI–Cocoli correlation was due entirely to *Piper aequale* and *Bactris major*, which had large population reductions at both sites (Figure 7a); without those two, the correlation became negative. For the Sherman–BCI comparison, the correlation remained even after removing the two *Piper* species (Figure 7b).

Impact of the 1998 dry season. No individual species at any of the sites, including the 10 sampled at BCI, showed a significant difference in mortality between census periods in any dbh category. At Cocoli, 19 of 26 species with ≥ 50 individuals at 10–99 mm dbh had higher mortality during 1998 than during the prior period, paralleling the elevated mortality seen forest-wide among saplings there. At Sherman, however, 27 of 41 species had lower mortality during 1998. The five species at BCI targeted because they had greatly elevated mortality during the 1983 drought showed no clear pattern of elevated mortality during 1998. In larger trees, ≥ 100 mm dbh, two of the species did have substantially elevated mortality (*Beilschmiedia* more than double), but *Guatteria* and *Poulsenia* did not (*Acalypha* had no individuals ≥ 100 mm dbh).

In contrast, elevated growth during the El Niño was discernable among individual species at all three sites. At both Sherman and Cocoli, the majority of species had higher sapling growth during the El Niño than during

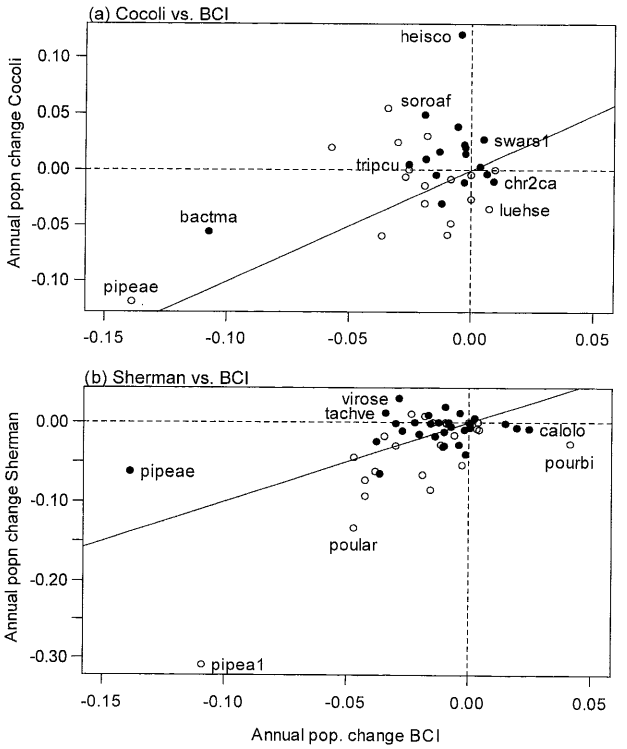

Figure 7. Comparison of population change of individual species at two sites; (a) Cocoli vs. BCI and (b) Sherman vs. BCI. Each point represents a single species, giving the rate of change during 1994–1998 (Cocoli), 1995–2000 (BCI) or 1996–1999 (Sherman). Any species with an initial population ≥ 20 at two different sites is included, and those with $N \geq 50$ at both sites have filled dots. Solid lines show equal rates of change at the two sites; dashed lines are at zero change. Species codes: bactma = *Bactris major*, chr2ca = *Chrysophyllum cainito*, tachve = *Tachigali versicolor*, virose = *Virola sebifera* and calolo = *Calophyllum longifolium*; other codes are identified in Figures 5–6.

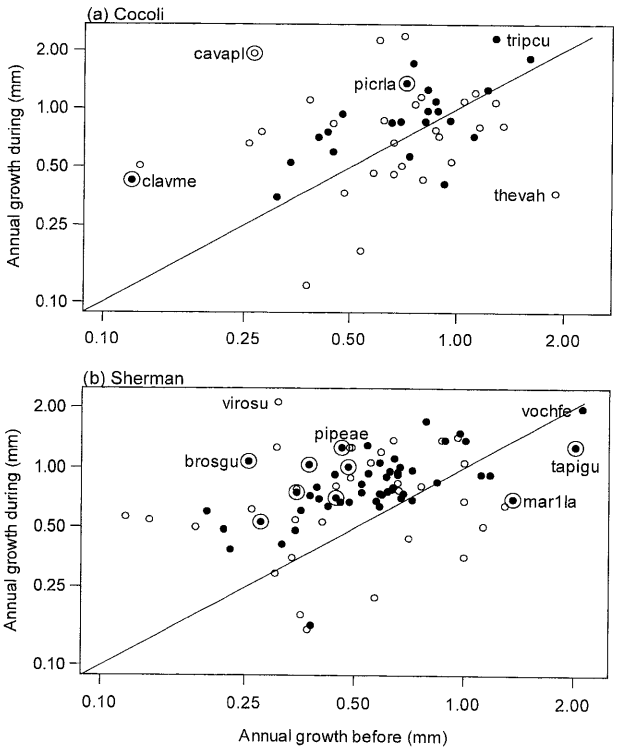

Figure 8. Growth rates at (a) Cocoli and (b) Sherman in the 10–19 mm dbh category, comparing the 1998 El Niño interval with the period before. Lines show equal growth. All species with ≥ 5 individuals are included, and species with ≥ 20 individuals are indicated by filled dots. Circled dots indicate significant differences. Four species were omitted from each graph because mean growth was ≤ 0 and could not be log transformed. Species codes: clavme = *Clavija mezii*, cavapl = *Cavanillesia platanifolia*, picrla = *Picramnia latifolia*, thevah = *Thevetia ahoua*, brosgu = *Brosimum guianense*, virosu = *Virola surinamensis*, marlla = *Marila laxiflora*, tapigu = *Tapirira guianensis* and vochfe = *Vochysia ferruginea*; other codes are identified in Figures 5–7.

the period before, and there were many species where the difference was significant (Figure 8). Growth rates of the 10 BCI species were generally higher during the 1998 El Niño period than during the 2 y before or the 2 y after, in saplings as well as in large trees. Each of the 10 species was divided into four dbh categories (10–19, 20–99, 100–199, ≥ 200 mm), and 6 of 10 species showed their highest growth rate during 1998 in most dbh categories. In three species, growth was significantly highest during 1998 in at least one dbh category, and in no case was El Niño growth significantly lower than growth during the other periods.

Climate and the 1997–98 El Niño

Rainfall during the dry season starting in November, 1997, was much lower than the prior dry seasons at all three sites, and lower than the following dry season at BCI (Table 1). At BCI, the 1997–98 dry season was the second most severe since 1930, with 156 mm; only 1982–83 had less dry-season rain, with 96 mm, and the mean since 1930 was 592 mm. At Sherman, the 1997–98 dry season had 226 mm, the third driest since 1961 and well below the 38-y mean (683 mm). At Cocoli, the 1997–98 dry season was drier than average (196 mm vs. a 19-y average of 278 mm), but not as severe as at BCI.

At Panama City, near Cocoli, mean monthly PAR rose from December 1997, to March 1998, during the El Niño-associated dry season, when values were close to or above 40 mol m^{-2} d^{-1}; no month had mean PAR close to 40 during 1995–1997. The overall mean PAR during the 1998 census interval was >10% higher than during the prior interval (Table 1). At BCI, however, the census interval did not so clearly capture the elevated El Niño PAR – monthly means were low in 1996, rose with the onset of El Niño in mid-1997, were high from December 1997, to March 1998, and remained high in 1998 before

dropping in 1999. Mean PAR during the 1998 census interval was higher than the period before or the period after, but the difference was < 5% (Table 1). At Sherman, PAR was high from December 1997, to April 1998, but data collection only started in September 1997, so we could not compare this with earlier dry seasons.

At BCI, monthly means of daily temperature minima were < 24° in 21 of 24 months during 1995 and 1996, but with the El Niño of 1997, minimum temperatures rose, and every month from July 1997, to July 1998, was >24°. Afterwards, temperatures fell and were again < 24° through 2000. Because the census interval of the 1998 dry season included only part of the warm period, the mean temperature of the 1998 census interval was only slightly higher than it was before or after (Table 1). Sherman likewise had elevated minimum temperatures, from February to June 1998, but data from the prior interval were incomplete (Table 1). Maximum temperature rose with minimum temperatures during the El Niño, at both BCI and Sherman. Unfortunately, temperature data from the Panama City site near Cocoli were missing during several months in 1998.

DISCUSSION

The three sites differed in forest-wide rates of growth and mortality. Most strikingly, Cocoli had low mortality, and it also had low growth among large trees; however, it had the highest sapling growth of the three sites. Sherman and BCI were very similar in all rates except for sapling growth, which was higher at the former. All these differences were manifest among individual species: although there were exceptions, most species at Cocoli had lower mortality than they did at BCI, and likewise for other comparisons.

We designed these studies to examine the climatic gradient across the isthmus of Panama and how it affects forest dynamics, and the climatic differences provide straightforward interpretation for the main differences we observed. Slow turnover and low productivity typify vegetation of dry regions, such as desert (Cody 2000), and tropical dry forests have 50–75% the productivity of wet forests (Murphy & Lugo 1986). At a 50-ha plot in very dry forest in India, overall forest mortality was low, below 1% y^{-1}, and adult growth rates were low (R. Sukumar, *pers. comm.*). Phillips *et al.* (1994) documented the general trend for forest turnover to correlate with precipitation across many sites in South America. Thus, we find it likely that low growth and mortality at Cocoli is – at least partly – due to the drier climate. Greater deciduousness at Cocoli (Condit *et al.* 2000) would limit growth of canopy trees and also explain high sapling growth, since more light reaches the lower levels of the forest when the canopy is deciduous, and few saplings drop leaves (Condit *et al.* 2000). Given lower growth, species must have lower mortality to persist in the forest.

These same interpretations are not supported at Sherman, which is less deciduous than BCI (Condit *et al.* 2000) yet had higher mortality. High sapling growth at Sherman relative to BCI is particularly difficult to explain, given greater deciduousness at BCI. These observations suggest the importance of factors other than climate.

Differences in the state of succession among the sites is one alternative factor that might be relevant to forest dynamics. Cocoli is clearly a successional forest, probably *c.* 100 y since large-scale clearing; both Sherman and BCI are more mature than this. The canopy at Cocoli includes a number of species which are likely to decline in abundance in the future – *Anacardium exelsum*, *Cavanillesia platanifolia*, *Spondias mombin* in particular. Generally, however, early successional species have high mortality and growth, so that the secondary nature of the Cocoli forest seems unlikely to be an explanation for low mortality there.

There are other factors that might influence growth and mortality at the three sites, such as soil nutrient status or the frequency of wind damage. Since Cocoli is drier, it may have fewer severe thunderstorms which cause treefalls than BCI or Sherman. Perhaps Sherman has a richer soil, and this is why saplings grow faster there. We do not have data to test these possibilities. To separate climatic influences from other factors affecting dynamics, we would need additional plots where climate and soils were all known; at this stage, we can only note that Cocoli's low rates of growth and mortality are consistent with expectations based on moisture availability and deciduousness.

Census intervals between late 1997 and early 1999 included the end of the harsh 1997–98 dry season that came at the end of the El Niño event. There was, however, no hint of increased tree mortality at BCI nor at Sherman during the 1998 interval. At BCI, we saw no unusual wilting during March and April 1998, such as was observed in 1983 (Leigh *et al.* 1990), and Engelbrecht *et al.* (2002) found no increase in BCI seedling mortality in 1998 relative to average years. We thus conclude that the 1998 drought, which had more rainfall than the 1983 drought at BCI, was not severe enough to affect tree mortality. At Cocoli, we did observe elevated mortality, but since the 1997–98 dry season at Cocoli was not especially severe (it was wetter than at BCI), it is doubtful that the extra mortality was caused by drought; we do not have alternative hypotheses for the increased mortality during 1998 at Cocoli.

On the other hand, we did find evidence for elevated growth rates during the 1998 census interval. For saplings at Sherman and Cocoli, and for all diameter classes in 10 species at BCI, 1998 growth was higher,

but not so for large trees at Cocoli, which had lower growth during 1998. Impact of the 1997–98 El Niño in central Panama thus contrasted with the impact in South-East Asia, where drought in early 1998 greatly elevated tree mortality and reduced tree growth (Aiba & Kitayama 2002, Nakagawa *et al.* 2000).

Our original hypothesis for increased growth at BCI during the 1983 El Niño was that increased mortality opened the canopy and admitted more light to the understorey, but since we found no increase in mortality at BCI nor at Sherman, this explanation fails in 1998. An alternative hypothesis for the El Niño impact was proposed by Wright *et al.* (1999). Drier weather brings more sunshine, and particularly in the forest understorey (since the canopy layer might be light-saturated), this could lead to relevant increases in PAR. Indeed, the El Niño of 1997–98 produced high PAR, and this was clearest during the long and dry 1997–98 dry season at both Cocoli and BCI (data were incomplete at Sherman). Higher PAR and greater growth during our 1998 census interval is consistent with Wright's insolation hypothesis: since increased sunshine ought to have its greatest impact in the understorey, failure to observe higher growth among large trees at Cocoli during 1998 is not inconsistent with the hypothesis. However, our censuses were designed on the premise that drought would have the biggest impact, and we would have timed them differently to test the cloud-cover hypothesis. Still another possibility, that temperature influences tree growth, could not be addressed with our censuses. The El Niño produced high minimum and maximum temperatures at BCI and Cocoli, particularly during the dry season of 1997–98, but the period of high temperature was divided between two census intervals, and mean temperatures during each interval were nearly identical.

The El Niño impact on growth held for many individual species: a few had significantly higher growth during 1998, many had elevated growth but not significantly, some showed reduced growth but not significantly, and a very few were reduced significantly. Due to sampling error, we cannot specify just how many species were affected by El Niño and how many were not – the results are consistent with the conclusion that nearly every single species was affected, but likewise with the conclusion that some species were affected while others were not. Other studies have found considerable variation in the extent to which species respond to climatic fluctuations (Becker *et al.* 1998, Chapin & Shaver 1985, Graumlich 1993).

When comparing dynamics of different forests, where many species are not shared, trends for the forest as a whole need not parallel trends seen in individual species. For instance, it would be possible for shared species to have identical demography across sites, with forest-wide differences caused entirely by changing species composition. But we found that trends for individual species paralleled forest-wide trends. There were, however, exceptions: species whose demography was opposite to the forest-wide patterns. Moreover, the tendency for mortality and growth rates to shift from site-to-site was mixed with a tendency for individual species' rates at two sites to be correlated. Both results are possible simultaneously because correlations were weak. Site to site variation in demography falls under the concept of the 'site factor' in temperate forestry, but few tropical studies have had sufficient data to incorporate a site factor (but see Vanclay 1994). We do not know of data that address whether individual tree species respond jointly to differences in the site factor in the tropics. In Panama, most did, but some did not.

Mortality rates were most conserved across sites: species occuring at two sites usually had similar rates at each. It was only a minority of species that differed, but in the BCI–Cocoli comparison, the exceptions all tended in the same direction – lower mortality at Cocoli. Growth rates were less conserved than mortality rates, with many species differing substantially between sites; indeed, a substantial majority of species had higher growth at Cocoli relative to BCI.

If mortality and growth rates were identical across sites, then changes in population size would be identical (assuming also identical reproductive rates across sites). But we found at most very weak correlations in rates of population change from site to site: species with expanding populations at one site were often declining at a second site. Evidently, the correlations in growth and mortality were so weak that the overall demographic result – population change – varied widely from site to site. Since we have not measured reproductive rates, we cannot say to what extent site variation in fecundity also contributed to variation in population growth.

Species whose demography varied considerably from site to site offer direct evidence that the forests are not at equilibrium in terms of species composition. Consider *Piper cordulatum*, for instance: at BCI, its mortality rate was 26% y^{-1} and growth 0.18 mm y^{-1}; at Sherman, growth was 0.29 mm y^{-1}, and no plant (of 16) died. The population at BCI was 3708 individuals in 1985, 394 in 1995 and 92 in 2000; at Sherman, it increased from 16 to 20 (Appendix 1). We believe this is one of the drought-sensitive species which has been unable to tolerate the recent spate of harsh dry seasons on BCI (Condit 1998*a*, Condit *et al.* 1996). Apparently, the wetter site at Sherman has not been affected by droughts the way BCI has.

A number of other species showed similar contrasts: *Lacistema aggregatum* was particularly interesting since it occurred in moderate numbers at all three sites (the only species that did), and its demography was different everywhere: mortality at BCI was 4.0% y^{-1}, at Sherman 1.4% y^{-1} and at Cocoli, 0.55% y^{-1}. Its population fell

substantially at BCI, declined by one individual at Sherman, but increased at Cocoli. *Triplaris cumingiana* had mortality at BCI of 3.9% y^{-1}, but only 0.2% y^{-1} at Cocoli, and its population at BCI fell from 294 to 259 but increased at Cocoli from 138 to 141. *Sorocea affinis* had high survival and growth at Cocoli compared with BCI; *Aspidosperma cruenta* had high survival and growth at Sherman relative to BCI; *Maquira guianensis*, in contrast, had high survival and growth at BCI relative to Sherman. In all cases, population changes differed as predicted, with steeper declines at the site with lower survival and growth (Appendix 1; Condit *et al.* 1996). All cases provide evidence that forest composition can change in different directions at nearby sites.

In sum, there were differences in the demography of forests over a short distance in Panama, likely associated with the climatic gradient but also with other, yet unknown, factors. There were fluctuations in demography associated with short-term climatic events, but the 1997–98 El Niño had a weaker impact than the 1983 event: it led to elevated tree growth, but had no effect on mortality. Against a general backdrop of consistent trends, demography of individual species differed between sites, and a few exceptional species even showed trends exactly opposite the rest of the forest. A number of species expanded their population at one site while declining at another site.

In general, sample sizes and time intervals were limiting. The short duration of an El Niño drought presents the problem of measuring a short-term response in species with low mortality and low growth. Changes in demography can only be studied with very large sample sizes (Hall *et al.* 1998), highlighting the need for large-scale plots in the tropics (Condit 1995). Forests change slowly, and observations of how climate affects demography must be long-term. It appears, though, that forests can change in composition even in the short term, and we predict that longer studies will show considerable species turnover where climates are shifting.

ACKNOWLEDGEMENTS

The US Department of Defense Legacy Program supported the census plots at Fort Sherman and Cocoli, both on former US military land, including an award specifically for examining the impact of the 1997–98 El Niño. The BCI plot has been supported by the National Science Foundation, the Smithsonian Scholarly Studies Program, the John D. and Catherine T. MacArthur Foundation, the World Wildlife Fund, the Earthwatch Center for Field Studies, the Geraldine R. Dodge Foundation, and the Alton Jones Foundation. We thank the many field workers who tagged and measured over a third of a million trees, S. Paton and the Environmental Sciences Program of the Smithsonian Tropical Research Institute for the climate data, and the Smithsonian Tropical Research Institute for logistical and financial support. This is a scientific contribution from the Center for Tropical Forest Science.

LITERATURE CITED

AIBA, S.-I. & KITAYAMA, K. 2002. Effects of the 1997–98 El Niño drought on rain forests of Mount Kinabalu, Borneo. *Journal of Tropical Ecology* 18:215–230.

BEARD, J. S. 1944. Climax vegetation in tropical America. *Ecology* 25:127–158.

BECKER, P. & WONG, M. 1993. Drought-induced mortality in tropical heath forest. *Journal of Tropical Forest Science* 5:416–419.

BECKER, P., RABENOLD, P. E., IDOL, J. R. & SMITH, A. P. 1988. Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. *Journal of Tropical Ecology* 4:173–184.

BECKER, P., LYE, O. C. & GOH, F. 1998. Selective drought mortality of dipterocarp trees: no correlation with timber group distributions in Borneo. *Biotropica* 30:666–671.

CAO, K. F. 2000. Water relations and gas exchange of tropical saplings during a prolonged drought in a Bornean heath forest, with reference to root architecture. *Journal of Tropical Ecology* 16:101–116.

CHAPIN, F. S. & SHAVER, G. R. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* 66:564–576.

CODY, M. L. 2000. Slow-motion population dynamics in Mojave Desert perennial plants. *Journal of Vegetation Science* 11:351–358.

CONDIT, R. 1995. Research in large, long-term tropical forest plots. *Trends in Ecology and Evolution* 10:18–22.

CONDIT, R. 1998*a*. Ecological implications of changes in drought patterns: shifts in forest composition in Panama. *Climatic Change* 39:413–427.

CONDIT, R. 1998*b*. *Tropical forest census plots*. Springer-Verlag and R. G. Landes Company, Berlin and Georgetown. 211 pp.

CONDIT, R. In press. Species richness and species ranges estimated from using tree census plots: how accurate are incomplete inventories? In Daly, D. (ed.) *Studies of neotropical flora*. Columbia University Press, New York.

CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 1992. Stability and change of a neotropical moist forest over a decade. *Bioscience* 42:822–828.

CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 1993. Identifying fast-growing native trees from the neotropics using data from a large, permanent census plot. *Forest Ecology and Management* 62:123–143.

CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* 65:419–439.

CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 1996. Changes in a tropical forest with a shifting climate: results from a 50 ha permanent census plot in Panama. *Journal of Tropical Ecology* 12:231–256.

CONDIT, R., FOSTER, R. B., HUBBELL, S. P., SUKUMAR, R., LEIGH, E. G., MANOKARAN, N. & LOO DE LAO, S. 1998. Assessing forest diversity on small plots: calibration using species-individual curves from 50 ha plots. Pp. 247–268 in Dallmeier, F. & Comiskey, J. A. (eds). *Forest biodiversity diversity research, monitoring, and modeling.* UNESCO, the Parthenon Publishing Group, Paris.

CONDIT, R., ASHTON, P. S., MANOKARAN, N., LAFRANKIE, J. V., HUBBELL, S. P. & FOSTER, R. B. 1999. Dynamics of the forest communities at Pasoh and Barro Colorado: comparing two 50 ha plots. *Proceedings of the Royal Society of London* Series B 354:1739–1748.

CONDIT, R., WATTS, K., BOHLMAN, S. A., PÉREZ, R., HUBBELL, S. P. & FOSTER, R. B. 2000. Quantifying the deciduousness of tropical forest canopies under varying climates. *Journal of Vegetation Science* 11:649–658.

CONDIT, R., ROBINSON, W. D., IBÁÑEZ, R., AGUILAR, S., SANJUR, A., MARTÍNEZ, R., STALLARD, R., GARCÍA, T., ANGEHR, G., PETIT, L., WRIGHT, S. J., ROBINSON, T. R. & HECKADON, S. 2001. Maintaining the canal while conserving biodiversity around it: a challenge for economic development in Panama in the 21st century. *Bioscience* 51:135–144.

CONDIT, R., PITMAN, N., LEIGH, E. G., CHAVE, J., TERBORGH, J., FOSTER, R. B., NÚÑEZ, P. V., AGUILAR, S., VALENCIA, R., VILLA, G., MULLER-LANDAU, H., LOSOS, E. & HUBBELL, S. P. 2002. Beta-diversity in tropical forest trees. *Science* 295:666–669.

CROAT, T. R. 1978. *Flora of Barro Colorado Island.* Stanford University Press, Stanford 943 pp.

D'ARCY, W. G. 1987. *Flora of Panama. Part I. Introduction and checklist.* Missouri Botanical Garden, St. Louis. 328 pp.

ENGELBRECHT, B. M. J., WRIGHT, S. J. & DE STEVEN, D. 2002. Survival and ecophysiology of tree seedlings during El Niño drought in a tropical moist forest in Panama. *Journal of Tropical Ecology* 18:569–579.

GELDENHUYS, C. J. 1993. Observations of the effects of drought on evergreen and deciduous species in the eastern Cape forests. *South African Journal of Botany* 59:522–534.

GELMAN, A., CARLIN, J. B., STERN, H. S. & RUBIN, D. B. 1995. *Bayesian data analysis.* Chapman and Hall/CRC, Boca Raton. 526 pp.

GENTRY, A. H. 1982. Patterns of neotropical plant species diversity. *Evolutionary Biology* 15:1–84.

GENTRY, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75:1–34.

GRAUMLICH, L. J. 1993. Response of tree growth to climatic variation in the mixed conifer and deciduous forest of the upper Great Lakes region. *Canadian Journal of Forest Research* 23:133–143.

HALL, P., ASHTON, P. S., CONDIT, R., MANOKARAN, N. & HUBBELL, S. P. 1998. Signal and noise in sampling tropical forest structure and dynamics. Pp. 63–78 in Dallmeier, F. & Comiskey, J. A. (eds). *Forest biodiversity diversity research, monitoring, and modeling.* UNESCO, the Parthenon Publishing Group, Paris.

HARMS, K. E., CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 2001. Habitat associations of trees and shrubs in a neotropical forest. *Journal of Ecology* 89:947–959.

HARRISON, R. D. 2001. Drought and the consequences of El Niño in Borneo: a case study of figs. *Population Ecology* 43:63–75.

HOLDRIDGE, L. R. 1967. *Life zone ecology.* Tropical Science Center, San Jose, Costa Rica. 206 pp.

HUBBELL, S. P. & FOSTER, R. B. 1983. Diversity of canopy trees in a neotropical forest and implications for conservation. Pp. 25–41 in Sutton, S. L., Whitmore, T. C. & Chadwick, A. C. (eds). *Tropical rain forest: ecology and management.* Blackwell Scientific Publications, Oxford.

LAURANCE, W. F., WILLIAMSON, G. B., DELAMÔNICA, P., ALEXANDRE, O., LOVEJOY, T. E., GASCON, C. & POHL, L. 2001. Effects of a strong drought on Amazonian forest fragments and edges. *Journal of Tropical Ecology* 17:771–785.

LEIGH, E. G. 1999. *Tropical forest ecology: a view from Barro Colorado Island.* Oxford University Press, New York. 245 pp.

LEIGH, E. G., WINDSOR, D. M., RAND, A. S. & FOSTER, R. B. 1990. The impact of the "El Niño" drought of 1982–83 on a Panamanian semideciduous forest. Pp. 473–486 in Glynn, P. W. (ed.). *Global ecological consequences of the 1982–83 El Niño-Southern Oscillation.* Elsevier, Amsterdam.

MURPHY, P. G. & LUGO, A. E. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17:67–88.

NAKAGAWA, M., TANAKA, K., NAKASHIZUKA, T., OHKUBO, T., KATO, T., MAEDA, T., SATO, K., MIGUCHI, H., NAGAMASU, H., OGINO, K., TEO, S., HAMID, A. A. & LEE, H. S. 2000. Impact of severe drought associated with the 1997–1998 El Niño in a tropical forest in Sarawak. *Journal of Tropical Ecology* 16:355–367.

NEWBERY, D. M., KENNEDY, D. N., PETOL, G. H., MADANI, L. & RIDSDALE, C. E. 1999. Primary forest dynamics in lowland dipterocarp forest at Danum Valley, Sabah, Malaysia, and the role of the understorey. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 354:1763–1782.

PACIOREK, C. J., CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 2000. The demographics of resprouting in tree and shrub species of a moist tropical forest. *Journal of Ecology* 88:765–777.

PHILLIPS, O. L., HALL, P., GENTRY, A. H., SAWYER, S. A. & VÁSQUEZ, R. 1994. Dynamics and species richness of tropical rain forests. *Proceedings of the National Academy of Sciences* 91:2805–2809.

PIPERNO, D. 1990. Fitolitos, arqueología y cambios prehistóricos de la vegetación en un lote de cincuenta hectáreas de la isla de Barro Colorado. Pp. 153–156 in Leigh, E. G., Rand, A. S. & Windsor, D. M. (eds). *Ecología de un bosque tropical: ciclos estacionales y cambios a largo plaza.* Smithsonian Tropical Research Institute, Balboa, República de Panamá.

PYKE, C. R., CONDIT, R., AGUILAR, S. & LAO, S. 2001. Floristic composition across a climatic gradient in a neotropical lowland forest. *Journal of Vegetation Science* 12:553–566.

ROSENZWEIG, M. L. 1995. *Species diversity in space and time.* Cambridge University Press, Cambridge. 436 pp.

RUBINOFF, I. & LEIGH, E. G. 1990. Dealing with diversity: the Smithsonian Tropical Research Institute and tropical biology. *Trends in Ecology and Evolution* 5:115–118.

SMITH, A. P., HOGAN, K. P. & IDOL, J. R. 1992. Spatial and temporal patterns of light and canopy structure in a lowland moist forest. *Biotropica* 24:503–511.

VANCLAY, J. K. 1994. *Modelling forest growth and yield.* CAB International, Wallingford. 312 pp.

WALSH, R. P. D. 1996. Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics. *Journal of Tropical Ecology* 12:385–407.

WOODS, P. 1989. Effects of logging, drought, and fire on structure and composition of tropical forests in Sabah, Malaysia. *Biotropica* 21:290–298.

WRIGHT, S. J., CARRASCO, C., CALDERON, O. & PATON, S. 1999. The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. *Ecology* 80:1632–1647.

Appendix 1. Abundance of 346 species censused in the Cocoli plot (4 ha) and the old-forest section of the Sherman plot (4.96 ha). Species names match those from Croat (1978) and Condit *et al.* (1996) except when listed in Appendix 2. Unnamed morphospecies are indicated with 'sp' and a number. The final line indicates a few plants which have not been matched with any morphospecies (usually because they were lacking leaves when censused). Families are abbreviated, omitting -aceae. For legumes (family Fabaceae), the subfamily is included (Mimos for Mimosoideae, etc.).

		Cocoli ≥ 10 mm			Cocoli ≥ 100 mm			Sherman ≥ 10 mm			Sherman ≥ 100 mm		
Species	Family	1994	1997	1998	1994	1997	1998	1996	1997	1999	1996	1997	1999
Abarema barbouriana	Fab: Mimos	0	0	0	0	0	0	7	9	9	3	3	3
Acacia melanoceras	Fab: Mimos	23	19	19	0	0	0	0	0	0	0	0	0
Acalypha diversifolia	Euphorbi	14	18	22	0	0	0	9	7	5	0	0	0
Acalypha macrostachya	Euphorbi	1	2	2	0	0	0	0	0	0	0	0	0
Adelia triloba	Euphorbi	5	6	6	1	1	1	0	0	0	0	0	0
Aegiphila panamensis	Verben	2	1	1	0	0	0	0	0	0	0	0	0
Albizia adinocephala	Fab: Mimos	55	53	57	9	6	6	0	0	0	0	0	0
Albizia procera	Fab: Mimos	2	2	2	0	0	0	0	0	0	0	0	0
Alchornea costaricensis	Euphorbi	2	1	1	1	1	1	0	0	0	0	0	0
Alchornea latifolia	Euphorbi	0	0	0	0	0	0	53	50	50	13	15	16
Alchornea sp 3	Euphorbi	0	0	0	0	0	0	9	7	6	4	4	4
Alibertia edulis	Rubi	253	228	224	0	0	0	1	1	1	0	0	0
Alseis blackiana	Rubi	4	4	4	2	3	3	0	0	0	0	0	0
Amaioua corymbosa	Rubi	12	13	13	0	0	0	86	85	86	6	5	5
Anacardium excelsum	Anacardi	128	124	124	125	121	122	0	0	0	0	0	0
Andira inermis	Fab: Papil	16	15	15	14	14	14	40	37	37	10	10	10
Annona hayesii	Annon	109	107	111	0	0	0	0	0	0	0	0	0
Annona purpurea	Annon	4	1	1	4	1	1	0	0	0	0	0	0
Annona spraguei	Annon	5	7	8	5	5	5	1	1	0	1	1	0
Antirhea trichantha	Rubi	87	82	80	63	61	57	0	0	0	0	0	0
Apeiba aspera	Tili	0	0	0	0	0	0	42	35	33	19	19	18
Apeiba tibourbou	Tili	0	0	0	0	0	0	4	4	4	4	4	4
Aphelandra scabra	Acanth	8	6	6	0	0	0	0	0	0	0	0	0
Aphelandra sinclairiana	Acanth	0	0	0	0	0	0	1	1	1	0	0	0
Ardisia bartlettii	Myrsin	0	0	0	0	0	0	48	48	49	0	0	0
Ardisia fendleri	Myrsin	0	0	0	0	0	0	5	4	4	0	0	0
Ardisia guianensis	Myrsin	0	0	0	0	0	0	1	0	0	0	0	0
Ardisia revoluta	Myrsin	3	3	3	2	2	2	0	0	0	0	0	0
Ardisia sp 5	Myrsin	0	0	0	0	0	0	16	16	16	3	3	3
Ardisia sp 6	Myrsin	0	0	0	0	0	0	1	0	0	0	0	0
Aspidosperma cruentum	Apocyn	0	0	0	0	0	0	303	304	308	75	75	75
Astronium graveolens	Anacardi	272	255	260	36	37	36	0	0	0	0	0	0
Attalea butyracea	Arec	35	30	31	35	30	31	0	0	0	0	0	0
Bactris barronis	Arec	12	12	13	0	0	0	36	38	37	0	0	0
Bactris coloniata	Arec	0	0	0	0	0	0	118	107	97	1	0	0
Bactris coloradonis	Arec	1	1	1	0	0	0	40	40	37	0	0	0
Bactris major	Arec	84	68	67	0	0	0	2	2	2	0	0	0
Bactris panamensis	Arec	0	0	0	0	0	0	36	33	29	0	0	0
Banara guianensis	Flacourti	0	1	1	0	0	0	0	0	0	0	0	0
Beilschmiedia pendula	Laur	0	0	0	0	0	0	58	56	58	11	10	10
Brosimum alicastrum	Mor	503	515	533	30	35	36	0	0	0	0	0	0
Brosimum guianense	Mor	0	0	0	0	0	0	157	159	162	21	22	21
Brosimum utile	Mor	0	0	0	0	0	0	308	307	311	157	157	154
Bunchosia odorata	Malpighi	3	3	6	1	1	1	0	0	0	0	0	0
Bursera simaruba	Burser	27	26	23	13	14	11	0	0	0	0	0	0
Byrsonima spicata	Malpighi	0	0	0	0	0	0	4	4	4	2	2	2

Appendix 1. *Continued*

		Cocoli ≥ 10 mm			Cocoli ≥ 100 mm			Sherman ≥ 10 mm			Sherman ≥ 100 mm		
Species	Family	1994	1997	1998	1994	1997	1998	1996	1997	1999	1996	1997	1999
Calophyllum longifolium	Clusi	0	0	0	0	0	0	122	117	119	28	28	28
Calycolpus warszewiczianus	Myrt	1	1	1	1	1	1	0	0	0	0	0	0
Calycophyllum candidissimum	Rubi	161	155	155	96	100	102	0	0	0	0	0	0
Capparis frondosa	Capparid	2	3	3	0	0	0	0	0	0	0	0	0
Carapa guianensis	Meli	0	0	0	0	0	0	113	108	110	20	20	21
Casearia arborea	Flacourti	1	1	1	0	0	0	1	0	0	0	0	0
Casearia arguta	Flacourti	1	1	1	0	0	0	0	0	0	0	0	0
Casearia commersoniana	Flacourti	30	28	27	5	3	3	51	49	51	11	10	11
Casearia guianensis	Flacourti	26	25	26	3	2	2	0	0	0	0	0	0
Casearia sylvestris	Flacourti	15	15	16	0	1	1	19	17	15	8	6	6
Cassia moschata	Fab: Caes	1	1	1	1	1	1	0	0	0	0	0	0
Cassipourea elliptica	Rhizophor	7	7	8	1	1	1	40	39	40	8	7	7
Cavanillesia platanifolia	Bombac	55	56	54	38	36	34	0	0	0	0	0	0
Cecropia insignis	Cecropi	0	0	0	0	0	0	11	9	15	5	5	5
Cecropia longipes	Cecropi	6	8	7	5	1	2	0	0	0	0	0	0
Cecropia obtusifolia	Cecropi	1	9	9	1	0	0	0	0	10	0	0	0
Cecropia peltata	Cecropi	1	3	3	1	0	0	2	1	7	0	0	0
Cedrela odorata	Meli	9	7	7	6	6	6	0	0	0	0	0	0
Cespedezia macrophylla	Ochn	0	0	0	0	0	0	62	60	56	25	25	25
Cestrum megalophyllum	Solan	0	0	0	0	0	0	5	3	3	0	0	0
Chamguava schippii	Myrt	0	0	0	0	0	0	8	7	8	0	0	0
Chlorophora tinctoria	Mor	9	8	9	1	1	1	0	0	0	0	0	0
Chomelia spinosa	Rubi	2	2	1	0	0	0	0	0	0	0	0	0
Chrysophyllum argenteum	Sapot	0	1	1	0	0	0	57	55	52	9	8	8
Chrysophyllum cainito	Sapot	73	69	70	6	5	6	0	0	0	0	0	0
Clavija costaricana	Theophrast	0	0	0	0	0	0	4	4	4	0	0	0
Clavija mezii	Theoprast	171	164	172	0	0	0	0	0	0	0	0	0
Clidemia densiflora	Melastomat	0	0	0	0	0	0	2	1	0	0	0	0
Clidemia sp 1	Melastomat	0	0	0	0	0	0	0	1	1	0	0	0
Coccoloba manzinellensis	Polygon	0	0	0	0	0	0	2	2	2	0	0	0
Coccoloba padiformis	Polygon	55	58	65	4	5	5	3	3	3	1	1	1
Cojoba rufescens	Fab: Mimos	30	20	22	2	3	2	0	0	0	0	0	0
Colubrina glandulosa	Rhamn	2	2	2	2	2	2	0	0	0	0	0	0
Colubrina heteroneura	Rhamn	1	1	1	0	0	0	0	0	0	0	0	0
Conostegia bracteata	Melastomat	0	0	0	0	0	0	45	41	43	0	0	0
Conostegia sp 1	Melastomat	0	0	0	0	0	0	1	0	0	0	0	0
Copaifera aromatica	Fab: Caesal	33	33	35	5	5	5	0	0	0	0	0	0
Cordia alliodora	Boragin	7	4	5	2	1	1	0	0	0	0	0	0
Cordia bicolor	Boragin	0	0	0	0	0	0	41	40	36	19	19	17
Coussarea curvigemmia	Rubi	609	603	616	10	15	13	0	0	0	0	0	0
Cremastosperma panamense	Annon	0	0	0	0	0	0	136	133	138	0	0	0
Crossopetalum parviflorum	Celastr	0	0	0	0	0	0	4	4	6	0	0	0
Cryosophila warscewiczii	Arec	2	3	4	2	2	2	0	0	0	0	0	0
Cupania cinerea	Sapind	1	1	1	0	0	0	0	0	0	0	0	0
Cupania latifolia	Sapind	1	0	0	0	0	0	0	0	0	0	0	0
Cupania rufescens	Sapind	7	8	8	0	0	0	0	0	0	0	0	0
Cupania scrobiculata	Sapind	2	2	0	0	0	0	319	302	317	19	17	17
Cupania sylvatica	Sapind	159	153	157	4	4	3	0	1	1	0	0	0
Cyathea petiolata	Cyathe	0	0	0	0	0	0	1	2	2	0	0	0
Cymbopetalum lanugipetalum	Annon	0	0	0	0	0	0	76	73	71	0	0	0
Dalbergia retusa	Fab: Papil	11	11	11	8	8	8	0	0	0	0	0	0
Dendropanax arboreus	Arali	14	14	15	4	4	4	445	435	425	66	65	67
Desmopsis panamensis	Annon	0	0	0	0	0	0	18	18	17	0	0	0
Diospyros artanthifolia	Eben	0	0	0	0	0	0	50	49	49	6	7	6
Diphysa robinioides	Fab: Papil	2	2	2	1	1	1	0	0	0	0	0	0
Discophora guianensis	Icacin	0	0	0	0	0	0	17	20	20	0	0	0

Appendix 1. *Continued*

Species	Family	Cocoli ≥ 10 mm			Cocoli ≥ 100 mm			Sherman ≥ 10 mm			Sherman ≥ 100 mm		
		1994	1997	1998	1994	1997	1998	1996	1997	1999	1996	1997	1999
Dussia sp 1	Fab: Papil	0	0	0	0	0	0	56	53	54	27	27	27
Elaeis oleifera	Arec	31	30	31	31	30	31	0	0	0	0	0	0
Erythrina costaricensis	Fab: Papil	0	0	0	0	0	0	14	11	11	0	0	0
Erythroxylum citrifolium	Erythroxyl	0	0	0	0	0	0	4	4	4	1	1	1
Erythroxylum macrophyllum	Erythroxyl	0	0	0	0	0	0	16	16	15	0	0	0
Erythroxylum panamense	Erythroxyl	4	3	3	0	0	0	0	0	0	0	0	0
Eugenia coloradoensis	Myrt	20	23	25	3	3	3	5	4	4	0	0	0
Eugenia principium	Myrt	647	710	782	0	0	0	0	0	0	0	0	0
Eugenia salamensis	Myrt	4	4	4	4	4	4	0	0	0	0	0	0
Eugenia sp 5	Myrt	0	0	0	0	0	0	2	2	2	1	1	1
Eugenia sp 6	Myrt	0	0	0	0	0	0	73	71	73	4	3	3
Euterpe precatoria	Arec	0	0	0	0	0	0	144	136	133	4	2	3
Euterpe sp 1	Arec	0	0	0	0	0	0	21	13	13	0	0	0
Faramea luteovirens	Rubi	0	0	0	0	0	0	4	4	4	0	0	0
Faramea multiflora	Rubi	0	0	0	0	0	0	5	5	4	0	0	0
Faramea occidentalis	Rubi	578	607	634	15	16	16	22	21	19	2	1	1
Ficus bullenei	Mor	2	2	2	1	1	1	0	0	0	0	0	0
Ficus citrifolia	Mor	1	1	1	1	1	1	1	0	0	0	0	0
Ficus insipida	Mor	9	8	9	6	6	6	0	0	1	0	0	0
Ficus maxima	Mor	2	2	2	1	1	1	4	4	4	1	1	1
Ficus nymphaeifolia	Mor	0	0	0	0	0	0	1	1	1	0	0	0
Ficus sp 6	Mor	0	0	0	0	0	0	1	0	0	0	0	0
Ficus tonduzii	Mor	0	0	0	0	0	0	3	3	3	1	1	1
Fissicalyx fendleri	Fab: Papil	1	1	1	0	0	0	0	0	0	0	0	0
Garcinia madruno	Clusi	0	0	0	0	0	0	196	193	195	43	41	40
Genipa americana	Rubi	18	18	17	0	0	0	0	0	0	0	0	0
Geonoma congesta	Arec	0	0	0	0	0	0	567	545	537	0	0	0
Geonoma cuneata	Arec	0	0	0	0	0	0	247	233	231	0	0	0
Geonoma deversa	Arec	0	0	0	0	0	0	1	1	1	0	0	0
Geonoma interrupta	Arec	0	0	0	0	0	0	10	7	7	0	0	0
Grias cauliflora	Lecythid	0	0	0	0	0	0	1	1	1	0	0	0
Guarea glabra	Meli	193	177	174	45	44	42	0	0	0	0	0	0
Guarea grandifolia	Meli	1	1	1	0	0	0	1	0	0	0	0	0
Guarea guidonia	Meli	0	0	0	0	0	0	1	1	1	1	1	1
Guarea sp 1	Meli	0	0	0	0	0	0	3	3	4	0	0	0
Guarea sp 2	Meli	0	0	0	0	0	0	49	49	49	5	5	5
Guatteria amplifolia	Annon	0	0	0	0	0	0	52	48	45	1	0	0
Guatteria dumetorum	Annon	0	0	0	0	0	0	178	166	166	54	53	52
Guazuma ulmifolia	Sterculi	2	2	2	1	1	1	0	0	0	0	0	0
Gustavia fosteri	Lecythid	0	0	0	0	0	0	1	1	1	0	0	0
Gustavia superba	Lecythid	0	0	0	0	0	0	6	5	5	2	1	1
Hampea appendiculata	Malv	0	0	0	0	0	0	2	4	5	0	1	1
Heisteria acuminata	Olac	0	0	0	0	0	0	173	171	179	9	8	8
Heisteria concinna	Olac	185	250	302	13	15	15	7	6	6	3	3	3
Henriettea succosa	Melastomat	0	0	0	0	0	0	18	16	15	3	4	4
Herrania pulcherium	Sterculi	0	0	0	0	0	0	18	13	12	0	0	0
Herrania purpurea	Sterculi	0	0	0	0	0	0	3	2	2	0	0	0
Hirtella americana	Chrysobalan	35	36	38	2	2	2	0	0	0	0	0	0
Hirtella racemosa	Chrysobalan	111	107	109	0	0	0	103	101	101	0	0	0
Hirtella triandra	Chrysobalan	0	0	0	0	0	0	6	6	5	0	0	0
Humiriastrum diguense	Humiri	0	0	0	0	0	0	13	13	14	5	5	5
Hymenaea courbaril	Fab: Caesal	5	5	4	1	1	1	0	0	0	0	0	0
Hymenolobium mesoamericanum	Fab: Caesal	0	0	0	0	0	0	11	11	11	1	1	1
Inga cocleensis	Fab: Mimos	0	0	0	0	0	0	45	36	34	7	6	5
Inga goldmanii	Fab: Mimos	0	0	0	0	0	0	11	10	10	2	2	3
Inga laurina	Fab: Mimos	42	37	33	9	10	10	0	0	0	0	0	0
Inga multijuga	Fab: Mimos	0	0	0	0	0	0	38	35	37	9	10	11
Inga nobilis	Fab: Mimos	0	0	0	0	0	0	3	3	2	2	2	2

Appendix 1. *Continued*

		Cocoli ≥ 10 mm			Cocoli ≥ 100 mm			Sherman ≥ 10 mm			Sherman ≥ 100 mm		
Species	Family	1994	1997	1998	1994	1997	1998	1996	1997	1999	1996	1997	1999
Inga pezizifera	Fab: Mimos	0	0	0	0	0	0	259	221	214	63	53	54
Inga punctata	Fab: Mimos	1	2	1	0	0	0	0	0	0	0	0	0
Inga sertulifera	Fab: Mimos	0	0	0	0	0	0	30	31	31	1	1	1
Inga spectabilis	Fab: Mimos	0	0	0	0	0	0	4	4	4	1	1	2
Inga vera	Fab: Mimos	44	36	39	2	1	1	0	0	0	0	0	0
Ixora floribunda	Rubi	93	98	98	3	4	5	0	0	0	0	0	0
Jacaranda caucana	Bignoni	2	2	2	1	1	1	0	0	0	0	0	0
Jacaranda copaia	Bignoni	0	0	0	0	0	0	57	56	55	29	28	28
Jacaratia spinosa	Caric	0	0	0	0	0	0	1	1	1	1	1	1
Lacistema aggregatum	Flacourti	47	49	52	2	2	2	205	200	204	5	4	5
Lacmellea panamensis	Apocyn	0	0	0	0	0	0	57	54	52	11	10	9
Laetia procera	Flacourti	0	0	0	0	0	0	3	3	3	1	1	1
Lafoensia punicifolia	Lythr	1	1	1	0	0	0	0	0	0	0	0	0
Leandra granatensis	Melastomat	0	0	0	0	0	0	2	2	1	0	0	0
Licania hypoleuca	Chrysobalan	0	0	0	0	0	0	78	78	80	15	15	14
Lindackeria laurina	Flacourti	1	1	1	0	0	0	0	0	0	0	0	0
Lonchocarpus latifolius	Fab: Papil	2	2	2	0	0	0	11	10	9	3	2	3
Lopimia dasypetala	Malv	2	2	2	0	0	0	0	0	0	0	0	0
Lozania pittieri	Flacourti	0	0	0	0	0	0	120	100	102	6	6	6
Luehea seemannii	Tili	23	19	20	2	4	4	0	0	0	0	0	0
Luehea speciosa	Tili	2	1	1	1	1	1	0	0	0	0	0	0
Macrocnemum roseum	Rubi	39	37	38	5	7	7	0	0	0	0	0	0
Mangifera indica	Anacardi	3	3	3	1	1	1	0	0	0	0	0	0
Manilkara bidentata	Sapot	0	0	0	0	0	0	245	250	258	61	59	60
Maquira guianensis	Mor	0	0	0	0	0	0	87	76	80	14	11	11
Maranthes panamensis	Chrysobalan	0	0	0	0	0	0	159	155	161	18	17	18
Margaritaria nobilis	Euphorbi	5	6	5	0	0	0	0	0	0	0	0	0
Marila laxiflora	Clusi	0	0	0	0	0	0	473	458	471	125	130	133
Matayba apetala	Sapind	0	0	0	0	0	0	166	159	166	14	15	15
Matayba glaberrima	Sapind	5	5	4	1	1	1	0	0	0	0	0	0
Maytenus schippii	Celastr	0	0	0	0	0	0	11	12	12	1	1	1
Meliosma glabrata	Sabi	0	0	0	0	0	0	13	11	12	3	3	3
Miconia affinis	Melastomat	0	0	0	0	0	0	26	25	26	0	1	1
Miconia argentea	Melastomat	4	4	4	0	0	0	0	0	0	0	0	0
Miconia elata	Melastomat	0	0	0	0	0	0	32	30	26	1	1	1
Miconia impetiolaris	Melastomat	3	3	5	0	0	0	0	0	0	0	0	0
Miconia ligulata	Melastomat	0	0	0	0	0	0	242	214	214	0	0	1
Miconia minutiflora	Melastomat	2	3	2	0	0	0	15	13	11	8	8	7
Miconia multispicata	Melastomat	0	0	0	0	0	0	7	4	4	0	0	0
Miconia nervosa	Melastomat	0	0	0	0	0	0	13	12	12	0	0	0
Miconia prasina	Melastomat	0	0	0	0	0	0	1	1	2	0	0	0
Miconia serrulata	Melastomat	0	0	0	0	0	0	10	9	7	0	0	0
Miconia simplex	Melastomat	0	0	0	0	0	0	225	219	223	0	0	0
Miconia sp 3	Melastomat	0	0	0	0	0	0	73	71	69	2	1	1
Miconia sp 5	Melastomat	0	0	0	0	0	0	1	1	2	1	1	1
Mollinedia darienensis	Monimi	0	0	0	0	0	0	159	153	159	0	0	0
Mortoniodendron anisophyllum	Tili	0	0	0	0	0	0	56	51	50	20	20	21
Mosannona garwoodii	Annon	0	0	0	0	0	0	2	2	2	1	1	1
Mouriri myrtilloides	Melastomat	0	0	0	0	0	0	42	41	43	0	0	0
Myrcia gatunensis	Myrt	34	31	28	0	1	1	79	77	79	20	17	16
Myrcia zetekiana	Myrt	0	0	0	0	0	0	49	48	47	0	0	0
Myrciaria sp 2	Myrt	0	0	0	0	0	0	20	20	20	5	5	5
Myriocarpa longipes	Urtic	2	1	1	1	1	1	0	0	0	0	0	0
Myrospermum frutescens	Fab: Papil	1	0	0	0	0	0	0	0	0	0	0	0
Nectandra lineata	Laur	3	3	3	1	1	1	0	0	0	0	0	0
Nectandra martinicensis	Laur	26	30	37	1	1	2	0	0	0	0	0	0
Nectandra purpurea	Laur	0	0	0	0	0	0	134	122	130	15	16	16
Neea amplifolia	Nyctagin	0	0	0	0	0	0	46	46	45	0	0	0
Neea delicatula	Nyctagin	38	38	40	3	3	3	0	0	1	0	0	0
Neea sp 2	Nyctagin	1	1	1	1	1	1	0	0	0	0	0	0

Appendix 1. *Continued*

Species	Family	Cocoli ≥ 10 mm			Cocoli ≥ 100 mm			Sherman ≥ 10 mm			Sherman ≥ 100 mm		
		1994	1997	1998	1994	1997	1998	1996	1997	1999	1996	1997	1999
Ochroma pyramidale	Bombac	1	2	2	1	1	1	0	0	2	0	0	0
Ocotea dendrodaphne	Laur	0	0	0	0	0	0	139	124	116	18	17	15
Ocotea ira	Laur	0	0	0	0	0	0	67	66	67	23	26	28
Ocotea puberula	Laur	0	0	0	0	0	0	4	4	3	0	0	0
Ocotea rubrinervis	Laur	14	13	14	0	0	0	0	0	0	0	0	0
Ocotea sp 5	Laur	0	0	0	0	0	0	3	2	1	0	0	0
Ocotea whitei	Laur	0	0	0	0	0	0	2	2	2	1	1	1
Oenocarpus mapora	Arec	3	3	3	0	0	0	256	251	249	56	60	58
Ormosia coccinea	Fab: Papil	0	0	0	0	0	0	14	12	13	3	3	2
Ormosia macrocalyx	Fab: Papil	15	16	17	2	2	2	0	0	0	0	0	0
Ouratea cocleensis	Ochn	0	0	0	0	0	0	39	38	37	0	0	0
Ouratea lucens	Ochn	70	70	76	0	0	0	0	0	0	0	0	0
Oxandra longipetala	Annon	0	0	0	0	0	0	33	33	33	0	0	0
Pachira quinata	Bombac	1	1	1	1	1	1	0	0	0	0	0	0
Pachira sessilis	Bombac	6	6	6	1	1	1	0	0	0	0	0	0
Palicourea guianensis	Rubi	3	3	2	0	0	0	8	5	4	0	0	0
Pentagonia macrophylla	Rubi	0	0	0	0	0	0	38	34	32	0	0	0
Pera arborea	Euphorbi	0	0	0	0	0	0	137	133	136	33	32	35
Perebea xanthochyma	Mor	0	0	0	0	0	0	743	709	707	103	105	105
Phoebe cinnamomifolia	Laur	5	5	5	1	0	0	13	12	11	1	1	1
Phyllanthus acuminatus	Euphorbi	0	0	0	0	0	0	1	1	1	0	0	0
Picramnia latifolia	Picramni	86	86	92	0	1	1	1	1	1	0	0	0
Piper aequale	Piper	21	15	13	0	0	0	66	58	56	0	0	0
Piper arboreum	Piper	6	7	5	0	0	0	28	15	12	0	0	0
Piper augustum	Piper	0	0	0	0	0	0	25	24	21	0	0	0
Piper colonense	Piper	0	0	0	0	0	0	1	0	1	0	0	0
Piper cordulatum	Piper	1	1	1	0	0	0	16	15	20	0	0	0
Piper culebranum	Piper	4	5	4	0	0	0	0	0	0	0	0	0
Piper grande	Piper	1	0	0	0	0	0	0	0	0	0	0	0
Piper hispidum	Piper	1	1	1	0	0	0	0	0	0	0	0	0
Piper reticulatum	Piper	181	175	178	0	1	1	0	0	0	0	0	0
Piper sp 5	Piper	0	0	0	0	0	0	0	0	1	0	0	0
Posoqueria latifolia	Rubi	148	150	154	16	17	19	5	5	5	0	0	0
Poulsenia armata	Mor	0	0	0	0	0	0	31	23	22	11	9	9
Pourouma bicolor	Cecropi	0	0	0	0	0	0	102	97	94	28	30	30
Pouteria campechiana	Sapot	51	48	45	13	13	13	0	0	0	0	0	0
Pouteria reticulata	Sapot	0	0	0	0	0	0	25	25	23	10	9	9
Pouteria sp 4	Sapot	0	0	0	0	0	0	1	1	1	0	0	0
Prockia crucis	Flacourti	2	1	1	0	0	0	0	0	0	0	0	0
Protium glabrum	Burser	0	0	0	0	0	0	55	46	42	0	0	0
Protium panamense	Burser	0	0	0	0	0	0	1063	1028	1046	96	97	97
Protium tenuifolium	Burser	593	643	694	35	37	38	2	2	2	0	0	0
Pseudobombax septenatum	Bombac	14	11	12	9	8	9	0	0	0	0	0	0
Pseudolmedia spuria	Mor	0	0	0	0	0	0	6	6	6	0	0	0
Psychotria acuminata	Rubi	0	1	1	0	0	0	0	0	0	0	0	0
Psychotria chagrensis	Rubi	0	0	0	0	0	0	6	4	5	0	0	0
Psychotria deflexa	Rubi	0	0	0	0	0	0	2	1	1	0	0	0
Psychotria elata	Rubi	0	0	0	0	0	0	34	29	26	0	0	0
Psychotria erecta	Rubi	0	0	0	0	0	0	6	5	8	0	0	0
Psychotria grandis	Rubi	8	7	7	0	0	0	0	0	0	0	0	0
Psychotria horizontalis	Rubi	5	5	7	0	0	0	0	0	0	0	0	0
Psychotria marginata	Rubi	0	0	1	0	0	0	0	0	0	0	0	0
Psychotria poeppigiana	Rubi	0	0	0	0	0	0	2	2	2	0	0	0
Psychotria suerrensis	Rubi	0	0	0	0	0	0	202	176	184	0	0	0
Pterocarpus rohrii	Fab: Papil	0	0	0	0	0	0	1	1	1	1	1	1
Quiina schippii	Quiin	0	0	0	0	0	0	79	76	78	4	4	4
Randia armata	Rubi	0	0	0	0	0	0	3	3	3	0	0	0
Rauvolfia littoralis	Apocyn	6	5	5	2	2	2	0	0	0	0	0	0
Rinorea lindeniana	Viol	75	75	79	0	0	0	0	0	0	0	0	0
Rosenbergiodendron formosum	Rubi	17	17	17	0	0	0	0	0	0	0	0	0
Sapindus saponaria	Sapind	3	3	3	1	1	1	0	0	0	0	0	0

Appendix 1. *Continued*

Species	Family	Cocoli ≥ 10 mm			Cocoli ≥ 100 mm			Sherman ≥ 10 mm			Sherman ≥ 100 mm		
		1994	1997	1998	1994	1997	1998	1996	1997	1999	1996	1997	1999
Sapium sp 1	Euphorbi	0	0	0	0	0	0	3	3	3	3	3	3
Saurauia yasicae	Actinidi	0	0	0	0	0	0	12	9	9	5	3	3
Schefflera morototoni	Arali	1	1	2	0	0	0	8	6	6	5	5	5
Senna dariensis	Fab: Caesal	1	1	1	0	0	0	0	0	0	0	0	0
Simarouba amara	Simaroub	0	0	0	0	0	0	107	102	95	44	40	39
Siparuna pauciflora	Monimi	2	3	3	0	0	0	1	1	1	0	0	0
Sloanea sp aff *meianthera*	Elaeocarp	0	0	0	0	0	0	123	116	116	41	41	40
Sloanea terniflora	Elaeocarp	36	35	34	2	2	2	1	1	1	1	1	1
Socratea exorrhiza	Arec	0	0	0	0	0	0	566	536	564	274	261	281
Solanum extensum	Solan	0	1	1	0	0	0	0	0	0	0	0	0
Solanum hayesii	Solan	0	2	1	0	0	0	0	0	0	0	0	0
Sorocea affinis	Mor	460	512	562	1	1	1	36	30	30	0	0	0
Spondias mombin	Anacardi	17	16	15	15	14	13	0	0	0	0	0	0
Spondias radlkoferi	Anacardi	7	12	9	2	2	2	1	1	1	0	0	0
Stemmadenia grandiflora	Apocyn	8	7	7	3	3	3	0	0	0	0	0	0
Sterculia apetala	Sterculi	12	12	13	2	2	2	0	0	0	0	0	0
Stylogyne standleyi	Myrsin	38	36	30	0	0	0	0	0	0	0	0	0
Swartzia simplex var *grandiflora*	Fab: Caesal	193	198	216	36	37	38	1	1	1	0	0	0
Swartzia simplex var *ochnacea*	Fab: Caesal	6	6	6	3	3	3	258	248	253	0	0	0
Swietenia macrophylla	Meli	4	4	4	1	1	1	0	0	0	0	0	0
Symphonia globulifera	Clusi	0	0	0	0	0	0	122	125	129	11	11	11
Synechanthus warscewiczianus	Arec	0	0	0	0	0	0	403	384	357	0	0	0
Tabebuia rosea	Bignoni	19	19	19	3	3	3	0	0	0	0	0	0
Tabernaemontana arborea	Apocyn	0	0	0	0	0	0	24	24	24	7	7	7
Tachigali versicolor	Fab: Caesal	0	0	0	0	0	0	443	436	459	8	9	9
Tapirira guianensis	Anacardi	0	0	0	0	0	0	571	545	558	113	112	117
Terminalia amazonia	Combret	2	2	2	1	1	1	5	5	5	3	3	3
Terminalia oblonga	Combret	3	4	4	1	1	1	0	0	0	0	0	0
Ternstroemia tepezapote	The	1	0	0	0	0	0	0	0	0	0	0	0
Tetrathylacium johansenii	Flacourti	3	3	3	1	1	1	0	0	0	0	0	0
Tetrorchidium gorgonae	Euphorbi	0	0	0	0	0	0	32	30	30	17	17	17
Theobroma bernoullii	Sterculi	0	0	0	0	0	0	127	125	124	56	59	56
Thevetia ahouai	Apocyn	23	22	23	0	0	0	0	0	0	0	0	0
Tocoyena pittieri	Rubi	0	0	0	0	0	0	22	22	22	10	11	10
Tovomita longifolia	Clusi	0	0	0	0	0	0	1253	1239	1256	123	129	129
Tovomita stylosa	Clusi	0	0	0	0	0	0	809	806	813	5	5	5
Trattinnickia aspera	Burser	0	0	0	0	0	0	22	21	21	9	10	10
Trichilia hirta	Meli	14	13	13	13	12	12	0	0	0	0	0	0
Trichilia martiana	Meli	12	10	13	0	0	0	0	0	0	0	0	0
Trichilia pleeana	Meli	315	301	297	184	182	179	0	0	0	0	0	0
Trichilia tuberculata	Meli	1	1	2	0	0	0	12	12	12	3	3	3
Trichospermum galeottii	Tili	2	5	5	0	1	1	2	1	1	2	1	1
Triplaris cumingiana	Polygon	138	138	141	17	19	20	0	0	0	0	0	0
Trophis racemosa	Mor	30	31	34	0	0	0	0	0	0	0	0	0
Turnera panamensis	Turner	5	6	6	0	0	0	0	0	0	0	0	0
Turpinia occidentalis	Staphyle	0	0	0	0	0	0	1	1	1	1	1	1
Unonopsis panamensis	Annon	0	0	0	0	0	0	482	475	480	5	5	5
Vantanea depleta	Humiri	0	0	0	0	0	0	27	26	26	12	13	13
Vernonanthura patens	Aster	0	1	0	0	0	0	0	0	0	0	0	0
Virola elongata	Myristic	0	0	0	0	0	0	213	214	222	35	33	33
Virola multiflora	Myristic	0	0	0	0	0	0	124	120	124	36	31	33
Virola sebifera	Myristic	0	0	0	0	0	0	213	223	233	43	42	42
Virola surinamensis	Myristic	0	0	0	0	0	0	33	31	34	7	6	6
Vismia baccifera	Clusi	0	0	0	0	0	0	13	9	10	0	0	0
Vismia macrophylla	Clusi	0	0	0	0	0	0	8	6	6	5	4	4
Vitex cooperi	Verben	6	6	6	3	3	3	0	0	0	0	0	0
Vochysia ferruginea	Vochysi	0	0	0	0	0	0	121	115	115	55	51	49

Appendix 1. *Continued*

Species	Family	Cocoli ≥ 10 mm			Cocoli ≥ 100 mm			Sherman ≥ 10 mm			Sherman ≥ 100 mm		
		1994	1997	1998	1994	1997	1998	1996	1997	1999	1996	1997	1999
Xylopia frutescens	Annon	5	4	4	2	2	2	0	0	0	0	0	0
Xylopia macrantha	Annon	0	0	0	0	0	0	298	290	297	22	22	22
Zanthoxylum juniperinum	Rut	1	1	1	0	0	0	1	1	1	0	0	0
Zanthoxylum panamense	Rut	1	1	1	0	0	0	0	0	0	0	0	0
Zuelania guidonia	Flacourti	15	12	11	4	3	3	0	0	0	0	0	0
Unidentified sp 2		1	0	0	0	0	0	0	0	0	0	0	0
Unidentified sp 1	Annon	3	3	3	0	0	0	0	0	0	0	0	0
Unidentified		0	0	0	0	0	0	7	2	6	2	1	1

Appendix 2. Tree species whose names have changed since Croat (1978), D'Arcy (1987) or Condit *et al.* (1996), with authorities for each. For completeness, we include names already changed in Condit *et al.* (1996) and which have not changed since; these are marked with asterisks. In all but one of the names listed here, each row refers to a group of plants which – in our plots – refer to a single well-defined morphospecies, and only the name changed (usually due to taxonomic revision of several species within a given genus, although some are simply spelling errors). The one more complicated case is in *Dendropanax*, where we used to separate two forms which we called *D. arboreus* and *D. stenodontus*; however, *D. stenodontus* is no longer considered a valid name, and we have decided that all of our *Dendropanax* fall within *D. arboreus*.

Current name	Condit *et al.* (1996) name	D'Arcy (1987) name	Croat (1978) name
Abarema barbouriana (Standl.) Barneby & J. W. Grimes	*Pithecellobium barbouriana*	*P. barbouriana*	*P. barbouriana*
Apeiba aspera Aubl.	*A. membranacea*	*A. membranacea*	*A. membranacea*
Aspidosperma cruentum Woods.	*A. cruenta*	*A. cruenta*	*A. cruenta*
Attalea butyracea (Mutis ex L. f.) Wess. Boer.	*Scheelea zonensis*	*S. zonensis*	*S. zonensis*
**Chamguava schippii* (Standl.) Landrum	*C. schippii*	*Psidium anglohondurense*	*P. anglohondurense*
Chlorophora tinctoria (L.) Gaudich.	*Maclura tinctoria*	*C. tinctoria*	
**Chrysochlamys eclipes* L. O. Wms.	*C. eclipes*	*Tovomitopsis nicaraguensis*	*T. nicaraguensis*
**Chrysophyllum argenteum* Jacq.	*Chrysophyllum argenteum*	*Cynodendron panamense*	*Cynodendron panamense*
Clavija costaricana Pittier		*Clavija costaricense*	
Coccoloba manzinellensis Beurl.	*C. manzanillensis*	*C. manzanillensis*	*C. manzanillensis*
Cojoba rufescens (Benth.) Britton & Rose	*Pithecellobium rufescens*	*P. rufescens*	*P. rufescens*
Cyathea petiolata (Hook.) R. M. Tryon	*Cnemidaria petiolata*		*Cnemidaria petiolata*
Dendropanax arboreus (L.) Dec. & Planch	*D. stenodontus, D. arboreus*	both names appear	both names appear
**Erythroxylum macrophyllum* Turcz.	*E. macrophyllum*	*E. macrophyllum*	*E. multiflorum*
Eugenia coloradoensis Standl.	*E. coloradensis*	*E. coloradensis*	*E. coloradensis*
Faramea multiflora A. Rich. ex DC.		*F. talamancarum*	
Ficus nymphaeifolia Mill.		*F. nymphaeaefolia*	*F. nymphiifolia*
**Garcinia intermedia* (Pittier) Hammel	*G. intermedia*	*Rheedia edulis*	*R. edulis*
**Garcinia madruno* (H. B. K.) Hammel	*G. madruno*	*Rheedia acuminata*	*R. acuminata*
Grias cauliflora L.		*G. cauliflora*	*G. fendleri*
**Guarea grandifolia* DC.	*G. grandifolia*	*Guarea grandifolia*	*G. multiflora*
**Guarea guidonia* (L.) Sleumer	*G. guidonia*	*Guarea guidonia*	*G. glabra*
Guarea sp 1	*G.* sp. nov.		
**Heisteria acuminata* (Humb. & Bonpl.) Engl.	*H. acuminata*	*H. acuminata*	*H. longipes*
**Hyeronima alchorneoides* Allemao	*H. alchorneoides*	both names appear	*H. laxiflora*
Inga laurina (Sw.) Willd.	*I. fagifolia*	*I. fagifolia*	*I. fagifolia*
Inga nobilis Willd.	*I. quaternata*	*I. quaternata*	*I. quaternata*
Lonchocarpus latifolius Kunth	*L. latifolia*	*L. pentaphylla*	*L. pentaphylla*
**Lopimia dasypetala* (Turcz.) Standl.	*L. dasypetala*	*L. dasypetala*	*Pavonia dasypetala*
Macrocnemum roseum (Ruiz & Pav.) Wedd.	*M. glabrescens*	*M. glabrescens*	*M. glabrescens*
Maquira guianensis (Standl.) C. C. Berg	*M. costaricana*	*M. costaricana*	*M. costaricana*
Miconia minutiflora (Bonpl.) DC.		*M. minutiflora*	*M. borealis*
Myriocarpa longipes Liebm.		*M. longipes*	*M. yzabelensis*
Nectandra lineata (Kunth) Rohwer	*N. globosa*	*N. globosa*	*N. globosa*
**Nectandra purpurea* (Ruiz & Pav.)Mez	*N. purpurea*	*N. purpurea*	*N. purpurascens*
**Ocotea puberula* (Rich.) Nees	*O. puberula*	*O. puberula*	*O. pyrimidata*
Ormosia coccinea (Aubl.) Jacks.	*O. croatii*	*O. coccinea*	*O. coccinea*
Pachira quinata (Jacq.) W. S. Alverson	*Pochota quinata*	*Bombacopsis quinata*	*B. quinata*
Pachira sessilis Benth.	*Pochota sessilis*	*Bombacopsis sessilis*	*B. sessilis*
**Pourouma bicolor* Mart.	*P. bicolor*	*P. guianensis*	*P. guianensis*
Pseudosamanea guachapele (Kunth) Harms		*Albizia guachapele*	*A. guachapele*
Psychotria poeppigiana Müll. Arg.		*Cephaelis tomentosa*	*C. tomentosa*
Rosenbergiodendron formosum (Jacq.) Fagerl.	*Randia formosa*	*Randia formosa*	*Randia formosa*
Sapium sp 1	*S.*sp. nov.		
Saurauia yasicae Loes.		*S. laevigata*	*S. laevigata*
**Schefflera morototoni* (Aubl.) Maguire, Stey. & Frod.	*S. morototoni*	*Didymopanax morototoni*	*D. morototoni*
Schizolobium parahyba (Vell.) S. F. Blake	*S. parahybum*	*S. parahybum*	*S. parahybum*
**Senna dariensis* (Britton & Rose) H. S. Irwin & Barneby	*S. dariensis*	*S. dariensis*	*Cassia fruticosa*
**Terminalia oblonga* (R. & P.) Steud.	*T. oblonga*	*T. oblonga*	*T. chiriquensis*
Trichilia martiana C. DC.		*T. tomentosa*	*T. tomentosa*
**Trichilia tuberculata* (Triana & Planch.) C. DC.	*T. tuberculata*	*T. tuberculata*	*T. cipo*
**Trichospermum galeottii* (Turcz.) Kosterm.	*T. galeottii*	*T. galeottii*	*T. mexicanum*
Vantanea depleta McPherson		*V. occidentalis*	*V. occidentalis*
Vernonanthura patens (H. B. K.) H. Robinson		*Vernonia patens*	*Vernonia patens*
Virola multiflora (Standl.) A. C. Sm.	*Virola* sp. nov.		
Zanthoxylum ekmanii (Urb.) Alain	*Z. belizense*	*Z. belizense*	*Z. belizense*
Zanthoxylum juniperinum Poepp.	*Z. procerum*	*Z. procerum*	*Z. procerum*