

Dynamics of the forest communities at Pasoh and Barro Colorado: comparing two 50-ha plots

Richard Condit^{1*}, Peter S. Ashton², N. Manokaran³, James V. LaFrankie⁴, Stephen P. Hubbell^{1,5} and Robin B. Foster^{1,6}

¹Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Unit 0948, APO, AA 34002-0948, USA

²Harvard Institute for International Development and Arnold Arboretum, 1 Eliot Street, Cambridge, MA 02138, USA

³Forest Research Institute of Malaysia, Kepong, 52109 Kuala Lumpur, Malaysia

⁴Center for Tropical Forest Science, National Institute of Education, 469 Bukit Timah Road, Singapore 1025

⁵Department of Ecology, Evolution, and Behavior, Princeton University, Princeton, NJ 08544, USA

⁶Department of Botany, Field Museum of Natural History, Chicago, IL 60605, USA

Dynamics of the Pasoh forest in Peninsular Malaysia were assessed by drawing a comparison with a forest in Panama, Central America, whose dynamics have been thoroughly described. Census plots of 50 ha were established at both sites using standard methods. Tree mortality at Pasoh over an eight-year interval was 1.46% yr⁻¹ for all stems ≥ 10 mm diameter at breast height (dbh), and 1.48% yr⁻¹ for stems ≥ 100 mm dbh. Comparable figures at the Barro Colorado Island site in Panama (BCI) were 2.55% and 2.03%. Growth and recruitment rates were likewise considerably higher at BCI than at Pasoh. For example, in all trees 500–700 mm in dbh, mean BCI growth over the period 1985–1995 was 6 mm yr⁻¹, whereas mean Pasoh growth was about 3.5 mm yr⁻¹. Examining growth and mortality rates for individual species showed that the difference between the forests can be attributed to a few light-demanding pioneer species at BCI, which have very high growth and mortality; Pasoh is essentially lacking this guild. The bulk of the species in the two forests are shade-tolerant and have very similar mortality, growth and recruitment. The Pasoh forest is more stable than BCI's in another way as well: few of its tree populations changed much over the eight-year census interval. In contrast, at BCI, over 10% of the species had populations increasing or decreasing at a rate of >0.05 yr⁻¹ (compared to just 2% of the species at Pasoh). The faster species turnover at BCI can probably be attributed to severe droughts that have plagued the forest periodically over the past 30 years; Pasoh has not suffered such extreme events recently. The dearth of pioneer species at Pasoh is associated with low-nutrient soil and slow litter breakdown, but the exact mechanisms behind this association remain poorly understood.

Keywords: tropical forest dynamics; tree demography; Pasoh; Barro Colorado Island

1. INTRODUCTION

We no longer think of tropical forests as stable and unchanging communities. At long time-scales, dramatic changes in forest composition associated with climatic shifts are conspicuous (Bush & Colinvaux 1990; Piperno & Becker 1996). But climatic shifts are also being well documented at much shorter time-scales. The impact of climatic shifts, such as drought, wind-storm and perhaps elevated carbon dioxide, are evident in our lifetimes. By observing changes in forest census plots, we can document the physiological and ecological mechanisms behind the changes, verify rates at which forests change, and ultimately develop predictions about longer-term and larger-scale shifts in tropical forests.

At Barro Colorado Island (BCI) in Central America, a 50-ha plot first censused in 1982 has allowed us to document changes in tree species composition and shifts in the demography of the forest. The large size of the plot

allowed evaluation of individual species on a case-by-case basis, and we could document extinction or population decline even in very rare trees. The main force behind some rather striking changes in the Barro Colorado forest was a severe 1983 El Niño drought that elevated both mortality and growth of the forest (Condit *et al.* 1992, 1995). About 10% of the species in the forest are restricted to moist soil microhabitats, and all of these species are undergoing sharp population declines (Condit *et al.* 1996*b*). Two moisture specialists were lost from the plot (Condit 1997).

We have been curious whether other tropical forests experience such shifts in mortality and growth and seemingly abrupt changes in species composition. Is the drought-prone, highly seasonal, semi-deciduous forest at Barro Colorado unusual? Or do all diverse tropical forests have a subset of species in rapid decline at any moment? The Forest Research Institute of Malaysia and the Center for Tropical Forest Science have now completed three censuses of a 50-ha plot in the Pasoh Forest in Peninsular Malaysia, providing an opportunity

* Author for correspondence (rick@eno.princeton.edu).

for detailed assessment of the dynamics of the whole forest and of individual tree species. Like most of the far-eastern equatorial tropics, Pasoh has an aseasonal climate and is evergreen. Does this lead to a community more stable than the one at Barro Colorado? Are there major differences in the dynamics and demography between the two forests and can these be traced to the differences in climate and deciduousness?

2. THE PLOTS

The Pasoh Forest Reserve is in the centre of the Malay peninsula, 140 km south-east of Kuala Lumpur. The reserve is a 2000-ha remnant of old-growth forest connected to a larger production forest, dominated by Dipterocarpaceae and classified as red meranti-keruing by Wyatt-Smith (1987). Rainfall is under 2000 mm yr⁻¹ and relatively aseasonal, with every month averaging more than 100 mm of rain (Kochummen *et al.* 1990). The canopy is evergreen. The forest is on level terrain overlying Triassic sediments and granite, with topographic variation of 25 m in 50 ha.

BCI is in the Panama Canal, and is mostly old-growth tropical forest dominated by Leguminosae and Bombacaceae. About 10% of the canopy is deciduous (R. Condit and K. Watts, unpublished data; Condit *et al.* 1996a). Rainfall is highly seasonal, with a strong four-month dry season from December through April, but the yearly total of 2500 mm exceeds that at Pasoh (Leigh *et al.* 1982). During 1983 and again in 1998—both strong El Niño years—the dry season was unusually severe, lasting five instead of four months. The 50-ha plot is on mainly level terrain on the island's summit overlying mostly Miocene basalts, with 28 m vertical variation.

The 50-ha census plot at Pasoh was established and censused for the first time in 1987; 815 species and 335 000 individuals were recorded (Manokaran *et al.* 1992; Condit *et al.* 1996c). Re-censuses were completed in 1990 and 1995. The Barro Colorado plot was first censused in 1982, with 305 species and 235 000 individuals tagged. The plot was re-censused in 1985, 1990 and 1995. Identical census methods were employed at the two sites: all free-standing woody stems ≥ 1 cm in diameter at breast height (dbh) were tagged and mapped precisely, and their dbhs recorded in each census. Condit (1998b) describes the methods in detail.

3. BACKGROUND FROM BARRO COLORADO

Using data from the first three censuses, we have documented changes in demography and abundance of individual species in the Barro Colorado forest. Across the forest as a whole, both mortality and growth rates were elevated during the 1982–1985 census period—the interval spanning the 1983 drought—relative to 1985–1990 (Leigh *et al.* 1990; Condit *et al.* 1992). About 75% out of 220 species common enough to analyse had higher mortality during the drought period (Condit *et al.* 1992, 1995).

We also examined changes in the abundance of individual species. Hubbell & Foster (1992) noted that 40% of the species in the plot changed in abundance by 3% yr⁻¹ or more between 1982 and 1985. Between 1982 and 1990,

27 species (12% of the community) had population growth (or decline) rates exceeding 5% yr⁻¹ (Condit *et al.* 1996b). Most of the declines were species associated with the slopes of the plot, where a perched water table keeps the soil moist through most dry seasons. Most of the increases were fast-growing, gap-demanding species. A population change of 5% yr⁻¹ is very fast for a tree—it leads to doubling (or halving) the population in just 15 years. Drought-sensitive species are being eliminated from the forest rapidly.

4. METHODS

We followed standard methods for calculating mortality, growth, recruitment and population change. Let the census interval be t , and the population sizes at time 0 and time t be n_0 and n_t . The number of survivors at time t is S_t , and so the number of recruits is $n_t - S_t$. Demographic rates are defined as the rate constants of population growth, calculated for mortality from

$$m = \frac{\ln n_0 - \ln S_t}{t}, \quad (1)$$

for recruitment from

$$r = \frac{\ln n_t - \ln S_t}{t}, \quad (2)$$

and for population growth from

$$\lambda = \frac{\ln n_t - \ln n_0}{t}. \quad (3)$$

Notice that $\lambda = r - m$. The time interval in equations (1)–(3) was found as the mean time interval for all individuals included in the calculation (n_0 in equations (1) and (3), n_t in equation (2)). For growth rate, we used mean dbh increment per year, but excluded extremes from the calculation—all individuals decreasing in size by $> 5\%$ yr⁻¹ or increasing by > 75 mm yr⁻¹. These methods were documented in detail in Condit *et al.* (1992, 1993a,b, 1995, 1996a,b,c). Here we employ identical methods with the Pasoh data, and in addition, we update the Barro Colorado results using the 1995 census data.

5. RESULTS

(a) Basic forest structure

Pasoh has a higher density of smaller individuals than Barro Colorado, but BCI has more large trees (table 1). As a result, BCI has a slightly higher basal area than Pasoh, 31.8 versus 30.3 m² ha⁻¹, for all stems ≥ 10 mm dbh. For stems ≥ 100 mm dbh, the difference is greater, 27.8 m² ha⁻¹ at BCI versus 24.4 m² ha⁻¹ at Pasoh.

According to a commonly used regression for biomass (Brown *et al.* 1989; Brown 1997), BCI has 405 t ha⁻¹ of above-ground vegetation and Pasoh 203 t ha⁻¹. This estimator ignores tree height, though, and Pasoh trees are taller than BCI trees; these biomass figures are probably unreliable except as very crude approximations.

(b) Forest turnover rate

Barro Colorado had a higher mortality rate than Pasoh, whether considering all stems ≥ 10 mm dbh or only trees ≥ 100 mm dbh (table 2). With the longest intervals available, BCI mortality was 2.64% yr⁻¹ for all

Table 1. Diameter at breast height distribution in 50-ha plots at Barro Colorado Island and Pasoh, based on 1995 census data

(Columns give the total number of individuals in 50 ha and per ha for each plot.)

dbh (mm)	BCI		Pasoh	
	total	no. ha ⁻¹	total	no. ha ⁻¹
10–49	177850	3557.0	244834	4896.7
50–99	29751	595.0	44805	896.1
100–199	13635	272.7	20092	401.8
200–299	3687	73.7	5047	100.9
300–399	1777	35.5	1889	37.8
400–499	941	18.8	808	16.2
500–999	1232	24.6	985	19.7
1000–1999	148	3.0	56	1.1
≥2000	15	0.3	0	0

stems, while Pasoh was 1.46% yr⁻¹ (1982–1995 at BCI, 1987–1995 at Pasoh). Mortality was especially high during the drought interval at BCI (1982–1985), but even after this remained higher than at Pasoh (table 2).

Recruitment was also higher at BCI, at least for all stems ≥10 mm dbh (table 2). Over 13 years at BCI, recruitment was 2.87% yr⁻¹, while it was just 1.65% yr⁻¹ at Pasoh over eight years at Pasoh. But for trees ≥100 mm dbh, recruitment was quite similar at the two forests, 2.66% yr⁻¹ at BCI and 2.79% yr⁻¹ at Pasoh (table 2).

Mortality and recruitment are not the only sources of population change. When a stem breaks but the plant survives, a tree can fall out of a dbh class. These instances were not tallied as mortality, yet they lead to loss from the population. Thus, if recruitment exactly equalled mortality, the overall population would decline due to the loss of these broken plants. At both BCI and Pasoh, recruitment has been only slightly higher than mortality for stems ≥10 mm dbh, and the total forest density has declined (over the full census periods: 235 349 to 229 071 at BCI, 335 361 to 320 382 at Pasoh). However, density of trees ≥100 mm dbh has increased slightly at BCI (20 882 to 21 459) and more so at Pasoh (26 556 to 28 997). This is reflected at Pasoh by the recruitment rate into the 100 mm dbh class that is nearly double mortality (table 2).

(c) Mortality as a function of dbh class

In species that reach the canopy at both BCI and Pasoh, mortality rate declined from 10 to about 50 mm dbh (figure 1). At larger dbhs, mortality was fairly constant or rose slightly with dbh, except during the drought interval at BCI, when mortality rose sharply in larger trees (see also Condit *et al.* 1995). In understorey species, mortality was nearly constant across all dbh classes (figure 2).

At all sizes up to 600 mm dbh, BCI trees had much higher mortality than Pasoh, for both canopy and understorey species (figures 1 and 2). For the very largest trees, the two forests had similar rates, but confidence limits are wide. During the 1982–1985 drought period, Barro Colorado had double or even triple the mortality of Pasoh

in large trees and in understorey species (figures 1b and 2b).

(d) Recruitment as a function of dbh class

Recruitment rate can also be assessed as a function of dbh class, by considering the rate of input of new stems into successively larger dbhs (figure 3). Recruitment was generally higher at BCI than at Pasoh for most dbhs, except near 100 mm (as table 1 shows). During 1990–1995 at BCI, a period with no major drought, recruitment rate was low at BCI, similar to the rate at Pasoh.

(e) Growth as a function of dbh class

In canopy tree species, growth rates at BCI were higher than at Pasoh, and dramatically so in some census intervals (figure 4). Small saplings, <100 mm dbh, grew 2 mm yr⁻¹ or less, with BCI saplings growing a small amount faster than at Pasoh (for example, 10–19 mm saplings at BCI grew 0.64 mm yr⁻¹, at Pasoh 0.59 mm yr⁻¹, a highly significant difference due to very large samples). But it was in larger trees where growth rates differed sharply between the plots, with BCI growth doubling that at Pasoh in certain dbh classes (figure 4).

Understorey species showed a surprising and opposite result, growing quite a bit faster at Pasoh than at BCI in dbh classes greater than 50 mm (figure 5). At smaller dbhs, growth rates were similar at the two plots, although faster during 1982–1985 at BCI. Understorey species had much lower growth rates than canopy species at both plots, in all censuses and dbh classes (comparing figures 4 and 5).

Examining the dbh distribution of understorey species at the two plots suggests that the high growth rate of this group at Pasoh is an artefact of how species were categorized as understorey or canopy. The 50-ha plot at Pasoh had 219 individuals in 1995 that were ≥300 mm dbh but classified as understorey species, whereas BCI had just seven such individuals. This suggests that some of the species called understorey at Pasoh would be classified as canopy species at BCI, and these would raise growth rates quite a bit in the larger dbhs of understorey trees (≥100 mm). The categories were based on qualitative estimates of the tallest tree in each species (Condit *et al.* 1995), and could easily be subject to a bias like this.

(f) Mortality and growth of individual canopy species

Figures 1–5 and table 2 show that overall forest turnover was quite a bit slower at Pasoh than at BCI. This contrast was reflected by individual species as well. In figures 6 and 7, mortality and growth rates are plotted in two dbh classes, 10–19 mm and 200–499 mm, for all species which had at least ten individuals alive at the start of the census period in both classes (1985 at BCI, 1987 at Pasoh). These two dbh classes conveniently summarize the range of growth and mortality rates each species exhibits throughout its ontogeny (above 10 mm dbh, anyway).

There was a wider range of mortality rates at BCI, especially in the sapling dbh class (figure 6). At Pasoh, the highest sapling mortality among the 146 common canopy species was in *Shorea leprosula* (Dipterocarpaceae), 11.7% yr⁻¹; at BCI, eight out of the 69 common canopy species had mortality rates higher than this (figure 6).

Table 2. *Mortality and recruitment rates at BCI and Pasoh*

(n_0 is the number of individuals alive at the beginning of the census interval. (a) Individuals ≥ 10 mm dbh. During the 1990 census at Pasoh, recruits were undercounted, and the recruitment estimates from the two intervals are thus not reliable (we put the recruitment figures for the two shorter intervals in bold). (b) Individuals ≥ 100 mm dbh. Since recruits ≥ 100 mm dbh were already tagged in the prior census (when they were < 100 mm dbh), there was no underestimate of recruitment in this category at Pasoh in 1990.)

site	interval	n_0	dead	recruits	mortality	recruitment
<i>(a)</i>						
BCI	1982–1985	235 349	19 881	33 079	2.66 ± 0.04	4.43 ± 0.05
	1985–1990	242 082	26 822	39 412	2.23 ± 0.03	3.34 ± 0.03
	1990–1995	244 025	27 634	21 776	2.52 ± 0.03	2.09 ± 0.03
BCI	1982–1995	235 349	70 003	73 035	2.64 ± 0.04	2.87 ± 0.02
	1985–1995	242 082	54 612	52 726	2.55 ± 0.02	2.61 ± 0.03
Pasoh	1987–1990	335 361	11 608	5744	1.17 ± 0.02	0.60 ± 0.02
	1990–1995	323 279	25 862	38 142	1.56 ± 0.02	2.37 ± 0.02
Pasoh	1987–1995	335 361	38 614	41 823	1.46 ± 0.02	1.65 ± 0.02
<i>(b)</i>						
BCI	1982–1985	20 882	1840	2036	2.75 ± 0.13	3.08 ± 0.14
	1985–1990	20 720	2064	3016	1.98 ± 0.09	2.58 ± 0.11
	1990–1995	21 231	1834	2394	1.89 ± 0.09	2.48 ± 0.10
BCI	1982–1995	20 882	5472	6457	2.26 ± 0.06	2.66 ± 0.07
	1985–1995	20 720	3829	4987	2.03 ± 0.07	2.62 ± 0.08
Pasoh	1987–1990	26 556	900	2283	1.16 ± 0.08	2.88 ± 0.12
	1990–1995	27 700	2274	4025	1.60 ± 0.07	2.79 ± 0.09
Pasoh	1987–1995	26 556	3095	6114	1.48 ± 0.06	2.83 ± 0.08

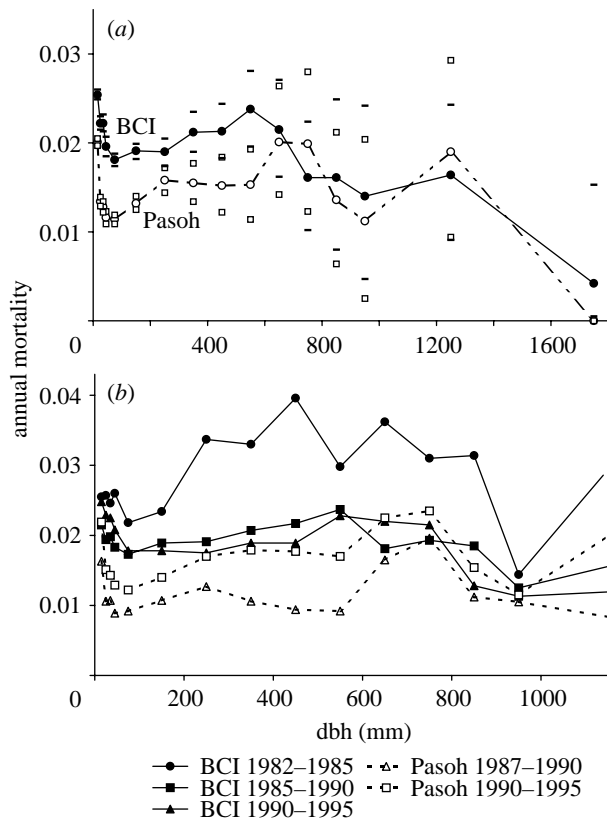


Figure 1. Mortality rates for Barro Colorado Island (BCI) and Pasoh canopy species as a function of dbh class. Rate for each dbh class (10–49, 50–99, 100–199, 200–299, etc., 1000–1499 and all trees ≥ 1500 mm dbh) using equation (1), with all individuals (of all species) included. Points are placed above the mid-point of each dbh class, with the rightmost point for the terminal dbh class. (a) Shows annualized rate

There was also a wider range of growth rates among individual species at BCI compared to Pasoh. The growth rate of *Cecropia insignis* (Moraceae) at BCI was five times the rate of the fastest growing species at Pasoh (*Xylopia ferruginea* v. *ferruginea*, Annonaceae; figure 7). Still, in both forests, a majority of species were clustered in a small demographic space, with mortality rates $< 3\%$ yr $^{-1}$ and growth rates < 2 mm yr $^{-1}$ in saplings and < 5 mm yr $^{-1}$ in larger trees.

We were concerned that there might be other very fast-growing species at Pasoh that were too rare to include in figure 7. So we calculated growth in the same two dbh classes for every species that had survivors over 1985–1995 at BCI and 1987–1995 at Pasoh. The fastest-growing species at Pasoh was *Macaranga hosei* (Euphorbiaceae), with saplings growing at 5.3 mm yr $^{-1}$. Only three out of 422 canopy species had mean sapling growth over 4 mm yr $^{-1}$. At BCI, 16 out of 141 canopy species grew faster than 4 mm yr $^{-1}$.

At BCI, the high growth and mortality rates among saplings were found in familiar gap-invading species, such as *Cecropia insignis*, *Zanthoxylum belizense* (Rutaceae) and *Alchornea costaricensis* (Euphorbiaceae). High growth among larger trees was found in canopy emergents that had very slow growth as saplings, especially *Tachigali versicolor* (Leguminosae). High mortality in the larger dbh class was observed in a few small species that just barely

Figure 1. (Cont.) over 1987–1995 at Pasoh, 1985–1995 at BCI. Small open squares give 95% confidence limits for Pasoh, dashes for BCI. Confidence limits were calculated assuming a binomial variance (see Condit *et al.* 1995); (b) gives annualized rates calculated from shorter intervals, as indicated in legend; confidence limits not shown.

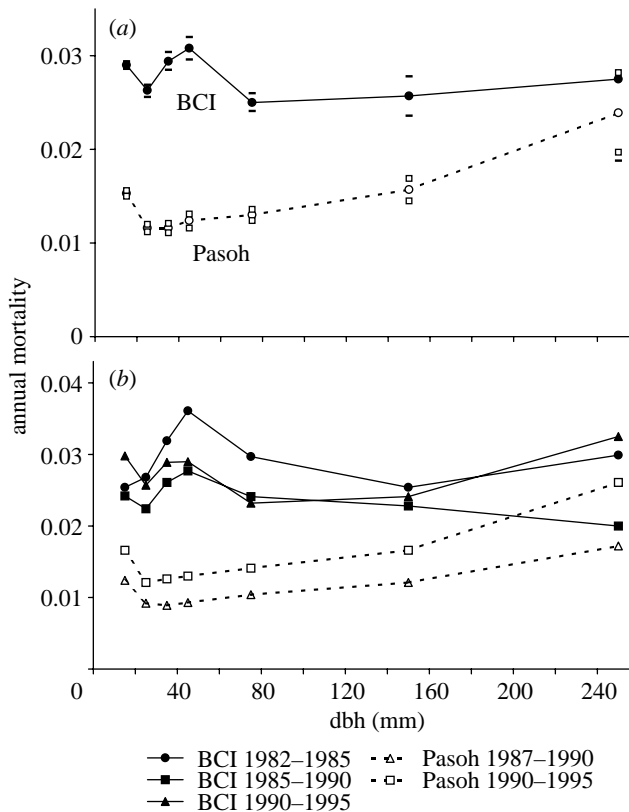


Figure 2. Mortality rates for BCI and Pasoh understorey species as a function of dbh class (10–19, 20–29, 30–39, 40–49, 50–99, 100–199 and 200–299 mm dbh, with points plotted above the mid-point of each class). See legend to figure 1.

reach 200 mm dbh (such as *Eugenia oerstedeana*, Myrtaceae). Two species at BCI—*Inga marginata* (Leguminosae) and *Ocotea oblonga* (Lauraceae)—stood out as having very high mortality at both the sapling and large tree stages. This is probably not their normal life history, but more likely a sign of pathology. Both are declining in abundance.

At Pasoh, high growth and mortality in saplings was found in several species of red meranti (*Shorea acuminata*, *S. leprosula*, *S. lepidota* and *S. parvifolia*), and the same species also had the highest growth as larger trees (figure 7). High mortality in the larger dbh class was observed especially in small canopy trees, such as the two *Xylopias*. Remarkably, *Xylopia ferruginea* v. *ferruginea* increased in abundance despite high mortality as both a sapling and a larger tree.

In understorey species, BCI also showed a much wider range of mortality and growth rates, with a few species growing and dying far faster than any species at Pasoh. In the 10–19 mm dbh class, the highest mortality rate at Pasoh over 1987–1995 was in *Urophyllum hirsutum* (Rubiaceae), at 4.2% yr⁻¹. Eleven understorey species at BCI had higher mortality, with *Palicourea guianensis* (Rubiaceae) and *Senna dariensis* (Leguminosae) the highest at 20% yr⁻¹. The highest growth rate in a common understorey species at BCI was in *Croton billbergianus* (Euphorbiaceae) and was far higher than any species at Pasoh (figure 8). Still, Pasoh had faster average growth of understorey species (see figure 5). This can be seen in figure 8 as the large number of species with

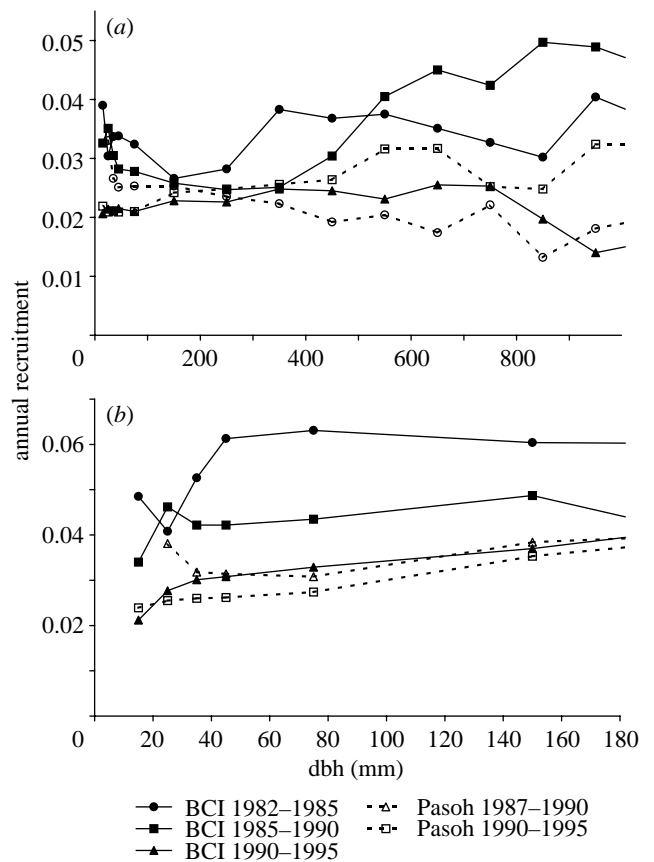


Figure 3. Recruitment rates for BCI and Pasoh, (a) for canopy species, (b) for understorey species. These are calculated from equation (2), with all individuals (all species) included. Dbh classes are identical to those used for mortality (figures 1 and 2), with points plotted above the mid-point of each class. Recruitment plotted at a given dbh class means the rate at which new recruits grew into that class; for example, recruitment at 300–399 mm dbh refers to recruits that grew past 300 mm dbh (the upper dbh is irrelevant).

growth of 1.5–2 mm yr⁻¹ as large saplings at Pasoh (the vertical axis in figure 8); these species are missing at BCI. This we attribute, as discussed above, to a different definition of ‘understorey species’ at Pasoh.

(g) Rate of population change

Pasoh has a more stable species composition than BCI. Over 1985–1995 at BCI, 23 out of 220 species (10.5%) changed by $\geq 5\%$ yr⁻¹. At Pasoh over 1987–1995, just 13 out of 650 did (2%). This difference was sharpest among those species declining in abundance: 20 species declined in abundance by $\geq 5\%$ yr⁻¹ at BCI, but just five species did at Pasoh. Histograms from the two plots are distinct with high statistical significance (figure 9). We deliberately made this comparison based on 1985–1995 data at BCI, omitting the drought interval of 1982–1985. Nevertheless, BCI had substantially more change.

Nearly all the species undergoing rapid population decline at BCI are species associated with the relatively moist slope soils (Condit *et al.* 1996b). Two of them, the palm *Geonoma interrupta* and the tree-fern *Cnemidaria petiolata*, are now extinct in the plot (table 3; Condit 1997). Other particularly sharp declines (table 3) were in the genus *Piper* (Piperaceae), an understorey group especially

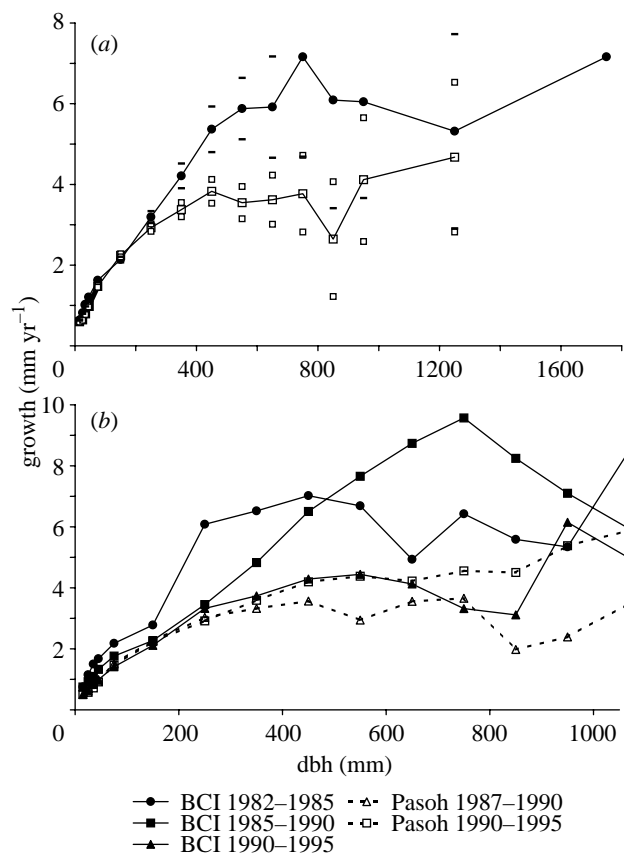


Figure 4. Growth rates at BCI and Pasoh, in millimetres per year, for all canopy species combined. Dbh classes as for mortality (figure 1). (a) 1987-1995 rates for Pasoh and 1985-1995 for BCI, annualized in each case. (b) Growth calculated from shorter census intervals, as indicated by legend. (a) Includes 95% confidence limits (small open squares for Pasoh, dashes for BCI), but not (b).

abundant in wet forests, and the fading canopy dominant *Poulsenia armata* (Moraceae).

The three abundant species at Pasoh that are undergoing conspicuous population decline are the fast-growing light red merantis, *Shorea leprosula*, *S. lepidota* and *S. parvifolia* (table 4). There are no examples like the dramatic declines at Barro Colorado, though (table 4 lists some of the most severe declines).

Between 1987 and 1995 at Pasoh, five species were lost from the census and eight new species were found. Taking the average of the two, the 'species turnover' was 0.8% out of the 815 species observed in 1987. Taking a comparable period at BCI, 1985-1995, without the drought, seven species invaded and 13 were lost (not including a single hybrid *Apeiba*, which died). This is a turnover of 3.3% out of the 306 species recorded in 1985.

6. DISCUSSION

The Pasoh forest is less dynamic than the Barro Colorado forest. Growth and mortality rates of the whole forest are substantially lower at Pasoh. There has been less species turnover during the 50-ha censuses at Pasoh, and Pasoh does not have rapidly changing populations to the degree that Barro Colorado does. Most intriguing is the complete absence of fast-growing tree species from the Pasoh plot.

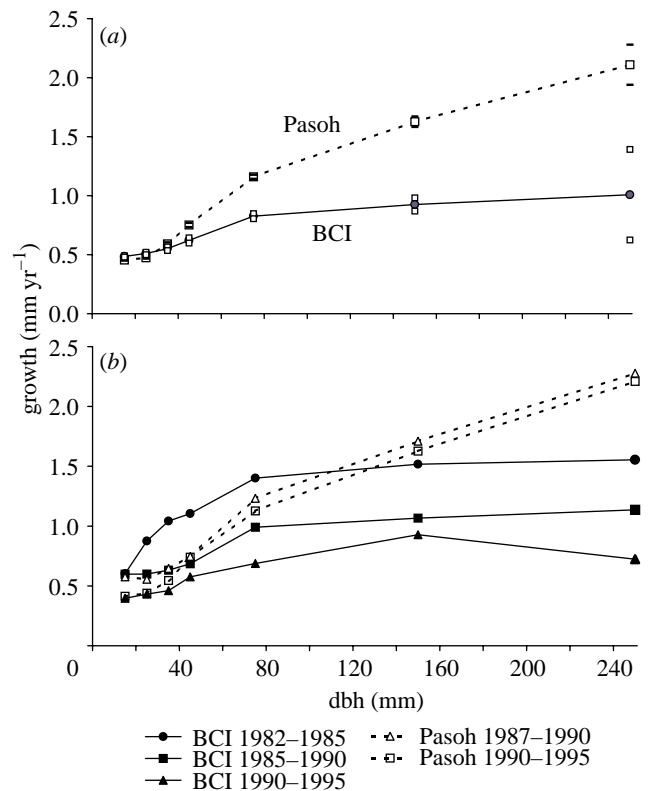


Figure 5. Growth rates of all understorey species combined. See legend to figure 4.

Indeed, the high growth rate of the BCI forest, relative to Pasoh, seems to be entirely due to a minority of species at BCI with very high growth rates. Careful inspection of figures 7 and 8 shows that the largest group of species at BCI have growth rates in exactly the same range as species at Pasoh, while a very small number of species at BCI have much higher growth. We believe that this observation is crucial for focusing hypotheses about why the two forests are different.

If growth rates at BCI were elevated because deciduous species allow more light to enter the forest in the dry season, we would anticipate that most species—across the board—would have higher growth at BCI than at Pasoh. Instead, it seems that growth rates of the bulk of the species in two forests—all shade-tolerant—are similar. What is different is that a small number of pioneer species at Barro Colorado are fairly abundant in the forest, whereas these species are virtually absent at Pasoh.

The difference in abundance of pioneer species in the two forests explains why growth rates in smaller dbh classes were only slightly higher at BCI than at Pasoh, whereas rates of larger dbh trees were much higher at BCI (see figure 4). This follows from the fact that pioneer trees are rare as saplings, but much more common as large trees, relative to shade-tolerant species (Condit *et al.* 1996a). Condit *et al.* (1998) showed that this dearth of saplings among pioneer species is a result of high growth rates, and is maintained even with steady recruitment.

Forest-wide mortality rates at Barro Colorado are elevated relative to Pasoh for the same reason—a few pioneer species with very high mortality are fairly common at BCI, but nearly absent at Pasoh. So understanding the

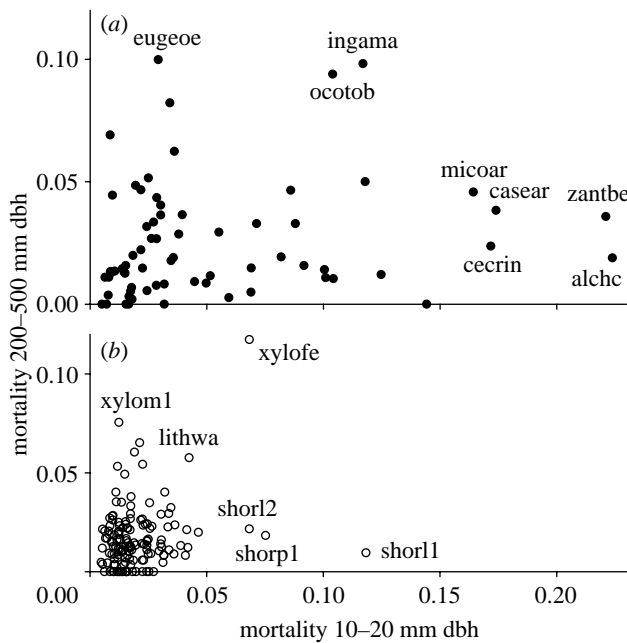


Figure 6. Mortality rates of individual canopy species, (a) for BCI, 69 species (1985–1995 annualized), (b) for Pasoh, 146 species (1987–1995 annualized). Mortality as a sapling is plotted against mortality as a large tree for each species. Only species that had \geq ten individuals at the start of the interval in both dbh classes are included. Species abbreviations for BCI: eugeoe, *Eugenia oerstediana* (Myrtaceae); ingama, *Inga marginata* (Leguminosae); ocotob, *Ocotea oblonga* (Lauraceae); micoar, *Miconia argentea* (Melastomataceae); casear, *Casearia arborea* (Flacourtiaceae); cecrin, *Cecropia insignis* (Moraceae); zantbe, *Zanthoxylum belizense* (Rutaceae); alchco, *Alchornea costaricana* (Euphorbiaceae). Abbreviations for Pasoh: xylofe, *Xylopia ferruginea v. ferruginea* (Annonaceae); xylo1, *X. magna*; lithwa, *Lithocarpus wallichianus* (Fagaceae); shor12, *Shorea lepidota* (Dipterocarpaceae); shorp1, *S. parvifolia*; shor11, *S. leprosula*.

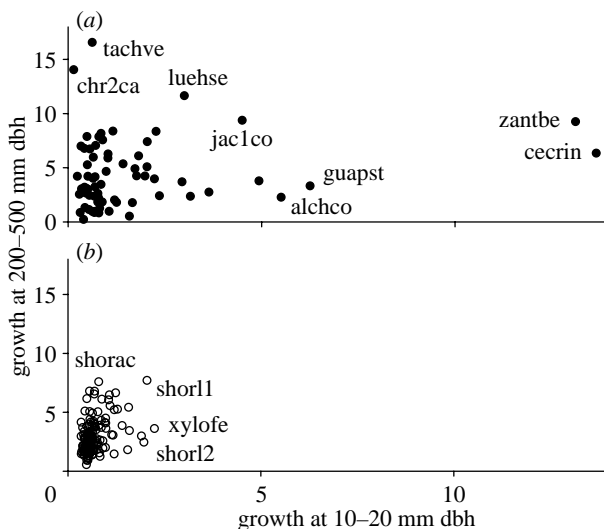


Figure 7. Annual growth rates of individual canopy species, (a) for BCI, 69 species (1985–1995), (b) for Pasoh, 146 species (1987–1995). Growth as sapling plotted against growth as large tree. Exactly the same species as those in figure 6 are included. Abbreviations for BCI: tachve, *Tachigali versicolor* (Leguminosae); chr2ca, *Chrysophyllum cainito* (Sapotaceae); jac1co, *Jacaranda copaia* (Bignoniaceae); guapst, *Guapira standleyanum* (Nyctaginaceae); and see figure 6 legend. Abbreviations for Pasoh: shorac, *Shorea acuminata*; and see figure 6 legend.

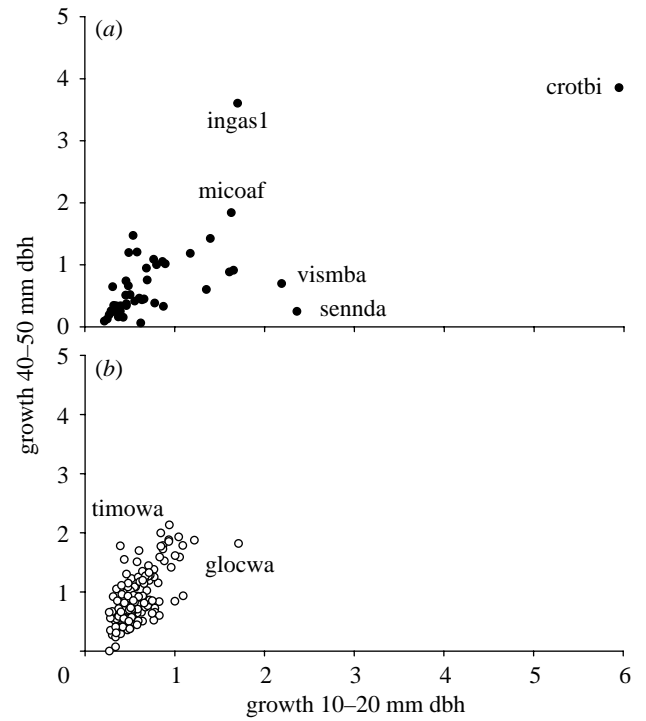


Figure 8. Annual growth rates of individual understorey species, (a) for BCI, 46 species (1985–1995), (b) for Pasoh, 153 species (1987–1995), including only species which had \geq ten individuals at the start of the interval in both dbh classes. Growth as small sapling plotted against growth as large sapling. Abbreviations for BCI: crotbi, *Croton billbergianus* (Euphorbiaceae); vismba, *Vismia baccifera* (Guttiferae); ingas1, *Inga* sp. (Leguminosae); sennda, *Senna dariensis* (Leguminosae); and micoaf, *Miconia affinis* (Melastomataceae). Abbreviations for Pasoh: glocwa, *Glochidion wallichianum* (Euphorbiaceae); and timowa, *Timonius wallichianus* (Rubiaceae).

difference in dynamics between these forests requires an understanding of why pioneer species persist. It appears that Barro Colorado has features that allow disturbance-demanding pioneer species to maintain substantial populations, while Pasoh does not.

A contrast in the abundance of pioneers was also observed between sites in Borneo, where Ashton & Hall (1992) found that plots at Bukit Mersing had higher overall growth and more pioneer species than plots at two other sites. Ashton & Hall suggested two main reasons for this difference. First, soil nutrient levels were higher at Bukit Mersing, and growth of pioneer species may be limited by soil nutrient status, while growth of shade-tolerant species is not. Second, drought is less common at Bukit Mersing than the other two sites, favouring a taller forest with more windthrows creating large gaps. Both these hypotheses seem applicable to the Barro Colorado–Pasoh contrast. However, even the Bukit Mersing site in Borneo had no trees growing at anywhere near the rates of *Cecropia*, *Zanthoxylum* or *Croton* at BCI.

We suggest that the BCI–Pasoh contrast is based on geology and climate. The siliceous, acid-reacting soil surface at Pasoh is low in nutrients, and coupled with the aseasonal climate, this leads to slow litter breakdown and a near complete and constant litter cover at Pasoh. In contrast, BCI soils are relatively rich, and litter cover becomes sparse during the wet season, possibly due to the

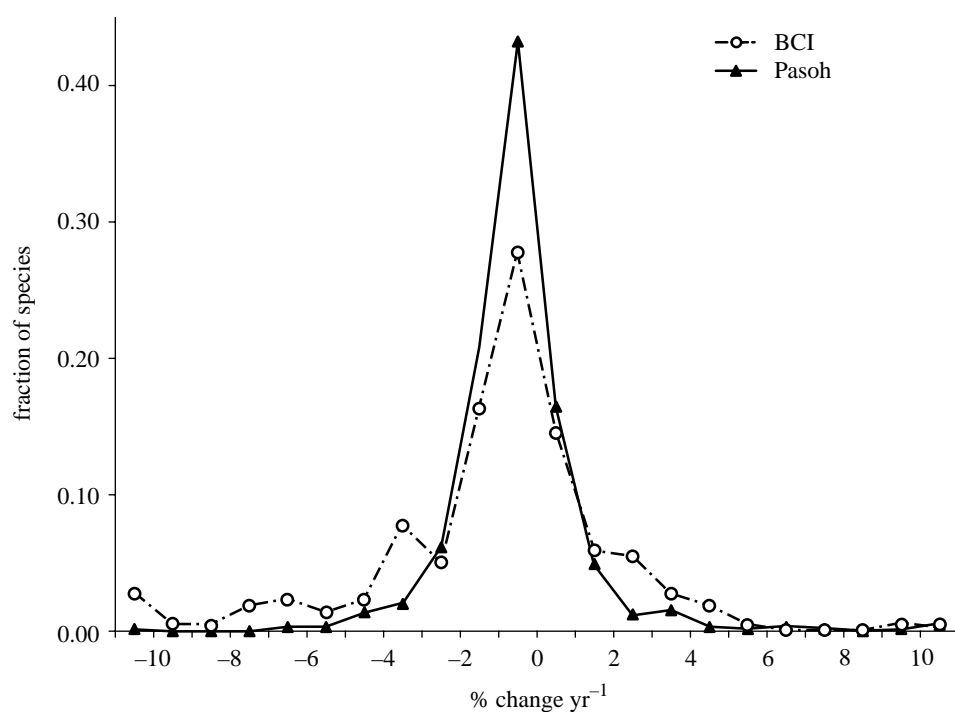


Figure 9. Histogram of rates of population change across two forest communities: Pasoh, 650 species (1987–1995); BCI, 220 species (1985–1995). Rates for each species were calculated from equation (3) (and multiplied by 100). All species that had ≥ 20 individuals in at least one census were included. A χ^2 -test comparing the two curves was calculated using intervals of one percentage point wide from -4 to $+4$, and combining all rates < -4 and $> +4$ (ten intervals all told) ($\chi^2 = 75.2$, d.f. = 9).

Table 3. *Rapidly changing populations in the BCI 50-ha plot*

(Only species that had ≥ 20 individuals in one census were considered. Of these, the five fastest declines and increases are included, plus the three fastest declines and increases among species with ≥ 500 individuals in a census. The two most dramatic extinctions are also included—the largest 1982 populations, which are now gone. The total number of individuals ≥ 10 mm dbh in each census is given, plus the population growth rate λ (see equation (3) in text).)

species and family	1982	1985	1990	1995	λ
<i>Geonoma interrupta</i> (Palmae)	19	14	3	0	—
<i>Cnemidaria petiolata</i> (Cyathaceae)	8	3	1	0	—
<i>Piper cordulatum</i> (Piperaceae)	3145	3709	1773	394	-15.9
<i>P. aequale</i>	220	159	60	52	-10.8
<i>P. culebratum</i>	120	65	53	30	-10.6
<i>Cestrum megalophyllum</i> (Solanaceae)	309	237	157	81	-10.0
<i>Acalypha diversifolia</i> (Euphorbiaceae)	1566	1205	823	530	-8.0
<i>Ocotea whitei</i> (Lauraceae)	1126	935	763	575	-4.9
<i>Eugenia galalonensis</i> (Myrtaceae)	963	1160	1382	1500	+3.3
<i>Chrysophyllum argenteum</i> (Sapotaceae)	425	480	685	707	+3.8
<i>Spondias mombin</i> (Anacardiaceae)	59	63	95	110	+4.8
<i>Cupania rufescens</i> (Sapindaceae)	55	72	96	109	+5.1
<i>Palicourea guianensis</i> (Rubiaceae)	376	661	1474	1055	+7.9
<i>Annona spraguei</i> (Annonaceae)	57	71	143	177	+8.5
<i>Psychotria graciliflora</i> (Rubiaceae)	10	14	44	57	+13.6

less acid soil (litter builds up during the dry season as many species shed leaves, though). Growth of pioneers may be nutrient-limited. In addition, many small-seeded pioneer species require bare soil to germinate (Guzmán-Grajales & Walker 1991; Molofsky & Augspurger 1992), and gaps at BCI have less litter than gaps at Pasoh due to the different decay rates. Finally, the ever-wet climate at Pasoh allows a denser sapling understorey than BCI (see table 1), and these waiting saplings can capture light gaps when they form, displacing the pioneer species, which must disperse into the gap. Thus, germination and growth in old forest may be too low for pioneer species to maintain populations in the Pasoh forest. Experimental

work on seed germination and growth could provide a test for these hypotheses.

There are a couple of alternative hypotheses explaining high pioneer populations at BCI, neither of which we currently favour. One is that part of BCI was cleared about 100 years ago and is now second-growth forest, and pioneer populations may be elevated there, just adjacent to the 50-ha plot. However, most of the 50-ha plot itself is old-growth, undisturbed for over 600 years, and there is currently no cleared land within 6 km of the plot. It seems unlikely that high-turnover tree populations would still be elevated 100 years after or 6 km away from the disturbances. Another hypothesis is that wind speeds are

Table 4. *Rapidly changing populations in the Pasoh 50-ha plot*

(Criteria for including species in this table exactly match those for BCI given in table 3.)

species and family	1987	1990	1995	λ
<i>Thottea grandifolia</i> (Aristolochiaceae)	25	13	1	-37.9
<i>Pandanus yvonii</i> (Pandanaeae)	23	23	13	-6.7
<i>Symplocos cochinchinensis</i> (Symplocaceae)	21	19	12	-6.6
<i>Mallotus griffithianus</i> (Euphorbiaceae)	41	35	26	-5.4
<i>Pinanga malayana</i> (Palmae)	236	210	153	-5.1
<i>Shorea parvifolia</i> (Dipterocarpaceae)	1707	1508	1194	-4.2
<i>Shorea lepidota</i> (Dipterocarpaceae)	1169	1066	824	-4.1
<i>Shorea leprosula</i> (Dipterocarpaceae)	3020	2765	2140	-4.1
<i>Gnetum gnemon</i> (Gnetaceae)	582	552	669	1.6
<i>Parospsia vareciformis</i> Passifloraceae	580	602	711	2.4
<i>Hopea dryobalanoides</i> (Dipterocarpaceae)	698	682	935	3.4
<i>Macaranga conifera</i> (Euphorbiaceae)	40	53	78	7.9
<i>Tarenna</i> species 11 (Rubiaceae)	26	26	59	9.6
<i>Eugenia cerina</i> (Myrtaceae)	6	5	22	15.3
<i>Diospyros lanceifolia</i> (Ebenaceae)	5	5	21	16.9
<i>Cleistanthus malaccensis</i> (Euphorbiaceae)	10	11	59	20.9

lower at Pasoh (S. Thomas, personal communication), and we have collected some wind data at Pasoh, indicating that in the understorey wind is nearly absent, whereas at BCI, there are stiff trade winds throughout the dry season. This could lead to smaller and less frequent tree-fall gaps at Pasoh and less area available to pioneer species. However, most windthrow is caused by rain squalls at BCI and Pasoh, and our impression is that treefall gaps are common at Pasoh. Data on gap formation rate comparable to studies at BCI (Brokaw 1982, 1985; Hubbell *et al.* 1999) could resolve this.

The rapid changes observed in tree populations at BCI, in contrast with Pasoh, are probably attributable to the droughty conditions at Barro Colorado. The BCI climate switched from a wetter to a drier mode about 30 years ago. Species requiring moist soils throughout the dry season were able to persist during the wetter times, but are now being eliminated by the frequent El Niño droughts (Condit *et al.* 1996b; Condit 1997, 1998a). Severe droughts have not struck Pasoh during the census period, and perhaps the climate is not as variable over decade time-scales as it is at Barro Colorado.

We appreciate that with a sample from just two forests, these hypotheses must remain speculation. But the contrast between BCI and Pasoh sets up a framework for examining other forests, and the Center for Tropical Forest Science (CTFS) network of plots will provide replicate data sets with which to do so. Each CTFS plot is large enough to examine the demography of individual species, and it is the results from individual species that are crucial to our hypotheses. With demography from many species in the community, we have been able to examine both forest-wide dynamics as well as the demography and population change of individual species. In another ten years, large-plot data sets will be available from moist forests in Thailand, Sarawak (Malaysia), Sri Lanka, Ecuador, Puerto Rico, Cameroon and the Congo, and precise comparisons of demographic patterns will provide a much larger data set on which to base hypotheses about factors affecting the dynamics of tropical forests.

We thank the Royal Society and David Newbery for organizing the meeting at which this paper was presented, and the College of Forest Resources at the University of Washington, which hosted the senior author while writing the paper. S. Bohlman, P. Hall, J. Greenberg, D. Newbery, G. Prance, K. Bible and C. Halpern offered useful comments. We also thank the Forest Research Institute of Malaysia for sponsoring and supporting the work at Pasoh, the Smithsonian Tropical Research Institute in Panama for support at BCI, and I. Rubinoff and E. Losos for maintaining the Center for Tropical Forest Science network of plots. K. M. Kochummen, E. S. Quah, S. Appanah, R. Pérez and over 100 fieldworkers from 12 countries have assisted in the plot censuses. The Pasoh project was also supported by the National Science Foundation (USA), the Rockefeller Foundation and the John Merck Fund, and the BCI project 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.

REFERENCES

- Ashton, P. S. & Hall, P. 1992 Comparisons of structure among mixed dipterocarp forests of north-western Borneo. *J. Ecol.* **80**, 459–481.
- Brokaw, N. V. L. 1982 The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* **14**, 158–160.
- Brokaw, N. V. L. 1985 Gap-phase regeneration in a tropical forest. *Ecology* **66**, 682–687.
- Brown, S. 1997 Estimating biomass and biomass change of tropical forests: a primer. UN FAO Forestry Paper 134. Rome: FAO.
- Brown, S., Gillespie, A. & Lugo, A. 1989 Biomass estimation methods for tropical forests with applications to forest inventory data. *Forest Sci.* **35**, 881–902.
- Bush, M. B. & Colinvaux, P. A. 1990 A pollen record of a complete glacial cycle from lowland Panama. *J. Vegetation Sci.* **1**, 105–118.
- Condit, R. 1997 Cambios en un bosque tropical con un clima cambiante: resultados de los censos realizados en la parcela de 50 hectáreas en la Isla de Barro Colorado en Panamá. In *Estudios sobre diversidad y ecología de plantas* (ed. R. Valencia & H. Balslev), pp. 231–240. Quito: Pontificia Universidad Católica del Ecuador.

- Condit, R. 1998a Ecological implications of changes in drought patterns: shifts in forest composition in Panama. *Climatic Change* **39**, 413–427.
- Condit, R. 1998b *Tropical forest census plots*. Berlin: Springer; Georgetown, TX: R. G. Landes Co.
- 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. 1993a Mortality and growth of a commercial hardwood, 'El Cativo', *Prioria copai-fera*, in Panama. *Forest Ecol. Mgmt* **62**, 107–122.
- Condit, R., Hubbell, S. P. & Foster, R. B. 1993b Identifying fast-growing native trees from the neotropics using data from a large, permanent census plot. *Forest Ecol. Mgmt* **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. *Ecol. Monogr.* **65**, 419–439.
- Condit, R., Hubbell, S. P. & Foster, R. B. 1996a Assessing the response of plant functional types in tropical forests to climatic change. *J. Vegetation Sci.* **7**, 405–416.
- Condit, R., Hubbell, S. P. & Foster, R. B. 1996b Changes in a tropical forest with a shifting climate: results from a 50 ha permanent census plot in Panama. *J. Trop. Ecol.* **12**, 231–256.
- Condit, R., Hubbell, S. P., LaFrankie, J. V., Sukumar, R., Manokaran, N., Foster, R. B. & Ashton, P. S. 1996c Species-area and species-individual relationships for tropical trees: a comparison of three 50 ha plots. *J. Ecol.* **84**, 549–562.
- Condit, R., Sukumar, R., Hubbell, S. P. & Foster, R. B. 1998 Predicting population trends from size distributions: a direct test in a tropical tree community. *Am. Nat.* **152**, 495–509.
- Guzmán-Grajoles, S. M. & Walker, L. R. 1991 Differential seedling responses to litter after Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* **23**, 407–414.
- Hubbell, S. P. & Foster, R. B. 1992 Short-term population dynamics of a neotropical forest: why ecological research matters to tropical conservation and management. *Oikos* **63**, 48–61.
- Hubbell, S. P., Foster, R. B., O'Brien, S. T., Harms, K. E., Condit, R., Wechsler, B., Wright, S. J. & Loo de Lao, S. 1999 Light gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* **283**, 554–557.
- Kochummen, K. M., LaFrankie, J. V. & Manokaran, N. 1990 Floristic composition of Pasoh Forest Reserve, a lowland rain forest in Peninsular Malaysia. *J. Trop. Forest Sci.* **3**, 1–13.
- Leigh Jr, E. G., Rand, S. A. & Windsor, D. M. (eds) 1982 *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Washington, DC: Smithsonian Institution Press.
- Leigh Jr, E. G., Windsor, D. M., Rand, S. A. & Foster, R. B. 1990 The impact of the 'El Niño' drought of 1982–1983 on a Panamanian semideciduous forest. In *Global ecological consequences of the 1982–1983 El Niño-Southern Oscillation* (ed. P. W. Glynn), pp. 473–486. Amsterdam: Elsevier Press.
- Manokaran, N., LaFrankie, J. V., Kochummen, K. M., Quah, E. S., Klahn, J., Ashton, P. S. & Hubbell, S. P. 1992 *Stand table and distribution of species in the 50-ha research plot at Pasoh Forest Reserve*. Research Data No. 1. Kepong, Malaysia: Forest Research Institute of Malaysia.
- Molofsky, J. & Augspurger, C. K. 1992 The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology* **73**, 68–77.
- Piperno, D. R. & Becker, P. S. 1996 Vegetational history of a site in the central Amazon basin derived from phytolith and charcoal records from natural soils. *Quat. Res.* **45**, 202–209.
- Wyatt-Smith, J. 1987 *Manual of Malayan silviculture for inland forest: red meranti-keruing forest*. Research Pamphlet No. 101. Kepong, Malaysia: Forest Research Institute of Malaysia.