

# Presence and absence of density dependence in a neotropical tree community

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## SUMMARY

We report dynamic data on the spatial pattern of sapling recruitment over a three-year interval in a 50 ha† mapped plot Barro Colorado Island (BCI), Panama. We analysed sapling recruitment of a given tree species against recruitment of all other competing tree species, as a function of distance to nearest conspecific adult tree. Strong negative conspecific effects of large trees on saplings were detectable in a few very common species, but not in many others. The power to detect conspecific effects was evaluated in model tree populations in which the strength of these effects was known *a priori*. The measured conspecific effects appear strong enough in the densest species to prevent them from assuming complete dominance. However, many species do not show these effects, and we conclude that these effects play only a limited contributing role to the maintenance of tree species diversity in the BCI forest.

## INTRODUCTION

The regulation of plant populations, particularly of long-lived plants such as trees, is very poorly understood. By regulation, we refer to the idea that there are clear limits to population size, and that the processes that generate these limits operate in a density-dependent manner (Silvertown 1982). In principle, density-dependent processes in plant populations can affect per head rates of birth, death and migration, or any combination of these rates. In practice density dependence is a more problematic concept to apply to sessile plants than to mobile animals.

As rooted organisms, sessile plants probably rarely if ever experience competition for resources from the population as a whole, but the spatial scales over which competition actually operates are poorly known. Most populations, even those of highly agile animals, are subdivided with respect to competition for resources, but competition is often an especially localized phenomenon in plants, which compete mainly with their immediate neighbours for limited light, water, and soil nutrients. For this reason, density is probably not the variable of choice in constructing neighbourhood models of plant competition. Rather, the number, size, and proximity of competing plants may be more appropriate variables (Pacala & Silander 1985; Silander & Pacala 1985). Most of the conceptual advances in the field of density dependence in plant populations have come through studies of monocultures, leading to the discovery of the limiting relation between stem density and mean weight per plant in self-thinning populations (White 1981). We

know considerably less about the prevalence and mechanics of density dependence in species-rich plant communities, such as tropical forests.

Nevertheless, it would be incorrect to argue that plants never compete at a distance. Non-neighbouring plants have been shown, for example, to compete for the attention of pollinators and seed dispersal agents in several species (see, for example, Howe & Vande Kerchove 1979). The question is whether such effects are ever strong enough to limit plant populations. We still lack a sufficient number of empirical studies to generalize about the spatial scales over which neighbourhood competitive effects operate on different plant life history stages and processes. Whatever the appropriate spatial scales turn out to be, it is clear that we must adopt an explicitly spatial approach to understanding density dependence in mixed-species plant communities, with mapped populations, at least until we better understand the connection between local neighbourhood effects and the regulation of plant populations as a whole.

This paper addresses the question of the prevalence and importance of density dependence in limiting the abundance of tree populations in a species-rich neotropical forest in Panama. The evidence on density dependence is phenomenological and non-experimental, and therefore our case is circumstantial. Nevertheless, most hypotheses for density dependence in plant populations have explicit spatial consequences, so the signature of density-dependence should be readily apparent in the unfolding fate of individual plants in precisely mapped plant communities.

† 1 hectare = 10<sup>4</sup> m<sup>2</sup>.

### THE BARRO COLORADO ISLAND FOREST: A CASE STUDY

Over the past decade we have been studying the population and community dynamics of a mapped, 50 ha plot of old growth forest on Barro Colorado Island (BCI), Panama (Hubbell & Foster 1983, 1986*a, b*). The organizing objective of this research has been to understand the maintenance of tree diversity in the BCI forest and the factors that determine patterns of relative tree species abundance. As part of this objective, we have assessed the phenomenological evidence for density dependence in tree populations in the plot, first from the static data on tree population density and dispersion obtained from the primary census and map completed in 1982 (Hubbell & Foster 1986*a*), and then from the short-term dynamic data on survival, growth, and recruitment obtained from the 1985 recensus (Condit *et al.* 1990). The plot is now being completely censused for the third time (1990), but the results of this recensus will not be known until next year.

BCI is an island of about 15 km<sup>2</sup> in artificial Gatun Lake in the zone of the Panama Canal. When the canal was finished, BCI was declared a nature reserve and it is now managed as a biological research station by the Smithsonian Tropical Research Institute. In 1980 we laid out the 50 ha plot in old-growth forest on the summit of the island (Hubbell & Foster 1983). The plot is on relatively uniform terrain, with gentle slopes on the eastern and southern margins, and with a seasonal swamp in the centre of about 2 ha in extent (figure 1). With the exception of a small piece of secondary forest about 75 years old at the north edge of the plot, the remaining *ca.* 49 ha is covered with old-growth forest that dates from precolombian times. Thorough palaeoecological surveys have revealed that the forest was never cleared for slash-and-burn agriculture, but occasional small clearings, probably

seasonal hunting camps, were made in the forest prior to 550 years BP (Piperno, personal communication). The BCI climate is seasonal, with a pronounced dry season from late December until April (Leigh *et al.* 1982).

Because the BCI flora is so well known (Croat 1978), BCI was an ideal site for a large-scale study of tropical forest dynamics. The 50 ha plot contains approximately 242 000 free-standing woody plants with stem diameters of 1 cm diameter at breast height (dbh) or larger, each of which has been tagged, mapped and identified to one of 306 species in the plot (Foster & Hubbell 1990). Species abundances range over 4.6 orders of magnitude, from 21 extremely rare species represented by a single individual apiece, to a very common shrub, *Hybanthus prunifolius* (Violaceae), represented by over 40 000 individuals in 1985 (figure 1) (Hubbell & Foster 1986*b*).

In this paper, the phenomenological evidence for density dependence in BCI tree species from the first and second censuses is reviewed. We exploit natural variation in local tree density to test hypotheses of density dependence. Tree densities both within and among species vary widely, as revealed when the 50 ha plot is tessellated into nearest neighbour polygons. For example, figure 2 is the Dirichlet tessellation for all canopy trees over 30 cm dbh, and is shown to convey a sense of the great range in local stand densities found within the plot. We then analyse density dependence in greater detail in two very common species, one exhibiting strong density dependence (*Trichilia tuberculata*, Meliaceae), and the other no detectable density dependence (*Quararibea asterolepis*, Bombacaceae). We conclude by modelling the dynamics of *Trichilia tuberculata*, and argue that the density dependence observed in this species is sufficient to limit the species at or near its present abundance. However, we also conclude that most of the remaining species in the BCI forest are probably nowhere near the densities at which

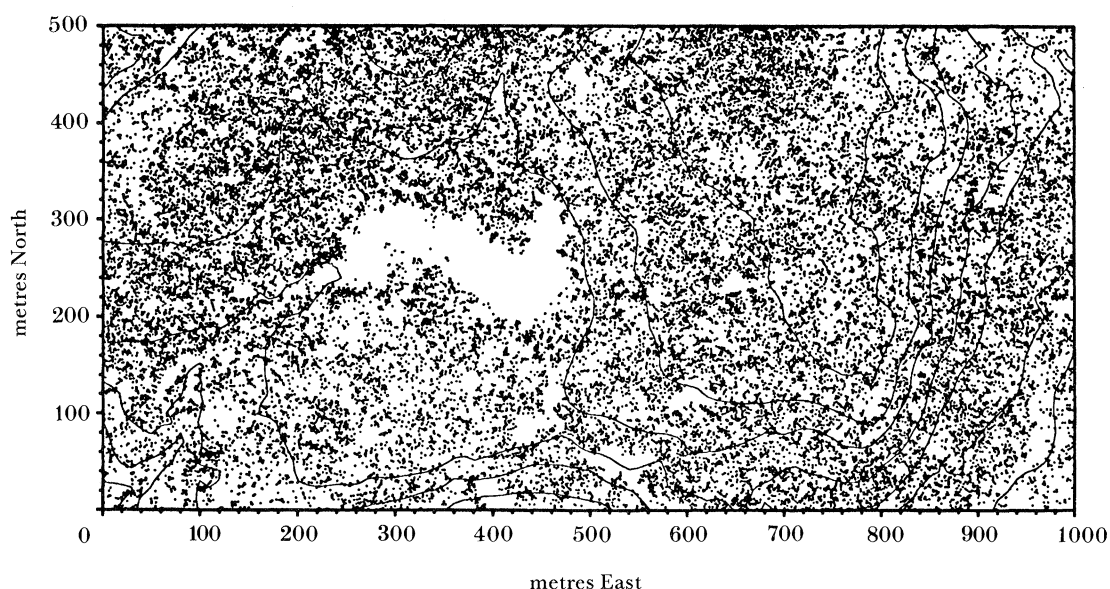


Figure 1. Map of the commonest species in the 50 ha plot on Barro Colorado Island, the shrub, *Hybanthus prunifolius* (Violaceae), with 41 106 individuals in the 1985 census. This species exhibited no detectable negative density dependence in recruitment.

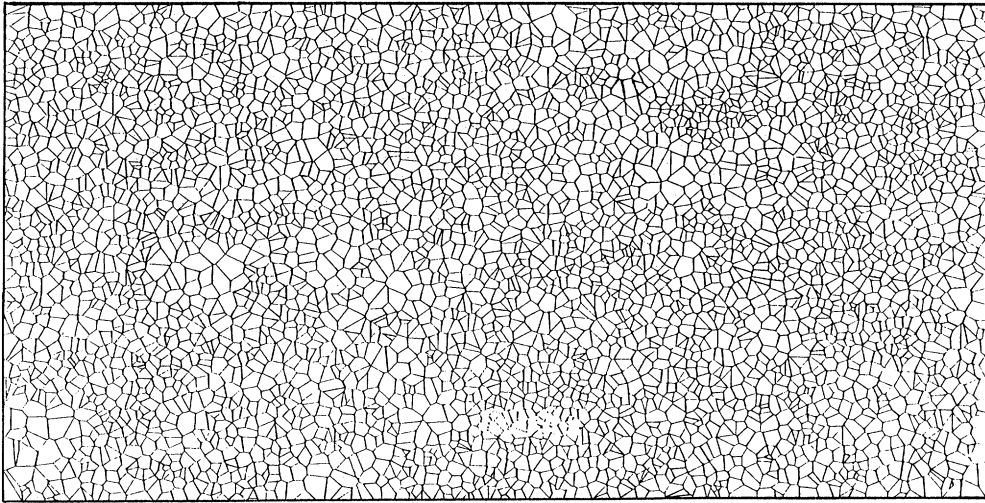


Figure 2. Dirichlet tessellation of the 50 ha plot for canopy trees greater than 30 cm dbh, showing the great variation in local tree densities in the plot. Each polygon defines the boundaries of the nearest neighbour region surrounding each canopy tree.

density dependence would begin to strongly influence their population dynamics.

#### THE SEARCH FOR DENSITY DEPENDENCE IN BCI TREE SPECIES

Are there density-dependent limits to the abundance of tree species in the BCI forest? The short answer is of course yes. An ultimate limit is set by the self-thinning law for each species growing in monoculture. However, the more interesting and difficult question is: are there non-trivial limits to tree abundance short of reaching a state of single-species dominance? If so, at what population densities of a given species in a mixed-species stand are these limits approached? What are the life history stages and processes at which density-dependence regulates the population? We cannot at present answer all these questions satisfactorily, but analyses of both the static, first-census data and the recensus data on short-term dynamics led us to the conclusion that only two or three of the most abundant tree species in the BCI forest are prevented by density dependence from increasing above present abundance levels in the plot (Hubbell & Foster 1986*a*, 1990*a*).

##### (a) Evidence from Population Dispersion

With the primary census data, we began looking for the spatial signature of density dependence at several spatial scales within the limits set by the 50 ha plot. The first study was a quadrat-based analysis of the relative dispersion of saplings and adults. We analysed how the adult (per head) production of saplings varied with local adult tree density, in quadrats ranging in size from  $4 \times 10^2 \text{ m}^2$  to  $10^5 \text{ m}^2$  (10 ha) (Hubbell & Foster 1986*a*). We found a strong local depression in the per head number of juveniles in the densest patches of adults in the two most common mature-phase, canopy tree species, *Trichilia tuberculata* (Meliaceae) and *Alseis blackiana* (Rubiaceae), particularly in the range of quadrat sizes of 1 ha and larger. Of the

remaining 46 canopy species examined, roughly half also showed significant but weak negative second-order terms in a quadratic regression of the number of small saplings per hectare on number of adults per hectare (Hubbell & Foster 1986*a*). However, these second-order effects, although statistically significant, were judged unlikely to be important to population regulation because they are grossly too small to limit populations to observed abundances, sometimes by several orders of magnitude. The density effects detected in the static data analysis were not strong enough to prevent any species, with the possible exception of *Trichilia* and *Alseis*, from assuming complete monospecific dominance or increasing to impossibly supersaturated tree densities.

We re-analysed the primary census data from a focal tree perspective, asking which species were likely to replace the current adult trees in the canopy, by using a tree replacement analysis modified from Horn (1975). Based on the distribution of saplings growing beneath the adults of each canopy tree species, we estimated the probabilities of self-replacement or replacement by other species in the next generation (Hubbell & Foster 1986*c*). The major conclusions from these analyses were that: (i) all species were capable of in-situ self-replacement; (ii) nevertheless, the probability of self-replacement was very low, as was the probability of replacement by any other specified species, and (iii) this low replacement rate was not because of any inability to self-replace but simply to the low frequency of any given species and the high species richness in the forest. We were unable to reject the null hypothesis that the collective set of probabilities of self-replacement were a random draw of the probabilities of any arbitrary pairwise species replacement. However, when the 10 commonest species were analysed individually, strong sapling avoidance of adults was found in two species, *Trichilia* and *Alseis*, and is visibly evident in *Trichilia* (figure 3).

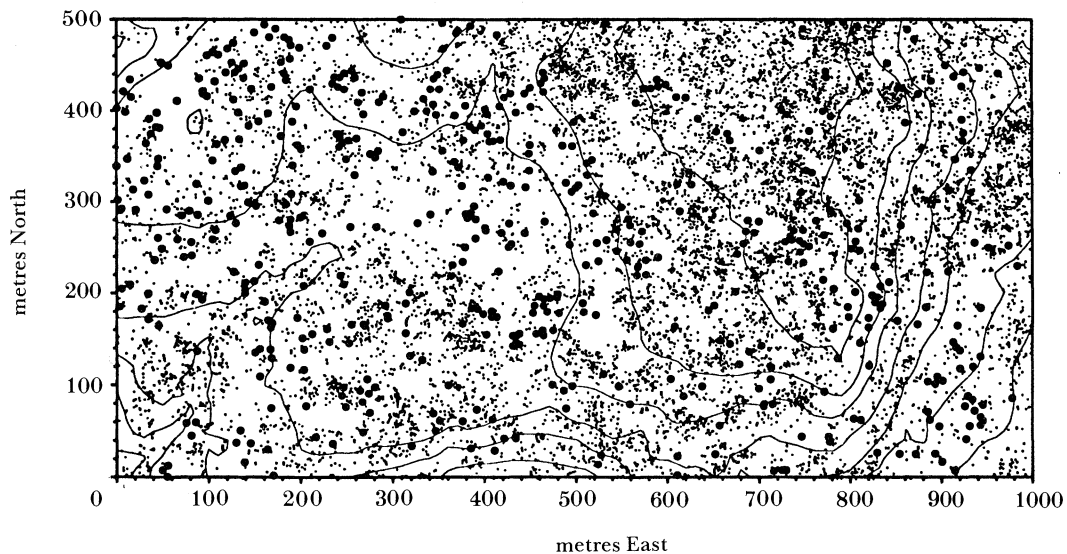


Figure 3. Map of the commonest canopy tree in the 50 ha plot, *Trichilia tuberculata* (Meliaceae). Large dots are adult trees greater than 30 cm dbh; small dots are all smaller *Trichilia* plants.

#### (b) Evidence from growth and survival patterns

When the plot was recensused in 1985, we had our first opportunity to analyse short-term rates of survival, growth, and recruitment of new saplings. In analysing the dynamic data, we again took a focal tree approach and analysed sapling performance as a function of adult tree proximity. First, we compared the growth and survival rates of 1–4 cm dbh saplings located beneath large trees of either the same or of different species, for canopy tree species (Hubbell & Foster 1990*a*). When all species were pooled and tested together, there was a 5.3% reduction in survival rate ( $p < 0.0001$ ), and 23.5% reduction in annual growth rate ( $p < 0.0003$ ), in saplings growing beneath conspecific vs. beneath heterospecific large trees.

When separate analyses of individual species were conducted, however, the results were less clear cut. It now appears that the pooled species results were driven in part by the behaviour of the two commonest species, which show strong conspecific effects. Table 1 compares the growth and survival performance of saplings beneath conspecific and heterospecific large trees for the 11 most common canopy species. Sample size were adequate to compare growth rate differences in three juvenile size classes, 1–2, 2–4 and 4–8 cm dbh, but sample sizes limited survival comparisons to one size class, 1–4 cm dbh.

Several conclusions can be drawn from these results: first, all significant conspecific effects on sapling growth and survival were negative in sign. Secondly, the only two species to show significant negative conspecific effects on both survival and growth were *Trichilia* and *Alseis*, the two most abundant canopy tree species, and the same two that showed local density dependence in the static first-census data. Thirdly, most common species did not exhibit detectable conspecific effects, and most were a long way from significance ( $p > 0.5$ ), not for lack of sample sizes (all species tested had more than 500 total saplings). Even species as abundant as the fifth most common canopy tree, *Quararibea asterolepis*

(Bombacaceae), showed no effect of neighbouring conspecific adult on sapling growth or survival (table 1). Fourth, being beneath a conspecific adult was more likely to affect sapling growth rate than survival rate. Finally, significant negative conspecific effects on growth occurred more often in the smaller size classes, which was not unexpected. More surprising was the suggestion that these negative effects may persist into quite large juvenile size classes (2–4 cm dbh), at least in some species. Overall, negative conspecific effects on growth were much more common than positive effects ( $p < 0.001$ ), although there was no difference in the case of survival (table 1).

These conspecific effects, when detected, appeared to be real and not due to spurious correlations. We tested all reasonable alternative hypotheses. For example, if conspecific adult trees happened to be closer on average to the test saplings than the heterospecific adult trees, or happened to be larger. In these cases, apparent conspecific effects could be due to competition from a closer or larger tree instead. We tested four alternative hypotheses for these effects: (i) conspecific adult trees are nearer; (ii) conspecific adult trees are larger; (iii) conspecific sites are shadier (higher canopy), and (iv) conspecific sites have higher overall competition because of higher stand densities. Although there were some significant differences in these variables, without exception the significant differences were not in the right direction to explain significant conspecific effects (table 2). Indeed, when negative conspecific effects were detected, they were found in spite of incidental effects in the opposite direction. For example, negative growth and survival effects were found in *Alseis* and *Trichilia* in spite of the fact that conspecific adult trees were on average farther from the test saplings and smaller in diameter, than were heterospecific large trees (table 2). Partial regression analyses confirmed the results of these univariate tests.

Table 1. Summary of juvenile growth and survival beneath conspecific against heterospecific large trees, over the interval 1982–1985 in the BCI 50 ha plot

(Growth rate differences are reported for three sapling size classes, 1–2 cm dbh, 2–4 cm dbh, and 4–8 cm dbh. Survival rate differences are reported for a single size class, 1–4 cm dbh. The entry of a ‘less-than’ symbol means that juvenile performance was worse in saplings beneath trees of the same species than beneath trees of other species. A ‘greater-than’ symbol means that performance was better beneath trees of the same species. Unbracketed symbols indicate significant differences in performance at  $p < 0.05$ ; symbols in brackets show non-significant differences. Note that all individually significant growth and survival rate differences represent poorer performance beneath conspecifics. Also, for growth rates, there are significantly more ‘less-than’ symbols (24) than ‘greater-than’ symbols (9) ( $p < 0.01$ ,  $\chi^2$ ). However, there are roughly equal numbers of species that show better survival beneath conspecifics (5 species) than beneath heterospecifics (6 species).

| tree species                   | family        | performance of different diameter classes (cm dbh) |     |     |                      |
|--------------------------------|---------------|--|-----|-----|----------------------|
|                                |               | growth rate<br>1–2                                 | 2–4 | 4–8 | survival rate<br>1–4 |
| <i>Alseis blackiana</i>        | Rubiaceae     | <  | (<) | (<) | <                    |
| <i>Beilschmiedia pendula</i>   | Lauraceae     | <  | <   | (>) | (<)                  |
| <i>Drypetes standleyi</i>      | Euphorbiaceae | (<)  | (<) | (<) | (>)                  |
| <i>Guatteria dumetorum</i>     | Annonaceae    | (>)  | (>) | (>) | (>)                  |
| <i>Ocotea skutchii</i>         | Lauraceae     | <  | (<) | (<) | (<)                  |
| <i>Poulsenia armata</i>        | Moraceae      | (<)  | <   | (>) | (<)                  |
| <i>Prioria copaiifera</i>      | Leguminosae   | (<)  | (<) | (>) | (>)                  |
| <i>Quararibea asterolepis</i>  | Bombacaceae   | (>)  | (<) | (>) | (>)                  |
| <i>Tabernaemontana arborea</i> | Apocynaceae   | <  | (>) | (<) | (<)                  |
| <i>Tetragastris panamensis</i> | Burseraceae   | (<)  | (<) | (<) | (>)                  |
| <i>Trichilia tuberculata</i>   | Meliaceae     | <  | <   | (<) | <                    |

Table 2. Tests of four alternative hypotheses to explain apparent conspecific effects, including (i) distance to neighbouring adult tree; (ii) size (diameter) of neighbouring adult tree; (iii) canopy height over conspecific against heterospecific site (shade), and (iv) stand density at conspecific against heterospecific site.

(In (i), a ‘less-than’ symbol means that the conspecific tree is on average closer than the heterospecific tree to the test sapling. In (ii), a ‘less-than’ symbol means that the conspecific tree is on average smaller in diameter than the heterospecific tree. In (iii), a ‘less-than’ symbol means that the conspecific site on average has lower canopy (younger forest) than does the heterospecific site. In (iv), a ‘less-than’ symbol means that the conspecific site on average has lower stand density than does the heterospecific site. Only differences significant at  $p < 0.05$  are shown; dashes show non-significance. The column headings 1, 2, and 4 refer to the juvenile diameter classes, 1–2, 2–4 and 4–8 cm dbh. See table 1 for the full species names.)

| species                | four alternative hypotheses |   |   |                |   |   |               |   |   |               |   |   |
|------------------------|-----------------------------|---|---|----------------|---|---|---------------|---|---|---------------|---|---|
|                        | adult distance              |   |   | adult diameter |   |   | Canopy height |   |   | stand density |   |   |
|                        | (cm dbh)                    |   |   | (cm dbh)       |   |   | (cm dbh)      |   |   | (cm dbh)      |   |   |
|                        | 1                           | 2 | 4 | 1              | 2 | 4 | 1             | 2 | 4 | 1             | 2 | 4 |
| <i>Alseis</i>          | >                           | > | > | <              | < | < | <             | < | – | –             | > | – |
| <i>Beilschmiedia</i>   | –                           | – | – | >              | – | – | <             | – | – | –             | – | – |
| <i>Drypetes</i>        | –                           | – | – | <              | – | – | –             | – | – | –             | – | – |
| <i>Guatteria</i>       | –                           | – | – | –              | – | – | –             | – | – | –             | – | – |
| <i>Ocotea</i>          | –                           | – | – | >              | > | – | –             | – | – | –             | – | – |
| <i>Poulsenia</i>       | <                           | – | – | –              | – | – | –             | – | – | –             | – | – |
| <i>Prioria</i>         | –                           | – | – | –              | – | – | –             | – | – | –             | – | – |
| <i>Quararibea</i>      | –                           | – | – | >              | > | – | –             | – | – | –             | – | – |
| <i>Tabernaemontana</i> | –                           | – | – | <              | – | – | <             | – | – | –             | – | – |
| <i>Tetragastris</i>    | –                           | – | – | –              | – | – | –             | – | – | –             | – | – |
| <i>Trichilia</i>       | >                           | > | > | <              | < | < | <             | – | – | –             | – | – |

### (c) Evidence from recruitment patterns

We examined sapling recruitment patterns for density dependence, again taking a focal adult approach. We tested whether sapling recruitment was inhibited near conspecific adult trees (Condit *et al.* 1990). We defined a recruit as any plant  $< 4$  cm dbh in 1985 that was not present in the first census, and therefore was  $< 1$  cm dbh in 1982. To set this analysis

in a community context, we compared new recruitment in a given species relative to the collective recruitment of all its competitors. We calculated the ratio of recruits of focal species  $i$  to all recruits, including the same and competing species, at each location as a function of distance from the nearest adult tree of the focal species. This relative recruitment analysis represented an improvement over most previous analyses, including ours, which had treated each species in isolation from

Table 3. *Recruitment pattern of new saplings relative to nearest conspecific adult in 15 shrub species, 19 understory treelet species, 25 midstory tree species, and 22 canopy tree species (modified from Condit et al. 1990)*

(‘Attracted pattern’ means that recruits were more abundant than expected near conspecific adults. ‘Repelled pattern’ means that recruits were less abundant than expected near conspecific adults. ‘Near’ is defined as one adult canopy radius. The proportion of species repelled within 1–5 crown radii is also reported).

| recruitment pattern  | trees  |            |          |        | total |
|--|--------|------------|----------|--------|-------|
|  | shrubs | understory | midstory | canopy |       |
| attracted pattern  | 13     | 8          | 3        | 3      | 27    |
| repelled pattern   | 0      | 3          | 4        | 6      | 13    |
| partially repelled pattern                                   | 1      | 2          | 4        | 7      | 14    |
| no pattern (indifferent)                                     | 1      | 6          | 14       | 6      | 27    |
| total number of species                                      | 15     | 19         | 25       | 22     | 81    |
| proportion of species<br>repelled or partially<br>repelled   | 0.07   | 0.26       | 0.32     | 0.59   | 0.33  |
| proportion of species<br>repelled within 1–5<br>canopy radii | 0.07   | 0.16       | 0.28     | 0.36   | 0.23  |

its competitors. We also, for the first time, analysed recruitment in species of all growth forms, from shrubs to canopy trees. We recognized four recruitment patterns: repelled, partially repelled, attracted and indifferent (Condit *et al.* 1990). Species exhibiting repelled patterns showed significant deficits in the number of recruits close to conspecific adults, and consistent repulsion to some distance from the adult tree. Partially repelled species showed inconsistent repulsion, with significant deficits of recruits at some nearby distance intervals, but not others. Attracted species showed significant over-representation of recruits close to adults. Indifferent species exhibited patterns that were indistinguishable from the random patterns of recruitment exhibited by all species collectively.

We also compared relative recruitment rates within one crown radius of the adult trees, and then within 1–5 crown radii, in the immediate neighbourhood. The results showed that several canopy tree species inhibited their own recruitment rate relative to that of other species immediately beneath their own canopy (table 3). However, this negative effect was much less prevalent among shrubs, understory treelets, and midstory trees. There was no effect even in the most common species in the plot, the shrub, *Hybanthus prunifolius* (figure 1), which accounts for almost one out of every six plants > 1 cm dbh in the plot. When the effect was present, it generally disappeared at the edge of the crown in most species. Only a few tree species inhibited recruitment beyond their crown in the near neighbourhood from 1–5 crown radii away, including *Trichilia*. Most species in fact showed the opposite, with significant excesses of recruitment in the immediate neighbourhood adjacent to the focal tree (Condit *et al.* 1990). We concluded that these negative conspecific effects, when they occurred, were too local to prevent the given species from becoming very common. Indeed, even strong repulsion effects in *Trichilia*, extending out several canopy radii, did not prevent this species from becoming the most abundant species in the BCI forest.

In theoretical models, confining conspecific inhibition of recruitment just to prevention of self-replacement results in an equilibrium tree community containing only three tree species (Hubbell 1980).

#### ANALYSING DENSITY DEPENDENCE IN *TRICHILIA* AND *QUARARIBEA*

The preceding analyses of static pattern and short-term dynamics all led to a similar conclusion, namely that detectable negative conspecific effects in BCI tree species are limited mainly to a few canopy trees, particularly those that are extremely abundant, and are less often found in shrubs and subcanopy tree species, regardless of abundance. However, they fall short of proof that these conspecific effects generate sufficiently strong density dependence to limit populations even of the most common canopy trees, let alone populations of the less common species. In the absence of experimental tests, the best remaining avenue for analysis is to model the observed local conspecific effects and evaluate their consequences for population-level regulation of total abundance.

We chose to examine two species in detail, *Trichilia tuberculata*, the most abundant canopy tree species in the BCI plot with 13 164 individuals > 1 cm dbh in 1985, and *Quararibea asterolepis*, the fifth most abundant canopy tree, with 2382 individuals greater than 1 cm dbh. The full details of the analyses and results will be presented in a separate paper (Condit *et al.* in preparation), but the main results are outlined here.

##### (a) *Density effects on recruitment*

To estimate density-dependence in recruitment rates, for each newly recruited sapling in 1985, we calculated the number of large conspecific trees (> 16 cm dbh) that were present in 1982 within 5, 10, 30, 50 and 75 m of the given sapling. We used the 1982 data for large trees because virtually all of the 1985 recruits entering the census at a diameter of 1 cm were alive in

1982. Because the number of recruits was large, it was possible to isolate and directly measure the effects of large conspecifics at different distances. We also considered whether the presence of large subadult trees also influenced recruitment rate.

**(b) Density effects on survival and growth**

We estimated density-dependence in survival and growth in plants in the following six size classes: 1–2, 2–4, 4–8, 8–16, 16–32 and 32 cm dbh and above. The effect of conspecific density of three size classes on the focal plant were considered; these size classes were 1–4, 4–16 and 16 cm dbh and above. Each focal plant was categorized by the number of conspecifics present within various distance intervals. In *Trichilia*, the distances began at 5 m, then increased to larger values (10, 15 and 50 m), while holding density within 5, 10 or 15 m at zero. In *Quararibea*, the same analyses were done, but the distance intervals had to be adjusted because of smaller sample sizes, to 7, 14, 21 and 50 m, respectively. With these adjustments, we were able to directly isolate the effect of conspecific density on one of the three size classes while holding density of the other two constant. For example, we allowed density of 1–4 cm dbh neighbours within 5 m to vary while holding the density of plants greater than 4 cm dbh within 5 m at zero. Statistical significance in growth or mortality was assessed both by chi-square comparisons and by multiple regression, to minimize errors due to correlated effects. There were 12 independent variables: the number of neighbours in the three size classes (1–4, 4–16, and 16+ cm dbh) and four distance intervals. Results of the multiple regression analysis bore out all conclusions from the chi-square tests, so we report only the  $\chi^2$  tests here.

**(c) Density dependent life tables**

The BCI plot was divided into 50, 100 × 100 m (1 ha) subplots. These hectares were grouped into six categories of adult density, based on the density of *Trichilia* trees greater than 30 cm dbh present in 1982, and five categories for *Quararibea*. For each of these density regions, a life table was constructed, based on approximately doubling size classes. Transition probabilities for each pair of size classes, and mortality data for each, were estimated from the 1982–85 census data. Transitions to smaller size classes were disallowed in this analysis, although this is an oversimplification since a small fraction of trees that lose their trunk manage to resprout and survive. All recruitment was attributed to trees > 30 cm dbh. An estimate of recruitment rate was determined for each of the six density regions by dividing the number of 1985 recruits by the number of 1982 trees greater than 30 cm dbh. The population rate of increase,  $\lambda$ , was calculated for each life table following standard procedures. To test whether differences in population growth rate were significant, we used a simple bootstrap procedure. We calculated  $\lambda$  values 100 times for life tables created from random subsets of hectares, and set the 5%  $\alpha$  level by the fifth largest  $\lambda$  value.

**(d) Population simulations**

A life table model was created that took into account density dependent effects on recruitment and size-specific survival and growth. The model kept track of individual plants in an explicitly spatial fashion within a 16 ha (400 × 400 m) model plot. Six doubling size classes were used: 1–2, 2–4, 4–8, 8–16, 16–32, and 32 cm dbh and above. Initial conditions assumed random dispersion of 25 plants divided randomly among the six size classes. We then calculated survival and growth probabilities for each individual as a function of the number of its conspecific neighbours. Density dependence in survival and growth was modelled by first defining baseline (maximal) growth and survival rates for individuals unaffected by conspecific neighbours. Growth and survival were then adjusted downward as the number of neighbours increased, assuming a linear effect of number of neighbours in each distance interval. The slope of the effect was estimated by regressing growth or mortality rate on number of neighbours.

Density dependence in recruitment was more problematic to model. We defined a baseline recruitment rate by calculating the density of recruits in regions of the plot with the lowest density of large conspecific neighbours. This assumes that regions that do not currently have many adult trees are suitable regeneration sites for saplings. This seems reasonable at least in *Trichilia* because these regions showed the highest recruit density recorded, which we call  $r_{\max}$ . Let  $a$  be the number of 32+ cm dbh trees in the plot. Then  $50 \cdot r_{\max}/a$  estimates the recruitment rate per head in the absence of density-dependent effects, such as when the population density is very low. Next we calculated the proportion of the 16 ha that fell within given distances and densities of large trees. The number of recruits in this area was reduced from the maximum recruit density by the appropriate density-dependent factor based on the regression analyses.

Each cycle of the model corresponded to a time step of three years as all parameter values were based on the three year intercensus period, 1982–85. Simulations were continued for up to 4000 cycles, and total population and numbers in each size class were recorded every 100 cycles.

**DENSITY DEPENDENCE IN *TRICHILIA*, AND ITS ABSENCE IN *QUARARIBEA***

**(a) Density dependence in recruitment**

The density of recruits in *Trichilia* was much lower in regions close to large conspecifics (figure 4a). In areas within 5 m of a large *Trichilia* tree, there were fewer than 15 recruits per hectare, whereas the mean for the whole plot was 32.6 ha<sup>-1</sup>. We were surprised to discover that the density of large conspecifics from 10–30 m away, 30–50 m away, and 50–75 m away all had significant, independent negative effects on recruit density in *Trichilia*. We did not test beyond 75 m because of small sample sizes. Figure 4b summarizes the effects from 10–75 m. In regions of the plot with fewer than 25 large plants within 75 m (and none



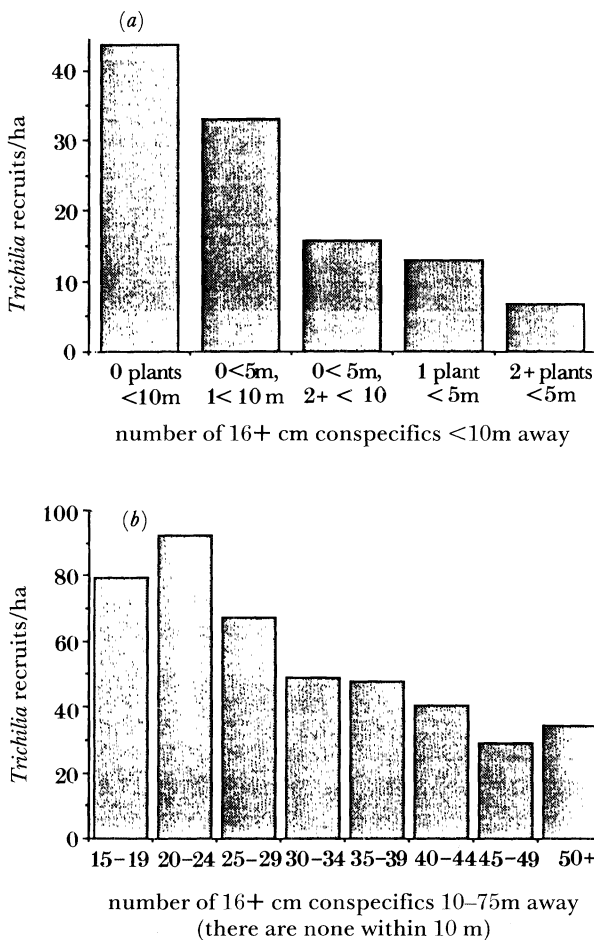


Figure 4. Effect of conspecific neighbours on recruitment rate per hectare in *Trichilia tuberculata*. (a) Effect of the number of large (16+ cm dbh) conspecifics less than 10 m away. (b) Effect of the number of large (16+ cm dbh) conspecifics at distances between 10 and 75 m away. There were none within 10 m for these calculations.

within 10 m), recruit density exceeded  $80 \text{ ha}^{-1}$ , more than tenfold greater than in regions very close to large neighbours (figure 4a the lowest point). The effect of local density of neighbouring 4–16 cm dbh plants on recruit density in *Trichilia* was just the opposite: in regions with more mid-sized neighbours, there were also more recruits. For example, in regions with no mid-sized neighbour within 5 m, recruit density was  $32.3 \text{ ha}^{-1}$ , whereas in regions with more than three mid-sized neighbours, the figure was 48.6. This difference was statistically significant. In *Quararibea*, there was no suggestion that large conspecifics were negatively associated with recruitment. Both large and mid-sized conspecifics showed positive associations with recruits in this species (figure 5a, b).

#### (b) Density dependence in survival and growth

There were extensive local density effects on survival in *Trichilia*. The most pronounced effects were negative, large trees within 5 m greatly reduced survival. Within 5 m, this effect persisted until young trees were 8 cm dbh (figure 6a, table 4). In addition, the effect of large neighbours on the smallest size class persisted as far as 15 m (table 4). Moreover, local density of mid-

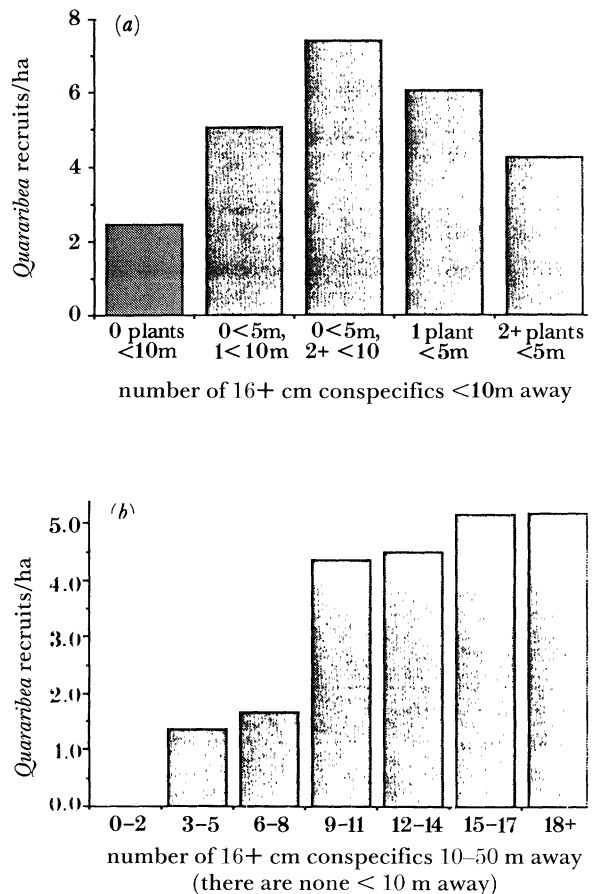


Figure 5. Effect of conspecific neighbours on recruitment rate per hectare in *Quararibea asterolepis*. (a) Effect of the number of large (16+ cm dbh) conspecifics less than 10 m away. (b) Effect of the number of large (16+ cm dbh) conspecifics at distances between 10 and 75 m away. There were none within 10 m for these calculations.

sized trees was also associated with reduced survival of the two smallest size classes (figure 6b). In contrast to the effects of large and mid-sized conspecifics, local density of small plants tended to be positively associated with survival in *Trichilia* (table 5). Growth effects were rather inconsistent, however, with some positive and some negative effects; and none were as great in magnitude as the strongest survival effects (table 5).

In *Quararibea*, we concluded that there is no credible evidence of systematic effects of local density on survival (figure 7, table 6). There were six tests showing a significant effect, but these were scattered, and as many were positive as were negative (table 6). The effects of local density on growth in *Quararibea* were similar, with only four tests showing significance, one positive and three negative.

In both *Trichilia* and *Quararibea*, density of large conspecifics between 10 and 50 m had no effect on survival or growth of any size class. Because there was no effect of the largest size class, we did not repeat the test with mid-sized trees as the independent variable.

#### (c) Density dependence in life tables

Figure 8 shows the hectares with highest and lowest density of adult trees in *Trichilia*. In the 16 lowest



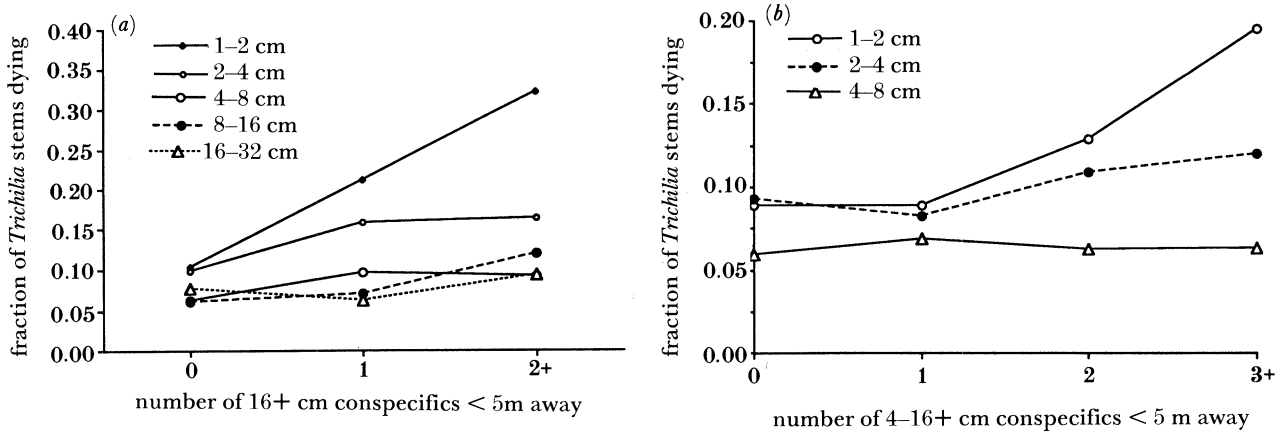


Figure 6. Effect of conspecific neighbours on mortality rate of different size classes of *Trichilia tuberculata*. (a) Fraction of plants dying between 1982 and 1985 as a function of the number of large (16+ cm dbh) conspecifics less than 5 m away. (b) Fraction of plants dying between 1982 and 1985 as a function of the number of medium-sized (4–16 cm dbh) conspecifics less than 5 m away.

Table 4. Conspecific density effects on survival in *Trichilia*

(The right-most columns are slopes of regressions of survival on density in a particular distance range. In doing the regressions, terminal size classes were combined so that sample size in any class was never below 20. A positive sign indicates survival increased with distance, a negative sign indicates a decline. Blanks indicate no significant effect, based on a  $\chi^2$  test. Boldface entries were used in the simulation model; others were not.)

|                                  |                     | distance/m    |               |               |       |
|----------------------------------|---------------------|---------------|---------------|---------------|-------|
| effect of 1–4 cm dbh size class  |                     |               |               |               |       |
| baseline survival                | size class affected | 0–5           | 5–10          | 10–15         | 15–20 |
| 0.903                            | 1–2 cm              | —             | +0.022        | —             | —     |
| 0.911                            | 2–4 cm              | +0.014        | —             | —             | —     |
| 0.949                            | 4–8 cm              | —             | —             | —             | —     |
| 0.950                            | 8–16 cm             | —             | —             | —             | —     |
| 0.938                            | 16–32 cm            | —             | —             | —             | —     |
| 0.843                            | 32+ cm              | +0.087        | +0.013        | —             | —     |
| effect of 4–16 cm dbh size class |                     |               |               |               |       |
|                                  | size class affected | 0–5           | 5–10          | 10–15         | 15–20 |
|                                  | 1–2 cm              | <b>–0.036</b> | —             | –0.024        | —     |
|                                  | 2–4 cm              | –0.011        | —             | —             | —     |
|                                  | 4–8 cm              | —             | —             | —             | —     |
|                                  | 8–16 cm             | —             | —             | —             | —     |
|                                  | 16–32 cm            | —             | —             | —             | —     |
|                                  | 32+ cm              | —             | —             | —             | —     |
| effect of 16+ cm dbh size class  |                     |               |               |               |       |
|                                  | size class affected | 0–5           | 5–10          | 10–15         | 15–20 |
|                                  | 1–2 cm              | <b>–0.109</b> | <b>–0.022</b> | <b>–0.020</b> | —     |
|                                  | 2–4 cm              | <b>–0.033</b> | <b>–0.013</b> | —             | —     |
|                                  | 4–8 cm              | <b>–0.015</b> | <b>–0.006</b> | —             | —     |
|                                  | 8–16 cm             | —             | —             | —             | —     |
|                                  | 16–32 cm            | —             | –0.029        | —             | —     |
|                                  | 32+ cm              | —             | —             | —             | —     |

ranking hectares, the population growth rate calculated from the corresponding life table was  $\lambda = 1.026$ , whereas in the four highest ranking hectares,  $\lambda = 0.917$ . Our bootstrap analyses indicated that a difference between two  $\lambda$  values of 0.056 would be statistically significant at the 5% level, so the difference between high and low density regions is very unlikely to be because of chance. There was a nearly monotonic decrease in  $\lambda$  from low to high density regions (figure 8). Population growth rate was uncorrelated with density in *Quararibea*. Although the lowest  $\lambda$  was found

at the lowest density, the greatest difference between  $\lambda$ s (0.04) was less than the critical value for statistical significance ( $p < 0.05$ ).

(d) Simulation results

Because of the fact that *Quararibea* did not exhibit density dependence, we simulated only the density-dependent growth of *Trichilia*. The parameters used to model density dependence in *Trichilia* survival and growth are given in tables 5 and 6. In the model we

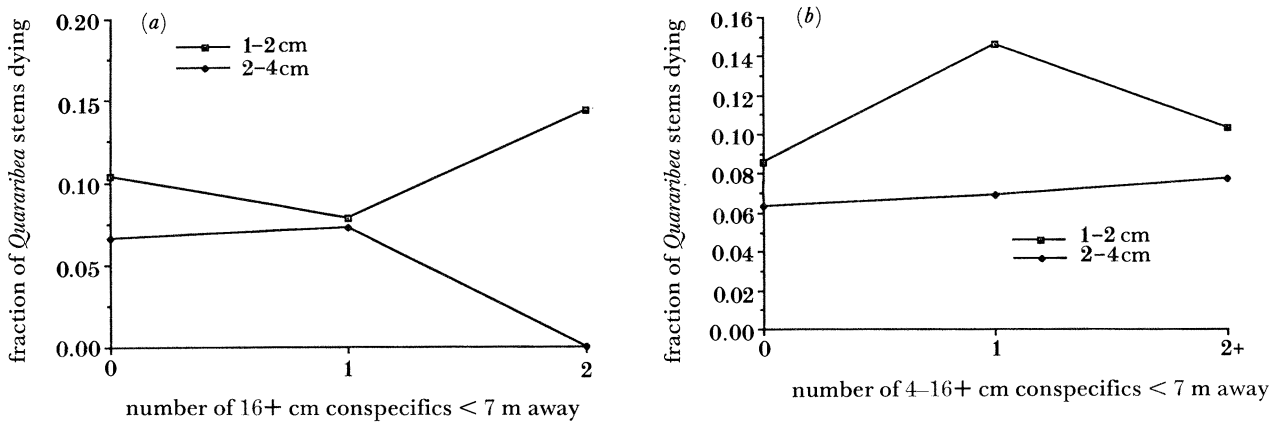


Figure 7. Effect of conspecific neighbours on mortality rate of different size classes of *Quararibea asterolepis*. (a) Fraction of plants dying between 1982 and 1985 as a function of the number of large (16+ cm dbh) conspecifics less than 7 m away. (b) Fraction of plants dying between 1982 and 1985 as a function of the number of medium-sized (4-16 cm dbh) conspecifics less than 7 m away.

Table 5. *Conspecific density effects on growth in Trichilia*

(See explanation for table 4. Growth rate of the largest size class is zero by definition)

|                                  |                     | distance/m    |        |        |        |
|----------------------------------|---------------------|---------------|--------|--------|--------|
| effect of 1-4 cm dbh size class  |                     |               |        |        |        |
| baseline growth                  | size class affected | 0-5           | 5-10   | 10-15  | 15-20  |
| 0.123                            | 1-2 cm              | —             | —      | —      | —      |
| 0.104                            | 2-4 cm              | —             | —      | —      | —      |
| 0.059                            | 4-8 cm              | -0.017        | —      | —      | —      |
| 0.040                            | 8-16 cm             | —             | —      | —      | —      |
| 0.062                            | 16-32 cm            | -0.013        | —      | —      | —      |
| 0.00                             | 32+ cm              | —             | —      | —      | —      |
| effect of 4-16 cm dbh size class |                     |               |        |        |        |
|                                  | size class affected | 0-5           | 5-10   | 10-15  | 15-20  |
|                                  | 1-2 cm              | —             | +0.011 | —      | -0.024 |
|                                  | 2-4 cm              | —             | —      | -0.032 | —      |
|                                  | 4-8 cm              | -0.011        | —      | —      | —      |
|                                  | 8-16 cm             | -0.019        | —      | —      | —      |
|                                  | 16-32 cm            | —             | —      | —      | —      |
|                                  | 32+ cm              | —             | —      | —      | —      |
| effect of 16+ cm dbh size class  |                     |               |        |        |        |
|                                  | size class affected | 0-5           | 5-10   | 10-15  | 15-20  |
|                                  | 1-2 cm              | <b>-0.026</b> | —      | —      | —      |
|                                  | 2-4 cm              | -0.030        | —      | —      | —      |
|                                  | 4-8 cm              | —             | +0.022 | —      | —      |
|                                  | 8-16 cm             | +0.041        | —      | —      | —      |
|                                  | 16-32 cm            | —             | —      | —      | —      |
|                                  | 32+ cm              | —             | —      | —      | —      |

used the clearest density effects (boldface in tables 5 and 6), those which were consistent with a simple, *a priori* hypothesis, namely that the largest size class should have its largest effects on the smallest size classes and at the shortest distances. The baseline survival and growth figures, those in the absence of local neighbours, are also given in tables 5 and 6.

The maximum recruit density in *Trichilia* was about 80 recruits per hectare, found in regions with the lowest density of large *Trichilia* trees (figure 4b). If this density of recruits were found throughout 50 ha, there would be 4000 recruits, or 8.5 recruits per adult. Depression factors were: 0.85 for regions which had one or more large conspecific within 5 m, 0.66 if one was 5-10 m

away (but none within 5 m), and 0.52 for regions that had more than 30 large conspecifics within 75 m (but none within 10 m). Thus, recruitment was almost completely eliminated within 5 m of large trees (85% eliminated), and reached its maximum density only in regions with less than 30 large trees within 75 m. These figures come directly from the data in figure 4, with some regions combined.

The model *Trichilia* population grew from 25 trees at the beginning to a maximum density of about 4200 trees in 16 ha in 500 cycles (1500 years). It remained at about this level for the remaining 1000 cycles of the model (figure 9a). Mortality rate of the smallest size class increased from 0.097 during the first 100 cycles to

Table 6. *Conspecific density effects on survival in Quararibea*

(See explanation for table 4. In this species, the baseline survival rate was simply the mean rate for the entire plot, since there was very little density dependence apparent.)

|                                  |                     | distance/m |        |        |
|----------------------------------|---------------------|------------|--------|--------|
| effect of 1–4 cm dbh size class  |                     |            |        |        |
| baseline survival                | size class affected | 0–7        | 7–14   | 14–21  |
| 0.895                            | 1–2 cm              | —          | —      | —      |
| 0.935                            | 2–4 cm              | —          | —      | —      |
| 0.940                            | 4–8 cm              | —          | —      | +0.048 |
| 0.959                            | 8–16 cm             | —          | —      | —      |
| 0.947                            | 16–32 cm            | —          | —      | —      |
| 0.928                            | 32+ cm              | —          | —      | +0.047 |
| effect of 4–16 cm dbh size class |                     |            |        |        |
|                                  | size class affected | 0–7        | 7–14   | 14–21  |
|                                  | 1–2 cm              | —          | —      | —      |
|                                  | 2–4 cm              | —          | –0.083 | —      |
|                                  | 4–8 cm              | —          | —      | —      |
|                                  | 8–16 cm             | +0.029     | —      | —      |
|                                  | 16–32 cm            | –0.044     | —      | —      |
|                                  | 32+ cm              | —          | —      | —      |
| effect of 16+ cm dbh size class  |                     |            |        |        |
|                                  | size class affected | 0–7        | 7–14   | 14–21  |
|                                  | 1–2 cm              | —          | —      | —      |
|                                  | 2–4 cm              | —          | —      | —      |
|                                  | 4–8 cm              | —          | —      | —      |
|                                  | 8–16 cm             | –0.039     | —      | —      |
|                                  | 16–32 cm            | —          | —      | —      |
|                                  | 32+ cm              | —          | —      | —      |

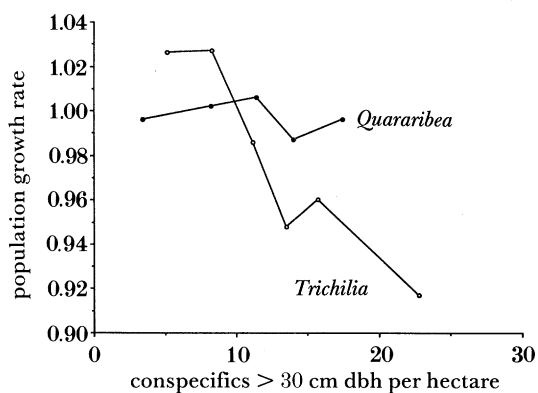


Figure 8. Comparative population growth rate ( $\lambda$ ), as a function of the density of large (> 30 cm dbh) conspecific trees per ha in *Trichilia tuberculata* and *Quararibea asterolepis*.

0.14 when the population peaked, and recruitment rate declined from 8.5 to 5.3. Figure 10*b* shows the relation between these two parameters and the total density of large trees. If all density dependence was removed from the model, then the population grew exponentially at an observed rate  $\lambda = 1.017$  (figure 9*a*). When we calculated  $\lambda$  from the set of life table parameters derived directly from field measurements, we obtained  $\lambda = 1.016$ . Moreover, the population levelled off at a realistic population density and with similar size class distributions to those observed in the 50 ha BCI plot (figure 10). Thus we believe we have accurately captured the essential features of density-dependent population growth in *Trichilia*.

We do not yet know the causes of the strong density-

dependence discovered in *Trichilia*, but we suspect that heart-rot fungi may be involved. In mahogany, also a member of the Meliaceae, heart-rot fungi are a major cause of tree death, especially in saplings near infected adults. Moreover, the fungus continues to live for a long time as a saprophyte on the wood of trees that it has killed, so it may contaminate areas previously occupied by the host species and prevent recruitment for several years or decades. *Trichilia tuberculata* does harbour a heart-rot fungus, but we know nothing about its life history or host relations. This interesting possibility merits further research.

## CONCLUSIONS

In this paper we have endeavoured to summarize the evidence for density dependence in regulating tree populations in a neotropical forest. Although the study is now a decade old, our conclusions must all be regarded as tentative because although we have monitored the forest for a decade, this only a small fraction of the lifespan of many of its member tree species. Nevertheless, there is a remarkable consistency among the answers we are getting, whether they are derived from analyses of the static, first-census data, from recensus data on short-term dynamics of survival, growth, and recruitment, or from detailed studies of density effects in individual BCI tree species.

The picture emerging from these studies is that, with the exception of one or two extremely abundant canopy and possibly midstory tree species, the vast majority of the species in the BCI forest are nowhere

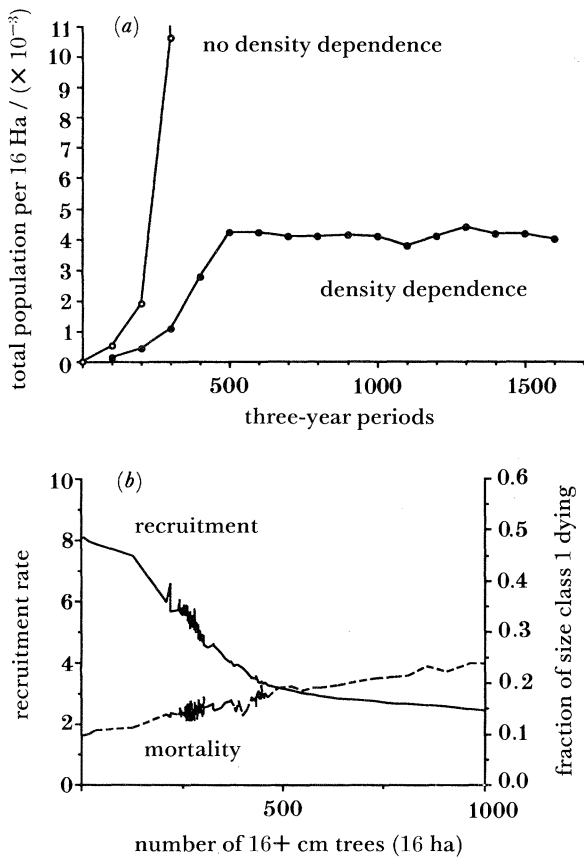


Figure 9. Simulation results for the growth of *Trichilia tuberculata* model populations in a 16 ha area (400 × 400 m). (a) Population growth curves with and without density dependence on survival, growth, and recruitment, as measured in the natural population. (b) Relation between recruitment rate per 16 ha and mortality rate per three-year cycle, as a function of the number of large (16 + cm dbh trees) per 16 ha.

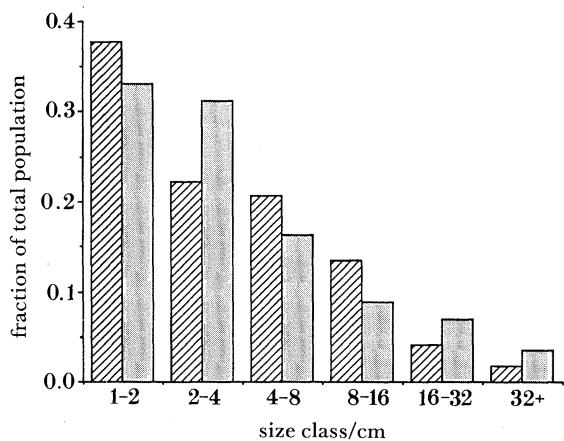


Figure 10. Comparison of the simulated (hatched bars) and observed (solid bars) size structure of the model and natural *Trichilia tuberculata* populations, after the model population reached more or less stable size structure (1000 three-year cycles).

near the densities at which density-dependent feedbacks can limit further population growth. One might argue that any density dependence at all, even density dependence too weak for us to detect, will ultimately limit a population. While certainly true in principle,

these theoretical limits may be unrealistically high for a space-limited plant population.

A plant population cannot increase beyond the ultimate limit set by the self-thinning law in a monospecific stand, the density at which local and global competitive effects become one and the same. The limits we seek cannot be the same as those setting the self-thinning limits for monocultures; otherwise the population should grow to these limits. But higher limits are simply not credible for any real plant population. Therefore the limits, if they exist, must be lower. However, our current evidence is that the measured strength of density dependence in most BCI trees fails to meet this criterion. The exceptions are a few species such as *Trichilia* in which lower density limits do exist, set by as yet unknown density dependent factors that are demonstrably sufficient to regulate the population at observed densities.

Our current working hypothesis is that density dependence sets upper, often unattainably high, limits to the abundance of trees in the BCI forest, but that most species are far below these limits, too rare to encounter each other often or experience significant conspecific density effects. This is not to argue against effects at larger spatial scales than we have examined. For example, there might well be inverse-density effects when tree populations become so sparse that they suffer from Allee effects because of limited attention from pollinators and seed dispersal agents.

We thank the large numbers of students who have helped with the field work on the project over the past decade. We thank the National Science Foundation, the Smithsonian Institution (Scholarly Studies Program), the World Wildlife Fund (U.S), the Geraldine R. Dodge Foundation, The W. Alton Jones Foundation, and Earthwatch, for their support.

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### Discussion

P. J. GRUBB (*Botany School, Cambridge University*). The point I wished to make in conversation earlier was that in some genera of woody plants represented by many species in a single forest stand the various species are strikingly various in leaf form, e.g. in *Diospyros* and *Eugenia* in various parts of the world, and they might plausibly be expected to respond to environmental conditions differently; and that in genera where this is not so, e.g. in *Strychnos* in Ghana, there is commonly wide variation between species in the size and form of the fruit and/or seeds, which seems likely to result in different conditions favouring establishment.

S. P. HUBBELL. My challenge to you is to show that these differences are of any material significance.

P. J. GRUBB. I accept the challenge!

C. D. THOMAS. (*Centre for Population Biology, Imperial College at Silwood Park, U.K.*). Many insects feed on more than one species of plant. Potentially, such insects could regulate the combined densities of all host plants, perhaps limiting the total density of individuals in plant genera or families. Has Professor Hubbell looked for density- or distance dependence at generic or family level?

S. P. HUBBELL. We have done some analyses pertinent to this issue. What we have found is that species in the same genus (*Inga* and *Ocotea*) and family (Lauraceae) do not interact negatively with one another, based on the same sorts of analyses presented here. For example, *Beilschmiedia pendula* and *Ocotea skutchii* in the Lauraceae have recruits closer to adults of the other species than one would expect by chance. This is probably because they fruit at the same time and share dispersers (toucans). In addition, nearby adults of one do not reduce survival of saplings of the other. We have not, however, combined all species within a family and looked for density dependence, and that is an interesting suggestion.