

Demographic and life-history correlates for Amazonian trees

Nascimento, Henrique E.M.^{1,2*}; Laurance, William F.^{1,2,3}; Condit, Richard^{1,4}; Laurance, Susan G.^{1,5}; D'Angelo, Sammya^{2,6} & Andrade, Ana C.^{2,7}

¹Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panamá; ²Biological Dynamics of Forest Fragments Project (BDFFP), National Institute for Amazonian Research (INPA), C.P. 478, Manaus, AM 69011-970, Brazil; ³E-mail laurancew@si.edu; ⁴E-mail condit@ctfs.si.edu; ⁵E-mail laurances@si.edu;

⁶E-mail sammya@inpa.gov.br; ⁷E-mail titina@inpa.gov.br; *Corresponding author; E-mail henrique@inpa.gov.br

Abstract

Questions: Which demographic and life-history differences are found among 95 sympatric tree species? Are there correlations among demographic parameters within this assemblage?

Location: Central Amazonian rain forest.

Methods: Using long-term data from 24 1-ha permanent plots, eight characteristics were estimated for each species: wood density, annual mortality rate, annual recruitment rate, mean stem diameter, maximum stem diameter, mean stem-growth rate, maximum stem-growth rate, population density.

Results: An ordination analysis revealed that tree characteristics varied along two major axes of variation, the major gradient expressing light requirements and successional status, and the second gradient related to tree size. Along these gradients, four relatively discrete tree guilds could be distinguished: fast-growing pioneer species, shade-tolerant subcanopy species, canopy trees, and emergent species. Pioneers were uncommon and most trees were canopy or emergent species, which frequently had low mortality and recruitment. Wood density was negatively associated with tree mortality, recruitment, and growth rates when all species were considered. Growth rates varied markedly among and within species, with pioneers exhibiting far faster and less variable growth rates than did the other species. Slow growth in subcanopy species relative to canopy and emergent trees was not a simple consequence of mean tree size, but apparently resulted from physiological constraints imposed by low-light and other conditions in the forest understorey.

Conclusions: Trees of Amazonian rain forests could be classified with some success into four relatively distinctive guilds. However, several demographic and life-history traits, such as those that distinguish early and late successional species, probably vary along a continuum, rather than being naturally grouped into relatively discrete categories.

Keywords: Amazon; Growth; Mortality; Rain forest; Recruitment; Tree guild; Tree life history; Wood density.

Nomenclature: Ribeiro et al. (1999).

Abbreviation: BDFFP = Biological Dynamics of Forest Fragments Project.

Introduction

Amazonian forests are the world's most diverse in tree species (Gentry 1990; Oliveira & Mori 1999; Turner 2001) and are experiencing very high rates of logging and deforestation (Nepstad et al. 1999; Laurance et al. 2001a). Demographic studies of individual tree species are needed to provide baseline ecological data that are essential for effective forest management and conservation in the tropics. Unfortunately, even basic information is unavailable for many Amazonian tree species, which have been understudied relative to other tropical regions and are often locally rare and patchily distributed (Laurance 2001).

Much of what is known about the demography and life history of tropical trees has been derived from long-term forest-dynamics studies in permanent plots (e.g. Lieberman et al. 1985; Primack et al. 1985; Hubbell & Foster 1986; Clark & Clark 1992; Condit et al. 1995, 1996a, b; O'Brien et al. 1995; Laurance et al. 2004). Such studies have revealed large variability in species-specific mortality, recruitment, and incremental-growth rates, which are frequently associated with life-history differences along a continuum between early and late successional trees (Condit et al. 1996a, b; Turner 2001); however, this simple gradient obscures considerable ecological variation among species (Welden et al. 1991; Clark & Clark 1992; Davies 1998). Additional features, such as wood density and allometric relationships among diameter, height and crown shape, also vary greatly among species and can be correlated with factors such as tree age, successional status, growth form, local environmental conditions, and phylogenetic affinities (Williamson 1984; Primack et al. 1985; O'Brien et al. 1995; Turner 2001; Poorter et al. 2003).

In this study we use long-term (18 years) data from 24 permanent 1-ha study plots, augmented with an extensive literature survey, to estimate a number of demographic and life-history parameters for 95 tree

species of the central Amazonian rain forest. We then test for associations among these traits to identify ecological differences and relationships within this species assemblage. The group of species we examined includes many of the most widespread and abundant trees in central Amazonia.

Methods

Study area

The study was conducted within the experimentally fragmented landscape of the Biological Dynamics of Forest Fragments Project (BDFFP), which is located about 80 km north of Manaus, Brazil (2°30' S, 60° W). Rain forests in the area are evergreen and *terra firme* (not seasonally flooded), occurring in the altitudinal range 50 - 100 m (Lovejoy et al. 1986). Rainfall varies between 1900 and 3500 mm annually with a pronounced dry season from June to October (Laurance 2001). The forest canopy is typically 30 - 37 m tall, with emergent trees to 55 m. Species richness of trees is very high and can exceed 280 species (≥ 10 cm DBH) per ha (Oliveira & Mori 1999).

The dominant soils in the study area are xanthic ferralsols, which are heavily weathered, acidic and very poor in nutrients such as P, Ca and K (Chauvel et al. 1987). Cation concentrations tend to be higher in more clayey soils, which are prevalent in flatter areas and ridge tops; these areas generally support greater tree biomass than do gullies and slopes, which have higher sand contents and lower cation concentrations (Laurance et al. 1999).

Plot description and species analysed

Since 1980, a long-term study of tree-community dynamics, biomass and composition has been conducted in fragmented and continuous forests in the BDFFP study area. For this study, data were pooled from 24 1-ha plots in undisturbed (unfragmented and unlogged) forest arrayed across an area spanning ca. 1000 km². All plots were located more than 300 m from the nearest forest-pasture edge to minimize the influence of edge effects on tree communities.

Following an initial, exhaustive census of all trees in the early mid-1980s, each plot was recensused 2-3 times at regular (typically 4 - 7 year) intervals to assess tree mortality, recruitment, and growth, with the final census conducted in mid-1999. Tree diameters were measured (to the nearest 1 mm) with DBH tapes at 1.3 m height or above any buttresses. Species identifications (often by recognized taxonomic experts; see Acknowledgements)

were based on sterile or fertile herbarium material collected for each tree, which is lodged in the BDFFP reference collection, Manaus, Brazil. About 1260 tree species (≥ 10 cm DBH) have been identified in the study area to date.

The 95 tree species examined (App. 1) in this study account for 23.1% of all stems, 8.8% of all identified tree species, 26% (61 of 235) of all tree genera, and 43% (25 of 61) of all tree families found in our 24 plots. This subset includes all species that were confidently identified to species level, for which at least ten individuals were present in the plots (mean sample size was 33.5 trees per species), and for which wood-density estimates were available. Wood density (specific gravity of dry wood) data were gleaned from a review of wood-density values in Amazonian trees (Fearnside 1997) and from an exhaustive survey of more than 130 publications and graduate theses (W.F. Laurance, S. D'Angelo, I. Ferraz, unpubl. database). When multiple wood-density estimates were available for a particular tree species, the mean of the estimates was used. Selected species encompassed a wide range of variation in growth form, stature, and successional status. Prior to undertaking our analysis, we tentatively assigned each species into one of four different tree guilds (pioneer, subcanopy, canopy, and emergent species) based on species descriptions in Ribeiro et al. (1999) and online data sources from the New York and Missouri Botanical Gardens. We then used our quantitative data on tree demography and life history of each species to assess the robustness of the *a priori* botanical and field-guild classifications.

Mortality, recruitment, and growth rates for individual species

Annualized mortality and recruitment rates were estimated by finding parameters describing these rates that maximized the likelihood of observing our data. This technique allows for variable census intervals between plots and censuses. Each species was considered separately, and the following refers to records of just one species.

Mortality. Let N_{ij} be the number of individuals found alive in plot i at the start of census interval j , and S_{ij} be the number of those found alive at the end of the interval. A single time interval, T_{ij} , is assumed for all individuals in a plot and census, and recorded to the nearest month (it took less than a month to finish a census of a single plot). Define the mortality parameter p as one minus the probability that a single individual tree survives one year, so the probability of a tree surviving T years is $(1 - p)^T$; assume this probability is constant for all individuals of the given species. For any arbitrary p ,

the likelihood L_{ij} of observing the S_{ij} survivors at time $T_{ij} = L_{ij} \text{ binom}(N_{ij}, S_{ij}, (1-p)^{T_{ij}})$

the binomial probability of observing S_{ij} successes out of N_{ij} trials, given a probability of success per trial of $(1-p)^{T_{ij}}$. The likelihood L_{tot} of observing all the data for this species is the product of the probabilities L_{ij} for all plots i and census intervals j :

$$L_{\text{tot}} = \prod_{i,j} L_{ij} \quad (1)$$

We located the value of p that maximizes L_{tot} , but as in any likelihood approach, we worked with $\log(L_{\text{tot}})$ and maximized the sum of $\log(L_{ij})$. We located the optimal p using the functions *dbinom* and *optimize* in the computer language R, version 1.6.2, starting with $p = 0.0125$ and constraining p to the interval $[0,1]$, otherwise using default settings. For compatibility with recruitment rate, we report the instantaneous mortality parameter, $m = \log(1-p)$, which equals the derivative of the number of survivors with respect to time, dS/dt (Condit et al. 1995, 1999).

To assign 95% confidence limits to p (and, hence, m), we bootstrapped across plots. If a species occurred in nine plots, we randomly drew nine plots, 1000 times, with replacement, and fit p each time; the 25th and 975th ranking values are the 95% confidence limits. When we selected a plot, all censuses of that plot and all individuals within the plot were included. By bootstrapping across plots, we assume that the plot is the unit of data, not the individual tree nor the individual census of a plot; thus, our confidence limits acknowledge that mortality events for individuals within a plot, even in different censuses, are not independent.

A problem arose with the bootstrap method for calculating confidence when no trees of a species died. The maximum likelihood value for p is of course 0, but all bootstrap replicates also return 0, because no dead trees can be chosen. To avoid the conclusion that no individual of this species will ever die, we estimated confidence intervals using the method of Condit et al. (1995). Let

$$N = \sum N_{ij} = S = \sum S_{ij}$$

be the number of individuals of this species summed over all plots and censuses, and let

$$T = \frac{\sum_{i,j} T_{i,j}}{ij}$$

be the arithmetic mean census interval for this species, across all plots and censuses. Then the upper 95% confidence limit p_u is the mortality parameter for which $\text{binom}(N, S, (1-p_u)^T) = 0.025$ (half of 5% because it is a two-tailed test). Since the binomial probability of observing N successes out of N trials is $(1-p_u)^{NT}$, it follows that: $p_u = \sqrt[NT]{0.025}$ and

$$m_u = -\log(1-p_u) = \frac{\log(40)}{Nt} \quad (2)$$

This is the highest mortality rate consistent with observing all N trees surviving, that is, the mortality at which the probability of observing all trees survive is 0.025. The lower confidence limit is 0. This same method can be used for calculating upper and lower confidence limits for any species, even with $N \neq S$ (Condit et al. 1995); we compared this method with the bootstrap methods, and the results were very similar.

Recruitment. The recruitment parameter r is analogous to the mortality parameter m , and

$$\frac{dN}{dT} = (r - m)N \quad (3)$$

describes the rate of population change in a species; this describes recruitment as a birth process, with r being the rate at which single individuals produce new trees. With this description of population change, the number of recruits R observed after T years is $R = S(e^{rT} - 1)$, where S is the number of survivors (the initial population) N does not appear in the formula for R . Given any arbitrary recruitment parameter, r , the likelihood L_{ij} of observing S_{ij} survivors and R_{ij} recruits after a census interval of T_{ij} years is

$$L_{ij} = \text{Poisson}(R_{ij}, S_{ij}(e^{rT_{ij}} - 1)) \quad (4)$$

the probability of observing R_{ij} events according to a Poisson with expectation $S(e^{rT} - 1)$. We located the value of r that maximized this probability across all plots and census intervals for each species, again using *optimize* in R, with an initial value of $r = 0.0125$ and constraining r to the interval $[0,1]$. Confidence limits were calculated with a bootstrap as for mortality. When no recruits were observed, an upper confidence limit was estimated as for mortality, but using the Poisson, not binomial; then

$$r_u = \frac{1}{T} \ln\left(\frac{\ln(40)}{S} + 1\right) \quad (5)$$

A problem arose with these calculations in plots with recruitment but no survivors. In this situation, the model produces a probability of zero for finding any recruits. Since a few species did recruit in plots where no trees were present, we had to use a separate likelihood model when $S_{ij} = 0$: the predicted value of $R = e^{rT} - 1$. This means the predicted recruitment with no survivors present is roughly half what it would be with one survivor. This is realistic in that it allows recruitment even with no trees present, but predicts less recruitment than with one tree present. The term $rT / 2$ is, however, arbitrary. We compared the likelihood estimate of r with the method used in Condit et al. (1999), and the two agree almost exactly in all species except the two *Cecropia* species; in both

species, most recruits appeared in plots where there were no *Cecropia* present, forcing use of the arbitrary likelihood calculation just described. Regardless, both methods estimated very high recruitment in *Cecropia* with broad and overlapping confidence intervals (due to the low number of samples).

Growth. The mean annual growth rate for each individual tree was estimated by subtracting its initial DBH (from the first census) from its final DBH (from the last census), and dividing this value by the total number of years between the two censuses. For each species, two estimates of growth rate were determined: the median growth rate; and the upper decile of the growth rate, which was used as an estimate of maximum growth rate for each species. The use of median and decile values, rather than the mean and absolute highest value, helped to minimize possible bias from outliers.

Data analysis

An ordination analysis, Global Non-metric Multidimensional Scaling (GNMDS), with the Sørensen similarity index, performing on PC-ORD package (McCune & Mefford 1999), was used to summarize major gradients in eight demographic and life-history features of trees (wood density, mean DBH, maximum DBH, median growth rate, maximum growth rate, mean mortality rate, mean recruitment rate, mean population density). All variables were equally weighted prior to analysis, using the standardization by the maximum method (Noy-Meir et al. 1975). Randomization tests were used to determine the number of ordination axes that explained significantly more variation in the data set than expected by chance (McCune & Mefford 1999).

We used one-way ANOVAs to assess differences among the four tree guilds for each demographic and life-history feature, followed by Tukey's tests to contrast sample means. Low growth rates in subcanopy trees might arise because they are smaller in size than canopy and emergent trees and as a result of physiological adaptation to low-light and other environmental conditions beneath the forest canopy (Thomas 1996). We attempted to discriminate between these two explanations by comparing relative effects of tree size (mean DBH) and tree guild on species growth rates using an ANCOVA. Linear regressions were used to assess interrelationships between demographic and life-history attributes. Because these are parametric tests, appropriate data transformations were used to reduce heteroscedasticity, improve normality, and increase linearity of relationships between response and predictor variables (tree mortality and recruitment rates, median growth rate, mean DBH, and maximum DBH).

Results

General differences among guilds

Two major gradients of variation among the 95 species were revealed by ordination analysis of the eight key demographic and life-history characteristics (Table 1). A randomization test ($n = 50$ runs) confirmed that the two axes explained significantly more variation than expected by chance ($P < 0.02$ in both cases). Axis 1, which captured 58% of the total variation in the data set, described a gradient from old-growth species with slow growth, high wood density, and low mortality and recruitment rates, to fast-growing pioneer species with opposite traits. Axis 2 captured 36% of the total variation and mainly described a gradient in tree size (mean and maximum DBH). Larger trees also exhibited some tendency to have lower mortality and recruitment, higher wood density, and higher population densities, than did smaller species (Table 1).

We then assessed the efficacy of our *a priori* classification of tree species into pioneer, subcanopy, canopy, and emergent guilds, based on the ordination analysis. Although species in the four guilds were moderately well separated in two-dimensional ordination space (Fig. 1), 18 species were re-allocated to different guilds based on their ordination scores. Two species initially classified as pioneers, *Inga capitata* and *Jacaranda copaia*, had low scores on axis 1 and were placed in the subcanopy group. Among emergent trees, two *Lecythidaceae* species (*Couratari stellata* and *Eschweilera amazoniciformis*) were re-allocated to the canopy guild, based on their low scores on axis 2. Substantial variation was evident within the canopy guild, and 14 species were re-allocated to the three other guilds (see the Appendix for details). Thus,

Table 1. Product-moment correlations between eight demographic features of Amazonian trees and two ordination axes (DBH = trunk diameter at breast height). Asterisks indicate significant correlations, using a Bonferroni-corrected probability value ($P = 0.003$) to reduce the likelihood of spurious correlations.

Variable	Axis 1	Axis 2
Wood density	-0.629 *	0.320 *
Mortality rate	0.728 *	-0.527 *
Recruitment rate	0.710 *	-0.395 *
Mean DBH	-0.017	0.839 *
Maximum DBH	-0.058	0.878 *
Median growth rate	0.849 *	-0.122
Maximum growth rate	0.890 *	-0.007
Population density	-0.300	0.319 *
Variation explained*	58.1%	36.1%

*Based on coefficients of determination for correlations between ordination distances and distances in the original n -dimensional space.

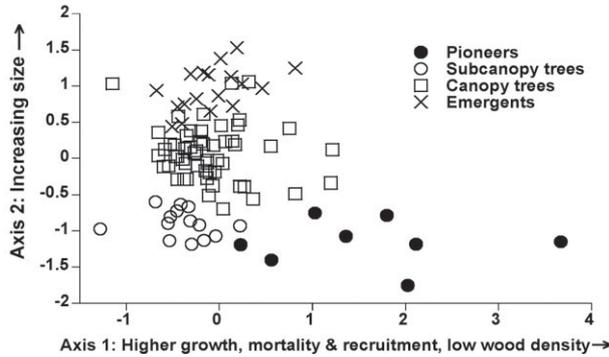


Fig. 1. Ordination of demographic features of 95 Amazonian rain forest tree species, using Non-metric Multidimensional Scaling. Axis lengths are proportional to the amount of variation explained by each axis.

our *a priori* classification of species into guilds was effective for about four-fifths of all tree species, with the remainder being reallocated into new guilds based on our multivariate analysis of demographic and life-history features. Hereafter all analyses will be based on this new classification.

Within our 95 relatively common species, the canopy guild was best represented (43 species), followed by subcanopy trees (22 species), emergent trees (21), and pioneers (9). Associations between tree taxonomy and guild status were relatively weak. Most (10 of 13) tree families with multiple (> 2) species were distributed among two or more guilds; only *Cecropiaceae*, *Lauraceae* and *Myristicaceae* were confined to a single guild, being entirely classified as pioneer, canopy, and subcanopy species, respectively. Even at the generic level, most (six of eight) genera with multiple (> 2) species were found in two or more guilds.

Mortality and recruitment rates

We evaluated demographic and life-history differences among and within the four guilds in greater detail. Annualized mortality and recruitment rates were generally low for the 95 species we studied, with mean values of just 1.06% and 0.94%, respectively. These averages, however, disguise considerable variability among species. About 60% and 72% of all species, respectively, had low (< 1%.a⁻¹) mortality and recruitment, whereas roughly a quarter had intermediate values (1–2%.a⁻¹) and nearly a tenth had high (2–10%.a⁻¹) mortality and recruitment.

Mortality ($F_{3,91} = 6.71$, $P = 0.0004$) and recruitment ($F_{3,91} = 5.78$, $P = 0.001$) both varied significantly among tree guilds (one-way ANOVAs; Fig. 2). Pioneers had significantly higher mortality than did the subcanopy

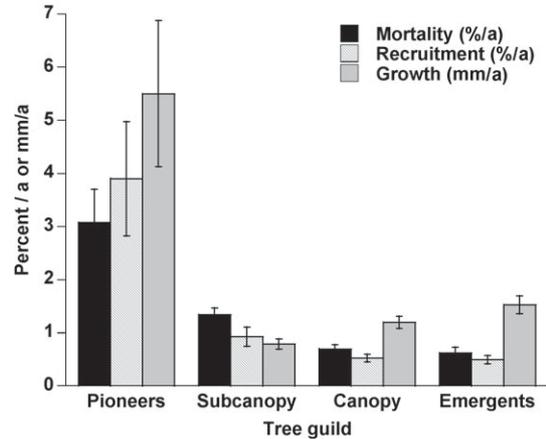


Fig. 2. Mean (\pm SE) mortality, recruitment, and growth rates for four guilds of Amazonian rain forest trees.

($P < 0.05$), canopy ($P < 0.001$), and emergent ($P < 0.001$) guilds. In addition, understory trees had significantly ($P < 0.01$) higher mortality than did emergent trees (Tukey's tests). Results were similar for recruitment rates, with pioneers having higher recruitment than subcanopy ($P < 0.01$), canopy ($P < 0.001$), and emergent ($P < 0.001$) species. On average, mortality and recruitment rates of pioneers were 2–6 times higher than those of subcanopy, canopy, and emergent species (Fig. 2).

Among the 95 species, there was a significant, positive relationship between mortality and recruitment rates ($F_{1,93} = 32.30$, $R^2 = 25.8\%$, $P < 0.0001$; linear regressions). For example, the pioneer *Cecropia sciadophylla* had both the highest mortality (6.5%.a⁻¹) and highest recruitment (10.4%.a⁻¹) of all species, and six of nine species with high (> 2%.a⁻¹) mortality also had similarly high recruitment.

Growth rates

Incremental-growth rates varied greatly among species, ranging from 0.25 mm.a⁻¹ in the subcanopy tree *Swartzia corrugata* to 16.0 mm.a⁻¹ in the pioneer *Cecropia sciadophylla*, with an overall mean of 1.6 ± 1.89 mm.a⁻¹. Among-guild differences were highly significant ($F_{3,91} = 27.01$, $P < 0.0001$; one-way ANOVA). As expected, pioneers had by far the highest growth rates, followed by emergent, canopy, and subcanopy species (Fig. 2). Growth rates were significantly higher in pioneers than the other guilds ($P < 0.001$), and significantly ($P < 0.0001$) higher in emergent and canopy species than in subcanopy species (Tukey's tests).

The analysis indicated that growth rates were influenced by tree size ($F_{1,82} = 3.99$, $P = 0.049$) and varied among the three non-pioneer guilds ($F_{2,82} = 8.65$, $P = 0.004$). Hence, subcanopy species had significantly lower

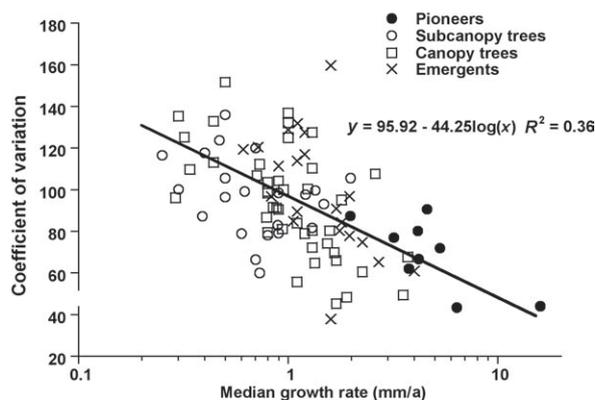


Fig. 3. Relationship between coefficients of variation in growth rates within each species and the median growth rate of that species.

growth rates than canopy and emergent species even when effects of varying tree size were removed statistically.

Within any species, growth rates often varied considerably among different individuals in the population. Coefficients of variation in growth ranged from 38% in the pioneer *Cecropia sciadophylla* to 160% in the emergent *Goupia glabra*. When coefficients of variation were compared to median growth rates (Fig. 3), the relationship was negative and highly significant ($F_{1,93} = 52.0$, $R^2 = 35.9\%$, $P < 0.0001$). Thus, fast-growing species tended to have less variable growth rates, whereas slower growing species were relatively more variable.

Wood density

Wood density ranged from 0.38 in the pioneer species *Pourouma bicolor* and *P. guianensis* to 1.20 in the understorey tree *Swartzia corrugata* (App. 1). Wood density varied strongly among tree guilds ($F_{3,91} = 10.62$, $P < 0.0001$; one-way ANOVA), with pioneers having significantly lower average wood density ($0.50 \pm 0.16 \text{ g.cm}^{-3}$) than subcanopy ($P < 0.05$), canopy ($P < 0.01$), and emergent ($P < 0.01$) species (Tukey's tests). Mean wood density varied little among subcanopy (0.69 ± 0.17), canopy (0.76 ± 0.15), and emergent ($0.78 \pm 0.15 \text{ g.cm}^{-3}$) species.

As expected, wood density was negatively related to tree growth (Fig. 4), accounting for 13–17% of the total variation in median ($F_{1,93} = 11.60$, $R^2 = 12.6\%$, $P = 0.001$) and maximum ($F_{1,93} = 13.60$, $R^2 = 16.7\%$, $P = 0.0004$) growth rates for each species. However, when pioneer species were removed, there was no relationship between wood density and growth ($F_{1,84} = 2.30$, $R^2 = 2.6\%$, $P = 0.13$). Thus, although species with the lowest wood densities tended to grow rapidly, and vice-versa, many species with intermediate wood density had variable growth rates (Fig. 4).

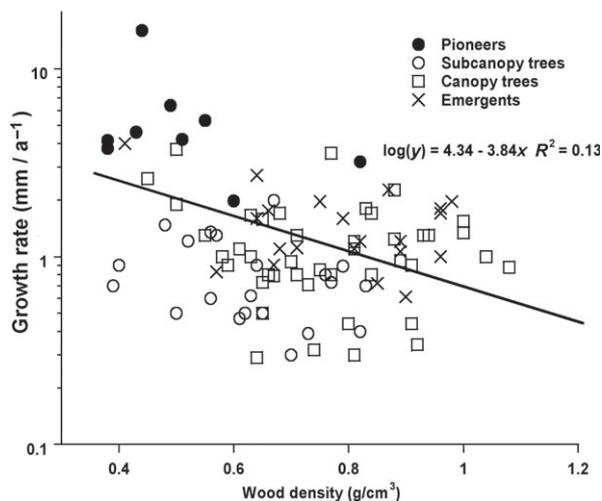


Fig. 4. Relationship between wood density and median growth rate in 95 Amazonian tree species.

Wood density was also negatively associated with species' mortality rates ($F_{1,93} = 14.17$, $R^2 = 13.3\%$, $P = 0.0003$) and to a lower degree with recruitment rates ($F_{1,93} = 7.67$, $R^2 = 7.6\%$, $P = 0.007$; linear regressions). Again, however, when pioneers were removed, neither mortality ($F_{1,84} = 3.30$, $R^2 = 3.7\%$, $P = 0.073$) nor recruitment ($F_{1,84} = 0.01$, $R^2 = 0.5\%$, $P = 0.99$) was significantly related to wood density. When the guilds were analysed separately, only subcanopy trees exhibited a significant relationship between wood density and mortality ($F_{1,21} = 13.21$, $R^2 = 40.3\%$, $P = 0.007$), and no guilds showed a significant relationship between wood density and recruitment.

Tree size

Indices of tree size (mean and maximum DBH) were negatively related to rates of mortality ($F_{1,93} = 14.18$, $R^2 = 13.2\%$, $P = 0.0003$; Fig. 5) and recruitment ($F_{1,93} = 12.56$, $R^2 = 11.9\%$, $P = 0.0006$; linear regressions using mean DBH data). These relationships were highly significant even when pioneers were excluded from the analysis (mortality: $F_{1,84} = 7.82$, $R^2 = 8.6\%$, $P = 0.005$; recruitment: $F_{1,84} = 7.05$, $R^2 = 7.7\%$, $P = 0.009$). Further, they remained significant even when effects of variation in wood density were removed with partial correlation analyses (mortality: $r = -0.360$, $P = 0.0007$; recruitment: $r = -0.301$, $P = 0.005$). Thus, even among non-pioneers and irrespective of variation in wood density, larger species tended to have lower mortality and recruitment than did smaller species.

In addition, tree size (mean DBH) was positively but rather weakly associated with the median ($F_{1,93} = 3.38$, $R^2 = 3.5\%$, $P = 0.069$) and maximum ($F_{1,93} = 7.79$, $R^2 = 7.7\%$,

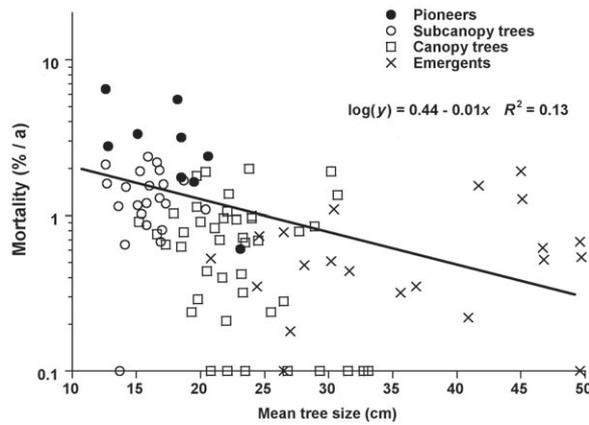


Fig. 5. Relationship between mean tree size and mean mortality rate in 95 Amazonian tree species.

$P=0.006$) growth rates of each species. Therefore, larger trees typically had faster absolute growth than smaller trees, even when small, fast-growing pioneer species were included. When pioneers were removed from the analysis, the association between tree size and growth rate was strengthened considerably (median growth rate: $F_{1,84} = 24.20$, $R^2 = 22.4\%$, $P < 0.0001$; maximum growth rate: $F_{1,84} = 34.30$, $R^2 = 28.9\%$, $P < 0.0001$; all linear regressions).

Population density

Significant associations between species' population density and demographic features partly resulted because old-growth species are common, and pioneers rare, in the undisturbed forests of our study area. The strongest correlates of population density were wood density ($F_{1,93} = 12.73$, $R^2 = 12.0$, $P = 0.0006$) and maximum DBH ($F_{1,93} = 12.47$, $R^2 = 11.8\%$, $P = 0.0006$), indicating that species that attained large sizes and high wood density were more abundant than small, light-wooded species. These relationships were still significant when pioneers were excluded, although the association with wood density was weakened considerably ($F_{1,84} = 4.43$, $R^2 = 5.0\%$, $P = 0.04$), whereas maximum DBH remained a relatively strong correlate of population density ($F_{1,84} = 8.29$, $R^2 = 9.0\%$, $P = 0.005$; linear regressions with log-transformed axes, except for wood density).

In addition, population density was negatively associated with mortality ($F_{1,93} = 6.85$, $R^2 = 6.9\%$, $P = 0.01$), recruitment ($F_{1,93} = 8.50$, $R^2 = 8.4\%$, $P = 0.004$), median growth ($F_{1,93} = 5.22$, $R^2 = 5.3\%$, $P = 0.025$), and maximum growth ($F_{1,93} = 4.99$, $R^2 = 5.1\%$, $P = 0.028$) rates. However, none of these relationships were significant when pioneers were excluded from the analysis ($F_{1,84} < 0.35$, $P > 0.5$; linear regressions).

Discussion

Guild classification

Using demographic and life-history data from a long-term study of forest dynamics, we find that trees of Amazonian *terra-firme* rain forests (≥ 10 cm DBH) can be classified into four relatively distinctive guilds (Fig. 1). Pioneer species, which are uncommon (nine species or 4% of all trees involved), usually have low wood density, high growth rates, rapid population turnover, and small sizes (trunk diameters). Subcanopy species, which are somewhat more abundant (22 species and 16% of all trees), are also typically small in size but have moderately low mortality and recruitment, moderate to high wood density, and consistently low growth rates. Canopy trees, the most abundant in both species and individuals (43 species and 41% of all trees), are large in size, with low mortality and recruitment, and moderate to high wood density, and moderate but variable growth rates. Finally, emergent trees, which are also common (21 species and 40% of all trees), overlap with canopy trees in their demographic and life-history characteristics and are mainly distinguished by virtue of their very large size. These guild classifications generally accord with those of other authors, except that the canopy and emergent guilds are sometimes merged into a single guild (e.g. Lieberman et al. 1985; Turner 2001).

At least among the eight demographic and life-history variables we measured, tree species are separated along two main axes of variation: one from light-demanding species (rapid growth, low wood density, high mortality and recruitment) to shade-tolerant species (with opposing traits); and a second gradient in tree size (stem diameter). Other authors (e.g. Turner 2001; Poorter et al. 2003) have also suggested that light requirements and adult stature represent relatively independent axes of architectural differentiation in tropical rain forest trees. Although additional axes of variation, such as moisture tolerance (e.g. Condit et al. 1996a), plant phenology (e.g. Garwood 1983), and interactions with animal mutualists (e.g. Wheelwright 1985), can contribute to the ecological differentiation of sympatric tree species, our results suggest that light requirements and tree stature are important ecological factors that help to distinguish Amazonian tree species.

As in all guild classifications, our categories inevitably obscure some differences among species within the same guild (cf. Clark & Clark 1992; Turner 2001). For example, a key difference among the four guilds relates to their degree of shade tolerance during different life stages. Pioneers are generally light-demanding during most stages of growth and reproduction. Many canopy and emergent species, however, persist for extended periods in the

understorey as shade-tolerant saplings or small trees, before rapidly ascending to the canopy if a nearby treefall increases understorey light levels, at which point they can intercept enough light to attain reproductive maturity (Denslow 1987). Understorey species are even more shade-tolerant, growing slowly throughout their lives and being the only guild capable of reproducing under shady conditions (e.g. Thomas 1996). Yet these differences actually reflect a continuum among species having varying degrees of shade tolerance, rather than discrete categories. Condit et al. (1996a) concluded that rain forest trees on Barro Colorado Island, Panama varied along a demographic gradient between slow-growing, shade-tolerant species vs. fast-growing, light demanding pioneers, with most species clustering near the shade-tolerant end of the gradient, while the remaining were continuously distributed over a wide range along the gradient.

Wood density

Wood density is strongly correlated with most measures of wood strength (Panshin & Dezeew 1970) and may be inversely related to tree growth rate, mortality rate, trunk snapping (Putz et al. 1983), successional status (Lawton 1984; Richards 1952), elevation (Williamson 1984), and windiness of the environment (Lawton 1984). In our study, wood density is significantly and negatively related to rates of tree growth (Fig. 4), mortality, and recruitment, but these relationships are weakened considerably when pioneer species (which have much lower wood densities and by far the highest growth, mortality, and recruitment of any guild) are excluded from the analysis. Among non-pioneers, the generally weak relationships between wood density and demographic parameters may arise in part because mean wood-density data are used in our analysis. Wood density can vary markedly among individuals in a population and during the lifetime of a tree (Lawton 1984); for example, in canopy and emergent trees, wood density may decline once individuals reach the full sunlight of the forest canopy, where growth rates increase considerably (Thomas 1996).

Nevertheless, when guilds were analysed individually, subcanopy trees exhibited a highly significant negative relationship between wood density and mortality rate. High-density wood may develop in subcanopy trees not only as a consequence of their slow growth (Fig. 2) in low-light conditions beneath the forest canopy; it may also help subcanopy trees withstand recurring physical damage from litter- and branch-fall, and from pathogen and insect attack in the humid understorey (Thomas 1996). The patterns we observed are consistent with the notion that high-density wood confers an important survival advantage for subcanopy species.

Tree growth

In the 95 species we examined, median growth increments follow a negative exponential distribution, with most (83%) species having low to moderate growth rates ($\leq 2 \text{ mm.a}^{-1}$) and the remainder ranging up to a maximum of 16 mm.a^{-1} . Although growth rates vary by nearly two orders of magnitude among species, our average across all species (1.59 mm.a^{-1}) was very close to that reported by Silva et al. (2002), who use growth bands to rigorously measure incremental growth in 272 randomly selected trees in a nearby forest reserve (1.64 mm.a^{-1}).

Within any single species, growth rates often vary markedly among individuals in the population, with over a third (37%) of all species having coefficients of variation (CV) in excess of 100%. The pronounced negative relationship between CV and median growth rate indicates that fast-growing species tended to exhibit more-uniformly high growth rates. This trend may arise because light-demanding pioneer species exhibit a 'grow fast or die' strategy, in which individuals located in treefall gaps grow rapidly whereas those in non-gap microhabitats frequently die. Slower-growing species, however, are more shade-tolerant and exhibit lower mortality than pioneers. For these species, natural spatial variability in crown position, soils, topography, nearby competitors, and tree sizes can create large variation in individual growth rates (e.g. Primack et al. 1985; Swaine et al. 1987). The net effect is that relatively slow-growing individuals of slow-growing species can persist in the population, whereas slow-growing individuals of fast-growing species often cannot.

Mortality and recruitment rates

Over the past two decades, mortality rates of trees in intact forests of our study area are quite low, both at the plot level ($1.23 \pm 0.45\% \text{ a}^{-1}$; Laurance et al. 2004) and in terms of the 95 species examined in this study ($1.06 \pm 1.03\% \text{ a}^{-1}$). These values are considerably lower than those observed in the Peruvian Amazon (Phillips et al. 1994), Costa Rica (Lieberman & Lieberman 1987), and central Panama (Condit et al. 1995), where mortality estimates exceeded $2\% \text{ a}^{-1}$. Because tree mortality is the principal driver of forest turnover (the average of mortality and recruitment rates), our forests appear to experience low dynamism relative to many other Neotropical rain forests.

Three factors appear to account for the low dynamism of central Amazonian forests. The first is the acidic, heavily weathered soils of the region (Chauvel et al. 1987; Richter & Babbar 1991), which limits rates of tree growth. This could lower mortality rates both by reducing the intensity of competition for light among individuals (Leigh 1999) and by favouring old-growth species with high-density

wood, which are less prone to stem breakage and other physical damage (Putz et al. 1983; ter Steege & Hammond 2001). Second, forest disturbances by convectional windstorms (Nelson et al. 1994), fires (Piperno & Becker 1996), lightning strikes (Magnusson et al. 1996), and wet-season flooding (Mori & Becker 1991) are limited in frequency and extent, further reducing tree mortality. Finally, central Amazonian forests have a relatively low density of lianas (Laurance et al. 2001b), which are major structural parasites of trees, and many small-statured trees (Nascimento & Laurance 2002), which may tend to limit the size of treefall gaps. Collectively, these factors may reduce the frequency and size of forest disturbances, thereby contributing to the low dynamism of forests in this region.

As a direct result of their low dynamism, central Amazonian rain forests are dominated by long-lived, old-growth tree species, with short-lived pioneers comprising only a small fraction of the tree community. Over 95% of the tree species we examined in this study were non-pioneers, and two-thirds of these had mortality rates of $< 1\% \cdot a^{-1}$. On average, emergent species exhibited the lowest mortality, followed by canopy, subcanopy, and pioneer species (Fig. 2), a pattern similar to that observed in Panamanian (Condit et al. 1995) and Malaysian (Manokaran & Kochummen 1987) rain forests.

An important implication of low mortality rates is that many central-Amazonian trees are expected to grow old. Among the species examined in this study, nearly 60% have estimated maximum longevitys of 200-500 years, and 15% had maximum longevitys of 500-1000 years, based on extrapolations from long-term growth and mortality data (Laurance et al. 2004). Such pronounced tree longevity has key implications for understanding forest dynamics, quantifying rates of carbon cycling, and improving forest-management strategies (Chambers et al. 1998; Martinez-Ramos & Alvarez-Buylla 1998). Of obvious relevance is that polycyclic logging may require unusually long intervals between cutting cycles, given the low growth rates and slow regeneration of many central-Amazonian tree species.

Acknowledgements. We thank R. Økland, P. Fine, N. Enright, N. Pitman, and C. Dick for commenting on the manuscript and many taxonomic experts who kindly identified tree species in our study area, especially W. Anderson, R. Barneby, C. Berg, B. Boom, M. Campos, L. Coelho, Paulo Apóstolo, J. Costa, D. Daly, A. Gentry, M. Kawasaki, N. Lepsch-Cunha, M. Hopkins, S. Mori, R. Hutchings, P. Maas, M. Nee, T. Pennington, G. Prance, R. Rankin-de Merona, W. Rodrigues, S. Renner, A. de Souza, L. Teixeira, M. Uehling, A. Vincentini and H. van der Werff. Support was provided by the NASA-LBA program, A.W. Mellon Foundation, Conservation, Food and Health Foundation, and Smithsonian Tropical Research Institute. This is Publication number 453 in the BDFFP technical series.

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Received 23 August 2004;

Accepted 26 October 2005.

Co-ordinating Editor: R.H. Økland.

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