

A time to grow and a time to die: a new way to analyze the dynamics of size, light, age, and death of tropical trees

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Abstract. In tropical rain forests, rates of forest turnover and tree species' life-history differences are shaped by the life expectancy of trees and the time taken by seedlings to reach the canopy. These measures are therefore of both theoretical and applied interest. However, the relationship between size, age, and life expectancy is poorly understood. In this paper, we show how to obtain, in a dynamic environment, age-related population parameters from data on size and light transitions and survival of individuals over single time steps. We accomplish this goal by combining two types of analysis (integral projection modeling and age-from-stage analysis for variable environments) in a new way. The method uses an index of crown illumination (CI) to capture the key tree life-history axis of movement through the light environment. We use this method to analyze data on nine tropical tree species, chosen to sample two main gradients, juvenile recruitment niche (gap/nongap) and adult crown position niche (subcanopy, canopy-emergent). We validate the method using independent estimates of age and size from growth rings and ¹⁴C from some of the same species at the same site and use our results to examine correlations among age-related population parameters. Finally, we discuss the implications of these new results for life histories of tropical trees.

Key words: age; crown illumination index; environmental stochasticity; integral projection model; La Selva, Costa Rica; light; Markov chains; mortality trajectory; remaining life expectancy; size structure; tropical trees.

INTRODUCTION

Most studies of tropical tree demography have focused on size, but in many cases the link between size and age remains the more important ecological question with consequences at both the ecosystem and population levels. For example, understanding this link is required at the ecosystem level to determine rates of forest turnover (Martinez-Ramos and Alvarez-Buylla 1998, Baker 2003, Vieira et al. 2005), and at the population level, for comparisons among species of longevity, time to reach the canopy, and age patterns of mortality (Baker 2003, Easdale et al. 2007). Despite the importance of quantifying and qualifying this link, there are relatively few estimates of the time it takes for trees of tropical wet forests to reach important demographic milestones, such as escaping juvenile mortality, reaching the canopy, reaching maximum size, and dying. Estimating tree ages at these key events is complex for two main reasons. First, many species have the potential to be very long lived, and no records to date capture the full life cycle of the oldest individuals of the longer-lived

species, nor are annual tree rings prevalent. Second, the relationship between size and age depends upon the environment and is not deterministic; size and age are not always linked simply by a single parameter. Data on annual growth increments indicate high interannual variability driven by stochastically varying environmental conditions (Clark and Clark 1992, 1999, 2006, Clark et al. 2003, 2007). Previous models have estimated the time it takes individuals to attain particular sizes and life expectancy by simulating size dependent growth increments. The new modeling framework we introduce here is the first to explicitly include the dynamics of light environment (via an index of crown illumination, CI) in the estimation of the time to attain particular sizes and life expectancy of tropical trees from size-dependent annual growth and survival data. Problems with previous approaches were reviewed by Baker (2003) and Martinez-Ramos and Alvarez-Buylla (1998); one key limitation is that many earlier formulations were deterministic. Lieberman et al. (1985) did introduce stochasticity but did not include the sampling effect of mortality (Wyckoff and Clark 2002), or the role of known environmental factors such as light (Baker 2003). The framework we introduce here captures the light dependence of demography, dynamics of light environment over the lifetimes of individuals, variability in

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growth across size, and the conditionality of growth on survival. The light environment is identified by an index of crown illumination (CI) provided for each tree in the data base at each time step.

Results from previous studies are diverse. Lieberman et al. (1985) modeled lifespan from growth data over one 13-year census interval for 45 species, by estimating the shortest possible time taken to reach the largest observed diameter, obtaining highest ages in the range of 500–650 years old. Fichtler et al. (2003) used ^{14}C and tree rings of a few individuals of five species and reported similar highest ages of 500–650 years. Both of these studies were conducted in Costa Rica, where volcanic soils are relatively high in nutrients. In contrast, in Amazonia where soils are lower in nutrients, tropical trees may attain higher ages; for example, one carbon-dating study from Central Amazonia reported tropical tree longevity as high as 900–1600 years old (Chambers et al. 1998); and carbon-dating studies at three Amazonian locations reported that 17–50% of trees with diameters >10 cm were more than 300 years old (Vieira et al. 2005). Previous estimation approaches (both modeling and physical) can lead to widely different predictions even from the same data sets (Martinez-Ramos and Alvarez-Buylla 1998).

Here we develop a method that combines recent progress in estimating age-specific demographic rates from stage-based matrix projection models in stochastic environments (Tuljapurkar and Horvitz 2006) with integral projection model (IPM) analysis (Ellner and Rees 2006). IPMs are similar to matrix projection models of population dynamics; time is discrete and future fate (survival and state) depends upon current state. The principal difference in IPMs is that the state variable used to describe a population is continuous rather than discrete and model parameters are estimated by regression relationships rather than counts (Ellner and Rees 2006). In our analysis, each state of the temporally varying environment is represented by a distinct integral projection model and there is a set of probability rules that governs which one is chosen at each time step. We show how this approach leads to new insights about tropical tree life histories by applying it to the extensive data base on tropical trees provided by Clark and Clark (2006). Previous work on the Clark and Clark (2006) data set indicated that over single time steps mortality and growth of trees depends upon size, but environment accounts for significant portions of the observed variability in demography (Clark and Clark 1992). However, these studies did not dynamically integrate these size effects with light specific dynamics across the life cycle to associate age with demographic events like reaching the canopy or dying because there were no analytical tools available to go from size to age. Our new analysis is able to integrate across ontogeny, incorporate unexplained heterogeneity in growth, capture variation in growth and survival driven by the light environment, and directly address the effect of changes

in the light environment that occur in parallel to changes in size driven by tree growth. Given recruitment of a cohort at age zero into a single small size class in a particular light environment, our approach uses a Markov chain approach to track the probability that at each subsequent age, individuals are found to be any size in any light environment, provided they survive; and survival at any age depends jointly upon size and light. Thus, the trajectories of individuals within a cohort are tracked throughout their lives. Since size is ontogenetically plastic and light is changing, the complete description of a life path of an individual from birth to death will include not only its size at each age, but also its light environment at that age.

We use this new method to go from single time step data on size transitions and survival to estimates of expectations of timing of key events in the life of a tree, including escaping juvenile mortality, reaching the canopy, achieving maximum size, and dying. We introduce a new method for estimation of first passage times to chosen specific sizes in a dynamic light environment. With this, first, we can compare our results on the relationship between size and age with independent estimates based on tree rings and ^{14}C . Second, for every species, given a recruitment light environment, we can estimate both average remaining life expectancy, and the average time they will take to reach the canopy for the first time. If the latter is larger than the former, it suggests that on average individuals recruiting into that light environment die before reaching the canopy, providing unique insight into the importance of gaps for different species within the study.

Below, we introduce the methods, and then, to illustrate the methods, present results in detail for two of the nine species, one of the more common short-lived pioneer species at the study site and a common emergent species in the old-growth forest on more fertile soils. The study site is La Selva Biological Station, located in lowland tropical rain forest in northwestern Costa Rica. Detailed results for the full set of nine species are available in Appendix C. We compare the full range of age trajectories obtained across all nine species and discuss life history implications revealed by our analysis.

METHODS

There are four main steps to our method that are applied to each species. First, we use the data to develop statistical models that describe the functional dependence of growth and survival in single time steps on size, by light environment. Second, we combine growth and survival models to create an integral projection model (IPM) for individuals based on their size in each light environment. Third, we develop a Markov chain model of light dynamics based on observed transitions of individuals among categories of light availability. Fourth, we analyze the stochastic dynamics of environment-dependent integral projection cohort models by

incorporating the environment-specific IPMs into a model that includes environmental (light) dynamics. Finally, we obtain age patterns of mortality, life expectancy, and expected first passage times to certain key sizes, conditional on initial environmental state.

Data and study species

The data set provided by Clark and Clark (2006) includes observations on 10 species taken between 1983 and 2000. One of these (*Pentaclethra macroleoba*) was only studied in 1998–2000 and lacks observations across some sizes. D. A. and D. B. Clark (*personal communication*) recommended we focus this analysis on the nine species for which there are many more observations that span the full size ranges, i.e., the six studied 1983–2000 and the three studied 1988–2000. These species span a range of sizes, recruitment needs, and adult habitat. Maximum observed diameters for the nine species range from 366 to 1870 mm. These species can be classified by the vertical stratum in which mature adults are found. (1) The smallest species *Cecropia obtusifolia* is a subcanopy tree; individuals are found in full sunlight only where the canopy is broken. (2) The next largest species, *Cecropia insignis*, *Simarouba amara*, and *Minquartia guianensis*, are canopy species; their crowns form a continuous layer of forest, and mature individuals are usually only fully illuminated from the top unless there is a break in the canopy. (3) The largest and tallest species, *Balizia* (= *Pithecellobium*) *elegans*, *Hymenobium mesoamericanum*, *Lecythis ampla*, *Dipteryx panamensis*, and *Hyeronima alchorneoides* are emergents; mature individuals are usually illuminated both from the top and laterally. A total of 3036 individuals across these nine species were tracked between 1983 and 2000. Data taken for each individual each year included a measurement of diameter, status (dead or alive) and a measure of the availability of light. The two species we focus on in the main text are *Cecropia obtusifolia* and *Dipteryx panamensis*, one subcanopy and one emergent.

Within each species, individuals were chosen to accumulate an unbiased sample of all post-establishment size classes for each study species. Consequently, the data indicate how growth and mortality change across the entire size range, and such data are just what is required to develop the statistical regression models of how these annual demographic rates depend upon size (see Appendix A: Fig. A1 for diameter of individuals on a natural log scale at time t and a year later; see Appendix A: Fig. A3 for survival data from t to $t+1$ for individuals as a function of diameter on a natural log scale). These regression models form the underpinnings of an integral projection model. More than 1000 mortality events were recorded.

For each individual tree at each census, a crown illumination index, CI, is provided, which indicates the amount of light received by each individual, as determined by the position of its crown with respect to openings in the surrounding canopy (Clark and Clark

2006). We used six categories chosen as biologically meaningful to facilitate computation: 1, 2, and 3 indicate low, medium, and high lateral light only (respectively corresponding to 1.5–1.75, 2–2.25, 2.5–2.75 in the data base), 4 indicates some overhead light, 5 indicates full overhead light, and 6 indicates that the crown was completely exposed, i.e., emergent, or in a gap (respectively corresponding to 3–3.5, 4–4.5, and 5 in the data base). Crown illumination varies over the life course of individuals due to changes in their own height as well as changes in the crown structure of neighboring trees, i.e., canopy dynamics (Clark and Clark 1992).

In what follows, we model changes in tree diameter and changes in crown illumination, or CI, separately. Changes in crown illumination are not confounded with changes in diameter (see Appendix A for a statistical analysis of this separation), because they can result from several sources. Increases in crown illumination can occur through growth in height, but also openings in the canopy due to growth, death, or branch loss of neighboring trees. Decreases in crown illumination can result from physical damage to the focal individual (stem breakage or being knocked over, due to falling branches or trees), or from the closing of canopy openings by lateral or upward ingrowth by neighboring plants. At large sizes, tree height reaches a characteristic plateau, for a given species, determining its position in the vertical stratum of the forest, whereas diameter may continue to increase. All these patterns may be species specific as they will be partly determined by species growth in height and die-back characteristics, but also species' wood density and resilience. In the development of models described in the rest of the *Methods* section, we therefore separate growth in diameter (including survival) from changes in crown illumination, although we allow crown illumination to influence growth rate and mortality as there is good evidence that light is a key covariate of growth and mortality in tropical trees (Clark and Clark 1992).

Demographic framework

Integral projection models are a useful way to study the dynamics of populations in which a continuous variable such as size is predictive of survival, growth (future size) and reproduction (Ellner and Rees 2006). Time is treated as discrete, the state of the system is described by a distribution of sizes at a given time, and the process is Markovian. Regression analysis is used to estimate parameters of functions that relate current size of an individual to its future size and status. In this paper, we adapt the IPM approach to address cohort dynamics, by which we mean the future fates of individuals already alive at a given time; thus we leave out the birth of new individuals at each time step. We use diameter as the main size measurement, taking the natural logarithm as Clark and Clark (1992) suggest that most intraspecific variation in mortality occurs for plants with a diameter of less than 40 mm. Our size-

structured population model tracks progression of a population vector \mathbf{n} , which can be thought of as a number density by size at t . Tracking is achieved by capturing transitions between different sizes:

$$n(y, t + 1) = \int_{\omega} p(y, x)n(x, t) dx. \tag{1}$$

The integral is taken across the entire range of possible sizes ω , and the kernel $p(y, x)$ includes transitions from size x to size y from time t to time $t + 1$, incorporating both survival and growth:

$$p(y, x) = s(x)g(y, x) \tag{2}$$

where $s(x)$ is the probability of survival at a given size x ; and $g(y, x)$, is the probability of transition from a size x at time t to a size y at time $t + 1$ through growth conditional on survival, and takes the form of a normal density function around y . Both components of $p(y, x)$ are defined by applying statistical models to the data. To include the role of light in demographic transitions, we estimate a separate kernel for each light environment, obtaining parameters for a different function $p_i(y, x, i)$ for each level i of crown illumination, CI. Later we show that the sequence of kernels experienced by a cohort is generated by a stochastic process model for the temporally varying light environment for each species.

To obtain statistical models of $s(x)$ by light environments, we fit a logistic regression to the data on size and status for each species according to

$$\text{logit}[s(x)] = m_i + m_s x(t) \tag{3}$$

where m_i is the light environment specific intercept, and m_s is the overall slope of size common to all light environments, and i indicates an index of light environment (details are in Appendix A). Although not all sizes are present in all light environments (e.g., very small individuals will generally not be observed in the highest light environments) we assume that we can extrapolate from the sizes that are available in each light environment to obtain the effect of light across the full size range.

The second component of Eq. 2, $g(y, x, i)$, is given by a linear regression linking size at $t + 1$, given size at t :

$$y = r_i + s_i x + \varepsilon \tag{4}$$

where r_i and s_i are the light-specific intercept and slope, the i index indicates a particular light environment, CI = i , and ε captures a deviation from the mean relationship for each observation. Again, although not all sizes are present in all light environments, we assume that we can extrapolate from the sizes that are available in each light environment to obtain the effect of light across the full size range. The function that enters Eq. 2, $g(y, x, i)$ will be a normal density function centered on y where y is the predicted size from the linear regression, given the size observed at t . The variance, σ_g^2 , of this normal density

function is defined from the error variance of the regression, i.e., by $\varepsilon \sim N(0, \sigma_g^2)$ (details in Appendix B).

To implement Eq. 2, a numerical approach for estimating the integral is used in which the total size range is divided into a large number of bins, S , so that the population is described by an $S \times 1$ vector and the transitions by an $S \times S$ matrix denoted \mathbf{q}_i when the light environment CI = i (Ellner and Rees 2006).

Markov chain for the light environment

For each species, having defined a matrix \mathbf{q}_i to estimate the integral kernel $p(y, x, i)$ for each crown illumination environment, CI = i , we also require the model of the stochastic environmental process, comprised by transitions between light environments. For each species, we estimated the average (across individuals) annual transition probabilities c_{ij} from crown illumination environment CI = j to crown illumination environment CI = i . For each species, the corresponding Markov matrix $\mathbf{c} = (c_{ij})$ is of size $K \times K$, where K is the number of crown illumination classes in which that species occurs. At each time t , the life-history transition matrix $\mathbf{q}(t)$ is chosen according to

$$\text{Pr}[q(t) = q_i | q(t - 1) = q_j] = c_{ij}. \tag{5}$$

Modeling light environment dynamics from observed transitions of individual trees differs from measuring forest canopy dynamics independently of the target species (e.g., Tuljapurkar et al. 2003). The transition probabilities, c_{ij} , include not only gap formation and closure (determined by the neighboring trees), but also the ability of individuals to occupy and traverse the vertical strata of the forest.

Size to age in variable environments

Temporal variability means that individuals experience a particular sequence of environmental states over time. Consider an individual who is size y at time $t = 1$. At time $t = 2$, the individual will be some size x after making growth and survival transitions according to the probabilities in the kernel that corresponds to the environment at that time. $P(y, x)$ is a random variable that takes on values $p(y, x, i)$. $P(y, x)(1)$ denotes the kernel at time 1, and so on over successive intervals. At each time t the kernel $P(y, x)(t)$ is determined by the environmental state at that time, similar to the process for stochastic population dynamics governed by IPMs in Ellner and Rees (2007). What we are doing here, however, is not stochastic population dynamics; we are interested only in growth and survival of existing individuals, not in the production of new individuals. To numerically estimate this process, we use the sequence of environments to find the value $p(y, x, i)$ at each time t and use the corresponding matrix \mathbf{q}_i to generate a product of matrices.

For each species, we have a set of K demographic transition matrices, \mathbf{q}_i , one for each crown illumination environment where individuals of the species are

present, each of size $S \times S$; and an environmental transition matrix, \mathbf{c} , of size $K \times K$, describing transitions between crown illumination environments. With these, to summarize all possible transitions among sizes within and among environments, we define the megamatrix, \mathbf{m} ,

$$\mathbf{m} = \mathbf{q}_i \mathbf{c}_{ij} \quad i, j = 1, \dots, K \quad (6)$$

an $SK \times SK$ matrix made up of $K \times K$ blocks each of size $S \times S$:

$$\mathbf{m} = \begin{pmatrix} \mathbf{q}_1 \mathbf{c}_{11} & \mathbf{q}_1 \mathbf{c}_{12} & \cdots \\ \mathbf{q}_2 \mathbf{c}_{21} & \mathbf{q}_2 \mathbf{c}_{22} & \cdots \\ \vdots & \vdots & \vdots \end{pmatrix}. \quad (7)$$

The megamatrix \mathbf{m} is at the heart of closed-form equations which quantify remaining life expectancy and age-specific survivorship conditional on initial environment in a Markovian environment. As in Tuljapurkar and Horvitz (2006), the fundamental matrix is defined, conditional on a particular environmental sequence, as

$$\mathbf{N} = \mathbf{I} + \mathbf{Q}(1) + \mathbf{Q}(2)\mathbf{Q}(1) + \mathbf{Q}(3)\mathbf{Q}(2)\mathbf{Q}(1) + \cdots \quad (8)$$

where \mathbf{Q} is a random variable that can take on the values \mathbf{q}_i , $\mathbf{Q}(1)$ is the environment at $t = 1$, and so on, \mathbf{I} is the identity matrix, and the series runs over all integers $t \geq 1$. The t th term after the first in Eq. 8, written as $\hat{\mathbf{Q}}(t)$, is a product of matrices that contains the probabilities of life history transitions between times 1 and $t + 1$. Conditional on the environmental sequence experienced by a cohort, the average times spent in each size before death are found in the elements of the matrix \mathbf{N} . For individuals born in environment i , the expected lifetimes are contained in the elements of the average of \mathbf{N} in Eq. 8 taken over all subsequent environmental sequences.

Tuljapurkar and Horvitz (2006) have shown that, for Markovian environments, for cohorts born in environment i , the average fundamental matrix is computed as

$$\mathbf{N}_i = \mathbf{I} + \left[\tilde{\mathbf{e}}(\mathbf{I} - \mathbf{m})^{-1} \tilde{\mathbf{q}}_i \right] \quad (9)$$

and survivorship to age z for cohorts born in environment i is computed as

$$l_i(z) = \left[\mathbf{e}'(\tilde{\mathbf{e}}\mathbf{m}^{z-1} \tilde{\mathbf{q}}_i) \right]_1. \quad (10)$$

Here $\tilde{\mathbf{q}}_i$ has K blocks each $S \times S$ with only the i th block being nonzero,

$$\tilde{\mathbf{q}}_i = [0 \cdots 0(\mathbf{q}_i)0 \cdots 0] \quad (11)$$

$\tilde{\mathbf{e}}$ has K blocks of $S \times S$ identity matrices,

$$\tilde{\mathbf{e}} = (\mathbf{I} \cdots \mathbf{I}) \quad (12)$$

\mathbf{e} is a column vector of all 1's, and the 1 in the subscript denotes the first column for size class 1.

The total expected remaining life time of an individual who starts in size y at time $t = 1$ is found by summing column y in \mathbf{N} . We emphasize that this is a calculation of

the mean life expectancy. The variance in life expectancy can also be obtained by related methods (Tuljapurkar and Horvitz 2006), but we do not do so in this paper. Survivorship to age z , $l(z)$ is computed from the $\hat{\mathbf{Q}}(z)$, which is of course conditional on the environmental sequence experienced by a cohort.

First passage times in Markovian environments

The matrix \mathbf{m} can also be used to estimate average times taken by surviving individuals to reach specified critical sizes. To do this, we extend existing theory (Kemeny and Snell 1976: chapter 3; Caswell 2001:113–114, 124–125), to the megamatrix. The mathematical analysis of this problem for the doubly Markov process described by the megamatrix has not, to our knowledge, been previously used in an ecological context. Technical details of how to accomplish this interesting and previously unexplored first passage time problem are given in Appendix B.

RESULTS

Demographic models: \mathbf{q}_i for each light environment

Growth models.—Linear regressions were used to obtain the r_i and s_i parameters for Eq. 4, and the associated variance of $g(y, x, i)$, σ_g^2 . In all species, the pattern of residuals suggested declining variance with size. This was most marked in *Cecropia* although it was also evident in other species (Appendix A: Fig. A1). We assumed that the variance could be modeled as

$$\sigma_g^2 = \phi \exp(-\gamma \hat{y}) \quad (13)$$

where ϕ and γ are estimated from the data pooled over all light environments and \hat{y} is the fitted value. For all species, this function provided a better fit than simple linear regression, and including size as a covariate significantly improved the model; for most species, adding light specific intercepts, and an interaction between light and size further improved the model (Appendix A: Table A1; Table A2 for parameter values). The first row in Fig. 1 shows the resulting predicted mean growth increment across the range of sizes for each light environments $CI = i$ for *Cecropia obtusifolia* and *Dipteryx panamensis*. Note that in all light environments, growth increment peaks at intermediate sizes (in line with scatter plots shown in Clark and Clark 1999). (Appendix A provides parameters from the fitted model for all species, their significance, and discussion of species-specific patterns.)

Survival models.—Logistic regressions were used to obtain the m_i and m_s parameters for Eq. 3. Patterns of residuals suggested the presence of nonlinearities, and we therefore used the Akaike information criteria to test whether a model including a polynomial term, i.e.,

$$\text{logit}(s) = m_i + m_s x(t) + m_p x(t)^2 \quad (14)$$

would improve the fit. This proved to be the case for all species ($P < 0.01$) except the two *Cecropia* ($P > 0.05$).

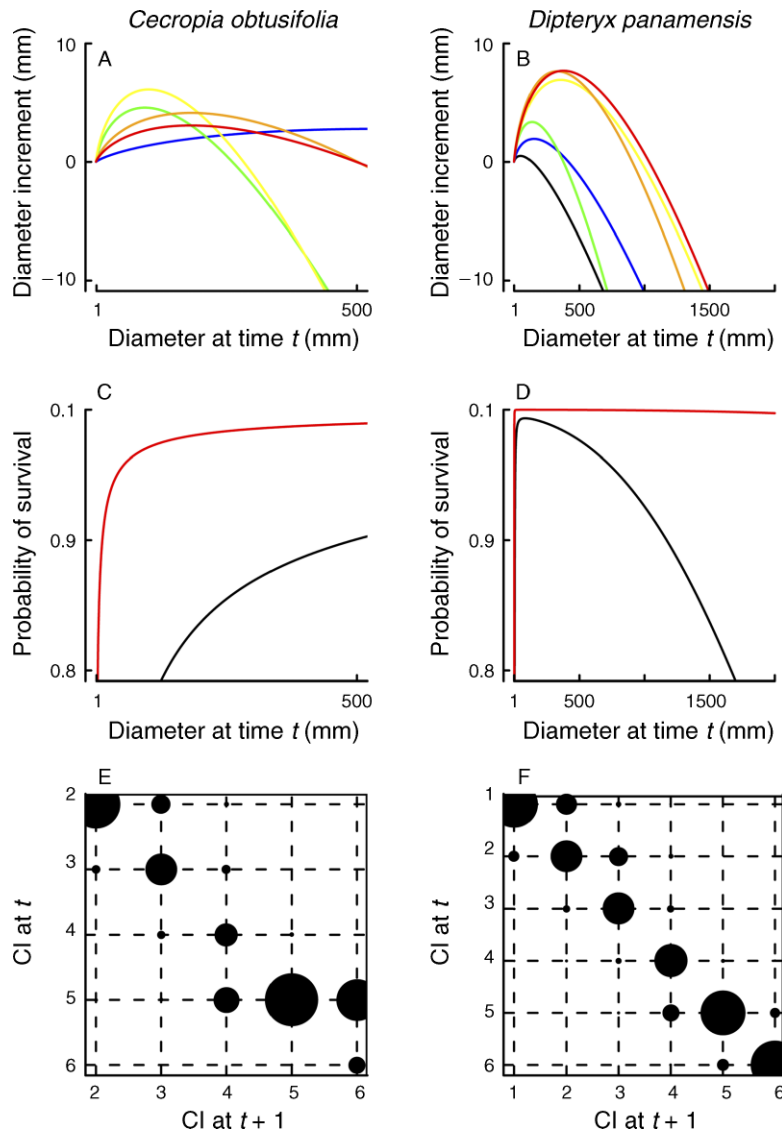


FIG. 1. Elements used to construct the full model illustrated for *Cecropia obtusifolia* and *Dipteryx panamensis*. Panels A and B show predicted growth increment across the observed size range in each of the six light environments obtained from a linear regression (Eq. 4). The black line is for crown illumination index CI=1, blue line is CI=2, green line is CI=3, yellow line is CI=4, orange line is CI=5, red line is CI=6. Categories 1, 2, and 3 indicate low, medium, and high lateral light only, category 4 indicates some overhead light, category 5 indicates full overhead light, and category 6 indicates that the crown was completely exposed, i.e., emergent, or in a gap. Panels C and D show predicted survival probability; the black line is for shaded environments (Eq. 3), the red line is light environments. Panels E and F indicate, by the sizes of the dots, the relative probabilities of transitions between light environments, used to build the matrix c . The smallest dots indicate probabilities of less than 1%, and the largest dots correspond to probabilities of between 85% and 95% (see Appendix A: Fig. A5 for more details).

The nonlinearity models the possibility that very large trees have a higher risk of dying (Laurance et al. 2000). However, *Cecropia* have never been observed to survive to sizes so large. The second row in Fig. 1 shows the resulting predicted survival probability across the range of sizes for two classes of light environments (CI = 1, 2, or 3 and CI = 4, 5, or 6) for *Cecropia obtusifolia* and *Dipteryx panamensis*. For the former, there is no decline of survival with size; for the latter, in shadier environments, there is a distinct decrease of survival probability

at larger sizes (Appendix A provides an illustration of the data [Fig. A3], significance tests of coefficients [Table A3], coefficients for all species [Table A4], the resulting predicted mean survival probability across the range of sizes across the range of light environments [Fig. A4], and discussion thereof.)

Numerical estimates of $p(y, x, i)$ by creation of matrices \mathbf{q}_i .—For all species, we numerically estimated the integral kernel $p(y, x, i)$ with a matrix by using $S = 300$ bins for the size range from 1 to 2000 mm resulting

in a matrix of 300×300 size categories based on the $\log(\text{diameter})$ (see Appendix A for details). Since these matrices have as the smallest size category, 1 mm, counting time for individuals begins by when they are recruited into this size class.

Environmental dynamics: Markov chains

Dipteryx panamensis is found in all six light environments; *Cecropia obtusifolia* was never observed in the darkest light environment (Fig. 1E, F). For both species, individuals tend to remain in the same light environment from one year to the next, with most non-stasis transitions taking place between adjacent categories (Fig. 1E, F). In shadier environments, individuals have a higher probability of transitioning to an even darker environment than to lighter conditions; in lighter environments, there is a higher probability of being in an even lighter environment the following year than of becoming shadier, in line with results in Clark et al. (1993). In the pioneer species *Cecropia obtusifolia*, transitions from the highest light environment to one with less light are frequent, indicating that this species is often overtopped. In contrast the emergent species *Dipteryx*, once it attains the status of being in the high light environment by breaking through the canopy, remains in high light (see Appendix A for results for all species and discussion thereof).

Remaining life expectancy in the Markovian environment

To estimate remaining conditional life expectancy, the mean time to death for individuals who have already attained a particular size, for each species we obtain the megamatrix \mathbf{m} , as in Eq. 6. Life expectancy is size and light dependent. This means, if you were writing insurance policies for trees, you would write a different one for trees in a gap or above the canopy than for trees of equivalent size in shaded conditions. For trees of equivalent size at a given point in time that differ in light environment, the expectation of future life is greater in the light (Fig. 2A, B). Species show very distinct patterns across size and with light. For *Cecropia obtusifolia*, remaining life expectancy increases, declines, and then increases steadily with size. For *Dipteryx panamensis*, remaining life expectancy peaks at very small sizes, and then steadily declines (Appendix C: Fig. C1 provides results for all nine species).

Age-specific mortality trajectories in the Markovian environment

The megamatrices \mathbf{m} allow estimation of the rate of change of survivorship with age by calculation of age-specific mortality curves $\mu_i(z)$ where z is age and the subscript i indicates that the mortality at age z is dependent on the initial environmental state of the individual (Horvitz and Tuljapurkar 2008). We first defined the recruitment environment as the crown illumination (CI) value for individuals of 1 mm diameter, i.e., we define being age 1 as having a 1 mm

diameter. Species such as *Dipteryx* may achieve this diameter within their first year, for *Cecropia* it might take longer, but there was insufficient data to address these differences in detail. We estimated the rate of change of survivorship up to 300 years of age for each “recruitment” environment, using closed form equations for expected survivorship $l_i(z)$ for an assemblage of cohorts recruiting into each environment and $\mu_i(z) = -\log_\lambda(l(z+1)/l_i(z))$ for each environment (Tuljapurkar and Horvitz 2006, Horvitz and Tuljapurkar 2008). We also calculated the mortality plateau $-\log(\lambda)$ and examined the approach to it asking whether it is reached by 300 years of age.

Lower age-specific mortality when seedlings recruit into the light is observed for both species. *Cecropia obtusifolia* approaches the plateau from above exhibiting negative senescence (Fig. 2C, D). By contrast, *Dipteryx panamensis* shows a classic asymmetric “bathtub-shaped” mortality, with very high mortality at early ages that falls rapidly to a minimum indicating an age at which the species escapes juvenile mortality, and then rises up towards the plateau from below exhibiting positive senescence that then levels off (see Appendix C: Fig. C2 for results for all nine species).

Expected first passage times in the Markovian environment

We estimated the expected time to reach various sizes of interest from particular starting sizes, conditional on survival. The target sizes included 100 mm, the usual lower threshold for including trees in forest inventory studies; 300 mm, the size associated with reaching the canopy (Clark and Clark 1999:993); 800 mm, which indicates fairly large trees; and finally 1200 mm and 1800 mm are quite large dominant trees. In addition, for each species we also estimated time to reach the maximum observed diameter. This type of analysis has not been presented previously in the context of a dynamic environment. Fig. 2 (last row) indicates absorption times to a size of 300 mm for a range of starting sizes. In general, the passage time to reach the canopy is quicker in lighter environments. For both species, there is a hump in the curve. This means that on average the very smallest trees are expected to reach the canopy sooner than trees that are a little bit bigger. This is particularly noticeable for *Cecropia obtusifolia*, and is attributable to higher variance in growth at small sizes (Appendix C shows results for all species; Fig. C3 and Table C1). Fig. 3 shows the time to attain various target sizes for a starting size of 10 mm, the size we consider as a threshold of juvenile “recruitment.” In all species, these increase monotonically. In all species the estimated relationship between size and the age at which this size is expected to be attained is in good agreement with measures taken by Fichtler et al. (2003) using tree rings and ^{14}C from fallen logs of the same species.

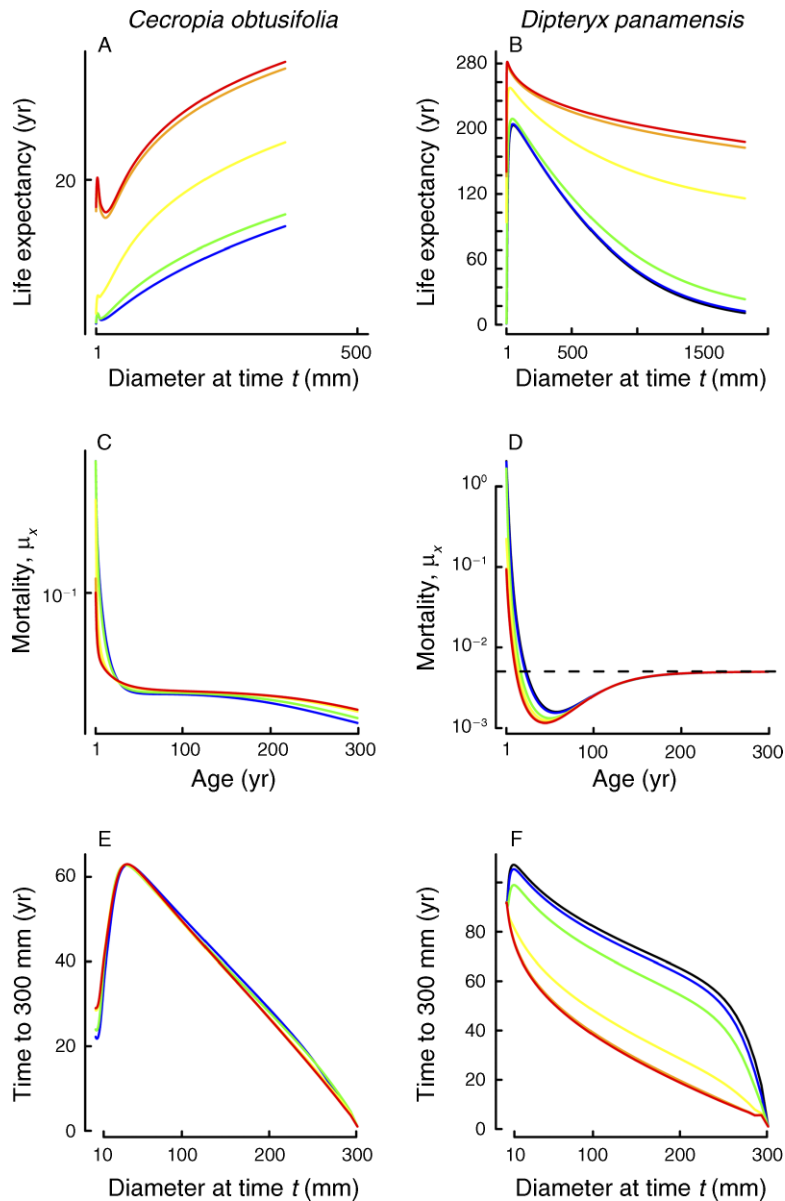


FIG. 2. Dynamics in *C. obtusifolia* and *D. panamensis*: (A, B) remaining life expectancy conditional on size (from Eq. 10) where sizes range from 1 mm (which we consider equivalent to the birth size) to maximum observed size for each species; (C, D) age-specific mortality trajectory (from Eq. 10); and (E, F) time to reach 300 mm, the size at which the canopy is reached, from a range of starting sizes, from 10 to 300 mm. Colors are for different crown illumination (CI) environments as in Fig. 1.

DISCUSSION

Size, light, life expectancy, and first passage times

Our results provide the first estimates of life expectancy, first passage time to chosen target sizes and age patterns of mortality for nine tropical tree species in a dynamic environment. These results are based on a detailed model of the interaction between growth, survival, plant size, and light.

The predicted survivorship, mortality rate, and first passage time trajectories exhibit some well known features and reveal some surprising patterns. Initial

light environment has considerable impact on expected remaining life span, as does size. Mortality trajectories indicate negative senescence for some species (the *Cecropia*) and a mortality plateau for others, not a monotonic increase in mortality with age. Most of the non-pioneer species exhibited very high mortality at the youngest ages with a sharp decrease to a minimum mortality at an intermediate age that is then followed by a slow rise to a plateau. This pattern results from changes in the size structure of a cohort as it ages. In early years, it is comprised of mostly very small individuals with low survival. These are replaced by

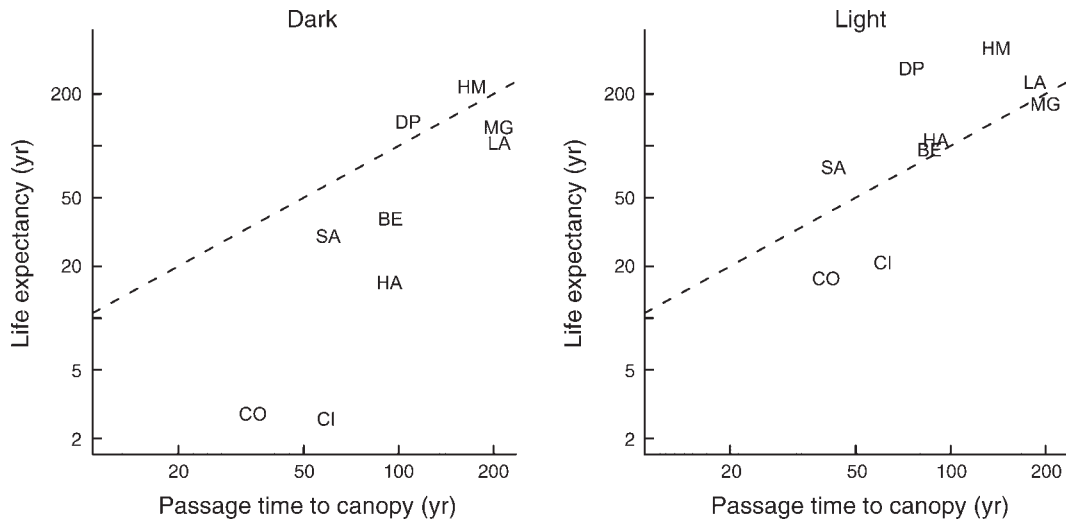


FIG. 3. Relationship between time to attain 300 mm, the size at which the canopy is reached, and remaining life expectancy of individuals of 10 mm diameter, starting in the darkest and lightest environment for each species (darkest and lightest crown illumination [CI] values, 1 and 6 for all species but *Cecropia obtusifolia* [2,6] and *Miconia* [1,5]). Note log scale. The dashed line indicates $y = x$. The correlation is significant in the dark ($P < 0.05$) and near significant in the light ($P < 0.055$).

larger individuals with better survival, but there is an age after which the cohort becomes gradually composed of very large trees that have lower survival. Consequently, many species are characterized by the bathtub-shaped pattern of mortality rates across age considered characteristic of humans. That tropical trees exhibit a mortality trajectory similar to humans is a novel result.

For all species, variance in growth declined with size, a pattern in line with results for maximum and mean growth rate obtained by Clark and Clark (1999). The implications of this pattern have not been previously appreciated: very small trees on average may reach a particular large size more rapidly than somewhat larger trees. The larger variance in growth for small trees coupled with fact that the survivors are more likely to be those who grow faster is a plausible explanation. This result underscores the important distinction between age and size: young plants can never reach a particular old age sooner than somewhat older plants. But small trees can reach a particular large size sooner than somewhat larger ones. Such non-monotonic first passage time patterns affect the relationship between size and remaining life expectancy and mortality rates, e.g., they lie behind the fact that average remaining life expectancy in the two *Cecropia* species initially declines with size. Greater physiological flexibility for pioneer species has been indicated in previous work (Bazzaz 1996) and here we show that the implications are complex. These complexities would be lost if only mean growth rate was considered and variance ignored, or size was simply assumed to show gradual, directional increases across the lifetime. The pattern in decreasing variance in growth with size is conspicuous when size is taken on the log scale (Appendix A: Fig. A1) at which we can

detect the key differences between growth and mortality (Clark and Clark 1992).

Estimates of remaining life expectancy, mortality rates, and first passage times depend on the demographic model used, which in turn relies on the underlying statistical models and corresponding data. This unique data set has broad coverage across size and light for all species, so that sampling error is small. However, survival in late age survival classes, corresponding to the largest individuals will heavily influence life expectancy, and this is where data is most sparse. Both Condit et al. (1993) and Clark and Clark (1992) explored mortality of large trees and suggested no particular patterns. Using the logistic regression (Eq. 14), we found significantly increased mortality at larger sizes for a range of species. However, we did not model the effect of the full range of light environments on all parameters in Eq. 14 but simply compared intercepts at two levels, light and dark. More data at this size range would allow more detailed estimates of this pattern (although these are difficult to obtain since the density of very large individuals in tropical species is low and their deaths are rare events). Our demographic model also fixes survival probability of trees with diameters of 2000 mm and above to survival at size 2000 mm, whereas in fact, it may continue to decline with size. More generally, a range of different statistical forms for growth and survival could be explored (see Appendix A).

Comparing our results with previous estimates

Fichtler et al. (2003) used a combination of tree rings and carbon-dating techniques to obtain age estimates for 12 individuals encountered as fallen trees across the range of species considered here. Our estimates of first

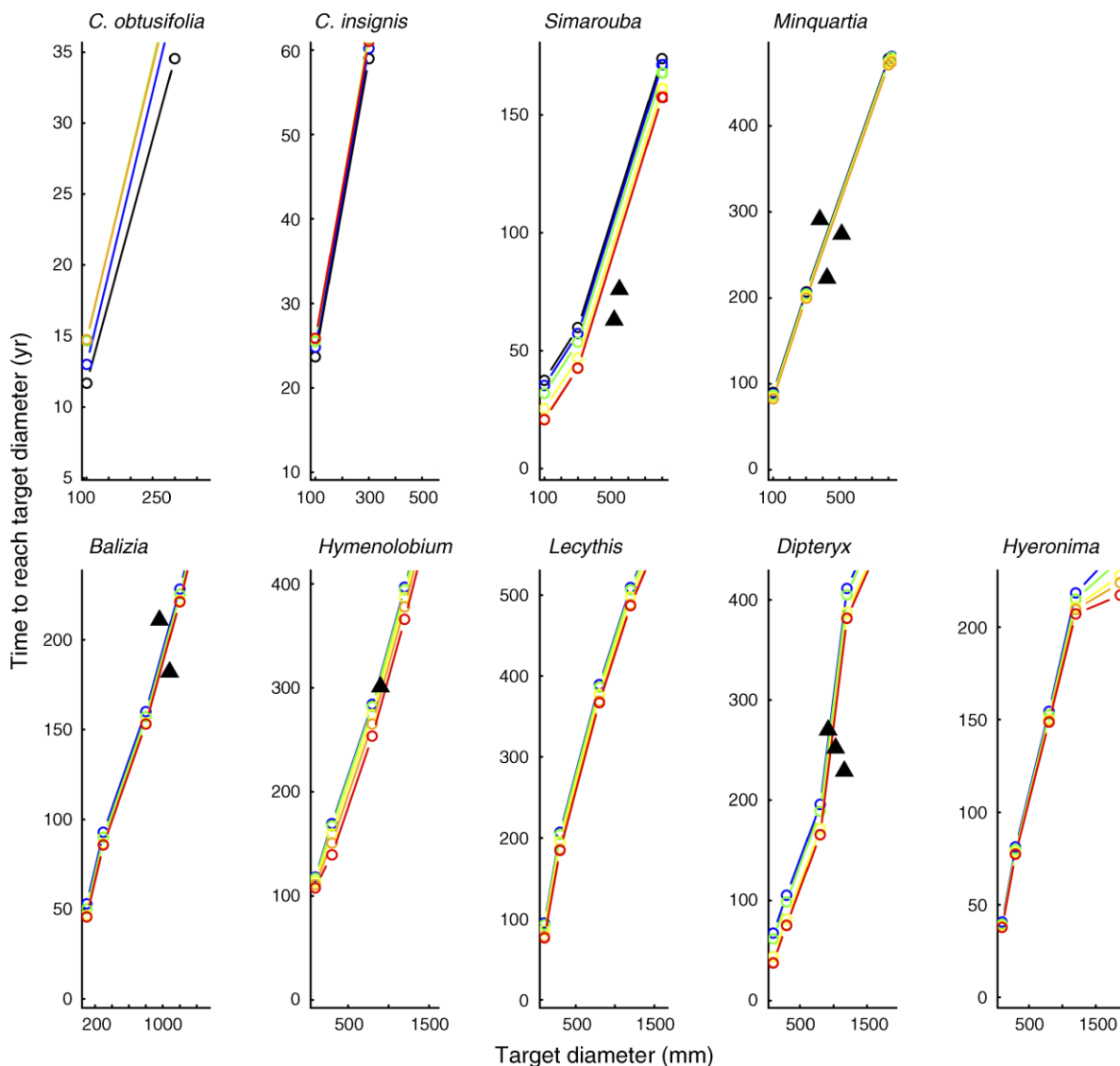


FIG. 4. For two species of *Cecropia* and seven other tropical tree species at La Selva, Costa Rica, first passage time to critical target sizes (300, 800, 1200, and 1800 mm and the largest observed diameter) for the starting size of 10 mm, depicted for initial crown illumination environments CI=1 (black line), CI=2 (blue line), CI=3 (green line), CI=4 (yellow line), CI=5 (orange line), and CI=6 (red line). Triangles indicate estimates from an independent study at the same location (Fichtler et al. 2003), based on tree rings and ¹⁴C analysis from fallen trees. The two *Simarouba* estimates were suspected to be underestimates, given the loss of some outer sapwood.

passage time at the observed sizes are very close to their estimates (Fig. 4), providing an independent validation of the methods used here.

Clark and Clark (1992) estimated time spent in each size class and first passage time to 300 and 1000 mm diameter based on maximum and median diameter growth increments. Our estimates of first passage time lie between these two estimates, e.g., for *Lecythis*, Clark and Clark (1992) predict 59 (maximum increment) to 462 (median increment) years to reach 30 cm; we predict between 96 (in the dark) and 76 (in the light) years. Our analysis is conditional on survival, and surviving trees tend to be faster growing due to the relationship between

size and mortality; it also includes growth increases through attaining higher light environments.

Lieberman et al. (1985) calculated longevity as the number of years it took to go from 100 mm diameter to the maximum observed diameter for the minimum growth trajectory for each species using the approach described in the *Introduction*. *Minquartia* is the only species common to both their data set and the current set of nine species. For this species, they reported a maximum diameter of 722 mm and estimated a “minimum age” of 188 years and a “projected life span” of 280 years. The “minimum age” is defined as the number of year to grow from 100 mm to the maximum

diameter based upon the maximum growth rate in their simulation, while the “projected life span” is defined as the number of years to grow from 100 mm to a size near the maximum diameter based upon the minimum growth trajectory in their simulation. Our estimates of how long it takes to reach the same target sizes are not really comparable to theirs, since we start counting time from a much smaller size (10 mm); unsurprisingly for *Minquartia*, our estimated first passage times from 10 mm to maximum observed size (820 mm) is the larger value of 482 years for individuals starting in the dark, and 475 for individuals starting in the light (Appendix C: Table C1).

Alvarez-Buylla and Martinez-Ramos (1992) aged gaps in a rain forest in Mexico using damage to stems of an understory palm species and found that *Cecropia obtusifolia* individuals with a stem diameter of 300–400 mm were located predominantly in gaps of between 21 and more than 35 years of age. Assuming that recruitment generally coincides with gap formation, this period is compatible (although slightly shorter) than our estimates of 34 years (Appendix C: Table C1).

Cross-species patterns in demography

To shed light on the processes allowing coexistence of many species apparently sharing the same resources, a broad program of research has been devoted to tropical tree life histories (Clark and Clark 1992). A currently favored process underlying coexistence is a growth–survival trade-off: if species that grow fast also suffer high mortality, this could create an equalizing mechanism (Adler et al. 2006) facilitating coexistence by making species more similar in population growth. For example, Gilbert et al. (2006) compared one-year growth increment with one-year survival for two different stages, seedlings and saplings, and showed that species that grew faster tended to have higher mortality. Here, a similar comparison can be obtained by plotting growth increment at a chosen size based on Eq. 4 vs. survival at that size from Eq. 14. However, a fundamental point is that in our analysis, even at the same chosen size, there are several possible pairs of growth and survival values, one for each light environment. Trade-offs are not necessarily apparent in any particular light environment. The comparison made by Gilbert et al. (2006), and indeed the entire theory of trade-offs, does not include variation in the environment through time, and differences in how individuals of a given species experience the environment (Orzack and Tuljapurkar 2001). Comparisons of demographic rates at a single age or size can consequently underestimate or overstate differences between species’ overall fitness (necessarily the outcome of the entire demographic schedule). Since equal fitness is required for coexistence, using only a single size or age may consequently obscure inference on the likelihood of species coexistence, a key question in tropical ecology.

Our framework allows a whole cohort perspective on this issue. Our results show a correlation between the number of years it will take to reach the canopy and the number of years of remaining life, for members of a cohort who have achieved a size of 10 mm in diameter; i.e., there is a correlation between log first passage time to a diameter of 300 mm from a diameter of 10 mm, and log remaining life expectancy at 10 mm (for the darkest starting environment for each species, $n = 9$, $\rho = 0.85$, $P \leq 0.01$; for the lightest starting environment, $n = 9$, $\rho = 0.72$, $P \leq 0.05$; Fig. 3). This is also consistent with a growth–survival trade-off, but now operating across large portions of the life cycle, and in a variable environment. Species which reach the canopy faster tend to have fewer survivors. The relationship does not persist on excluding the two *Cecropia*, which have the clearest claim to being a distinct functional group (shorter life spans, higher sensitivity to light, particularly in survival, and considerable variance in growth) and thereby might drive the correlation ($n = 7$, $\rho = 0.72$, $P > 0.5$ and $n = 7$, $\rho = 0.59$, $P > 0.1$). However, sample size is small (only nine species), so it is difficult to determine whether this is chiefly an issue of power.

Another way to compare the importance of gaps for different species is to estimate survivorship to the canopy of individuals recruiting into different crown illumination environments (Fig. 5) by combining our estimates of time taken to attain the canopy from different recruitment crown illumination environments (Fig. 2E, F) with estimates of survivorship over age given different recruitment crown illumination environments (from which Fig. 2C, D). If recruitment occurs into shaded environments, *Balizia* has the highest chance of attaining the canopy, and *Hyeronima* the lowest, whereas if recruitment occurs in high light environments, *Dipteryx* individuals have a probability close to 1 of attaining the canopy, i.e., recruitment light environment leads to differences in the fraction of individuals of each species that will reach the canopy.

Several other demographic features are also likely to be important in allowing coexistence. First, the model we use for light transitions averages over individual experiences of light conditions, and may thereby neglect some of the variability that is important to coexistence. Second, we only analyze cohort dynamics, and so do not include the effects of differences in recruitment, although for example, *Cecropia* tend to recruit more frequently into the light (Alvarez-Buylla and Martinez-Ramos 1992, Condit et al. 1995), and, by contrast, *Lecythis* and *Minquartia* tend to recruit into dark environments (Clark and Clark 1992). A third related issue is that of species differences in fertility. All three are interesting avenues for further development. Estimates of the survivorship of cohorts over the period required to reach the canopy for different recruitment environments provide an indication of magnitude of successful recruitment from the seed crop for at least one individual to recruit to the canopy (Fig. 5).

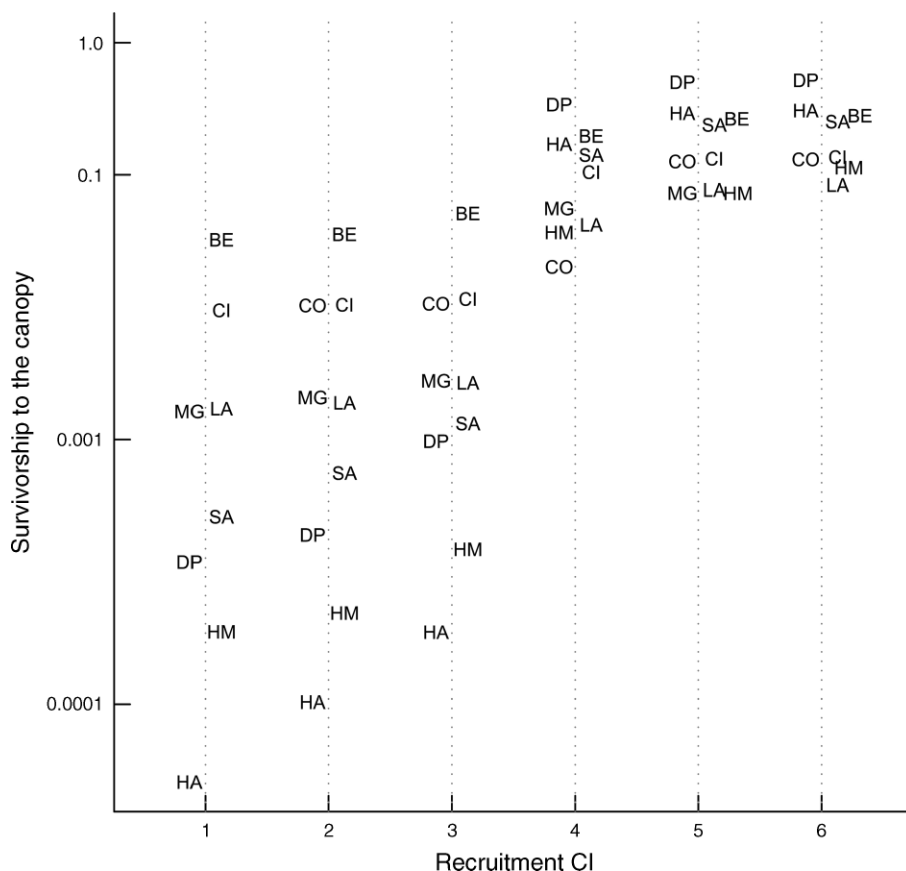


FIG. 5. Relationship between recruitment crown illumination environment (x-axis) and cohort survivorship to the canopy on a log scale (y-axis), i.e., the proportion of a cohort recruiting into each crown illumination category expected to successfully reach the canopy. To estimate this value, the age of attaining the canopy is taken as the estimate of absorption time at 300 mm for each species; survivorship at this age is estimated from Eq. 10. Species codes are: CO, *Cecropia obtusifolia*; CI, *Cecropia insignis*; SA, *Simarouba amara*; MG, *Minuartia guianensis*; BE, *Balizia elegans*; HM, *Hymenolobium mesoamericanum*; LA, *Lecythis ampla*; DP, *Dipteryx panamensis*; and HA, *Hyeronima alchorneoides*.

These results (Figs. 3 and 5) also provide insights into the importance of recruitment environments for different tree species. For example, *Hyeronima*, although an emergent, and part of a group that features considerable shade tolerance, has seemingly low chances of successfully making it to the canopy when recruiting into shaded environments (Figs. 3 and 5). *Lecythis* and *Minuartia*, which recruit into the shade (Clark and Clark 1992) have much higher chances. Clark and Clark (1999) organized species into four groups according to their regeneration pattern. In group I, *Lecythis* and *Minuartia* regenerated mostly in the dark. In group II, *Hymenolobium*, *Simarouba*, and *Dipteryx* recruited in the shade but with increasing size tended toward lighter environments. In group III, *Hyeronima* and *Balizia* recruited in lighter environments but survived well at intermediate sizes in the shade. Finally, in group IV, the two *Cecropias* remained mostly in the light through juvenile phases. This classification accords well with the results in Figs. 3 and 5.

Forest dynamics and turnover

Here we report on only nine of the over 320 tree species at La Selva (Hartshorn and Hammel 1994), so that direct extrapolation to forest dynamics is not possible. However, these species span a representative range of juvenile recruitment niches and adult canopy-position niches and may capture much of the scope of demographic diversity. Our results suggest that it takes a minimum of 60 years to reach the canopy, and generally ≥ 200 years for individuals recruiting into shady conditions. Even though one of our most interesting results is that, much like humans, trees show “bathtub” mortality rates, and life expectancy peaks at surprisingly low sizes (often ≤ 50 mm) life expectancy remains high for large trees, and survivorship for example of *Dipteryx* at age 300 is 0.2, so that trees with life spans of >300 years may be relatively abundant, in agreement with Fichtler et al. (2003) and Lieberman et al. (1985). Forest turnover is consequently likely to be on the order of at least hundreds of years, with negative implications for rates of carbon absorption (Vieira et al. 2005).

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APPENDIX A

Obtaining models of the demography and changing light environment (*Ecological Archives* E090-196-A1).

APPENDIX B

Technical details of methods for obtaining absorbing times (*Ecological Archives* E090-196-A2).

APPENDIX C

Life-history results for all nine species (*Ecological Archives* E090-196-A3).