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Response of recruitment to light availability across a tropical lowland rainforest community

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Summary

1. Many hypotheses about species coexistence involve differential resource use and trade-offs in species' life-history traits. Quantifying resource use across most species in diverse communities, although, has seldom been attempted.

2. We use a hierarchical Bayesian approach to quantify the light dependence of recruitment in 263 woody species in a 50-ha long-term forest census plot in Panama. Data on sapling recruitment were obtained using the 1985–1990 and 1990–1995 census intervals. Available light was estimated for each recruit from yearly censuses of canopy density.

3. We use a power function (linear log–log relationship) to model the light effect on recruitment. Different responses of recruitment to light are expressed by the light effect parameter b. The distribution of b had a central mode at 0.8, suggesting that recruitment of many species responds nearly linearly to increasing light.

4. Nearly every species showed increases in recruitment with increasing light. Just nine species (3%) had recruitment declining with light, while 198 species (75%) showed increasing recruitment in both census intervals. Most of the increases in recruitment were decelerating, i.e. the increase was less at higher light ($b < 1$). In the remaining species, the response to light varied between census intervals (24 species) or species did not have recruits in both intervals (41 species).

5. *Synthesis*. Nearly all species regenerate better in higher light, and recruitment responses to light are spread along a continuum ranging from modest increase with light to a rather strict requirement for high light. These results support the hypothesis that spatio-temporal variation in light availability may contribute to the diversity of tropical tree species by providing opportunities for niche differentiation with respect to light requirements for regeneration.

Key-words: Barro Colorado Island, hierarchical Bayesian model, life-history traits, light requirements, niche partitioning, Panama, regeneration niche, shade tolerance, tropical rain forest

Introduction

Many hypotheses about species coexistence involve differential resource use and trade-offs in species' life-history traits (e.g. Tilman 1982, 2004; Rees *et al*. 2001; Silvertown 2004). Understorey light availability is one of the most limiting resources in tropical rain forests (Whitmore 1996), and its spatio-temporal variation is an important component of the regeneration niche and gap dynamics hypotheses for species coexistence (Grubb 1977; Denslow 1987). Treefall gaps increase heterogeneity in light conditions and may contribute to the diversity of tropical tree species by providing opportunities for niche differentiation with respect to light requirements (Ricklefs 1977; Brokaw 1985).

Empirical studies quantifying niche differentiation in regeneration have yielded inconsistent conclusions. Several studies suggest that species differentially respond to light levels, even if variations are subtle, and that tight species packing along the small range of light environments may

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contribute to coexistence (Denslow 1980; Kobe 1999; Svenning 2000; Poorter & Arets 2003). However, other studies conclude that many species in tropical rain forests share similar light requirements. While Hartshorn (1980) estimated that half of the tree species of the tropical lowland rain forest at La Selva, Costa Rica, required gaps for regeneration; other studies found that >80% of the tree species at Barro Colorado Island (BCI), Panama, regenerate at low light levels (Hubbell & Foster 1986; Welden *et al.* 1991; Condit, Hubbell & Foster 1996); and Wright *et al.* (2003) concluded that most of the same BCI species have intermediate light requirements.

Quantifying resource use in highly diverse communities is challenging because it theoretically involves measuring the continuous environmental variation of the resource and continuous variation in species responses (Lieberman, Lieberman & Peralta 1989; Wright *et al.* 2003). This is often not feasible, and previous studies have usually simplified the problem by either focusing on a small number of species (e.g. Brown & Whitmore 1992; Clark & Clark 1992; Van der Meer, Sterck & Bongers 1998; Svenning 2000; Poorter & Arets 2003; Uriarte *et al.* 2005; Queenborough *et al.* 2007), grouping species into broad growth form classes (Dupuy & Chazdon 2006), or using few categories of environmental conditions (e.g. gap/non-gap; Welden *et al.* 1991; Condit, Hubbell & Foster 1996; Barker, Press & Brown 1997).

Moreover, if forest inventories form the basis of the analyses, the samples usually contain only few individuals of the many rare species (Pitman *et al.* 1999). As a consequence, there are few studies quantifying the light response of recruitment across entire diverse tropical rain forest communities (but see Welden *et al.* 1991 for an analysis of 155 species).

In this study, we aim to quantify the response of recruitment to light availability across more than 80% of the 300 tree and shrub species occurring at BCI, Panama, and our approach explicitly addresses all three problems. Forest census data from the 50-ha Forest Dynamics Plot (FDP) at BCI provided information on the spatial location of more than 50 000 recruits of 263 species. Yearly canopy census data allowed an estimate of light availability across the 50-ha FDP with a spatial resolution of 5 m. We used a hierarchical Bayesian approach to quantify the response of recruitment to light availability for all species. The hierarchical Bayesian approach combines the probability models for the spatial distribution of recruits within species and the variation of the light response across species, including rare ones (e.g. Clark 2005; Condit *et al.* 2006). Moreover, the posterior distribution of parameter estimates provides direct information about the uncertainty associated with the parameter estimates (Ellison 2004).

We explore how the response of recruitment to light is distributed across the tree community and how it is related to the abundance of the species. Furthermore, we calculate a comparable measure of light requirements for recruitment, the light level at which recruitment falls to 50% of the maximum under high light. Our estimates of the sensitivity of recruitment to light availability can serve in a classification of tree species into functional groups (Swaine & Whitmore 1988).

Materials and methods

STUDY SITE

We analysed data from a 50-ha forest census plot on BCI, Panama (9°9′N, 79°51′W). Barro Colorado Island is a 1567-ha island in the Panama Canal, covered with tropical lowland moist forest. The plot consists of 48 ha of undisturbed old-growth forest and 2 ha of secondary forest about 100 years old (Foster & Brokaw 1982). The climate on BCI is warm throughout the year, but rainfall is seasonal with most of the 2500 mm falling from April to November (Windsor 1990; Windsor, Rand & Rand 1990). Elevation of the plot is 120–155 m a.s.l. (Hubbell & Foster 1983). Detailed descriptions of flora, fauna, geology and climate can be found in Croat (1978), Leigh, Rand & Windsor (1982) and Leigh (1999).

RECRUITMENT DATA

All freestanding woody individuals ≥1 cm diameter at breast height (d.b.h.) were mapped, identified to species and measured in 1981–1983, 1985 and every 5 years thereafter (http://www.ctfs.si.edu; Hubbell & Foster 1983; Condit 1998). In this study, we use the census intervals from 1985 to 1990 and 1990 to 1995 and define every individual absent in the first census of each interval but present in the second as a recruit. To avoid edge effects of the light availability calculation, we excluded all recruits within 20 m of any edge of the plot. In the 1990 census, 33 069 recruits of 252 species were recorded, and in the 1995 census, 17 809 recruits of 233 species. We divided the plot (excluding the 20 m perimeter) into 17 664 5×5 m grid cells and computed the number of recruits of each species in each grid cell.

ESTIMATION OF LIGHT AVAILABILITY

Yearly canopy censuses were conducted from 1983 to 1996, except for 1994. We use the canopy census data to produce an index of the amount of light reaching any point in the forest. The canopy census includes a record of the height at which vegetation intersected vertical lines above points on a square, 5-m grid across the 50 ha. Presence versus absence of vegetation was recorded in six height intervals, 0–2, 2–5, 5–10, 10–20, 20–30 and ≥30 m, with the assistance of an ocular range finder. A single census of all 20 301 points on the grid was done annually.

If vegetation was present in a height interval, we assume it casts shade below exactly as would a flat circle of diameter 5 m placed at the vertical midpoint of the cell (for the topmost height category, we assumed the circle was at 35 m). For any point below, the vegetation obscures a section of the sky. Using trigonometry, we calculate the angle of sky so obscured by vegetation at position C, denoted α_c (see Appendix S1 in Supporting Information). The total amount of sky obscured at any point P is the sum of α_c over all cells C that are near enough to cast shade; we assume that points with a horizontal distance of ≤20 m from C are near enough. These assumptions mean that each cell of vegetation reduces light, even if there is another cell above it: the top layer removes a certain quantity of light, and the next layer below removes more. This approach seems reasonable, in that several layers of leaves directly above a point reduce light to a level lower than a single layer would. The assumption that the presence of vegetation can be modelled as a horizontal circle of diameter 5 m is arbitrary, and we acknowledge that this is only a crude way of converting canopy density above a point to light reaching the point. By using many surrounding points and many vertical layers (cf. Connell, Lowman & Noble 1997), we suggest that this method may be some-

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what better at estimating light than methods based on only the tallest nearby trees (Lieberman *et al.* 1995) or the top layer of vegetation (Welden *et al.* 1991).

We calculated the shading index for each point of the plot's 5-m grid at height $z = 2$ m because this is the approximate height of recruits at 1 cm d.b.h. For each grid cell, we averaged the shading index s at its four corners and for all years of a census interval, i.e. 6 years for the first interval (1985–1990) and 5 years for the second (1990–1995; no canopy census was done in 1994).

To convert the estimates of mean shading to an estimate of light availability at each grid cell and in each census interval, we made use of 396 direct measurements of relative irradiance by Wirth, Weber & Ryel (2001), who provide a probability distribution of irradiance l at 1 m height in December 1993 at BCI. We matched their distribution of irradiance with our probability distribution of canopy shading, s. We assumed the 5th, 25th, 50th, 75th and 95th percentiles of the two distributions match, allowing a simple conversion of each value s to l by using the regression line through the percentiles (Appendix S1). Using this conversion, we found that average light availability in the understorey was 2% in both census intervals.

HIERARCHICAL BAYESIAN MODEL

We used a hierarchical Bayesian framework to assess the light response of recruitment across the tree and shrub species at BCI. Our model involves a data model, a process model and parameter models (Fig. 1).

Data enter our model as observed recruit numbers $O_{i,j}$ of each species (i) in each 5×5 m grid cell (j). We assume that $O_{i,j}$ varies around the predicted $R_{i,j}$ following a negative binomial distribution (data model or likelihood)

$$O_{i,j} \sim \text{NegBinomial}(R_{i,j}, c_i).$$

Recruit distributions are not only affected by the light conditions but also by the distribution of seed trees, spatially heterogeneous seed dispersal by animals or spatially heterogeneous soil conditions (e.g. Uriarte *et al.* 2005; Comita, Condit & Hubbell 2007). The negative binomial incorporates the resulting spatial autocorrelation of recruit numbers at < 5 m into the clumping parameter c_i. Autocorrelation of recruitment at larger scales (> 5 m) was negligible: autocorrelation for adjacent grid cells was < 0.2 for 252 of the 263 species we studied, and there was no correlation in recruitment across cells separated by 20 m or more.

We compared seven functional relationships to describe the dependence of the number of recruits on light availability: constant, linear, semi-log, log–log, sigmoid and Michaelis–Menten. For each model, we judged the fit to data using the Akaike Information Criterion (AIC; Akaike 1974). When all 263 species were tested, the log–log relationship was selected as the best model for the highest proportion of species (excluding the constant model). For the species, for which the log–log relationship was not the best model, the best model was significantly better than the log–log relationship (i.e. AIC difference > 2) only in 36 cases.

Thus, we use a power function (log–log relationship) to model the light effect on recruitment (process model). The log of the predicted number of recruits $R_{i,j}$ of each species (i) in each 5×5 m grid cell (j) given light availability l_j is

$$\log_{10}(R_{i,j}) = a_i + b_i \log_{10}(l_j).$$

In this model, a_i represents a measure of the mean log of the number of recruits to be expected, and b_i measures the strength of the light response of species i. For values of $b < 0$, the number of recruits decreases with increasing light. For $0 < b < 1$, the number of recruits increases in a decelerating way with increasing light; for $b = 1$, it is a linear relationship; and for $b > 1$, the number of recruits increases in an accelerating way with light (Fig. 2).

We then describe the variation of a and b across the community (parameter model). We used normal distributions for both parameters,

$$a_i \sim \text{Normal}(\mu_a, \sigma_a),$$
$$b_i \sim \text{Normal}(\mu_b, \sigma_b),$$

with hyperparameters μ_a and μ_b describing the community-wide means of a and b, and σ_a and σ_b measuring the between-species variation of both characteristics. Model runs without hyperdistributions confirmed that both variables were normally distributed across the community. These runs also revealed that for species with > 100 recruits, parameter estimates were largely determined by the data, whereas for species with < 100 recruits, parameter estimates for b were 'pulled' towards the community-wide mean.

As we did not have prior knowledge of the parameters, we used non-informative flat priors for all parameters:

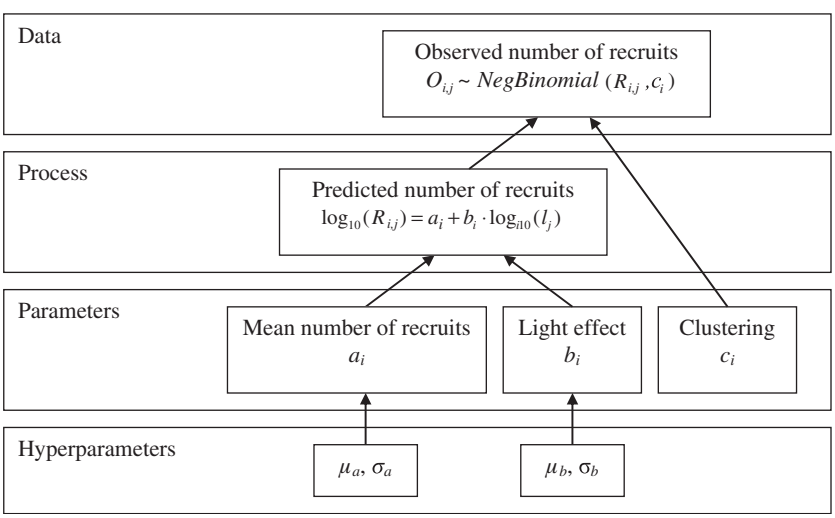

Fig. 1. Graphical representation of the hierarchical model.

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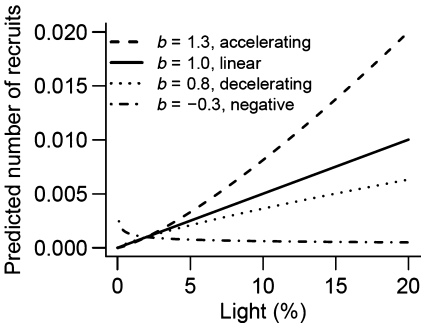

Fig. 2. Illustration of the three types of light response of recruitment: negative ($b < 0$), decelerating ($0 < b < 1$) and accelerating ($b > 1$). The number of recruits at average light conditions is 0.001 in all three cases ($a = -3$).

$$
\begin{aligned}
c_i &\sim \text{Uniform}(0, 100),\\
\mu_a &\sim \text{Uniform}(-10, 1),\\
\mu_b &\sim \text{Uniform}(-5, 5),\\
\sigma_a, \sigma_b &\sim \text{Uniform}(0, 2).
\end{aligned}
$$

We restricted c to values <100 because for $c > 10$, the negative binomial already approximates a spatially homogeneous Poisson distribution (Bolker 2008). Altogether, the joint posterior distribution for the full model is:

$$
\begin{aligned}
&P(R, a, b, c, \mu_a, \sigma_a, \mu_b, \sigma_b | O, l)\\
&\propto \prod_{i=1}^{spp} \prod_{j=1}^{17644} \text{NegBinomial}(O_{i,j} | R_{i,j}, c_i)\\
&\times \prod_{i=1}^{spp} \text{Normal}(a_i | \mu_a, \sigma_a) \times \prod_{i=1}^{spp} \text{Normal}(b_i | \mu_b, \sigma_b) \times \prod_{i=1}^{spp} \text{Unif}(c_i | 0, 100)\\
&\times \text{Unif}(\mu_a | -10, 1) \times \text{Unif}(\mu_b | -5, 5) \times \text{Unif}(\sigma_a | 0, 2) \times \text{Unif}(\sigma_b | 0, 2),
\end{aligned}
$$

with *spp* being the number of species with recruits in the respective census interval. The last three lines denote the likelihood, the priors and the hyperpriors, respectively.

MODEL IMPLEMENTATION AND DIAGNOSTICS

Posterior distributions of the parameters were obtained using a Markov chain Monte Carlo method that is a hybrid of the Metropolis–Hastings algorithm and the Gibbs sampler (Gelman *et al.* 1995; Condit *et al.* 2006). Parameter values are sequentially updated as in the Gibbs sampler, but acceptance depends on the likelihood ratios as in the Metropolis–Hastings algorithm (Muller-Landau *et al.* 2008). The proposal distribution is a normal distribution centred on the current value of the given parameter. The step width for each parameter, i.e. the standard deviation of the proposal distribution, is constantly adjusted during the burn-in period in such a way that the acceptance rate is kept around 0.25 (Gelman *et al.* 1995).

To speed up the convergence of the Gibbs sampler, we weakened the correlation of a and b by centring the light data at average $\log_{10}$ light ($\bar{l}$)

$$\log_{10}(R_{i,j}) = a_i + b_i(\log_{10}(l_j) - \bar{l}).$$

Thus, a_i measures the mean log of the predicted number of recruits at average light conditions. Mean $\log_{10}$ of l was -1.7 for the period 1985–1990 and -1.8 for 1990–1995. We used an average value of $\bar{l} = -1.7$, corresponding to a relative irradiance of 2%, for the analysis of both periods to keep parameter estimates comparable.

We monitored convergence by running two chains with different initial values and used Gelman and Rubin's convergence diagnostics and a value of 1.1 to detect the convergence (Gelman & Rubin 1992; Gelman *et al.* 1995). Convergence required 500–5100 iterations. We used a burn-in period of 7000 iterations and additional 10 000 iterations were used for analysis. We computed the posterior parameter distributions for observed recruit numbers and light availability estimations for two intervals (1985–1990, 1990–1995). All analyses were carried out using the software package R version 2.5.0 (R Development Core Team 2007). The R-code is available in Appendix S2.

ANALYSIS OF RESULTS

From the posterior distributions, we computed the mean and 95% credible intervals (CI) of all parameters for the two periods (1985–1990, 1990–1995). We define maximum recruitment as recruitment at high light conditions, where high light is 20% relative irradiance, since 20% is close to the brightest the forest understorey ever gets. For each species, we calculated the light level at which the recruitment falls to 50% (*Light50*) of maximum recruitment. To compare model fits with data, we calculated the mean number of observed recruits in ten light intervals corresponding to 10th percentiles of light estimates across the 50-ha plot. Total abundance of each species across 50 ha in 1990 (i.e. number of individuals ≥1 cm d.b.h.) was used in comparing species. All BCI inventory data, including recruitment, can be downloaded from http://www.ctfs.si.edu.

Results

COMMUNITY-LEVEL PATTERN OF LIGHT RESPONSE

Mean posterior estimates of the light response of recruitment (b) ranged from −0.6 to 3.3, with most species falling between 0 and 1, i.e. these species take advantage of higher light levels with a decelerating response of recruitment to light (Fig. 3; Table S1). When mean posterior estimates of b were compared between census intervals, 101 species (38%) showed a decelerating response of recruitment with increasing light availability ($0 < b < 1$) in both census intervals, 54 species (21%) showed an accelerating response ($b > 1$), and recruitment of nine species (3%) decreased with light availability ($b < 0$). For the remaining 99 species (38%), b indicated different types of light response for the two census intervals or species did not have recruits in both intervals.

For 97 species, the 95% CI of b did not include zero in either census interval. There were only three species with a negative b and a CI that did not include zero: *Xylopia macrantha* in both census intervals, *Trichilia tuberculata* only in the first interval, and *Drypetes standleyi* and *Licania platypus* only in the second interval. There were 18 species with $b > 1$ and a 95% CI > 1 in both intervals, i.e. an accelerating response of recruitment to light availability. These included many species of the common pioneer genera, e.g. *Cecropia*, *Croton*, *Miconia*, *Palicourea*, *Spondias*, *Zanthoxylum*. Posterior estimates of the community-wide mean of b (μ_b) were 0.80 for 1985–1990 and 0.85 for 1990–1995, and the standard deviation (σ_b) was 0.76 and 0.72, for the two census intervals, respectively.

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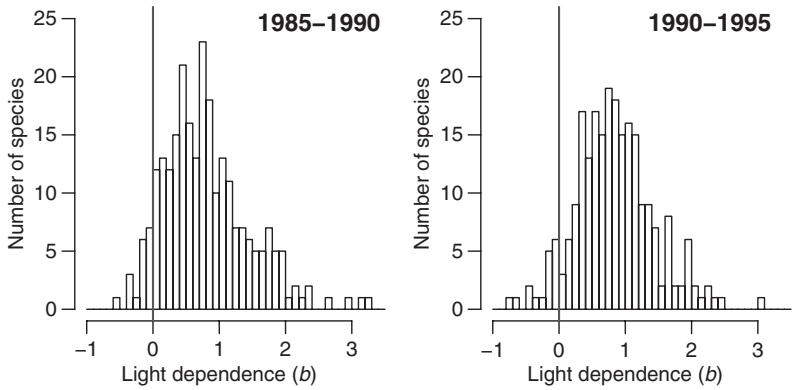

Fig. 3. Mean posterior estimates of the light dependence of recruitment (*b*) for the tree species at BCI, Panama, for the two census intervals (1985–1990 and 1990–1995).

OTHER PARAMETERS

Mean posterior estimates of the log of the mean number of recruits at average light conditions (*a*) ranged from −4.3 to −0.88 (i.e. 0.02–53 recruits per hectare; Fig. 4 and Table S1). The minimum roughly corresponded to one individual in the sampling area, while the maximum corresponded to about 0.1 individuals per 5 × 5 m grid cell. Posterior estimates of the community-wide mean of *a* (μ_a) were −3.017 and −3.162, and posterior estimates of the standard deviation (σ_a) were 0.88 and 0.84, for the two census intervals, respectively. The distribution of *a* across the community was skewed to the right.

The distribution of the clustering parameter of the negative binomial was bimodal (Fig. 4; Table S1). Thirty species showed pronounced clustering ($c < 1$) in both census intervals, 32 only in the first and nine only in the second census interval, while for the majority of the species either spatial clustering did not occur or could not be detected due to the small number of recruits ($c > 10$). The correlation between *b* and *c* is −0.13 in the first census interval and −0.18 in the second, indicating that recruits of more light-demanding species tend to be slightly more clustered than recruits of shade-tolerant species.

CONSISTENCY BETWEEN CENSUS INTERVALS

Comparing mean posterior estimates for the two census intervals showed that the log of the mean number of recruits (*a*) tended to be slightly higher in the first census interval 1985–1990 than in the second census interval 1990–1995 (Fig. 5a). However, parameter estimates were consistent over the two intervals. Likewise, the estimates of the strength of the light

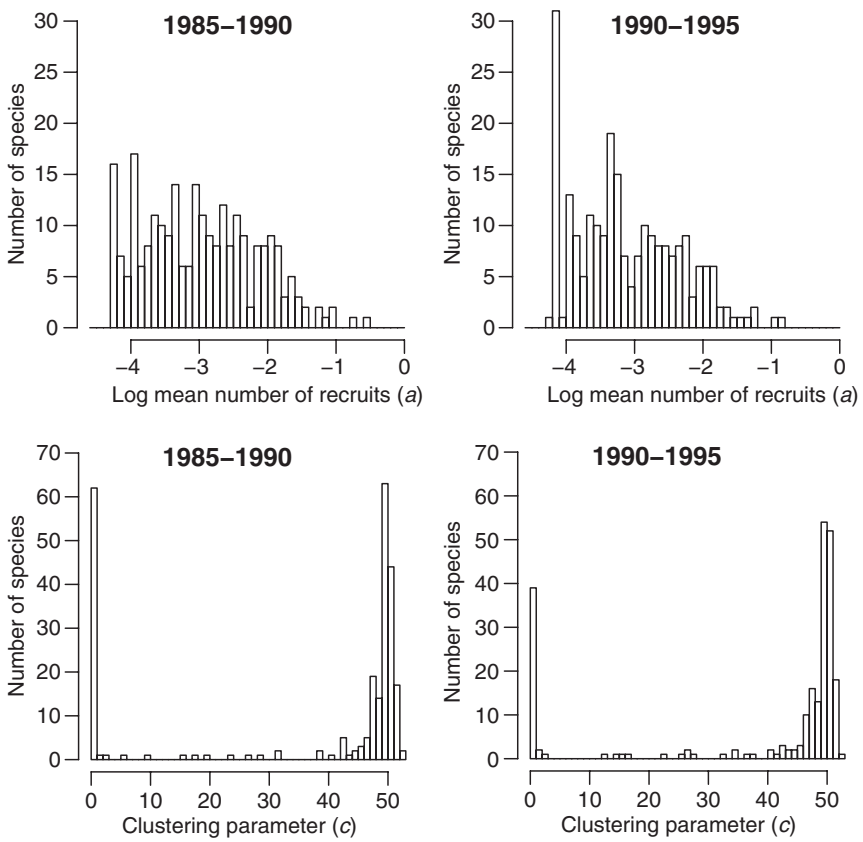

Fig. 4. Mean posterior estimates of the log10 of the mean number of recruits at average light conditions (*a*) and the clustering parameter of the negative binomial distribution (*c*) for the tree species at BCI, Panama, for the two census intervals (1985–1990 and 1990–1995).

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response of recruitment (b) were consistent over the two analysed time intervals (Fig. 5b).

OBSERVED VERSUS PREDICTED RECRUITMENT RATES

Mean posterior parameter estimates predicted the mean number of recruits under different light conditions. Model fits are shown for two species with positive (*Trichilia pallida*) and negative (*Trichilia tuberculata*) response to light (Fig. 6). Model fits for the remaining species are available in Fig. S1.

UNCERTAINTY AND SAMPLE SIZE

The uncertainty of parameter estimates decreased rapidly with the number of recruits (Fig. 7). When recruit numbers were low, the 95% CI of a spanned up to an order of magnitude (Fig. 7a). Likewise, CIs for b ranged over more than one type of light response, i.e. $b < 0$, $0 < b < 1$, $b > 1$, when few recruits were available for parameter estimation (Fig. 7b). However, for 46% of the species with >20 recruits, parameter estimates significantly determined the type of light response (95% CI of b neither including 0 nor 1), as opposed to 7% of the species with <20 recruits. When the number of recruits increased to >50 (100), this proportion increased to 59% (66%), as opposed to 10% (15%) for species with <50 (100) recruits. Below ten recruits, spatial aggregation could not be detected, but also for larger numbers of recruits, the clustering parameter c often did not contain information and varied over the entire range of allowed values (0–100) (Fig. 7c).

LIGHT RESPONSE AND ABUNDANCE

Across the community, the strength of the light response of recruitment (b) decreased slightly with abundance. In a linear regression, the effect of $\log_{10}$ of abundance on b was significant ($P < 0.0001$, $n = 233$, $r^2 = 0.07$, intercept $= 1.19$, slope $= -0.155$). While b varied over a broad range for species with intermediate abundance, the most abundant species had a b close to zero, i.e. showed hardly any response of recruit numbers to light availability. For rare species (<50 recruits), however, b was largely determined by the community-wide mean and the relationship is not informative for them.

LIGHT REQUIREMENTS FOR RECRUITMENT

The light intensity where recruitment fell to 50% of maximum recruitment (*Light50*) was heavily skewed to the right (Fig. 8). Fifty-six species (22% of the total) in the first interval had

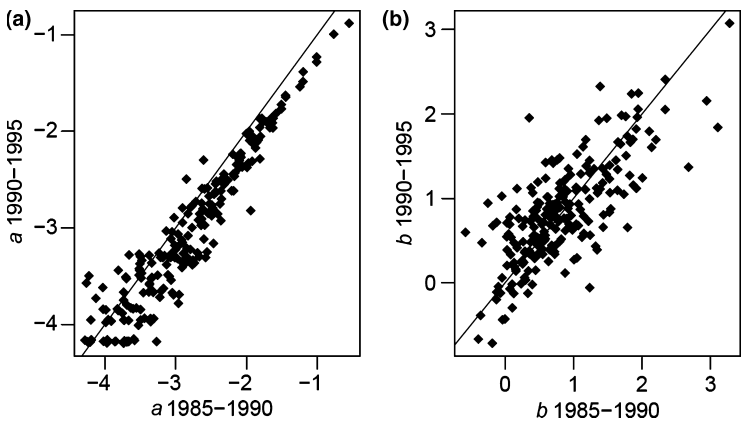

Fig. 5. Posterior means of parameters of the light dependence of recruitment for the tree species at BCI, Panama, for the two census intervals (1985–1990, 1990–1995). Parameters are (a) $\log_{10}$ of the mean number of recruits at average light conditions a, and (b) the light effect b. The line represents the 1:1 relationship.

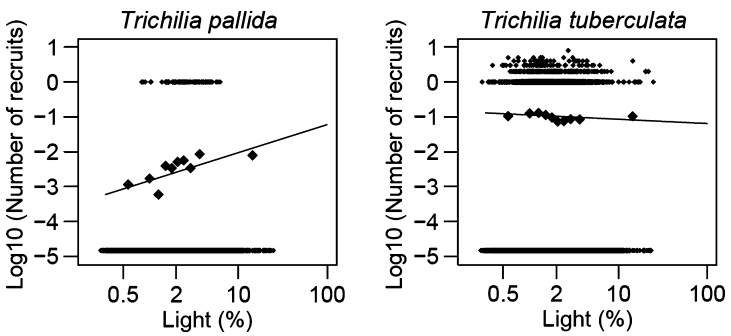

Fig. 6. Model fit for the predicted number of recruits at different light conditions vs. the observed number of recruits for two selected species. Mean number of recruits in intervals of tenth percentiles of light in the 5 × 5 m grid cells (large dots), observed number of recruits in the 5 × 5 m grid cells (small dots), predicted number of recruits using posterior means for the second interval 1990–1995 (line). Grid cells without recruits were assigned a small number ($1.5e^{-5}$).

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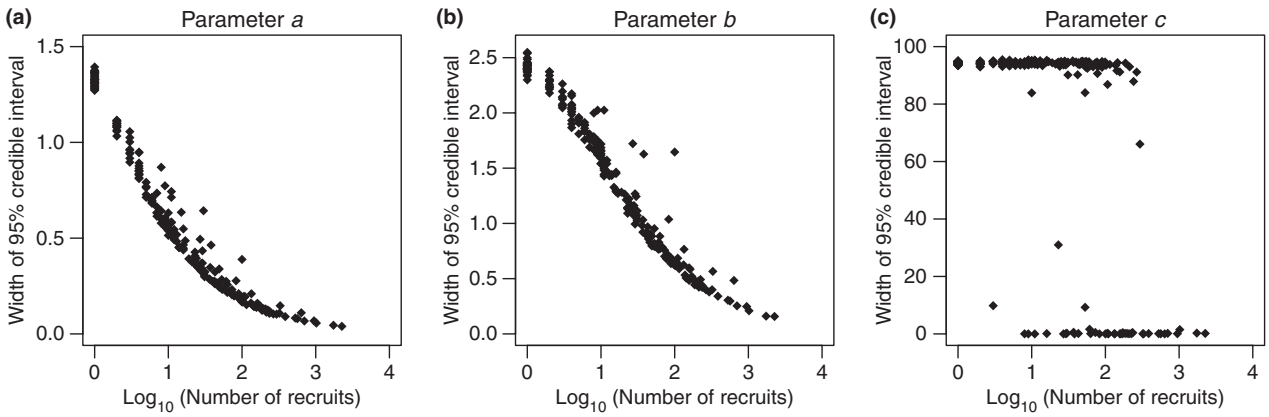

Fig. 7. Uncertainty of estimates (width of the 95% credible interval) of (a) the $\log_{10}$ of the mean number of recruits at average light conditions *a*, (b) the light dependence of recruitment *b*, and (c) the clustering parameter of the negative binomial distribution *c* as a function of the number of sampled recruits. Uncertainty estimates are given for 233 tree species at BCI, Panama, for the second census interval (1990–1995).

Light50 < 2%, the understorey light average, i.e. they recruited well at low light. At the opposite end, 81 species (32% of the total) in the first interval had *Light50* > 10% and thus only recruited well at high light. The second census interval had similar results, with 35 species recruiting well at average light and 84 requiring high light. The median *Light50* in the two census intervals was 7.7% and 8.5%.

Discussion

Our results broadly support the notion that light requirements for recruitment are distributed along a continuum (Denslow 1987; Wright *et al.* 2003) and that species belong to broad regeneration guilds rather than partitioning the light gradient at a fine scale (Hubbell & Foster 1986). The distribution of the light response of recruitment (*b*) had a strong central mode, with many species showing a nearly linear light response, suggesting that the majority of species share intermediate light requirements for recruitment (Wright *et al.* 2003). Using the hyperparameters of the posterior distribution of light dependence across the community, recruitment of 13% of the species is expected to decrease with increasing light availability, while recruitment of 87% of the species benefits from higher light, 46% in a decelerating manner and 41% in an accelerating manner.

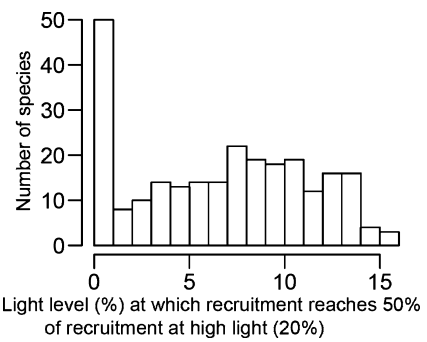

Fig. 8. Estimates of the light level at which recruitment falls to 50% of recruitment under high light conditions (i.e. at 20% light, *Light50*) for the tree species at BCI, Panama. Estimates are based on the means of posterior means of the species' parameters from both census intervals (1985–1990, 1990–1995).

Recruitment of only 20% of the species reached 50% or more of their maximum recruitment at light levels lower than the average in the forest understorey at BCI suggesting that relatively few species recruit well in the deepest forest shade. Thus, the ability to regenerate at low-light conditions may not be as widespread among tree species at BCI as we thought (Hubbell & Foster 1986; Welden *et al.* 1991; Condit, Hubbell & Foster 1996). Rather, nearly all species regenerate better in increasing light, and they are spread along a continuum from modest response to a rather strict requirement for high light. Species specialized to recruit in high-light conditions ($b > 1$) are more common (41%) than expected from the rarity of large gaps (Hubbell & Foster 1986; Hubbell *et al.* 1999).

Our results are consistent with the findings of a community-wide analysis of sapling distributions with respect to light in a temperate rain forest in Chile (Lusk, Chazdon & Hofmann 2006). In that study, half the species were randomly distributed with respect to canopy openness, whilst the remainder was non-randomly distributed. The majority of tree species were also found to have intermediate shade tolerance, and niche overlap was not smaller than expected.

There are several caveats we must consider. The basis of our analysis is the distribution of saplings with respect to the estimated light levels integrated over 6 years during which the recruit surpassed the 1 cm d.b.h. threshold. Based on mean growth at 1 cm d.b.h. (< 1 mm year^{-1}), we estimate the average age of individuals reaching the 1 cm d.b.h. threshold to be 10–20 years. Therefore, the establishment of seedlings and subsequent growth and mortality may have occurred under light conditions different from those at the time of the study (Denslow 1987; Kobe 1999). However, we believe that our approach gives reasonable estimates of light requirements for recruitment not only for fast-growing species, but also for slower-growing species, due to the temporal correlation of light availability caused by the slow dynamics of the canopy cover (the correlation between the light estimates for both census intervals was 0.76).

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Recruitment success in terms of our study integrates both growth and survival of plants during the 5 years of the census interval. Growth and mortality of seedlings and saplings are likely to vary with light availability (e.g. Montgomery & Chazdon 2002; Iriarte & Chazdon 2005; Aiba & Nakashizuka 2007). Since recruits only enter our census at 1 cm d.b.h., we cannot separate the impact of light on growth from the impact on survival.

Another concern is that our calculated light availability obviously is only a rough index of the light environment in the forest, unable to capture spatial variation at scales < 5 m horizontally or vertically. Measuring light directly at every recruit, however, would involve prohibitive time and labour. Until laser-mapping data of the forest are available, the method we propose offers an objective and straightforward measure of how much vegetation is blocking the sky above any tree of any height. The consistency of the derived light response between the two census intervals indicates that our light index contains information relevant to the species' performance. Interestingly, our light estimation procedure is similar to the index that best described gap light index obtained by hemispherical photographs in a temperate forest in Japan (Takashima, Kume & Yoshida 2006). The latter estimates also accounted for shading from topography, but we ignored this at BCI due to the relatively flat topography.

The power function does not capture the saturation of recruit numbers at very high light levels for some pioneer species with $b > 1$ (e.g. *Cecropia insignis*, *Croton billbergianus*, *Miconia argentea*, *Palicourea guianensis*, *Spondias radlkoferi*; Fig. S1). Thus for these species, we overestimate the number of recruits at very high light and predicted recruit numbers beyond light levels found in forests gaps (c. 20%) should be used with caution.

A final caveat is the low number of individuals per area for the many rare species in such a diverse forest (Pitman *et al.* 1999). Hierarchical Bayesian methods explicitly account for this problem by superimposing a form of variation across the community and by providing direct measures of uncertainty associated with parameter estimates (e.g. Clark 2005; Condit *et al.* 2006). We could significantly determine the type of light response (i.e. negative, decelerating or accelerating) for nearly half of the species (44%) with at least 20 recruits. For 167 (75%) of the 224 species with recruits in both census intervals, light response was consistent across the two intervals, i.e. mean posterior estimates of light dependence indicated the same type of light response (negative, decelerating or accelerating). However, applying the rather strong criterion, that the width of the 95% CI of b be < 0.5, about 100 recruits were necessary. This is certainly a large number for rare species. The main point of the Bayesian approach, however, is that the response of rare species need not be known to estimate the community-wide variation.

Conclusions

Light response of recruitment is only one aspect of species' performance under heterogeneous environmental conditions. To arrive at a more complete understanding of species' life-history traits, differential response of growth and survival to light conditions have to be analysed for different ontogenetic stages (Clark & Clark 1992; Poorter *et al.* 2005). Such analyses will allow extending existing species classifications into functional groups on the basis of light (or other resource) dependence of all vital rates in several life stages (Condit, Hubbell & Foster 1996). Ultimately, only mechanistic models accounting for species differences will allow investigations of the consequences of species' similarities or differences for coexistence and to determine the relative importance of niche partitioning versus chance events (Grubb 1977; Brokaw & Busing 2000; Wright 2002).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Calculation of the shading index using canopy density and conversion of the shading index to relative irradiance.

Appendix S2. R code to generate posterior distributions of the parameters of the hierarchical Bayesian model.

Figure S1. Model fits for the predicted number of recruits at different light conditions versus the observed number of recruits for the woody species at Barro Colorado Island, Panama.

Table S1. Posterior means, lower and upper limits of the credible interval (CI−, CI+) of the parameters of the hierarchical Bayesian model and the light level at which recruitment falls to 50% (*Light50*) of recruitment at 20% light for the woody species at Barro Colorado Island, Panama.

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Appendix S1

Calculation of the shading index using canopy density and conversion of the shading index to relative irradiance

1. Calculation of the shading index using canopy density

Consider an arbitrary point *P* whose three-dimensional coordinates in the forest are *x, y, z*, and consider a cell of vegetation *C* whose midpoint is at position x_c, y_c, z_c (Fig. 1). Call the horizontal distance between the two points d_c, calculated from *x* and *y* coordinates, and the vertical distance $h_c = z_c - z$. Assume the vegetation in the cell is a horizontal circle of radius *r*. Then the formula for the angle α of sky obscured by the layer of vegetation is

$$\alpha_c = \arctan\left(\frac{d_c + r}{h_c}\right) - \arctan\left(\frac{d_c - r}{h_c}\right) \quad \text{if } d_c \le 20 \text{ m}$$

$$\alpha_c = 0 \quad \text{if } d_c > 20 \text{ m},$$

as we assume vegetation further than 20 m away (horizontal distance) have no impact on the light reaching a point. We estimate the total shading at point *P* as

$$s_p = \sum_c \alpha_c \ ,$$

where the summation means over all cells *c* in the 50-ha plot.

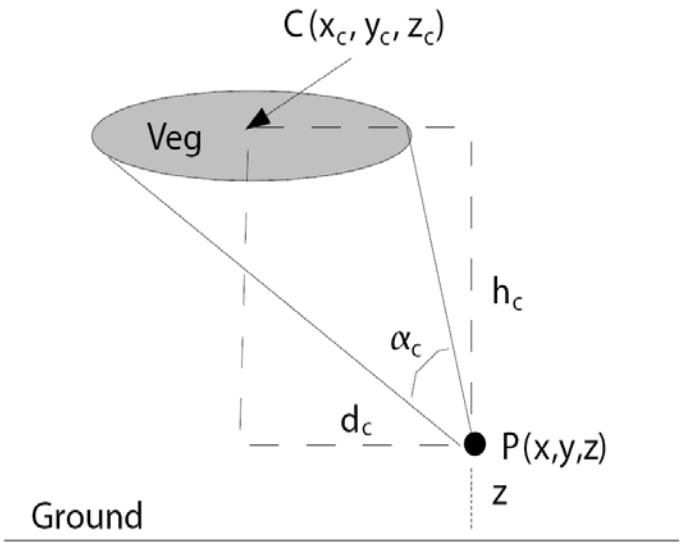


Figure 1: Diagram of the calculation converting vegetation density to shading. Point *P* at horizontal coordinates *x, y*, and height *z*, is where an estimate of shading is needed. The vegetation cell (Veg) has midpoint (vertical and horizontal) at point *C*. We assume the amount of light removed (*i.e.,* shading) by the vegetation cell is proportional to the angle α_c.

2. Conversion of the shading index to relative irradiance

We assumed a linear relationship between the log of relative irradiance *l* (data from Wirth *et al.* 2001) and the shading index *s* (for the period 1990–95 to be temporally closer to the light measurements which were carried out in 1993) and performed a quadratic regression through 5th, 25th, 50th, 75th and 95th percentiles of both distributions, assuming that the lowest estimate of *s* for any tree individual (a *Prioria copaifera* tree with a dbh > 1.2 m) in any census interval corresponds to 100% light (Fig. 2). Thus, $l = e^{-0.01351-0.08043 \cdot s-0.00315 \cdot s^2}$. Distributions of estimated light are given in Fig. 3. The spatial distribution of recruits closely follows the distribution of estimated light across the 50-ha plot (Fig. 4).

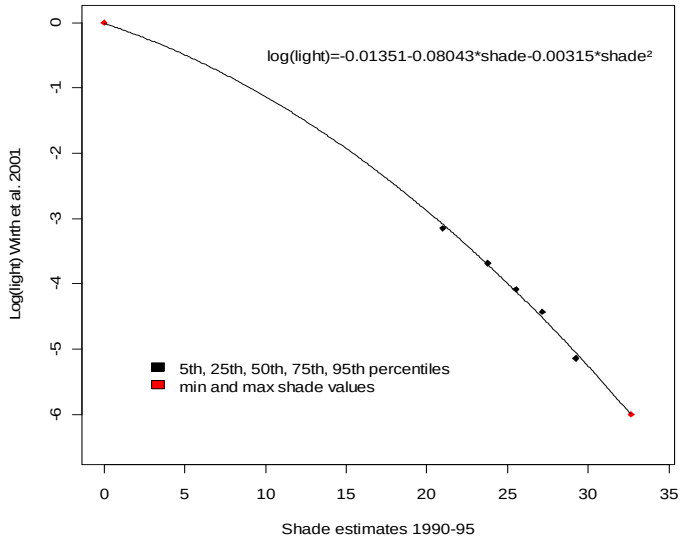


Figure 2: Conversion of shade estimates to relative irradiance.

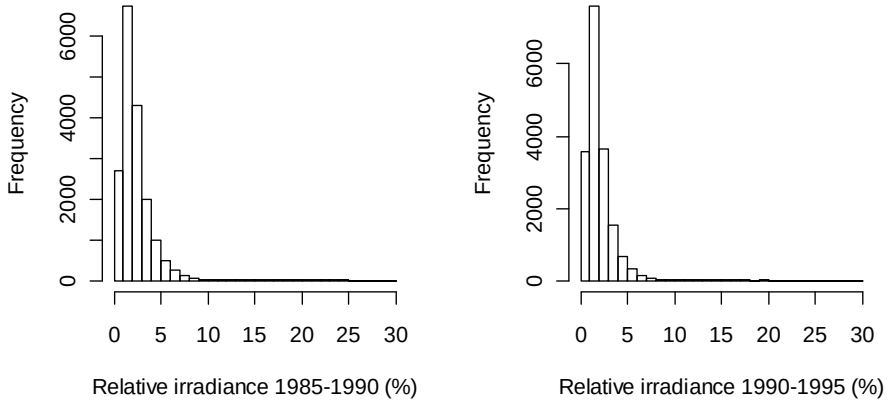


Figure 3: Distribution of estimated light at 2 m in the center of 5 m × 5 m quadrats across the 50-ha plot on Barro Colorado Island, Panama.

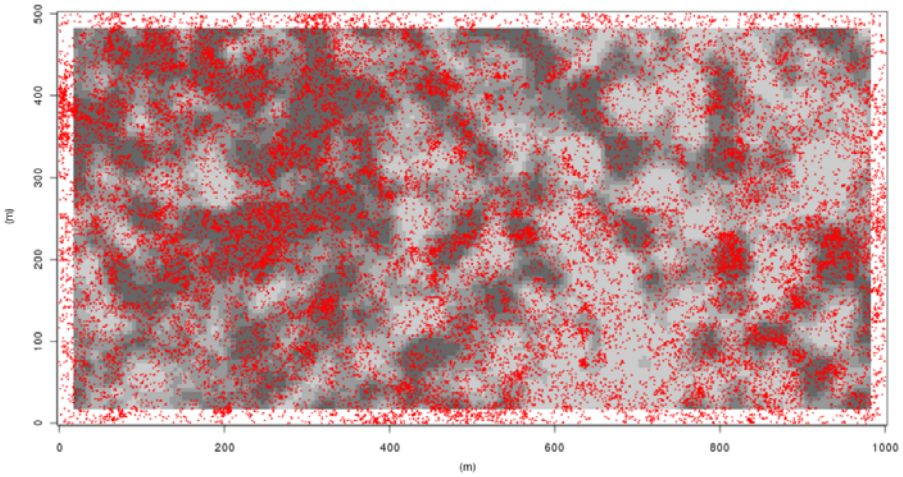


Figure 4: Spatial distribution of recruits (1985−1990; red dots) with respect to estimated light at 2 m height across the 50-ha plot. Darker shades of grey indicate higher light availability.

References

Wirth, R., Weber, B. & Ryel, R.J. (2001) Spatial and temporal variability of canopy structure in a tropical moist forest. *Acta Oecologica*, **22**, 235–244.

Appendix S2

R code to generate posterior distributions of the parameters of the hierarchical Bayesian model

```
# Functions for fitting a power function to the number of recruits per species given available light, hyperdistributions of
# the log of the mean number of recruits at average light availability (a) and light-dependence (b), and the clumping
# parameter of the negative binomial distribution (k) using a hybrid of the Gibbs sampler and the Metropolis-Hastings
# algorithm. These functions should source in R2.5.0, and given a table of data in the correct format, will produce the
# posterior distribution of all parameters.

# The matrix of data has one row per species and columns with the number of recruits in each 5 m × 5 m quadrat.
# normlight is a vector with centered light data: log10 of relative irradiance in each 5 m × 5 m quadrat – mean(log10 of
# relative irradiance all 5 m × 5 m quadrats).
# spp is a character vector with species' acronyms

# The four hyperparameters are the mean (MuA) and SD (SdA) of the log of the mean number of recruits at average
# light availability (a) and mean (MuB) and SD (SdB) of the light-dependence (b). The argument start.param sets their
# starting values.

# start.scale sets the initial step size for the proposal distribution of the Metropolis-Hastings algorithm, the step size is
# adjusted scale.burnin steps (burn-in), so that acceptance rate is kept around 0.25. The number of cycles run by the
# Gibbs sampler is the argument steps, and the current state will be printed to the screen every showstep steps. The
# argument whichuse defines the post burn-in phase; estimates based on the Gibbs sampler are drawn from those steps.

library(coda)

metrop.normLight.Gibbs=function(data,start.param=c(1,0),start.scale=c(0.1,0.01),scale.burnin=7000,steps=17000,
  whichuse=7000:17000,showstep=100)
{
  MuA1=SdA1=MuB1=SdB1=MuA2=SdA2=MuB2=SdB2=matrix(nrow=steps,ncol=3)
  MuA1[1,1]=MuA2[1,1]=log10(sum(data[,])/(dim(data)[1]*dim(data)[2]))
  SdA1[1,1]=SdA2[1,1]=start.param[1]
  MuB1[1,1]=MuB2[1,1]=start.param[2]
  SdB1[1,1]=SdB2[1,1]=start.param[1]
  MuA1[1,3]=SdA1[1,3]=MuB1[1,3]=SdB1[1,3]=MuA2[1,3]=SdA2[1,3]=MuB2[1,3]=SdB2[1,3]=start.scale[1]

  nospp=length(spp)
  spa1=spb1=spk1=drawsa1=drawsb1=drawsk1=scalea1=scaleb1=scalek1=matrix(ncol=steps,nrow=nospp)
  spa2=spb2=spk2=drawsa2=drawsb2=drawsk2=scalea2=scaleb2=scalek2=matrix(ncol=steps,nrow=nospp)
  rownames(spa1)=rownames(spb1)=rownames(drawsa1)=rownames(drawsb1)=rownames(spk1)=rownames(drawsk1)
    =rownames(scalea1)=rownames(scaleb1)=rownames(scalek1)=spp
 rownames(spa2)=rownames(spb2)=rownames(drawsa2)=rownames(drawsb2)=rownames(spk2)=rownames(drawsk2)
  =rownames(scalea2)=rownames(scaleb2)=rownames(scalek2)=spp

  # chain 1 is initialized with average values
  spa1[,1]=log10(sum(data[,])/(dim(data)[1]*dim(data)[2]))
  spb1[,1]=0
  spk1[,1]=10

  # chain 2 is initialized with more extreme values
  spa2[,1]=-3
  spb2[,1]=2
  spk2[,1]=1
```

```
  convergence = matrix(data=NA, ncol=3, nrow=nospp)

  scalea1[,1] = scaleb1[,1] = scalea2[,1] = scaleb2[,1] = start.scale[2]
  scalek1[,1] = scalek2[,1] = start.scale[1]


for(i in 2:steps)
 {
  adjust=ifelse((i <= scale.burnin), T, F)

  MuA1[i,] = metrop1step(func=mu.aGibbs,start.param=MuA1[i-1,1],scale.param=MuA1[i-1,3],SdA=SdA1[i-1,1],
    spa=spa1[,i-1],adjust.scale=adjust)
  SdA1[i,] = metrop1step(func=sd.aGibbs,start.param=SdA1[i-1,1],scale.param=SdA1[i-1,3],MuA=MuA1[i,1],
    spa=spa1[,i-1],     adjust.scale=adjust)
  MuB1[i,] = metrop1step(func=mu.bGibbs,start.param=MuB1[i-1,1],scale.param=MuB1[i-1,3],SdB=SdB1[i-1,1],
    spb=spb1[,i-1],adjust.scale=adjust)
  SdB1[i,] = metrop1step(func=sd.bGibbs,start.param=SdB1[i-1,1],scale.param=SdB1[i-1,3],MuB=MuB1[i,1],
    spb=spb1[,i-1],adjust.scale=adjust)

  MuA2[i,] = metrop1step(func=mu.aGibbs,start.param=MuA2[i-1,1],scale.param=MuA2[i-1,3],SdA=SdA2[i-1,1],
    spa=spa2[,i-1],adjust.scale=adjust)
  SdA2[i,]=metrop1step(func=sd.aGibbs,start.param=SdA2[i-1,1],scale.param=SdA2[i-1,3],MuA=MuA2[i,1],
    spa=spa2[,i-1],adjust.scale=adjust)
  MuB2[i,]=metrop1step(func=mu.bGibbs,start.param=MuB2[i-1,1],scale.param=MuB2[i-1,3],SdB=SdB2[i-1,1],
    spb=spb2[,i-1],adjust.scale=adjust)
  SdB2[i,]=metrop1step(func=sd.bGibbs,start.param=SdB2[i-1,1],scale.param=SdB2[i-1,3],MuB=MuB2[i,1],
    spb=spb2[,i-1],adjust.scale=adjust)

  for(j in 1:nospp)
  {
    nexta = metrop1step(func=spa.Gibbs, start.param=spa1[j,i-1],scale.param=scalea1[j,i-1],N=data[j,], spb=spb1[j,i-1],
      spk=spk1[j,i-1],MuA=MuA1[i,1], SdA=SdA1[i,1], MuB=MuB1[i,1], SdB=SdB1[i,1],adjust.scale=adjust)
    spa1[j,i] = nexta[1]
    drawsa1[j,i] = nexta[2]
    scalea1[j,i] = nexta[3]

    nextb = metrop1step(func=spb.Gibbs, start.param=spb1[j,i-1], scale.param=scaleb1[j,i-1], N=data[j,], spa=spa1[j,i],
      spk=spk1[j,i-1], MuA=MuA1[i,1], SdA=SdA1[i,1], MuB=MuB1[i,1], SdB=SdB1[i,1], adjust.scale=adjust)
    spb1[j,i] = nextb[1]
    drawsb1[j,i] = nextb[2]
    scaleb1[j,i] = nextb[3]

     nextk = metrop1step(func=spk.Gibbs, start.param=spk1[j,i-1], scale.param=scalek1[j,i-1], N=data[j,], spa=spa1[j,i],
       spb=spb1[j,i], adjust.scale=adjust)
    spk1[j,i] = nextk[1]
    drawsk1[j,i] = nextk[2]
    scalek1[j,i] = nextk[3]

    nexta = metrop1step(func=spa.Gibbs, start.param=spa2[j,i-1],scale.param=scalea2[j,i-1],N=data[j,], spb=spb2[j,i-1],
      spk=spk2[j,i-1],MuA=MuA2[i,1], SdA=SdA2[i,1], MuB=MuB2[i,1], SdB=SdB2[i,1], adjust.scale=adjust)
    spa2[j,i] = nexta[1]
    drawsa2[j,i] = nexta[2]
    scalea2[j,i] = nexta[3]

    nextb = metrop1step(func=spb.Gibbs, start.param=spb2[j,i-1], scale.param=scaleb2[j,i-1], N=data[j,], spa=spa2[j,i],
      spk=spk2[j,i-1], MuA=MuA2[i,1],SdA=SdA2[i,1], MuB=MuB2[i,1], SdB=SdB2[i,1], adjust.scale=adjust)
```

```
  spb2[j,i] = nextb[1]
  drawsb2[j,i] = nextb[2]
  scaleb2[j,i] = nextb[3]

  nextk = metrop1step(func=spk.Gibbs, start.param=spk2[j,i-1], scale.param=scalek2[j,i-1], N=data[j,], spa=spa2[j,i],
    spb=spb2[j,i], adjust.scale=adjust)
  spk2[j,i] = nextk[1]
  drawsk2[j,i] = nextk[2]
  scalek2[j,i] = nextk[3]

  if(i%%showstep==0 & i>=500)
  {
    g = gelman.diag(mcmc.list(mcmc(spa1[j,((i-500)+1):i]), mcmc(spa2[j,((i-500)+1):i])), confidence = 0.95,
      transform=T, autoburnin=F)
    if (g[[1]][1] < 1.1 & !converged[j,1])  convergence[j,1] = i

    g = gelman.diag(mcmc.list(mcmc(spb1[j,((i-500)+1):i]), mcmc(spb2[j,((i-500)+1):i])), confidence = 0.95,
      transform=T, autoburnin=F)
    if (g[[1]][1] < 1.1 & !converged[j,2])  convergence[j,2] = i

    g = gelman.diag(mcmc.list(mcmc(spk1[j,((i-500)+1):i]), mcmc(spk2[j,((i-500)+1):i])), confidence = 0.95,
      transform=T, autoburnin=F)
    if (g[[1]][1] < 1.1 & !converged[j,3])  convergence[j,3] = i

   write.table(convergence, file="convergence.txt", sep="\t")
  } # convergence test

} # species loop

write.table(t(round(spa1[,i], digits=4)), file="spa1.txt", sep="\t", append=T, col.names=F)
write.table(t(round(spb1[,i], digits=4)), file="spb1.txt", sep="\t", append=T, col.names=F)
write.table(t(round(spk1[,i], digits=4)), file="spk1.txt", sep="\t", append=T, col.names=F)
write.table(t(round(spa2[,i], digits=4)), file="spa2.txt", sep="\t", append=T, col.names=F)
write.table(t(round(spb2[,i], digits=4)), file="spb2.txt", sep="\t", append=T, col.names=F)
write.table(t(round(spk2[,i], digits=4)), file="spk2.txt", sep="\t", append=T, col.names=F)

write.table(t(drawsa1[,i]), file="drawsa1.txt", sep="\t", append=T, col.names=F)
write.table(t(drawsb1[,i]), file="drawsb1.txt", sep="\t", append=T, col.names=F)
write.table(t(drawsk1[,i]), file="drawsk1.txt", sep="\t", append=T, col.names=F)
write.table(t(drawsa2[,i]), file="drawsa2.txt", sep="\t", append=T, col.names=F)
write.table(t(drawsb2[,i]), file="drawsb2.txt", sep="\t", append=T, col.names=F)
write.table(t(drawsk2[,i]), file="drawsk2.txt", sep="\t", append=T, col.names=F)

write.table(t(MuA1[i,]), file="mua1.txt", sep="\t", append=T, col.names=F)
write.table(t(SdA1[i,]), file="sda1.txt", sep="\t", append=T, col.names=F)
write.table(t(MuA2[i,]), file="mua2.txt", sep="\t", append=T, col.names=F)
write.table(t(SdA2[i,]), file="sda2.txt", sep="\t", append=T, col.names=F)
write.table(t(MuB1[i,]), file="mub1.txt", sep="\t", append=T, col.names=F)
write.table(t(SdB1[i,]), file="sdb1.txt", sep="\t", append=T, col.names=F)
write.table(t(MuB2[i,]), file="mub2.txt", sep="\t", append=T, col.names=F)
write.table(t(SdB2[i,]), file="sdb2.txt", sep="\t", append=T, col.names=F)

write.table(t(scalea1[,i]), file="scalea1.txt", sep="\t", append=T,col.names=F)
write.table(t(scaleb1[,i]), file="scaleb1.txt", sep="\t", append=T,col.names=F)
write.table(t(scalek1[,i]), file="scalek1.txt", sep="\t", append=T,col.names=F)
```

```
  cat(i, "\n")

  } # steps loop
}


# likelihood of the mean of the normal hyperdistribution for a
mu.aGibbs=function(MuA,spa,SdA)
{
 if(SdA<=0) return(-Inf)
 llike = dnorm(spa, mean=MuA, sd=SdA, log=T)
 return(sum(llike) + dunif(MuA, min=-10, max=1, log=T))
}

# likelihood of the standard deviation of the normal hyperdistribution for a
sd.aGibbs=function(SdA,spa,MuA)
{
 if(SdA<=0) return(-Inf)
 llike = dnorm(spa, mean=MuA, sd=SdA, log=T)
 return(sum(llike) + dunif(SdA, min=0, max=2, log=T))
}

# likelihood of the mean of the normal hyperdistribution for b
mu.bGibbs=function(MuB,spb,SdB)
{
 if(SdB<=0) return(-Inf)
 llike = dnorm(spb, mean=MuB, sd=SdB, log=T)
 return(sum(llike) + dunif(MuB, min=-5, max=5, log=T))
}

# likelihood of the standard deviation of the normal hyperdistribution for b
sd.bGibbs=function(SdB,spb,MuB)
{
 if(SdB<=0) return(-Inf)
 llike = dnorm(spb, mean=MuB, sd=SdB, log=T)
 return(sum(llike) + dunif(SdB, min=0, max=2, log=T))
}

# likelihood of the constant of the linear relationship between log light and log
# recruitment
spa.Gibbs=function(spa,N,spb,spk,MuA,SdA,MuB,SdB)
{
 if(spk<0) return(-Inf)
 pred.nr = 10^(spa+spb*normlight)
 if(any(pred.nr<0)) return(-Inf)
 llike=sum(dnbinom(N,mu=pred.nr,size=spk,log=T))+dnorm(spa,mean=MuA,sd=SdA,log=T)
 return(llike)
}

# likelihood of the coefficient of light in the linear relationship between log
# light and log recruitment
spb.Gibbs=function(spb,N,spa,spk,MuA,SdA,MuB,SdB)
{
 if(spk<0) return(-Inf)
 pred.nr = 10^(spa+spb*normlight)
 if(any(pred.nr<0)) return(-Inf)
```

```
 llike=sum(dnbinom(N,mu=pred.nr,size=spk,log=T))+dnorm(spb,mean=MuB,sd=SdB,log=T)
 return(llike)
}

# likelihood of the cluster parameter of the negative binomial distribution
spk.Gibbs=function(spk,spa,spb,N)
{
 if(spk<0) return(-Inf)
 pred.nr = 10^(spa+spb*normlight)
 if(any(pred.nr<0)) return(-Inf)
 llike=sum(dnbinom(N,mu=pred.nr,size=spk,log=T))+dunif(spk,min=0,max=100,log=T)
 return(llike)
}

# A generic routine for taking a single Metropolis step given any probability function, func, an initial parameter,
# start.param, and a scaling parameter for # the step size, scale.param. It returns the next parameter value as well as an
# acceptance indicator (0 if the value was accepted, 1 if rejected), and the new scale parameter. If adjust.scale=T, the
# scale parameter is adjusted to keep the acceptance rate at around 0.25, adjust.scale should be T only for
# steps<which.use (only during burnin period). Based on programs by Richard Condit and Helene Muller-Landau.
metrop1step=function(func,start.param,scale.param,adjust.scale=T,...)
{
 new.scale = scale.param
 probaccept = 0.25
 multreject = 0.975
 multaccept = multreject^(-(1-probaccept)/probaccept)
 origlike = func(start.param,...)
 newval = rnorm(1,mean=start.param,sd=scale.param)
 newlike = func(newval,...)

if(!is.finite(newlike))
  accept = F
  else
  {
    if(newlike>=origlike) accept = T
      else
      {
        likeratio=exp(newlike-origlike)
        if(runif(1)<likeratio) accept = T
          else accept = F
      }
  }

 if(accept)
 {
   if(adjust.scale)  new.scale=multaccept*scale.param
   return(c(newval,0,new.scale))
 }
   else
   {
     if(adjust.scale)  new.scale=multreject*scale.param
     return(c(start.param,1,new.scale))
   }
}
```

Response of recruitment to light availability across a tropical lowland rainforest community

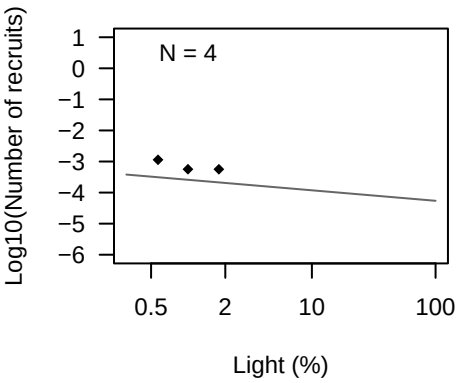
Nadja Rüger, Andreas Huth, Stephen P. Hubbell, and Richard Condit

Supporting Information

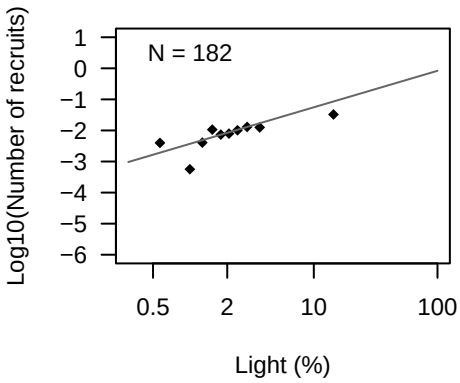
Figure S1:

Model fit for the predicted number of recruits at different light conditions vs. the observed number of recruits for the woody species at Barro Colorado Island, Panama. Observed mean number of recruits (1985–1990) in intervals of 10-percentiles of light in the 5 × 5 m quadrats (dots, only means different from zero are plotted), and predicted number of recruits using posterior means for the second interval 1985–1990 (line).

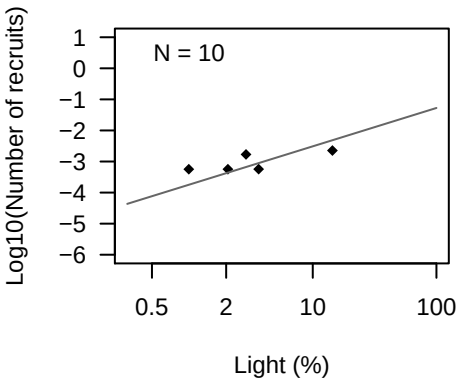
Acacia melanoceras



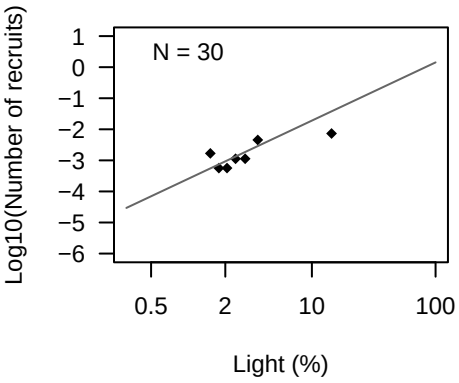
Acalypha diversifolia



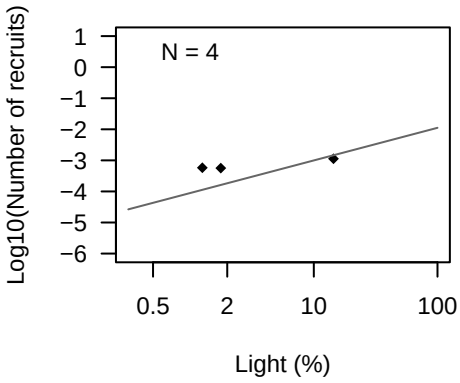
Acalypha macrostachya



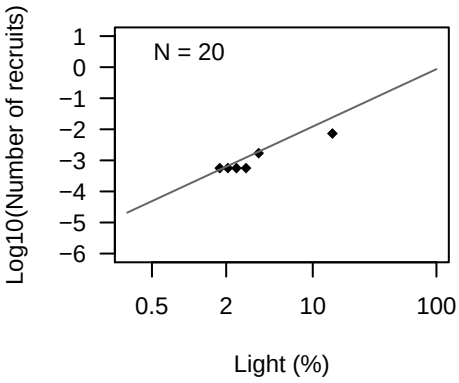
Adelia triloba



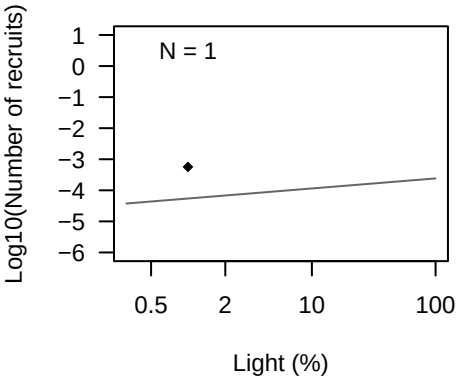
Aegiphila panamensis



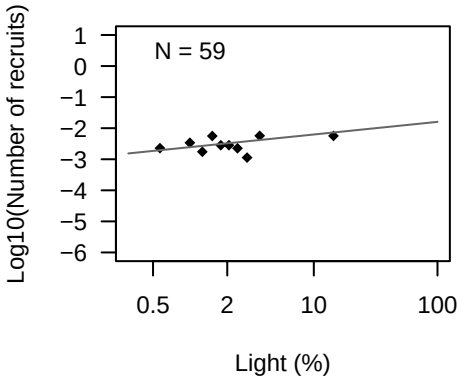
Alchornea costaricensis



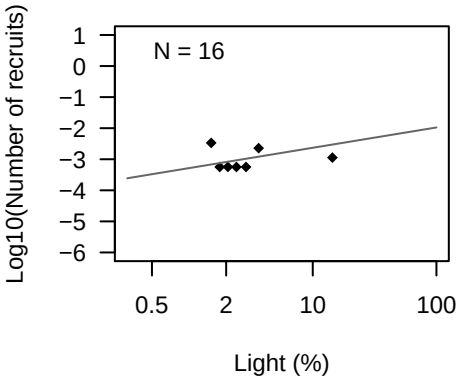
Alchornea latifolia



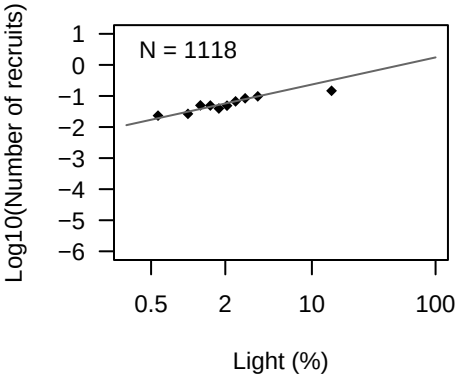
Alibertia edulis



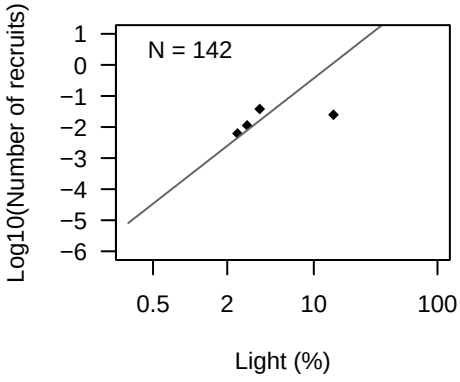
Allophylus psilospermus



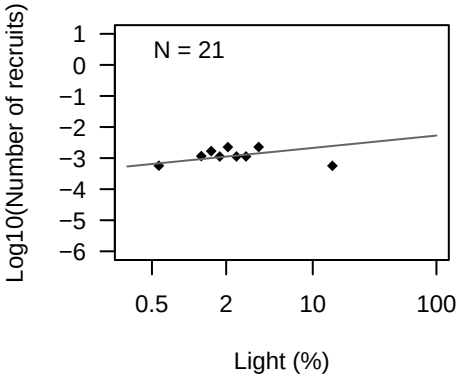
Alseis blackiana

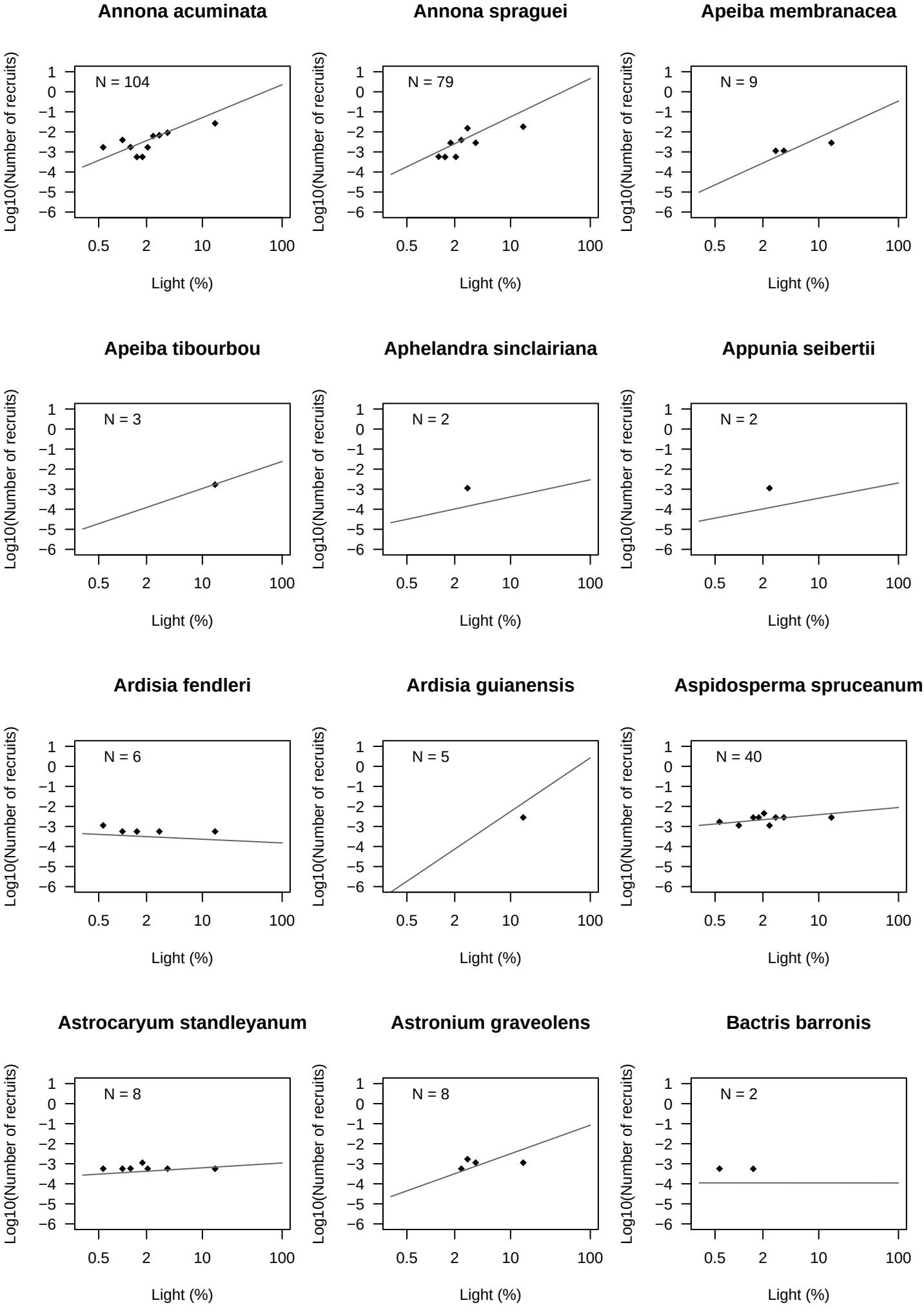


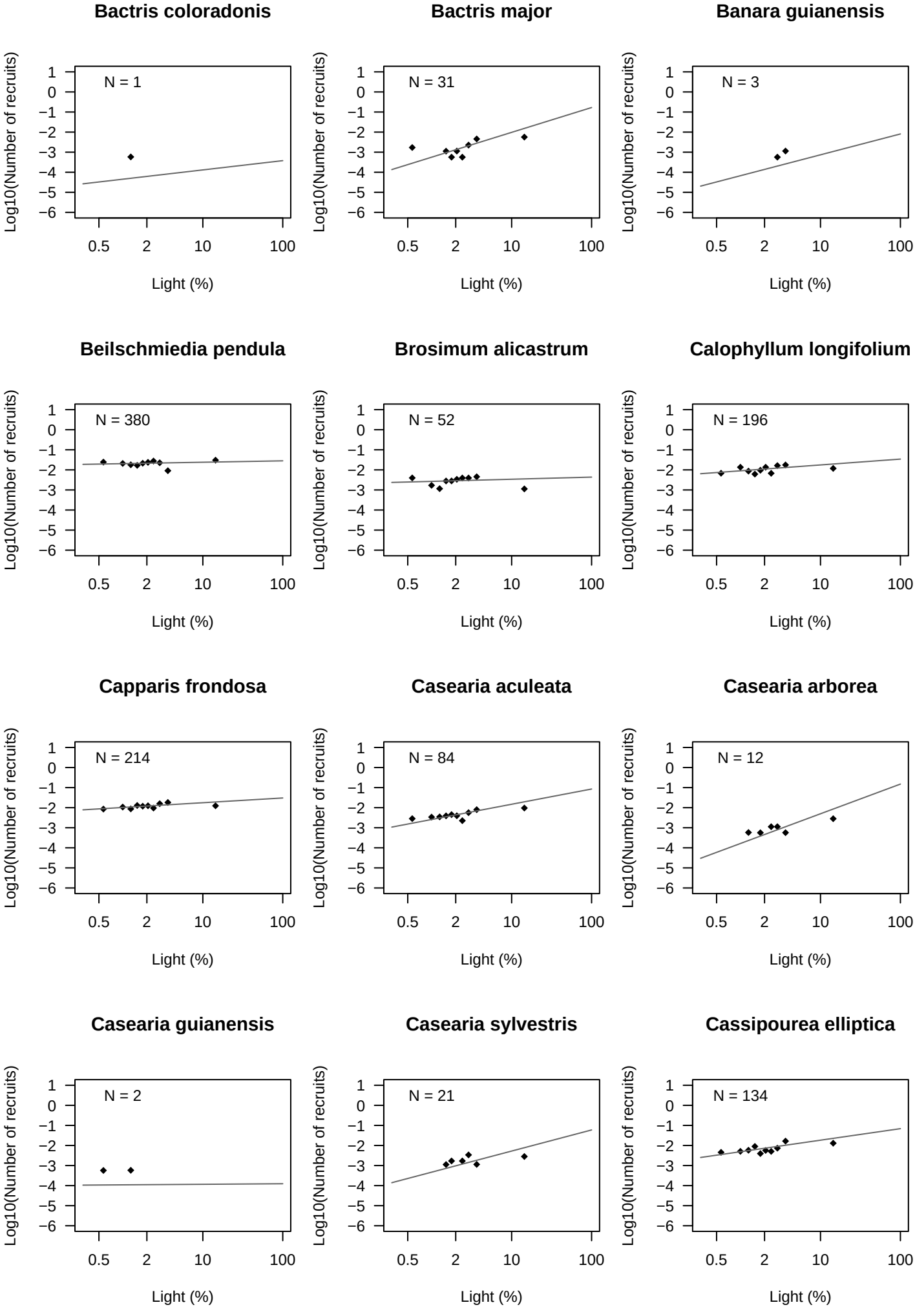
Anaxagorea panamensis



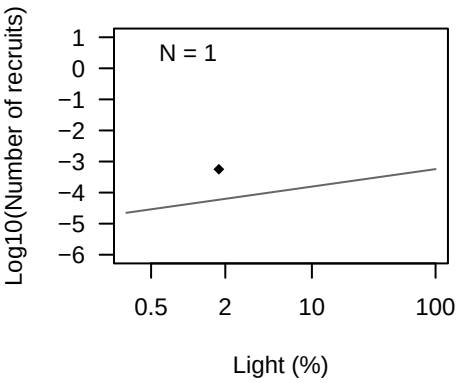
Andira inermis



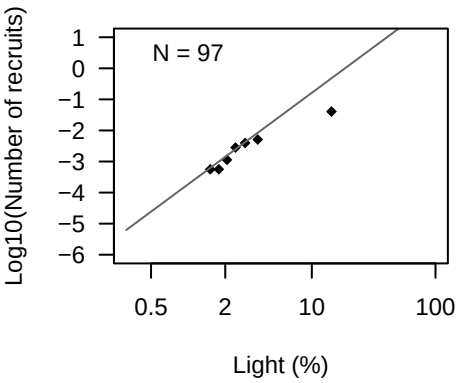

Annona acuminata
N = 104
Annona spraguei
N = 79
Apeiba membranacea
N = 9
Apeiba tibourbou
N = 3
Aphelandra sinclairiana
N = 2
Appunia seibertii
N = 2
Ardisia fendleri
N = 6
Ardisia guianensis
N = 5
Aspidosperma spruceanum
N = 40
Astrocaryum standleyanum
N = 8
Astronium graveolens
N = 8
Bactris barronis
N = 2
Log10(Number of recruits)
Light (%)
1
0
−1
−2
−3
−4
−5
−6
0.5
2
10
100


Bactris coloradonis
N = 1
Bactris major
N = 31
Banara guianensis
N = 3
Beilschmiedia pendula
N = 380
Brosimum alicastrum
N = 52
Calophyllum longifolium
N = 196
Capparis frondosa
N = 214
Casearia aculeata
N = 84
Casearia arborea
N = 12
Casearia guianensis
N = 2
Casearia sylvestris
N = 21
Cassipourea elliptica
N = 134
Log10(Number of recruits)
Light (%)
1
0
−1
−2
−3
−4
−5
−6
0.5
2
10
100

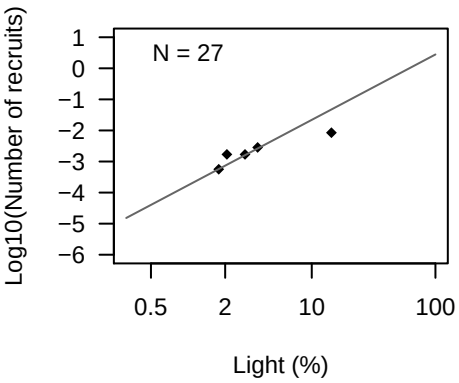
Cavanillesia platanifolia



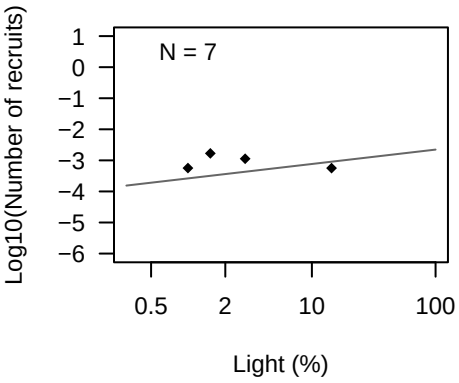
Cecropia insignis



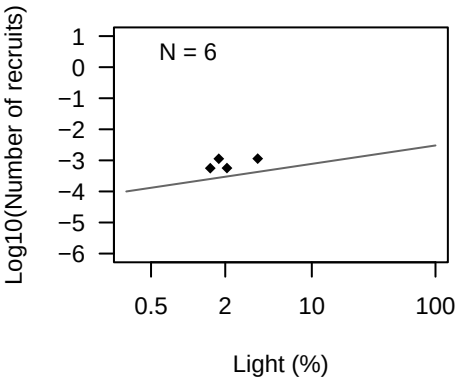
Cecropia obtusifolia



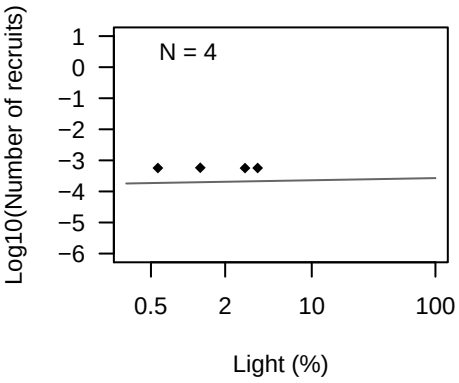
Cedrela odorata



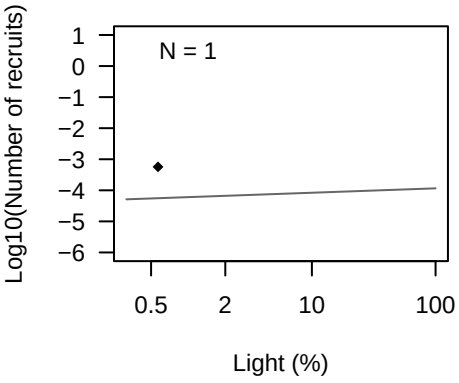
Ceiba pentandra



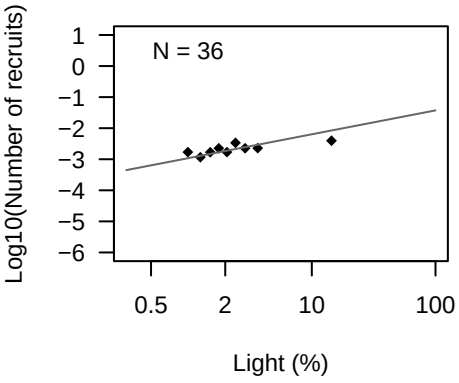
Celtis schippii



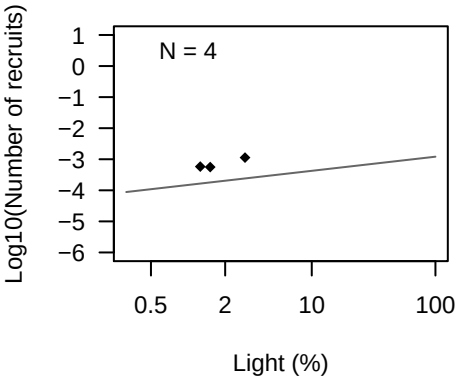
Cespedesia spathulata



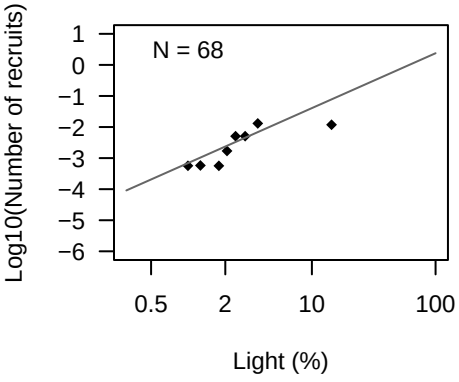
Cestrum megalophyllum



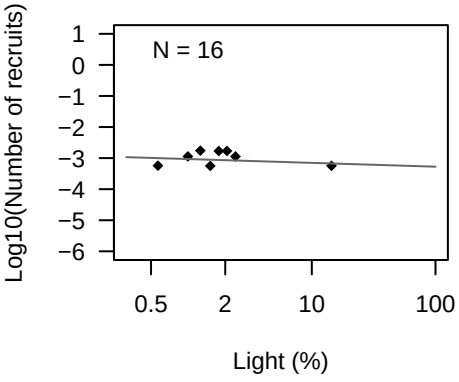
Chamaedorea tepejilote



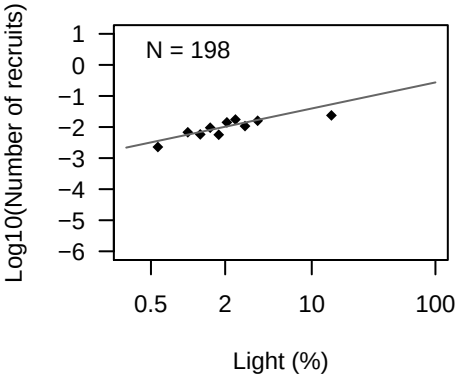
Chamguava schippii

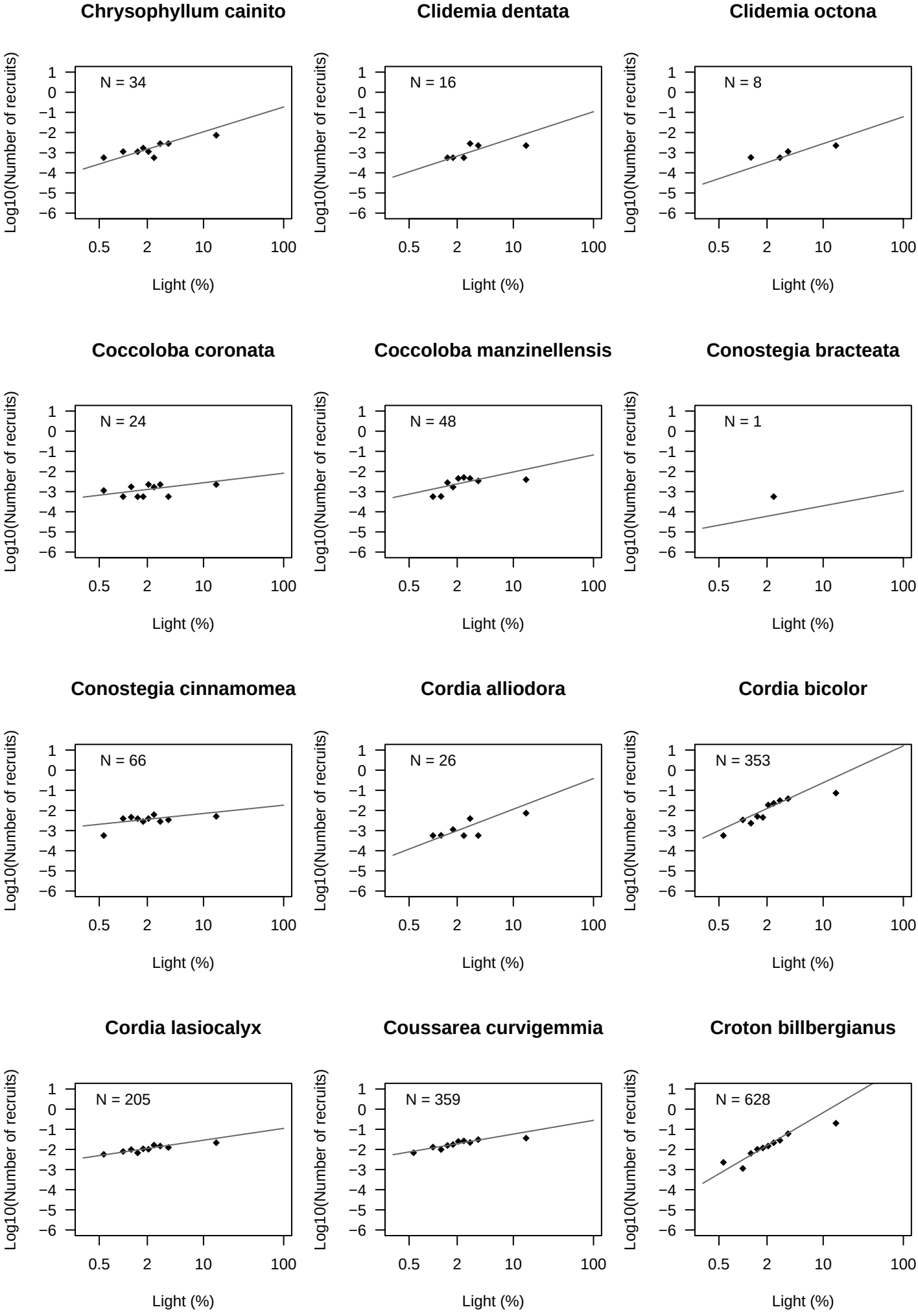


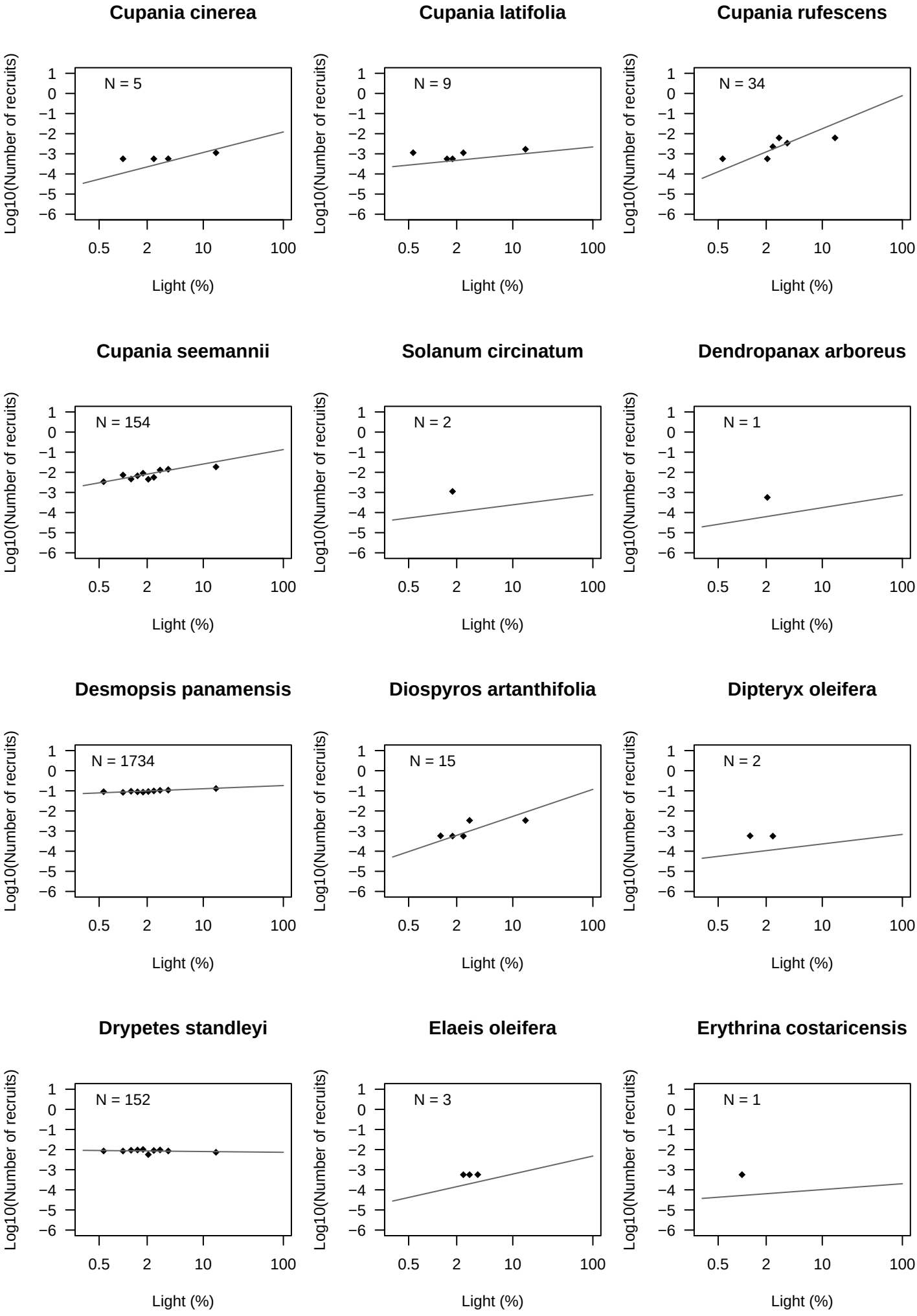
Chrysochlamys eclipes

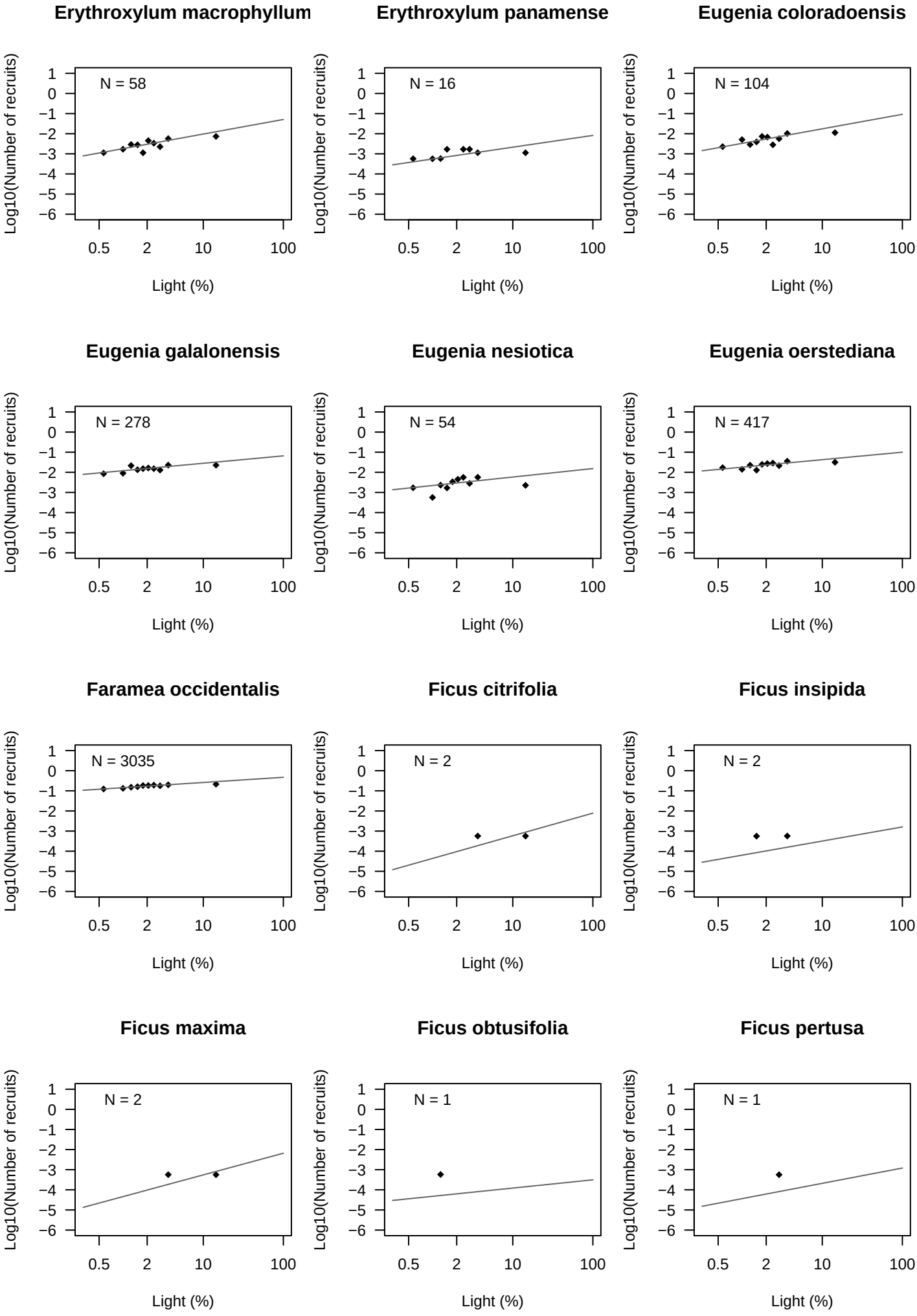


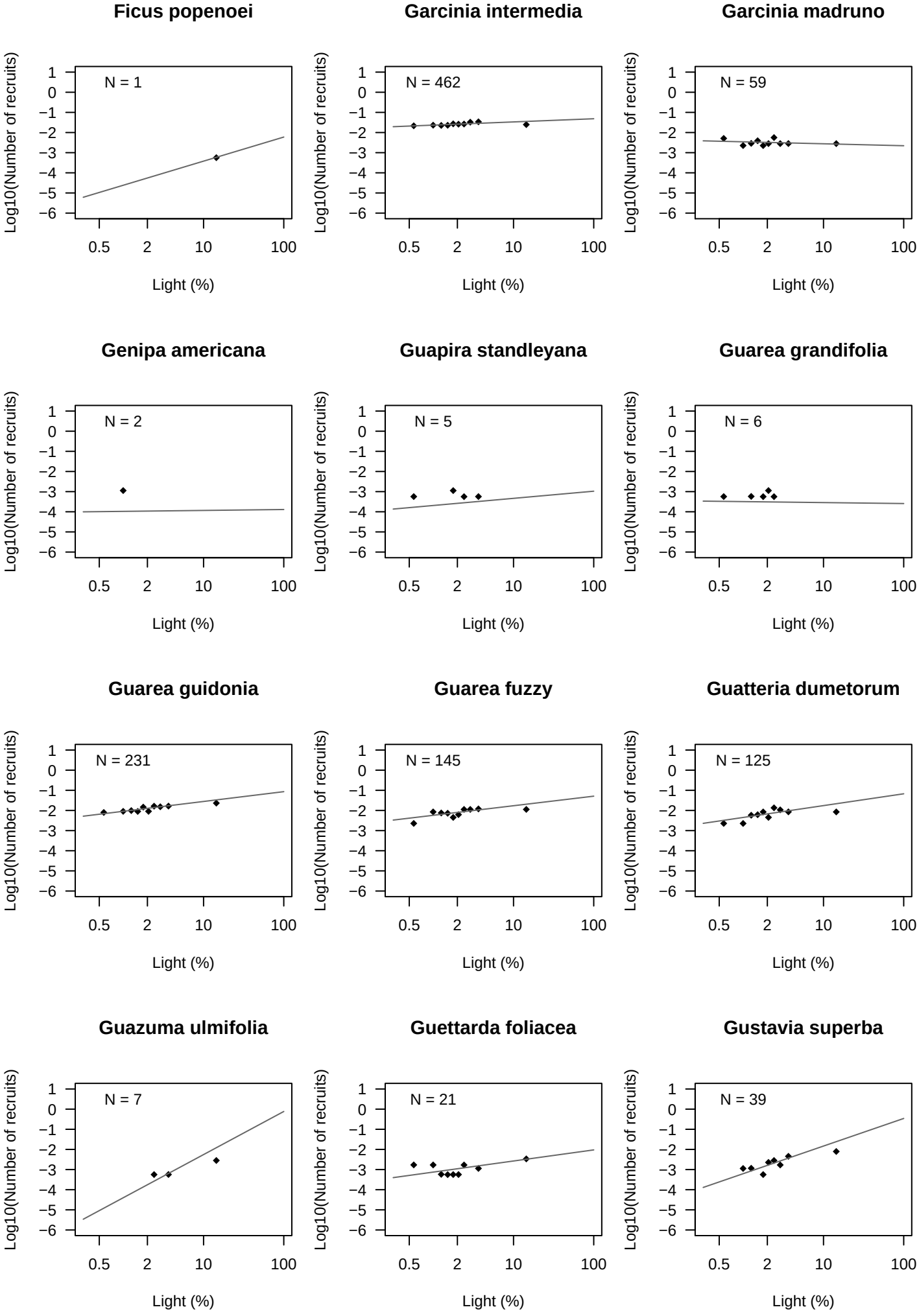
Chrysophyllum argenteum



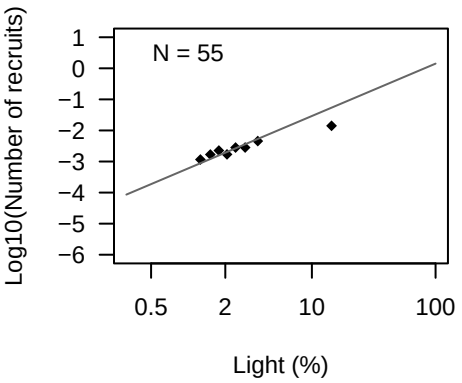

Chrysophyllum cainito
N = 34
Clidemia dentata
N = 16
Clidemia octona
N = 8
Coccoloba coronata
N = 24
Coccoloba manzinellensis
N = 48
Conostegia bracteata
N = 1
Conostegia cinnamomea
N = 66
Cordia alliodora
N = 26
Cordia bicolor
N = 353
Cordia lasiocalyx
N = 205
Coussarea curvigemmia
N = 359
Croton billbergianus
N = 628
Log10(Number of recruits)
Light (%)
1
0
−1
−2
−3
−4
−5
−6
0.5
2
10
100


Cupania cinerea
N = 5
Cupania latifolia
N = 9
Cupania rufescens
N = 34
Cupania seemannii
N = 154
Solanum circinatum
N = 2
Dendropanax arboreus
N = 1
Desmopsis panamensis
N = 1734
Diospyros artanthifolia
N = 15
Dipteryx oleifera
N = 2
Drypetes standleyi
N = 152
Elaeis oleifera
N = 3
Erythrina costaricensis
N = 1
Log10(Number of recruits)
Light (%)
1
0
−1
−2
−3
−4
−5
−6
0.5
2
10
100

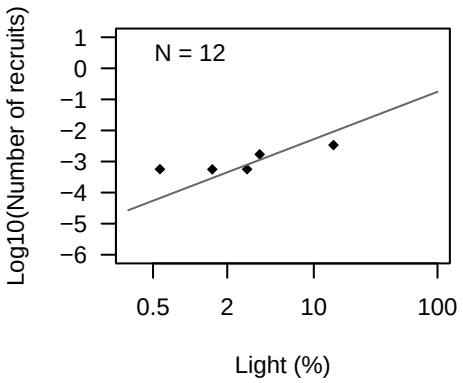

Erythroxylum macrophyllum
N = 58
Erythroxylum panamense
N = 16
Eugenia coloradoensis
N = 104
Eugenia galalonensis
N = 278
Eugenia nesiotica
N = 54
Eugenia oerstediana
N = 417
Faramea occidentalis
N = 3035
Ficus citrifolia
N = 2
Ficus insipida
N = 2
Ficus maxima
N = 2
Ficus obtusifolia
N = 1
Ficus pertusa
N = 1
Log10(Number of recruits)
Light (%)
1
0
−1
−2
−3
−4
−5
−6
0.5
2
10
100


Ficus popenoei
N = 1
Garcinia intermedia
N = 462
Garcinia madruno
N = 59
Genipa americana
N = 2
Guapira standleyana
N = 5
Guarea grandifolia
N = 6
Guarea guidonia
N = 231
Guarea fuzzy
N = 145
Guatteria dumetorum
N = 125
Guazuma ulmifolia
N = 7
Guettarda foliacea
N = 21
Gustavia superba
N = 39
Log10(Number of recruits)
Light (%)
1
0
−1
−2
−3
−4
−5
−6
0.5
2
10
100

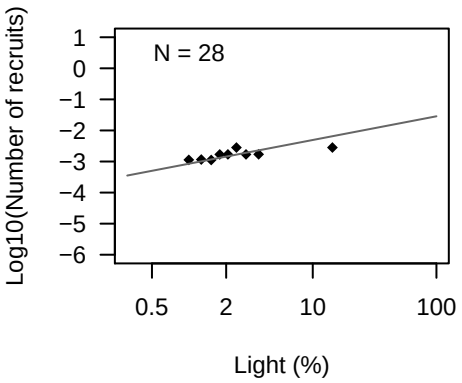
Hamelia axillaris



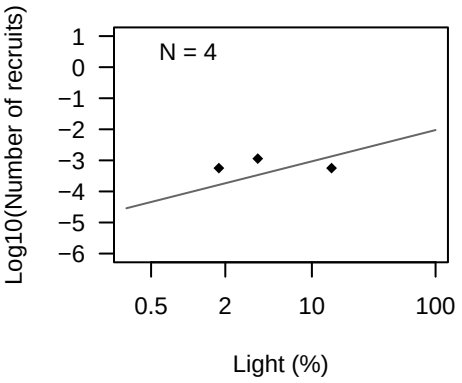
Hampea appendiculata



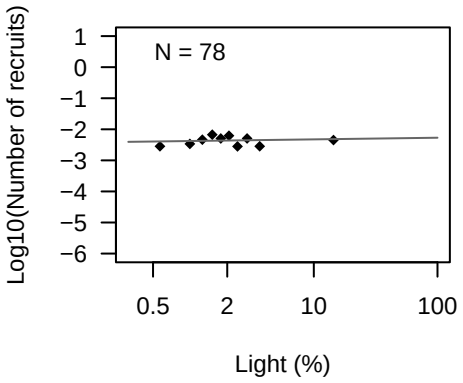
Hasseltia floribunda



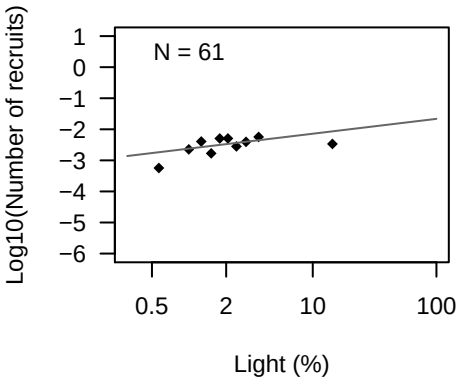
Heisteria acuminata



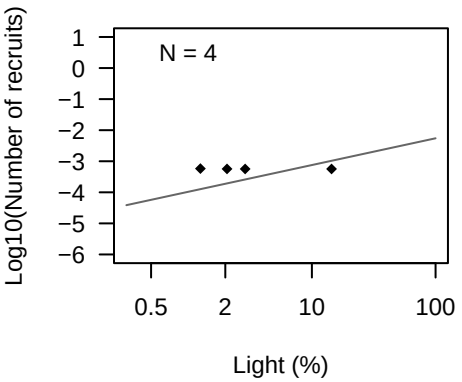
Heisteria concinna



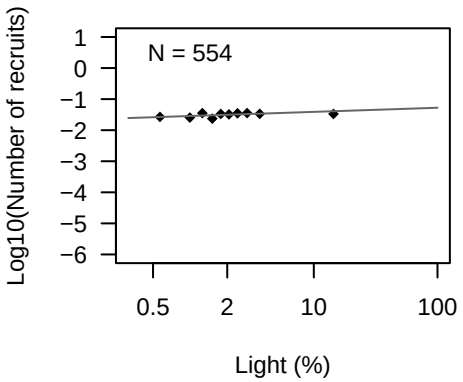
Herrania purpurea



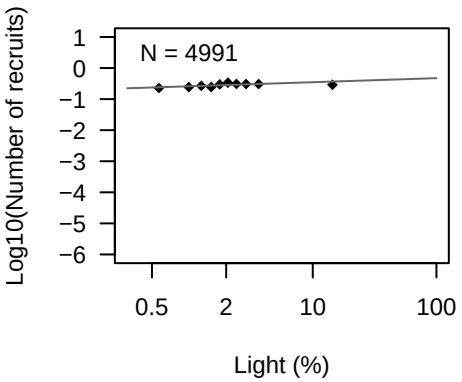
Hirtella americana



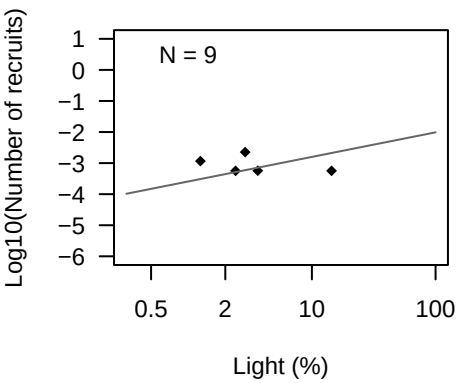
Hirtella triandra



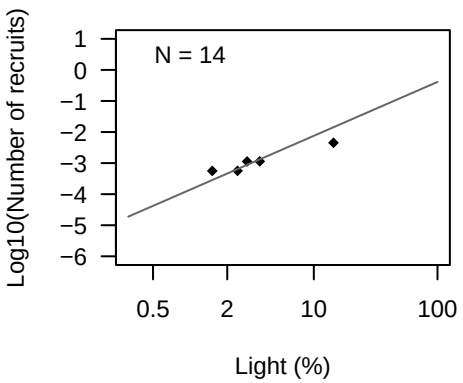
Hybanthus prunifolius



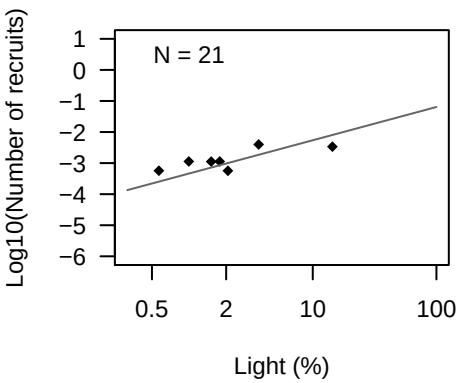
Hieronyma alchorneoides

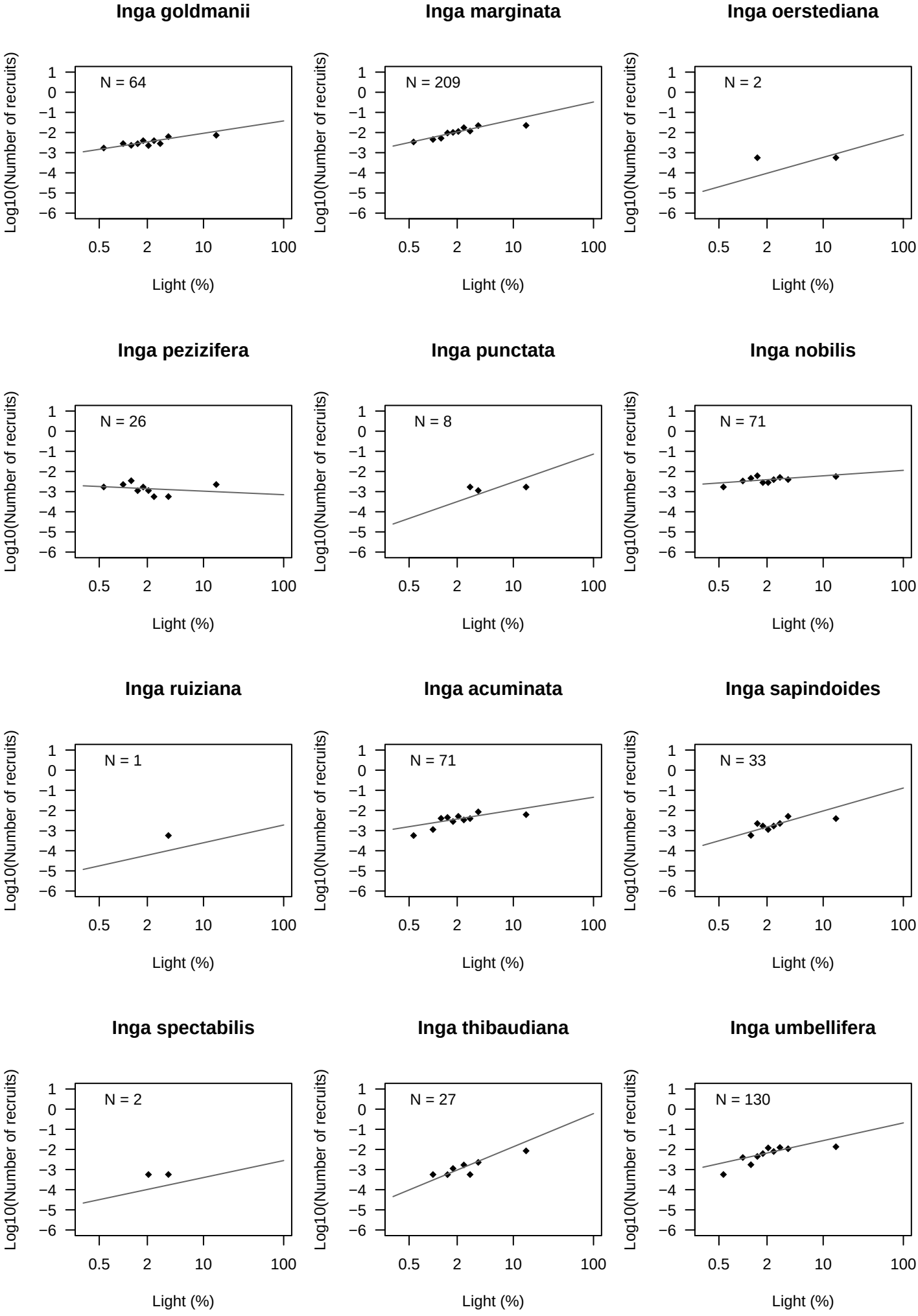


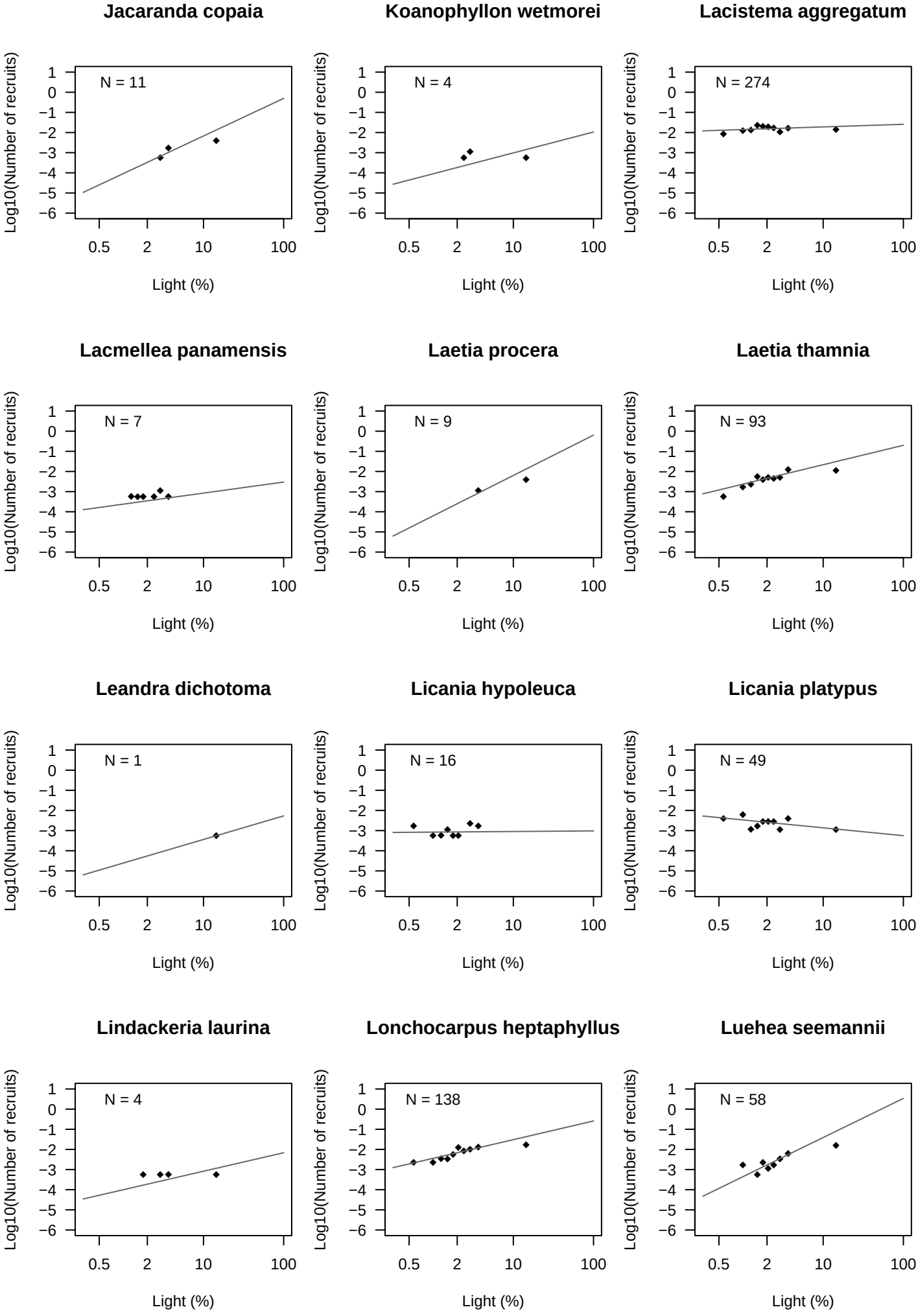
Inga cocleensis

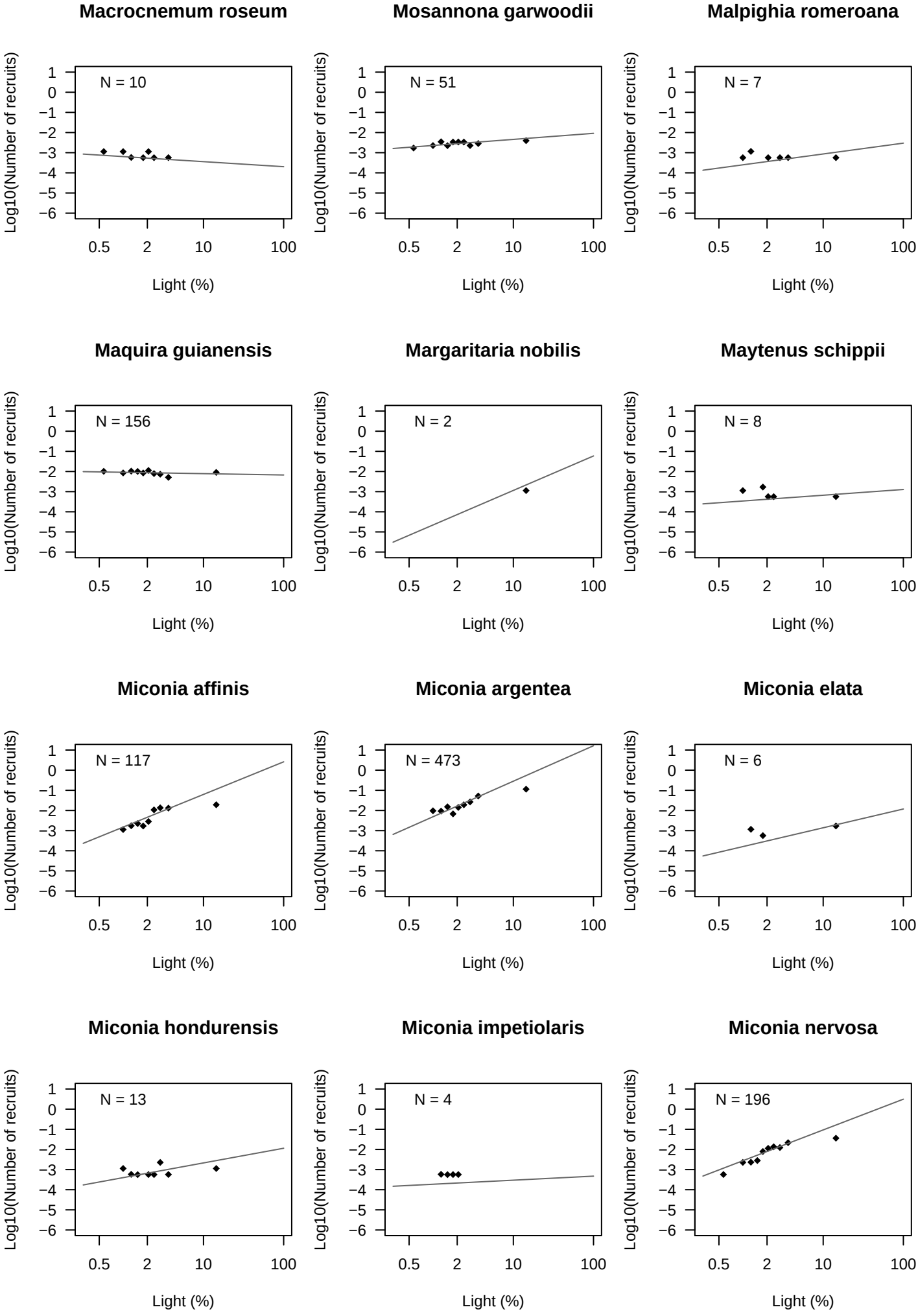


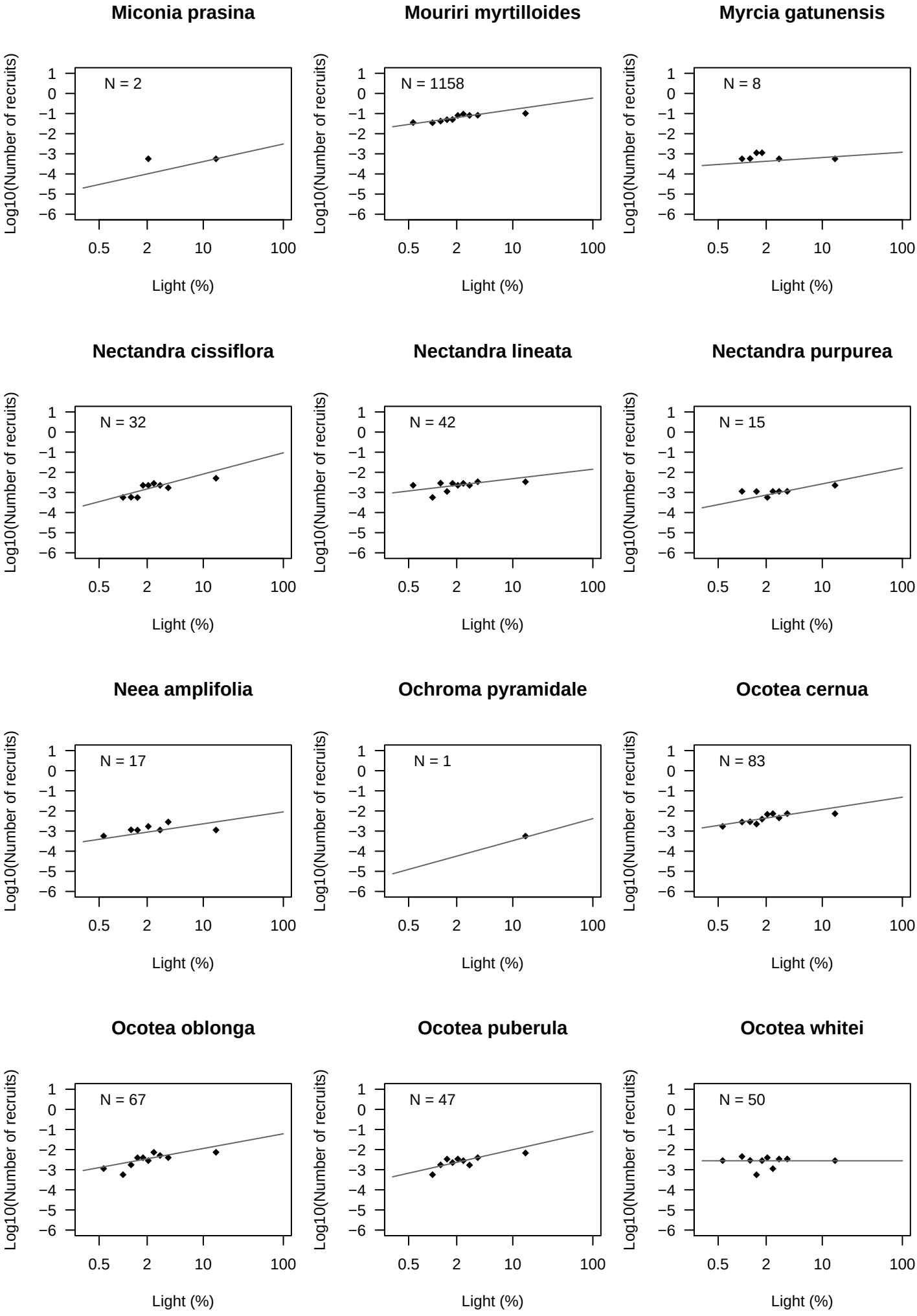
Inga laurina

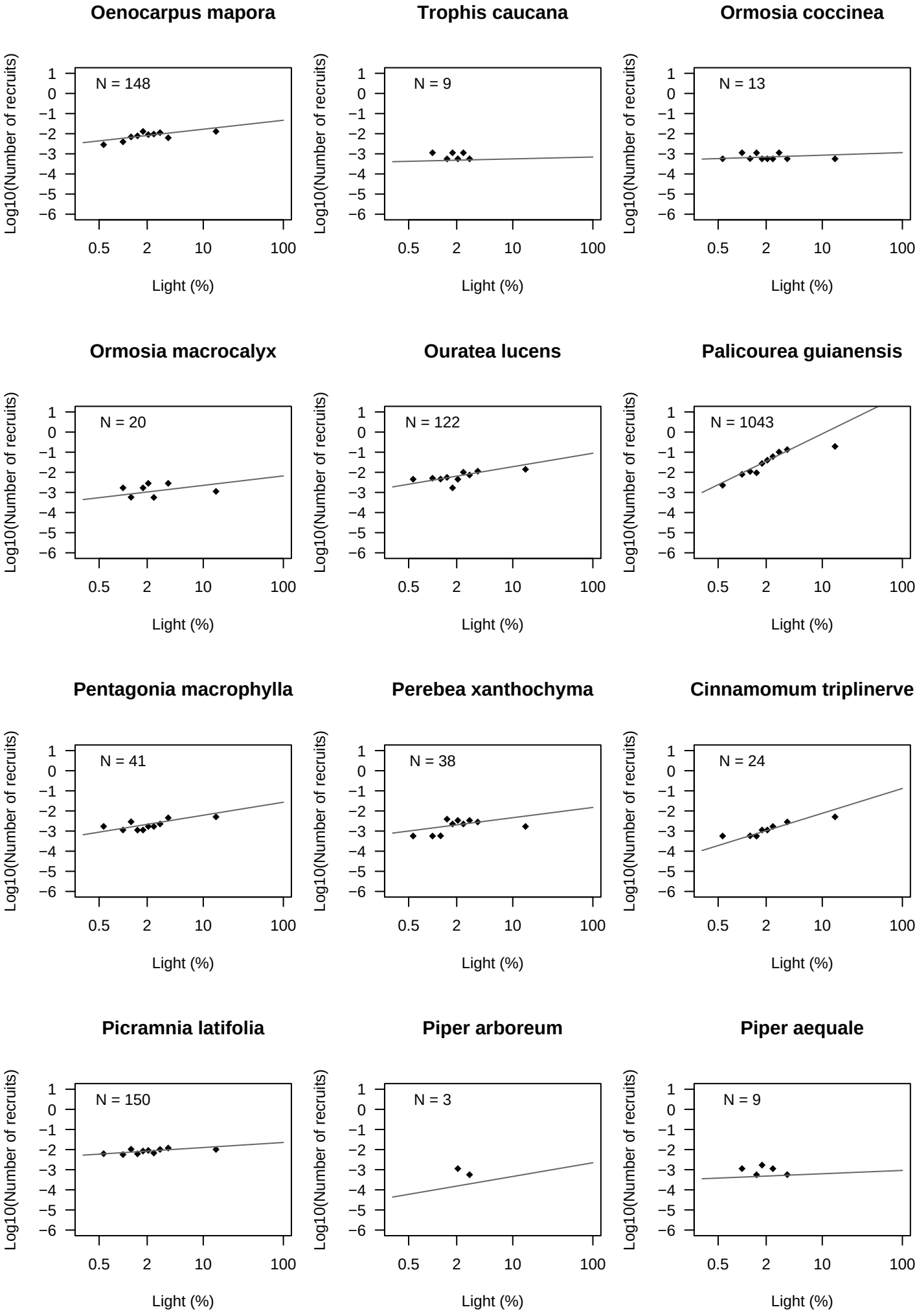



Inga goldmanii
N = 64
Inga marginata
N = 209
Inga oerstediana
N = 2
Inga pezizifera
N = 26
Inga punctata
N = 8
Inga nobilis
N = 71
Inga ruiziana
N = 1
Inga acuminata
N = 71
Inga sapindoides
N = 33
Inga spectabilis
N = 2
Inga thibaudiana
N = 27
Inga umbellifera
N = 130
Log10(Number of recruits)
Light (%)
1
0
−1
−2
−3
−4
−5
−6
0.5
2
10
100

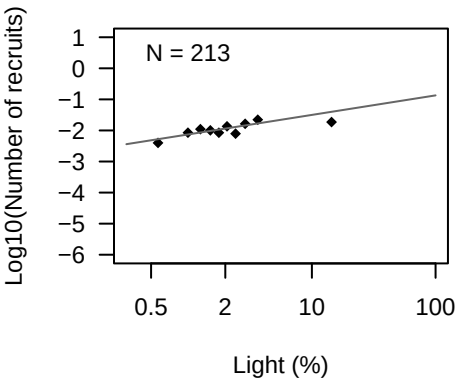

Jacaranda copaia
N = 11
Koanophyllon wetmorei
N = 4
Lacistema aggregatum
N = 274
Lacmellea panamensis
N = 7
Laetia procera
N = 9
Laetia thamnia
N = 93
Leandra dichotoma
N = 1
Licania hypoleuca
N = 16
Licania platypus
N = 49
Lindackeria laurina
N = 4
Lonchocarpus heptaphyllus
N = 138
Luehea seemannii
N = 58
Log10(Number of recruits)
Light (%)
1
0
−1
−2
−3
−4
−5
−6
0.5
2
10
100


Macrocnemum roseum
N = 10
Mosannona garwoodii
N = 51
Malpighia romeroana
N = 7
Maquira guianensis
N = 156
Margaritaria nobilis
N = 2
Maytenus schippii
N = 8
Miconia affinis
N = 117
Miconia argentea
N = 473
Miconia elata
N = 6
Miconia hondurensis
N = 13
Miconia impetiolaris
N = 4
Miconia nervosa
N = 196
Log10(Number of recruits)
Light (%)
1
0
−1
−2
−3
−4
−5
−6
0.5
2
10
100

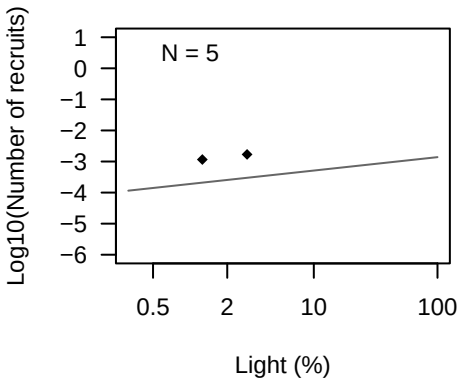

Miconia prasina
N = 2
Mouriri myrtilloides
N = 1158
Myrcia gatunensis
N = 8
Nectandra cissiflora
N = 32
Nectandra lineata
N = 42
Nectandra purpurea
N = 15
Neea amplifolia
N = 17
Ochroma pyramidale
N = 1
Ocotea cernua
N = 83
Ocotea oblonga
N = 67
Ocotea puberula
N = 47
Ocotea whitei
N = 50
Log10(Number of recruits)
Light (%)
1
0
−1
−2
−3
−4
−5
−6
0.5
2
10
100


Oenocarpus mapora
N = 148
Trophis caucana
N = 9
Ormosia coccinea
N = 13
Ormosia macrocalyx
N = 20
Ouratea lucens
N = 122
Palicourea guianensis
N = 1043
Pentagonia macrophylla
N = 41
Perebea xanthochyma
N = 38
Cinnamomum triplinerve
N = 24
Picramnia latifolia
N = 150
Piper arboreum
N = 3
Piper aequale
N = 9
Log10(Number of recruits)
Light (%)
1
0
−1
−2
−3
−4
−5
−6
0.5
2
10
100

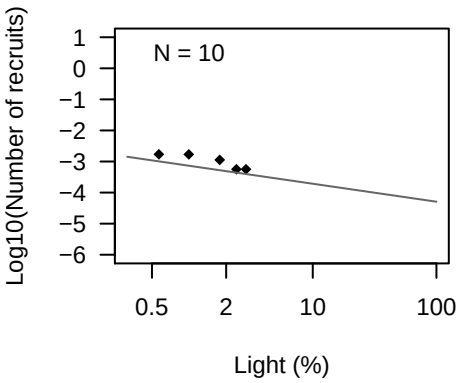
Piper cordulatum



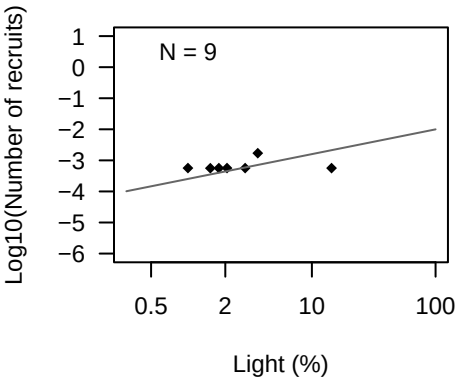
Piper colonense



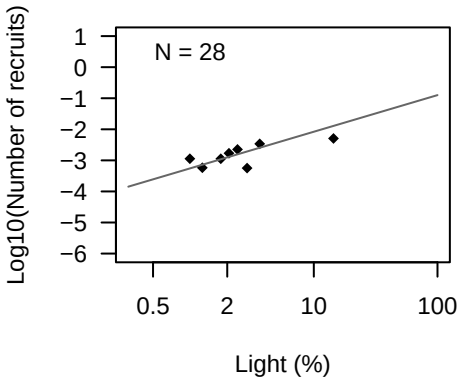
Piper perlasense



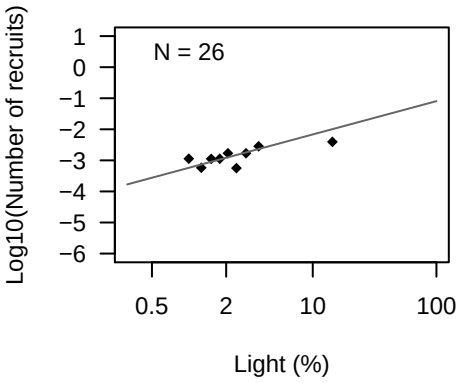
Piper reticulatum



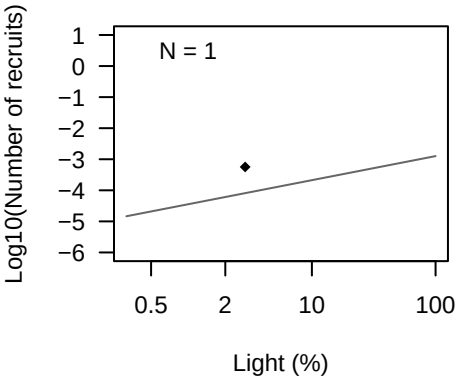
Platymiscium pinnatum



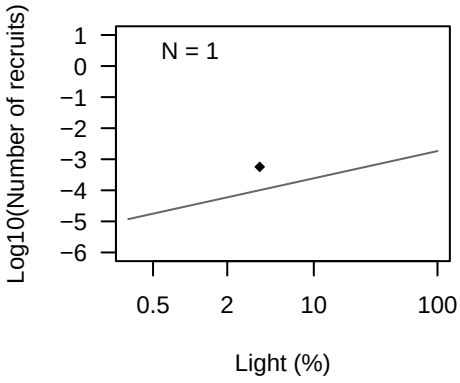
Platypodium elegans



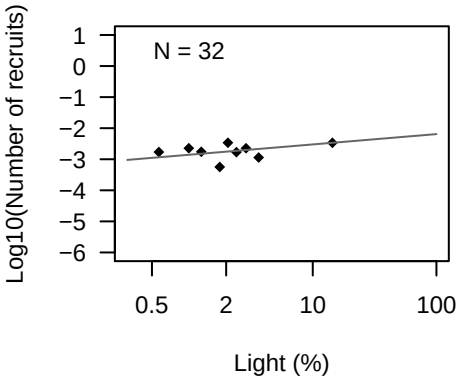
Pachira quinata



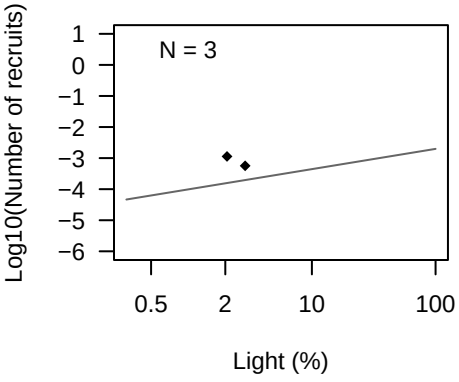
Posoqueria latifolia



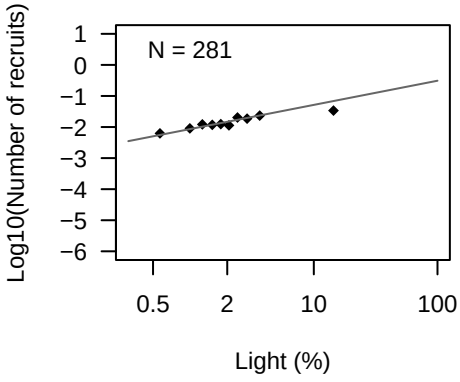
Poulsenia armata



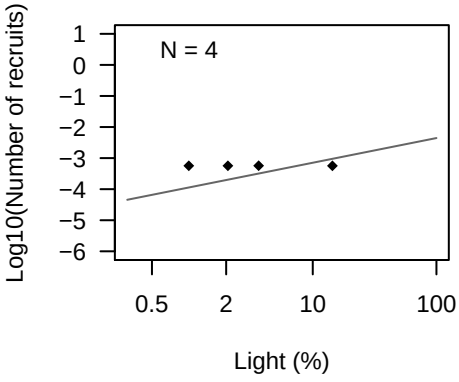
Pourouma bicolor



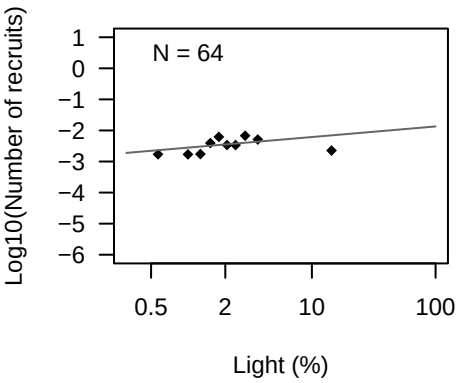
Pouteria reticulata



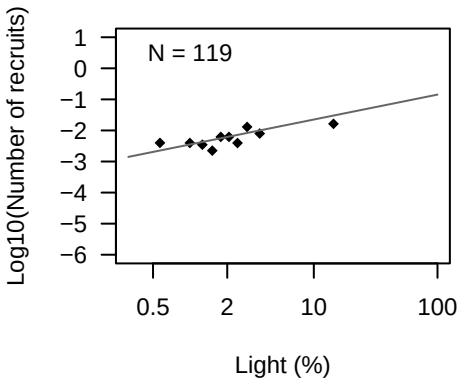
Pouteria stipitata



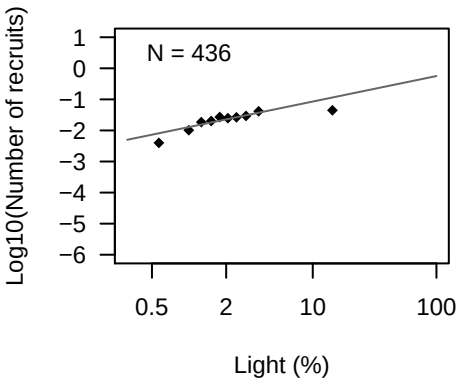
Prioria copaifera



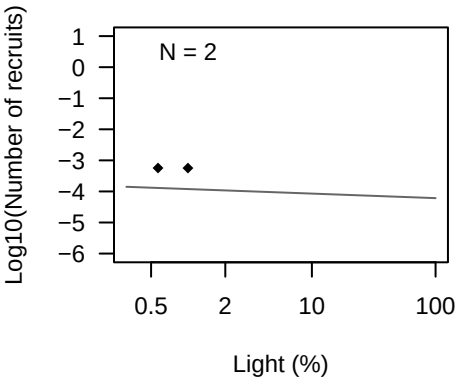
Protium costaricense



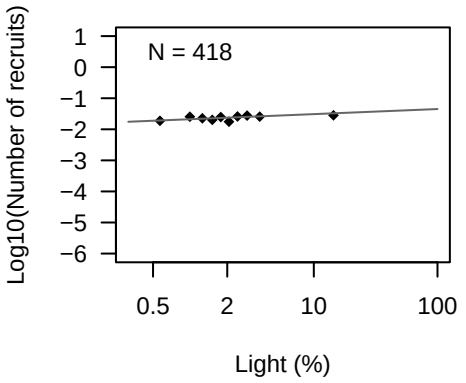
Protium panamense



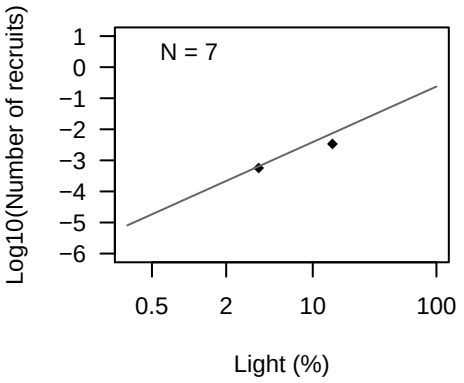
Protium confusum



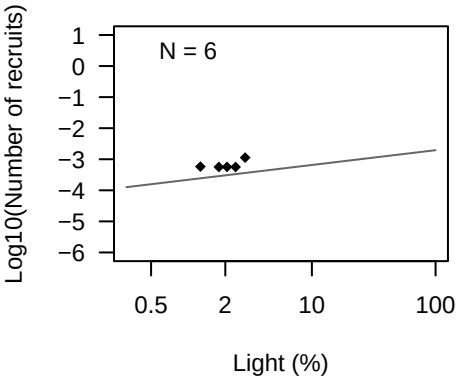
Protium tenuifolium



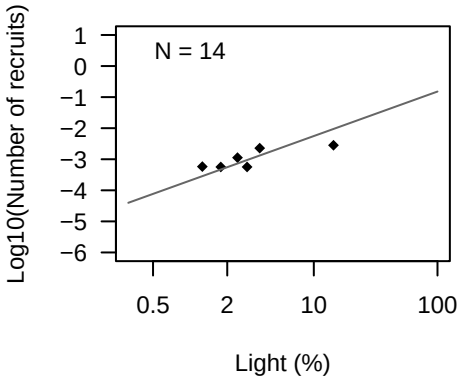
Pseudobombax septenatum



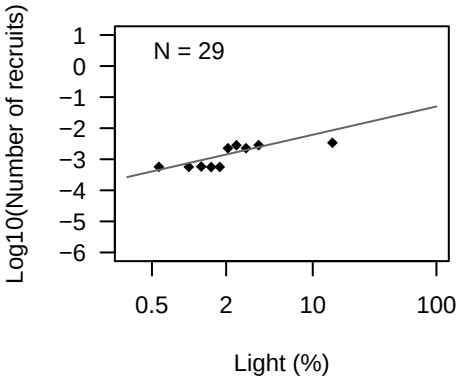
Psidium friedrichsthalianum



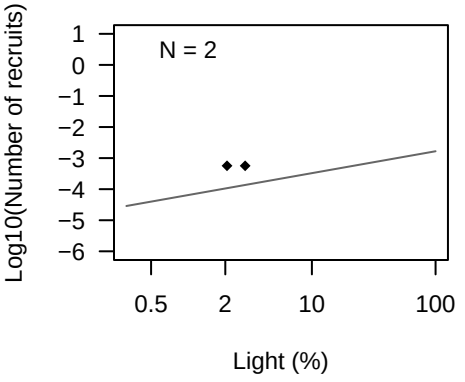
Psychotria acuminata



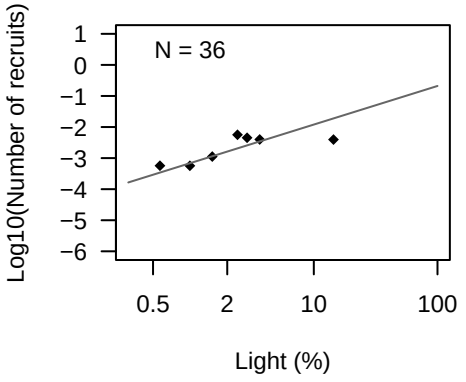
Psychotria deflexa



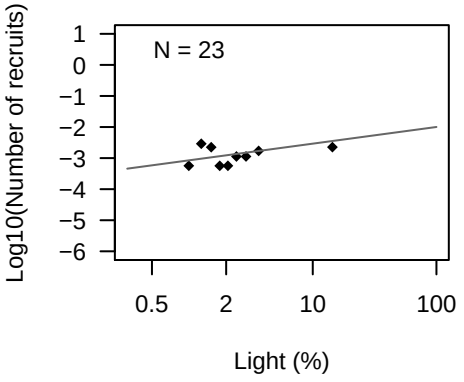
Psychotria hoffmannseggian

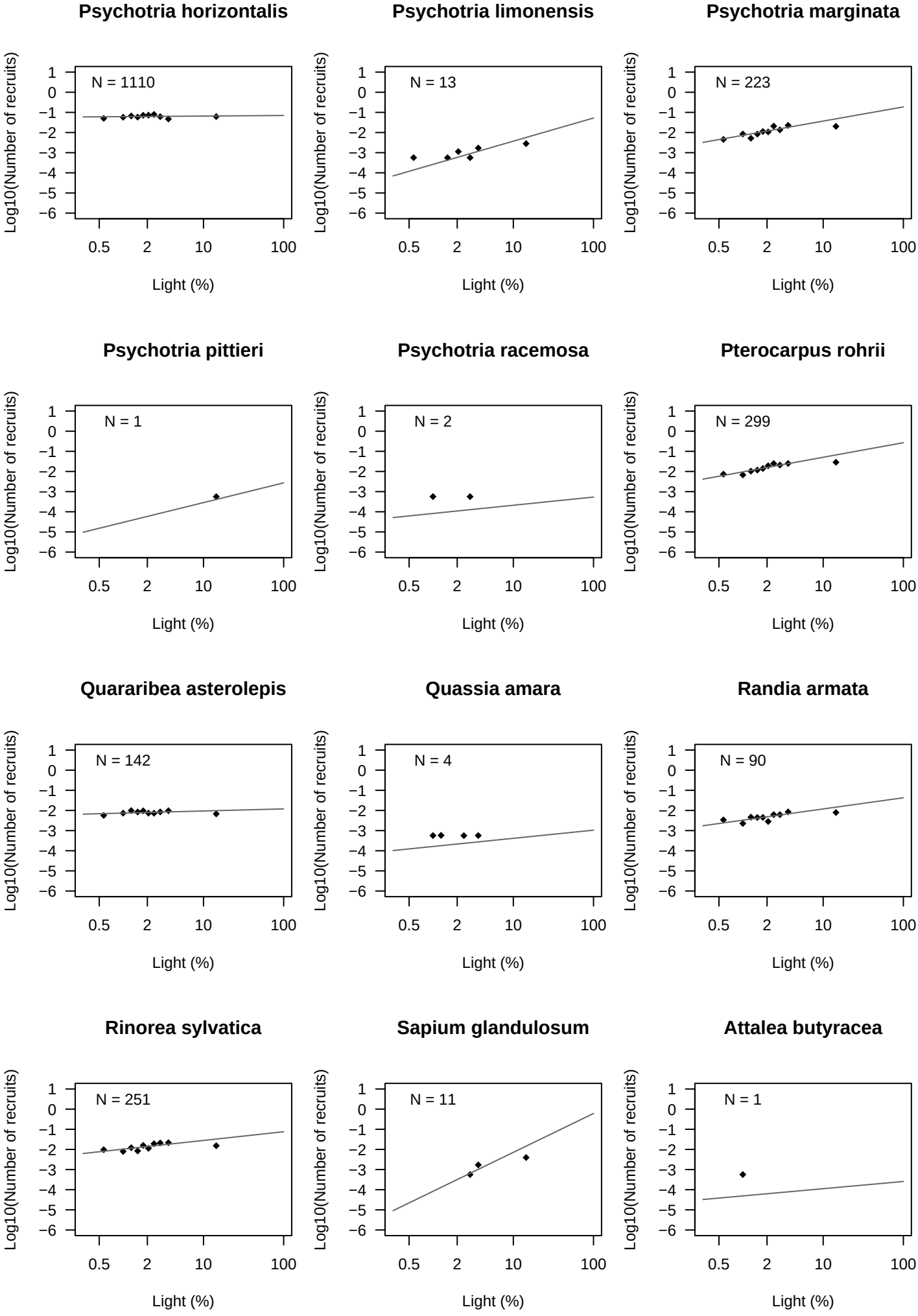


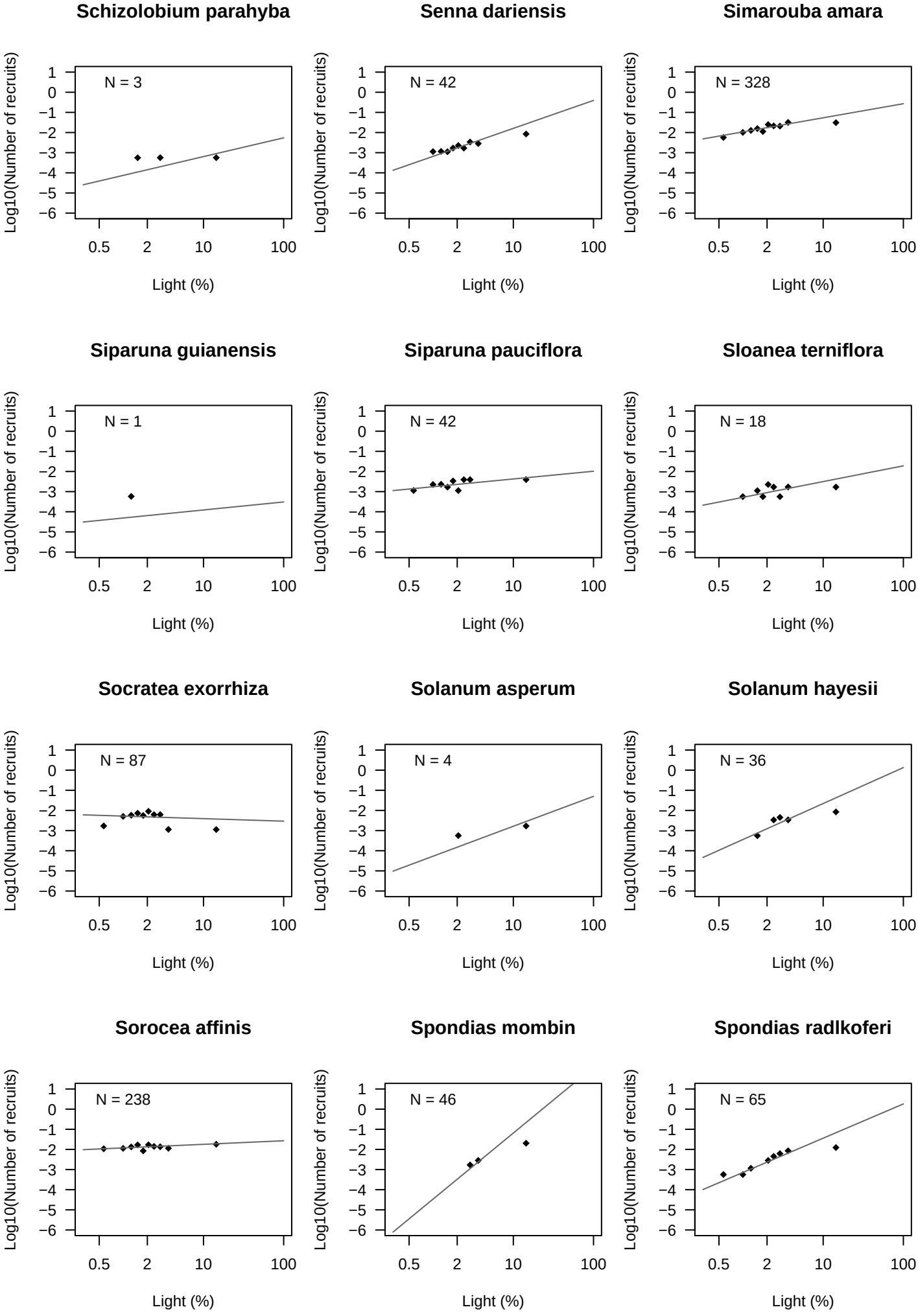
Psychotria graciliflora

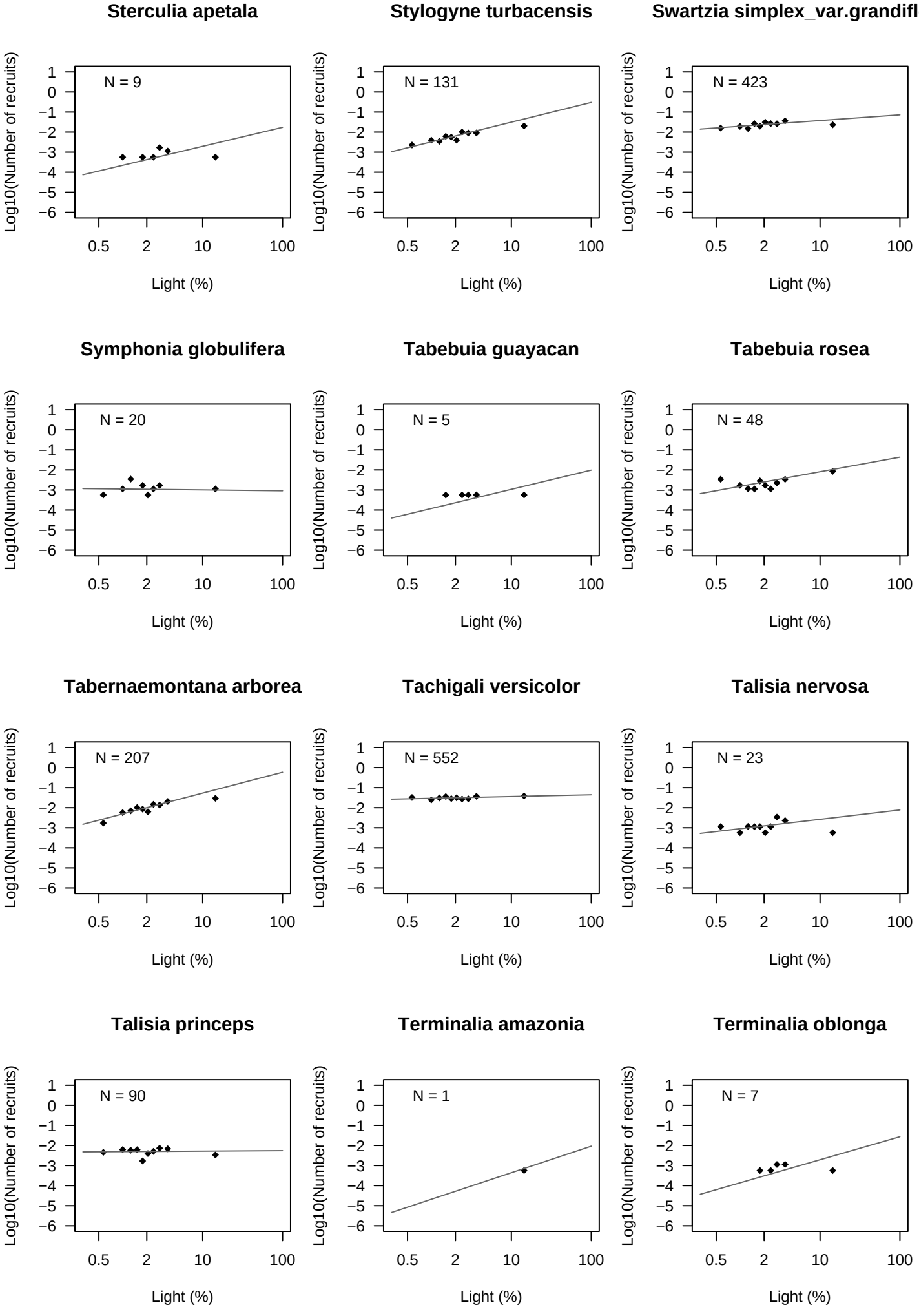


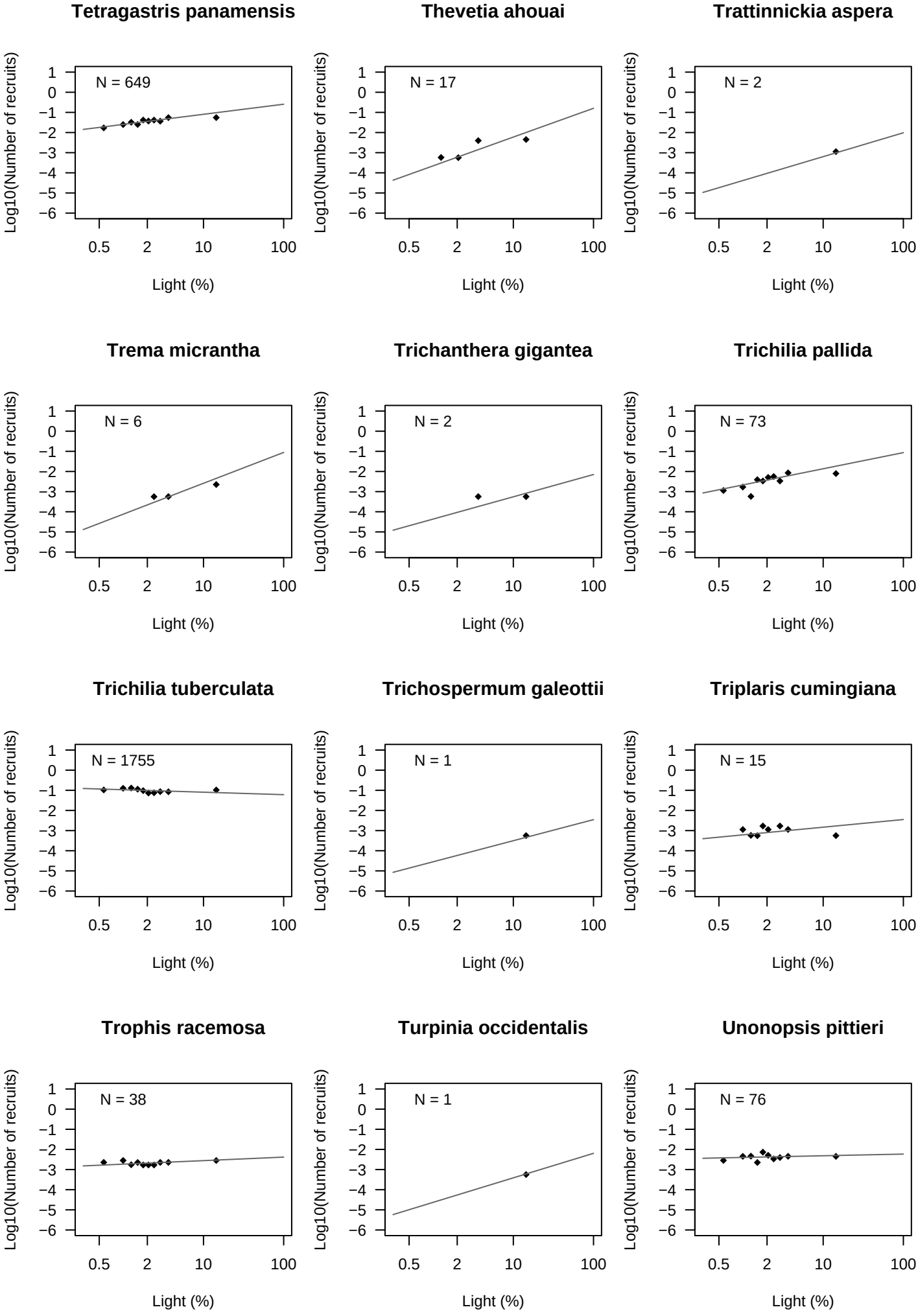
Psychotria grandis



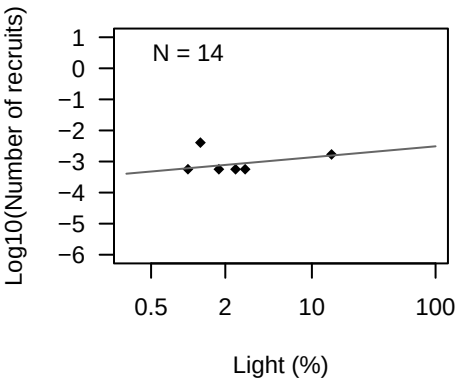

Psychotria horizontalis
N = 1110
Psychotria limonensis
N = 13
Psychotria marginata
N = 223
Psychotria pittieri
N = 1
Psychotria racemosa
N = 2
Pterocarpus rohrii
N = 299
Quararibea asterolepis
N = 142
Quassia amara
N = 4
Randia armata
N = 90
Rinorea sylvatica
N = 251
Sapium glandulosum
N = 11
Attalea butyracea
N = 1
Log10(Number of recruits)
Light (%)
1
0
−1
−2
−3
−4
−5
−6
0.5
2
10
100


Schizolobium parahyba
N = 3
Senna dariensis
N = 42
Simarouba amara
N = 328
Siparuna guianensis
N = 1
Siparuna pauciflora
N = 42
Sloanea terniflora
N = 18
Socratea exorrhiza
N = 87
Solanum asperum
N = 4
Solanum hayesii
N = 36
Sorocea affinis
N = 238
Spondias mombin
N = 46
Spondias radlkoferi
N = 65
Log10(Number of recruits)
Light (%)
1
0
−1
−2
−3
−4
−5
−6
0.5
2
10
100

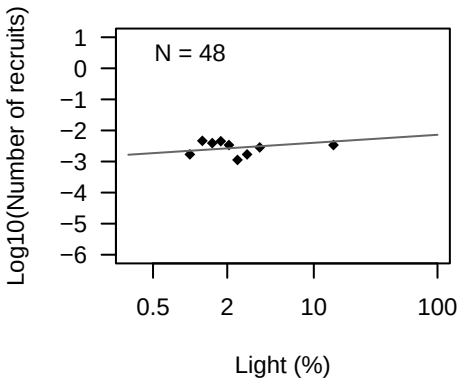

Sterculia apetala
N = 9
Stylogyne turbacensis
N = 131
Swartzia simplex_var.grandiflo
N = 423
Symphonia globulifera
N = 20
Tabebuia guayacan
N = 5
Tabebuia rosea
N = 48
Tabernaemontana arborea
N = 207
Tachigali versicolor
N = 552
Talisia nervosa
N = 23
Talisia princeps
N = 90
Terminalia amazonia
N = 1
Terminalia oblonga
N = 7
Log10(Number of recruits)
Light (%)
1
0
−1
−2
−3
−4
−5
−6
0.5
2
10
100


Tetragastris panamensis
N = 649
Thevetia ahouai
N = 17
Trattinnickia aspera
N = 2
Trema micrantha
N = 6
Trichanthera gigantea
N = 2
Trichilia pallida
N = 73
Trichilia tuberculata
N = 1755
Trichospermum galeottii
N = 1
Triplaris cumingiana
N = 15
Trophis racemosa
N = 38
Turpinia occidentalis
N = 1
Unonopsis pittieri
N = 76
Log10(Number of recruits)
Light (%)
1
0
−1
−2
−3
−4
−5
−6
0.5
2
10
100

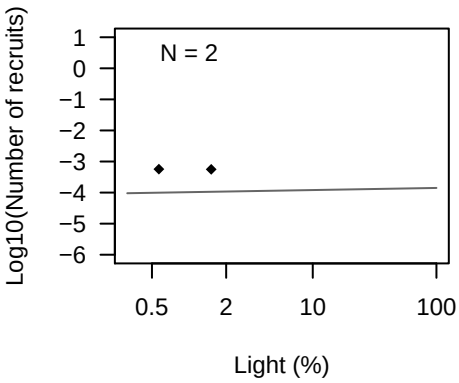
Urera baccifera



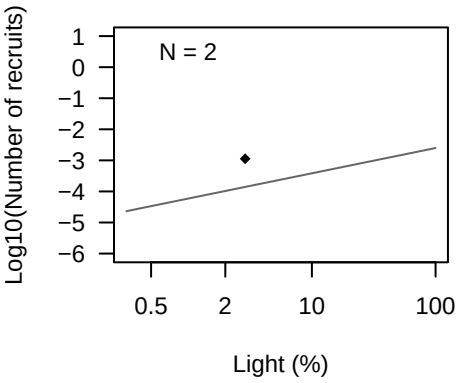
Virola sebifera



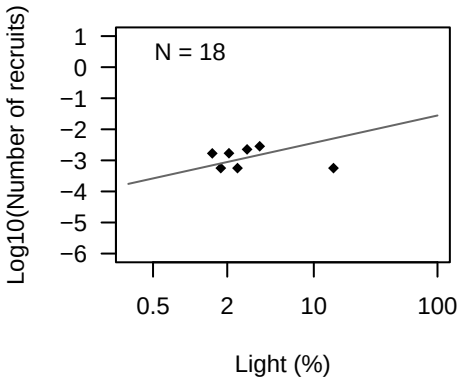
Virola multiflora



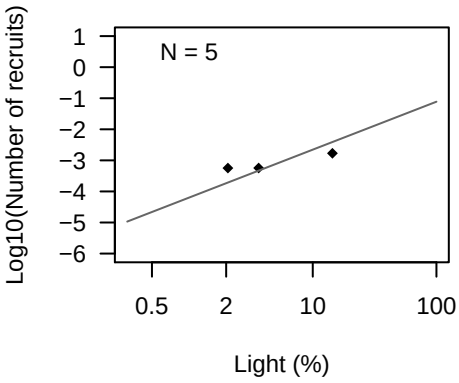
Virola surinamensis



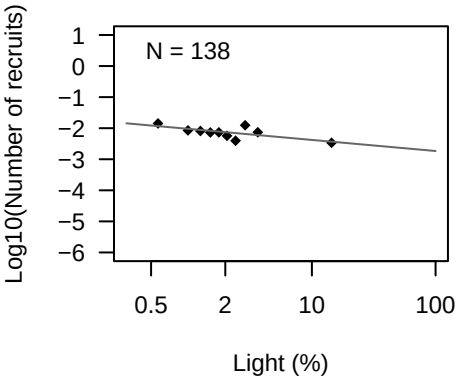
Vismia baccifera



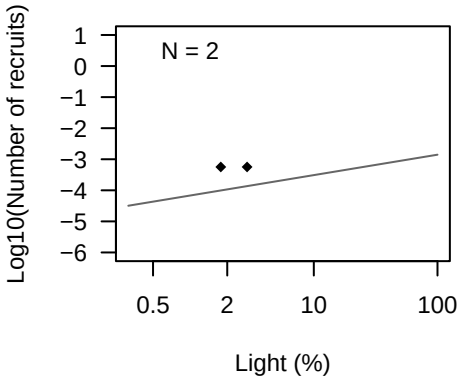
Vochysia ferruginea



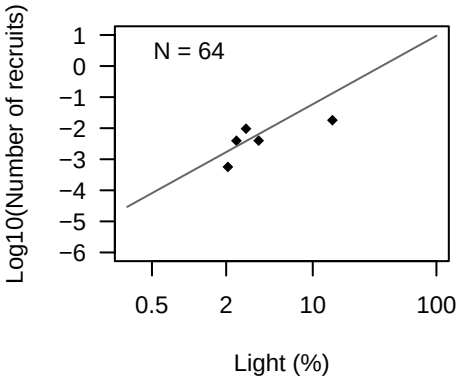
Xylopia macrantha



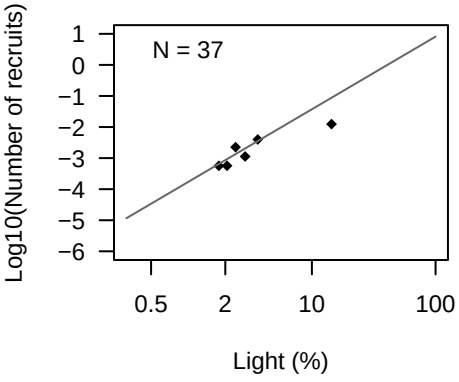
Xylosma oligandra



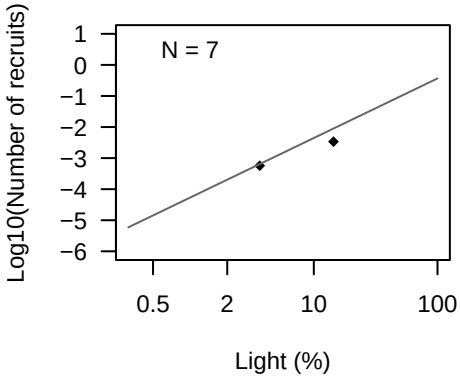
Zanthoxylum ekmanii



Zanthoxylum panamense



Zanthoxylum acuminatum



Zuelania guidonia

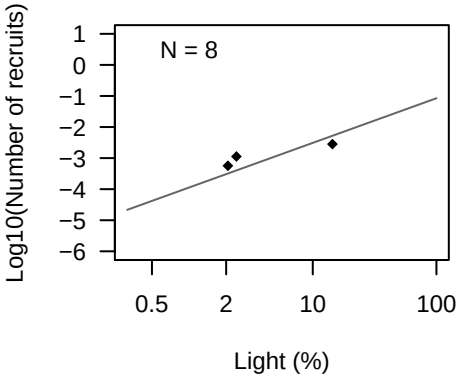


Table S1: Posterior means, lower and upper limits of the credible interval (CI -, CI +) of the log of the mean number of recruits (a), the light effect (b), the clustering parameter of the binomial distribution (c), and the light level at which recruitment falls to 50% of recruitment at 20% light (Light50) for two census intervals (1985-1990, 1990-1995) and tree species in the 50-ha Forest Dynamics Plot at Barro Colorado Island, Panama. Dashes indicate no recruitment in the respective census interval.

Species	Parameters											
	a						*b*					
	1985-1990			1990-1995			1985-1990			1990-1995		
	mean	CI -	CI +	mean	CI -	CI +	mean	CI -	CI +	mean	CI -	CI +
Acacia melanoceras	-3.69	-4.12	-3.3	-4.18	-4.91	-3.58	-0.34	-1.37	0.79	0.47	-0.74	1.74
Acalypha diversifolia	-2.08	-2.16	-2	-2.23	-2.32	-2.13	1.17	0.88	1.43	1.1	0.76	1.44
Acalypha macrostachya	-3.38	-3.67	-3.08	-3.28	-3.66	-2.95	1.23	0.46	2.06	1.45	0.39	2.42
Adelia triloba	-3.03	-3.28	-2.79	-3.69	-4.13	-3.26	1.87	1.17	2.66	1.16	0.19	2.24
Aegiphila panamensis	-3.74	-4.22	-3.35	-3.75	-4.18	-3.33	1.05	-0.01	2.01	1.52	0.56	2.5
Alchornea costaricensis	-3.2	-3.46	-2.97	-3.65	-4.1	-3.23	1.85	1.29	2.42	2.24	1.23	3.23
Alchornea latifolia	-4.17	-4.86	-3.54	-	-	-	0.32	-0.88	1.53	-	-	-
Alibertia edulis	-2.49	-2.62	-2.37	-2.76	-2.93	-2.61	0.41	-0.02	0.82	0.85	0.35	1.37
Allophylus psilospermus	-3.09	-3.32	-2.87	-3.5	-3.86	-3.17	0.65	-0.04	1.35	0.83	-0.08	1.76
Alseis blackiana	-1.24	-1.27	-1.21	-1.54	-1.58	-1.49	0.87	0.76	0.99	1.11	0.97	1.27
Anaxagorea panamensis	-2.61	-2.82	-2.38	-2.3	-2.5	-2.11	3.11	2.22	3.97	1.84	1.06	2.71
Andira inermis	-2.95	-3.15	-2.76	-3.69	-4.13	-3.25	0.4	-0.25	1.06	-0.02	-1.16	1.01
Annona acuminata	-2.44	-2.57	-2.33	-2.54	-2.67	-2.42	1.64	1.32	1.97	1.1	0.7	1.49
Annona spraguei	-2.59	-2.73	-2.45	-2.6	-2.75	-2.47	1.91	1.45	2.38	1.82	1.42	2.25
Apeiba membranacea	-3.55	-3.93	-3.19	-3.83	-4.32	-3.38	1.82	1.01	2.61	1.27	0.22	2.28
Apeiba tibourbou	-3.91	-4.46	-3.41	-3.97	-4.55	-3.45	1.35	0.27	2.52	1.07	0	2.18
Aphelandra sinclairiana	-3.99	-4.52	-3.4	-3.98	-4.53	-3.41	0.86	-0.29	1.97	1.2	0.01	2.3
Appunia seibertii	-3.98	-4.52	-3.44	-	-	-	0.76	-0.42	1.97	-	-	-
Ardisia bartlettii	-	-	-	-4.17	-4.94	-3.57	-	-	-	0.79	-0.49	1.9
Ardisia fendleri	-3.51	-3.84	-3.16	-3.37	-3.69	-3.06	-0.19	-1.08	0.77	-0.72	-1.58	0.14
Ardisia guianensis	-4.13	-4.66	-3.61	-3.73	-4.18	-3.33	2.68	1.85	3.63	1.37	0.28	2.27
Aspidosperma spruceanum	-2.66	-2.79	-2.53	-2.85	-3.02	-2.67	0.36	-0.1	0.87	0.34	-0.24	0.93
Astrocaryum standleyanum	-3.37	-3.69	-3.09	-	-	-	0.24	-0.68	1.17	-	-	-
Astronium graveolens	-3.5	-3.91	-3.13	-3.3	-3.6	-3.05	1.42	0.53	2.57	1.18	0.42	1.96
Attalea butyracea	-4.2	-4.89	-3.57	-	-	-	0.36	-0.83	1.69	-	-	-
Bactris barronis	-3.95	-4.5	-3.42	-	-	-	0	-1.33	1.07	-	-	-
Bactris coloradonis	-4.21	-4.89	-3.52	-	-	-	0.46	-0.81	1.69	-	-	-
Bactris major	-2.88	-3.09	-2.69	-3.33	-3.63	-3.03	1.24	0.6	1.86	-0.06	-0.94	0.78
Banara guianensis	-3.86	-4.34	-3.37	-4.18	-4.85	-3.52	1.04	0.04	2.25	0.7	-0.6	1.84
Beilschmiedia pendula	-1.67	-1.72	-1.61	-1.96	-2.03	-1.9	0.07	-0.1	0.27	-0.07	-0.31	0.15
Brosimum alicastrum	-2.54	-2.66	-2.43	-2.85	-3.05	-2.68	0.11	-0.3	0.56	-0.3	-0.87	0.29
Calophyllum longifolium	-1.96	-2.04	-1.89	-2	-2.07	-1.92	0.29	0.01	0.59	0.37	0.13	0.65
Capparis frondosa	-1.92	-1.98	-1.86	-2.31	-2.41	-2.22	0.24	0.02	0.45	-0.01	-0.34	0.35
Casearia aculeata	-2.36	-2.46	-2.27	-2.62	-2.75	-2.48	0.76	0.43	1.07	0.89	0.41	1.29
Casearia arborea	-3.34	-3.66	-3.07	-3.36	-3.66	-3.06	1.48	0.76	2.19	1.28	0.47	2.11
Casearia guianensis	-3.95	-4.55	-3.43	-3.95	-4.47	-3.44	0.03	-1.14	1.16	0.71	-0.4	1.97
Casearia sylvestris	-3.01	-3.23	-2.81	-3.18	-3.42	-2.93	1.05	0.42	1.7	0.3	-0.47	1.07
Cassipourea elliptica	-2.14	-2.22	-2.06	-2.34	-2.44	-2.25	0.57	0.28	0.85	0.5	0.16	0.87
Cavanillesia platanifolia	-4.2	-4.91	-3.57	-4.17	-4.9	-3.58	0.56	-0.79	1.71	0.72	-0.56	1.86
Cecropia insignis	-2.85	-3.04	-2.66	-2.49	-2.64	-2.36	2.94	2.4	3.46	2.16	1.65	2.69
Cecropia longipes	-	-	-	-4.21	-4.97	-3.64	-	-	-	1.31	0.11	2.52
Cecropia obtusifolia	-3.13	-3.36	-2.87	-3.03	-3.25	-2.82	2.11	1.48	2.87	1.79	1.26	2.35
Cedrela odorata	-3.44	-3.79	-3.13	-	-	-	0.46	-0.45	1.32	-	-	-
Ceiba pentandra	-3.53	-3.91	-3.2	-4.01	-4.6	-3.49	0.59	-0.42	1.56	1.42	0.21	2.5
Celtis schippii	-3.69	-4.07	-3.24	-4.18	-4.93	-3.54	0.07	-1.04	1.08	0.78	-0.43	1.97
Cespedesia spathulata	-4.18	-4.9	-3.6	-	-	-	0.14	-1.11	1.45	-	-	-
Cestrum megalophyllum	-2.74	-2.9	-2.59	-3.36	-3.7	-3.06	0.77	0.27	1.28	0.76	-0.05	1.61
Chamaedorea tepejilote	-3.69	-4.11	-3.26	-3.8	-4.29	-3.32	0.45	-0.5	1.53	0.86	-0.07	1.98
Chamguava schippii	-2.63	-2.77	-2.48	-2.59	-2.74	-2.45	1.77	1.32	2.2	1.51	1.04	2
Chrysochlamys eclipes	-3.07	-3.28	-2.87	-3.11	-3.34	-2.89	-0.12	-0.84	0.59	0.72	0	1.44
Chrysophyllum argenteum	-1.99	-2.06	-1.92	-2.37	-2.48	-2.28	0.84	0.6	1.07	1.03	0.67	1.35
Chrysophyllum cainito	-2.83	-3	-2.66	-2.85	-3.02	-2.68	1.23	0.71	1.71	1.3	0.74	1.81

Species	Parameters											
	a						*b*					
	1985-1990			1990-1995			1985-1990			1990-1995		
	mean	CI -	CI +	mean	CI -	CI +	mean	CI -	CI +	mean	CI -	CI +
Cinnamomum triplinerve	-2.98	-3.19	-2.78	-3.2	-3.44	-2.94	1.23	0.68	1.81	0.99	0.23	1.7
Clidemia dentata	-3.17	-3.44	-2.92	-3.63	-4.01	-3.25	1.3	0.62	1.96	1.35	0.47	2.28
Clidemia octona	-3.49	-3.82	-3.15	-3.52	-3.85	-3.17	1.34	0.51	2.2	1.12	0.16	2.08
Coccoloba coronata	-2.89	-3.07	-2.73	-3.26	-3.52	-2.98	0.47	-0.09	1.09	0.51	-0.3	1.35
Coccoloba manzinellensis	-2.62	-2.75	-2.48	-2.8	-2.96	-2.63	0.85	0.36	1.25	1.02	0.44	1.56
Colubrina glandulosa	-	-	-	-4.18	-4.86	-3.53	-	-	-	1.15	0.05	2.35
Conostegia bracteata	-4.22	-4.94	-3.59	-4.18	-4.94	-3.57	0.74	-0.48	2.02	0.64	-0.51	1.92
Conostegia cinnamomea	-2.44	-2.55	-2.34	-2.63	-2.77	-2.49	0.41	0.02	0.86	0.79	0.29	1.21
Cordia alliodora	-3	-3.23	-2.8	-3.23	-3.48	-2.96	1.52	0.94	2.12	0.84	0.06	1.63
Cordia bicolor	-1.9	-1.97	-1.83	-2.13	-2.21	-2.05	1.83	1.56	2.08	1.67	1.36	1.95
Cordia lasiocalyx	-1.95	-2.02	-1.89	-2.09	-2.18	-2.02	0.59	0.34	0.81	0.52	0.25	0.79
Coussarea curvigemmia	-1.72	-1.76	-1.66	-1.9	-1.96	-1.85	0.68	0.5	0.86	0.44	0.24	0.67
Croton billbergianus	-1.81	-1.87	-1.73	-2.28	-2.4	-2.19	2.34	2.07	2.59	2.05	1.63	2.4
Cupania cinerea	-3.65	-4.06	-3.25	-	-	-	1.02	0.06	2.08	-	-	-
Cupania latifolia	-3.32	-3.6	-3.05	-3.66	-4.09	-3.23	0.39	-0.48	1.29	0.33	-0.63	1.42
Cupania rufescens	-2.9	-3.09	-2.7	-2.94	-3.15	-2.74	1.64	1.01	2.2	1.34	0.76	1.9
Cupania seemannii	-2.09	-2.16	-2.01	-2.23	-2.32	-2.15	0.72	0.49	0.96	0.79	0.47	1.09
Dendropanax arboreus	-4.2	-4.89	-3.53	-	-	-	0.64	-0.75	1.84	-	-	-
Desmopsis panamensis	-1.01	-1.03	-0.99	-1.23	-1.26	-1.2	0.16	0.08	0.24	0.14	0.04	0.24
Diospyros artanthifolia	-3.21	-3.49	-2.99	-3.31	-3.59	-3.03	1.34	0.64	2	0.39	-0.43	1.22
Dipteryx oleifera	-3.97	-4.61	-3.49	-4.19	-4.86	-3.58	0.47	-0.68	1.7	0.95	-0.21	2.13
Drypetes standleyi	-2.07	-2.14	-2.01	-2.35	-2.46	-2.25	-0.04	-0.29	0.23	-0.44	-0.79	-0.1
Elaeis oleifera	-3.84	-4.3	-3.33	-	-	-	0.89	-0.22	2.01	-	-	-
Erythrina costaricensis	-4.19	-4.9	-3.54	-4.16	-4.85	-3.54	0.29	-0.98	1.63	0.74	-0.51	1.89
Erythroxylum macrophyllum	-2.52	-2.63	-2.4	-2.75	-2.9	-2.59	0.72	0.31	1.1	0.34	-0.19	0.88
Erythroxylum panamense	-3.08	-3.31	-2.87	-3.3	-3.6	-3.03	0.58	-0.14	1.25	0.56	-0.24	1.39
Eugenia coloradoensis	-2.26	-2.35	-2.17	-2.51	-2.63	-2.4	0.72	0.43	1.01	0.37	-0.02	0.78
Eugenia galalonensis	-1.81	-1.86	-1.76	-1.87	-1.94	-1.82	0.37	0.18	0.56	0.73	0.54	0.96
Eugenia nesiotica	-2.53	-2.65	-2.42	-2.67	-2.81	-2.53	0.42	-0.01	0.83	0.66	0.15	1.18
Eugenia oerstediana	-1.63	-1.68	-1.59	-1.91	-1.97	-1.84	0.37	0.19	0.53	0.48	0.24	0.72
Faramea occidentalis	-0.76	-0.78	-0.75	-0.99	-1.01	-0.97	0.26	0.19	0.32	0.22	0.14	0.3
Ficus bullenei	-	-	-	-4.19	-4.89	-3.55	-	-	-	1.09	-0.07	2.26
Ficus citrifolia	-4.02	-4.66	-3.51	-	-	-	1.12	-0.05	2.2	-	-	-
Ficus costaricana	-	-	-	-4.2	-4.93	-3.55	-	-	-	0.99	-0.12	2.27
Ficus insipida	-3.99	-4.55	-3.44	-3.85	-4.34	-3.43	0.7	-0.38	1.86	1.42	0.34	2.41
Ficus maxima	-4.01	-4.61	-3.48	-	-	-	1.08	-0.1	2.17	-	-	-
Ficus obtusifolia	-4.2	-4.89	-3.55	-3.95	-4.5	-3.41	0.41	-0.86	1.7	0.56	-0.53	1.81
Ficus pertusa	-4.21	-4.89	-3.58	-4.18	-4.84	-3.55	0.76	-0.47	2.04	0.95	-0.23	2.17
Ficus popenoei	-4.26	-4.94	-3.62	-	-	-	1.2	-0.01	2.44	-	-	-
Ficus trigonata	-	-	-	-4.18	-4.9	-3.6	-	-	-	0.91	-0.35	2.05
Garcinia intermedia	-1.58	-1.62	-1.54	-1.81	-1.87	-1.76	0.16	0	0.31	0.16	-0.04	0.36
Garcinia madruno	-2.49	-2.6	-2.38	-2.87	-3.07	-2.71	-0.1	-0.52	0.28	-0.04	-0.61	0.56
Genipa americana	-3.97	-4.52	-3.4	-	-	-	0.05	-1.07	1.3	-	-	-
Guapira standleyana	-3.58	-3.97	-3.24	-4.17	-4.88	-3.54	0.35	-0.67	1.39	0.38	-0.81	1.56
Guarea fuzzy	-2.1	-2.17	-2.03	-2.37	-2.48	-2.28	0.47	0.19	0.72	0.54	0.18	0.89
Guarea grandifolia	-3.51	-3.86	-3.2	-3.44	-3.76	-3.13	-0.05	-1.09	0.81	1.03	0.14	1.83
Guarea guidonia	-1.89	-1.95	-1.83	-2.07	-2.14	-2	0.49	0.26	0.69	0.5	0.24	0.75
Guatteria dumetorum	-2.17	-2.25	-2.09	-2.47	-2.59	-2.36	0.59	0.31	0.85	0.81	0.43	1.2
Guazuma ulmifolia	-3.75	-4.17	-3.36	-3.88	-4.43	-3.4	2.14	1.36	2.93	1.61	0.53	2.61
Guettarda foliacea	-2.96	-3.17	-2.78	-3.78	-4.27	-3.37	0.55	-0.13	1.17	0.34	-0.81	1.45
Gustavia superba	-2.79	-2.96	-2.62	-3.22	-3.48	-2.93	1.37	0.88	1.81	1.92	1.33	2.62
Hamelia axillaris	-2.71	-2.86	-2.55	-2.73	-2.89	-2.57	1.69	1.28	2.07	1.64	1.18	2.15
Hampea appendiculata	-3.35	-3.65	-3.05	-3.53	-3.88	-3.17	1.52	0.82	2.28	1.23	0.38	2.14
Hasseltia floribunda	-2.84	-3.01	-2.66	-3.21	-3.49	-2.98	0.76	0.19	1.44	1.46	0.74	2.17
Heisteria acuminata	-3.74	-4.17	-3.3	-3.67	-4.08	-3.27	1.01	-0.06	1.95	0.27	-0.76	1.31
Heisteria concinna	-2.36	-2.45	-2.27	-2.93	-3.11	-2.73	0.05	-0.32	0.39	0.58	-0.06	1.2

Species	Parameters											
	a						*b*					
	1985-1990			1990-1995			1985-1990			1990-1995		
	mean	CI -	CI +	mean	CI -	CI +	mean	CI -	CI +	mean	CI -	CI +
Herrania purpurea	-2.48	-2.58	-2.36	-2.79	-2.97	-2.64	0.48	0.08	0.87	1.19	0.68	1.72
Hieronyma alchorneoides	-3.35	-3.65	-3.05	-3.97	-4.53	-3.47	0.79	-0.1	1.56	1.11	0.04	2.26
Hirtella americana	-3.72	-4.18	-3.34	-4.17	-4.86	-3.57	0.86	-0.24	1.88	0.77	-0.42	2.04
Hirtella triandra	-1.5	-1.54	-1.47	-1.77	-1.82	-1.72	0.13	-0.02	0.27	0.24	0.05	0.43
Hybanthus prunifolius	-0.55	-0.56	-0.53	-0.88	-0.9	-0.86	0.13	0.07	0.19	0.19	0.12	0.27
Inga acuminata	-2.42	-2.53	-2.33	-2.52	-2.64	-2.4	0.64	0.27	0.99	0.25	-0.16	0.66
Inga cocleensis	-3.34	-3.67	-3.07	-3.51	-3.89	-3.18	1.73	1.08	2.4	1.05	0.13	1.96
Inga goldmanii	-2.47	-2.57	-2.36	-3.16	-3.4	-2.91	0.61	0.23	0.98	1.02	0.3	1.74
Inga laurina	-3.01	-3.22	-2.81	-3.31	-3.58	-3.01	1.07	0.47	1.72	0.68	-0.2	1.49
Inga marginata	-1.97	-2.04	-1.9	-2.33	-2.42	-2.22	0.88	0.64	1.13	1.22	0.91	1.55
Inga nobilis	-2.41	-2.51	-2.3	-2.86	-3.03	-2.68	0.27	-0.09	0.65	0.24	-0.31	0.83
Inga oerstediana	-4.02	-4.6	-3.51	-4.17	-4.88	-3.51	1.12	-0.01	2.27	0.54	-0.7	1.75
Inga pezizifera	-2.85	-3.02	-2.69	-3.36	-3.67	-3.07	-0.18	-0.78	0.4	0.68	-0.21	1.52
Inga punctata	-3.5	-3.86	-3.17	-3.95	-4.52	-3.43	1.39	0.51	2.24	1.11	-0.08	2.15
Inga ruiziana	-4.22	-4.96	-3.6	-	-	-	0.88	-0.26	2.22	-	-	-
Inga sapindoides	-2.82	-2.99	-2.64	-3.32	-3.6	-3.02	1.14	0.64	1.68	1.61	0.9	2.34
Inga spectabilis	-3.99	-4.54	-3.48	-	-	-	0.84	-0.38	2.01	-	-	-
Inga thibaudiana	-3.02	-3.24	-2.81	-2.89	-3.08	-2.71	1.65	1.03	2.12	1.67	1.05	2.32
Inga umbellifera	-2.18	-2.26	-2.1	-2.62	-2.74	-2.47	0.88	0.59	1.18	0.96	0.53	1.39
Jacaranda copaia	-3.48	-3.8	-3.14	-3.34	-3.61	-3.03	1.87	1.12	2.6	1.7	0.96	2.44
Koanophyllon wetmorei	-3.74	-4.17	-3.31	-4.19	-4.92	-3.56	1.04	-0.1	2.03	1.13	-0.16	2.28
Lacistema aggregatum	-1.81	-1.86	-1.76	-1.96	-2.02	-1.9	0.13	-0.05	0.33	0.47	0.25	0.7
Lacmellea panamensis	-3.46	-3.81	-3.16	-3.67	-4.09	-3.26	0.55	-0.46	1.46	0.4	-0.77	1.39
Laetia procera	-3.6	-4.01	-3.23	-3.84	-4.35	-3.39	2	1.11	3.05	1.24	0.22	2.35
Laetia thamnia	-2.34	-2.44	-2.25	-2.49	-2.61	-2.37	0.96	0.66	1.27	0.8	0.4	1.19
Leandra dichotoma	-4.26	-5.03	-3.64	-	-	-	1.17	-0.16	2.32	-	-	-
Licania hypoleuca	-3.07	-3.28	-2.84	-3.3	-3.6	-3	0.03	-0.7	0.67	0.39	-0.47	1.16
Licania platypus	-2.59	-2.71	-2.45	-2.97	-3.18	-2.79	-0.39	-0.83	0.03	-0.67	-1.29	-0.06
Lindackeria laurina	-3.73	-4.21	-3.32	-3.96	-4.54	-3.44	0.92	-0.12	1.93	0.88	-0.23	2
Lonchocarpus heptaphyllus	-2.16	-2.24	-2.08	-2.43	-2.55	-2.32	0.93	0.67	1.2	1.35	0.95	1.71
Luehea seemannii	-2.77	-2.94	-2.61	-3	-3.22	-2.79	1.94	1.54	2.34	2.06	1.53	2.52
Macrocnemum roseum	-3.27	-3.6	-2.96	-4.18	-4.86	-3.59	-0.25	-1.2	0.6	0.94	-0.25	2.12
Malpighia romeroana	-3.44	-3.79	-3.16	-3.94	-4.52	-3.43	0.54	-0.41	1.45	0.69	-0.46	1.84
Maquira guianensis	-2.06	-2.12	-1.99	-2.37	-2.47	-2.26	-0.07	-0.32	0.19	-0.12	-0.5	0.22
Margaritaria nobilis	-4.14	-4.74	-3.58	-	-	-	1.71	0.55	2.8	-	-	-
Maytenus schippii	-3.38	-3.69	-3.09	-3.66	-4.08	-3.27	0.29	-0.61	1.2	0.36	-0.64	1.44
Miconia affinis	-2.34	-2.46	-2.22	-2.51	-2.63	-2.38	1.62	1.22	2.03	1.45	1	1.88
Miconia argentea	-1.78	-1.85	-1.72	-1.87	-1.94	-1.79	1.76	1.55	1.99	1.97	1.7	2.27
Miconia elata	-3.51	-4.01	-3.07	-	-	-	0.93	-0.19	1.97	-	-	-
Miconia hondurensis	-3.18	-3.45	-2.94	-3.31	-3.59	-3.03	0.73	0.03	1.48	0.44	-0.41	1.25
Miconia impetiolaris	-3.67	-4.1	-3.29	-4.18	-4.85	-3.56	0.2	-0.86	1.27	0.76	-0.42	1.98
Miconia nervosa	-2.1	-2.19	-2.01	-2.27	-2.36	-2.17	1.53	1.24	1.82	1.39	1.05	1.7
Miconia prasina	-4	-4.61	-3.46	-	-	-	0.88	-0.27	2.04	-	-	-
Mosannona garwoodii	-2.55	-2.66	-2.43	-2.59	-2.73	-2.47	0.3	-0.14	0.71	0.03	-0.42	0.48
Mouriri myrtilloides	-1.2	-1.22	-1.17	-1.38	-1.42	-1.35	0.57	0.48	0.68	0.61	0.48	0.74
Myrcia gatunensis	-3.37	-3.66	-3.08	-3.58	-4	-3.23	0.26	-0.66	1.08	0.49	-0.5	1.46
Nectandra cissiflora	-2.82	-2.98	-2.66	-3.08	-3.3	-2.85	1.06	0.55	1.57	1.12	0.47	1.77
Nectandra lineata	-2.64	-2.77	-2.52	-2.9	-3.08	-2.72	0.47	-0.01	0.94	0.9	0.32	1.45
Nectandra purpurea	-3.13	-3.36	-2.88	-3.38	-3.71	-3.11	0.79	0.09	1.48	1.02	0.17	1.84
Neea amplifolia	-3.05	-3.28	-2.85	-3.26	-3.53	-3.01	0.59	-0.04	1.32	1.24	0.49	1.92
Ochroma pyramidale	-4.25	-4.92	-3.56	-4.18	-4.9	-3.58	1.1	-0.14	2.37	0.87	-0.39	2
Ocotea cernua	-2.35	-2.45	-2.25	-2.7	-2.84	-2.55	0.61	0.25	0.94	0.87	0.39	1.37
Ocotea oblonga	-2.46	-2.56	-2.35	-2.65	-2.79	-2.52	0.73	0.37	1.12	0.86	0.41	1.31
Ocotea puberula	-2.63	-2.77	-2.5	-2.91	-3.09	-2.72	0.9	0.48	1.35	0.76	0.17	1.39
Ocotea whitei	-2.56	-2.68	-2.43	-3.25	-3.53	-2.98	0	-0.45	0.43	-0.43	-1.26	0.31
Oenocarpus mapora	-2.09	-2.16	-2.02	-2.25	-2.34	-2.16	0.45	0.19	0.71	0.15	-0.18	0.45

Species	Parameters											
	a						*b*					
	1985-1990			1990-1995			1985-1990			1990-1995		
	mean	CI -	CI +	mean	CI -	CI +	mean	CI -	CI +	mean	CI -	CI +
Ormosia coccinea	-3.16	-3.41	-2.93	-3.29	-3.57	-3.03	0.13	-0.63	0.89	-0.13	-0.96	0.67
Ormosia macrocalyx	-2.98	-3.17	-2.79	-3.32	-3.62	-3.05	0.47	-0.18	1.11	0.76	-0.08	1.6
Ouratea lucens	-2.19	-2.27	-2.11	-2.44	-2.55	-2.34	0.67	0.38	0.94	0.76	0.39	1.16
Pachira quinata	-4.22	-4.99	-3.6	-	-	-	0.77	-0.39	2.02	-	-	-
Pachira sessilis	-	-	-	-4.19	-4.91	-3.56	-	-	-	0.95	-0.24	2.18
Palicourea guianensis	-1.45	-1.49	-1.4	-1.63	-1.69	-1.57	1.95	1.76	2.12	2.25	2.02	2.5
Pentagonia macrophylla	-2.67	-2.8	-2.53	-3.3	-3.59	-3.02	0.65	0.16	1.11	0.39	-0.4	1.26
Perebea xanthochyma	-2.69	-2.83	-2.56	-3.26	-3.53	-3.02	0.51	0.01	0.98	0.48	-0.4	1.29
Picramnia latifolia	-2.08	-2.14	-2	-2.27	-2.35	-2.17	0.25	-0.02	0.5	0.26	-0.08	0.59
Piper aequale	-3.32	-3.63	-3.05	-3.67	-4.12	-3.29	0.17	-0.71	0.95	0.87	-0.17	1.86
Piper arboreum	-3.81	-4.31	-3.39	-3.86	-4.42	-3.36	0.68	-0.45	1.88	1.45	0.3	2.49
Piper colonense	-3.59	-4	-3.23	-4.15	-4.82	-3.54	0.43	-0.69	1.39	0.56	-0.75	1.79
Piper cordulatum	-1.94	-2	-1.87	-2.82	-2.98	-2.65	0.63	0.38	0.89	1.02	0.43	1.51
Piper perlasense	-3.31	-3.59	-3.02	-3.94	-4.47	-3.41	-0.58	-1.39	0.21	0.6	-0.48	1.77
Piper reticulatum	-3.36	-3.66	-3.06	-3.94	-4.52	-3.44	0.8	-0.11	1.6	0.49	-0.74	1.64
Platymiscium pinnatum	-2.9	-3.08	-2.71	-2.79	-2.97	-2.63	1.18	0.59	1.7	1.7	1.26	2.18
Platypodium elegans	-2.92	-3.11	-2.75	-3.12	-3.34	-2.89	1.07	0.55	1.66	0.93	0.18	1.62
Posoqueria latifolia	-4.23	-4.95	-3.59	-3.5	-3.85	-3.16	0.88	-0.38	2.05	0.12	-0.89	1.01
Poulsenia armata	-2.76	-2.91	-2.6	-3.33	-3.65	-3.05	0.33	-0.21	0.83	-0.12	-0.99	0.76
Pourouma bicolor	-3.81	-4.3	-3.39	-3.44	-3.78	-3.11	0.65	-0.36	1.78	0.94	0.05	1.8
Pouteria reticulata	-1.83	-1.89	-1.78	-2.09	-2.16	-2.02	0.78	0.58	0.98	0.91	0.64	1.15
Pouteria stipitata	-3.71	-4.15	-3.3	-3.51	-3.88	-3.14	0.8	-0.27	1.87	1.48	0.56	2.37
Prioria copaifera	-2.45	-2.56	-2.34	-2.83	-2.99	-2.65	0.34	-0.05	0.73	0.14	-0.45	0.68
Protium confusum	-3.97	-4.54	-3.45	-	-	-	-0.15	-1.44	1.07	-	-	-
Protium costaricense	-2.21	-2.29	-2.13	-2.61	-2.76	-2.49	0.8	0.53	1.08	1.18	0.79	1.62
Protium panamense	-1.64	-1.69	-1.6	-1.86	-1.92	-1.81	0.82	0.64	0.98	0.52	0.3	0.74
Protium tenuifolium	-1.63	-1.67	-1.58	-1.96	-2.03	-1.9	0.16	-0.01	0.32	0.45	0.21	0.69
Pseudobombax septenatum	-3.66	-4.07	-3.27	-4.18	-4.88	-3.58	1.79	0.93	2.71	0.66	-0.62	1.82
Psidium friedrichsthalianum	-3.52	-3.86	-3.15	-3.49	-3.85	-3.16	0.48	-0.6	1.36	0.44	-0.55	1.33
Psychotria acuminata	-3.26	-3.57	-3.01	-3.49	-3.86	-3.15	1.43	0.75	2.16	0.66	-0.3	1.53
Psychotria chagrensis	-	-	-	-3.93	-4.49	-3.4	-	-	-	0.39	-0.84	1.47
Psychotria deflexa	-2.85	-3.04	-2.68	-3.33	-3.62	-3.05	0.91	0.36	1.51	1.09	0.28	1.91
Psychotria graciliflora	-2.79	-2.99	-2.6	-2.79	-3.05	-2.55	1.24	0.57	1.98	0.57	-0.31	1.42
Psychotria grandis	-2.91	-3.1	-2.74	-3.41	-3.73	-3.1	0.54	-0.04	1.17	0.52	-0.41	1.37
Psychotria hoffmannseggiana	-3.98	-4.59	-3.48	-	-	-	0.71	-0.47	1.85	-	-	-
Psychotria horizontalis	-1.2	-1.23	-1.17	-1.48	-1.52	-1.44	0.03	-0.07	0.15	0.2	0.05	0.34
Psychotria limonensis	-3.23	-3.55	-2.95	-3.26	-3.54	-2.99	1.15	0.27	2.06	0.59	-0.29	1.37
Psychotria marginata	-1.93	-1.99	-1.86	-2.04	-2.12	-1.97	0.7	0.49	0.95	0.87	0.57	1.17
Psychotria pittieri	-4.23	-4.91	-3.61	-	-	-	0.98	-0.19	2.29	-	-	-
Psychotria racemosa	-3.96	-4.55	-3.44	-	-	-	0.41	-0.71	1.65	-	-	-
Pterocarpus rohrii	-1.8	-1.86	-1.75	-2.05	-2.13	-1.99	0.72	0.53	0.91	0.93	0.7	1.18
Quararibea asterolepis	-2.1	-2.18	-2.03	-2.3	-2.4	-2.21	0.1	-0.18	0.39	-0.02	-0.36	0.3
Quassia amara	-3.67	-4.04	-3.27	-3.96	-4.52	-3.42	0.4	-0.55	1.53	1.07	-0.06	2.19
Randia armata	-2.31	-2.4	-2.22	-2.55	-2.67	-2.42	0.56	0.22	0.87	0.56	0.06	0.95
Rauvolfia littoralis	-	-	-	-4.19	-4.88	-3.57	-	-	-	0.86	-0.3	2.13
Rinorea sylvatica	-1.86	-1.92	-1.8	-2.11	-2.2	-2.04	0.43	0.22	0.67	0.29	-0.03	0.6
Sapium glandulosum	-3.5	-3.83	-3.17	-3.85	-4.32	-3.37	1.93	1.22	2.65	1.96	1	2.9
Schizolobium parahyba	-3.85	-4.38	-3.39	-4.17	-4.89	-3.53	0.93	-0.22	1.95	0.7	-0.73	1.82
Senna dariensis	-2.76	-2.93	-2.61	-3.38	-3.71	-3.08	1.39	0.96	1.86	2.33	1.65	2.98
Simarouba amara	-1.76	-1.81	-1.71	-1.89	-1.96	-1.83	0.7	0.52	0.89	0.93	0.66	1.15
Siparuna guianensis	-4.19	-4.9	-3.57	-	-	-	0.4	-0.83	1.67	-	-	-
Siparuna pauciflora	-2.64	-2.77	-2.5	-2.97	-3.16	-2.77	0.38	-0.07	0.8	0.35	-0.33	0.95
Sloanea terniflora	-3.05	-3.26	-2.83	-3.67	-4.07	-3.23	0.78	0.09	1.47	0.73	-0.3	1.71
Socratea exorrhiza	-2.32	-2.41	-2.23	-2.44	-2.56	-2.33	-0.13	-0.47	0.22	-0.2	-0.57	0.21
Solanum asperum	-3.82	-4.33	-3.39	-3.84	-4.34	-3.4	1.49	0.51	2.55	1.95	0.98	2.85
Solanum circinatum	-3.97	-4.59	-3.47	-4.18	-4.84	-3.52	0.5	-0.74	1.64	0.94	-0.26	2.11

Species	Parameters											
	a						*b*					
	1985-1990			1990-1995			1985-1990			1990-1995		
	mean	CI -	CI +	mean	CI -	CI +	mean	CI -	CI +	mean	CI -	CI +
Solanum hayesii	-2.91	-3.12	-2.73	-3.15	-3.39	-2.9	1.79	1.21	2.36	1.74	1.15	2.42
Solanum steyermarkii	-	-	-	-4.19	-4.88	-3.56	-	-	-	1.03	-0.27	2.18
Sorocea affinis	-1.87	-1.92	-1.82	-2.17	-2.25	-2.09	0.18	-0.02	0.4	0.42	0.13	0.72
Spondias mombin	-3.48	-3.75	-3.23	-3.47	-3.81	-3.16	3.28	2.9	3.68	3.07	2.44	3.68
Spondias radlkoferi	-2.63	-2.79	-2.48	-2.74	-2.91	-2.57	1.7	1.26	2.19	1.98	1.6	2.4
Sterculia apetala	-3.37	-3.67	-3.06	-3.59	-3.97	-3.25	0.95	0.15	1.82	0.93	-0.01	1.92
Stylogyne turbacensis	-2.19	-2.27	-2.11	-2.24	-2.32	-2.16	0.98	0.73	1.26	0.63	0.31	0.95
Swartzia simplex_var.grandiflora	-1.62	-1.66	-1.58	-1.86	-1.92	-1.81	0.28	0.12	0.43	0.06	-0.15	0.27
Symphonia globulifera	-2.97	-3.17	-2.78	-3.06	-3.29	-2.85	-0.04	-0.67	0.57	0.06	-0.63	0.82
Tabebuia guayacan	-3.64	-4.01	-3.25	-3.83	-4.26	-3.32	0.95	-0.08	1.95	1.28	0.16	2.31
Tabebuia rosea	-2.6	-2.73	-2.46	-3.12	-3.33	-2.88	0.73	0.31	1.21	0.85	0.2	1.63
Tabernaemontana arborea	-2	-2.07	-1.94	-2.02	-2.09	-1.94	1.04	0.82	1.26	1.09	0.84	1.34
Tachigali versicolor	-1.51	-1.54	-1.46	-1.72	-1.77	-1.67	0.09	-0.05	0.23	0.54	0.34	0.74
Talisia nervosa	-2.91	-3.1	-2.73	-3.36	-3.65	-3.07	0.47	-0.18	1.1	0.33	-0.49	1.3
Talisia princeps	-2.3	-2.39	-2.22	-2.5	-2.61	-2.38	0.02	-0.3	0.37	0.55	0.16	0.96
Terminalia amazonia	-4.28	-5.01	-3.63	-4.16	-4.89	-3.56	1.32	0.15	2.58	0.43	-0.69	1.76
Terminalia oblonga	-3.52	-3.86	-3.18	-3.42	-3.76	-3.14	1.15	0.22	1.95	0.79	-0.17	1.61
Tetragastris panamensis	-1.44	-1.48	-1.41	-1.64	-1.69	-1.6	0.5	0.36	0.63	0.35	0.19	0.53
Thevetia ahouai	-3.22	-3.77	-2.69	-3.72	-4.18	-3.29	1.43	0.28	2.69	1.35	0.42	2.43
Trattinnickia aspera	-4.03	-4.6	-3.54	-3.84	-4.41	-3.4	1.18	-0.01	2.31	1.38	0.28	2.42
Trema micrantha	-3.66	-4.08	-3.28	-3.28	-3.58	-3.03	1.53	0.62	2.47	1.07	0.26	1.8
Trichanthera gigantea	-4.03	-4.62	-3.48	-3.62	-4.04	-3.25	1.11	-0.02	2.3	1.29	0.32	2.22
Trichilia pallida	-2.43	-2.53	-2.32	-2.63	-2.77	-2.5	0.8	0.44	1.11	0.89	0.42	1.32
Trichilia tuberculata	-1.01	-1.03	-0.98	-1.28	-1.32	-1.25	-0.12	-0.22	-0.03	-0.11	-0.24	0.01
Trichospermum galeottii	-4.23	-4.97	-3.62	-	-	-	1.05	-0.2	2.27	-	-	-
Triplaris cumingiana	-3.1	-3.32	-2.88	-3.3	-3.59	-3.02	0.38	-0.36	1.07	1.13	0.34	1.95
Trophis caucana	-3.32	-3.64	-3.07	-	-	-	0.09	-0.79	0.88	-	-	-
Trophis racemosa	-2.68	-2.83	-2.54	-2.92	-3.11	-2.73	0.18	-0.35	0.65	1.12	0.53	1.67
Turpinia occidentalis	-4.26	-5.02	-3.64	-3.57	-3.93	-3.22	1.22	0.04	2.51	0.73	-0.24	1.72
Unonopsis pittieri	-2.37	-2.47	-2.28	-2.75	-2.91	-2.61	0.08	-0.29	0.44	0.33	-0.23	0.89
Urera baccifera	-3.11	-3.4	-2.84	-3.49	-3.9	-3.13	0.35	-0.44	1.22	1.95	0.96	2.99
Virola multiflora	-3.97	-4.53	-3.41	-4.16	-4.8	-3.52	0.07	-1.1	1.28	0.69	-0.47	1.92
Virola sebifera	-2.58	-2.69	-2.45	-3.31	-3.59	-3.03	0.26	-0.21	0.7	0.67	-0.15	1.54
Virola surinamensis	-3.99	-4.49	-3.45	-	-	-	0.81	-0.27	1.94	-	-	-
Vismia baccifera	-3.05	-3.26	-2.83	-3.04	-3.3	-2.84	0.88	0.19	1.61	0.62	-0.13	1.34
Vismia macrophylla	-	-	-	-4.2	-4.92	-3.58	-	-	-	1.03	-0.09	2.4
Vochysia ferruginea	-3.73	-4.17	-3.36	-3.95	-4.52	-3.44	1.54	0.54	2.47	0.88	-0.24	1.99
Xylopia macrantha	-2.13	-2.21	-2.05	-2.27	-2.36	-2.17	-0.36	-0.66	-0.08	-0.39	-0.71	-0.07
Xylosma oligandra	-3.97	-4.53	-3.44	-4.17	-4.92	-3.55	0.66	-0.47	1.87	0.69	-0.45	1.93
Zanthoxylum acuminatum	-3.7	-4.08	-3.31	-3.53	-3.91	-3.2	1.92	1.11	2.81	1.12	0.19	2.05
Zanthoxylum ekmanii	-2.77	-2.94	-2.57	-2.77	-3	-2.54	2.2	1.68	2.76	1.7	0.88	2.5
Zanthoxylum panamense	-3.07	-3.3	-2.83	-3.54	-3.9	-3.16	2.34	1.71	2.96	2.41	1.7	3.2
Zuelania guidonia	-3.52	-3.89	-3.18	-3.27	-3.53	-2.99	1.44	0.54	2.27	0.81	0.01	1.6

Species	Parameters							
	c						*Light50*	
	1985-1990			1990-1995			1985-90	1990-95
	mean	CI -	CI +	mean	CI -	CI +	mean	mean
Acacia melanoceras	46	0.025	94	51	0.94	96	0	0.05
Acalypha diversifolia	0.054	0.032	0.083	0.03	0.015	0.047	0.11	0.11
Acalypha macrostachya	47	0.089	94	0.0019	1e-04	0.0052	0.11	0.12
Adelia triloba	0.0058	0.0016	0.011	50	4.3	99	0.14	0.11
Aegiphila panamensis	49	0.97	95	50	2.4	95	0.1	0.13
Alchornea costaricensis	49	3.3	98	0.009	4e-04	0.026	0.14	0.15
Alchornea latifolia	50	1.8	97	-	-	-	0.02	-
Alibertia edulis	0.063	0.0071	0.16	47	0.0088	95	0.04	0.09
Allophylus psilospermus	52	3.8	98	50	0.76	94	0.07	0.09
Alseis blackiana	0.18	0.15	0.21	0.17	0.12	0.22	0.09	0.11
Anaxagorea panamensis	0.0028	0.0018	0.0039	0.0018	0.0011	0.0026	0.16	0.14
Andira inermis	49	1.3	96	50	0.29	94	0.04	0
Annona acuminata	0.1	0.035	0.19	17	0.04	84	0.13	0.11
Annona spraguei	0.025	0.011	0.041	0.33	0.017	1.6	0.14	0.14
Apeiba membranacea	48	0.55	95	50	0.39	95	0.14	0.12
Apeiba tibourbou	50	5.1	100	50	5	100	0.12	0.1
Aphelandra sinclairiana	48	0.017	95	49	0.13	95	0.09	0.11
Appunia seibertii	48	0.14	94	-	-	-	0.08	-
Ardisia bartlettii	-	-	-	47	0.095	94	-	0.08
Ardisia fendleri	49	0.89	95	51	4.4	100	0	0
Ardisia guianensis	45	0.0044	94	48	1.7	96	0.15	0.12
Aspidosperma spruceanum	50	3.1	97	50	6	100	0.03	0.03
Astrocaryum standleyanum	49	0.058	95	-	-	-	0.01	-
Astronium graveolens	0.0079	1e-04	0.035	47	0.089	95	0.12	0.11
Attalea butyracea	48	4.8	99	-	-	-	0.03	-
Bactris barronis	49	0.17	94	-	-	-	0	-
Bactris coloradonis	50	0.12	94	-	-	-	0.04	-
Bactris major	0.0069	0.0014	0.015	48	0.021	95	0.11	0
Banara guianensis	49	0.93	96	51	5.5	100	0.1	0.07
Beilschmiedia pendula	0.065	0.046	0.084	0.12	0.05	0.21	0	0
Brosimum alicastrum	49	0.39	95	50	3.4	98	0	0
Calophyllum longifolium	0.021	0.014	0.028	0.051	0.028	0.08	0.02	0.03
Capparis frondosa	42	0.13	93	52	6.1	100	0.01	0
Casearia aculeata	49	1.9	96	47	0.13	95	0.08	0.09
Casearia arborea	48	0.098	94	50	5.2	99	0.13	0.12
Casearia guianensis	50	1.2	95	50	9e-04	94	0	0.08
Casearia sylvestris	50	0.27	94	50	1.2	95	0.1	0.02
Cassipourea elliptica	0.061	0.027	0.12	27	0.027	91	0.06	0.05
Cavanillesia platanifolia	50	2.5	97	50	5.4	100	0.06	0.08
Cecropia insignis	0.03	0.017	0.045	0.018	0.0096	0.028	0.16	0.14
Cecropia longipes	-	-	-	50	0.048	94	-	0.12
Cecropia obtusifolia	0.028	0.0041	0.072	51	4.8	99	0.14	0.14
Cedrela odorata	50	3.2	97	-	-	-	0.04	-
Ceiba pentandra	50	4.2	98	51	5.8	100	0.06	0.12
Celtis schippii	50	5	100	51	5.4	100	0	0.08
Cespedesia spathulata	51	4.7	99	-	-	-	0	-
Cestrum megalophyllum	47	0.041	95	51	5.2	100	0.08	0.08
Chamaedorea tepejilote	50	4.2	99	49	4.1	99	0.04	0.09
Chamguava schippii	0.08	0.016	0.19	1.2	0.012	9.3	0.14	0.13
Chrysochlamys eclipes	50	2.6	97	48	0.22	95	0	0.08
Chrysophyllum argenteum	0.39	0.045	0.94	47	0.19	95	0.09	0.1
Chrysophyllum cainito	51	2.3	96	52	5.5	99	0.11	0.12
Cinnamomum triplinerve	52	3.4	97	50	1.8	96	0.11	0.1
Clidemia dentata	50	4.8	99	46	0.026	93	0.12	0.12
Clidemia octona	45	0.16	94	50	5	100	0.12	0.11
Coccoloba coronata	51	5.9	99	51	5.9	100	0.05	0.05

Species	Parameters							
	c						*Light50*	
	1985-1990			1990-1995			1985-90	1990-95
	mean	CI -	CI +	mean	CI -	CI +	mean	mean
Coccoloba manzinellensis	50	0.21	94	49	2	96	0.09	0.1
Colubrina glandulosa	-	-	-	50	1.5	96	-	0.11
Conostegia bracteata	49	0.034	94	50	0.17	94	0.08	0.07
Conostegia cinnamomea	0.029	0.008	0.061	27	0.039	90	0.04	0.08
Cordia alliodora	28	0.0067	92	51	2.4	97	0.13	0.09
Cordia bicolor	0.068	0.049	0.087	0.07	0.04	0.11	0.14	0.13
Cordia lasiocalyx	0.15	0.059	0.27	37	0.04	94	0.06	0.05
Coussarea curvigemmia	0.26	0.13	0.43	40	0.19	93	0.07	0.04
Croton billbergianus	0.031	0.026	0.038	0.03	0.018	0.045	0.15	0.14
Cupania cinerea	49	0.068	94	-	-	-	0.1	-
Cupania latifolia	50	1.6	96	51	1.5	95	0.03	0.02
Cupania rufescens	0.052	0.0043	0.15	13	0.0029	31	0.13	0.12
Cupania seemannii	42	0.14	94	45	0.077	94	0.08	0.08
Dendropanax arboreus	50	4.8	99	-	-	-	0.07	-
Desmopsis panamensis	1.4	0.87	2	1.2	0.52	2	0	0
Diospyros artanthifolia	49	0.017	96	50	0.15	95	0.12	0.03
Dipteryx oleifera	49	1.5	95	50	0.24	95	0.05	0.1
Drypetes standleyi	47	0.085	94	52	6.4	99	0	0
Elaeis oleifera	50	4.8	99	-	-	-	0.09	-
Erythrina costaricensis	50	2.4	96	49	0.084	95	0.02	0.08
Erythroxylum macrophyllum	48	0.074	94	50	1.9	96	0.08	0.03
Erythroxylum panamense	50	5.9	100	52	6.2	100	0.06	0.06
Eugenia coloradoensis	42	0.064	94	50	3.2	96	0.08	0.03
Eugenia galalonensis	0.18	0.082	0.3	0.25	0.09	0.49	0.03	0.08
Eugenia nesiotica	50	5.9	100	0.14	0.0026	0.57	0.04	0.07
Eugenia oerstediana	0.15	0.095	0.2	0.065	0.036	0.1	0.03	0.05
Faramea occidentalis	0.69	0.59	0.8	0.6	0.46	0.74	0.01	0.01
Ficus bullenei	-	-	-	50	3.2	97	-	0.11
Ficus citrifolia	50	0.12	95	-	-	-	0.11	-
Ficus costaricana	-	-	-	50	1.8	96	-	0.1
Ficus insipida	50	4.4	100	50	2	97	0.07	0.12
Ficus maxima	50	3.1	97	-	-	-	0.11	-
Ficus obtusifolia	52	2.5	95	50	5.6	100	0.04	0.06
Ficus pertusa	50	0.58	95	51	1.2	96	0.08	0.1
Ficus popenoei	51	5.6	100	-	-	-	0.11	-
Ficus trigonata	-	-	-	52	5.2	99	-	0.09
Garcinia intermedia	0.58	0.22	1.1	33	0.16	91	0	0
Garcinia madruno	50	2.8	97	51	0.044	95	0	0
Genipa americana	49	4.6	99	-	-	-	0	-
Guapira standleyana	49	0.18	95	51	4.6	99	0.03	0.03
Guarea fuzzy	47	0.22	93	51	4.5	99	0.05	0.06
Guarea grandifolia	50	4.5	99	49	3.3	97	0	0.1
Guarea guidonia	20	0.14	86	48	0.26	95	0.05	0.05
Guatteria dumetorum	47	0.12	94	47	0.17	95	0.06	0.08
Guazuma ulmifolia	51	0.42	95	50	5.7	100	0.14	0.13
Guettarda foliacea	51	1.4	96	50	1.8	97	0.06	0.03
Gustavia superba	51	0.83	94	47	0.016	95	0.12	0.14
Hamelia axillaris	45	0.11	94	0.059	0.0096	0.15	0.13	0.13
Hampea appendiculata	51	5.4	100	51	5.6	100	0.13	0.11
Hasseltia floribunda	0.021	0.0022	0.063	46	0.097	95	0.08	0.12
Heisteria acuminata	50	0.92	95	51	5.5	100	0.1	0.02
Heisteria concinna	52	5.6	100	49	4.1	98	0	0.06
Herrania purpurea	43	0.062	94	27	0.018	90	0.05	0.11
Hieronyma alchorneoides	49	0.76	95	48	2.8	97	0.08	0.11
Hirtella americana	50	4.7	99	50	5.2	100	0.09	0.08
Hirtella triandra	0.32	0.19	0.47	16	0.12	66	0	0.01

Species	Parameters							
	c						*Light50*	
	1985-1990			1990-1995			1985-90	1990-95
	mean	CI -	CI +	mean	CI -	CI +	mean	mean
Hybanthus prunifolius	0.67	0.61	0.74	0.51	0.43	0.6	0	0.01
Inga acuminata	49	0.1	95	49	0.6	95	0.07	0.01
Inga cocleensis	50	0.42	95	50	5.1	100	0.13	0.1
Inga goldmanii	44	0.029	94	48	0.006	94	0.06	0.1
Inga laurina	50	3.7	98	50	4.4	98	0.1	0.07
Inga marginata	0.089	0.044	0.14	37	0.055	93	0.09	0.11
Inga nobilis	46	0.17	95	50	0.51	94	0.02	0.01
Inga oerstediana	49	4.3	99	49	0.027	95	0.11	0.06
Inga pezizifera	48	0.044	94	50	4	99	0	0.07
Inga punctata	50	0.67	95	51	1	96	0.12	0.11
Inga ruiziana	50	4.7	99	-	-	-	0.09	-
Inga sapindoides	48	0.11	96	50	0.34	96	0.11	0.13
Inga spectabilis	50	5.1	100	-	-	-	0.09	-
Inga thibaudiana	49	4.8	100	0.025	0.0031	0.065	0.13	0.13
Inga umbellifera	15	0.063	85	49	2.2	96	0.09	0.1
Jacaranda copaia	49	0.88	95	48	0.12	95	0.14	0.13
Koanophyllon wetmorei	48	0.18	93	50	2.8	97	0.1	0.11
Lacistema aggregatum	0.81	0.094	2.4	44	0.11	94	0	0.05
Lacmellea panamensis	50	1	96	51	2.7	97	0.06	0.04
Laetia procera	0.049	4e-04	0.21	49	0.072	95	0.14	0.11
Laetia thamnia	48	0.051	95	41	0.075	93	0.1	0.08
Leandra dichotoma	49	2.9	98	-	-	-	0.11	-
Licania hypoleuca	49	0.057	95	51	4	99	0	0.03
Licania platypus	50	1.5	96	50	2.8	96	0	0
Lindackeria laurina	51	4.8	99	47	0.13	94	0.09	0.09
Lonchocarpus heptaphyllus	48	0.19	95	0.19	0.011	0.5	0.09	0.12
Luehea seemannii	27	0.072	91	49	4.8	99	0.14	0.14
Macrocnemum roseum	0.02	1e-04	0.15	50	0.74	95	0	0.1
Malpighia romeroana	50	0.28	95	49	5.1	98	0.06	0.07
Maquira guianensis	5.5	0.042	29	42	0.092	93	0	0
Margaritaria nobilis	50	5.2	99	-	-	-	0.13	-
Maytenus schippii	49	0.7	95	50	1.9	96	0.02	0.03
Miconia affinis	0.028	0.015	0.044	0.045	0.012	0.096	0.13	0.12
Miconia argentea	0.071	0.055	0.087	0.034	0.025	0.043	0.13	0.14
Miconia elata	0.0033	0	0.015	-	-	-	0.1	-
Miconia hondurensis	49	0.056	94	51	3.1	97	0.08	0.04
Miconia impetiolaris	50	2.4	96	50	2.7	96	0.01	0.08
Miconia nervosa	0.062	0.039	0.092	0.11	0.029	0.23	0.13	0.12
Miconia prasina	51	6.3	100	-	-	-	0.09	-
Mosannona garwoodii	51	4.4	99	50	3.9	99	0.02	0
Mouriri myrtilloides	0.86	0.54	1.2	0.29	0.21	0.4	0.06	0.06
Myrcia gatunensis	50	3.1	97	49	0.84	94	0.01	0.05
Nectandra cissiflora	41	0.054	93	51	5	100	0.1	0.11
Nectandra lineata	50	0.87	95	51	0.12	95	0.05	0.09
Nectandra purpurea	50	0.86	95	50	2.4	97	0.08	0.1
Neea amplifolia	51	4.5	99	49	0.088	94	0.06	0.11
Ochroma pyramidale	50	6	100	49	4.4	99	0.11	0.09
Ocotea cernua	47	0.043	96	47	0.024	95	0.06	0.09
Ocotea oblonga	49	0.14	95	48	0.023	95	0.08	0.09
Ocotea puberula	47	0.052	94	50	2.2	96	0.09	0.08
Ocotea whitei	2.5	0.0051	8.7	49	1	95	0	0
Oenocarpus mapora	38	0.061	95	48	0.13	94	0.04	0
Ormosia coccinea	49	1.6	96	50	2.3	97	0	0
Ormosia macrocalyx	49	1.2	95	49	0.083	94	0.05	0.08
Ouratea lucens	50	4.9	98	50	3.3	97	0.07	0.08
Pachira quinata	49	0.79	95	-	-	-	0.08	-

Species	Parameters							
	c						*Light50*	
	1985-1990			1990-1995			1985-90	1990-95
	mean	CI -	CI +	mean	CI -	CI +	mean	mean
Pachira sessilis	-	-	-	51	0.065	94	-	0.1
Palicourea guianensis	0.091	0.077	0.1	0.051	0.043	0.06	0.14	0.15
Pentagonia macrophylla	50	3.5	98	49	0.2	95	0.07	0.03
Perebea xanthochyma	48	0.019	95	51	5.4	100	0.05	0.05
Picramnia latifolia	39	0.1	94	43	0.13	94	0.01	0.01
Piper aequale	49	0.29	94	50	0.23	94	0	0.09
Piper arboreum	49	2.6	97	2.6	1e-04	9.8	0.07	0.12
Piper colonense	51	5.6	100	50	1.5	96	0.04	0.06
Piper cordulatum	0.056	0.031	0.083	48	0.096	95	0.07	0.1
Piper perlasense	51	4.6	99	50	0.71	95	0	0.06
Piper reticulatum	51	4.5	100	51	3.9	98	0.08	0.05
Platymiscium pinnatum	51	5.5	100	43	0.015	95	0.11	0.13
Platypodium elegans	51	5	99	47	0.077	94	0.1	0.1
Posoqueria latifolia	48	0.28	95	51	5.4	100	0.09	0
Poulsenia armata	49	2.9	96	50	1.4	96	0.02	0
Pourouma bicolor	51	0.8	95	47	0.026	95	0.07	0.1
Pouteria reticulata	0.49	0.12	1.1	52	7.5	99	0.08	0.09
Pouteria stipitata	50	1.5	96	50	1.6	95	0.08	0.13
Prioria copaifera	0.25	0.011	1	49	0.96	95	0.03	0
Protium confusum	50	2.1	96	-	-	-	0	-
Protium costaricense	32	0.069	93	45	0.074	94	0.08	0.11
Protium panamense	0.23	0.14	0.34	0.24	0.075	0.48	0.09	0.05
Protium tenuifolium	0.16	0.1	0.23	0.12	0.047	0.22	0	0.04
Pseudobombax septenatum	50	0.55	95	49	3.1	98	0.14	0.07
Psidium friedrichsthalianum	50	2.8	98	50	1.2	96	0.05	0.04
Psychotria acuminata	46	0.024	95	50	5.9	100	0.12	0.07
Psychotria chagrensis	-	-	-	51	4.7	100	-	0.03
Psychotria deflexa	47	0.012	94	51	3.4	99	0.09	0.11
Psychotria graciliflora	0.0043	0.0014	0.008	0.0017	5e-04	0.0035	0.11	0.06
Psychotria grandis	48	0.052	94	43	0.001	94	0.05	0.05
Psychotria hoffmannseggiana	50	5.4	100	-	-	-	0.07	-
Psychotria horizontalis	0.23	0.18	0.27	0.12	0.086	0.15	0	0.01
Psychotria limonensis	0.0055	3e-04	0.017	15	0.0061	84	0.11	0.06
Psychotria marginata	0.19	0.075	0.35	0.037	0.021	0.057	0.07	0.09
Psychotria pittieri	50	3.3	98	-	-	-	0.1	-
Psychotria racemosa	49	3.3	97	-	-	-	0.04	-
Pterocarpus rohrii	0.93	0.13	2.6	34	0.16	91	0.08	0.09
Quararibea asterolepis	0.19	0.035	0.48	47	0.1	95	0	0
Quassia amara	50	2.5	97	50	0.009	93	0.04	0.1
Randia armata	51	1.6	95	46	0.089	95	0.06	0.06
Rauvolfia littoralis	-	-	-	48	1.9	95	-	0.09
Rinorea sylvatica	0.06	0.036	0.087	0.038	0.017	0.062	0.04	0.02
Sapium glandulosum	51	4.7	99	48	0.0025	95	0.14	0.14
Schizolobium parahyba	52	2.9	98	50	4.8	100	0.1	0.07
Senna dariensis	50	5.2	100	49	0.15	94	0.12	0.15
Simarouba amara	0.16	0.096	0.25	0.088	0.049	0.14	0.07	0.09
Siparuna guianensis	50	0.057	94	-	-	-	0.04	-
Siparuna pauciflora	50	0.059	95	48	0.053	94	0.03	0.03
Sloanea terniflora	50	3.4	97	50	2.7	97	0.08	0.08
Socratea exorrhiza	18	0.02	67	35	0.057	93	0	0
Solanum asperum	52	4.1	99	51	3.2	97	0.13	0.14
Solanum circinatum	51	3.6	97	50	1.9	96	0.05	0.1
Solanum hayesii	0.079	0.0059	0.24	50	0.26	95	0.14	0.13
Solanum steyermarkii	-	-	-	51	4.3	99	-	0.1
Sorocea affinis	43	0.29	95	42	0.043	94	0	0.04
Spondias mombin	32	0.092	92	0.11	0.02	0.25	0.16	0.16

Species	Parameters							
	c						*Light50*	
	1985-1990			1990-1995			1985-90	1990-95
	mean	CI -	CI +	mean	CI -	CI +	mean	mean
Spondias radlkoferi	0.046	0.014	0.094	46	0.13	94	0.13	0.14
Sterculia apetala	50	0.81	95	50	1.7	97	0.1	0.1
Stylogyne turbacensis	47	0.14	95	49	2	97	0.1	0.07
Swartzia simplex_var.grandiflora	48	0.77	94	25	0.14	88	0.02	0
Symphonia globulifera	50	0.23	95	48	0.064	95	0	0
Tabebuia guayacan	49	2	96	50	5	99	0.1	0.12
Tabebuia rosea	48	0.059	95	51	5.3	99	0.08	0.09
Tabernaemontana arborea	48	0.34	94	0.23	0.066	0.51	0.1	0.11
Tachigali versicolor	0.19	0.12	0.25	0.085	0.054	0.12	0	0.06
Talisia nervosa	23	0.012	89	49	5.2	99	0.05	0.02
Talisia princeps	44	0.041	94	49	4.7	100	0	0.06
Terminalia amazonia	50	8e-04	94	50	4.7	99	0.12	0.04
Terminalia oblonga	51	3.1	97	49	4.4	98	0.11	0.08
Tetragastris panamensis	0.22	0.16	0.3	0.14	0.085	0.21	0.05	0.03
Thevetia ahouai	0.00036	1e-04	9e-04	46	0.026	95	0.12	0.12
Trattinnickia aspera	50	4.7	99	50	2.4	97	0.11	0.12
Trema micrantha	49	0.24	96	44	0.015	94	0.13	0.1
Trichanthera gigantea	50	0.91	95	45	0.051	95	0.11	0.12
Trichilia pallida	50	2.7	96	50	0.7	95	0.08	0.09
Trichilia tuberculata	0.21	0.19	0.25	0.17	0.14	0.21	0	0
Trichospermum galeottii	51	0.14	95	-	-	-	0.1	-
Triplaris cumingiana	51	5.5	98	51	3.4	98	0.03	0.11
Trophis caucana	50	0.86	95	-	-	-	0	-
Trophis racemosa	51	1.5	95	51	2.7	97	0	0.11
Turpinia occidentalis	48	0.46	93	47	0.0023	94	0.11	0.08
Unonopsis pittieri	50	0.073	95	50	4.8	99	0	0.03
Urera baccifera	0.004	2e-04	0.012	0.0044	1e-04	0.014	0.03	0.14
Virola multiflora	51	5.5	100	50	4.3	98	0	0.07
Virola sebifera	49	4	98	50	5.3	99	0.01	0.07
Virola surinamensis	51	1.7	96	-	-	-	0.09	-
Vismia baccifera	9.5	0.014	72	0.025	5e-04	0.11	0.09	0.07
Vismia macrophylla	-	-	-	50	4	98	-	0.1
Vochysia ferruginea	50	5.2	98	49	1.4	95	0.13	0.09
Xylopia macrantha	0.1	0.03	0.22	22	0.031	87	0	0
Xylosma oligandra	51	1.8	96	50	0.12	95	0.07	0.07
Zanthoxylum acuminatum	50	0.26	95	51	3.8	98	0.14	0.11
Zanthoxylum ekmanii	0.031	0.013	0.055	0.0022	9e-04	0.004	0.15	0.13
Zanthoxylum panamense	0.054	0.0091	0.13	47	0.027	95	0.15	0.15
Zuelania guidonia	52	5.4	99	50	4.9	100	0.12	0.08