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Patterns of woody plant species abundance and diversity in the seedling layer of a tropical forest

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Abstract

Questions: 1. How does the composition and diversity of established seedlings compare to that of larger size classes in tropical forests? 2. How do species abundances in the seedling layer vary with adult abundance and life history strategies?

Location: Barro Colorado Island (BCI), Panama.

Methods: We inventoried woody seedlings ≥ 20 cm tall and < 1 cm DBH in ca. 20 000 1-m^2 quadrats within the BCI 50-ha Forest Dynamics Plot, where all trees and shrubs ≥ 1 cm DBH have been identified. We compared diversity and composition of seedlings to that of larger size classes and tested whether adult abundance, growth form, and shade tolerance contributed to variation in seedling abundance among species.

Results: We encountered 60056 seedlings of 332 tree, shrub, and liana species. Diversity of tree seedlings was lower than that of trees ≥ 1 cm DBH. Species abundances in the seedling layer increased non-linearly with reproductive adult abundance, such that *per capita* seedling abundance declined with adult abundance. *Per capita* seedling abundance was highest for canopy tree species and lowest for understorey trees. For canopy trees, shade-tolerant species had significantly higher *per capita* seedling abundance than more light-demanding species.

Conclusions: The woody seedling layer on BCI is composed of a subset of the species present in larger size classes. Most species were present in less than 1% of seedling plots, suggesting strong recruitment limitation. Tree species abundance in the seedling layer is largely a function of reproductive adult abundance, but is also influenced by life history strategies and compensatory processes.

Keywords: Advanced regeneration; Barro Colorado Island; Forest dynamics plot; Life history strategy; Recruitment limitation; Seedling bank; Shade tolerance.

Abbreviations: BCI = Barro Colorado Island; DBH = Diameter at 1.3 m.

Nomenclature: Correa et al. (2004).

Introduction

Recent studies have highlighted the importance of seed dispersal and seedling establishment in the regeneration of tree species and the maintenance of diversity in both temperate and tropical forests (e.g. Dalling et al. 1998a; Lambers et al. 2002; Nathan & Muller-Landau 2000; Wang & Smith 2002). However, once established, tree seedlings can spend decades in the forest understorey waiting for openings in the canopy to provide adequate light for growth into the canopy layer (Antos et al. 2005; Delissio et al. 2002). Therefore, a substantial portion of a tree's life can be spent as an established seedling or small sapling in the shaded understorey (Hubbell 1998). This life stage may be particularly crucial to the success of shade-tolerant species and species lacking viable seed banks, which comprise the majority of species in most tropical tree communities (Vazquezyanes & Orozcosegovia 1993; Whitmore 1989).

When an opening does occur in the forest canopy, these gaps are often filled in by preexisting seedlings and saplings that established in the shade prior to gap formation (Brokaw & Scheiner 1989; Connell 1989; Uhl et al. 1988). The seedling bank therefore serves as the template upon which gap phase dynamics act to produce patterns of adult tree species diversity and relative abundances (Brokaw & Busing 2000; Brokaw & Scheiner 1989). Thus, identifying community-wide patterns of established seedling abundance and diversity in the forest understorey is critical to our overall understanding of tropical forest dynamics.

A species' abundance in the seedling bank will be a function of three demographic rates: recruitment into the seedling bank, survival of established seedlings, and growth out of the seedling layer into larger size classes. The upper limit of recruitment into the seedling layer is governed by seed production of reproductive adults in the community. Species abundance in the seedling layer is therefore likely to increase with reproductive adult abundance. If the number of seedlings produced per adult is constant, then we would expect a linear relationship between seedling and adult species abundances. However, studies from both temperate and tropical forests have shown that seedling establishment and survival are negatively influenced by conspecific density (Harms et al. 2000; Lambers et al. 2002; Wright et al. 2005a). Negative density dependence can generate a rare species advantage, or community compensatory trend (Connell et al. 1984), whereby species that are abundant in the community have lower rates of seed and seedling survival compared to rarer species. Thus, while the absolute number of established seedlings is expected to increase with increasing reproductive adult abundance, the number of seedlings per adult may decline as a result of compensatory processes during establishment.

Variation in the number of seedlings per reproductive adult (hereafter referred to as *per capita* seedling abundance) may also result from differences in life history strategies among species. For example, *per capita* seedling abundance may vary with growth form. Trees in the canopy will have more resources to devote to reproduction than understorey trees, which typically reproduce in the shade and have smaller canopies and root systems with which to capture resources. Thus, we would expect canopy tree species to have more seedlings per reproductive adult than smaller-stature species. Variation in *per capita* seedling abundance may also result from differences in species' shade tolerance. Tropical tree species are known to vary greatly in the amount of light required for regeneration (Whitmore 1998).

Shade-tolerant, climax species are capable of establishing and persisting in the shaded understorey. At the other end of the spectrum, light-demanding pioneer species require canopy gaps for establishment and survival, and grow quickly in high light conditions (Hubbell & Foster 1992). Pioneer species are therefore expected to have fewer individuals per reproductive adult in the seedling bank compared to more shade-tolerant species, since pioneers cannot persist in the shade, and they grow quickly into larger size classes when in gaps.

Testing community-level hypotheses concerning the seedling layer in tropical forests is challenging because most tropical tree species are rare and clumped in dispersion (Condit et al. 2000). Numerous samples spread over a large area are therefore needed to assess fully community-wide patterns of seedling abundance and diversity. With this objective in mind, we began a long-term, community-wide survey of established seedlings and small saplings in the 50-ha Forest Dynamics Plot on Barro Colorado Island (BCI), Panama (Hubbell & Foster 1983). We established ca. 20 000 1-m^2 seedling plots at 5-m intervals across the BCI plot and censused all woody seedlings and small saplings ≥ 20 cm in height and < 1 cm DBH within each plot. To our knowledge, this is the largest census of woody seedlings at a single study site to date. In addition, these data can be directly linked to an existing 25-year dataset on the dynamics of trees and shrubs ≥ 1 cm DBH in the BCI 50-ha plot, providing an unprecedented opportunity to explore community-wide patterns of species abundance and diversity across life stages.

Here we present results from the initial BCI 50-ha plot seedling census and examine established seedling density, diversity and abundance for 396 tropical tree, shrub, and liana species. We model the relationship between established seedling and adult tree abundances in the BCI tree community. We then test whether variation in *per capita* seedling abundance among species can be explained by differences in life history strategies, namely shade tolerance and growth form.

Methods

Study site

The study was conducted in the 50-ha Forest Dynamics Plot (500 m × 1000 m) on Barro Colorado Island (BCI), Panama (9°9' N, 79°51' W) (Hubbell & Foster 1983; Hubbell et al. 1999). BCI is classified as tropical moist forest and receives a mean of 2600 mm of rain per year, most of which falls during the 8-month wet season from May to December (Windsor 1990). More detailed descriptions of the climate, geology, and flora of BCI can be found in Croat (1978), Leigh et al. (1982), and Leigh (1999). The BCI 50-ha plot was established in 1980, and all trees and shrubs ≥ 1 cm DBH in the plot were mapped, identified to species, and measured between 1982 and 1983 (Condit 1998; Hubbell & Foster 1983). The BCI plot has been recensused at 5-year intervals since 1985.

Field methodology

In 2001, we established a permanently marked 1 m × 1 m seedling plot in the center of each 5 m × 5 m subquadrat of the 50-ha plot for a total of 20 000 plots (total area sampled = 2 ha). Between January and October 2001, all woody plants greater than 20 cm in height and less than 1 cm DBH (hereafter referred to simply as *seedlings*) were tagged, mapped and identified to species within each 1-m^2 plot. Seedlings were not censused in 366 seedling plots to avoid pre-existing research plots within those areas. Lianas were not measured in the census of stems ≥ 1 cm DBH, however liana seedlings were included in the seedling census if they were not yet entwined in or climbing on another plant. Palm seedlings (family *Arecaceae*) were excluded from the seedling census because they lack measurable woody stems. A small percentage of tagged seedlings (< 0.5%) could not be positively identified. In nearly all cases, unidentified individuals were seedlings lacking leaves or that had died shortly after being tagged, but before the species identification could be confirmed in the field by one of the head botanists. Thus, few, if any, of the unidentified individuals are likely to represent species that were not already included in the census.

Analyses

Species were assigned to one of five growth forms based on architecture and maximum height attained: lianas (woody vines), shrubs (< 4 m tall), understorey trees (4 - 10 m tall), midstorey trees (10 - 20 m tall), and canopy trees (≥ 20 m tall) (Hubbell and Foster 1986). For tree species, we calculated estimates of diversity for the seedling layer, for all saplings and trees ≥ 1 cm DBH, and for reproductive-size trees. We determined the number of reproductive-size trees of each species based on species-specific estimates of the DBH at which individuals on BCI become fully reproductive (R. Foster, unpubl. data; Wright et al. 2005b) . Shrubs were not included in the diversity estimates because many shrub species are reproductive at sizes < 1 cm DBH, and we could not confidently differentiate between juveniles and adults based on our current datasets. We also excluded six tree species in the genus *Ficus* (*Moraceae*) that first establish as hemi-epiphytes and seven rare tree species for which the minimum reproductive size is not known.

We calculated diversity in the sampled area separately for each group (seedlings, all trees ≥ 1 cm DBH, and only reproductive-size trees) using Fisher's alpha and rarefaction, both of which are largely independent of sample size (Magurran 1988). For estimates of diversity based on rarefaction, we calculated the mean number of species found in a random sample of 1000 individuals. As a measure of evenness we calculated Hurlbert's probability of interspecific encounter (Hurlbert 1971), which is related to rarefaction and is also independent of sample size (Olszewski 2004).

We examined variation in species abundance in the seedling layer for 178 understorey, midstorey and canopy tree species with at least one seedling and one reproductive-size adult found in the seedling and tree censuses, respectively. We modeled the relationship between seedling abundance and reproductive adult abundance as:

$$S = a * R^b \qquad (1)$$

where S is the number of established seedlings, R is the number of reproductive-size adults in the 2000 census of stems ≥ 1 cm DBH, a is the mean density-independent seedling production per reproductive adult, and b captures the effect of species abundance on *per capita* seedling abundance. If b is equal to 1, there is no effect of adult abundance on the number of seedlings per reproductive adult. Values of b less than one indicate a negative effect of adult abundance on *per capita* seedling abundance, and values greater than one indicate a positive effect. Similar power functions have been used previously to detect density dependence during the seed to seedling transition (Harms et al. 2000; Wright et al. 2005a) and to demonstrate a rare species advantage in sapling recruitment (Welden et al. 1991) . In addition, the power function can be easily evaluated using least squares regression by first log transforming both sides of the equation:

$$\log (S) = \log (a) + b * \log (R) \qquad (2)$$

To test whether reproductive adult abundance has a negative effect on the *per capita* number of seedlings, consistent with a rare species advantage, we examined 95% confidence intervals around the fitted parameters to determine if b is significantly less than 1. Since the seedling census includes individuals from multiple cohorts and various ages, we repeated the analysis using data on reproductive adult abundances in the 1990 census, the 1995 census, and the 1990, 1995, and 2000 censuses combined. We compared r^2 values of the models to assess which estimate of reproductive adult abundance was the best predictor of seedling abundance.

To determine how life history strategies affect seedling abundances, we examined differences in *per capita* seedling abundance among growth forms and among shade tolerance guilds. For each tree species having at least one reproductive-size adult in the BCI 50-ha plot in 2000, we calculated *per capita* seedling abundance by first multiplying the number of seedlings encountered by 25 to account for the fact that we sampled 4% of each 5 m × 5 m quadrat. We then calculated the *per capita* seedling abundance for each species by dividing the estimated total seedling abundance by the number of reproductive-size adults alive in the 2000 census.

To examine the effect of growth form on *per capita* seedling abundance, we tested for differences in *per capita* seedling abundance among canopy, understorey, and midstorey tree species. We also tested whether shade tolerance affects *per capita* seedling abundance by classifying tree species as light-demanding, shade-tolerant or intermediate based on published species classifications (Condit et al. 1995; Condit et al. 1996; Hubbell & Foster 1987; Hubbell et al. 1999; Welden et al. 1991). *Per capita* seedling abundances were highly skewed and variances were not equal among groups, thus we tested for significant differences in *per capita* seedling abundance among growth forms and among shade tolerance guilds using Kruskal-Wallis rank sum tests.

Species' shade tolerance is governed by a trade-off between maximum growth rate in sun and survival in shade (Hubbell & Foster 1992). Thus, we also used maximum sapling growth rates as a continuous measure of species' shade tolerance. Growth rates were calculated as in Welden et al. (1991) for each 1-2 cm DBH sapling over the census interval following its recruitment into the census of trees ≥ 1 cm DBH. We excluded individuals for which the DBH was measured on different stems in the two censuses due to stem breakage or resprouting. In total 165 tree species had at least 10 saplings for which we could calculate growth rates. For these species, we used the 90th quantile of sapling growth rates for each species as a measure of that species' maximum sapling growth. Using the 90th quantile rather than the highest single growth rate avoided potential bias from a single individual or a single DBH measurement error. We then tested for a correlation between maximum sapling growth rate and *per capita* seedling abundance. For this analysis, we used log transformed values of maximum sapling growth rate and log transformed values of *per capita* seedling abundance plus 0.05 (to deal with values of zero) in order to meet assumptions of normality and constant variance.

Lastly, we used an ANCOVA to test whether reproductive adult abundance, growth form, and shade tolerance guild each explained a significant amount of the variation in total (raw) seedling abundance when all three independent variables were included in the analysis. This test allowed us to determine whether there was a significant *per capita* effect of reproductive adult abundance (i.e. whether the coefficient *b* significantly differs from 1) when growth form and shade tolerance were also taken into account. All analyses were carried out using the software package R version 2.0.1 (R Development Core Team, Anon. 2005).

Table 1. Number of species and individuals of each growth form encountered in the census of seedlings ≥20 cm in height and < 1 cm DBH in 19 634 1-m^2 plots in the Barro Colorado Island 50-ha Forest Dynamics Plot, Panama.

	Number of species	Number of individuals
Canopy trees	82	22 621
Midstorey trees	61	6547
Understorey trees	41	8682
Shrubs	51	11 798
Lianas	96	10134
Total	331	60056*

* including 274 unidentified individuals.

Results

Seedling density and diversity

We encountered a total of 60 056 seedlings of 332 tree, shrub, and liana species in the 19 634 1-m^2 plots included in the 2001 census of seedlings (Table 1; App. 1). The most speciose growth forms were canopy trees and lianas, represented by 82 and 96 species in our census, respectively (Table 1). Besides the 96 liana species, we identified only 7 species that have not been encountered in the BCI plot censuses of stems ≥1 cm DBH. All but one of these species were small shrubs that rarely, if ever, grow to be > 1 cm DBH. The exception was *Inga vera* (*Fabaceae*), a midstorey tree previously encountered on BCI (Croat 1978) but never in the BCI 50-ha plot censuses.

Of the 305 tree and shrub species previously identified in the censuses of stems ≥ 1 cm DBH (excluding palms), 228 were also encountered in the census of seedlings. A plot of the mean number of tree species encountered in the seedling layer as a function of the number individuals censused suggests that our census captured nearly all species present in the seedling layer, since the number of new species encountered begins to level off at sample sizes larger than 35 000 (Fig. 1). According to both Fisher's alpha values and estimates of diversity based on rarefaction, tree species diversity was lower in the seedling layer compared to all trees ≥1 cm DBH and to only reproductive-size trees (Table

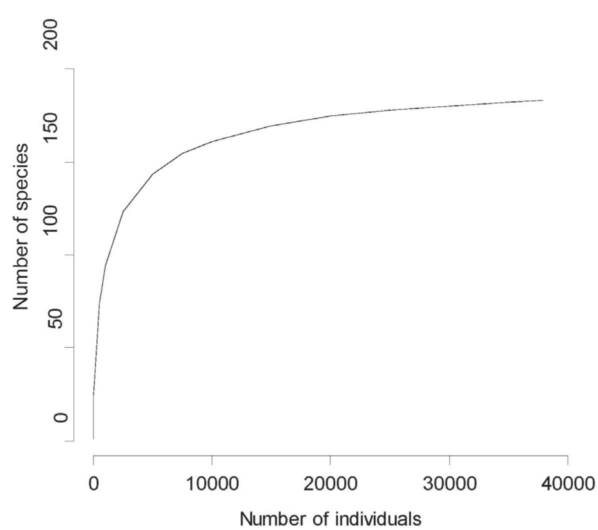

Fig. 1. Mean number of tree species encountered as a function of the number of individuals surveyed in a census of seedlings in the Barro Colorado Island 50-ha Forest Dynamics Plot, Panama. The mean number of species encountered for a given sample size, *N*, was calculated from 100 random draws of *N* individuals from the seedling census data.

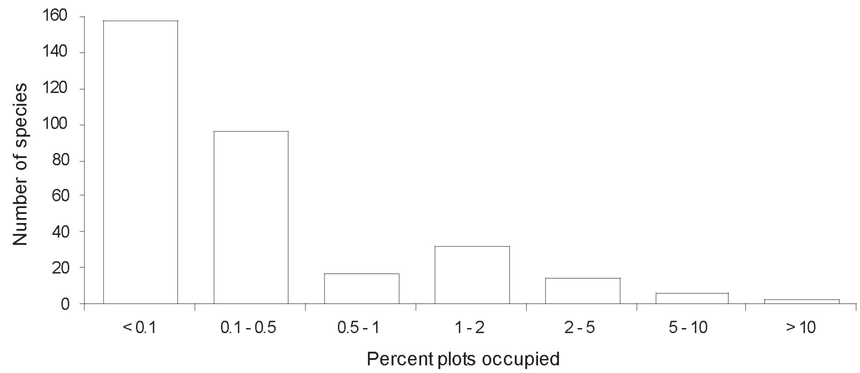

Fig. 2. Percentage of seedling plots in which each species was present in a census of 19 634 1-m^2 seedling plots in the Barro Colorado Island 50-ha Forest Dynamics Plot, Panama.

2). However, evenness in the seedling layer was similar to that of all trees ≥ 1 cm DBH and greater than that of reproductive-size trees.

The number of seedlings per 1-m^2 plot ranged from 0 to 133, with a mean density of 3.1 seedlings/m^2. Approximately one quarter of the plots did not contain seedlings in the size classes included in our census. Overall, 78% of the 1-m^2 plots contained 4 or fewer individuals. The number of species per plot ranged from 0 to 20, with a mean of 2.2 species/m^2 over all seedling plots and a mean of 3.0 species/m^2 in occupied plots. The handful of plots having extremely high seedling densities (> 50 individuals/m^2) were located near and dominated by one of four species (*Ocotea whitei* (*Lauraceae*), *Beilschmiedia pendula* (*Lauraceae*), *Pouteria reticulata* (*Sapotaceae*), and *Quararibea asterolepis* (*Bombacaceae*)), all of which produce large seeds that tend to drop beneath the crown and germinate well in the shade. For instance, in the 1-m^2 plot having 133 seedlings, 131 belonged to *O. whitei*.

The most abundant species in the seedling census, *Beilschmiedia pendula* (*Lauraceae*), accounted for 9.5% of all seedlings, but occurred in only 5.5% of the seedling plots (App. 1). The second most abundant species in the seedling census, *Faramea occidentalis* (*Rubiaceae*), was present in 13.3% of the seedling plots, more than any other species. Most other species were encountered in very few plots. Approximately half the species were found in less than 0.1% of the seedling plots, and over 85% of the species were present in less than 1.0% of the plots (Fig. 2).

Variation in seedling abundance

The abundance of reproductive-size adults in 2000 explained 33% of the variation in seedling abundance among species ($r^2 = 0.33$, $df = 176$, $P < 0.0001$; Fig. 3). The slope of the regression line for the log transformed data was significantly less than 1 ($b = 0.70$, 95% confidence intervals: 0.55 - 0.85), indicating that although absolute seedling abundance increased with species adult abundance, *per capita* seedling abundance declined. Neither the slope of the regression line, nor the amount of variation in seedling abundance explained by reproductive adult abundance changed substantially when using data on reproductive adult abundance from the 1990 ($r^2 = 0.31$, $b = 0.71$) or 1995 ($r^2 = 0.32$, $b = 0.72$) censuses, nor when combining data from 1990, 1995, and 2000 ($r^2 = 0.33$, $b = 0.72$). Consequently, we used data on the abundances of reproductive-size adults in only the 2000 census for subsequent analyses.

Estimates of *per capita* seedling abundance for individual species ranged widely from 0 to 1371.4 seedlings per reproductive adult (Fig. 4). *Per capita* seedling abun-

Table 2. Diversity of tree seedlings (≥ 20 cm tall and < 1 cm DBH), all saplings and trees ≥ 1 cm DBH, and reproductive-size trees in the Barro Colorado Island 50-ha Forest Dynamics Plot, Panama. Seedlings were censused in ca. 20 000 1-m^2 plots located throughout the 50-ha plot. Individuals ≥ 1 cm DBH and reproductive-size trees were sampled in the entire 50 ha. Numbers of species and individuals encountered and estimates of diversity are for all understorey, midstorey, and canopy tree species, with the exception of seven rare species for which minimum reproductive size was not known and six tree species which start out as hemi-epiphytes.

	No. species encountered	No. individuals encountered	Fisher's α	Rarefaction ($N = 1000$)	Hurlbert's evenness
Seedlings[1]	183	37849	24.99	94.99	0.95
Stems ≥ 1 cm DBH[2]	226	153795	26.02	122.08	0.95
Reproductive-size trees[2]	209	28453	30.57	120.01	0.88

[1] Total sample area = 2 ha; [2] Total sample area = 50 ha.

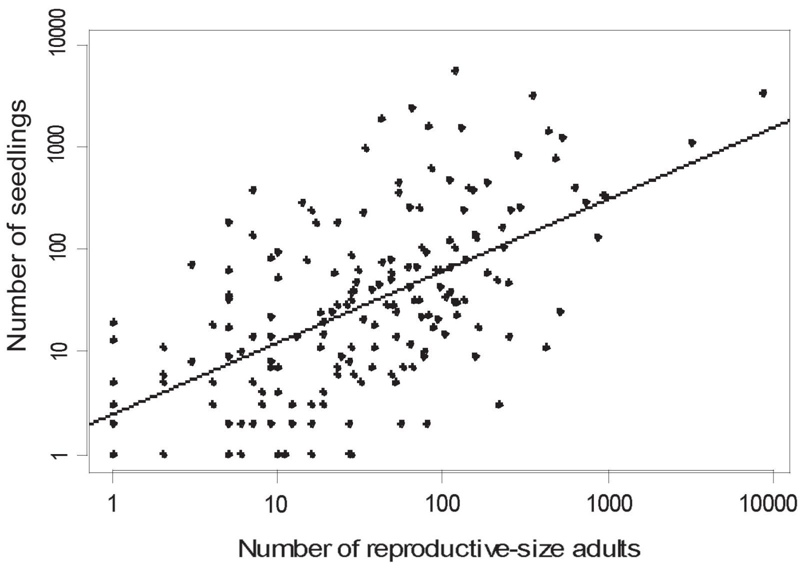

Fig. 3. Relationship between seedling abundance and reproductive-size adult abundance for 178 tree species in the Barro Colorado Island 50-ha Forest Dynamics Plot. Note both axes are log transformed. The slope of the regression line is significantly less than one, indicating that the number of seedlings per reproductive adult declines with increasing reproductive adult abundance.

dance differed significantly among growth forms with canopy, midstorey, and understorey tree species having means of 123.3, 60.0, and 15.8 seedlings per reproductive adult, respectively (Kruskal-Wallis $\chi^2 = 12.25$, $df = 2$, $P = 0.002$; Fig. 4).

Per capita seedling abundance did not vary significantly among shade tolerance guilds for midstorey or understorey tree species, or for all tree species combined (Table 3). However, for canopy trees, *per capita* seedling abundance differed significantly among the three shade tolerance guilds, with shade-tolerant species having nearly four times as many seedlings per reproductive adult as light-demanding species (Table 3). Similarly, canopy tree species showed a significant negative correlation between log transformed values of *per capita* seedling abundance and maximum sapling growth rate ($r = -0.43$, $df = 67$, $P = 0.0002$), while midstorey and understorey tree species did not (midstorey: $r = -0.02$, $df = 51$, $P = 0.9146$; understorey: $r = 0.05$, $df = 41$, $P = 0.7705$; Fig. 5).

The ANCOVA results confirm that growth form, shade tolerance, and reproductive adult abundance all contribute significantly to the variation in absolute seedling abundance (Table 4). The slope of the regression of log (seedling abundance) on log (reproductive adult abundance) remained significantly less than one ($b = 0.68$, 95% confidence intervals: 0.48-0.87) when growth form and shade tolerance were included in the analysis, indicating that the number of seedlings per reproductive adult declines with reproductive adult abundance. Interaction terms between reproductive adult abundance, growth form, and shade tolerance were not significant (Table

Table 3. Comparison of per capita seedling abundance among 141 tree species of three shade tolerance guilds on Barro Colorado Island, Panama. Species means, standard deviations (in parentheses), and number of species (*N*) in each group are reported separately for each growth form. Kruskal-Wallis rank sum tests were used to test for significant differences in per capita seedling abundance among shade tolerance guilds

	Shade tolerance guild			
	Light-demanding	Intermediate	Shade-tolerant	Kruskal-Wallis rank sum test
Canopy trees	70.16	243.38	272.11	$\chi^2 = 7.4372$
	(120.98)	(350.91)	(367.35)	$N = 57$; $df = 2$
	$N = 22$	$N = 16$	$N = 19$	$P = 0.0243$
Midstorey trees	59.96	30.44	87.96	$\chi^2 = 0.2443$
	(135.97)	(49.11)	(220.83)	$N = 50$; $df = 2$
	$N = 12$	$N = 6$	$N = 32$	$P = 0.6662$
Understorey trees	15.03	14.45	21.02	$\chi^2 = 0.9601$
	(23.73)	(13.31)	(26.68)	$N = 34$; $df = 2$
	$N = 6$	$N = 4$	$N = 24$	$P = 0.6188$
All trees	58.83	159.02	113.19	$\chi^2 = 2.8064$
	(116.34)	(293.69)	(250.97)	$N = 141$; $df = 2$
	$N = 40$	$N = 26$	$N = 75$	$P = 0.2458$

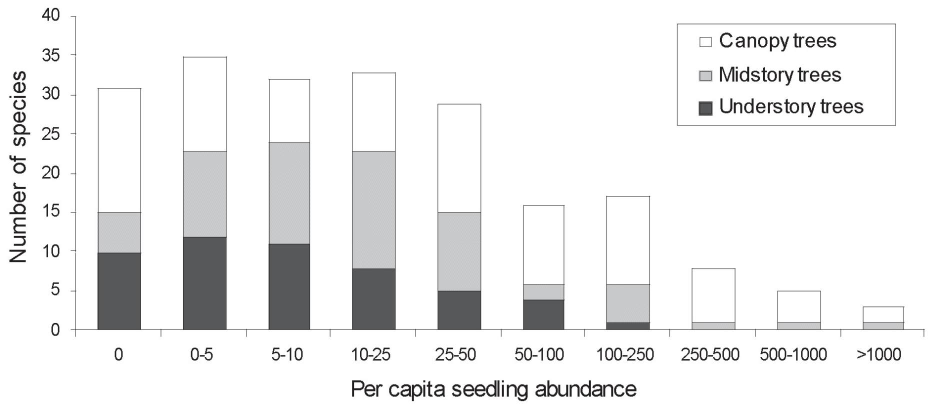

Fig. 4. Variation in per capita seedling abundance of 209 tree species on Barro Colorado Island, Panama.

Table 4. Results of an ANCOVA examining variation in seedling abundance among tree species in the Barro Colorado Island 50-ha Forest Dynamics Plot, Panama. Reproductive adult abundance was a covariate, and shade tolerance guild and growth form were factors in the analysis. Values of reproductive adult abundance and seedling abundance were natural-log transformed. *P*-values in bold denote significance.

	df	SS	MS	*F*	*P*-value
Reproductive adult abundance (R)	1	126.68	126.68	56.43	**< 0.0001**
Growth form (GF)	2	34.07	17.03	7.59	**0.0008**
Shade tolerance guild (SG)	2	24.57	12.29	5.47	**0.0053**
R × GF	2	6.82	3.41	1.52	0.2231
R × SG	2	0.98	0.49	0.22	0.8051
GF × SG	4	12.51	3.13	1.39	0.2401
R × GF × SG	4	8.35	2.09	0.93	0.4491
Residuals	122	273.85	2.25		

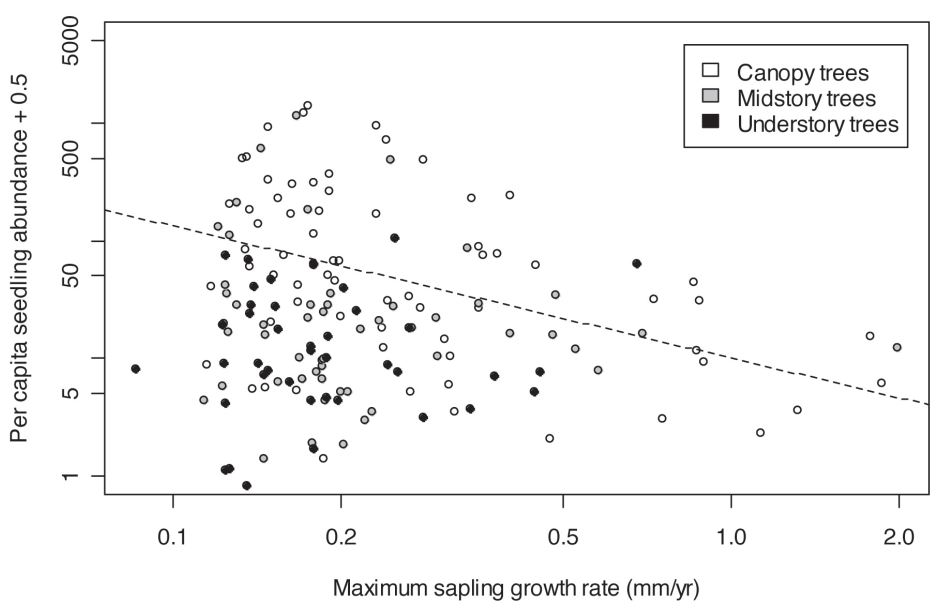

Fig. 5. Relationship between per capita seedling abundance and maximum sapling growth rate for 165 tree species on Barro Colorado Island, Panama. There is a significant correlation between the two variables for canopy tree species (dashed line), but not for understorey or midstorey tree species.

4).

Discussion

Diversity and composition of the seedling layer

In the BCI 50-ha Forest Dynamics Plot, the composition of tree and shrub species in the seedling layer consists largely of species that have been previously identified in censuses of large saplings and trees ≥1 cm DBH. We encountered only a handful of woody species in the seedling layer that are small shrubs that do not grow to be > 1 cm DBH and only one tree species that was not previously identified in the 50-ha plot. Liana species make a substantial contribution to the diversity of the seedling layer, accounting for nearly 30% of species encountered in the seedling census. This proportion is consistent with estimates of the overall contribution of lianas to woody plant species richness on Barro Colorado Island and in other tropical forests (Gentry 1991; Schnitzer & Carson 2001; Schnitzer & Bongers 2002).

Not all species present in the BCI plot were found in the seedling layer; 25% of tree and shrub species previously identified in the census of stems ≥ 1 cm DBH were not encountered in the seedling census. This may be a result of the fact that, despite the large number of seedling plots, the seedling census covers a total of only 4% of the area inside the 50-ha plot. Thus, rare species may be present in the seedling layer at densities too low to detect with our level of sampling effort. However, the species-individual plot (Fig. 1) suggests that few species present in the seedling layer of the 50-ha plot were missed in our census. Although we cannot directly compare seedling and tree species richness due to differences in total area sampled, estimates of diversity based on sample size-independent indices suggest species richness (on a per individual basis) is lower for seedlings compared to trees in the 50-ha plot. This lower diversity of seedlings may be the result of tree species failing to reproduce or reproducing irregularly. Fecundity and seedling establishment are known to vary greatly from year to year on BCI, and the variation tends to be asynchronous among species (De Steven 1994; De Steven & Wright 2002). The species composition and abundances in the seedling layer at a single point in time therefore reflects recent variation in fecundity and establishment (De Steven & Wright 2002).

Seedling density and recruitment limitation

We found that the mean density of woody seedlings ≥ 20 cm tall and < 1cm DBH in the BCI 50-ha plot is 3.1 plants/m^2. By comparison, Harms et al. (2004) reported the mean density of seedlings 10-50 cm in height on BCI is 6.1 seedlings/m^2, suggesting that the inclusion of seedlings < 20 cm tall would have more than doubled our estimate of seedling density. However, the occurrence of 100+ seedlings in some of our 1-m^2 plots proves that much higher densities of seedlings, at least of some species, can be supported. This is consistent with Wright's (2002) assertion that, in tropical forests, understorey plant density, and therefore competition between understorey plants, is suppressed by herbivores and by asymmetric competition with canopy plants. Previous studies suggest that low established seedling density on BCI is also due in part to limited seed arrival (Dalling et al. 2002; Hubbell et al. 1999; Muller-Landau et al. 2002; Svenning & Wright 2005) and high seed and early seedling mortality due to pathogen attack or unsuitable environmental conditions (Augspurger 1984; Dalling et al. 1998b; Farris-Lopez et al. 2004; Molofsky & Augspurger 1992).

As a consequence of the low density of individuals in the seedling layer, few species will be competing in each seedling plot. On average there were only 2.2 species/m^2, and the majority of species were present in less than 1% of the seedling plots. This is consistent with results of a preliminary census of seedlings in a 5-ha portion of the BCI plot reported by Hubbell et al. (1999) and reinforces their conclusion that the majority of species in the BCI forest are severely recruitment limited. Previous studies have shown that seedlings and saplings present in the understorey before gap formation play a large role in filling in treefall gaps (Brokaw & Scheiner 1989; Connell 1989; Uhl et al. 1988). For example, Uhl et al. (1988) found that 4 years after gap formation, advanced regeneration accounted for between 83% and 97% of all trees > 1 m tall in their study gaps. Since individuals present in the seedling layer prior to gap formation will constitute the majority of species competing for a site when an opening in the canopy forms, only a very small subset of species from the BCI community will be competing for any given site. Theoretical studies have shown that recruitment limitation can maintain local diversity by allowing competitively inferior species to persist in the community by winning sites where superior species are absent (Hurtt & Pacala 1995).

Species abundances in the seedling layer

We found that adult abundance, growth form, and shade tolerance all explain a significant proportion of the variation in seedling abundance among tree species in the BCI forest. Reproductive adult abundance accounted for approximately one-third of the total variation in seedling abundance. Absolute seedling abundance increased with reproductive adult abundance; however, there was a negative effect of reproductive adult abundance on the number of seedlings per reproductive adult in the BCI community, consistent with a rare species advantage or community compensatory trend. This may be the result of local-scale negative density dependence during the seed-to-seedling transition in the BCI tree community (Harms et al. 2000; Wright et al. 2005a), but since we examined only static seedling abundances we cannot determine whether the observed pattern is due to higher recruitment and seedling establishment or to lower seedling mortality of rare species. Welden et al. (1991) also found a negative relationship between sapling recruitment and species abundance in the BCI 50-ha plot, suggesting that this pattern holds for larger size classes as well.

The number of seedlings per reproductive adult varied by several orders of magnitude among species. We found that life history strategy accounted for a significant portion of this variation in *per capita* seedling abundance. As predicted, canopy tree species had the highest *per capita* seedling abundance, followed by midstorey and then understorey tree species. Canopy trees tend to delay reproduction until their crowns are exposed to direct sunlight. Thus, canopy trees have more resources to devote to reproduction than smaller stature trees reproducing in the shaded understorey. Even when exposed to full sun, understorey trees have less crown area with which to capture light compared to canopy trees.

Differences in species' shade tolerance also explained some of the variation in *per capita* seedling abundance. Saplings of light-demanding species tend to have high mortality in the shade and grow quickly into larger size classes if in a gap (Hubbell & Foster 1992). This results in a skewed size class distribution with few seedling and saplings relative to adults, in contrast to shade-tolerant species which tend to have many seedlings and saplings relative to adults (Wright et al. 2003). Thus, we expected *per capita* seedling abundance to increase with increasing shade tolerance. Shade-tolerant species did have higher *per capita* seedling abundance than light-demanding species. However, the difference in *per capita* seedling abundance among shade tolerance guilds was significant only for canopy tree species. Also, only canopy tree species showed a significant correlation between maximum sapling growth and *per capita* seedling abundance, suggesting that shade tolerance plays a weaker role in structuring midstorey and understorey tree communities. Of the species on BCI for which shade tolerance guild is known, 39% of canopy tree species are light-demanding while only 24% and 18% of midstorey and understorey trees are light-demanding, respectively (Table 3). Canopy trees are able to grow to heights at which they escape shading, while midstorey and understorey trees can be shaded even at their maximum stature. Thus, for smaller tree species, shade-tolerance may be a more successful life history strategy than shade-intolerance.

The remaining, unexplained variation in *per capita* seedling abundance may be due to chance alone or may also result from differences in other species traits, such as seed size or susceptibility to natural enemies. Seed mass varies over several orders of magnitude among tree species on BCI (Foster 1982). Large seeded species tend to produce fewer seeds than smaller seeded species (Westoby et al. 1992), which could result in lower *per capita* seedling abundances. However, large seeds also tend to have higher seedling establishment and survival (Westoby et al. 1996), which may cancel out differences in seed production. Variation in susceptibility to seed predators, pathogens and herbivores may also contribute to unexplained variation in *per capita* seedling abundance. High rates of seed and seedling attack would reduce the proportion of individuals recruiting and surviving in the seedling layer, and thus lower *per capita* seedling abundances of more vulnerable species.

Conclusions and future directions

A substantial portion of a tree's life can be spent as a seedling or small sapling in the shaded understorey (Delissio et al. 2002; Hubbell 1998), yet few community-wide surveys of the seedling layer have been conducted in tropical forests (but see Connell et al. 1984; Webb 1997). This study represents the most comprehensive census of seedlings and small saplings undertaken in a tropical forest to date. Although the current results represent only a single snapshot of the seedling layer, they offer insights into patterns of regeneration and diversity in tropical tree communities. We found that the woody seedling layer on BCI is composed of a subset of the species present in larger size classes. Overall seedling density and individual species' densities in the seedling layer are relatively low, confirming that recruitment limitation is strong in the BCI forest. Lastly, our results demonstrate that tropical tree species abundance in the seedling layer is largely a function of reproductive adult abundance, but is also influenced by life history strategies and compensatory processes.

Here we examined seedling composition, diversity, and species abundances at the scale of the entire 50-ha plot. However, both the seedling and tree data sets are spatially explicit, making it possible to study variation in the seedling layer at smaller spatial scales within the 50-ha sample area. In future analyses, we will examine differences in seedling abundances and diversity among different edaphic habitat types found in the BCI plot (Harms et al. 2001) and in varying light environments.

The data presented here from the initial BCI 50-ha plot seedling census will also serve as a baseline for annual recensuses of the nearly 20 000 1-m^2 seedling plots, which are presently under way. These censuses will yield spatially-explicit, dynamic data on seedling performance for the 331 tree, shrub and liana species tagged in the initial census. These data will allow us to examine the effects of life history strategy and adult abundance on seedling dynamics, and will offer new insights into the processes shaping species abundances in the seedling layer and maintaining diversity in the BCI tree community.

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For App. 1, see also JVS/AVS Electronic Archives; www.opuluspress.se/

App. 1. Species encountered in the 2001 census of 19 634 1-m^2 seedling plots and the 2000 census of all trees and shrubs ≥1 cm DBH in the Barro Colorado Island 50-ha Forest Dynamics Plot, Panama. Species were grouped into growth form categories based on architecture and maximum adult stature: L = liana, S = shrub, U = understorey tree, M = midstorey tree, T = canopy tree. Tree species were further grouped in shade tolerance guilds: G = gap specialist/light-demanding, S = shade-tolerant, I = intermediate. Maximum sapling growth rates were also used as an estimate of species' shade tolerance (see Text for details). Dashes indicate insufficient data.

Species	Family	Growth form	No. seedlings	% plots present	No. stems ≥ 1 cm DBH	No. reproductive adults	Shade tolerance guild	Max. sapling growth (mm/year)
Unidentified	-	-	274	-	-	-	-	-
Abarema macradenia	Fabaceae-Mimosoideae	T	0	0	1	1	-	-
Abuta racemosa	Menispermaceae	L	301	1.42	-	-	-	-
Acacia hayesii	Fabaceae-Mimosoideae	L	285	1.02	-	-	-	-
Acacia melanoceras	Fabaceae-Mimosoideae	U	0	0	10	4	-	-
Acalypha diversifolia	Euphorbiaceae	S	172	0.73	492	332	-	-
Acalypha macrostachya	Euphorbiaceae	U	7	0.03	43	37	G	0.444
Adelia triloba	Euphorbiaceae	U	23	0.11	161	81	G	0.252
Aegiphila cephalophora	Verbenaceae	L	159	0.74	-	-	-	-
Aegiphila elata	Verbenaceae	L	86	0.43	-	-	-	-
Aegiphila panamensis	Verbenaceae	M	6	0.03	62	49	I	0.227
Alchornea costaricensis	Euphorbiaceae	T	43	0.18	228	96	G	0.868
Alchornea latifolia	Euphorbiaceae	M	2	0.01	2	1	-	-
Alibertia edulis	Rubiaceae	U	68	0.31	356	62	S	0.137
Allophylus psilospermus	Sapindaceae	M	43	0.17	111	63	S	0.216
Alseis blackiana	Rubiaceae	T	1250	4.67	7867	533	S	0.137
Amaioua corymbosa	Rubiaceae	U	5	0.02	26	2	-	0.179
Anacardium excelsum	Anacardiaceae	T	25	0.1	24	21	-	-
Anaxagorea panamensis	Annonaceae	S	63	0.18	749	-	-	-
Andira inermis	Fabaceae-Papilionoideae	T	1	0.01	284	5	S	0.138
Annona acuminata	Annonaceae	S	50	0.25	498	-	-	-
Annona spraguei	Annonaceae	M	21	0.09	134	33	G	0.694
Apeiba membranacea	Tiliaceae	T	39	0.18	269	111	I	0.89
Apeiba tibourbou	Tiliaceae	M	6	0.02	30	23	G	-
Aphelandra sinclairiana	Acanthaceae	S	2	0.01	6	4	-	-
Appunia seibertii	Rubiaceae	S	0	0	3	1	-	-
Ardisia bartlettii	Myrsinaceae	S	1	0.01	6	-	-	-
Ardisia guianensis	Myrsinaceae	S	2	0.01	19	8	-	-
Ardisia pellucida	Myrsinaceae	S	4	0.02	0	-	-	-
Ardisia standleyana	Myrsinaceae	U	7	0.04	99	23	-	0.085
Aristolochia tonduzii	Aristolochiaceae	L	1	0.01	-	-	-	-
Arrabidaea verrucosa	Bignoniaceae	L	8	0.04	-	-	-	-
Aspidosperma spruceanum	Apocynaceae	T	187	0.73	478	23	S	0.126
Astronium graveolens	Anacardiaceae	T	20	0.09	76	19	-	0.277
Banara guianensis	Flacourtiaceae	U	0	0	1	-	-	-
Beilschmiedia pendula	Lauraceae	T	5693	5.47	2318	118	I	0.171
Bignoniaceae morphsp. 1	Bignoniaceae	L	1	0.01	-	-	-	-
Brosimum alicastrum	Moraceae	T	365	1.72	900	54	I	0.162
Brosimum guianense	Moraceae	T	0	0	3	0	-	-
Byttneria aculeata	Sterculiaceae	L	1	0.01	-	-	-	-
Callichlamys latifolia	Bignoniaceae	L	340	1.42	-	-	-	-
Calophyllum longifolium	Clusiaceae	T	235	1.05	1130	16	I	0.191
Capparis frondosa	Capparaceae	S	1647	7.32	2990	-	-	-
Casearia aculeata	Flacourtiaceae	U	62	0.29	420	91	S	0.154
Casearia arborea	Flacourtiaceae	T	12	0.06	139	64	G	0.265
Casearia commersoniana	Flacourtiaceae	U	0	0	21	3	-	0.217
Casearia guianensis	Flacourtiaceae	U	1	0.01	16	10	-	-
Casearia sylvestris	Flacourtiaceae	M	5	0.03	150	51	S	0.22
Cassipourea elliptica	Rhizophoraceae	M	102	0.48	1007	119	S	0.175
Cavanillesia platanifolia	Bombacaceae	T	3	0.02	21	16	-	-
Cecropia insignis	Cecropiaceae	T	67	0.23	716	112	G	1.771
Cecropia longipes	Cecropiaceae	T	0	0	12	0	-	-
Cecropia obtusifolia	Cecropiaceae	M	18	0.07	101	38	G	1.989
Cedrela odorata	Meliaceae	T	5	0.02	8	1	G	-
Ceiba pentandra	Bombacaceae	T	2	0.01	54	27	G	1.13
Celtis iguanaea	Ulmaceae	L	32	0.16	-	-	-	-
Celtis schippii	Ulmaceae	M	3	0.02	122	12	I	0.17
Ceratophytum tetragonolobum	Bignoniaceae	L	55	0.18	-	-	-	-
Cespedesia spathulata	Ochnaceae	T	0	0	2	1	-	-

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App. 1, cont.

Species	Family	Growth form	No. seedlings	% plots present	No. stems ≥ 1 cm DBH	No. reproductive adults	Shade tolerance guild	Max. sapling growth (mm/year)
Cestrum megalophyllum	Solanaceae	S	9	0.05	50	-	-	-
Chamguava schippii	Myrtaceae	U	32	0.15	381	71	S	0.176
Chimarrhis parviflora	Rubiaceae	T	0	0	3	0	-	-
Chiococca alba	Rubiaceae	L	5	0.01	-	-	-	-
Chomelia barbellata	Rubiaceae	L	2	0.01	-	-	-	-
Chondrodendron tomentosum	Menispermaceae	L	30	0.15	-	-	-	-
Chrysochlamys eclipes	Clusiaceae	S	18	0.09	399	295	-	-
Chrysophyllum argenteum	Sapotaceae	T	179	0.9	671	17	G	0.19
Chrysophyllum cainito	Sapotaceae	T	286	1.24	134	14	G	0.135
Cinnamomum triplinerve	Lauraceae	T	82	0.41	61	9	G	0.343
Clidemia dentata	Melastomataceae	S	7	0.04	14	-	-	-
Clidemia octona	Melastomataceae	S	4	0.02	12	-	-	-
Clidemia septuplinervia	Melastomataceae	S	18	0.07	1	-	-	-
Clitoria javitensis	Fabaceae-Papilionoideae	L	60	0.26	-	-	-	-
Cnestidium rufescens	Connaraceae	L	66	0.28	-	-	-	-
Coccoloba coronata	Polygonaceae	M	40	0.2	114	29	S	0.125
Coccoloba manzinellensis	Polygonaceae	U	14	0.07	401	13	I	0.152
Coccoloba parimensis	Polygonaceae	L	341	1.63	-	-	-	-
Cojoba rufescens	Fabaceae-Mimosoideae	M	0	0	2	0	-	-
Colubrina glandulosa	Rhamnaceae	T	0	0	4	1	-	-
Combretum decandrum	Combretaceae	L	8	0.04	-	-	-	-
Combretum laxum	Combretaceae	L	33	0.14	-	-	-	-
Connarus panamensis	Connaraceae	L	5	0.03	-	-	-	-
Connarus turczaninowii	Connaraceae	L	340	1.64	-	-	-	-
Conostegia bracteata	Melastomataceae	S	6	0.02	10	-	-	-
Conostegia cinnamomea	Melastomataceae	S	29	0.13	125	-	-	-
Cordia alliodora	Boraginaceae	T	75	0.29	94	43	G	0.858
Cordia bicolor	Boraginaceae	M	107	0.49	765	234	G	0.527
Cordia lasiocalyx	Boraginaceae	M	257	1.2	1282	295	S	0.296
Coussarea curvigemmia	Rubiaceae	U	134	0.67	2079	863	S	0.176
Coutarea hexandra	Rubiaceae	U	0	0	1	-	-	-
Croton billbergianus	Euphorbiaceae	U	382	0.84	358	151	G	0.677
Cupania cinerea	Sapindaceae	M	0	0	6	0	-	-
Cupania latifolia	Sapindaceae	T	8	0.04	43	3	I	0.193
Cupania rufescens	Sapindaceae	T	19	0.1	94	1	I	0.281
Cupania seemannii	Sapindaceae	U	50	0.22	1212	216	S	0.161
Davilla nitida	Dilleniaceae	L	59	0.28	-	-	-	-
Dendropanax arboreus	Araliaceae	T	6	0.03	103	29	-	0.146
Desmopsis panamensis	Annonaceae	U	1103	5.27	11291	3252	S	0.142
Diospyros artanthifolia	Ebenaceae	M	36	0.15	87	5	S	0.174
Dipteryx oleifera	Fabaceae-Papilionoideae	T	48	0.24	45	30	I	0.117
Doliocarpus dentatus	Dilleniaceae	L	1	0.01	-	-	-	-
Doliocarpus major	Dilleniaceae	L	736	3.07	-	-	-	-
Doliocarpus multiflorus	Dilleniaceae	L	11	0.05	-	-	-	-
Doliocarpus olivaceus	Dilleniaceae	L	285	1.28	-	-	-	-
Drypetes standleyi	Euphorbiaceae	T	618	2.43	2193	85	S	0.137
Enterolobium schomburgkii	Fabaceae-Mimosoideae	T	0	0	13	0	-	-
Erythrina costaricensis	Fabaceae-Papilionoideae	U	0	0	113	80	S	0.156
Erythroxylum macrophyllum	Erythroxylaceae	M	79	0.35	245	48	S	0.124
Erythroxylum panamense	Erythroxylaceae	U	15	0.08	102	102	S	0.124
Eugenia coloradoensis	Myrtaceae	T	184	0.88	655	5	I	0.148
Eugenia galalonensis	Myrtaceae	U	397	1.81	1581	144	S	0.136
Eugenia nesiotica	Myrtaceae	M	452	2.02	515	54	S	0.13
Eugenia oerstediana	Myrtaceae	M	1909	8.17	1926	42	S	0.167
Faramea occidentalis	Rubiaceae	U	3394	13.31	26754	8772	S	0.188
Ficus bullenei	Moraceae	T (H)	0	0	1	-	-	-
Ficus citrifolia	Moraceae	T (H)	0	0	1	-	-	-
Ficus colubrinae	Moraceae	T (H)	0	0	1	-	-	-
Ficus costaricana	Moraceae	T (H)	1	0.01	11	7	-	-
Ficus crocata	Moraceae	T	0	0	6	4	-	-
Ficus insipida	Moraceae	T	0	0	16	1	-	-
Ficus maxima	Moraceae	T	0	0	8	2	-	-
Ficus obtusifolia	Moraceae	T (H)	0	0	6	6	-	-
Ficus pertusa	Moraceae	T	0	0	1	-	-	-
Ficus popenoei	Moraceae	T (H)	0	0	4	2	-	-

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App. 1, cont.

Species	Family	Growth form	No. seedlings	% plots present	No. stems ≥ 1 cm DBH	No. reproductive adults	Shade tolerance guild	Max. sapling growth (mm/year)
Ficus tonduzii	Moraceae	M	0	0	27	6	-	-
Ficus yoponensis	Moraceae	T	0	0	6	5	-	-
Fischeria blepharopetala	Asclepiadaceae	L	3	0.02	-	-	-	-
Forsteronia myriantha	Apocynaceae	L	16	0.08	-	-	-	-
Forsteronia viridescens	Apocynaceae	L	17	0.09	-	-	-	-
Garcinia intermedia	Clusiaceae	M	485	2.3	4409	110	S	0.126
Garcinia madruno	Clusiaceae	M	71	0.34	374	3	S	0.143
Genipa americana	Rubiaceae	T	2	0.01	70	6	-	0.115
Guapira standleyana	Nyctaginaceae	T	28	0.14	165	50	S	0.307
Guarea ”fuzzy” (morphosp.)	Meliaceae	M	62	0.32	1037	96	S	0.125
Guarea grandifolia	Meliaceae	T	9	0.05	66	5	-	0.195
Guarea guidonia	Meliaceae	M	286	1.37	1838	743	S	0.168
Guatteria dumetorum	Annonaceae	T	32	0.16	1038	67	S	0.238
Guazuma ulmifolia	Sterculiaceae	T	7	0.04	61	23	G	-
Guettarda foliacea	Rubiaceae	U	22	0.1	303	74	S	0.148
Gustavia superba	Lecythidaceae	M	407	1.7	753	639	G	0.401
Hamelia axillaris	Rubiaceae	S	51	0.24	88	-	-	-
Hamelia patens	Rubiaceae	S	0	0	1	-	-	-
Hampea appendiculata	Malvaceae	M	52	0.25	27	10	I	-
Hasseltia floribunda	Flacourtiaceae	M	14	0.06	543	254	S	0.201
Heisteria acuminata	Olacaceae	U	14	0.07	106	52	S	0.146
Heisteria concinna	Olacaceae	M	59	0.3	953	184	S	0.185
Herrania purpurea	Sterculiaceae	U	25	0.12	511	511	G	0.178
Heteropterys laurifolia	Malpighiaceae	L	18	0.09	-	-	-	-
Hieronyma alchorneoides	Euphorbiaceae	T	11	0.05	78	28	G	0.314
Hippocratea volubilis	Hippocrateaceae	L	352	1.61	-	-	-	-
Hiraea faginea	Malpighiaceae	L	13	0.06	-	-	-	-
Hiraea grandifolia	Malpighiaceae	L	94	0.4	-	-	-	-
Hiraea reclinata	Malpighiaceae	L	999	4.27	-	-	-	-
Hiraea smilacina	Malpighiaceae	L	36	0.18	-	-	-	-
Hirtella americana	Chrysobalanaceae	T	3	0.02	30	0	I	0.192
Hirtella triandra	Chrysobalanaceae	M	339	1.64	4760	937	S	0.185
Hura crepitans	Euphorbiaceae	T	9	0.05	105	76	-	-
Hybanthus prunifolius	Violaceae	S	3286	12.07	31934	-	-	-
Hylenaea praecelsa	Hippocrateaceae	L	12	0.06	-	-	-	-
Inga acuminata	Fabaceae-Mimosoideae	U	259	1.12	368	63	S	0.249
Inga goldmanii	Fabaceae-Mimosoideae	T	10	0.05	341	6	I	0.167
Inga laurina	Fabaceae-Mimosoideae	T	18	0.08	75	4	-	0.179
Inga marginata	Fabaceae-Mimosoideae	T	953	4.03	398	34	S	0.241
Inga mucuna	Fabaceae-Mimosoideae	T	0	0	4	0	-	-
Inga multijuga	Fabaceae-Mimosoideae	T	59	0.29	154	49	-	0.876
Inga nobilis	Fabaceae-Mimosoideae	M	23	0.12	663	121	S	0.205
Inga oerstediana	Fabaceae-Mimosoideae	T	2	0.01	3	0	I	-
Inga pezizifera	Fabaceae-Mimosoideae	T	3	0.02	120	1	-	0.358
Inga punctata	Fabaceae-Mimosoideae	T	0	0	20	3	-	0.445
Inga ruiziana	Fabaceae-Mimosoideae	T	0	0	12	0	I	0.328
Inga sapindoides	Fabaceae-Mimosoideae	M	39	0.19	250	28	G	0.191
Inga spectabilis	Fabaceae-Mimosoideae	T	4	0.02	17	8	-	-
Inga thibaudiana	Fabaceae-Mimosoideae	M	17	0.08	55	5	G	0.337
Inga umbellifera	Fabaceae-Mimosoideae	M	46	0.23	830	41	S	0.189
Inga vera	Fabaceae-Mimosoideae	M	8	0.04	0	0	-	-
Jacaranda copaia	Bignoniaceae	T	17	0.08	264	165	G	0.755
Koanophyllon wetmorei	Asteraceae	S	0	0	3	2	-	-
Lacistema aggregatum	Flacourtiaceae	U	245	1.15	1404	134	S	0.15
Lacmellea panamensis	Apocynaceae	M	32	0.16	98	28	-	0.353
Laetia procera	Flacourtiaceae	T	0	0	26	6	-	-
Laetia thamnia	Flacourtiaceae	U	25	0.13	451	52	S	0.177
Lafoensia punicifolia	Lythraceae	T	0	0	5	2	-	-
Leandra dichotoma	Melastomataceae	S	0	0	1	-	-	-
Licania hypoleuca	Chrysobalanaceae	M	11	0.06	127	18	S	0.146
Licania platypus	Chrysobalanaceae	T	13	0.06	282	1	-	0.148
Lindackeria laurina	Flacourtiaceae	M	2	0.01	70	56	-	-
Lonchocarpus heptaphyllus	Fabaceae-Papilionoideae	T	63	0.31	734	31	G	0.189
Lozania pittieri	Flacourtiaceae	U	0	0	3	0	-	-
Luehea seemannii	Tiliaceae	T	51	0.2	217	48	G	0.353

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App. 1, cont.

Species	Family	Growth form	No. seedlings	% plots present	No. stems ≥ 1 cm DBH	No. reproductive adults	Shade tolerance guild	Max. sapling growth (mm/year)
Lycianthes maxonii	Solanaceae	S	68	0.24	0	-	-	-
Macfadyena unguis-cati	Bignoniaceae	L	192	0.84	-	-	-	-
Machaerium floribundum	Fabaceae-Papilionoideae	L	1	0.01	-	-	-	-
Machaerium isadelphum	Fabaceae-Papilionoideae	L	12	0.06	-	-	-	-
Machaerium milleflorum	Fabaceae-Papilionoideae	L	91	0.44	-	-	-	-
Machaerium pittieri	Fabaceae-Papilionoideae	L	65	0.28	-	-	-	-
Machaerium seemannii	Fabaceae-Papilionoideae	L	36	0.17	-	-	-	-
Maclura tinctoria	Moraceae	T	0	0	1	0	-	-
Macrocnemum roseum	Rubiaceae	M	1	0.01	91	28	G	0.145
Malpighia romeroana	Malpighiaceae	S	13	0.06	43	-	-	-
Maquira guianensis	Moraceae	M	9	0.05	1460	156	S	0.177
Marcgravia nepenthoides	Marcgraviaceae	L	1	0.01	-	-	-	-
Margaritaria nobilis	Euphorbiaceae	U	0	0	3	-	I	-
Marila laxiflora	Clusiaceae	M	0	0	21	9	-	0.093
Maripa panamensis	Convolvulaceae	L	420	1.95	-	-	-	-
Marsdenia crassipes	Asclepiadaceae	L	2	0.01	-	-	-	-
Mascagnia hiraea	Malpighiaceae	L	847	2.76	-	-	-	-
Mascagnia morphosp. 1	Malpighiaceae	L	2	0.01	-	-	-	-
Mascagnia ovatifolia	Malpighiaceae	L	172	0.8	-	-	-	-
Maytenus schippii	Celastraceae	M	5	0.03	81	32	-	0.113
Mendoncia gracilis	Acanthaceae	L	19	0.1	-	-	-	-
Mendoncia litoralis	Acanthaceae	L	11	0.06	-	-	-	-
Miconia affinis	Melastomataceae	U	31	0.15	375	117	G	0.377
Miconia argentea	Melastomataceae	M	102	0.44	600	75	G	0.484
Miconia elata	Melastomataceae	U	1	0.01	17	1	I	0.213
Miconia hondurensis	Melastomataceae	U	5	0.02	55	7	-	0.265
Miconia impetiolaris	Melastomataceae	U	0	0	14	8	-	0.198
Miconia morphosp. 15	Melastomataceae	S	0	0	1	-	-	-
Miconia nervosa	Melastomataceae	S	68	0.3	292	-	-	-
Miconia prasina	Melastomataceae	U	0	0	2	-	-	-
Mikania leiostachya	Asteraceae	L	17	0.09	-	-	-	-
Morphospecies 1	Malpighiaceae	L	37	0.18	-	-	-	-
Mosannona garwoodii	Annonaceae	M	32	0.16	436	136	S	0.154
Mouriri myrtilloides	Melastomataceae	S	2376	10.07	6512	2535	-	-
Myrcia gatunensis	Myrtaceae	U	14	0.07	48	9	-	0.202
Myrospermu frutescens	Fabaceae-Papilionoideae	T	5	0.03	13	4	-	-
Nectandra ”fuzzy” (morphosp.)	Lauraceae	T	0	0	3	0	-	-
Nectandra cissiflora	Lauraceae	T	22	0.11	197	0	S	0.265
Nectandra lineata	Lauraceae	M	136	0.66	98	7	G	0.246
Nectandra purpurea	Lauraceae	M	2	0.01	75	7	-	0.18
Neea amplifolia	Nyctaginaceae	S	26	0.13	64	-	-	-
Ochroma pyramidale	Bombacaceae	M	1	0.01	9	2	-	-
Ocotea cernua	Lauraceae	M	67	0.34	222	69	S	0.186
Ocotea oblonga	Lauraceae	T	95	0.47	148	10	I	0.402
Ocotea puberula	Lauraceae	T	33	0.17	138	5	I	0.231
Ocotea whitei	Lauraceae	T	2407	1.91	429	65	S	0.232
Odontocarya morphosp. 1	Menispermaceae	L	6	0.03	-	-	-	-
Odontocarya tamoides	Menispermaceae	L	1	0.01	-	-	-	-
Omphalea diandra	Euphorbiaceae	L	16	0.08	-	-	-	-
Ormosia amazonica	Fabaceae-Papilionoideae	T	0	0	1	0	-	-
Ormosia coccinea	Fabaceae-Papilionoideae	T	6	0.03	88	2	-	0.158
Ormosia macrocalyx	Fabaceae-Papilionoideae	T	11	0.06	107	2	-	0.142
Ouratea lucens	Ochnaceae	S	300	1.41	1193	196	-	-
Pachira quinata	Bombacaceae	T	0	0	1	1	-	-
Pachira sessilis	Bombacaceae	T	0	0	16	2	-	-
Palicourea guianensis	Rubiaceae	S	107	0.45	867	-	-	-
Paragonia pyramidata	Bignoniaceae	L	190	0.88	-	-	-	-
Parathesis macrocalyx	Myrsinaceae	S	4	0.02	0	-	-	-
Passiflora ambigua	Passifloraceae	L	3	0.02	-	-	-	-
Paullinia baileyi	Sapindaceae	L	263	1.24	-	-	-	-
Paullinia bracteosa	Sapindaceae	L	96	0.43	-	-	-	-
Paullinia fibrigera	Sapindaceae	L	133	0.64	-	-	-	-
Paullinia fuscescens var. *glabrata*	Sapindaceae	L	3	0.02	-	-	-	-
Paullinia glomerulosa	Sapindaceae	L	28	0.14	-	-	-	-
Paullinia morphosp. 1	Sapindaceae	L	6	0.03	-	-	-	-

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App. 1, cont.

Species	Family	Growth form	No. seedlings	% plots present	No. stems ≥ 1 cm DBH	No. reproductive adults	Shade tolerance guild	Max. sapling growth (mm/year)
Paullinia pinnata	Sapindaceae	L	2	0.01	-	-	-	-
Paullinia pterocarpa	Sapindaceae	L	156	0.75	-	-	-	-
Paullinia rugosa	Sapindaceae	L	46	0.22	-	-	-	-
Paullinia turbacensis	Sapindaceae	L	539	2.31	-	-	-	-
Pentagonia macrophylla	Rubiaceae	U	3	0.02	308	218	S	0.135
Perebea xanthochyma	Moraceae	M	5	0.03	242	32	S	0.187
Petrea volubilis	Verbenaceae	L	344	1.49	-	-	-	-
Phryganocydia corymbosa	Bignoniaceae	L	298	1.26	-	-	-	-
Picramnia latifolia	Picramniaceae	U	245	1.14	1047	259	S	0.137
Piper aequale	Piperaceae	S	29	0.12	51	-	-	-
Piper arboreum	Piperaceae	U	2	0.01	22	12	-	0.188
Piper aristolochiaefolium	Piperaceae	L	8	0.04	-	-	-	-
Piper colonense	Piperaceae	S	0	0	22	18	-	-
Piper cordulatum	Piperaceae	S	18	0.08	92	-	-	-
Piper darienense	Piperaceae	S	149	0.49	0	-	-	-
Piper imperialis	Piperaceae	U	0	0	1	1	-	-
Piper reticulatum	Piperaceae	U	10	0.05	123	77	I	0.341
Piper schiedeanum	Piperaceae	S	1	0.01	4	-	-	-
Pisonia aculeata	Nyctaginaceae	L	2	0.01	-	-	-	-
Pithecoctenium crucigerum	Bignoniaceae	L	98	0.44	-	-	-	-
Platymiscium pinnatum	Fabaceae-Papilionoideae	T	230	1.03	147	33	S	0.183
Platypodium elegans	Fabaceae-Papilionoideae	T	28	0.13	124	23	G	0.241
Pleonotoma variabilis	Bignoniaceae	L	54	0.26	-	-	-	-
Posoqueria latifolia	Rubiaceae	M	4	0.02	72	19	-	0.123
Poulsenia armata	Moraceae	T	7	0.04	1404	58	S	0.318
Pouruma bicolor	Cecropiaceae	T	22	0.11	59	9	G	0.445
Pouteria fossicola	Sapotaceae	T	0	0	3	2	-	-
Pouteria reticulata	Sapotaceae	T	1616	4.55	1401	81	S	0.133
Pouteria stipitata	Sapotaceae	M	9	0.05	71	24	I	0.186
Prestonia morphsp. 1	Apocynaceae	L	4	0.02	-	-	-	-
Prestonia obovata	Apocynaceae	L	18	0.09	-	-	-	-
Prionostema aspera	Hippocrateaceae	L	490	2.17	-	-	-	-
Prioria copaifera	Fabaceae-Caesalpinioideae	T	94	0.37	1382	79	S	0.167
Protium confusum	Burseraceae	M	1	0.01	4	0	-	-
Protium costaricense	Burseraceae	M	28	0.14	758	26	S	0.247
Protium panamense	Burseraceae	M	122	0.61	2899	109	S	0.177
Protium tenuifolium	Burseraceae	M	449	1.9	2853	184	S	0.179
Pseudobombax septenatum	Bombacaceae	T	1	0.01	16	6	G	-
Psidium friedrichsthalianum	Myrtaceae	U	3	0.02	53	4	-	0.123
Psychotria acuminata	Rubiaceae	S	112	0.48	12	-	-	-
Psychotria brachiata	Rubiaceae	S	1	0.01	0	-	-	-
Psychotria capitata	Rubiaceae	S	1	0.01	0	-	-	-
Psychotria chagrensis	Rubiaceae	S	22	0.09	6	-	-	-
Psychotria cyanococca	Rubiaceae	S	7	0.03	2	-	-	-
Psychotria deflexa	Rubiaceae	S	72	0.29	15	-	-	-
Psychotria graciliflora	Rubiaceae	S	106	0.34	52	-	-	-
Psychotria grandis	Rubiaceae	U	3	0.02	46	19	S	0.197
Psychotria hoffmannseggiana	Rubiaceae	S	310	1.38	1	-	-	-
Psychotria horizontalis	Rubiaceae	S	1086	4.76	3939	-	-	-
Psychotria limonensis	Rubiaceae	S	46	0.18	22	-	-	-
Psychotria marginata	Rubiaceae	S	318	1.4	554	-	-	-
Psychotria psychotriifolia	Rubiaceae	S	4	0.02	0	-	-	-
Psychotria racemosa	Rubiaceae	S	39	0.18	0	-	-	-
Psychotria tenuifolia	Rubiaceae	S	28	0.09	0	-	-	-
Pterocarpus rohrii	Fabaceae-Papilionoideae	T	62	0.31	1464	5	S	0.179
Quararibea asterolepis	Bombacaceae	T	3187	6.5	2200	350	S	0.154
Quassia amara	Simaroubaceae	U	2	0.01	131	80	-	0.124
Randia armata	Rubiaceae	U	771	3.45	1003	481	S	0.139
Rauvolfia littoralis	Apocynaceae	U	0	0	1	-	-	-
Rhynchosia pyramidalis	Fabaceae-Papilionoideae	L	64	0.28	-	-	-	-
Rinorea sylvatica	Violaceae	S	532	2.04	2314	1160	-	-
Rosenbergiodendron formosum	Rubiaceae	U	0	0	4	4	-	-
Rourea glabra	Connaraceae	L	29	0.14	-	-	-	-
Sapium broadleaf	Euphorbiaceae	T	0	0	4	2	-	-
Sapium glandulosum	Euphorbiaceae	T	3	0.02	40	8	G	-

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App. 1, cont.

Species	Family	Growth form	No. seedlings	% plots present	No. stems ≥ 1 cm DBH	No. reproductive adults	Shade tolerance guild	Max. sapling growth (mm/year)
Schizolobium parahyba	Fabaceae-Caesalpinioideae	T	0	0	17	0	-	-
Senna dariensis	Fabaceae-Caesalpinioideae	S	28	0.13	66	-	-	-
Serjania circumvallata	Sapindaceae	L	71	0.34	-	-	-	-
Serjania mexicana	Sapindaceae	L	10	0.05	-	-	-	-
Serjania rhombea	Sapindaceae	L	38	0.19	-	-	-	-
Simarouba amara	Simaroubaceae	T	255	1.21	1230	72	I	0.353
Siparuna guianensis	Siparunaceae (Monimiaceae)	M	0	0	30	11	-	-
Siparuna pauciflora	Siparunaceae (Monimiaceae)	U	35	0.17	315	105	S	0.242
Sloanea terniflora	Elaeocarpaceae	T	7	0.04	493	9	S	0.123
Smilax mollis	Smilacaceae	L	4	0.02	-	-	-	-
Smilax spinosa	Smilacaceae	L	3	0.02	-	-	-	-
Solanum adhaerens	Solanaceae	L	13	0.07	-	-	-	-
Solanum asperum	Solanaceae	S	5	0.03	7	-	-	-
Solanum hayesii	Solanaceae	M	8	0.04	50	27	G	0.578
Solanum steyermarkii	Solanaceae	S	0	0	1	1	-	-
Sorocea affinis	Moraceae	S	317	1.55	2832	1511	-	-
Spachea membranacea	Malpighiaceae	U	0	0	13	8	-	-
Spondias mombin	Anacardiaceae	T	2	0.01	83	16	-	1.318
Spondias radlkoferi	Anacardiaceae	T	86	0.4	260	28	G	0.382
Sterculia apetala	Sterculiaceae	T	7	0.04	56	10	I	0.236
Stizophyllum inaequilaterum	Bignoniaceae	L	2	0.01	-	-	-	-
Stizophyllum riparium	Bignoniaceae	L	9	0.04	-	-	-	-
Strychnos brachistantha	Loganiaceae	L	73	0.35	-	-	-	-
Strychnos darienensis	Loganiaceae	L	1	0.01	-	-	-	-
Strychnos panamensis	Loganiaceae	L	18	0.09	-	-	-	-
Strychnos toxifera	Loganiaceae	L	3	0.02	-	-	-	-
Stylogyne turbacensis	Myrsinaceae	S	223	1.12	681	121	-	-
Swartzia simplex var. *continentalis*	Fabaceae-Papilionoideae	U	335	1.65	2892	969	S	0.123
Swartzia simplex var. *grandiflora*	Fabaceae-Papilionoideae	U	828	3.92	2662	282	S	0.124
Symphonia globulifera	Clusiaceae	T	14	0.07	160	7	S	0.151
Tabebuia guayacan	Bignoniaceae	T	15	0.05	69	19	-	0.15
Tabebuia rosea	Bignoniaceae	T	59	0.29	245	22	I	0.199
Tabernaemontana arborea	Apocynaceae	T	140	0.69	1506	156	I	0.2
Tachigali versicolor	Fabaceae-Caesalpinioideae	T	384	1.28	2485	7	S	0.174
Talisia nervosa	Sapindaceae	U	11	0.06	747	420	S	0.126
Talisia princeps	Sapindaceae	M	77	0.39	633	15	S	0.121
Terminalia amazonia	Combretaceae	T	1	0.01	47	16	I	0.473
Terminalia oblonga	Combretaceae	T	1	0.01	89	27	-	0.186
Ternstroemia tepezapote	Theaceae	U	0	0	1	1	-	-
Tetracera hydrophila	Dilleniaceae	L	1	0.01	-	-	-	-
Tetracera portobellensis	Dilleniaceae	L	50	0.24	-	-	-	-
Tetragastris panamensis	Burseraceae	T	1557	6.05	4230	129	S	0.163
Tetrapterys goudotiana	Malpighiaceae	L	37	0.16	-	-	-	-
Tetrathylaceum johansenii	Flacourtiaceae	T	0	0	7	6	-	-
Theobroma cacao	Sterculiaceae	U	0	0	18	11	-	-
Thevetia ahouai	Apocynaceae	U	7	0.03	74	66	I	0.28
Thinouia myriantha	Sapindaceae	L	166	0.81	-	-	-	-
Tocoyena pittieri	Rubiaceae	M	2	0.01	7	5	-	-
Tournefortia hirsutissima	Boraginaceae	L	1	0.01	-	-	-	-
Trattinnickia aspera	Burseraceae	T	0	0	66	18	-	-
Trema micrantha	Ulmaceae	M	1	0.01	28	11	-	-
Trichanthera gigantea	Acanthaceae	U	0	0	7	7	-	-
Trichilia pallida	Meliaceae	M	30	0.15	519	121	S	0.185
Trichilia tuberculata	Meliaceae	T	1440	6.11	11977	434	S	0.134
Trichospermum galeottii	Tiliaceae	M	0	0	10	6	-	-
Triplaris cumingiana	Polygonaceae	M	28	0.13	259	46	I	0.479
Trophis caucana	Moraceae	U	81	0.37	175	138	S	0.189
Trophis racemosa	Moraceae	M	41	0.2	285	37	S	0.13
Turpinia occidentalis	Staphyleaceae	T	8	0.03	72	9	G	-
Uncaria tomentosa	Rubiaceae	L	1	0.01	-	-	-	-
Unonopsis pittieri	Annonaceae	M	164	0.79	656	230	S	0.268
Urera baccifera	Urticaceae	S	4	0.02	16	13	-	-
Verbesina gigantea	Asteraceae	S	0	0	1	-	-	-
Vernonanthura patens	Asteraceae	S	1	0.01	0	-	-	-
Virola multiflora	Myristicaceae	T	2	0.01	47	9	-	0.312
Virola sebifera	Myristicaceae	M	47	0.24	1615	251	S	0.2

→

App. 1, cont.

Species	Family	Growth form	No. seedlings	% plots present	No. stems ≥ 1 cm DBH	No. reproductive adults	Shade tolerance guild	Max. sapling growth (mm/year)
Virola surinamensis	Myristicaceae	T	17	0.09	200	87	-	0.166
Vismia baccifera	Clusiaceae	U	11	0.05	55	38	G	0.455
Vismia macrophylla	Clusiaceae	M	0	0	1	-	-	-
Vochysia ferruginea	Vochysiaceae	T	5	0.02	21	4	-	0.728
Xylopia macrantha	Annonaceae	M	130	0.64	1220	160	S	0.234
Xylosma oligandra	Flacourtiaceae	S	8	0.04	95	70	-	-
Zanthoxylum acuminatum	Rutaceae	M	4	0.02	116	10	G	0.298
Zanthoxylum ekmanii	Rutaceae	T	21	0.1	234	93	G	1.866
Zanthoxylum panamense	Rutaceae	T	24	0.12	143	18	G	0.264
Zanthoxylum setulosum	Rutaceae	M	0	0	1	1	-	-
Zuelania guidonia	Flacourtiaceae	M	3	0.02	36	4	I	0.145