

Influence of a common palm, *Oenocarpus mapora*, on seedling establishment in a tropical moist forest in Panama

Krista Farris-Lopez^{*1}, Julie S. Denslow[†], Barry Moser^{*‡} and Heather Passmore^{*}

^{*} Department of Biological Sciences, Louisiana State University, 202 Life Sciences Building, Baton Rouge, LA 70803, USA

[†] USDA Forest Service, Institute of Pacific Islands Forestry, 23 E. Kawili St., Hilo, HI 96720, USA

[‡] Department of Experimental Statistics, Louisiana State University, 101 Administration Building, Baton Rouge, LA 70803, USA

(Accepted 21st July 2003)

Abstract: Plants often modify microsite conditions important for seedling establishment. In tropical moist forest, advance regeneration in the form of shade-suppressed seedlings is a major component of regrowth in new gaps. Tree seedlings may be filtered by the composition and structure of the forest understorey. In a lowland forest in Central Panama, we examined light availability, litter accumulation and the seedling community (abundance, diversity and composition) under and away from the canopies of a common subcanopy, clonal palm, *Oenocarpus mapora*, and tested whether seedling abundance varies as a function of changes in understorey light conditions and leaf litter depth. We found evidence that leaf litter was five times deeper and light availability 27% lower under *O. mapora* canopy than where it was absent. The probability of finding a seedling in plots under *O. mapora* canopies was 33% lower than in plots without the palm. Plots under *O. mapora* canopies also had 49% fewer species of seedlings and those seedlings came from significantly larger seeds than seedlings in plots not under the palm. Overall, seedling density was positively correlated with light availability and negatively correlated with leaf litter depth. A transplant experiment confirmed that for at least one large-seeded species of dicot, seedlings are negatively affected by the reduction in light availability and increase in leaf litter. Under *O. mapora*, seedlings of *Gustavia superba* (Lecythidaceae) had lower survivorship and biomass accumulation than away from the palm. Thus, site conditions produced by large, clonal, multi-layered palms such as *O. mapora* may reduce establishment of small-seeded and shade-intolerant species, potentially affecting species composition in the understorey seedling pool.

Key Words: leaf litter, light availability, palms, seed size, shade tolerance

INTRODUCTION

In mesic forests, seedlings and saplings established in the understorey are a major component of the regrowth in new gaps (Ashton 1992, Brokaw 1985, Morin 1994, Uhl *et al.* 1988). In the understorey these seedlings often are suppressed and their growth and survival are often low unless a tree-fall gap or other disturbance creates more favourable light conditions (Canham *et al.* 1994, Denslow *et al.* 1990, Fraver *et al.* 1998, Pereira de Souza & Valio 2001, Poulson & Platt 1989, 1996). As a result, environmental conditions in the understorey may influence the composition, relative abundance and

distribution of seedlings present when treefalls provide opportunity for growth into the overstorey (Denslow 1987, George & Bazzaz 1999, Hubbell & Foster 1986, Kobe *et al.* 1995, Montgomery & Chazdon 2001, Pacala *et al.* 1996).

In tropical forests, light availability in the understorey is typically below 2% of that above the canopy and is likely to be one of the most limiting resources for seedling establishment and growth (Chazdon & Fetcher 1984, Kabakoff & Chazdon 1996). However, understorey light is spatially variable and this variability may be attributed in large part to the distribution of understorey trees and shrubs (Canham *et al.* 1994, Denslow *et al.* 1991, George & Bazzaz 1999, Kabakoff & Chazdon 1996, Montgomery & Chazdon 2001). Species-specific differences in crown geometry and tree architecture have been shown to influence spatial distribution of

¹ Corresponding author. 180 Sutton Rd, Bryson City, NC 28731, USA
Email: kristalopez@yahoo.com

understorey light environments in both temperate and tropical forests (Canham *et al.* 1994, Kabakoff & Chazdon 1996). In addition to light availability, tree seedling establishment has been shown to be sensitive to microsite conditions such as soil moisture, nutrient supply and leaf litter distribution (Augsburger 1983, 1984a; Facelli 1994, Garwood 1983, Molofsky & Augspurger 1992). The extent to which a particular overstorey species alters environmental conditions may determine the effect of that species on seedling establishment.

In tropical forests, palms, in particular, may influence microsite conditions important for seedling establishment and growth. Palms are often abundant in the canopy as well as lower strata where they can account for 60–70% of the total cover in neotropical forests (Balslev *et al.* 1987, Borchsenius 1997, Kahn & de Granville 1992, Kahn *et al.* 1988, Martínez Ramos *et al.* 1988, Peres 1994). High densities of palms have been suggested to reduce the abundance of seedlings and saplings of some species (Denslow *et al.* 1991, Pinero *et al.* 1986). The effects may be non-specific, affecting only seedling densities, or they may differentially influence emergence and survival of certain types of species, thereby influencing the composition and spatial structure of the seedling bank. *Oenocarpus mapora* Bailey (Arecaceae) is a long-lived, clonal, subcanopy palm that may reach high densities in second-growth and old-growth forests (De Steven 1986, 1989). Populations of *O. mapora* are relatively resilient to disturbance because of their clonal habit (De Steven 1989) and their multi-layered canopy composed of large fronds may have long-lasting impacts on environmental conditions in the understorey of a moist tropical forest in central Panama.

We tested the hypothesis that *Oenocarpus mapora* creates unsuitable microsite conditions for seedling establishment, survival and growth in the forest understorey. Specifically, we asked whether light availability and leaf litter distribution are affected by proximity to these palms and, if so, how these microsite conditions affect seedling density, diversity and composition. We predicted that forest understoreys where *O. mapora* palms are abundant would be more shaded, have greater accumulation of leaf litter, and have lower seedling density and diversity than areas free of *O. mapora*. We predicted that in general, microsites with low light availability and high leaf litter accumulation would harbour fewer species of small-seeded, light-demanding species. We predicted that large-seeded species would be more likely to establish under *O. mapora* because larger seeds produce larger seedlings and provide more carbon reserves in low light environments, but that even large-seeded species would be negatively affected by *O. mapora*. We further tested whether seedling survivorship and growth were reduced by proximity to *O. mapora* with a transplant experiment using seedlings of

a common, large-seeded subcanopy tree, *Gustavia superba* (H.B.K.) Berg (Lecythydaceae).

MATERIALS AND METHODS

Study site

The study sites were located on Barro Colorado Island, in Lake Gatun, Panama (BCI, 9°10'N, 79°51'W). The forests on BCI receive *c.* 2600 mm of annual rainfall, most of which occurs between May and December (Dietrich *et al.* 1982, Foster & Brokaw 1982). Detailed descriptions of the vegetation on BCI are found in Croat (1978), Hubbell & Foster (1986), and Leigh *et al.* (1996). We used two old-growth stands, Armour and Zetek, and one late second-growth stand, Barbour (*c.* 100 y old) (Knight 1975). These study stands were a subset of a chronosequence of forest stands described by Denslow & Guzman (2000). There were no significant differences in mean stand heights, tree densities, seedling densities, basal areas or light levels among the three stands (Denslow & Guzman 2000).

Microsite and vegetation sampling

In each stand, microsite conditions and vegetation were sampled in two parallel 160-m transects composed of contiguous 1-m² quadrats. Each transect was established well inside the forest edge and separated from other transects by at least 20 m (Denslow & Guzman 2000).

Incident light availability was measured at 75 cm from ground level using PAR sensors (LiCor™ LI190SA) attached to LiCor Plant Canopy Analysers (LiCor™ PCA2000) operating in two sensor mode (Denslow & Guzman 2000) during 1995. Readings were taken at 1-m intervals along each transect when the sun was obscured by continuous cloud cover or near the horizon. Above-canopy light levels were estimated concurrently with an instrument positioned outside of the forest where it had an unobscured view of the sky within 52° of zenith; per cent transmittance of photosynthetically active radiation (%TPAR) was calculated as the ratio of below-canopy to above-canopy readings. Where readings within 0.5 m of the sampling point were obscured by trees or fallen logs, the point was recorded as missing data. TPAR for each quadrat was estimated as the average of two measurements.

Palms were recorded as present for all quadrats in which *O. mapora* covered at least half the quadrat at any given height and absent for those in which *O. mapora* covered less than half of the quadrat in May 1999. Palm size-class was also recorded for each genet based on the classification of the largest ramet. Palms were classified as juvenile for individuals less than 1 m, immature for

individuals or clonal genets greater than 1 m but less than 8 m tall, and adult for clonal individuals greater than 8 m tall. *Oenocarpus mapora* generally reproduces sexually when it reaches 8 m tall (De Steven 1989).

Leaf-litter distribution was measured at 0.5-m intervals along each transect in May 2000; the values for both leaf-litter layers and leaf-litter depth per 1-m² plot are averages from the two measurements which were independent for each 1-m² plot. Leaf-litter depth was measured on a metal probe inserted into the leaf litter to the soil surface. The number of leaf-litter layers was estimated by counting the number of leaves penetrated by the inserted metal probe. Number of leaf layers and depth of leaves were significantly, but not strongly, correlated ($r^2 = 0.30$, $P < 0.0001$). The effect of number of leaf layers on seedling abundance was similar to leaf-litter depth, so only data on leaf-litter depth are presented.

Oenocarpus mapora and litter distributions were sampled several years after measurements of light availability and seedling distribution. However studies of *Oenocarpus* demography suggest that population turnover of this species in these forests is low. A six-year demographic study of *O. mapora* near our study sites (De Steven 1989) showed that survivorship is high, ramet production is generally low, and seedling and juvenile recruitment is low in our sites. Thus we believe that correlations between environmental measurements and palm populations are not likely to be spurious.

Within each plot along the transect, all woody seedlings, except palms and lianas, 20–100 cm tall were identified to species at the same time that light availability was measured, and abundance per species per plot was tallied. We used a relatively large minimum seedling size of 20 cm to sample primarily established individuals rather than new germinants. Each species of seedling was placed into a seed size class based on average dry seed weight: 1 = 10–100 g, 2 = 1–10 g, 3 = 0.1–1 g, 4 = 0.01–0.1 g, 5 = 1–10 mg, 6 = 0.1–1 mg, 7 = 0.01–0.1 mg following Foster (1996). The absolute number of species present in plots both under and away from *O. mapora* canopy is reported for each site. Because sample sizes varied between palm and non-palm plots, we also used a species richness estimator to account for sample-size bias. Estimates of species richness are highly dependent on the number of individuals and the area sampled. The incidence-based coverage estimator, ICE, was used to compare species diversities. ICE is a non-parametric method of estimating species richness based on the number of species found in less than 10 quadrats (Chazdon *et al.* 1998, Lee & Chao 1994). The principle for ICE measurements is that the needed information about undiscovered species (those not sampled) lies in the number of rare species already found. ICE is a robust estimator of species richness and is reported to be insensitive to sample size (Chazdon *et al.* 1998, Colwell & Coddington 1995). ICE values

were generated using EstimateS software (Colwell & Coddington 1995).

Transplant experiment design

To examine the effects of *O. mapora* on seedling survival and growth for one species of dicot, we conducted a transplant experiment. Seedlings of a common subcanopy tree, *Gustavia superba* were grown from seed in May 1999. Adults of *Gustavia superba* are typically 10–12 m tall and occur in old-growth as well as secondary forests on BCI (Foster & Brokaw 1982). *Gustavia superba* is a large-seeded, mammal-dispersed species that survives well in understorey environments (Sork 1987). A total of 256 1-mo-old seedlings were blocked by size and planted bare-rooted at eight sites in a late-secondary forest on BCI. Seedlings were planted in groups of four with one plant at each corner of a quadrat measuring 25 cm on a side. To test the importance of palm litter, half of the seedlings were covered by a litter treatment. Four quadrats were placed beneath each of eight adult *O. mapora* palms 25 cm from its base, and four more quadrats were placed approximately 2 m away from the *O. mapora* individual. Two of the four quadrats for each palm and non-palm site were covered by palm litter. Dead leaves from *O. mapora* fall with the rachis often still attached to the stem, so that much of the litter hangs suspended above the ground. To simulate natural leaf litter conditions, three palm fronds were suspended 30 cm above ground level laid across string tied to corner posts located outside of each seedling quadrat. This height was typical for suspended leaf litter of adult *O. mapora* palms.

After 7 mo, mortality was recorded and all surviving seedlings were harvested. Stem height, total leaf area, and above-ground dry mass were measured. Pathogen and herbivore damage was estimated as the per cent leaf area missing by tracing leaves and holes in leaves on paper and calculating leaf area missing from damaged leaves using a LiCor 1000 area meter.

Statistical analyses

We analysed the fixed effects of palm presence or absence and size class on complementary log-transformed %TPAR. Because light availability was shown to be spatially correlated in these stands (Denslow & Guzman 2000), plots that are close together may not be independent samples. To account for this spatial dependency, an ANOVA was performed using a first-order autoregressive covariance structure [Sp(POW) in PROC MIXED (SAS V.8 SAS Institute 1998)] which incorporates spatial dependencies into the model. Spatial dependence was estimated by $Sp = \sigma^2 \rho^{d_{ij}}$ where the variance σ^2 , is

multiplied by ρ , the spatial correlation parameter where $|\rho| < 1$, and d_{ij} represents the absolute distance between plots of the i th and j th observations in the data set. Tukey's test was used to do *a posteriori* multiple treatment comparisons. We examined the effects of palm presence, leaf litter, and light availability on the probability of seedling occurrence using logistic regression analyses. Because seedling density is also spatially autocorrelated (Denslow & Guzman 2000), a first order autoregressive covariance structure [Sp(POW)] was used for all logistic regression models using PROC LOGISTIC of SAS (SAS V.8 SAS Institute 1998).

To test for differences in seed size for species of seedlings occurring in palm and non-palm plots, we used contingency table analyses with the Likelihood Ratio chi-square (G^2) test and a Kolmogorov–Smirnov two-sample test to examine differences in seed size distributions. Importance values (IV) were calculated for seedlings present in nine or more plots as the average of relative abundance and relative frequency for each species. We used IV to compare relative importances of common species with and without the presence of *O. mapora*.

Seedling growth parameters were analysed using split-plot ANOVA with site and plot factors as covariates. The model used for the split plot analyses is:

$$Y_{ijkl} = P_i + B_j + \sigma_{ij} + L_k + P_iL_k + \sigma_{ijk} + \sigma_{ijkl}$$

where P = palm canopy treatment, B = block (eight replicates), σ_{ij} is the variance used to test the effect of the main treatment P , L = palm litter treatment, P_iL_k = palm and litter treatment interaction, and σ_{ijk} = the error term used to test for the effects of litter treatment and σ_{ijkl} = error term used to test for the effects of the interaction term Palm \times Litter. Stem length and herbivory were log-transformed whereas the square roots of leaf area and dry mass were used to normalize residuals. To test the effects of palm canopy and palm litter treatments on seedling survival the macro GlimMix in PROC MIXED (SAS V.8.2 SAS Institute 1998) was used with a binomial error and logit link function.

RESULTS

Microhabitat characteristics

Oenocarpus mapora modifies the environment of the forest floor in several ways. Light levels ranged from 0.06–8.1%. The presence of *O. mapora* reduced light availability to seedlings by 27% of *O. mapora*-free sites (0.80 ± 0.3 %TPAR vs. 1.07 ± 0.03 %TPAR (mean \pm SE) for *O. mapora* and *O. mapora*-free sites respectively; $F = 4.66$, $df = 1, 808$, $P < 0.03$). Light availability also decreased as a function of *O. mapora* size class. Juvenile *O. mapora* palms reduced light availability by 13%,

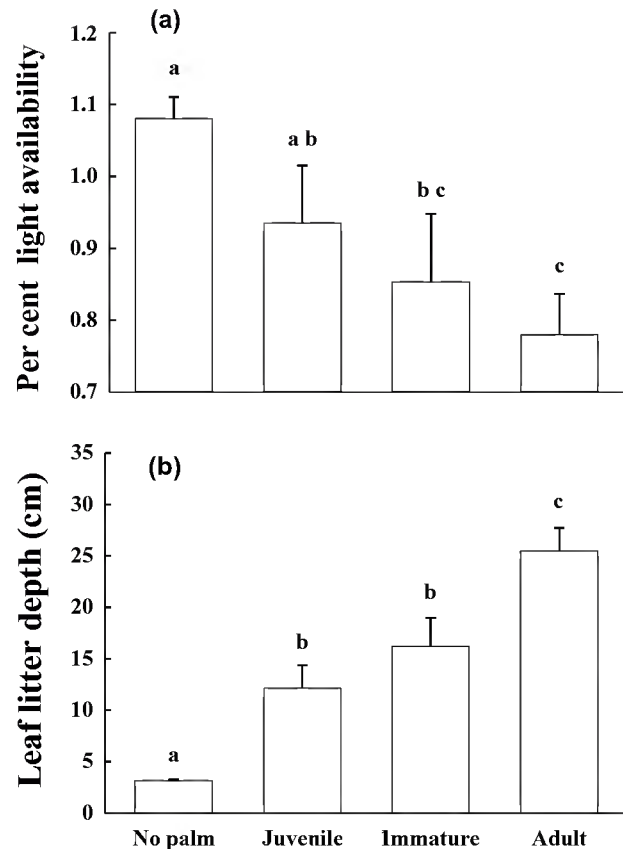


Figure 1. Effect of *Oenocarpus mapora* on light availability (a) measured as per cent transmittance of photosynthetically active radiation, and leaf litter depth (b) measured as distance from bare soil to the uppermost leaf. Bars show means with standard errors for plots with No palm (away from *O. mapora* canopy) and plots under *O. mapora* in three palm size classes: juvenile, immature and adult. Shared letters indicate that means are not significantly different at $P < 0.05$. ANOVA test statistic for the effects of *O. mapora* on light availability (all palm size classes pooled) $F = 4.66$, $df = 1, 808$, $P < 0.03$, and leaf litter accumulation $F = 164$, $df = 1, 956$, $P < 0.01$. Data are from three sites on Barro Colorado Island.

immature *O. mapora* by 21% and adult *O. mapora* by 28% of *O. mapora*-free understorey (Figure 1a). Leaf litter depth ranged between 0 and 117 cm. Leaf-litter depth was greater in plots under *O. mapora* canopy of all size classes than in plots not under *O. mapora* ($F = 164$, $df = 3, 956$, $P < 0.0001$). Less than 5% of the plots measured had no leaf litter and, of those plots, only two were under palms. Mean leaf-litter depth increased with palm size and was 381%, 506% and 797% greater in the juvenile, immature and adult *O. mapora* plots respectively, than non-*O. mapora* plots (Figure 1b).

Oenocarpus mapora creates microsite conditions unfavourable for the establishment of many seedlings. Light availability was a strong predictor of seedling occurrence. Seedling presence was positively correlated with light availability regardless of palm presence (Figure 2). However, light availability alone did not account for the low seedling occurrence under larger palms. Seedling

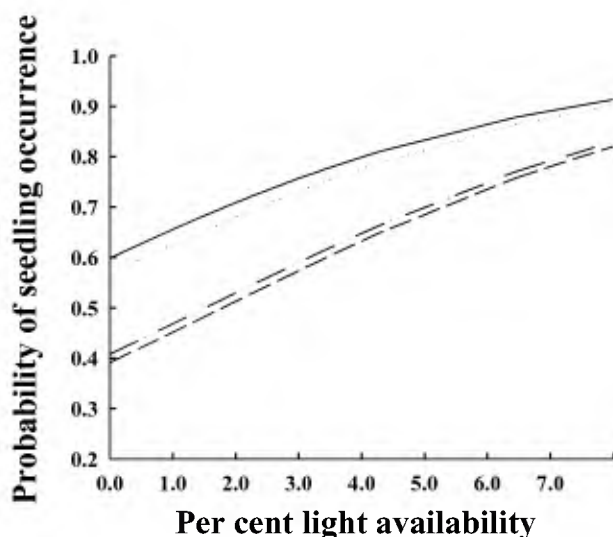


Figure 2. Logistic regression of the probability of seedling occurrence as a function of light availability (measured as per cent transmittance of photosynthetically active radiation) for plots away from *Oenocarpus mapora* (solid line) and plots under *O. mapora* for three palm size classes: Juvenile (dotted line), Immature (dashed and dotted line) and Adult (dashed line). Goodness of fit deviance is 1.32, $df = 852$, likelihood ratio = 27.6, $df = 3$, $P < 0.0001$.

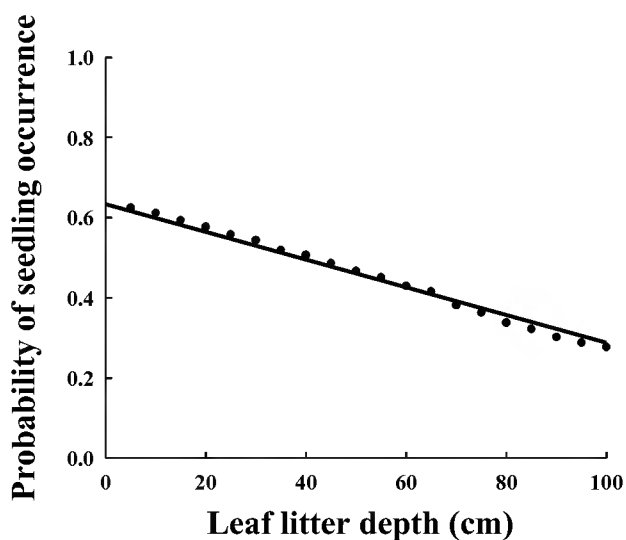


Figure 3. Logistic regression of the probability of seedling occurrence as a function of leaf litter depth. Dots are average probabilities at 5 cm increments starting at 0. The regression equation is: $y = -0.019x + 0.653$ with a likelihood ratio = 12.2, $df = 1$, $P < 0.0005$.

presence under immature and adult palms was 33% lower than non-palm sites of the same light level (Figure 2). Therefore larger palms had an additional impact on seedling establishment in addition to decreasing light availability. We found that leaf-litter accumulation also influenced seedling density. The probability of seedling presence decreased as leaf-litter depth increased (Figure 3). The greater leaf-litter accumulation under

Table 1. Number of quadrats in which at least one seedling was present in plots for *O. mapora* present and absent categories. Total number of seedlings and observed number of species as well as estimated total number of species (ICE) are presented for each site on Barro Colorado Island. Mean \pm SE are provided in parentheses for both observed and estimated seedling species under and away from *O. mapora* canopies. Seedling density was significantly lower where *O. mapora* was present ($F = 3.75$, $df = 956$, $P < 0.01$). Mean number of species was also lower where *O. mapora* was present ($F = 28.4$, $df = 4$, $P < 0.006$).

	Number of quadrats	Number of seedlings	Observed number of species	ICE species estimates
<i>O. mapora</i> present			(30 \pm 8)	(56 \pm 12)
Armour	128	199	35	63
Zetek	130	127	34	73
Barbour	62	38	20	31
<i>O. mapora</i> absent			(58 \pm 4)	(93 \pm 8)
Armour	192	245	61	110
Zetek	190	337	54	88
Barbour	258	326	58	83

larger *O. mapora* palms, apparently contributes to reduced seedling establishment in these microsites.

Mean seedling densities were generally low (0.9–1.65 seedlings m^{-2}). Seedling densities were significantly lower under *O. mapora* canopy than in palm-free plots ($F = 3.75$, $df = 1$, 956, $P < 0.01$) (Table 1). Because seedling densities are low under *O. mapora*, we expected the number of observed species to be low as well. Mean number of species observed in quadrats under *O. mapora* palms was 49% lower than quadrats away from *O. mapora* ($F = 28.4$, $df = 4$, $P < 0.006$) (Table 1). To take into account the differences in sample sizes, we estimated the asymptotic or total number of species in the species pools for palm and non-palm sites for each stand using an incidence-based coverage estimator (ICE) (Table 1). Estimated total number of species of seedlings in sites under *O. mapora* was 40% lower than in sites away from *O. mapora* ($F = 6.3$, $df = 4$, $P < 0.06$) (Table 1).

The most abundant species in the seedling community differed between plots under and away from *O. mapora*. The most abundant species in plots away from *O. mapora* was *Tetragastris occidentalis* (Engl.) Kuntze (Burseraceae); however, under *O. mapora* canopies *Beilschmiedia pendula* (Sw.) Hemsl. (Lauraceae) was more abundant. Of the most common species (present in at least nine plots), the Importance Values of only four were greater in palm than in non-palm plots (Table 2). *Beilschmiedia pendula*, for example, is a shade-tolerant (Lovelock *et al.* 1996, Welden *et al.* 1991), large-seeded species (Harms & Dalling 1997) with disease resistance (Gilbert *et al.* 1994), whose relative importance in the seedling pool was markedly greater in *O. mapora* plots than in non-palm plots. Under *O. mapora* canopies, seedlings were of species with significantly larger seeds than seedlings established in non-palm plots ($G^2 = 33.5$, $df = 6,680$, $P < 0.0001$). Relative frequencies for each seed size category for palm and non-palm plots are shown in Figure 4. The distribution of seed size was

Table 2. Importance values (IV) calculated as the average relative frequency and relative abundance for species found in nine or more quadrats for the three sites on Barro Colorado Island. Each species is categorized into a seed size class¹: 1 = 100–10 g, 2 = 10–1 g, 3 = 1–0.1 g, 4 = 0.1–0.01 g, 5 = 1–0.1 mg, 6 = 0.1–0.01 mg.

Species (family)	+ Palm IV	– Palm IV	Seed size
<i>Beilschmiedia pendula</i> (Lauraceae)	37	2	2
<i>Tetragastris panamensis</i> (Burseraceae)	27	24	3
<i>Faramea occidentalis</i> (Rubiaceae)	19	21	3
<i>Mouriri myrtilloides</i> (Melastomataceae)	12	19	4
<i>Pouteria reticulata</i> (Sapotaceae)	11	8	3
<i>Capparis frondosa</i> (Capparidaceae)	6	8	3
<i>Swartzia simplex</i> var. <i>grandiflora</i> (Fabaceae Caesalpinioideae)	6	3	3
<i>Hybanthus prunifolius</i> (Violaceae)	4	4	4
<i>Alseis blackiana</i> (Rubiaceae)	4	6	6
<i>Cupania sylvatica</i> (Sapindaceae)	4	6	3
<i>Garcinia intermedia</i> (Guttiferaceae)	3	4	? ²
<i>Swartzia simplex</i> var. <i>ochracea</i> (Fabaceae Caesalpinioideae)	3	3	3
<i>Ouratea lucens</i> (Ochnaceae)	3	4	4
<i>Desmopsis panamensis</i> (Annonaceae)	3	3	3
<i>Gustavia superba</i> (Lecythidaceae)	2	2	2
<i>Rinorea sylvatica</i> (Violaceae)	2	11	4
<i>Coussarea curvigenmia</i> (Rubiaceae)	1	4	5
<i>Psychotria horizontalis</i> (Rubiaceae)	1	5	5
<i>Psychotria deflexa</i> (Rubiaceae)	1	3	5
<i>Psychotria marginata</i> (Rubiaceae)	1	4	5
<i>Simarouba amara</i> (Simaroubaceae)	1	2	4
<i>Stylogyne standleyi</i> (Myrsinaceae)	0	4	4

¹ Seed size classes follow Foster (1996).

² Seed size not available.

also significantly different for seedlings established under *O. mapora* canopy and non-palm sites as determined by the Kolmogorov–Smirnov two-sample test ($D = 0.18$, $P < 0.0004$).

Transplant experiment

Survival of *G. superba*, was 38% lower for seedlings planted under *O. mapora* canopy vs. those planted away from palms ($F = 6.88$, $df = 1,7$, $P < 0.03$). Seedling survival was reduced by 45% under palm-litter treatments compared with controls ($F = 11.8$, $df = 1,14$, $P < 0.004$).

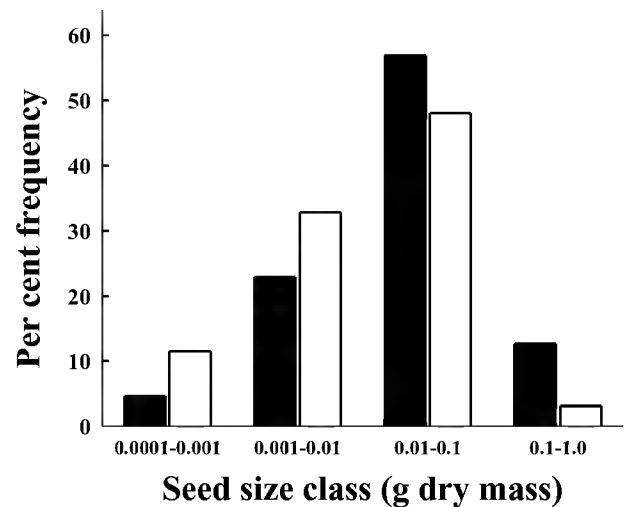


Figure 4. The distribution of seed sizes among seedlings established under *Oenocarpus mapora* canopy (shaded bars) and away from *O. mapora* canopies (clear bars) ($G^2 = 33.5$, $df = 6,680$, $P < 0.0001$).

Seedling growth rates were slow and stem height was often reduced as a result of stem loss from pathogens and herbivory. *Oenocarpus mapora* canopy significantly reduced stem length ($F = 5.32$, $df = 1,7$, $P < 0.02$) but not leaf area or dry mass (Table 3). The presence of suspended litter significantly increased total % herbivory ($F = 5.64$, $df = 1,14$, $P < 0.02$) but had no effect on growth as measured by changes in stem length, leaf area or dry mass (Table 3).

DISCUSSION

This study provides evidence that seedling establishment in the understorey is influenced by the variation of microsite conditions on the forest floor created by the overstorey vegetation. Our findings suggest that the palm *O. mapora* reduces light availability and increases leaf litter accumulation below its canopy, thereby creating areas that are not conducive for the establishment of some species of seedlings. We suggest that overstorey vegetation, such as palms, that reduce light availability

Table 3. Survival, growth, and herbivory parameter means \pm SE for transplanted seedlings ($n = 256$) of *Gustavia superba* planted under and away from *O. mapora* canopy ($n = 8$), with an additional sub-treatment of suspended leaf litter *O. mapora* ($n = 16$) on Barro Colorado Island. The presence or absence of the treatment is denoted by positive or negative symbols respectively.

	Palm		Litter	
	+	–	+	–
Survival (%)	41	66	38	70
Stem length (cm)	13.6 \pm 1.04	14.9 \pm 1.03	13.72 \pm 0.04	14.8 \pm 1.03
Dry mass (g)	0.62 \pm 0.002	0.72 \pm 0.001	0.63 \pm 0.002	0.72 \pm 0.001
Leaf area (cm ²)	87.4 \pm 0.39	119 \pm 0.27	98.7 \pm 0.30	106.9 \pm 0.19
Herbivory (% total area)	8.8 \pm 1.4	6.5 \pm 1.3	11.2 \pm 1.4	5.1 \pm 1.2

and/or create deep litter accumulation may act as an environmental filter selecting for seedling traits such as large seed and seedling size, shade tolerance and disease resistance that promote survival under such circumstances.

High light interception by the multilayered *O. mapora* canopy reduces light levels on the forest floor, thereby reducing the likelihood of seedling establishment. Light availability appears to be the primary factor limiting growth and survival for many tree seedlings in forest environments (Augspurger 1984b, Saverimuttu & Westoby 1996). For example, Kobe (1999) showed that increasing light levels from < 1 to 20% full sun, decreases mortality rates for species with a variety of life histories and Kitajima (1994) found that relative growth rates of seedlings at BCI were higher for sun-grown than for shade-grown plants for both pioneer and shade-tolerant species. Our data show a strong effect of light availability on seedling abundance even at very low light levels (< 2%). Metcalfe & Grubb (1997) also showed positive responses in seedling growth to increases in light availability from 0–0.5 to 1% for several tropical rain-forest species in Singapore. Therefore, small differences in TPAR may have a dramatic effect on seedling growth and survival in shaded tropical forest understorey habitats. The low density of seedlings found in palm sites suggests that light availability may be below the compensation points for many shade-tolerant tree species (Augspurger 1983, 1984b; Clark & Clark 1987, Denslow *et al.* 1990). However, variation in light availability alone is not a strong predictor of patterns of seedling distribution (Denslow & Guzman 2000, Nicotra *et al.* 1999, Welden *et al.* 1991).

Our data also suggest that the effects of low light availability are compounded by the effects of litter accumulation under palms. Leaf litter from *O. mapora* accumulates during the dry season when decay rates are slow and reaches its greatest depths at the beginning of the rainy season when the majority of seedlings germinate (Garwood 1983). This litter may present a physical barrier for newly germinating seedlings establishing their roots in mineral soil or emerging from below the litter. Leaf litter also can affect seedling establishment by changing light availability, microclimates and nutrient availability (Facelli & Facelli 1993, Facelli & Pickett 1991, Molofsky & Augspurger 1992). Leaf litter may reduce evaporation from the soil surface, which may enhance seedling establishment in dry months in seasonally dry forests (Molofsky & Augspurger 1992). However, high humidity may also facilitate pathogen damage to seedlings. Allelopathic effects may inhibit seedling growth and large falling fronds may inflict direct mortality by crushing seedlings established below the canopy (Aide 1987, Metcalfe & Grubb 1997, Torti *et al.* 2001). The impact of leaf litter cover on seedling establishment

varies by species of seedling, habitat type, and timing of germination (Molofsky & Augspurger 1992). For example, Molofsky & Augspurger (1992) found that in high-light environments seedling survival in the large-seeded species, *Gustavia superba*, was greater when seeds were buried under thick litter than when seeds were placed on top of litter. However, in the deep shade, litter depth had no effect on seedling survival, regardless of seed position (Molofsky & Augspurger 1992).

We found evidence that seedlings under *O. mapora* originate from larger seeds on average than do seedlings away from palms. It is likely that large seed size increases establishment success for seedlings. For example, large seed size has been correlated with seedling longevity in shaded environments (Leishman & Westoby 1994, Saverimuttu & Westoby 1996). The relative success of large-seeded species is often high in deep litter in comparison with small-seeded seedlings (Cintra 1997, Molofsky & Augspurger 1992, Svenning 2001). Large seeds produce large seedlings, which may provide a considerable competitive advantage in shaded environments (Fenner 1987, Westoby *et al.* 1992) as well as facilitate resprouting following physical damage (Dalling & Harms 1999, Harms & Dalling 1997). Large initial seedling height also promotes emergence through leaf litter (Molofsky & Augspurger 1992) and most likely provides resistance to physical damage from falling litter (Aide 1987, Clark & Clark 1991).

Finally, palm abundance also may affect seedling distributions through effects on seed dispersal. Large seeds may penetrate the multi-layered canopy of *O. mapora* more readily than do small seeds. However, palms are also roosting sites for frugivorous bats which may disperse small seeds to palm sites. Thus, the effects of palms on the composition of the seedling pool beneath them is likely due to a combination of factors, including those that influence seed availability, seed survival and germination, and seedling survival.

The degree to which *O. mapora* may reduce the size and diversity of the seedling bank at the stand level will depend on the density of this species. Populations of *O. mapora* can be high in both old-growth and late second-growth forests, where it forms large dense clones on Barro Colorado Island (De Steven 1986, 1989). Denslow & Guzman (2000) suggested that low seedling densities in those stands were associated with an increase in palm density with stand age. Our study provides evidence that both seedling density and diversity are reduced under *O. mapora* canopy which suggests that the regeneration pool may be substantially different than it would be if *Oenocarpus mapora* was absent.

Although our study focuses on a single abundant species of palm, we expect the pattern to be similar for any understorey species that either produces copious litter or markedly reduces light levels at ground level (Denslow

et al. 1991, George & Bazzaz 1999). These studies suggest that a fuller understanding of forest regeneration processes should encompass not only aspects of forest structure that promote seedling establishment, such as canopy openings, but also structural components such as understorey development that may reduce seedling abundance and alter composition.

ACKNOWLEDGEMENTS

We would like to thank the Smithsonian Tropical Research Institute for logistical support. The study was supported by grants from the A. W. Mellon Foundation to the Smithsonian Institution and the National Science Foundation for research on tropical forest succession by R. Chazdon and J. Denslow. We would also like to thank S. DeWalt, O. Lopez, K. Harms, W. Platt, L. Coley, S. Torti, and D. Mason for their comments on the manuscript.

LITERATURE CITED

- AIDE, T. M. 1987. Limbfalls: a major cause of sapling mortality for tropical forest plants. *Biotropica* 19:284–285.
- ASHTON, P. M. 1992. Establishment and early growth of advanced regeneration of canopy trees in moist mixed-species forest. Pp. 101–122 in Kelty, M. J., Larson, B. C. & Oliver, C. D. (eds). *The ecology and silviculture of mixed-species forests: a Festschrift for David M. Smith*. Kluwer Academic, Dordrecht.
- AUGSPURGER, C. K. 1983. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *Journal of Ecology* 71:759–771.
- AUGSPURGER, C. K. 1984a. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65:1705–1712.
- AUGSPURGER, C. K. 1984b. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology* 72:777–795.
- AUGSPURGER, C. K. & KELLY, C. K. 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia* 61:211–217.
- BALSLEV, H., LUTEYN, J., ØLLGAARD, B. & HOLM-NIELSEN, L. B. 1987. Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Botanica* 92:37–57.
- BORCHSENIUS, F. 1997. Palm communities in western Ecuador. *Principes* 41:93–99.
- BROKAW, N. V. L. 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66:682–687.
- CANHAM, C. D., FINZI, A. C., PACALA, S. W. & BURBANK, D. H. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research* 24:337–349.
- CHAZDON, R. L. & FETCHER, N. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology* 72:553–564.
- CHAZDON, R. L., COLWELL, R. K., DENSLLOW, J. S. & GUARIGUATA, M. R. 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. Pp. 285–309 in Dallmeier, F. & Comiskey, J. A. (eds). *Forest biodiversity research, monitoring and modelling: conceptual background and Old World case studies*. Parthenon Publishing, Carnforth.
- CINTRA, R. 1997. Leaf litter effects on seed and seedling predation of the palm *Astrocaryum murumuru* and the legume tree *Dipteryx micrantha* in Amazonian forest. *Journal of Tropical Ecology* 13:709–725.
- CLARK, D. A. 1985. Seedling dynamics of a tropical tree: impacts of herbivory and mersitem damage. *Ecology* 66:1884–1892.
- CLARK, D. A. & CLARK, D. B. 1987. Analisis de la regeneración de árboles del dosel en bosque muy húmedo tropical: aspectos teóricos y prácticos. *Revista Biología Tropical* 35:41–54.
- CLARK, D. A. & CLARK, D. B. 1991. The impact of physical damage on canopy tree regeneration in tropical rain forest. *Journal of Ecology* 79:447–457.
- COLEY, P. D. 1983. Herbivory and defense characteristics of tree species in a lowland tropical forest. *Ecological Monographs* 53:209–233.
- COLWELL, R. K. & CODDINGTON, J. 1995. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society, London B* 345:101–118.
- CROAT, T. B. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford. 943 pp.
- DALLING, J. W. & HARMS, K. E. 1999. Damage tolerance and cotyledonary resource use in the tropical tree *Gustavia superba*. *Oikos* 85:257–264.
- DE STEVEN, D. 1986. Comparative demography of a clonal palm (*Oenocarpus mapora* subsp. *mapora*) in Panama. *Principes* 30:100–104.
- DE STEVEN, D. 1989. Genet and ramet demography of *Oenocarpus mapora* subsp. *mapora*, a clonal palm of Panamanian tropical moist forest. *Journal of Ecology* 77:579–596.
- DENSLLOW, J. S. 1987. Tropical rain forest gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18:431–451.
- DENSLLOW, J. S. & GUZMAN, G. S. 2000. Variation in stand structure, light, and seedling abundance across a tropical moist forest chronosequence, Panama. *Journal of Vegetation Science* 11:201–212.
- DENSLLOW, J. S., NEWELL, E. & ELLISON, A. M. 1991. The effect of understorey palms and cyclanths on the growth and survival of *Inga* seedlings. *Biotropica* 23:225–234.
- DENSLLOW, J. S., SCHULTZ, J. C., VITOUSEK, P. M. & STRAIN, B. S. 1990. Growth responses of tropical shrubs to treefall gap environments. *Ecology* 71:165–179.
- DIETRICH, W. E., WINDSOR, D. M. & DUNNET, T. 1982. Geology, climate, and hydrology of Barro Colorado Island. Pp. 21–46 in Leigh, E. G., Rand, A. & Windsor, D. (eds). *The ecology of a tropical forest: seasonal rhythms and long-term changes* (First edition). Smithsonian Institution Press, Washington, DC.
- FACELLI, J. M. 1994. Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. *Ecology* 75:1727–1735.
- FACELLI, J. M. & FACELLI, E. 1993. Interactions after death: plant litter controls priority effects in a successional plant community. *Oecologia* 96:277–283.

- FACELLI, J. M. & PICKETT, S. T. A. 1991. Plant litter: its dynamics and effects on plant community structure. *Botanical Review* 57:1–32.
- FENNER, M. 1987. Seedlings. *New Phytologist* 106:35–47.
- FOSTER, R. B. 1996. Seasonal rhythm of fruitfall on Barro Colorado Island. Pp.151–172 in Leigh, E. G., Rand, A. & Windsor, D. (eds). *The ecology of a tropical forest: seasonal rhythms and long-term changes* (Second edition). Smithsonian Institution Press, Washington, DC.
- FOSTER, R. B. & BROKAW, N. V. L. 1982. Structure and history of the vegetation of Barro Colorado Island. Pp. 67–81 in Leigh, E. G., Rand, A. & Windsor, D. (eds). *The ecology of a tropical forest: seasonal rhythms and long-term changes* (Second edition). Smithsonian Institution Press, Washington, DC.
- FRAVER, S., BROKAW, N. V. L. & SMITH, A. P. 1998. Delimiting gap phase in the growth cycle of a Panamanian forest. *Journal of Tropical Ecology* 14:673–684.
- GARWOOD, N. C. 1983. Seed germination in a seasonal tropical forest in Panama: a community study. *Ecological Monographs* 53:158–181.
- GEORGE, L. O. & BAZZAZ, F. A. 1999. The fern understorey as an ecological filter: emergence and establishment of canopy tree seedlings. *Ecology* 80:833–845.
- GILBERT, G. S., HUBBELL, S. P., & FOSTER, R. B. 1994. Density and distance-to-adult effects of a canker disease of trees in a moist tropical forest. *Oecologia* 98:100–118.
- HARMS, K. E. & DALLING, J. W. 1997. Damage and herbivory tolerance through resprouting as an advantage of large seed size in tropical trees and lianas. *Journal of Tropical Ecology* 13:481–491.
- HUBBELL, S. P. & FOSTER, R. B. 1986. Biology, chance, and history and the structure of tropical rain forest communities. Pp.314–329 in Diamond, J. & Case, T. (eds). *Community ecology*. Harper & Row, New York.
- KABAKOFF, R. P. & CHAZDON, R. L. 1996. Effects of canopy species dominance on understorey light availability in low-elevation secondary forest stands in Costa Rica. *Journal of Tropical Ecology* 12:779–788.
- KAHN, F. & DE GRANVILLE, J. J. 1992. *Palms in forest ecosystems of Amazonia*. Ecological Studies 95. Springer-Verlag, Berlin. 226 pp.
- KAHN, F., MEHIA, K. & DE CASTRO, A. 1988. Species richness and density of palms in terra firme forests of Amazonia. *Biotropica* 20:266–269.
- KITAJIMA, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428.
- KITAJIMA, K. & AUGSPURGER, C. K. 1989. Seed and seedling ecology of a monocarpic tropical tree, *Tachigalia versicolor*. *Ecology* 70:1102–1114.
- KNIGHT, D. H. 1975. A phytosociological analysis of species-rich tropical forest on Barro Colorado Island, Panama. *Ecological Monographs* 45:259–284.
- KOBE, R. K. 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology* 80:187–201.
- KOBE, R. K., PACALA, S. W., SILANDER, J. A. & CANHAM, C. D. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications* 5:517–532.
- LEE, S. M. & CHAO, A. 1994. Estimating population size via sample coverage for closed capture-recapture methods. *Biometrics* 50:88–97.
- LEIGH, E. G., RAND, A. S. & WINDSOR, D. M. (eds) 1996. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. (Second edition). Smithsonian Institution Press, Washington, DC. 503 pp.
- LEISHMAN, M. R. & WESTOBY, M. 1994. The role of large seed size in shaded conditions: experimental evidence. *Functional Ecology* 8:205–214.
- LOVELOCK, C. E., KYLLO, D. & WINTER, K. 1996. Growth responses to vesicular arbuscular mycorrhizae and elevated CO₂ in seedlings of a tropical tree, *Beilschmieda pendula*. *Functional Ecology* 10:662–667.
- MARTÍNEZ-RAMOS, M., SARUKHAN, J. & PINERO, D. 1988. The demography of tropical trees in the context of forest gap dynamics: the case of *Astrocaryum mexicanum* at Los Tuxtlas tropical rain forest. Pp. 293–313 in Davy, A. J., Hutchings, M. J. & Watkinson, A. R. (eds). *Plant population ecology*. Blackwell Scientific, Oxford.
- MCCULLOUGH, D. G. 1977. *The path between the seas: the creation of the Panama Canal, 1870–1914*. Simon & Schuster, New York. 622 pp.
- METCALFE, D. J. & GRUBB, P. J. 1997. The responses to shade of seedlings of very small-seeded tree and shrub species from tropical rain forest in Singapore. *Functional Ecology* 11:215–221.
- MOLOFSKY, J. & AUGSPURGER, C. J. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology* 73:68–77.
- MONTGOMERY, R. A. & CHAZDON, R. L. 2001. Forest structure, canopy architecture, and light transmittance in tropical wet forests. *Ecology* 82:2707–2718.
- MORIN, H. 1994. Dynamics of balsam fir forests in relation to spruce budworm outbreaks in the boreal zone of Quebec. *Canadian Journal of Forest Research* 24:730–741.
- NICOTRA, A. B., CHAZDON, R. L. & IRIARTE, S. V. B. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* 80:1908–1926.
- PACALA, S. W., CANHAM, C. D., SAPONARA, J., SILANDER, J. A., KOBE, R. K. & RIBBENS, E. 1996. Forest models defined by field measurements: estimation, error analyses, and dynamics. *Ecological Monographs* 66:1–43.
- PEREIRA DE SOUZA, R. & VALIO, I. F. M. 2001. Seed size, seed germination, and seedling survival of Brazilian tropical tree species differing in successional status. *Biotropica* 33:447–457.
- PERES, C. A. 1994. Composition, density and fruiting phenology of arborescent palms in an Amazonian terra firme forest. *Biotropica* 26:285–294.
- PINERO, D., MARTINEZ-RAMOS, M., MENDOZA, A., ALVAREZ-BUYLLA, E. & SARUKHAN, J. 1986. Demographic studies in *Astrocaryum mexicanum* and their use in understanding community dynamics. *Principes* 30:108–116.
- POULSON, T. L. & PLATT, W. J. 1989. Gap light regimes influence canopy tree diversity. *Ecology* 70:553–555.
- POULSON, T. L. & PLATT, W. J. 1996. Replacement patterns of beech and sugar maple in Warren Woods, Michigan. *Ecology* 77:1234–1253.
- SAS INSTITUTE. 1998. Version 8.2. edition. SAS Institute. Cary.
- SAVERIMUTTU, T. & WESTOBY, M. 1996. Seedling longevity under deep shade in relation to seed size. *Journal of Ecology* 84:681–689.

- SORK, V. L. 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. *Ecology* 68:1341–1350.
- SVENNING, J. C. 2001. On the role of microenvironmental heterogeneity in the ecology and diversification of Neotropical rain-forest palms (Arecaceae). *Botanical Review* 67:1–53.
- TORTI, S. D., COLEY, P. D. & KURSAR, T. A. 2001. Causes and consequences of monodominance in tropical lowland forests. *American Naturalist* 157:141–153.
- UHL, C., CLARK, K., DEZZEO, N. & MAQUIRINO, P. 1988. Vegetation dynamics in Amazonian treefall gaps. *Ecology* 69:751–763.
- WELDEN, C. W., HEWETT, S. W., HUBBELL, S. P. & FOSTER, R. B. 1991. Sapling survival, growth, and recruitment: relationship to canopy height in a Neotropical forest. *Ecology* 72:35–50.
- WESTOBY, M., JURADO, E. & LEISHMAN, M. 1992. Comparative evolutionary ecology of seed size. *Trends in Ecology and Evolution* 7:368–372.