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

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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 understory. 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 understory 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 understory seedling pool.

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

INTRODUCTION

In mesic forests, seedlings and saplings established in the understory are a major component of the regrowth in new gaps (Ashton 1992, Brokaw 1985, Morin 1994, Uhl et al. 1988). In the understory 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 understory 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 understory 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, understory light is spatially variable and this variability may be attributed in large part to the distribution of understory 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
understorey light environments in both temperate and tropical forests (Canham et al. 1994, Kabakov & 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 (Augspurger 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, Borchesnius 1997, Kahn & de Granville 1992, Kahn et al. 1988, Martinez 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 (Areceae) 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 understory 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 understory. 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 understories 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 (Lecythidaceae).

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; percent 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 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 placed 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 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 $Sp = \sigma^2 \rho^{d_i}$ where the variance $\sigma^2$, is
multiplied by $\rho$, 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 $O. \text{mapora}$.

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:

$$Y_{ijkl} = P_i + B_j + a_{ij} + L_k + I_{ij} + \sigma_{ijk} + \epsilon_{ijkl}$$

where $P_i$ = palm canopy treatment, $B_j$ = block (eight replicates), $a_{ij}$ is the variance used to test the effect of the main treatment $P$, $L_k$ = palm litter treatment, $I_{ij}$ = palm and litter treatment interaction, and $\sigma_{ijk} = \epsilon_{ijkl}$ is the error term used to test for the effects of litter treatment and $\sigma_{ijk} = \epsilon_{ijkl}$ is error term used to test for the effects of the interaction term $P$ x $L$. 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

$Oenocarpus \text{mapora}$ modifies the environment of the forest floor in several ways. Light levels ranged from 0.06–8.1%. The presence of $O. \text{mapora}$ reduced light availability to seedlings by 27% of $O. \text{mapora}$-free sites ($0.80 \pm 0.3\% \text{TPAR}$ vs. $1.07 \pm 0.03\% \text{TPAR}$ (mean ± SE) for $O. \text{mapora}$ and $O. \text{mapora}$-free sites respectively; $F = 4.66$, $df = 1, 808$, $P < 0.03$). Light availability also decreased as a function of $O. \text{mapora}$ size class. Juvenile $O. \text{mapora}$ palms reduced light availability by 13%, immature $O. \text{mapora}$ by 21% and adult $O. \text{mapora}$ by 28% of $O. \text{mapora}$-free understory (Figure 1a). Leaf litter depth ranged between 0 and 117 cm. Leaf-litter depth was greater in plots under $O. \text{mapora}$ canopy of all size classes than in plots not under $O. \text{mapora}$ ($F = 164$, $df = 3, 956$, $P < 0.0001$). 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 $O. \text{mapora}$ plots respectively, than non-$O. \text{mapora}$ plots (Figure 1b).

$Oenocarpus \text{mapora}$ 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
Impacts of palms on seedling establishment

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 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.) Kurtze (Burseraceae); however, under O. mapora canopies Beltschmiediapendula (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). Beltschmiediapendula, 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 (G² = 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>
<thead>
<tr>
<th>O. mapora present</th>
<th>Number of quadrats</th>
<th>Number of seedlings</th>
<th>Observed number of species</th>
<th>ICE species estimates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Armour</td>
<td>128</td>
<td>199</td>
<td>(30 ± 8)</td>
<td>(56 ± 12)</td>
</tr>
<tr>
<td>Zetek</td>
<td>130</td>
<td>127</td>
<td>34</td>
<td>73</td>
</tr>
<tr>
<td>Barbour</td>
<td>62</td>
<td>38</td>
<td>20</td>
<td>31</td>
</tr>
<tr>
<td>O. mapora absent</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Armour</td>
<td>192</td>
<td>245</td>
<td>(58 ± 4)</td>
<td>(93 ± 8)</td>
</tr>
<tr>
<td>Zetek</td>
<td>190</td>
<td>337</td>
<td>54</td>
<td>88</td>
</tr>
<tr>
<td>Barbour</td>
<td>258</td>
<td>326</td>
<td>58</td>
<td>83</td>
</tr>
</tbody>
</table>

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 ± 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).
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 class: 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.

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

1 Seed size classes follow Foster (1996).
2 Seed size not available.

Table 3. Survival, growth, and herbivory parameter means ± SE for transplanted seedlings (n = 256) of Gustavia superba planted under and away from Oenocarpus 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.

<table>
<thead>
<tr>
<th></th>
<th>Palm</th>
<th>Litter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survival (%)</td>
<td>41</td>
<td>66</td>
</tr>
<tr>
<td>Stem length (cm)</td>
<td>13.6 ± 1.04</td>
<td>14.9 ± 1.03</td>
</tr>
<tr>
<td>Dry mass (g)</td>
<td>0.62 ± 0.002</td>
<td>0.72 ± 0.001</td>
</tr>
<tr>
<td>Leaf area (cm²)</td>
<td>87.4 ± 0.39</td>
<td>119 ± 0.27</td>
</tr>
<tr>
<td>Herbivory (% total area)</td>
<td>8.8 ± 1.4</td>
<td>6.5 ± 1.3</td>
</tr>
</tbody>
</table>

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 understory 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

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).
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 rainforest species in Singapore. Therefore, small differences in TPAR may have a dramatic effect on seedling growth and survival in shaded tropical forest understory 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, Molosky & Augspurger 1992). Leaf litter may reduce evaporation from the soil surface, which may enhance seedling establishment in dry months in seasonally dry forests (Molosky & 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 (Cittra 1997, Molosky & 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 (Molosky & 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 understory 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.

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LITERATURE CITED


