

EFFECTS OF CANOPY OPENNESS ON SEEDLING SURVIVAL AND GROWTH AFTER SELECTIVE LOGGING IN A MONODOMINANT LOWLAND SWAMP FOREST IN COSTA RICA

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The mechanism proposed to explain tree monodominance in tropical forests is that the dominant species forms a dense canopy and produces shade-tolerant seedlings, which together favor self-replacement. Under this hypothesis, seedlings of monodominant species should have limited ability to respond to drastic increases in understory light, like those resulting from logging. Therefore, monodominant species should lose their seedling dominance after logging-induced canopy opening. To test this hypothesis, the current study measured seedling survival and growth of the monodominant species, *Prioria copaiifera*, and its main competitor, *Pentaclethra macroleoba*, in two forest stands that differ in logging history and in an unlogged stand in southeastern Costa Rica. Although, growth rates and survival of previously established seedlings were similar for both species across the three stands, seedling survival and growth decreased as light increased, with the effect being more pronounced for *Prioria* than for *Pentaclethra*. The study also investigated the ability of *Prioria* to respond to changing light environments by transplanting seedlings into logging-induced canopy gaps. Contrary to prediction, *Prioria* seedlings survived and grew better in gap centers than in gap edges or under a closed canopy. This result contrasts with established seedlings that cannot acclimate to changes in light conditions. Therefore, we conclude that continued *Prioria* dominance in selectively logged forests depends more on seedling production after canopy disturbance than on the established seedling present before disturbances.

Keywords: Light environment, monodominance, *Pentaclethra macroleoba*, *Prioria copaiifera*, seedling growth

INTRODUCTION

Monodominant forests are scattered throughout the tropics (Connell & Lowman 1989, Ter-Steege et al. 2019), with at least 22 species from eight families creating monodominant stands (Peh et al. 2011). Several mechanisms may contribute to monodominance, including ecto-mycorrhizal associations, poor dispersal of large seeds, shade tolerance and the persistence of seedlings in the forest floor (Nascimento & Proctor 1997, Torti et al. 2001, Kazmierczak et al 2016, Corrales et al. 2016). Hart et al. (1989) proposed that the seedlings of monodominant species grow and survive better in low-light environments than non-monodominant species. They hypothesised that low levels of understory light imposed by a dense canopy of adult monodominant trees create

conditions that facilitate their shade-tolerant regeneration, thus limiting the regeneration of non-shade-tolerant plants (Read et al. 2015). Although some evidence suggests that monodominant stands maintain shadier and more homogeneous understory light conditions than mixed stands, there is little information about the growth and survival responses of seedlings of monodominant species to changes in understory light environment (Torti et al. 2001, Read et al. 2015).

Selective logging is a widespread practice in tropical areas, but its practice may disrupt the stability of monodominant forests. Originally designed as a strategy to lessen the impact of logging and ensure the sustainability of forest ecosystems, selective logging has pronounced

effects on light conditions, seedling recruitment, forest structure, and ecosystem functions (Shima et al. 2018, Yguel et al. 2019). Logging generates large gaps and increases the amount of light in the understory (Yamada et al. 2013), which can affect the physiological performance of seedlings and, ultimately, their recruitment and establishment (Duah-Gyamfi et al. 2014). Therefore, direct light to the understory can lead to changes in species composition and canopy structure of logged forests, which usually favor recruitment of early-successional species at the detriment of shade-tolerant ones (Laing et al. 2019).

Prioria copaifera (Fabaceae) and *Pentaclethra macroleoba* (Fabaceae) are two tropical tree species that form monodominant stands in Central America and along the northern Pacific coasts of South America (Condit et al. 1993, Hartshorn & Hammel 1994). Since the early nineteenth century, these species have been intensively harvested to the point that *Prioria* is currently considered a threatened species (Jiménez-Madrigal et al. 2002). Despite several studies documenting the adverse effects of timber extraction on the dominance of *Prioria*, few studies have addressed the impacts of timber extraction on seedling growth and survival (Linares 1996, Grauel & Putz 2004, Valverde-Barrantes & Rocha 2014). This study examined how *Prioria* and *Pentaclethra* seedlings responded to changes in light conditions. If, as predicted for shade-tolerant species, seedlings of *Prioria* cannot respond to increases in light in a natural setting, seedling growth and survival should decrease after logging (Hart et al. 1989; Valladares et al. 2016). It is also expected that seedlings of these species should allocate more resources to belowground organs under lower light conditions (Montgomery & Chazdon 2002, Balderrama & Chazdon 2005).

MATERIALS AND METHODS

Study area

This study was conducted in three forest stands located near Gandoca-Manzanillo Wildlife Refuge, Talamanca, Costa Rica (9° 37' N, 82° 38' W). The vegetation in this area is a humid tropical forest (Herrera 1986), with average precipitation ranging from 2500 to 3100 mm year⁻¹ and temperatures ranging

between 25 and 27 °C. Average monthly precipitation ranges from 408 mm in July to 163 mm in September. However, precipitation is lowest in September and October, and locals consider August to October as the dry season, which corresponds to the peak of the logging season. The soils are predominantly Hydric Psamments, sandy alluvial soils weathered by periodic flooding. *Prioria copaifera* is the dominant tree, representing as much as 60% of the basal area in these forests (Valverde-Barrantes & Rocha 2014). *Carapa guianensis* and *P. macroleoba* are found interspersed among *Prioria* trees and are the second and third most abundant species in undisturbed stands, respectively (Appendix 1).

Traditional logging with heavy machinery took place on two 15-ha logging tracts of forest in the study area in 1988 and 1997. Official records of the logging operation in 1997 indicated the removal of nearly 60% of the basal area in each stand (on average, seven trees ha⁻¹), most of which were large *Prioria* and *C. guianensis* trees (diameter at breast height 60 cm) (Quirós & Finegan 1994). There were no official records available for the logging operations conducted in 1988. An adjacent 33 ha tract of undisturbed forest was used as a native undisturbed stand for comparisons. The site was visited in November 2000 to characterise the light environment, forest structure and diversity, and measure seedling recruitment, growth and survival. The sites were referred to as L-02 and L-12, with 2 and 12-years post-logging, respectively, and the unlogged forest as ULF.

Light environment

Two 50 transects were established in each of the logged and unlogged forest stands to describe the light environment in October 2020. In recently logged areas, the located plots were away from highly disturbed or compacted areas such as skid roads or log staging zones. Hemispherical photographs were taken every 5 m along the transect, a total of 11 photographs per plot. A high-resolution digital camera equipped with a 180 ° fisheye lens was used to take the hemispherical photographs at 1.5 m height in low ambient light following Oberbauer et al. (1993) and Whitmore et al. (1993).

The HemiView Hemispheric Image Analysis System was used to analyse the hemispherical photographs taken at each site. HemiView combines information on canopy structure with sun trajectory data to model the photosynthetic active radiation intercepted at various strata beneath the canopy. Following the recommendations of HemiView, the hemispherical photographs were analysed using eight azimuth divisions (45-degree divisions) and 18 zenith divisions (5-degree divisions). For each photo, the program characterised the light environment of the understory by estimating the number and duration of sun flecks. Then, the proportion of solar radiation penetrating to the understory, relative to that in the open (by removing the canopy), was calculated as the global site factor (GSF) (Anderson 1964). The GSF values ranged from 0, being complete light interception by the canopy, to 1, being standardised to the incoming radiation at the full open site. A linear mixed model was used to test for differences in GSF between forest stands using the lmer function in the lme4 package (Bates et al. 2014). For this analysis, the hemispherical photographs were nested within transects, and each transect was treated as a random effect within the forest. A Tukey's post hoc test was conducted for comparison of the light environment between forest stands.

Modelling seedling growth and survival

Seedling growth and survival was examined at each of the three sites in November 2000, May 2001 and December 2001. Ten 5m × 5m

sampling plots were established on each side of the 50m transect used to describe the light environment for a total of 20 plots. The sampling, conducted at 6-month intervals, allowed the study to evaluate growth and survival during the rainy and drier seasons, respectively (Figure 1). The densities of 50–150 cm tall *Prioria* and *Pentaclethra* seedlings were measured in each 5m × 5m sample plot. Together with *Carapa guianensis*, these three species were the most common (Appendix 1). Due to the abundance of seedlings in these plots, ten 5m × 5m subplots were selected randomly from each plot to measure seedling growth and mortality. All seedlings were tagged and measured for total height, stem diameter at 15 cm from the ground, and the number of leaves (leaflets in *Prioria*). Growth was evaluated based on increment in seedling height and stem diameter for the first six months of the study (November 2000–May 2001) and again in the following six months (May 2001–December 2001).

Due to the highly skewed distribution of growth in the seedling population, the differences in diameter and height increments were tested between sites using a permutation test with 9999 iterations (Fraker & Peacor 2008). Next, survival analysis via maximum likelihood estimation was used to parameterise mortality models for populations of *Prioria* and *Pentaclethra* seedlings. Seedling survival (L) was assumed to follow a negative binomial distribution of the form:

$$L\left(\frac{N}{X}\right) = F(T)^X (1-F(T))^{(N-X)}$$

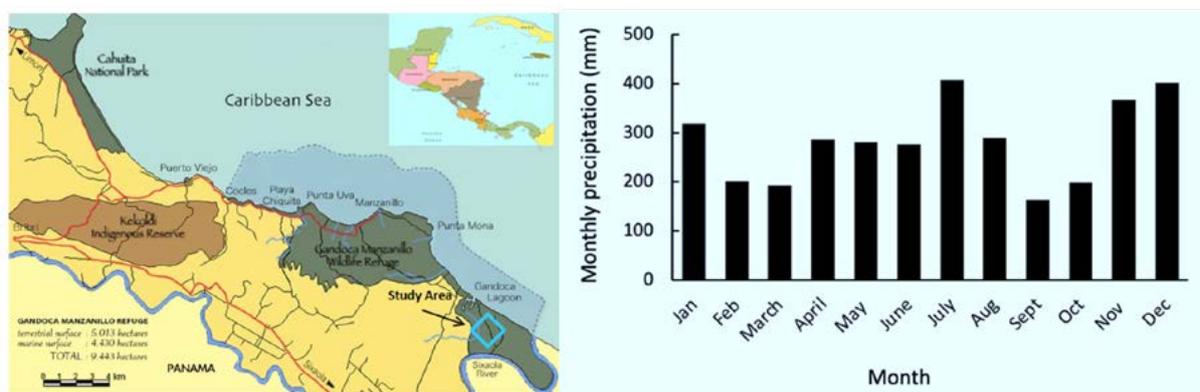


Figure 1 Location of the study area and average monthly precipitation reported for the area; the green areas in the map represents legally protected areas in the region including protected coral reefs, brown area is an indigenous reserve

Where, N is the number of seedlings at the start of the monitoring, X is the number of seedlings that died, and $F(T)$ is the probability of mortality over the 1-year interval. The goal of the study was to characterise mortality as a function of light, where $F(T)$ was specified as a function of light availability, defined by the GSF of each plot.

Plotting seedling survival (S) showed a monotonically decreasing function along a gradient of increasing light (Figure 1), thus, a simple two-parameter negative exponential function was implemented, where survival is a function of background survival at low light (A) raised to the power of the species-specific sensitivity to light (β) multiplied by the light availability (Kobe 1999):

$$S(\text{light}, \beta) = A^{(-\beta \times \text{light})}$$

where, $0 < A < \infty$, and $\beta \geq 0$. When $\beta = 0$, there is no effect of light on seedling survival, and values close to 1 indicated perfect light sensitivity. Parameters A and β were estimated for both *Prioria* and *Pentaclethra* seedlings at all three sites to test whether light was influential on seedling survival. Optimisation of the model and likelihood ratio tests ($p < 0.05$) for each parameter were carried out in R version 2.8.1 (R Core Team 2009) following Bolker (2008).

Transplant experiments

The effect of light on the growth and survival of *Prioria* seedlings were evaluated by transplanting greenhouse-grown seedlings across a gradient of canopy openness. Seeds of *Prioria* were recalcitrant and lacked dormancy, and frequently sprout before dispersal. Freshly fallen seeds were collected from the unlogged forest stand and planted in 1-gallon plastic bags with a 1:1 mix of native soil from the unlogged forest stand and sand. Bags were placed in a shade house using a cloth which allowed 70% transmittance of light for germination. After germination, the seedlings were grown in the shade house for 90 days. Seedlings were watered as needed to maintain the soil close to its water carrying capacity.

Seedlings were then transplanted to four gaps in the logged *Prioria* forest stand at three different locations to simulate a gradient of

canopy openness, (1) gap: in the center of the gap opening, (2) edge: on the border of the gap opening and (3) shade: 20 m into the undisturbed forest from the edge of the gap opening. A total of 20 *Prioria* seedlings were transplanted in each light environment per gap (20 seedlings \times 3 light conditions \times 4 gaps), 50 cm apart from each other, arranged in a grid within 2.5 m \times 2.5 m plots. They were sprayed with insecticidal pyrethroids to reduce the risk of mortality due to herbivory during the establishment of the transplants, as recommended by Balderrama and Chazdon (2005). Plant height, stem diameter at 15 cm height, and leaf number were measured every three months for one year.

Prior to transplanting, 20 greenhouse-grown seedlings were dissected into leaf, stem and root biomass portions. The parts were dried at 65 °C for 48 hours and weighed with an analytical balance (± 0.001 g resolution) for estimates of initial seedling biomass. At the end of the experiment, 20 seedlings were randomly selected from each treatment and harvested to determine treatment effects on biomass productivity and allocation patterns between leaves, stems and roots (Popma & Bongers 1991). Total leaf area was quantified using a leaf area meter, and dry biomass fractions were weighed for leaves, stems and roots.

Five growth parameters were derived using the dry biomass and leaf area measurements of each seedling: relative biomass growth rate (RGR_m), unit leaf rate (E , biomass per unit leaf area per year), leaf area ratio (LAR , leaf area/total seedling biomass), leaf weight fraction (LWF , total leaf weight/total seedling dry weight) and specific leaf area (SLA , total leaf area/total leaf dry weight, $\text{cm}^2 \text{g}^{-1}$). Root–shoot allometry was estimated as the slope of the relationship between above- and below-ground biomass. The RGR_m and E were calculated following the formulae of Popma and Bongers (1991) using 440 days as the total seedling growth period. The variables were estimated using the Hunt et al. (2002) plant growth analysis software. A linear mixed effect model was used to test for differences in growth parameters for seedlings growing in the three light environments using the lme function in the $nlme$ package, R 2.9.0 (2009). The models used seedling growth (diameter and height) as response variable with treatment, and time

of measurement as fixed predictor variables, and site nested within time as a random term. The model was fitted using a log-maximum likelihood method assuming normal error distributions. Tukey's post hoc test was used for comparison among forest stands.

For the gap experiment, a censored Cox's proportional hazard test was conducted to compare seedling survival among treatments (Cox & Oakes 1984). This analysis typically examines the effects of several risk factors or conditions, simultaneously, on survival time. In this study, it was used to test for the effect of seedling location within gaps in each forest stand on survival time. Cox's proportional hazard test was conducted using R 2.9.0 (R Core Team 2009), as recommended by Crawley (2013).

RESULTS

Light environment

Light environments, as described by hemispherical photographs taken at 1.5 m height, differed among the three sites, with more light reaching the understory at sites logged 2 years post-logging, followed by sites logged 12 years post-logging and the unlogged site (Table 1). Direct and diffuse radiation fluxes were on average two to three times higher in the logged sites than in the

undisturbed forest (diffuse light, $F = 11.0$, $p < 0.001$, direct light, $F = 10.1$, $p < 0.001$). Sunfleck number ($F = 2.89$, $p < 0.01$) and total light ($F = 6.47$, $p = 0.0007$) were also greater in logged forest. The GSF (i.e., the proportion of total light penetrating to the understory), adequately characterised the light gradient across the sites and indicated that L-02 and unlogged forest had the largest differences in light environment, with L-12 maintaining intermediate GSF values ($F = 10.2$, $p = 0.0005$). GSF values ranged between 0.05 and 0.13 (Table 1), showing that only 0.5% of the total light penetrated to the understory of the unlogged forest compared to 13% in the most recently logged (L-02) site.

Modelling seedling growth and survival

Seedling growth differed among sites, but *Prioria* and *Pentaclethra* seedlings maintained similar patterns of growth within sites (Table 2). In the most recently logged site (L-02), seedling diameter and height showed accelerated growth during the first six months of the study. Seedling growth slowed during the second six-month interval so that the total growth increment for L-02 seedlings was equal to seedling growth increment in the first six months (Table 2, Appendix 2). Diameter increments in L-02 were, on average, higher for *Pentaclethra* than *Prioria* seedlings and

Table 1 Mean (\pm standard deviation) for sunfleck number, sunfleck duration, direct and diffuse radiation, and global site factor resulting from the analysis of hemispherical photographs from three forest stands of *Prioria copaiifera* dominated forest using the program HemiView

Site	L-02	L-12	ULF
Sunfleck number per subplot	15.0 ^A (12.2–18.0)	14.0 ^A (12.2–16.1)	9.5 ^B (7.5–11.5)
Sunfleck duration (min m ⁻²)	129.5 ^A (98.5–160.5)	123.1 ^A (101.4–144.8)	62.1 ^B (45.2–79.1)
Direct radiation (MJ m ⁻²)	1406.7 ^A (972.9–1584.3)	903.0 ^{AB} (753.9–1227.7)	514.5 ^B (351.3–764.6)
Diffuse radiation (MJ m ⁻²)	136.0 ^A (95.2–154.7)	83.2 ^A (68.8–110.8)	46.3 ^B (29.1–56.4)
Global site factor (GSF)	0.13 ^A (0.10–0.16)	0.10 ^A (0.07–0.12)	0.05 ^B (0.03–0.06)

Sites differed in time of recovery since timber extraction, L-02: 2 years, L-12: 12 years, ULF: unlogged forest; letters indicate statistically significant differences among sites for each factor using Tukey–Kramer HSD test

Table 2 Mean increment in diameter and height for seedling of *Prioria copaifera* and *Pentaclethra macroloba* in three forest stands differing in time of recovery since timber extraction

	Diameter increment (mm)			Height increment (cm)		
	Site					
	L-02	L-12	ULF	L-02	L-12	ULF
<i>Prioria</i>						
First six months	0.41 ^A (0.19–0.61)	0.39 ^A (0.22–0.61)	0.10 ^B (0.02–0.12)	8.98 ^A (5.86–14.8)	2.80 ^B (1.87–4.87)	1.90 ^B (1.22–3.12)
Second six months	0.39 (0.23–0.62)	0.49 (0.33–0.81)	0.24 (0.15–0.39)	8.14 ^A (4.5–12.6)	6.83 ^{AB} (5.43–8.23)	3.27 ^B (2.13–4.41)
<i>Pentaclethra</i>						
First six months	0.89 ^A (0.45–1.34)	0.40 ^A (0.21–0.60)	0.17 ^B (0.03–0.20)	9.10 ^A (5.75–14.7)	0.49 ^B (0.00–1.31)	0.27 ^B (0.00–3.07)
Second six months	0.72^A (0.51–1.23)	0.35 ^B (0.07–0.42)	0.05 ^B (0–0.07)	10.44 ^A (4.1–14.5)	3.90 ^{AB} (0.65–8.45)	-1.38 ^B (-9.4–3.05)

Sites differed in time of recovery since timber extraction, L-02: 2 years, L-12: 12 years, ULF: unlogged forest; diameter and height increments were determined for the first six months (November 2000–May 2001) and for the second six months (June 2001–December 2001) of in-situ seedling monitoring; numbers in parenthesis indicate 95% confidence interval of the means; letters indicate significant differences among sites for each species resulting from the permutation tests using 9999 iterations; bold numbers indicate statistically significant differences in growth between species within each site (Tukey–Kramer HSD test)

remained higher for the entire duration of the study (Table 2, Appendix 2). Seedlings in the L-02 site had the greatest increases in height by the end of the year for both species, whereas seedlings in the L-12 and unlogged forest sites had slower but steady growth increments during the year for both diameter and height. Diameter increments in seedlings were similar among sites after one year, despite having significant differences in the first six months, during the rainy season, suggesting that diameter growth was constant only for seedlings in the sites with less light. On the other hand, proportional mortality was higher in the unlogged forest stand.

Light availability affected seedling survival (Table 3), and there was moderate correspondence between the seedling survival data and the fitted models (Figure 2). Both species showed a statistically significant decrease in survival as light increased (Figure 2, Table 3). The results showed differential reduction in survival probability between species, i.e., the slope of the fitted models differed (Figure 1). In the case of *Prioria*, β parameters across all sites tended to be higher than those reported for *Pentaclethra* (Figure 2).

Validation with transplant experiments

Seedling survival and growth of *Prioria* was greater in higher light environments. Seedlings transplanted in the center of gaps had higher survival and growth than seedlings in gap edges and shaded forest treatments (Figure 2). Seedlings planted in gap edge and shaded forest treatments started showing decreased survival after six months (Cox's likelihood ratio tests, $\chi^2 = 10.6$, $df = 4$, $p = 0.03$) with no significant effect of the initial size of seedlings on survival ($Z = 0.80$, $df = 4$, $p = 0.42$). By the one-year mark, seedling survival in the shaded forest treatments was < 60%, compared to 85% in gaps (Figure 2). *Prioria* seedlings grew more in gaps ($F = 16.1$, $df = 2$, $p < 0.0001$), and were on average, 13 and 28% taller than seedlings in gap edges and the shaded forest, respectively (Figure 3). Additionally, seedling diameter was 36% larger in gaps than in the shaded forest ($F = 32.7$, $df = 2$, $p < 0.0001$), and seedlings developed 43 and 58% more foliar area in gaps than in the gap edges or shaded forest treatments, respectively ($F = 20.8$, $df = 2$, $p < 0.0001$), despite no differences in leaflet number ($F = 0.89$, $df = 2$, $p = 0.46$).

Table 3 Maximum likelihood parameter (A and β) estimates (95% confidence interval) for best fit seedling survival model applied to seedling populations of *Prioria copaifera* and *Pentaclethra macroloba* in three monodominant *Prioria* stands near Talamanca, Costa Rica with varying recovery times after timber extraction

	Parameter	All sites	L-02	L-12	ULF
<i>Prioria</i> seedlings	n	617	93	179	345
	A	1.3 (1–1.2)	0.3 (1–1.7)	0.4 (0.2–0.9)	1.6 (1.2–2.2)
	β	12.8 (9.1–16.8)	1.9 (-10.1–13.2)	4.9 (-2.7–12.9)	14.3 (8.5–21.0)
<i>Pentaclethra</i> seedlings	n	116	57	48	31
	A	0.7 (0.4–1.3)	0.1 (> 0.0–0.7)	0.6 (0.1–2.0)	0.8 (0.4–1.9)
	β	6.3 (0.6–12.4)	-1.9 (-12.3–10.7)	3.4 (-7.6–13.7)	-1.5 (-11.7–12.5)

Sites differed in time of recovery since timber extraction, L-02: 2 years, L-12: 12 years, ULF: unlogged forest, A = background survival at low light, β = change in survival due to light sensitivity; site codes correspond to those in Table 1, a positive β indicates that survivorship decreases as light, for positive values of β , higher value indicates that the same level of light has a greater negative impact on survival; bolded parameter estimates are significantly different from zero (Cox’s likelihood ratio test)

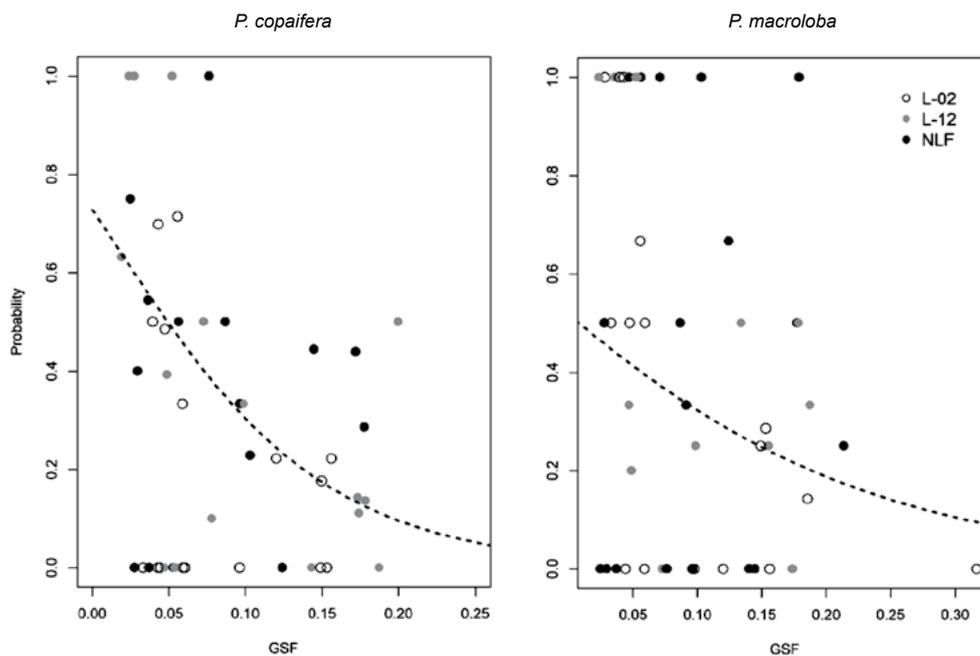


Figure 2 Seedling survival probability as a function of light availability (a) *Prioria copaifera* and (b) *Pentaclethra macroloba* under the canopy of a *Prioria* stand; global site factor (GSF) represents the total amount of light (direct and indirect) reaching the understory relative to that of a completely open area, and can assume values between 0 (no incoming solar radiation) to 1 (maximum incoming solar radiation), therefore light availability increases from left to right on the x-axis; points correspond to measured seedling survival in plots, 2 years following timber extraction (L-02), 12 years following timber extraction (L-12), and in an unaltered forest patch (ULF); lines are log-linear survival models fits

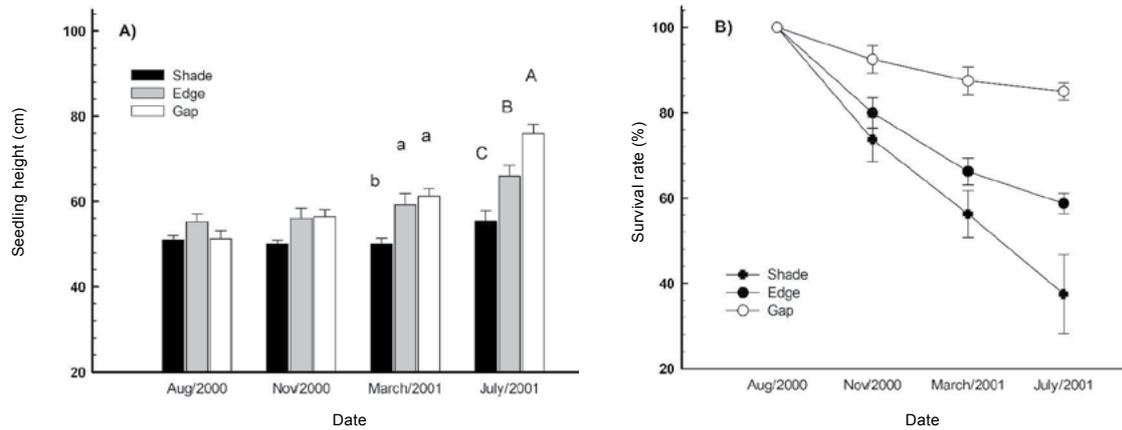


Figure 3 (A) Mean (\pm standard error) seedling height and (B) seedling survival for *Prioria copaiifera* seedlings transplanted into three different light environments (gap, edge and shade) in a recently logged, monodominant *Prioria* stand; letters denote statistical differences among treatments.

Seedling biomass allocation was consistent among treatments, despite the differences in survival (Figure 2). Across all six variables measured, seedlings in the gap, edge and shade environments showed no substantial differences in allocation. (Table 4). Only relative biomass growth rate (RGR_m) showed significant differences among treatments, with higher growth rates in forest gaps. Confidence intervals were broad, suggesting sizable intraspecific variation in growth. On the other hand, metrics comparing allocation to above- vs. below-ground biomass were similar across treatments, indicating little plasticity in allocation patterns, irrespective of the light environment.

DISCUSSION

The findings revealed that the survivorship of previously established *Prioria* and *Pentaclethra* seedlings and saplings decrease as canopy opening and understory light increased. These findings support the idea that seedlings of monodominant species are not tolerant of abrupt changes in canopy cover. It was also found that seedlings of these two species had similar height and diameter increments when growing in the same stand. In contrast, the study also showed that greenhouse-grown *Prioria* seedlings transplanted to the center of the gaps had greater survival and growth than seedlings transplanted under full canopy shade

Table 4 Plant growth variables for transplanted *Prioria copaiifera* seedlings grown in gap, edge and shade conditions in a logged area of a *Prioria copaiifera* monodominant forest in Costa Rica.

	Gap	Edge	Shade
Relative growth rate ($g\ g^{-1}\ year^{-1}$)	1.17 ^A (1.10–1.24)	0.63 ^B (0.55–0.70)	0.14 ^C (0.04–0.23)
Unit leaf rate ($g\ cm^{-2}\ year^{-1}$)	0.03 (0–0.082)	0.03 (-0.02–0.08)	0.24 (0.05–0.43)
Leaf area ratio ($cm^2\ g^{-1}$)	36.39 (11.74–61.04)	34.94 (11.51–58.36)	37.05 (12.13–61.98)
Leaf weight fraction ($g\ g^{-1}$)	0.259 (0.123–0.359)	0.250 (0.08–0.42)	0.260 (0.09–0.47)
Specific leaf area ($cm^2\ g^{-1}$)	141 (68–213)	141 (75–208)	146 (63–220)
Root-shoot allometry	1.16 (-0.30–2.62)	1.14 (-1.41–3.71)	1.18 (-1.39–9.79)

Values represent parameter means (and 95% confidence interval) after 1 yr; letters indicate statistically significant differences among sites for each factor using Tukey–Kramer HSD test

or in gap edges. The growth of transplanted *Prioria* seedlings contradicted the expected relationship between light environment and survival of seedlings of monodominant tropical. Thus, indicating that recently established seedlings of *Prioria* can survive and thrive in open areas. Similarly successful survival and growth rates of young seedlings of other closely related monodominant species have been reported (Hall et al. 2019). These findings suggest that young seedlings cope easily with enhanced light conditions, in contrast to seedlings of unknown age growing under previously shaded conditions.

Light environment

The GSF values observed in this study suggest that light conditions in the understory of the undisturbed *Prioria* forest were like the typically found in mature tropical forests (Montgomery & Chazdon 2002). Even the most recently logged area (L-02) showed lower irradiance values than those reported for the typical logged tropical forest (Yguel et al. 2019). Besides, light conditions were homogeneous in the unlogged forest and were consistent with previous measurements of light availability in a *Gilbertiodendron* monodominant forest in Congo (Hart 1995, Torti et al. 2001, Hall et al. 2019). These results validate the notion that monodominant forests tend to be shadier and less variable in light conditions than forests that are more diverse. Peh et al. (2014) suggested that such light conditions limit the number of species present in monodominated forests and facilitate the establishment and persistence of monodominant stands.

Seedling growth and survival

This study also showed that canopy openness does not affect growth and survival in the same manner. In a previous study, higher seedling mortality was reported in unlogged forest than in logged forest, where mortality rates were 50% compared to 11–20% respectively (Valverde-Barrantes & Rocha 2014). In agreement with the hypothesis, the seedling survival model suggested that the survival probability of *Prioria* seedlings decreases significantly as more light becomes available (Figure 1), showing similar survivorship rates

to those reported for unlogged *Prioria* forests in Panama (López & Kursar 2007). Moreover, Yamada et al. (2013) showed that the legacy of selective logging on the tree community is still evident decades later, indicating changes in species composition and forest structure in the logged forest compared with unlogged forest. It was argued that the effects of selective logging are exerted via influences on tree demography rather than functional trait composition.

The current model suggests that even small increases in the understory light environment can reduce the survival of previously established *Prioria* and *Pentaclethra* seedlings. This effect is consistent with other seedling studies in closed canopies, however the response was more pronounced for *Prioria* seedlings than what has been reported (Numata et al. 2006, Comita et al. 2010, Muscarella et al. 2013). Thus, monodominance is possibly associated with large numbers of recruits rather than tolerance to stressful conditions for previously established seedlings (Valverde-Barrantes & Rocha 2014, Record et al. 2016).

Transplanting experiment

In contrast with observations of seedlings established before the beginning of this study, the growth and survival of transplanted seedlings were higher in gap centers than for gap edges or in the shaded forest understory (Figure 2). Seedlings used in the transplanting experiment came from freshly dispersed seeds, and most of them still had attached cotyledons when transplanted into the forest from the shade house. These results suggested that the apparent contradiction in the findings may result from differences in the age of the seedlings, where the inability of old *Prioria* and *Pentaclethra* seedlings to respond to sudden light changes may be explained by differences in resource availability when exposed to higher radiation. *Prioria* and *Pentaclethra* have considerable reserves in their cotyledons, a common trait among monodominant species (66.3–145.7 g in *Prioria*). Thus, it is argued that large seeds play an essential role in maintaining a dominant seedling bank. Resources provided in the seed contribute to the survival of the seedlings and their ability to respond to changes in the

light environment, maintaining a dominant seedling bank.

The results from the transplant experiment supported the idea that recently recruited *Prioria* seedlings can take advantage of gap formation. A study performed with *Pentaclethra* using a more extreme gradient in light environments obtained similar results (Oberbauer & Strain 1985). In addition, multiple acclimation studies indicate that nursery conditions influence the ability of tropical seedlings to respond to changes in the light environment conditions where plants grow (Hogan & Machado 2002). Since we maintained the seedlings of *Prioria* under a 30% shade cloth before being transplanted, we recognize that the relatively high exposure of the seedlings to light before transplanting might have contributed to their lower survival and growth when transplanted into the understory.

Torti et al. (2001) proposed that adults of the monodominant tropical tree, *Gilbertiodendron dewevrei* in northeastern Congo, significantly modify the understory environment, making it difficult for other species to regenerate. The study suggested that adult trees form a dense, uniform canopy and seedling tolerance to low light levels is conducive to establishing those monodominant stands. As it was found in this study, large seeds of *G. dewevrei* represented an additional trait that improves seedling establishment, and thus contributes to the dominance of a single species. Henkel et al. (2005) pointed out that persistent monodominant species may result from the high seed production and limited dispersal of seeds, thereby establishing a large seedling bank independent of the light environment. Valverde-Barrantes & Rocha (2014) reported high seedling abundance in the understory of the same *Prioria* stands studied here. Thus, the ability of monodominant species to persist as seedlings in the understory might confer a higher probability of reaching and dominating the canopy (Hart 1995, Record et al. 2016).

Contrary to Popma and Bongers (1991), the present study found no positive correlation between relative biomass growth rate (RGR_m) and unit leaf rate (E) for *Prioria* seedlings. Other variables related to leaf production and plant biomass, such as the leaf area ratio, leaf weight fraction, and SLA in the transplant

experiment, were almost identical across light environments, providing little support for the hypothesis of increased allocation to below-ground organs in seedlings growing in lower light conditions. The similarity between seedling leaf investment and biomass accumulation among treatments described a coordinated increase of biomass throughout the plant, rather than shifting allocation to below-ground structures, as hypothesised (Table 4). The trend to allocate resources equally among compartments is typical of light-demanding seedlings, suggesting that *Prioria* seedlings can grow and survive in a wide range of light conditions (Montgomery & Chazdon 2002, Fenner & Thompson 2005).

CONCLUSIONS

In summary, the results showed that light conditions can affect the growth and survival of *Prioria* and *Pentaclethra*, two monodominant-stand forming species. Based on the transplant experiment results for *Prioria*, the remaining resources available in the cotyledon, which depend on seedling age at the time of gap formation, appear to affect the response of seedlings after the establishment of a gap. Slow acclimation to light conditions and limited shifts in seedling allocation suggests a restricted, yet plastic response. The findings indicated that the ability of these species to maintain their dominance is due to steady seed production and the establishment of persistent and dense seedling banks, where seed resources may determine seedling growth in response to gap formation. It was argued that maintenance of monodominance in *Prioria* after selective logging may depend more on the ability of the remaining trees to produce seeds and establish new seedlings after the logging disturbance. Future research should focus on light interactions with other abiotic and biotic drivers of forest dynamics across tree life stages within monodominant forests.

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Appendix 1 Number of trees (N), basal area (BA), relative abundance (RA), relative dominance (RD) and importance value index (IVI) for the five top species (≥ 2.5 cm DBH) for a two-year (L-02) and twelve-year (L-12) old logged stand and an unlogged stand (ULF) of *Prioria copaiifera* forest in the Caribbean lowlands of Costa Rica; species ranked for IVI

	Stems ha ⁻¹	BA (m ² ha ⁻¹)	RA (%)	RD (%)	IVI (%)
L-02					
<i>Pentaclethra macroloba</i>	340 (9)	15.10 (0.74)	21.25	43.79	32.52
<i>Musa textilis</i>	570 (12)	4.10 (0.05)	35.63	11.85	23.74
<i>Prioria copaiifera</i>	150 (5)	10.80 (1.72)	9.38	31.37	20.37
<i>Simira maxonii</i>	120 (5)	0.55 (0.05)	7.50	1.39	4.45
<i>Quararibea bracteolosa</i>	40 (4)	1.70 (0.74)	2.50	4.98	3.74
Total	1620 (18)	34.50 (0.60)	-	-	-
L-12					
<i>Prioria copaiifera</i>	240 (8)	35.60 (2.92)	15.48	70.17	42.83
<i>Pentaclethra macroloba</i>	190 (7)	7.50 (0.63)	12.26	14.78	13.52
<i>Musa textilis</i>	120 (6)	1.80 (0.08)	7.74	3.57	5.66
<i>Simira maxonii</i>	100 (4)	0.30 (0.02)	6.45	0.67	3.56
<i>Carapa guianensis</i>	70 (4)	0.50 (0.06)	4.52	0.91	2.71
Total	1670 (21)	50.78 (1.26)	-	-	-
ULF					
<i>Prioria copaiifera</i>	150 (6)	32.50 (3.89)	10.00	62.39	36.19
<i>Pentaclethra macroloba</i>	260 (10)	8.20 (0.60)	17.33	15.62	16.48
<i>Simira maxonii</i>	80 (5)	3.90 (0.87)	5.33	7.39	6.36
<i>Carapa guianensis</i>	120 (6)	1.50 (0.17)	8.00	2.85	5.43
<i>Rinorea dasydeana</i>	110 (5)	0.30 (0.02)	7.33	0.57	3.95
Total	2500 (21)	52.10 (1.38)	-	-	-

Appendix 2 Mean (standard deviation) for initial height, diameter and number of leaflets and subsequent increments in height, diameter and number of leaflets of *Prioria copaifera* seedlings transplanted gap, edge and shade environments in a recently logged monodominant *Prioria* stand and monitored for a 1-year period (August 2000–July 2001)

Measurement	August 2000			November 2000			March 2001			July 2001		
	Initial			Increment			Increment			Increment		
	Diameter (mm)	Height (cm)	Leaflets (N)	Diameter (mm)	Height (cm)	Leaflets (N)	Diameter (mm)	Height (cm)	Leaflets (N)	Diameter (mm)	Height (cm)	Leaflets (N)
Nursery	4.80 ^a (1.12)	59.73 ^a (12.03)	10.90 ^a (4.15)	-	-	-	-	-	-	-	-	-
Gap	4.61 ^a (1.49)	51.21 ^a (15.10)	11.14 ^a (4.41)	1.29 ^a (0.15)	4.77 ^a (4.93)	1.69 ^a (0.55)	2.21 ^a (2.70)	4.90 ^a (2.03)	4.59 ^a (0.95)	3.73 ^a (4.86)	13.41 ^a (2.89)	5.25 ^a (1.13)
Edge	4.82 (1.50)	55.23 ^a (15.10)	10.63 ^a (4.41)	0.64 ^a (0.54)	0.31 ^a (6.90)	-1.29 ^B (1.96)	0.42 ^B (0.34)	3.050 ^{AB} (4.31)	2.05 ^B (1.85)	0.60 ^B (0.20)	4.97 ^B (0.81)	2.05 ^B (1.24)
Shade	4.51 ^a (1.49)	50.98 ^a (13.55)	11.03 ^a (4.62)	0.23 ^B (0.10)	-0.49 ^a (1.99)	-1.28 ^B (1.73)	0.09 ^B (0.29)	-1.16 ^B (1.24)	0.46 ^B (1.82)	0.35 ^B (0.49)	3.08 ^B (3.45)	0.45 ^B (0.86)

Analysis of variance table

Light condition	0.98 NS	2.3 NS	0.28 NS	4.70 **	1.49 NS	4.75 **	8.59 ***	4.38 **	15.72 ****	20.82 ****	20.84 ****	9.79 ****
Location	1.9 NS	1.64 NS	1.40 NS	1.44 NS	1.54 NS	1.75 NS	2.71 *	2.01 *	6.20 ****	6.95 ***	6.22 ****	2.53 **

Letters indicate statistically significant differences among light conditions for each indicator of growth using Tukey–Kramer HSD test ($p = 0.05$); NS = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, **** = $p < 0.0001$, **** indicates probability values for each source of variation in the analysis of variance