

## Ecology of *Aglaia mackiana* (Meliaceae) Seedlings in a New Guinea Rain Forest<sup>1</sup>

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### ABSTRACT

The large seeds of *Aglaia mackiana* (Meliaceae) germinate and produce vigorous seedlings under closed canopies or in large gaps. To assess seedling ecology after germination, we measured growth, herbivore damage, and survivorship of seedlings over one year. The sample included shaded seedlings from dispersed seeds, undispersed seeds under parent trees, and seedlings transplanted to gaps. We quantified the light environment using hemispherical canopy photographs taken above seedlings at the beginning and end of the one-year study.

Seedlings transplanted to gaps grew faster and had more leaves, larger total leaf surface area, longer secondary roots, and greater root mass than shaded seedlings. Seedlings in gaps did not differ from shaded seedlings in survivorship or amount of herbivore- and pathogen-caused leaf damage.

The canopy photographs taken one year apart suggest there is a rough equilibrium in closed canopies with slight changes occurring around an average light level. Sites with < 0.06 ISF (a unitless, relative measure of canopy openness or reflected sunlight) tended to remain the same with minor fluctuations toward brighter or darker. Sites with canopy openness > 0.06 ISF tended to close; few gaps grew larger.

Seedlings under parent trees and seedlings away from parent trees had similar amounts of leaf damage and virtually identical survivorship after 18 months, but seedlings under parent trees had slower growth rates and smaller total leaf surface areas. Dispersal did not strongly benefit seeds via escaping high levels of mortality or competition around the parent.

*Key words:* Meliaceae; Papua New Guinea; seed dispersal; seedling ecology; treefall gaps; tropical rain forest.

TREEFALL GAPS PLAY VITAL ROLES IN THE DYNAMICS of most tropical rain forests by allowing higher amounts of sunlight to reach the forest floor than under intact, closed canopies. Greater insolation provides a regeneration niche (Grubb 1977) where shade intolerant plants can establish and grow (Brokaw 1987, Denslow 1987), and most rain forest trees require gaps at some point in order to attain adulthood (Hartshorn 1978, Clark & Clark 1992). Additionally, gaps are probably important to the maintenance of high plant diversity in tropical rain forests (Connell 1978, Connell *et al.* 1984,

Denslow 1985, 1987, Brandani *et al.* 1988, Ashton 1989).

Three sources of individuals form the regrowth in new gaps: the seedbank, new seed rain, and the persistent seedling bank. Many studies have focused on the role of seedbanks on regeneration within treefall gaps (*e.g.*, Hopkins & Graham 1983, Uhl & Clark 1983, Saulei & Swaine 1988, Chandrashekhara & Ramakrishnan 1993). The high insolation, particularly elevated far-red wavelengths (Chazdon & Fetcher 1984), and elevated ground temperatures in treefall gaps (Fetcher *et al.* 1985) can trigger germination in dormant heliophilic plants, and a new second growth plant community can quickly develop, especially in large gaps.

The second major component determining the

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composition of regrowth in gaps is newly arrived seeds (Schupp *et al.* 1989, Denslow & Gomez Diaz 1990). Gaps can act as aerodynamic sinks for wind-dispersed species (Augsburger & Franson 1988). Some vertebrate seed dispersers are attracted to gaps and differentially move seeds into older gaps; others appear to avoid gaps and, consequently, rarely disperse seeds into gaps (Hoppe 1988, Levey 1988, Schupp *et al.* 1989).

The third major source of gap plants, the seedling bank established prior to gap formation, might be the most important component but has been the least studied (Clark 1994). Although gap formation kills some vegetation (Brandani *et al.* 1988), many of the forest understory and ground layer plants are not damaged, or resprout if damaged. Established seedlings can rapidly take advantage of the increased sunlight because they are already well developed and may be at a competitive advantage relative to germinating seedlings.

Studies on the responses of established plants to gap formation are difficult because it is seldom possible to predict or manipulate gap formation (*e.g.*, Burton & Mueller-Dombois 1984, Uhl *et al.* 1988), thereby precluding the collection of baseline data. Nonetheless, gap formation is probably critical for the release of "dormant" or "suppressed" seedlings experiencing extremely slow growth rates in the understory (DeSteven 1994). Rain forest seedlings experience fairly high, stochastic probabilities of death because of physical disturbance and falling debris (Augsburger 1983, Aide 1987, Mack 1997). Small, dormant seedlings that are not released by gap formation are unlikely to survive for many years, even if they have adequate resources for maintenance and defense.

To investigate the responses of dormant seedlings of one species of New Guinean canopy tree to gap formation, we experimentally transplanted seedlings from shade into natural gaps of various sizes. We examined responses in survivorship, growth, biomass allocation, incidence of herbivore damage, and morphology of *Aglaia mackiana* seedlings. Because gaps are not discrete, unambiguous entities (Lieberman *et al.* 1989), we used hemispherical canopy photos to quantify canopy openness above seedlings.

## METHODS

**STUDY AREA.**—This study was conducted at the Crater Mountain Biological Research Station, 10 km east of Haia, Simbu Province, Papua New Guinea (06°43.4'S, 145°05.6'E) in the Crater

Mountain Wildlife Management Area on traditional lands of the Pawaiian people. The study area spanned 950–1200 m elevation in the valley of the Oo River in the Pio drainage. The area is entirely forested with openings and patches of second growth forest formed by landslips and treefall gaps. The vegetation spans the transition from mixed evergreen hill forest to submontane forest (Paijmans 1976). Tree diversity is high with no strongly dominant canopy tree species (Wright *et al.* 1997).

**STUDY SPECIES.**—The species studied was provisionally called *Aglaia* aff. *flavida* Merrell et Perry (Meliaceae) (C. Pannell, pers. comm.; Pannell 1992) in several previous publications (Mack 1995, 1997). Recently the species has been described as a new species, *Aglaia mackiana* (Pannell 1997), hereafter called *Aglaia*. Adult trees occur in low density in the study area. The seeds are large (115 g) and widely dispersed by *Casuarium bennetti*, a large, flightless bird endemic to hill and montane forest of New Guinea (Mack 1995). Seeds germinate shortly after abscission and produce vigorous seedlings that are a common component of the forest understory.

**SEEDLING SAMPLES.**—During July–August 1990, 237 established seedlings under six mature trees were tagged and measured. These seedlings were re-censused and measured six times between 1990–1993 to compare growth and survivorship with that of seedlings from dispersed seeds.

During June–July 1990, we established seven 100-m belt transects following randomly chosen compass bearings 5 m from randomly chosen points on trails. No transects passed under mature *Aglaia* trees. All *Aglaia* seedlings found within 5 m of the transect were mapped, tagged, and measured. In March 1992, the transects were revisited and seedlings were remeasured for comparison with the seedlings under parent trees.

Two hundred seventy-two dormant seedlings < 150 cm tall in closed forest and away from adult trees were selected for a transplant experiment. Dormancy was readily determined by the absence of new leaves and the degree of epiphytic growth on stems and leaves. Fifty-four of these seedlings were taken from the population that was already being monitored in random transects and were divided among three treatments. None of these 54 had exhibited significant growth the previous year. Seedlings were randomly assigned to one of three treatments: transplant group—105 seedlings were transplanted to 20 gaps within 75 m of their ori-

gin; replant group—100 seedlings were dug up similarly to the transplant group, but were then replanted in the same site they were taken from to control for effects of digging up and manipulating the seedlings; and control group—67 seedlings selected as controls remained *in situ*. The three groups were established from 30 March–22 April 1992. Larger initial sample sizes were used for the transplant and replant groups than controls because we expected that the manipulation would cause some mortality.

**MEASUREMENTS.**—*Aglaiia* has compound leaves that grow from meristems just below the terminal bud. Thus, the youngest leaf is topmost and the oldest leaf lowest on the stem. We determined new leaf production by tagging the topmost leaf at the beginning of the study and counting leaves above the tagged leaf at the end of the study. Leaflets on developing leaves are folded (closed) along their midvein; such immature leaves were excluded in leaf counts. We measured height from the ground to the tip of the terminal bud. At the end of the study, we excluded from analyses all seedlings obviously damaged by falling debris and > 5 cm shorter than their starting height.

Plants were re-censused in June 1992, October 1992, and from March–April 1993. At each census the height of each surviving seedling was measured and the number of leaves and leaflets were counted. The June 1992 height measurement was used as the initial height because planting and ground settling after planting caused some spurious changes in height (see below). The few seedlings dead at the June census were considered due to transplant shock and excluded from the analyses. At the end of the experiment, all seedlings were carefully excavated and the length of the primary taproot and the longest secondary root was recorded. The roots of each seedling were washed, placed in envelopes, and dried to constant weight.

To measure the light environment, we took hemispherical canopy photos directly above transplant (before and after transplanting), replant, and control seedlings at the beginning of the study (time 1) and at the end of the study (time 2). Photographs were taken on Kodak Tri X film (ASA 400) using a Nikon F3 body with databack and a Nikkor 50 mm lens with a Spiratone 8mm fisheye converter lens. Canopy photographs were analyzed with the video image analysis program, CANOPY, and hardware described in Rich *et al.* (1993). CANOPY provided a mean annual direct site factor (DSF) and indirect site factor (ISF) for each

hemispherical photograph. The DSF is a relative measure of direct sunlight (canopy openness along the path of the sun above the point where the photograph was taken). The ISF is a relative measure of reflected sunlight (overall canopy openness above the point where the photograph was taken). ISF and DSF calculated from hemispherical canopy photographs have been shown to be strongly correlated with photosynthetic photon flux density (Chazdon & Field 1987, Rich *et al.* 1993).

Each photograph (time 1 and time 2) was analyzed twice (trials A and B). If the difference in ISF between trials A and B for any photograph was > 0.005, the image was reanalyzed twice (trials C and D). If the difference between trials C and D was > 0.005, the mean of trials A, B, C, and D was used for the site. If the difference between trials A and B or C and D was < 0.005, the mean of the two trials was used as the value for each site at time 1 and time 2. For comparisons among sites for the entire study period, the mean of photos from time 1 and time 2 was used. Thus, the value used to characterize a site was the mean of at least four analyses: two of the photograph taken at the beginning of the study (time 1) and two of the photograph taken at the end of the study (time 2).

**HERBIVORE DAMAGE.**—The herbivores and pathogens of *Aglaiia* are unknown. We only once observed an herbivorous insect, a lepidopteran larva, feeding on *Aglaiia* leaves. Some leaflet damage appeared to have been caused by other leaf-chewing insects. Most damage appeared to have resulted from a pathogen that caused leaf tissue to turn brown, die, and fall away, leaving a thin brown margin on the remaining green leaflet tissue. Presumed pathogen damage occurred throughout leaflet blades, whereas presumed herbivore damage was confined to leaflet margins.

In order to analyze leaf surface area and leaf damage, we traced all 867 leaves (3705 leaflets) of 190 seedlings at the end of the study. We also traced 95 leaves (373 leaflets) from 29 seedlings found under parent trees. Because we had marked the topmost leaf at the beginning of the study, we could compare damage to leaves produced after treatments were imposed. Missing and damaged areas were colored black on the tracings. The tracings were later cut out and leaflet surface areas (damaged and undamaged) measured by image analysis (Agvision, Decagon Instruments; Pullman, Washington). Leaflets were pooled to obtain the total surface area (assuming no damage) and the damaged area for each leaf; then leaves were pooled to

yield the intact and damaged surface areas of new (posttreatment) and old (pretreatment) leaves on each seedling.

**STATISTICAL ANALYSES.**—We used one-way ANOVAs to identify significant effects and post hoc Student-Newman-Keuls tests to identify means that differed significantly. Unpaired Bonferroni *t*-tests were used when comparing only two means. All regressions used the least squares method and Pearson correlation coefficients are given in the results.

## RESULTS

**THE LIGHT ENVIRONMENT (CANOPY PHOTOS).**—We used ISF as a measure of canopy openness. DSF was strongly correlated with ISF in this study ( $R^2 = 0.866$ ,  $P \ll 0.0001$ ) as in previous studies (Chazdon & Field 1987, Turner 1990, Dirzo *et al.* 1992).

Seedlings transplanted to gaps experienced a substantial shift in light availability. The mean ISF prior to transplanting was 0.04839 ( $N = 76$  photos,  $SD = 0.01462$ ) whereas the mean ISF after transplanting was 0.09750 ( $N = 86$  photos,  $SD = 0.03389$ ); the mean change in ISF for seedlings transplanted to gaps was + 0.04489 ( $N = 74$ ,  $SD = 0.03046$ ;  $t = 12.2$ ,  $P \ll 0.0001$ ).

Initial assignment of seedlings to closed forest versus gaps was based on our subjective estimation of canopy closure. Distinguishing gaps from non-gaps is not a simple matter (Canham 1989, Lieberman *et al.* 1989) because canopy openness is a continuum and other factors can modify gap effects (*e.g.*, penumbral effects; Smith *et al.* 1989). There was some overlap in the ISF among transplants in the smallest gaps or on the edges of gaps and those in fairly open forest (note overlap in Fig. 1 along the x-axis). The sites we subjectively called gaps were mostly above ISF 0.06. Overall, our distinction between forest and gap was reliable; the mean initial ISF (time 1) for transplant sites, 0.09750, was significantly greater than the mean value for replant sites, 0.04638 ( $t = 12.97$ ,  $P \ll 0.0001$ ) and control sites, 0.04978 ( $t = 10.38$ ,  $P \ll 0.0001$ ). ISF values for replant and control sites did not differ significantly ( $t = 1.08$ ,  $P = 0.285$ ).

During the year between taking the first and second canopy photographs at each site, significant changes in canopy openness occurred. Gaps (transplant sites) tended to close, with only 5/80 sites becoming more open after one year than they were initially (Fig. 1). Conversely, roughly equal numbers of closed sites tended to open ( $N = 53$ ) or

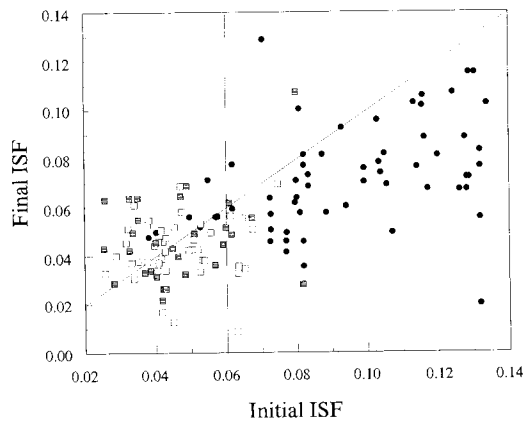


FIGURE 1. Change in light environment over *Aglaia* seedlings in one year. The x-axis shows ISF values (a measure of canopy openness) obtained from hemispherical canopy photographs (see Methods) at the beginning of the study. The y-axis shows ISF values calculated from photographs taken at the same sites one year later. Closed circles are transplant sites, shaded squares are control sites, and open squares are replant sites. The diagonal line represents  $y = x$ . Points below the line indicate sites where the canopy closed and points above the line represent sites where the canopy opened. The vertical line at ISF = 0.06 approximates the distinction between closed canopy and gaps.

close ( $N = 66$ ) after one year. The mean ISF for the replant sites and control sites did not change substantially over the course of the year [replants mean ISF = 0.04637 (time 1) to 0.04271 (time 2),  $t = 1.74$ ,  $P = 0.084$ ; controls mean ISF = 0.04978 (time 1) to 0.04532 (time 2),  $t = 1.08$ ,  $P = 0.282$ ]. The mean ISF for gap sites, however, showed a marked decrease in ISF one year later [mean ISF = 0.09750 (time 1) to 0.07317 (time 2),  $t = 5.59$ ,  $P \ll 0.0001$ ].

**INITIAL SEEDLING GROUPS.**—Transplant, replant, and control groups did not differ significantly in the initial number of leaves or in the initial height (Table 1). Transplanting and replanting seedlings affected seedling height because some seedlings were inadvertently planted slightly deeper than when initially found. Thus, replant seedlings lost nearly 4 cm and transplant seedlings 2 cm, although groups still did not differ significantly (Table 1). Because we expected transplanted seedlings to grow larger than controls, this bias was conservative.

**SURVIVORSHIP.**—By the end of the study, 11 transplants, 15 replants, and 7 controls had died. An additional 6 transplants, 10 replants, and 8 controls

TABLE 1. Growth and morphological characteristics for *Aglaia mackiana* seedlings transplanted to gaps, replanted in closed forest, and unmanipulated controls in shade. Means with different letters in the superscript are significantly different at  $P < 0.02$ ; means with the same or no letter in the superscript are not significantly different at  $P > 0.05$  (Student-Newman-Keuls tests).

Variable	Transplants (in gaps)			Replants (in shade)			Controls (in shade)			ANOVA results
	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	
$\bar{x}$ initial height (cm)	69.7	24.91	88	73.5	22.79	75	76.5	28.76	52	$F = 0.23$ ; $P = 0.79$
$\bar{x}$ height postmanipulation (cm)	67.5	24.62	88	69.4	23.04	68	76.5	28.76	52	$F = 1.25$ ; $P = 0.29$
$\bar{x}$ final height (cm)	78.3	25.90	88	74.0	23.74	68	78.6	28.59	50	$F = 0.67$ ; $P = 0.52$
$\bar{x}$ height increase (cm)	11.9 <sup>a</sup>	10.41	85	4.6 <sup>b</sup>	4.19	68	4.5 <sup>b</sup>	6.96	50	$F = 23.02$ ; $P < 0.0001$
$\bar{x}$ initial no. leaves	4.2	1.64	88	4.3	1.48	68	4.1	1.56	50	$F = 0.16$ ; $P = 0.85$
$\bar{x}$ final no. leaves	4.8 <sup>a</sup>	1.66	88	3.6 <sup>b</sup>	1.77	68	4.2 <sup>c</sup>	1.78	50	$F = 8.05$ ; $P < 0.001$
$\bar{x}$ no. new leaves/seedling	2.14 <sup>a</sup>	1.10	86	0.75 <sup>b</sup>	0.69	63	0.82 <sup>b</sup>	0.68	39	$F = 53.69$ ; $P < 0.0001$
$\bar{x}$ new leaf surface area (cm <sup>2</sup> )/seedling	601.7 <sup>a</sup>	490.0	69	303.7 <sup>b</sup>	293.4	36	305.9 <sup>b</sup>	275.2	33	$F = 9.44$ ; $P < 0.001$
$\bar{x}$ surface area/new leaf (cm <sup>2</sup> )	258.1	169.7	77	211.5	138	35	261.1	214.2	32	$F = 0.97$ ; $P = 0.38$
Length of taproot (cm)	20.6 <sup>a</sup>	6.64	85	20.7 <sup>a</sup>	7.50	67	28.8 <sup>b</sup>	9.50	50	$F = 20.58$ ; $P < 0.0001$
Longest secondary root (cm)	21.9 <sup>a</sup>	12.27	85	3.2 <sup>b</sup>	9.12	66	17.0 <sup>b</sup>	11.37	50	$F = 12.94$ ; $P < 0.0001$
Dry root mass (g)	8.7 <sup>a</sup>	6.64	84	6.1 <sup>b</sup>	4.86	63	6.7 <sup>b</sup>	6.3	47	$F = 3.62$ ; $P = 0.03$
Proportion of new leaf area damaged/seedling	0.055	0.083	68	0.047	0.088	35	0.062	104	32	$F = 0.22$ ; $P = 0.80$

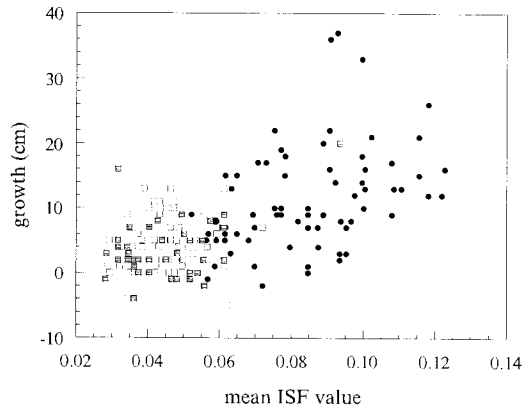


FIGURE 2. *Aglaia mackiana* seedling height increase in relation to canopy openness. The ISF value on the x-axis is the mean ISF calculated from the photographs taken at the beginning and the end of the study. Open squares represent replanted seedlings, closed squares are controls, and dots are transplanted seedlings.

could not be relocated and were presumed dead. Overall survivorship was 79 percent. Treatments did not differ in survival if only known deaths were considered as mortality ( $\chi^2 = 1.97$ ,  $df = 2$ ,  $P > 0.3$ ), or if lost seedlings were pooled with known deaths ( $\chi^2 = 3.62$ ,  $df = 2$ ,  $P > 0.1$ ).

GROWTH AND LEAF PRODUCTION.—Seedlings transplanted into gaps grew more than twice as much in height as replant and control seedlings (Table 1); replant and control seedlings did not exhibit significantly different growth (Table 1). Seedlings transplanted to gaps were not significantly taller than replant or control seedlings at the end of the study (Table 1), but a difference might have been obscured by our tendency to plant seedlings deeper than they were originally.

*Aglaia* seedlings appeared to exhibit a change in growth response at light levels above ISF 0.06 (Fig. 2). In closed sites, ISF had a negligible but statistically significant influence on height increase ( $c = 0.16$ ,  $R^2 = 0.026$ ,  $N = 104$ ,  $P \ll 0.001$ ). In gaps ( $ISF > 0.06$ ), however, the correlation was stronger ( $c = 0.39$ ,  $R^2 = 0.15$ ,  $N = 74$ ,  $P \ll 0.001$ ).

By the end of the experiment, transplant seedlings had significantly more leaves than replants and controls (Table 1). Control seedlings also had significantly more leaves than replant seedlings (Table 1); perhaps manipulation had caused some leaf loss so that transplanted seedlings compensated for with new growth, but shaded replants could not. Seedlings transplanted to gaps produced signifi-

TABLE 2. Growth and morphological data collected from *Aglaia mackiana* seedlings growing under maternal parent trees (from undispersed seeds) and away from adult trees (from dispersed seeds). Numbers are means  $\pm$  SD (N).

Variable	Seedlings away from adult trees	Seedlings under parent trees	Statistics
Survivorship (%) after 18 mo	80.3 (137)	78.1 (237)	$\chi^2 = 0.004$ , $df = 1$ , $P > 0.9$
No. leaves/seedling	$3.42 \pm 1.92$ (137)	$3.46 \pm 1.56$ (237)	$t = 0.23$ ; $P = 0.81$
Height increase (cm/yr)	$4.2 \pm 5.44$ (46)	$2.5 \pm 2.25$ (110)	$t = 2.08$ ; $P = 0.043$
Undamaged leaf surface area/seedling (cm <sup>2</sup> )	$765.4 \pm 674.9$ (50)	$492.6 \pm 280.5$ (29)	$t = 2.5$ ; $P = 0.014$
Proportion herbivore-pathogen damage	$0.1315 \pm 0.0858$ (50)	$0.1585 \pm 0.1071$ (29)	$t = 1.19$ ; $P = 0.239$

cantly more new leaves than replant or control seedlings (Table 1). Replant and controls did not differ in the number of new leaves produced (Table 1). Consequently, seedlings transplanted to gaps had a greater surface area of new leaves than replants or controls, which did not differ from each other (Table 1). New leaves on transplant seedlings did not differ in size from new leaves on controls or replants (Table 1).

**ROOT GROWTH.**—Primary roots of control plants were significantly longer than primary roots of transplant and replant seedlings (Table 1). Primary roots of transplants and replants were not significantly different (Table 1). This suggests that taproots were damaged and shortened during the initial manipulation. Greater care was practiced when digging up the seedlings at the end of the study. The point where taproots had been broken one year earlier was often apparent.

The longest secondary root on transplant seedlings was significantly longer than those on replants and controls (Table 1). Transplant seedlings had conspicuously greater numbers of secondary roots (A. Mack, pers. obs.). This difference is apparent in the data for root mass (Table 1): transplant seedlings had significantly greater root mass than replants or controls.

**HERBIVORE AND PATHOGEN DAMAGE TO LEAVES.**—Herbivore damage to new leaves did not differ among the three groups of seedlings. Average loss of new leaf surface area ranged from 4.7 percent in replants to 6.2 percent in control seedlings (Table 1). Likewise, damage to leaves was not correlated with canopy openness (ISF) ( $R^2 = 0.001$ ;  $N = 128$ ,  $P > 0.9$ ), nor was percent damage to old leaves and percent damage to new leaves correlated ( $R^2 = 0.003$ ,  $N = 66$ ,  $P > 0.9$ ) among all seedlings.

**SURVIVORSHIP UNDER PARENT TREES.**—The survivorship of seedlings (>2-yr-old) from undispersed seeds under parent trees (80.3%) was not significantly different from the survivorship of seedlings from dispersed seeds on four belt transects (78.5%) after 19 mo (Table 2).

**HEIGHT GROWTH AND LEAF PRODUCTION UNDER PARENT TREES.**—Seedlings under parent trees showed significantly less annual height increase than seedlings from dispersed seeds (Table 2). We compared the surface areas of old leaves on seedlings away from parent trees (control seedlings from the experimental manipulation above) to old leaves of seedlings under parent trees and found that seedlings from dispersed seeds (controls) had significantly greater average surface areas (Table 2). Leaf surface area damaged by herbivores or pathogens did not differ between leaves of seedlings growing under parent trees and leaves of control seedlings (Table 2).

## DISCUSSION

**SURVIVAL OF AGLAIA SEEDLINGS.**—Although seedlings of several taxa exhibit higher survival in gaps (Augspurger 1984, Augspurger & Kelly 1984, Denslow *et al.* 1990, Popma & Bongers 1991), this was not the case with *Aglaia* seedlings transplanted to gaps over the course of one year. Gap formation probably did not have an immediate effect on the survival of *Aglaia* seedlings if undamaged during gap formation.

Numerous studies, mostly in Central America (Clark & Clark 1984, Howe *et al.* 1985, Schupp 1988, Kitajima & Augspurger 1989, Willson & Whelan 1990), have demonstrated very low survivorship of seedlings under parent trees. *Aglaia* seedling survival from dispersed seeds (away from adult

trees) was no better than that of fallen seeds under parent trees (Table 2).

**GROWTH RESPONSES OF *AGLAI*A SEEDLINGS.**—Seedlings moved to gaps showed a rapid release from dormancy. These seedlings had 2.5 times the height growth and produced twice as many leaves and leaf surface area as seedlings in shade. Transplants to gaps had longer secondary roots and greater root dry mass (Table 1) similar to a study of *Virola* seedlings (Fisher *et al.* 1991). Because growth responses can be delayed due to transplant shock (Struve & Joly 1992), the data probably underestimate how seedlings *in situ* responded to gap formation. Small gaps close rather quickly from lateral ingrowth of adjacent trees (Fetcher *et al.* 1985); so a rapid response to increased light availability will maximize growth before light levels return to closed-canopy conditions.

Gap formation stimulates germination of dormant seeds (Garwood 1983, Lawton & Putz 1988, Horvitz & Schemske 1994) and triggers new growth in herbs, seedlings, and saplings, all potentially competitors for light (Uhl *et al.* 1988). Thus, rapid growth is advantageous in order to minimize shading from competitors on the forest floor. Growth rates of *Aglaiia* seedlings in gaps (12 cm/yr; Table 1) did not approach those of pioneer species that germinate upon canopy opening, but at 75 cm tall (Table 1), dormant *Aglaiia* seedlings have a substantial height advantage over germinating seeds. A germinating seedling would require a growth rate of 87 cm/yr to overtop a released *Aglaiia* seedling in one year, 50 cm/yr to overtop in two years, or 37 cm/yr to overtop in three years. Shade tolerant species, such as *Aglaiia*, may partially compensate for slower growth rates than competing pioneer species by having an initial height advantage over competitors.

Seedlings under parent trees had an equally high survivorship as that of seedlings away from parent trees, but their growth rates and leaf surface areas were lower. The reduction in growth rate and leaf surface area of seedlings from undispersed seeds could be due to competition with the large mother tree and the large numbers of nearby siblings. *Aglaiia* seedling density under parent trees is often > 50 times greater under parent trees than away from parent trees (A. Mack, pers. obs.). Hubbell and Foster (1990) documented greater negative effects on growth of saplings near conspecifics than near nonconspecifics. Dispersal might benefit *Aglaiia* by reducing intraspecific competition.

**LEAF MORPHOLOGY.**—Plants grown in shade might adjust to the different light environment after gap formation by producing different kinds of leaves (Canham 1989, Popma *et al.* 1992). Seedlings transplanted to gaps did not have different leaf morphology in terms of leaflet number, leaf surface area, or leaf mass of new leaves. The main response was an increase in foliar surface area due to an increase in leaf number. We did not, however, assess possible changes in new leaves such as nitrogen content, fiber content, leaf thickness, leaf toughness, or size and number of stomata (Mulkey *et al.* 1993).

**HERBIVORE AND PATHOGEN DAMAGE.**—We did not quantify damage to leaves caused by identifiable sources, but instead measured the amount of leaf surface area that was removed by all sources combined. Unlike some findings (Dudt & Shure 1994), percent damage to leaves was not correlated to canopy openness (ISF). This suggests that leaves produced in gaps are not more vulnerable to herbivory.

Percent damage to old leaves and damage to new leaves were not correlated, suggesting that variation in leaf damage is not strongly correlated with seedling genotype, at least over the length of this study. If pathogens are transmitted among leaves within seedlings, one also might expect a correlation between damage to old leaves and new leaves. Additionally, there was no significant difference between herbivore damage to seedlings under parent trees and seedlings away from parent trees. Pathogen infection or herbivore infestation do not appear to be strongly affected by density or nearest-neighbor distances.

**THE LIGHT ENVIRONMENT.**—The mean beginning and final ISF values for the control and replant sites only changed by 8–9 percent of initial ISF. This represents a < 0.5 percent change in canopy openness. However, this belies the dynamic nature of the forest canopy. Twenty-four sites under closed canopies became more open by > 20 percent of their original ISF and 38 sites became more closed by > 20 percent of their original ISF. The shifts toward increased or decreased canopy openness above specific sites tended to compensate for each other over a large spatial scale, but small-scale canopy dynamics above specific sites might have had important implications for the seedlings at those sites (Chazdon & Percy 1991).

Because treefall gaps play a significant role in rain forest ecology (Pickett 1983, Brokaw 1985,

Denslow 1987), substantial attention has been devoted to rates of gap formation (Clark 1990). Less attention has been devoted to rates of gap closure (Fetcher *et al.* 1985) though these data are equally important to studies of forest dynamics (Dirzo *et al.* 1992). There was a dramatic reduction in canopy openness in gaps; in one year the mean ISF for the gap sites decreased by 25 percent of the initial mean (roughly a 2.4 % decrease in canopy openness). Although some gaps can become larger due to die-off and treefalls along their edges (Denslow & Hartshorn 1994), only one gap in this study exhibited a marked increase in ISF (Fig. 1). Thus, in closed forest (roughly those points < 0.06 ISF; Fig. 1) the canopy is essentially in equilibrium, with some points becoming more open and others darker, whereas in gaps (those points with ISF > 0.06; Fig. 1) the tendency is for the canopy to close. In a forest in equilibrium, the gap formation rate would balance the gap closure rate. In this study, there may be a discernible distinction between gaps and closed forest around 0.06 ISF (Fig. 1). However, it is important to note that the numerical value 0.06 ISF is not directly applicable to other studies and other sites because ISF is a relative measure (not calibrated to photon flux) and because of the substantial error inherent to the analysis of hemispherical canopy photographs.

SEEDLING ECOLOGY.—*Aglaiia* seedlings survive in

shade either under the parent tree or away after dispersal where they persist for years as “dormant” seedlings. Gap formation above such seedlings triggers new growth. These seedlings (“advanced regeneration” of some authors) have a competitive head start on more rapidly-growing successional species that germinate from the seedbank upon gap formation. Previously established seedlings can constitute a major component of regrowth in gaps (Uhl *et al.* 1988). Sustainable forest logging operations (*e.g.*, Hartshorn 1989a, b) should try to minimize damage to extant seedlings in order to maximize regeneration of shade tolerant species *cf.* heliophilic successional species.

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## LITERATURE CITED

- ADDI, T. M. 1987. Limbfalls: a major cause of sapling mortality for tropical forest plants. *Biotropica* 19: 284–285.
- ASHFORD, P. S. 1989. Species richness in tropical forests. In L. B. Holm-Nielsen, I. C. Nielsen, and H. Balslev (Eds.), *Tropical forests: botanical dynamics, speciation and diversity*, pp. 239–251. Academic Press, New York, New York.
- AUGSPURGER, C. K. 1983. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *J. Ecol.* 71: 759–771.
- . 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light gaps, and pathogens. *Ecology* 65: 1705–1712.
- , AND S. E. FRANSON. 1988. Input of wind-dispersed seeds into light-gaps and forest sites in a Neotropical forest. *J. Trop. Ecol.* 4: 239–252.
- , AND C. K. KELLY. 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia (Berl.)* 61: 211–217.
- BRANDANI, A., G. S. HARTSHORN, AND G. H. ORIANS. 1988. Internal heterogeneity of gaps and species richness in Costa Rican tropical wet forest. *J. Trop. Ecol.* 4: 99–119.
- BROKAW, N. V. L. 1985. Treefalls, regrowth and community structure in tropical forests. In S. T. A. Pickett and P. S. White (Eds.), *The ecology of natural disturbance and patch dynamics*, pp. 53–71. Academic Press, New York, New York.
- . 1987. Gap-phase regeneration of three pioneer species in a tropical forest. *J. Ecol.* 75: 9–20.
- BURTON, P. J., AND D. MUELLER-DOMBOIS. 1984. Response of *Metrosideros polymorpha* seedlings to experimental canopy opening. *Ecology* 65: 779–791.
- CANHAM, C. D. 1989. Different responses to gaps among shade-tolerant tree species. *Ecology* 70: 548–550.
- CHANDRASEKHARA, U. M., AND P. S. RAMAKRISHNAN. 1993. Germinable soil seedbank dynamics during the gap phase of a humid tropical forest in the Western Ghats of Kerala, India. *J. Trop. Ecol.* 9: 455–467.
- CHAZDON, R. L., AND N. FETCHER. 1984. Light environments of tropical forest. In H. A. Mooney and C. Vazquez-



- Yanes (Eds.). Physiological ecology of plants of the wet tropics, pp. 27–36. Dr W. Junk Publishers, The Hague, The Netherlands.
- , AND C. B. FIELD. 1987. Photographic estimation of photosynthetically active radiation: evaluation of a computerized technique. *Oecologia* (Berl.) 73: 525–532.
- , AND R. W. PEARCY. 1991. The importance of sunflecks for forest understory plants. *BioScience* 41: 760–766.
- CLARK, D. A. 1994. Plant demography. In L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (Eds.). *La Selva: ecology and natural history of a Neotropical rain forest*, pp. 90–105. University of Chicago Press, Chicago, Illinois.
- , AND D. B. CLARK. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *Am. Nat.* 124: 769–788.
- , AND ———. 1992. Life history diversity of canopy and emergent trees in a Neotropical rain forest. *Ecol. Monogr.* 62: 315–344.
- CLARK, D. B. 1990. The role of disturbance in the regeneration of Neotropical moist forests. In K. S. Bawa and M. Hadley (Eds.). *Reproductive ecology of tropical forest plants, man and biosphere series 7*: 291–304. Parthenon Publishing Co., Park Ridge, New Jersey.
- CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* (Wash. DC) 199: 1302–1310.
- , J. G. TRACEY, AND L. J. WEBB. 1984. Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. *Ecol. Monogr.* 54: 141–164.
- DENSLow, J. S. 1985. Disturbance-mediated coexistence of species. In S. T. A. Pickett and P. White (Eds.). *The ecology of natural disturbance and patch dynamics*, pp. 307–324. Academic Press, New York, New York.
- . 1987. Tropical rain forest gaps and tree species diversity. *Annu. Rev. Ecol. Syst.* 18: 431–451.
- , AND A. E. GOMEZ DIAZ. 1990. Seed rain to tree-fall gaps in a Neotropical rain forest. *Can. J. For. Res.* 20: 642–648.
- , AND G. K. HARTSHORN. 1994. Tree-fall gap environments and forest dynamic processes. In L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (Eds.). *La Selva: ecology and natural history of a Neotropical rain forest*, pp. 120–127. University of Chicago Press, Chicago, Illinois.
- , J. C. SCHULTZ, P. M. VITOUSEK, AND B. R. STRAIN. 1990. Growth responses of tropical shrubs to treefall gap environments. *Ecology* 71: 165–179.
- DESTEVEN, D. 1994. Tropical tree seedling dynamics: recruitment patterns and their population consequences for three canopy species in Panama. *J. Trop. Ecol.* 10: 369–383.
- DIRZO, R., C. C. HORVITZ, H. QUEVEDO, AND M. A. LOPEZ. 1992. The effects of gap size and age on the understory herb community of a tropical Mexican rain forest. *J. Ecol.* 80: 809–822.
- DUDT, J. E., AND D. J. SHURE. 1994. The influence of light and nutrients on foliar phenolics and insect herbivory. *Ecology* 75: 86–98.
- FETCHER, N., S. E. OBERBAUER, AND B. R. STRAIN. 1985. Vegetation effects on microclimate in lowland tropical forest in Costa Rica. *Int. J. Biometeor.* 29: 145–155.
- FISHER, B. L., H. F. HOWE, AND S. J. WRIGHT. 1991. Survival and growth of *Virola surinamensis* yearlings: water augmentation in gap and understory. *Oecologia* (Berl.) 86: 292–297.
- GARWOOD, N. 1983. Seed germination in a seasonal tropical forest in Panama: a community study. *Ecol. Monogr.* 53: 159–181.
- GRUBB, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52: 107–145.
- HARTSHORN, G. S. 1978. Treefalls and tropical forest dynamics. In P. B. Tomlinson and M. H. Zimmermann (Eds.). *Tropical trees as living systems*, pp. 617–638. Cambridge University Press, New York, New York.
- . 1989a. Application of gap theory to tropical forest management: natural regeneration on strip clear-cuts in the Peruvian Andes. *Ecology* 70: 567–569.
- . 1989b. Gap-phase regeneration and tropical tree species richness. In L. B. Holm-Nielsen, I. C. Nielsen, and H. Balslev (Eds.). *Tropical forests: botanical dynamics, speciation and diversity*, pp. 65–73. Academic Press, New York, New York.
- HOPKINS, M. S., AND A. W. GRAHAM. 1983. The species composition of soil seedbanks beneath tropical rain forests in north Queensland, Australia. *Biotropica* 15: 90–99.
- HOPPEs, W. G. 1988. Seedfall patterns of several species of bird-dispersed plants in an Illinois woodland. *Ecology* 69: 320–329.
- HORVITZ, C. C., AND D. W. SCHEMSKE. 1994. Effects of dispersers, gaps, and predators on dormancy and seedling emergence in a tropical herb. *Ecology* 75: 1949–1958.
- HOWE, H. E., E. W. SCHUPP, AND L. C. WESTLEY. 1985. Early consequences of seed dispersal for a Neotropical tree (*Virola surinamensis*). *Ecology* 66: 781–791.
- HUBBELL, S. P., AND R. B. FOSTER. 1990. Structure, dynamics and equilibrium status of old growth forest on Barro Colorado Island. In A. H. Gentry (Ed.). *Four Neotropical forests*, pp. 522–541. Yale University Press, New Haven, Connecticut.
- KITAJIMA, K., AND C. K. AUGSPURGER. 1989. Seed and seedling ecology of a monocarpic tropical tree, *Tachigalia versicolor*. *Ecology* 70: 1102–1114.
- LAWTON, R. O., AND F. E. PUTZ. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology* 69: 764–777.

- LEVY, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology* 69: 1076–1089.
- LIEBERMAN, M., D. LIEBERMAN, AND R. PERLATA. 1989. Forests are not just Swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology* 70: 550–552.
- MACK, A. L. 1995. Distance and non-randomness of seed dispersal by the Dwarf Cassowary, *Casuarius bennetti*, in Papua New Guinea. *Ecography* 18: 286–295.
- . 1997. Spatial distribution, fruit production, and seed removal of a rare, dioecious canopy tree species (*Aglaia* aff. *flavida* Merr. et Perr.) in Papuan rainforest. *J. Trop. Ecol.* 13: 305–316.
- MURKEY, S., S. J. WRIGHT, AND A. P. SMITH. 1993. Comparative physiology and demography of three Neotropical forest shrubs: alternative shade-adaptive character syndromes. *Oecologia (Berl.)* 96: 526–536.
- PAIJMANS, K. 1976. New Guinea vegetation. National University Press, Canberra, Australia.
- PANNELL, C. M. 1992. A taxonomic monograph of the genus *Aglaia* Lour. (Meliaceae), Kew Bull. Additional Series edition, Vol. 16. HMSO, London, England.
- . 1997. A new, cassowary-dispersed species of *Aglaia* (Meliaceae, section Amoorra) from Papua New Guinea. *Kew Bull.* 52: 715–717.
- PICKETT, S. T. A. 1983. Differential adaptation of tropical tree species to canopy gaps and its role in community dynamics. *Trop. Ecol.* 24: 68–84.
- POPMA, J., AND F. BONGERS. 1991. Acclimation of seedlings of three Mexican tropical rain forest tree species to a change in light availability. *J. Trop. Ecol.* 7: 85–97.
- , ———, AND M. J. A. WERGER. 1992. Gap-dependence and leaf characteristics of trees in a tropical lowland rain forest in Mexico. *Oikos* 63: 207–214.
- RICH, P. M., D. B. CLARK, D. A. CLARK, AND S. F. OBERBAUER. 1993. Long-term study of solar radiation regimes in a tropical wet forest using quantum sensors and hemispherical photography. *Agr. For. Meteorol.* 65: 107–127.
- SAULEL, S. M., AND M. D. SWAINE. 1988. Rain forest seed dynamics during succession at Gogol, Papua New Guinea. *J. Ecol.* 76: 1133–1152.
- SCHUPP, E. W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. *Oikos* 51: 71–78.
- , H. F. HOWE, C. K. AUGSPURGER, AND D. J. LEVEY. 1989. Arrival and survival in tropical treefall gaps. *Ecology* 70: 562–564.
- SMITH, W. K., A. K. KNAPP, AND W. A. REINERS. 1989. Penumbra effects on sunlight penetration in plant communities. *Ecology* 70: 1603–1609.
- STRUVE, D. K., AND R. J. JOLY. 1992. Transplanted red oak seedlings mediate transplant shock by reducing leaf surface area and altering carbon allocation. *Can. J. For. Res.* 22: 1441–1448.
- TURNER, I. M. 1990. Tree seedling growth and survival in a Malaysian rain forest. *Biotropica* 22: 146–154.
- UHL, C., AND K. CLARK. 1983. Seed ecology of selected Amazon basin successional species. *Bot. Gaz.* 144: 419–424.
- , ———, N. DEZZEO, AND P. MAQUIRINO. 1988. Vegetation dynamics in Amazonian treefall gaps. *Ecology* 69: 751–763.
- WILLSON, M. E., AND C. J. WHELAN. 1990. Variation in postdispersal survival of vertebrate-dispersed seeds: effects of density, habitat, location, season, and species. *Oikos* 57: 191–198.
- WRIGHT, D. D., J. H. JESSEN, P. BURKE, AND H. G. de SILVA GARZA. 1997. Tree and liana enumeration and diversity on a one-hectare plot in Papua New Guinea. *Biotropica* In press.