

## FICUS STUPENDA GERMINATION AND SEEDLING ESTABLISHMENT IN A BORNEAN RAIN FOREST CANOPY<sup>1</sup>

TIMOTHY G. LAMAN<sup>2</sup>

Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138 USA

**Abstract.** Factors limiting seed germination and seedling establishment of the hemiepiphyte *Ficus stupenda* were investigated with two field experiments conducted in a Bornean rain forest canopy. In Experiment 1, seeds of *F. stupenda* were planted in potential establishment sites averaging 31 m above the ground in each of 45 dipterocarp trees. Twenty seeds each were planted in a total of 336 sites. Germination, survivorship, and growth were monitored over 1 yr, and examined in relation to microsite and host tree characteristics. The presence of substrate with good moisture retention (soil, rotting wood, or moss) was the most important factor for germination. Such substrates were most frequently associated with knothole sites in the canopy, which had the highest level of establishment success. Seedling survival to 12 mo was low (1.3% of planted seeds), especially considering that the best available sites in each tree were selected. Only 0.04% of seedlings showed vigorous growth after 12 mo. A seed-harvesting ant in the genus *Pheidole* significantly reduced germination success, and herbivory and desiccation killed many seedlings at later stages. In Experiment 2, seedling growth in natural canopy sites was compared with growth of seedlings in artificial planter boxes raised into the canopy in order to assess the relative quality of canopy sites. Planters were superior to natural sites for seedling survivorship and supported much more rapid seedling growth with a positive response to light level. Higher growth rates in planters compared with natural sites showed that water stress appeared to be the critical factor limiting seedling growth in the canopy, even in this very wet climate. Sites in the canopy with the optimal combination of conditions for fig seedling establishment appear to be very scarce. *Ficus* population densities may be limited by both biotic and abiotic factors reducing early recruitment success.

**Key words:** Borneo; canopy; *Ficus*; fig; germination; hemiepiphyte; rain forest; seedling establishment.

### INTRODUCTION

Seeds of hemiepiphytic or “strangler” figs (*Ficus* sp.) germinate on host trees where they spend the first part of their lives as epiphytes until their extending roots reach the ground (Putz and Holbrook 1986). Despite continued interest in the ecology of rain forest figs (Janzen 1979, Bronstein and McKey 1989), the difficulty of access to the canopy has limited studies of fig germination and seedling establishment.

Previous work has shown that fig seeds, which often have a viscous water-absorbing coating, require high humidity and light for germination (King 1888, Bessey 1908, Ramirez 1976, Titus et al. 1990). Establishment sites for fig seedlings have been described as places on host trees with accumulations of organic matter or soil where the seedling has access to water and light (Bessey 1908, Galil 1984, Putz and Holbrook 1986). There is some indication that certain host taxa provide superior establishment sites (Guy 1977, Michaloud and Michaloud-Pelletier 1987, Putz and Holbrook 1989, Daniels and Lawton 1991). However, no study prior to

this one has taken an experimental approach to investigate the specific properties of canopy establishment sites that promote *Ficus* seed germination and seedling establishment.

As first observed by Corner (1940), hemiepiphytic figs colonize a relatively small proportion of rain forest trees, despite their prolific seed production and dispersal. The question of what limits fig population densities remains unanswered, but Galil and Meiri (1981) speculate that limitations to seed germination and seedling establishment could be responsible.

To examine these possible limitations, I conducted seed planting experiments in natural canopy sites and in artificial planters raised into tree crowns to address the following questions: (1) What is the likelihood of successful germination and establishment for seeds dispersed to canopy sites? (2) What factors affect fig seed germination success in canopy microsites? (3) What establishment site characteristics are critical for seedling survivorship and growth over 1 yr?

### METHODS

#### Study site

This study was conducted at the Cabang Panti Research Site, located at 1° south latitude in Gunung Palung National Park, West Kalimantan, Indonesian Bor-

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<sup>2</sup> Present address: Arnold Arboretum of Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138 USA.

neo. The park is a 90 000-ha region of uninhabited primary rain forest. The mean annual rainfall of 4300 mm (M. Leighton, *unpublished data*) is relatively evenly distributed throughout the year. Some years have a dry month with <100 mm of rainfall, which usually falls between June and September. One longer drought of several months duration has been recorded in the last 8 yr.

The Cabang Panti Research Site is an ≈1500-ha portion of the reserve spanning a range of habitat types from peat swamp and freshwater swamp forest to mossy forest at 1100 m elevation near the summit of Mt. Palung. This study was confined to lowland forest on alluvium and sandstone foothills up to an elevation of ≈100 m above sea level. The study trees were widely dispersed along a 2-km strip of this habitat. This area has the tallest trees of the habitats in the research site, and its canopy is dominated by emergent trees in the Dipterocarpaceae that are 50–60 m tall. This forest formation is commonly referred to as lowland mixed dipterocarp forest (Ashton 1964).

#### *Study species and tree selection*

*Ficus stupenda* Miq. is one of the more common species of large hemiepiphytic figs at Cabang Panti with an approximate abundance of 20 adults/km<sup>2</sup> in the lowland forest (M. Leighton and T. Laman, *unpublished data*). It has distinctive leaf venation, which allowed young individuals to be confidently identified to species. Seeds of *F. stupenda* are ≈2 mm in diameter and had high germination rates in preliminary experiments (Laman 1994). In a survey of *F. stupenda* with roots in the ground, 86% were occupying host trees in the Dipterocarpaceae (Laman 1994). I therefore confined canopy experiments to this tree family. Important criteria for study tree selection were climbability and safety. This limitation precluded random selection of experimental trees. Forty-five trees were chosen that each contained at least five potential establishment sites such as branch crotches, knotholes, and knobs on the bole. Trees that were entirely epiphyte free and only offered bare bark sites for establishment were rejected. All study trees were over 70 cm dbh (diameter at breast height), occupied the upper canopy level or emergent stratum, and had typical dipterocarp architecture with a clear hole to ≈30 m and a domed crown.

For the most common dipterocarp species, five or more individuals were included to allow evaluation of host species differences. These were (followed by number of each species in study): *Dipterocarpus sublamellatus* (14), *Shorea hopeifolia* (5), *S. johorensis* (9), *S. parvifolia* (8). Six additional species were included to represent the diversity of host species available to *F. stupenda*. These included: *S. gibbosa* (2), *S. lamellata* (2), *S. leprosula* (1), *S. longisperma* (1), *S. parvistipulata* (2), and *S. pauciflora* (1). Five of the study trees contained adult *F. stupenda* to allow a test of the effect of adult presence on fig establishment. Planting

sites in these five trees were either on the host or in crevices between the host and fig.

Study trees were climbed using “single rope technique” adapted from cavers and mountaineers (Perry 1978, Nadkarni 1988, Laman 1994, *in press a*). For rigging access lines over 40 m high branches, the equipment used was a 30-kg (65 lb) pull compound bow firing a fiberglass fishing arrow with 11-kg (25 lb) test monofilament line fed from an open faced fishing reel.

#### *Canopy seed planting experiment*

The *F. stupenda* seeds used in this experiment were obtained from ripe figs that fell to the ground at a single tree in November 1991. A nearly pure preparation of seeds was obtained from the fraction that sank in water. Seeds were air dried and sealed in plastic bags in batches of 20. The viability of seeds used in the experiment was confirmed at the time canopy experiments were initiated by planting 100 seeds from the same homogenized group on soil in a shade house and watering them daily. Ninety-four seeds germinated, indicating a high level of viability.

In late November 1991 seeds were planted in canopy sites. In each of the 45 trees, the five best sites were selected based on where I had observed natural *F. stupenda* establishment, plus up to seven additional sites, depending on the range of sites available. All sites were >50 cm apart and were permanently marked with a numbered aluminum tag. At each planting site, 20 seeds were scattered within a 10 × 10 cm area without manipulating the substrate. A total of 340 sites were planted with a total of 6800 seeds. One site was lost when a dead branch fell off. Three others became inaccessible during the study, leaving 336 sites for data analysis.

Over the course of 1 yr, seed germination and seedling survivorship and growth were monitored in the canopy sites. Eighteen days after planting, a check of seed germination was performed in which a subsample of 19 of the 45 trees were climbed, and 152 of the 336 sites examined (almost all viable seeds germinated within 18 d in earlier germination trials). The number of seeds germinated in each site, and the number of seedlings with herbivore damage was recorded. After 7 mo and again after 12 mo, all sites were examined and data were recorded on the number of living seedlings and the length of the longest leaf, number of leaves, and stem length for each seedling. Signs of herbivory or drought stress were also recorded.

#### *Microsite level variables*

In order to examine what factors affected fig seed germination and establishment, data were collected on a number of potentially important variables. The statistical approach used (explained further below) made it possible to separate microsite level effects (unique to each canopy site) from tree level effects (common across all seed planting sites in a given tree). The following variables were used.

*Height above ground.*—Mean ( $\pm 1$  SD) site height was  $30.8 \pm 5.0$  m,  $N = 336$ .

*Site type.*—The site was categorized as: crotch = the fork where a branch leaves the trunk or a large branch divides; knothole = hole left where branch broke off; branch = the upper surface of a branch; bole = on the tree bole at a bulge or epiphyte clump.

*Substrate type.*—The substrate on which seeds were planted was categorized as (followed by percent of sites in each category): rotting wood (7%); soil (30%); moss (26%); leaf litter (24%); bark (13%).

*Soil quantity.*—The volume of soil accessible to germinating seedlings in each site was estimated visually. Soil quantity was transformed with the function  $\log(1 + \text{soil volume})$  for use as a continuous variable, or divided into five categories: 0, 0.1–0.2, 0.3–0.5, 0.6–1.0,  $>1.0$  L, for use as a categorical variable.

*Rain protection.*—Sheltering from rain that might dislodge seeds or seedlings (by overhanging epiphytes or branches) was estimated from 1 (0–20% shelter) to 5 (80–100% shelter).

*Canopy cover.*—Cover above the site was estimated from 1 (0–20% cover) to 5 (80–100% cover). This variable differed from the rain protection variable in that a site could have complete rain protection and still be exposed to light from the side. This variable reflects overall openness and perhaps proneness to desiccation.

*Light level.*—Sepia paper integrating light meters (ILMs) (Friend 1961, Sullivan and Mix 1983) were used to measure solar radiation at canopy microsites relative to an open gap control site in late 1992. ILMs were deployed on wire supports 10 cm above the substrate of each canopy site for periods of 7–14 d, matched in time with sets of control ILMs placed in a large gap. Based on several calibration curves reported in D. Ackerly and M. Latham (*unpublished data*), a slope of 0.40 for the relationship of exposed paper layers to  $\log(\text{total light})$  was used in calculating the relative percent illumination in the canopy sites relative to the gap site, as follows:

$$\frac{\text{sample light}}{\text{gap light}} = \frac{1}{10^{k(\text{NO} - \text{Ns})}}$$

where  $k$  = slope,  $N_s$  = number of sheets exposed at sample site, and  $\text{NO}$  = number of sheets exposed at reference site. Ants in some trees damaged ILMs resulting in 50 of the 336 sites with missing values. Light level was arcsine transformed for use as a continuous variable and divided into five classes (0–20, 21–40%, etc.) when used as a categorical variable.

#### *Tree level variables*

*Tree species.*—See *Study species and tree selection* above for list of species used.

*Tree dbh.*—Tree diameter was used as a measure of tree size. Tree dbh was treated as a continuous variable in regression models, and divided into four classes (70–

90, 91–110, 111–130, and  $>130$  cm) for contingency table analyses.

*Pheidole ant presence.*—Ants in the genus *Pheidole* that harvested *Ficus* seeds were discovered in the canopy of some study trees.

*F. stupenda presence.*—Five trees in the sample hosted adult *F. stupenda*.

*Epiphyte load.* Overall epiphyte load was estimated visually to the nearest 10%. Epiphyte load was arcsine transformed for use as a continuous variable in regression models and divided into five classes (0–20, 21–40%, etc.) for contingency table analyses.

Ten natural *F. stupenda* seedlings were encountered in the canopy during the study and their fates were followed. All died by the next time they were checked. Natural seed input to experimental sites was therefore unlikely to have been a significant source of error.

#### *Canopy planter box experiment*

In parallel with the planting experiment in natural canopy sites, a smaller scale experiment was conducted to examine the growth of seedlings placed in the canopy in planter boxes relative to those in natural sites. Planter boxes were constructed from polyvinyl chloride plastic roof gutter material ( $10 \times 12 \times 20$  cm) and were filled with 2 L of high organic content alluvial soil. Seeds used were from the same batch as those used in the natural site planting experiment, and both experiments were initiated simultaneously. Two *F. stupenda* seedlings were grown in each of 10 planters for 3 wk before planters were moved into the canopy. One planter was placed against the upper bole of each of 10 dipterocarp study trees. Planter box heights were 26–33 m above the ground. The side of the planter tied against the tree bole was covered with window screen only, allowing rapid drainage of excess water and the potential for fig roots to contact the host trunk. Planter box seedlings were monitored after 7 and 12 mo. Seedling survivorship and stem height, stem diameter, maximum leaf length, and number of leaves were recorded. Light level at each planter location was measured as described above with ILMs.

#### *Statistical analysis*

To analyze effects on *Ficus* germination success, discrete and continuous variables were combined in multiple regression models using the general linear modeling procedure in the computer program Data Desk (Velleman 1989). Computations were based on partial sums of squares (Type IV), which revealed the effects of individual variables over and above others included in each model. With this design, it was possible to take into account the unbalanced nature of the experiment due to the different types of sites available from tree to tree.

Since experimental planting sites were grouped in different trees, each unique in location as well as other characteristics, it was suspected that a tree effect would

TABLE 1. Establishment site type vs. seed germination and seedling establishment success (percent of total seeds planted that were alive as seedlings at each time after planting). Twenty seeds were planted per site.

Establishment site type	Time after planting					
	18 d		7 mo		12 mo	
	<i>N</i> (sites % checked)	<i>N</i> (sites % checked)	<i>N</i> (sites % checked)	<i>N</i> (sites % checked)	<i>N</i> (sites % checked)	<i>N</i> (sites % checked)
Branch	24.2 26	1.1 42	0.5 43			
Bole	24.9 34	1.4 63	0.4 66			
Crotch	21.8 82	2.1 185	0.8 191			
Knothole	37.0 10	10.1 36	6.0 36			
Total for all sites	23.9 152	2.7 326	1.3 336			

account for a significant amount of the variation. An initial model therefore tested 18-d seed germination success (arcsine transformed proportion of seeds germinated in each site) vs. tree species and tree number (the within-tree grouping variable). Three tree species containing 145 planting sites were included (10 *D. sublamellatus*, 4 *S. hopeifolia*, and 4 *S. johorensis*). Tree number was nested within tree species. Both species and tree number had significant effects on the number of seedlings alive in canopy sites at 18 d. Tree species accounted for 12.2% of the variation in germination level ( $F = 3.94$ ,  $df = 2$ ,  $P = 0.04$ ), while tree number explained 23.2% of the variation ( $F = 3.15$ ,  $df = 15$ ,  $P < 0.001$ ).

Based on this result, further analysis of germination success was divided into two parts. First, controlling for tree effects by including tree number in the model, factors affecting germination at the site level were examined (microsite-level analysis). Second, tree characteristics responsible for the differences in germination success between trees were examined (tree-level analysis), while controlling for microsite differences by including the main effect from the microsite level analysis in the model. Continuous variables were transformed as necessary to meet the assumptions of normality (Sokal and Rohlf 1981). Up to two-way interactions were tested for in the models, but are not reported when they did not contribute significantly to the model.

For the analysis of survivorship at 7 mo, the sample size of remaining seedlings was inadequate for multiple regression analysis. Contingency tables were used to examine which independent variables had significant effects on seedling survivorship. Variables having significant effects in two-way contingency table analysis were tested in multiway tables to examine patterns of interaction among them.

## RESULTS

### Canopy seed planting experiment

**Germination and establishment success.**—Of all seeds planted in canopy sites, 23.9% germinated, but

TABLE 2. Establishment site type vs. success level (percent of sites with one or more living seedlings present) at each census after planting.

Establishment site type	Time after planting					
	18 d		7 mo		12 mo	
	<i>N</i> (sites % checked)	<i>N</i> (sites % checked)	<i>N</i> (sites % checked)	<i>N</i> (sites % checked)	<i>N</i> (sites % checked)	<i>N</i> (sites % checked)
Branch	80.8 26	7.1 42	4.7 43			
Bole	88.2 34	12.7 63	7.6 66			
Crotch	62.2 82	12.4 185	3.7 191			
Knothole	80.0 10	16.7 36	13.9 36			
Total for all sizes	72.4 152	12.3 326	5.7 336			

only 2.7% survived to 7 mo, and 1.3% (85 of 6720 seeds planted) remained alive at the end of 1 yr (Table 1).

Of the four establishment site categories, knotholes had 10 times higher establishment success compared with other site types by the end of the year (Table 1). The crotch and knothole data provide unbiased measures of success in those site types because all available sites in these categories containing organic deposits were planted with seeds. The bole and branch sites used were higher quality sites than random locations on boles and branches.

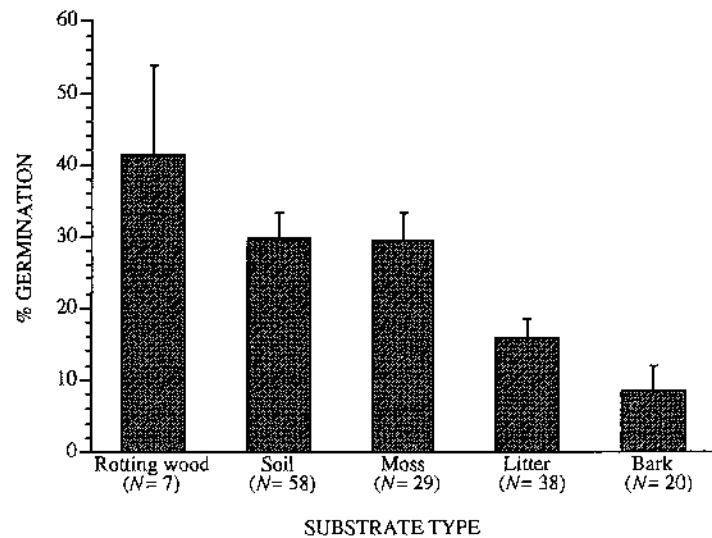
A total of 72.4% of the sites checked supported at least some seed germination at 18 d (Table 2). Only 12.3% (40 sites) of sites checked contained seedlings at 7 mo, however, and only 5.7% (a total of 19 sites) had seedlings alive at 12 mo. Knotholes stand out again in this analysis as the establishment site with the highest success after 12 mo.

**Factors affecting germination.**—Examining the effects of microsite-level variables on germination level with a general linear model revealed that substrate type had a significant effect on initial germination in the canopy (Table 3). Substrate type was the only variable that accounted for a significant portion of the variance

TABLE 3. Microsite effects on germination. ANOVA table for general linear model of microsite level variables vs. 18-d seed germination success (arcsine-transformed proportion of seeds germinated in each site). Transformations of other variables are explained in the methods. Includes all 19 trees with total of 152 sites surveyed at 18 d after planting seeds. The variable "tree number" is included to control for tree level effects. Partial sums of squares are reported.

Source	df	SS	MS	F	P
Tree number	18	5.57	0.31	4.06	<0.001
Substrate type	4	1.21	0.30	3.98	0.005
Site type	3	0.03	0.01	0.12	0.94 NS
Height above ground	1	0.07	0.07	0.98	0.32 NS
Soil quantity	1	0.06	0.06	0.79	0.38 NS
Rain protection	4	0.46	0.11	1.50	0.21 NS
Canopy cover	4	0.10	0.02	0.32	0.86 NS
Residual	116	8.85	0.08		
Total	151	18.43			

FIG. 1. Germination success of *F. stipenda* seeds in natural canopy sites by substrate type. Sampled at 18 d after planting in 19 canopy trees with a total of 152 planting sites. Values shown are means and bars indicate 1 SE. Significant differences exist among groups (see Table 3). Sample sizes in parentheses equal the number of sites examined at 18 d past planting of seeds.



(6.6%), over and above variance among trees (which accounted for 30.2% of the variance). None of the other variables contributed significantly to improving the model. Note that despite large differences in germination level among site types (Table 1), site type itself did not have a significant effect on germination. The model (Table 3) indicates that differences between site type are attributable to differential distribution of substrate types among site categories. Light level was missing for 24 cases and is not included in the model shown in Table 3. A model with light level included is still significant for substrate and tree number, but shows no significant effect for light. There was thus no evidence that light level in the canopy affects germination.

Some substrate types were significantly better than others for germination (Table 3, Fig. 1). Rotting wood, found in knotholes and some crotches of broken branches, was an excellent substrate for germination. This substrate was rare, however, as only seven such

sites were found in the 152-site subsample checked at 18 d. Soil and moss also promoted high germination rates on the order of 30%, while litter and bark were poorer substrates for germination.

A second general linear model examining the effects of tree level variables on germination showed that tree species and the presence of *Pheidole* seed harvesting ants had significant effects (Table 4). Tree species accounted for 9.9% of the variance, while ants accounted for 3.1%, over and above the variance due to the main effect in the microsite-level analysis, substrate type, which accounted for 6.7% of the variance. The reduction in germination due to the presence of ants was predicted based on observations of this ant species harvesting fig seeds (Laman, *in press b*).

*Factors affecting establishment and growth.*—Water stress and herbivory were the principal observed causes of seedling mortality. Signs of water stress were found in 55% of the 85 seedlings alive at 12 mo. Herbivore damage was seen on 11% of the living seedlings at 18 d, and at 12 mo on 16% of the remaining 85 seedlings.

Factors affecting seedling establishment at 7 mo were examined using contingency tables to test for associations between variables describing sites and the presence or absence of seedlings, and interactions between these variables. For microsite-level variables, substrate type was the only factor to have an effect ( $\chi^2 = 30.39$ ,  $df = 4$ ,  $P < 0.001$ ), just as at the germination stage. Contrary to expectations, sites with seedlings surviving were not associated with particular light levels or soil quantities.

For variables at the whole-tree level, *Pheidole* ant presence still had significant effects, as at 18 d ( $\chi^2 = 5.93$ ,  $df = 1$ ,  $P = 0.02$ ). The reduction in germination due to *Pheidole* ants carried over as a significant effect on establishment. Out of 84 canopy sites with ants present, only four had any live seedlings. Three other

TABLE 4. Tree level effects on germination. ANOVA table for general linear model of tree level variables vs. 18-d seed germination success (arcsine-transformed proportion of seeds germinated in each site). Transformations of other variables are explained in the *Methods*. Includes all 19 trees with total of 152 sites surveyed at 18 d after planting seeds. The variable "substrate type," the only main effect detected in microsite-level analysis, is included to control for microsite level effects. Partial sums of squares are reported.

Source	df	SS	MS	F	P
Substrate type	4	1.24	0.31	3.89	0.005
Tree species	3	1.84	0.61	7.71	<0.001
Tree dbh	1	0.28	0.28	3.50	0.06 NS
<i>Pheidole</i> ant presence	1	0.58	0.58	7.26	0.008
<i>F. stipenda</i> adult	1	0.02	0.02	0.30	0.58 NS
Epiphyte load	1	0.18	0.18	2.32	0.13 NS
Residual	140	11.12	0.08		
Total	151	18.43			

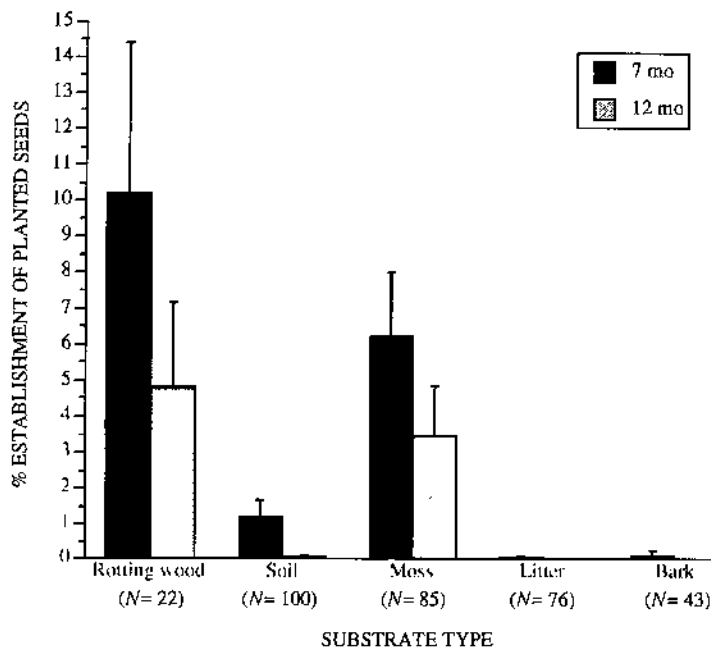


FIG. 2. Establishment of *F. stupenda* seedlings in natural canopy sites in relation to substrate type at 7 and 12 mo after planting. Values are the mean percent of seeds planted per site that are living seedlings at each time period, shown by substrate category. Bars show 1 SE. Sample sizes are number of sites sampled at 7 mo. At 12 mo, sample sizes by substrate type were: 22, 101, 89, 79, and 45, respectively.

tree-level variables, tree species, tree dbh, and epiphyte load had possible effects on the presence of seedlings. Survival was higher than expected by chance in *Dipterocarpus sublamellatus* hosts and lower than expected in *Shorea johorensis* and *S. parvifolia*. Sites with surviving seedlings were also fewer in large diameter trees and in trees with high epiphyte loads. An examination of the interdependence of these variables with multiway contingency tables showed that substrate type and ants had a distinct effect independent of all other factors. Tree species, tree dbh, and epiphyte load, on the other hand, were all significantly intercorrelated so the effects of these variables on establishment cannot be separated. The presence of a *F. stupenda* adult on the host tree did not have a significant effect on seedling survival.

The 40 sites with seedlings remaining alive at 7 mo were spread across 20 trees. One tree, a *Shorea longisperma*, had eight sites with living seedlings. It was not possible to determine if this was due to properties of the species or just that individual. No other tree had more than three sites with seedlings remaining, and most had only one.

Since substrate type appears to be an important factor for germination and establishment, the pattern of survivorship at 7 and 12 mo (Fig. 2). While bare soil was an excellent substrate for germination, it was not good for longer term survival (compare Fig. 2 to Fig. 1). Rotting wood and moss continued to be good substrates for seedling establishment and subsequent survival.

Seedling size was analyzed in relation to site characteristics. The largest seedling in each tree at 7 mo was used because including multiple seedlings from

the same site or the same tree in a model would bias the result heavily to sites and trees with more than one seedling. This reduced the sample to 20 seedlings. The longest leaf length was used as a measure of seedling growth. This measure was highly correlated with both seedling height and the number of leaves for the fig seedlings in this study (T. G. Laman, unpublished data). A general linear model was constructed in which microsite-level and tree-level variables were mixed since only one site per tree was used. The factors tested for effects on growth were substrate type, light level, soil quantity, epiphyte load, and height above ground. Five of the sites were missing values for light level, thus the sample was reduced to 15 for the model including all these variables. Light level showed a significant negative relationship with growth accounting for 48.2% of the variance in seedling size ( $F = 8.46$ ,  $df = 1$ ,  $P = 0.02$ ). The largest surviving seedlings were found in sites with lower light levels. None of the other variables had significant effects on growth with this data set.

Whether the seedlings surviving to 12 mo had grown significantly since the 7-mo measurements was examined for the 85 seedlings remaining in 19 sites. In 8 of the 19 sites, leaves supported at the end of the year were smaller than at 7 mo. Of the other 11 sites, 6 showed increases in size of >25%. However, even among the largest seedlings from the six most successful sites, three of them were quite small in size, with maximum leaf sizes between 12 and 19 mm. The other three sites produced much larger seedlings with maximum leaf lengths of 46–56 mm and heights of 50–80 mm. To look at how unique the properties of these three most successful sites were, I determined how

many sites in the whole study had traits that fell within the range of values spanned by these sites. The range of traits in the sites were a substrate of soil, moss, or rotting wood, light level between 9 and 23%, and soil greater than 0.5 L if on soil or moss, while no soil required if on rotting wood. Sixty out of the total 336 sites fell within these ranges.

#### Canopy planter box experiment

In the parallel experiment using ten artificial planter boxes raised into the canopy, survivorship and growth were far greater than in the natural canopy sites. The overall establishment success in planters was 30%, compared with 5.4% for germinated seeds in natural sites. Where two seedlings were alive in the same planter, only the larger one was used in analysis of growth. All the seedlings alive at the end of the year were of similar size or much larger than the largest three seedlings from the canopy planting experiment. These had a range of maximum leaf lengths from 46 to 180 mm, and height from 62 to 145 mm.

For seedlings in canopy planter boxes, growth was positively correlated with light exposure (Fig. 3). The regression is still highly significant if the plant at the highest light level in Fig. 3 is excluded. This result supports the prediction that given adequate water and nutrients, fig seedlings will grow faster in a higher light environment.

## DISCUSSION

### Germination

Results of the present study, those of a preliminary germination trial I carried out in planters at ground level (Laman 1994), and the results of earlier studies (Galil and Meiri 1981, Titus et al. 1990) all support the view that the most critical factor for fig seed germination is moisture availability. The significant effects of substrate on germination presented here can best be explained through the moisture conditions substrates create for seeds. Although substrate moisture content was not measured directly in this study, levels of germination success paralleled the expected moisture holding properties of each substrate type. More porous substrates like rotting wood, moss, and soil have a higher water holding capacity than bark and dead leaves (ter Steege and Cornelissen 1989).

Seed harvesting by ants of the genus *Pheidole* was a significant factor affecting germination success. Eleven of the 45 canopy trees were found to contain this ant species, and it thus could have a significant impact on *Ficus* reproduction in the Bornean rain forest. Additional details of this interaction, and implications of possible seed predation on hemiepiphytes by ants in the canopy are examined further in a separate paper (Laman, *in press b*). I also observed lygaeid bugs feeding on fig seeds below fruiting figs, and they appear to be another potential source of mortality whose level

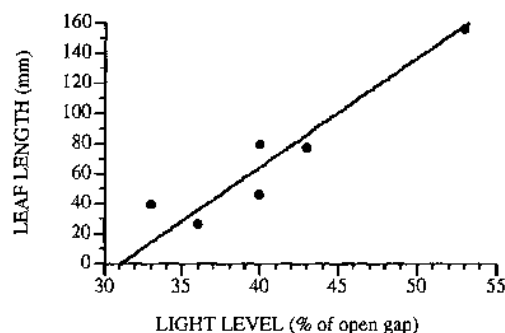


FIG. 3. Relationship between light exposure and seedling size represented by length of largest leaf for *F. stupenda* seedlings grown in planter boxes in the canopy for 7 mo. Adjusted  $R^2 \approx 0.86$ .

of importance in Borneo is not yet clear. Bugs in this family are known fig seed predatory specialists in Africa (Slater 1972), but this behavior has not been previously reported from Borneo. While I only observed these bugs on the ground, if they are attracted to the canopy of fruiting figs, they could be sources of significant seed mortality in canopy sites near the parent plant.

In the analysis of germination success, tree species also had a significant effect independent of the other critical factors, i.e., substrate type and ants. Germination was significantly higher in *Dipterocarpus sublamellatus* than in two *Shorea* species. Due to the restrictions on tree selection in the design of this experiment as discussed in the methods, however, some biases could have entered into tree selection. The possibility that different dipterocarp species vary in their suitability as fig hosts thus remains speculative.

### Establishment

Successful establishment in canopy sites was low, especially considering that I selected known preferred sites for seed planting. Interpreting the results of the seed planting experiment in light of the parallel experiment in planter boxes points to water availability as the most critical factor limiting seedling establishment. The faster growth of the seedlings in planters reveals that they provided resources that were superior to even the best of the 336 natural sites. The 2-L volume of the planter box not only provided ample soil with nutrients, but also considerable water-retaining capacity. It was not possible to measure water availability directly in this experiment, but water stress is directly related to light exposure, other things being equal. The light levels at the planter boxes with seedlings at the end of the year ranged from 33 to 43%. This is higher than the light levels at the best canopy seed planting sites, which ranged from 9 to 23%. I examined the light levels at all 40 sites that had seedlings at 7 mo to see how seedlings at higher light levels fared. There were 11 sites with light levels over 30%. However, in all but

two of those, the seedlings died before 12 mo, and the remaining two showed no growth. The seedlings in the two planter boxes with light levels over 43% also died, apparently of desiccation. Since the planter boxes presumably contain more than ample nutrients for plants of this size, water availability is likely to have been the most important factor for these seedlings. These observations suggest that while requiring high light levels for rapid growth, *F. stupenda* seedlings experience serious water stress in the canopy. Sites with high light exposure are likely to be the most water stressed, and this could explain why there was a negative effect of light level on growth in the natural site planting experiment after 7 mo. My results are thus consistent with the interpretation that a reliable water supply could be the most important characteristic of an establishment site.

Independent evidence also supports the idea that nutrients are unlikely to be as important as water as a limiting factor for fig establishment. Putz and Holbrook (1989) showed through a nutritional analysis of *Ficus* seedling leaves that there was no evidence that they were nutrient limited. Nadkarni (1981, 1984) has also shown that nutrients in the canopy in general do not appear to be limiting factors for epiphyte growth. In fact, she found that trees extend roots into epiphyte mats to harvest excess nutrients in the canopy (Nadkarni 1981).

The strong correlation between light level and growth in the planter box seedlings indicates that as long as water is not limiting, high light promotes seedling growth. Fast growth appears to be possible in *F. stupenda* under high light conditions. Sites providing adequate water supplies in high light locations in the canopy may be exceedingly rare, and characteristics of the establishment site that allow it to trap and hold water may be the most critical.

Substrate type had a significant effect on establishment success, as it did for germination, but the pattern of optimal substrates shifted such that moss was far superior to soil at 7 and 12 mo. While for germination the critical feature of the substrate may be the ability to keep the seed moist, additional properties undoubtedly become important as the seedling grows. Establishment success was best on rotting wood and mats of moss, both of which provide a good matrix for rooting and anchoring the seedling, as well as holding water. Perhaps soil offers both a less solid anchor, and dries out more quickly than moss or dead and rotting wood. These observations are in accordance with Michaloud and Michaloud-Pelletier's (1987) record that 80% of the sites where they observed successfully established figs were places where mutilation or damage had occurred to the tree, presumably offering dead wood substrates. Evidence from studies of epiphyte establishment also suggest that the presence of mosses on a branch increases the probability that a seed will lodge at a given site and germinate (Bennett 1986).

In addition to characteristics of the establishment sites, various sources of mortality unrelated to site features also appear to affect seedling establishment. Seed collection by ants had a significant effect, and there was ample evidence of herbivory on seedlings. Determining precisely to what degree such factors contribute to mortality relative to environmental factors was not possible in this experiment. Sixty of the 336 sites fell within the range of site variables that defined the three best sites at the end of the year, suggesting that these sites were not particularly unique. Perhaps chance encounters with seed predators, herbivores, dislodgement, or being covered by falling leaves could have a major impact on fig establishment in the canopy. In addition, the fact that in each of the best canopy planting sites, there was a single seedling that was considerably larger than the others suggests that very small-scale microsite factors such as exactly where the seedling takes root could have a major effect on early growth.

#### *Establishment on conspecific hosts*

The inclusion in the experiment of five dipterocarps hosting adult *F. stupenda* allowed me to test whether fig seedlings would germinate on conspecifics. The canopy planting sites selected in these trees represented the range of available crotches and other sites, including many crevices between fig roots or stems and host trunk or branches. *F. stupenda* seeds readily germinated in these sites, and there was no statistically significant effect of being in a conspecific fig, either for germination or establishment. With only five fig trees in the sample, however, the power to detect any differences was limited. The fact that germination occurred in these cases, however, is consistent with the conclusion of Titus et al. (1990) that there is no evidence for autotoxic effects against germination in fig crowns.

#### *Ecological implications*

The positive correlation between light and growth of fig seedlings in the artificial planter experiment, in addition to their inability to survive low light conditions in the understory (Laman 1994), supports the view that the hemiepiphytic habit is an adaptation to exploit the high light environment of the canopy (Dobzhansky and Murca-Pires 1954, Ramirez 1977, Putz and Holbrook 1986, Daniels and Lawton 1991). While plants germinating at ground level in the rain forest may often be limited by light and to a lesser extent by water, for hemiepiphytes it appears that light is plentiful and water is the primary limiting factor. Thus even in a very wet climate, water stress can be a major limitation in the canopy, pointing out the tremendous difference between canopy and terrestrial microclimates.

Overall establishment of 1.3% in this experiment is higher than that reported for other small-seeded rain forest plants such as shrubs in the Melastomataceae

(Ellison et al. 1993), or *Cecropia* (Alvarez-Buylla and Garcia-Barrios 1991). However, these experiments are not directly comparable since I planted seeds specifically into potential safe sites. Large-seeded rain forest species on the other hand, often have much higher establishment success (e.g., Augspurger 1984, Howe 1990). For small-seeded plants that do not have a large store of nutrients to help with establishment, the establishment site must meet specific requirements to sustain the young seedling.

*Limitations on fig recruitment.*—Sites in the canopy where the optimal combination of conditions come together for fig seedling establishment appear to be very scarce. Also, a variety of sources of mortality must be avoided for a seedling to be successful. These findings support the speculations of Galil and Meiri (1981) and M. Leighton (*personal communication*) that relatively low abundances of figs in the forest compared with the abundance of potential host trees could be due to limitations to seedling establishment. If successful seed dispersal to good sites alone had been the factor limiting fig recruitment, then I would have expected much higher establishment success in this study. Thus we can conclude that postdispersal factors appear to be very significant limitations to establishment. Seed dispersal could additionally be a major limiting step (Laman, *in press c*).

*Maintenance of species diversity in Ficus.*—The presence of  $\geq 20$  similar hemiepiphytic figs in one forest such as at this study site (T. G. Laman, *unpublished data*) raises the question of how this diversity is maintained. Benzing (1981) has suggested for epiphytes that an inability to saturate potential establishment sites with seeds, combined with patchy and shifting target sites, could account for multiple species with identical requirements for coexistence, and Grubb (1986) has extended the idea to plants in general. If other fig species face limitations to establishment similar to *F. stipenda*, numerous species may be able to coexist while exploiting identical or very similar lifestyles as hemiepiphytes without competing with one another.

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