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Factors affecting the distribution of a neotropical hemiepiphyte

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FACTORS AFFECTING THE DISTRIBUTION OF
A NEOTROPICAL HEMIEPIPHYTE

A Thesis

Presented to

The Faculty of the Department of Biology
San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Gregory W. Massa

December 1996

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Abstract

FACTORS AFFECTING THE DISTRIBUTION OF A NEOTROPICAL HEMIEPIPHYTE

by Gregory W. Massa

The distribution of *Marcgravia serrae*, a primary hemiepiphyte, was investigated on host trees at La Selva Biological Station, Costa Rica. A total of 1181 trees on four soil types and four topographic positions was examined for *M. serrae* presence. The hemiepiphyte showed preferences for tree trunks with relatively higher densities of bryophytes, but not for a particular soil type or topographic position. Bryophyte mats may be reservoirs of water or nutrients, may protect the hemiepiphyte seedlings from allelopathic effects of bark, or may improve a seed's ability to establish on a tree. A seed germination study was conducted to examine allelopathic effects of three tree barks (*Dipteryx panamensis*, *Hyeronima oblonga*, and *Terminalia oblonga*). Germination rate was highest on *Dipteryx*, and lowest on *Terminalia*. Differential seed predation may also influence the germination site of *M. serrae*. Seeds placed on the ground were removed more frequently than those placed on trees.

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Introduction

Hemiepiphytes are plants that spend part of their lives as true epiphytes, with no connection to the ground, and another part with an "umbilical" connection to the soil (Williams-Linera and Lawton 1995). Primary hemiepiphytes begin life in a tree and drop roots to the ground (e.g., strangler figs), while secondary hemiepiphytes germinate in the soil and later lose their connections as they climb a tree by means of adventitious roots (e.g., many Araceae). These growth forms have evolved independently many times, and are found in 25 families and roughly 59 genera (Williams-Linera and Lawton 1995). Almost 1500 species have been identified, with more likely to be discovered as botanists continue collecting from the poorly known forest canopy (Williams-Linera and Lawton 1995). The plant families with the most hemiepiphytes include Moraceae, Clusiaceae, Araliaceae, and Araceae (Williams-Linera and Lawton 1995).

Hemiepiphytes, like epiphytes and lianas, are structural parasites, dependent upon trees to provide mechanical support during some, if not all, of their lives (Stevens 1987). This dependency is generally detrimental to the trees that support these life forms, reducing stem diameter growth (Featherly 1941, Putz 1982, Clark and Clark 1990) and fecundity (Stevens 1987). In addition, hemiepiphytes may compete with the host tree for light, water and nutrients (Clark and Clark 1990). Hemiepiphytes and lianas may also increase the accessibility of the host tree canopy to foliovores (Montgomery and Sundquist 1978, Charles-Dominique *et al.* 1981). For these reasons, trees that possess characteristics to reduce their suitability for the colonization and growth of hemiepiphytes may have a selective advantage over trees that do not possess these characteristics.

Bark characteristics, such as roughness or shedding, or tree attributes, such as buttressing, may influence distributional patterns in hemiepiphytes. For example, *Hura*

crepitans L. (Euphorbiaceae) is a common host of hemiepiphytes because its spiny bark may facilitate seedling establishment, while *Quararibea asterolepis* Pittier (Bombacaceae), with smooth, peeling bark, hosts few hemiepiphytes (Todzia 1986). In Corcovado National Park in Costa Rica, the distributions of seven species of epiphyte vary with respect to host branch angle, diameter, and height, and in one case, bark texture (Kernan and Fowler 1995). Bark porosity and pH, as well as the makeup of the bryophyte mat, may also influence epiphyte distributions (ter Steege and Cornelissen 1989).

Another way trees may reduce the frequency of colonization by hemiepiphytes is the chemical inhibition of seed germination (allelopathy). For example, the barks of certain species of *Quercus* in Mexico are inhibitory to the germination and early growth of epiphytic orchids (Frei and Dodson 1972). Talley *et al.* (1996a) found a similar allelopathic effect on the germination of *Rhus radicans* L. (Anacardiaceae), a root-climbing liana, by some hardwood trees in Alabama, USA. However, data on allelochemical interactions between hemiepiphytes and their hosts is lacking.

Many plant distributions are influenced by soil type and nutrient status, as well as topography (e.g., Huston 1980, Johnston 1992, Oliveira-Filho *et al.* 1994, Clark *et al.* 1995). This is expected for terrestrially rooted plants, but the effects of soil and topography on primary hemiepiphytes, which must first survive an epiphytic stage, is unknown.

Finally, hemiepiphyte distributions may be affected by habits of their dispersers or influenced by unequal seed predation pressures. For example, *Platypodium elegans* J. Vogel, a leguminous tree from Panama, largely escapes colonization by hemiepiphytes because its wind dispersed seeds do not attract the frugivorous birds and bats that carry hemiepiphyte seeds (Todzia 1986). *Ficus microcarpa* L. (Moraceae), an Asian

hemiepiphyte, has a two-phase seed dispersal in which seeds pass first through the gut of birds and then are moved by ants attracted to the seeds' elaiosomes (Kaufmann *et al.* 1991). *Pheidole* ants at La Selva Biological Station, Costa Rica, harvest seeds from the forest floor and kill most of them, but significantly benefit some by depositing seeds in favorable germination sites (Levey and Byrne 1993).

This paper addresses whether *Marcgravia serrae* de Roon (Marcgraviaceae), a primary hemiepiphyte, exhibits preferences for certain host tree characteristics, soil types, or topographic positions. In addition, it will examine allelopathic effects of tree barks on the germination of *M. serrae* seeds. Finally, it will explore the influence of seed predators on the distribution of this plant.

Species Description

One taxon of hemiepiphytes is Marcgraviaceae, a strictly neotropical family of (mostly) woody hemiepiphytes. Approximately 75% of the 130 or so species in the family are epiphytic or hemiepiphytic (Putz and Holbrook 1986). The family is easily identifiable by either vegetative or floral characters, but the presence of saccate nectaries subtending the flowers is the most obvious feature. The form and location of these nectaries chiefly determines generic placement (Gentry 1993). *Souroubea* has a brush-type inflorescence with nectaries immediately subtending each flower, while *Norantea* has the nectaries subtending each pedicel. In *Marcgravia*, the inflorescence has been reduced to a wheel-like ring of flowers subtended by these nectaries, always fewer in number than the flowers (see Sazima *et al.* 1993 for diagrams of these inflorescences). Pollination in Marcgraviaceae has received some attention (Bailey 1922, Howard 1970, Sazima and Sazima 1980, Sazima *et al.* 1993), although the pollen vectors of most species remain in doubt, and most species appear to be autogamous (Bedell, personal communication, cited in Gentry and Dodson 1987).

In some genera, including *Marcgravia* and *Norantea*, the juvenile climbing shoots differ from the mature shoots in leaf form and in the presence of adventitious roots that anchor the plant to the substrate. In many species, the switch between the juvenile and adult forms is reversible but the stimulus that causes the change is unknown.

Marcgravia serrae is a common plant in old-growth forest at La Selva but is almost completely absent from second-growth and selectively logged forest. Juvenile *Marcgravia serrae* are commonly found climbing the trunks of trees in the shaded understory of primary forest at La Selva. The seeds appear to germinate on the lower portion of tree trunks (within the first two meters) or at the immediate base of the tree. The plant is not found on the forest floor, with the exception of occasional small individuals climbing large boulders (personal observation). Kelly (1985) notes a similar pattern for *Marcgravia brachysepala* in Jamaica. Once established, tiny hair-like roots grow down to the forest floor as the shoot climbs the tree by means of adventitious roots. On the basis of this phenomenon, this species can be classified as a primary hemiepiphyte, although hemiepiphytic Marcgraviaceae have been previously described as being entirely secondary hemiepiphytes (Madison 1977, Benzing 1987, Williams-Linera and Lawton 1995). Leaf size at this stage is generally 1-2 (3) cm in length and 0.5 cm in width. The square stem at the earliest stage is approximately 1 mm in diameter. At some point in the plant's development, it will produce adult leaves, generally after the stem is at least 5 mm in diameter and the plant is more than a few meters in height. These adult leaves are much larger (approximately 8 times the size of the juvenile leaves) and are formed on long (1 m or more), round, pendulous branches that hang away from the tree trunk. It is at the end of these branches that an inflorescence may develop (Figure 1).

Figure 1. The inflorescence and adult foliage of *Marcgravia serrae*. One red nectary is visible to the right of the base of the inflorescence.

M. serrae has small greenish flowers and nectaries that turn red upon maturing. The flowers appear to open only at night and are most likely pollinated by two small, long-tongued bats, *Hylonycteris underwoodi* and *Lichonycteris obscura* (M. Tschapka, personal communication). The wings of the bats hit the flowers and get dusted with pollen as the bats stick their tongues into the nectaries at the center of the inflorescence. Hummingbirds also visit the inflorescences to obtain the nectar but most likely do not transfer pollen (due to the diurnally closed flowers). The plant is also capable of self-fertilization (unpublished data). Upon maturation of the fruit, the fruit wall falls away in two pieces to reveal a mass of very small (<1 mm in length), sticky, bright red seeds embedded in red flesh. These fruits are eaten by many birds, especially euphonias and tanagers (B. Loiselle, personal communication). At higher elevations, the fruits are also eaten by *Sturnira* bats (B. Loiselle, personal communication), but Gutierrez (1996) found no *Marcgravia* seeds in bat fecal samples at La Selva.

Methods

1. Study Site.

The La Selva Biological Station of the Organization for Tropical Studies consists of a 1550-ha reserve near Puerto Viejo de Sarapiquí in the Atlantic lowlands of Costa Rica (10° 26' N, 84° 00' W; elevation 37-150 m; Figure 2). It is classified in the Holdridge life zone system as tropical wet forest (Hartshorn and Hammel 1994) and has a mean annual rainfall of 3962 mm. Average monthly rainfall varies from a low of 152 mm in March to a high of 480 mm in July (Sanford *et al.* 1994).

This study was restricted to the "original La Selva" of McDade and Hartshorn (1994), excluding swamps, secondary forest, disturbed areas and the 12.4 ha of restricted access plots. The remaining 500+ ha of the original La Selva reserve has been surveyed and mapped according to a grid system, with posts placed in the forest every 50 m along

Figure 2. The location of La Selva Biological Station, Costa Rica ($10^{\circ} 26' \text{ N}$, $84^{\circ} 00' \text{ W}$).

lines at 100 m intervals. The accuracy of post placement is ± 20 cm (Clark *et al.* 1995), which provides a convenient platform for systematic sampling methods. Maps based on this grid are stored in the station's Geographic Information System (ARC/INFO 7.0, on Sun Sparc II workstations). Available coverages include soils, topography, streams, land use, and trails.

La Selva's flora is estimated to include nearly two thousand species (Hammel and Grayum 1982, Hammel 1986), of which approximately 1,680 have been recorded (Hartshorn and Hammel 1994). Of these plants, two families of gymnosperms are represented, as well as eight families of pteridophytes and 122 families of flowering plants. La Selva is particularly rich in epiphytes and hemiepiphytes, with these growth forms comprising 23% of all vascular plant species (Hartshorn and Hammel 1994). Much of the forest is dominated by *Pentaclethra macroloba* (Willd.) Kuntze (Mimosaceae) (Hartshorn and Hammel 1994), although palms are very common as well (31 native species, Chazdon 1985; 25% of all woody stems ≥ 10 cm dbh, Lieberman *et al.* 1990).

II. Population structure of *Marcgravia serrae*.

To evaluate the population structure of *Marcgravia serrae*, I sampled the 500+ ha area systematically at the intersections of a 150 m by 200 m grid (every third post along every other line); additional sites were later added due to the limited distributions of the Alluvial, Arboleda and Stream soil types (described below; Figure 3). At each grid intersection, I set up a 10 m radius plot with the grid post at its center. I censused every tree within these plots over 10 cm diameter at breast height for the presence of *M. serrae*. All searching was done from the ground with 8 x 35 binoculars. When I encountered an individual of *M. serrae*, I measured its diameter, estimated the maximum height to which it had climbed, and recorded its growth stage (juvenile or adult; see Species Description).

Figure 3. Soil types, streams and plot locations in a 500+ ha area of old-growth forest at La Selva Biological Station, Costa Rica.

III. Host tree characteristic and habitat preferences.

To examine the influence of host tree factors on the distribution of *M. serrae*, I classified each tree in my plots greater than 10 cm dbh according to the following variables: diameter at breast height or above buttresses (measured with a diameter tape when possible and estimated when the trunk had buttresses too large to get above), presence or absence of buttresses or stilt roots, bark type (a scale of 1 [smooth] to 5 [very rough with large fissures]), number of climbing stems on the trunk, and moss and liverwort load of the trunk (5 point scale--0 [no moss] to 4 [entire trunk and branches covered with a thick mat of bryophytes]). I also noted the species of tree if it was easily identifiable; however, this was not a major focus, as my intent was to relate *Marcgravia serrae* presence with site variation and morphological features of the tree.

I used Hierarchical Logistic Regression Analysis (Tabachnik and Fidell 1996) to develop a predictive model of the presence or absence of *M. serrae* based on physical habitat characteristics. Logistic Regression requires that all independent variables are, in fact, independent. Therefore, I used Loglinear Analysis (Tabachnik and Fidell 1996), a type of multi-way frequency analysis, to determine if any significant dependencies existed among independent variables. All of the categorical host tree variables were entered into this analysis. Significant associations occurred between bark type, buttressing, host tree species, number of climbers, and trunk moss load. Because associated variables are essentially measuring the same factor in slightly different ways, I choose trunk moss load to represent all of these variables. I based this decision upon my own observations of which factor seemed most important biologically. Upon completion of the Loglinear Analysis, I ran the Logistic Regression with host trunk moss load and host tree diameter as predictors of the presence or absence of *M. serrae*.

The Logistic Regression Analysis recodes categorical variables into new variables. The number of new variables created is one less than the number of categories in the original variable. For example, if a categorical variable had three levels (low, medium and high), the computer program would create two new dichotomous variables to represent the categories. One variable would represent the low value, coded 1 if the original value was low and 0 otherwise. The second new variable would represent the medium value, coded 1 if the original value was medium and 0 otherwise. The high value would be represented by codes of 0 for both of these variables. The five level categorical variable representing host trunk bryophyte load was re-coded in this manner, resulting in four new variables in the analysis.

To determine if topography influences the distribution of *Marcgravia serrae*, I classified each sample plot into one of four categories, based upon local slope and topography. *Slope base* was defined as occurring at the point at which a slope broke and changed angle to become less steep. *Slope crest* was defined to include the upper break point of a slope. The mid-slope areas were categorized based upon the slope of the site: *gentle slopes* were those with an angle of less than 15°, while *steep slopes* were those sites with an angle of 15° or greater. I measured all slopes with a clinometer.

In order to determine if soil type influences the distribution of *Marcgravia serrae*, I classified each plot according to soil type. La Selva's soils vary greatly in color, nutrient status and texture (D. A. Clark personal communication). The 1:10 000 soils map of the reserve (Sancho and Mata 1987) demarcates 23 consociations (mapping unit in which ≥ 75% of the area is one soil type) and one complex (an area where two or more dissimilar soils occur together in an inseparable pattern) (Sollins *et al.* 1994). Here, I have grouped related soil consociations into four categories (Residual, Arboleda, Alluvial, and Stream

soils), following Clark *et al.* (1995) and my own field notes. I created a coverage of these categories on La Selva's GIS and used it to classify my sites according to soil type.

Residual soils (Ultisol) are very acidic, low in exchangeable bases, and rich in organic matter (Sollins *et al.* 1994). Arboleda soil (Inceptisol) is less acidic than the Residual soil, with extractable P levels intermediate between Residual and Alluvial soils (Sollins *et al.* 1994; J. S. Denslow and G. Chaverri, unpublished data cited in Clark *et al.* 1995). Alluvial soils (Inceptisol) are found on gently undulating terrain along the major rivers bordering La Selva. These soils are the least acidic of the four soil types and are highest in exchangeable bases (Sollins *et al.* 1994). The Stream soils (Inceptisol) occur in the valley bottoms of the major streams of La Selva. These soils are poorly to moderately drained, highly acidic, and poor in exchangeable bases (Sollins *et al.* 1994).

The analyses for host tree characteristics and edaphic factors (soil and topographic position) were done separately because of differences in the scale of the measured variables. In addition, I performed separate analyses for soil and topographic position because the sample size would have varied widely among groups had I done them together, and may have introduced bias in the analysis

I performed Analyses of Covariance (ANCOVA; Tabachnik and Fidell 1996) to determine whether the distribution of *M. serrae* is affected by soil type or topographic position. In Analysis of Covariance, the relationships between a dependent variable and one or more independent variables are examined after the effects of the covariates are removed (Tabachnik and Fidell 1996). One of the requirements of this test is that the chosen covariates must be correlated to the dependent variable. Therefore, I did a Pearson Pairwise Correlation Analysis (Sokal and Rohlf 1995) on the number of *M. serrae* per plot, the sum of the circumferences of all trees in the plot, the number of trees per plot, and the average moss score per plot (the sum of the moss scores of a plot

divided by the number of trees in that plot). For topographic position, the average moss score and number of trees per plot were chosen as covariates. For soil type, only the average moss score per plot was significantly correlated with *M. serrae* abundance, and was the only covariate chosen.

IV. Seed Germination Experiment

I used a one-way ANOVA design and planned orthogonal comparisons (Sokal and Rohlf 1995) to determine if seed germination of *Marcgravia serrae* varied in samples containing bark material from different tree species (*Pentaclethra macroloba* (Willd.) Kuntze (Mimosaceae), *Dipteryx panamensis* (Pittier) Record (Fabaceae), *Hyeronima oblonga* (Tul.) Muell.Arg. (Euphorbiaceae), *Terminalia oblonga* (Ruiz & Pavón) Steudel (Combretaceae), and *Cordia alliodora* (Ruiz & Pavón) Oken (Boraginaceae)). I chose these trees because of they are relatively abundant at La Selva, and are in different taxonomic families. I shaved strips from the outer bark of *Pentaclethra*, *Hyeronima*, and *Cordia*, while large peeling strips were taken from *Terminalia*, and smaller, flaking chips from *Dipteryx*. I then ground these barks separately in a Wiley-mill and placed three replicates of 5 grams of each into separate petri dishes. Subsequently, I deposited 50 *Marcgravia serrae* seeds on top of each bark sample and watered with a spray bottle until saturated. I also placed seeds on moistened filter paper as a control. The petri dishes were then put in a shade house, with light levels approximating those in primary forest. I checked the petri dishes once daily for seed germination and counted all seedlings. The control treatment and the barks of *Pentaclethra* and *Cordia* molded very quickly and were removed from the analysis.

V. Seed Predation Experiment

I performed this experiment along approximately 300 meters of the Camino Experimental Sur trail at La Selva Biological Station. This section of mature forest

grows on uplifted alluvial soils of gentle topography. *Marcgravia serrae* is very common in this area.

I harvested seeds from one mature *Marcgravia serrae* fruit collected near the study area. I placed 25 seeds on each of 32 microscope slides (for a total of 800 seeds). I then haphazardly chose sixteen individuals of *Pentaclethra macroloba* (Mimosaceae), the dominant tree at La Selva, as sites at which to place seeds of *M. serrae*. The trees were of approximately equal diameter and located at least three meters from the trail. Each slide was attached to a tree at breast height or placed on the ground at a distance of 2 meters from the same tree. Therefore, I placed 16 paired sets of slides in the field. The slides were set out between 8 and 8:30 a.m. on 24 July 1996. I returned to the sites at two hour intervals to count how many seeds remained on the slides, until a heavy rain at 3:30 p.m. forced the termination of the experiment. Insects observed harvesting seeds were collected and later identified by the ALAS (Arthropods of La Selva) project. In order to determine if differential seed predation was occurring at my study site, I performed a paired samples *t*-test (Sokal and Rohlf 1995) on the number of seeds remaining on each microscope slide at the end of the experiment.

Results

1. Population structure of *Marcgravia serrae*.

Marcgravia serrae is very common at La Selva (Tables 1 and 2). A total of 670 individuals were observed climbing 396 trees (33.5% of 1181 trees >10 cm dbh in the plots). Of these, only 23 (3.4%) had adult foliage; 647 (96.6%) had no horizontal branches and were classified as juvenile. These correspond to densities of 6.7 adult *M. serrae*/ha and 189 juvenile *M. serrae*/ha. The largest individual found within the study plots had a diameter of 9.4 cm and ascended approximately 40 meters into the forest canopy.

Table 1. Size class structure of *Marcgravia serrae* in 3.42 ha of old-growth tropical wet forest at La Selva, Costa Rica.

<i>Marcgravia</i> dbh (mm)	No. juveniles	No. adults
1	623	2
2	42	3
3	10	2
4	5	0
5	6	0
6	0	4
7	0	1
8	0	1
9	0	1
10+	0	18

Table 2. Size class structure of 3.42 ha of tropical wet forest at La Selva, Costa Rica, and size-specific occupation of host trees by *Marcgravia serrae*.

Tree dbh (cm)	No. trees	Σ tree dbh	No. juvenile	No. adult
			<i>Marcgravia</i>	<i>Marcgravia</i>
(10-20)	643	9711.5	293	4
(20.1-30)	210	5072.6	119	3
(30.1-40)	127	4386.4	56	6
(40.1-50)	98	4402.0	58	1
(50.1-60)	58	3118.9	79	5
(60.1-70)	27	1718.7	28	2
(70.1-80)	8	584.3	5	1
(80.1-90)	8	674.3	2	1
(>90)	2	182.8	7	0

II. Habitat and host tree preferences

The Loglinear Analysis showed significant dependencies among the variables. There were six three-way associations: buttress*number of climbers*moss load, buttress*number of climbers*bark type, buttress*number of climbers*tree species, number of climbers*moss load*bark type, number of climbers*mossload*tree species, and moss load*bark type*tree species.

The Logistic Regression showed that among the measured host tree factors, the presence of *M. serrae* varied only with the bryophyte load of the host tree trunk. A test of the full model with both predictors against a constant-only model was statistically reliable ($\chi^2=67.8$, $p<0.001$), indicating that the predictor variables reliably distinguished between trees with *M. serrae* and those without. Eighty-four per cent of trees without *M. serrae* were successfully predicted by the model, while only 51% of trees with *M. serrae* were predicted correctly. The overall success rate was 69%. Table 3 shows regression coefficients (*B*) for the significant variables in the model.

M. serrae abundance did not differ among topographic positions or soil types. These ANCOVA results can be seen in Tables 4 and 5, respectively.

III. Seed predation

Seed removal by insects was greater on the ground than it was on tree trunks (paired samples t-test; $t_{(15)}=3.52$; $p=0.003$; Figure 4). The only organisms seen removing seeds were small leaf litter ants in the genus *Pheidole*.

IV. Seed germination

Germination of *M. serrae* seeds varied among experimental treatments (one-way ANOVA; Table 6). Germination on the bark of *Dipteryx panamensis* was greatest, while germination on *Terminalia oblonga* was lowest (planned orthogonal comparisons; Table 7). In addition, the bark of *Terminalia* delayed germination of *M. serrae* seeds (Figure 5).

Table 3. Coefficients of the significant predictor variables of the Logistic Regression Analysis of the presence of *Marcgravia serrae* as a function of tree characteristics. See text for a description of the analysis.

Variables	<i>B</i>
Moss Load	
Moss(1)	-3 . 64
Moss(2)	-2 . 65
Moss(3)	-0 . 51
Moss(4)	-5 . 18
Constant	1 . 80

Table 4. One-way ANCOVA comparing mean abundance of *Marcgravia serrae* among topographic position (base, gentle slope, steep slope, and crest) with average moss score and number of trees per plot as covariates.

Source	Sum of Squares	df	Mean Square	F-Ratio	p
Topography	49.47	3	16.49	1.17	0.329
Avg. Moss	510.41	1	510.41	36.15	<0.001
No. Trees	134.04	1	134.04	9.49	0.003
Error	833.00	59	14.11		

Table 5. One-way ANCOVA comparing mean abundance of *Marcgravia serrae* among soil types (Residual, Arboleda, Alluvial, and Streams) with average moss score per plot as covariate.

Source	Sum of Squares	df	Mean Square	F-Ratio	p
Soil Type	19.49	3	6.50	0.27	0.844
Avg. Moss	580.15	1	580.15	24.97	<0.001
Error	766.73	33	23.23		

Table 6. One-way ANOVA comparing mean germination of *Marcgravia serrae* seeds placed on samples on bark from three tree species (*Dipteryx panamensis*, *Hyeronima oblonga*, and *Terminalia oblonga*).

Source	Sum of Squares	df	Mean Square	F-Ratio	p
Bark Species	38.89	2	19.44	6.034	0.037
Error	19.33	6	3.22		

Table 7. Germination of *Marcgravia serrae* seeds on tree barks. Three replicates of 50 seeds each in each treatment. Treatments with the same letter under "Group membership" do not differ significantly at $p < 0.05$ (planned orthogonal comparisons; Sokal and Rohlf 1995).

Bark	Mean seed germination	Std. Dev. seed germination	Group membership
<i>Dipteryx panamensis</i>	40 . 33	1 . 53	a
<i>Hyeronima oblonga</i>	36 . 67	2 . 31	ab
<i>Terminalia oblonga</i>	35 . 33	2 . 08	b

Figure 4. Total number of *Marcgravia serrae* seeds remaining over time on microscope slides placed in the forest on the ground or attached to a tree at breast height. Sixteen replicates of 25 seeds each in each treatment.

Figure 5. Mean number of *Marcgravia serra* seeds germinated on different bark substrates over time. Three replicates of 50 seeds each in each treatment.

Discussion

The density of adult *Marcgravia serrae* (6.7/ha on 2% of all trees over 10 cm dbh) in the La Selva forest appears to be similar to published studies from La Selva and other lowland rain forest sites. Clark and Clark (1990) found that 13% of trees at La Selva supported hemiepiphytes, but they did not determine the species of hemiepiphytes. On Barro Colorado Island, Panama, 9.8% of the trees were occupied by at least one of 20 hemiepiphyte species studied (Todzia 1986). In San Carlos, Venezuela, 13% of the trees supported *Clusia* spp. and *Ficus* spp. hemiepiphytes (Putz 1983).

Marcgravia serrae was not distributed evenly over possible host trees; thus, *M. serrae* is one of many mechanical parasites known to show preferences among possible hosts (e.g., Todzia 1986, Daniels and Lawton 1991, Kernan & Fowler 1995, Talley *et al.* 1996a, b). The fact that *M. serrae* abundance is associated with the bryophyte load of the host tree is consistent with findings for epiphytes (e.g., ter Steege and Cornelissen 1989) and may be due to a number of reasons.

First, *M. serrae* may be water limited in this forest, as hemiepiphytes are generally accepted as being most common in cloud forests and pluvial forests (where annual rainfall may be twice what it is at La Selva) (Williams-Linera and Lawton 1995). For instance, the epiphytic phase of *Ficus* hemiepiphytes have much lower stomatal densities than conspecifics in the tree phase (Holbrook and Putz 1996), indicating that water conservation is important in hemiepiphytes not connected to the ground. A heavy mat of bryophytes may retain stemflow water and provide necessary water for seed germination or help prevent drying of *M. serrae*'s roots during the epiphytic phase. In fact, bryophyte mats have very high water storage capacities when compared to bark, dead wood, and humus or litter (ter Steege and Cornelissen 1989). Alternatively, the bryophytes may simply be an indicator of wetter microsites. Humidity in tropical rain

forests is highest in the first few meters above the forest floor (Croat 1988), where bryophytes are most commonly found and where *M. serrae* most often germinates (personal observation). Indeed, the absence of *M. serrae* in secondary forest at La Selva (personal observation) may be due to lower humidity caused by the different physical structure of the forest.

Second, *M. serrae* may derive some nutritional benefit from the bryophyte mat, as these mats are reservoirs of nutrients (Nadkarni 1981). Bryophyte mats may also contain nitrogen-fixing cyanobacteria, another possible source of nutrients for epiphytes (A. Bien, personal communication). In addition, nutrient levels in stemflow water increase towards the base of the tree where young, epiphytic *M. serrae* would be most dependent upon those nutrients (Croat 1988). However, because *M. serrae* becomes rooted in the ground, I expect any effect of this type to be temporary.

Third, moss on the tree trunks may provide a mechanical "catch-basin" upon which seeds will easily become lodged. The raised, uneven surface created by the mat of bryophytes may make falling seeds more likely to hit and stick to a tree covered with a heavy layer of mosses than they would to a bare, smooth barked tree.

Finally, a heavy moss load on the tree trunk may provide some measure of protection against allelochemicals found in tree bark (Frei 1973, ter Steege and Cornelissen 1989). Seeds germinating on moss may be less subject to inhibition by bark chemicals than those germinating directly on the bark. In addition, because adventitious-root-climbers like *M. serrae* are in intimate contact with the host tree, a layer of moss between the bark and the roots may lessen the uptake of toxic substances. In fact, sub-lethal doses of allelopathic chemicals may even stimulate growth (Rice 1984, cited in Talley *et al.* 1996b).

Marcgravia serrae occurred independently of host tree size. This is not surprising in terms of the ability of the plant to climb different size hosts, because adventitious-root climbers are not limited by tree size as are tendril climbers or twining vines (Putz 1995). However, big trees may be larger "targets" for seeds dropped or defecated by aerial dispersal agents (Talley *et al* 1996a). This does not appear to be important for *M. serrae*, whose distribution may depend more upon the availability of suitable microsites on hosts.

Sloughing bark is an often-cited mechanism by which trees shed epiphytes (Johansson 1974, Kelly 1985, Todzia 1986, ter Steege & Cornelissen 1989, Zimmerman & Olmstead 1992, Talley *et al.* 1996a, b). Due to interactions with other variables, I was unable to specifically test for the effect of bark type. I expect that bark type in this forest would only indirectly influence the distribution of *M. serrae*, possibly through its effect on bryophyte loads of the host trunk (ter Steege and Cornelissen 1989).

Soil type and topographic position are also commonly associated with variation in plant distributions (e.g., Huston 1980, Johnston 1992, Oliveira-Filho *et al.* 1994, Clark *et al.* 1995). Soil types at La Selva have been shown to influence other plant distributions (e.g., palms; Clark *et al.* 1995), but have no effect upon the presence of *M. serrae* when the average moss loads of the sites are taken into account. Perhaps establishment of the epiphytic phase and growth up the host tree trunk are greater selective pressures for *M. serrae* than is soil type or topographic position in this forest.

Marcgravia serrae seeds were taken rather quickly from the forest floor in my experiment. This is not a surprising result, based upon the absence of *M. serrae* seedlings on the ground at La Selva. The *Pheidole* ants that took the seeds are common leaf litter seed predators at La Selva and have been shown to consume most of the seeds they harvest (Levey and Byrne 1993). *Marcgravia* seeds gathered by *Pheidole* ants have

also been found incorporated into the walls of the ants' carton nests (Briceño and Loiselle 1993). Levey and Byrne (1993) have hypothesized that patterns of plant regeneration may be due to differential seed harvesting by leaf-litter ants. My results appear to support this hypothesis.

This study confirms the presence of preferences of a hemiepiphyte for different habitats and attempted to provide some explanation for the observed patterns. Seed predation certainly appears to be an important factor. More experimental work is needed, however, to determine whether the association with trunk moss load is a causal relationship. If so, what determines how much moss will occur on a particular tree? Finally, the efficacy of the inhibition of hemiepiphyte seed germination and early growth by trees could be a fruitful subject for future study.

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