

## SEED AND SEEDLING ECOLOGY OF NEOTROPICAL MELASTOMATACEAE<sup>1</sup>

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**Abstract.** Models of gap-phase regeneration in tropical wet forests are based primarily on studies of canopy trees. These paradigms are derived from studies of a small number of species whose life history traits place them easily into “pioneer” or “climax” species. Woody plants of the forest understory, subcanopy trees and shrubs, are known to affect significantly regeneration dynamics in treefall gaps, yet we lack fundamental information on life history characteristics of understory plants that could permit their incorporation into gap regeneration models. We investigated intra- and interspecific variability in early life history characteristics of understory Melastomataceae species of different growth forms and adult distributions from the lowland tropical rain forest at La Selva Biological Station, Costa Rica. We examined germination patterns *in vitro* (22 species), effects on germination of passage through birds (5 species), seedling establishment in the field (3 species), and growth in different light environments (8 species).

Established seedlings were significantly more abundant in gaps than in nearby understory sites. This pattern was generally applicable to all melastomes studied, regardless of the habitat where adults were normally most abundant. Seedlings were more common in the root pits and on the root mounds of uprooted trees, even though there was less light available to the seedlings in these microsites than elsewhere in the gaps. In a series of germination trials *in vitro*, most seeds germinated readily within 1–2 wk. Comparisons of germination rates between seeds collected from bird droppings and seeds extracted from fruits by hand gave varied results. With one exception, seeds of shade-tolerant species germinated more slowly following passage through birds, while seeds from high-light-demanding species germinated more rapidly after passing through birds.

Seeds of three common species were sown directly into different microsites within gaps and understory control sites. In contrast to the germination trials, emergence percentages in the field ranged from 4% in understory sites to 21% in gap centers. Survival after 1 yr was low (0.1%–0.4%). After 1 yr, these seedlings were small (<2 cm tall) and produced few leaves. In similar light environments in the shade-house, melastome seedling survival was between 80% and 100%, and growth increased with increasing light levels from 2% (corresponding to understory sites) to 20% (small gap centers) of full sun. With the exception of two species common to abandoned pastures and river banks, the species used in the shade-house growth experiments did not show significant increases in growth with increases in light from 20% to 40%. Suites of early life history traits described for tropical tree species are not consistent with the variation in pattern seen within this one family of understory species.

**Key words:** *Costa Rica; gap dynamics; light; Melastomataceae; seed germination; seedling establishment; seedling growth; seedlings; seeds.*

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## INTRODUCTION

The ability of buried seeds and suppressed forest seedlings to respond rapidly to increased light levels following a treefall has long been recognized as a crucial stage in plant life history, and is a fundamental component of stand regeneration in tropical forests (e.g., Schulz 1960, Vázquez-Yánes 1974, Ng 1978, Denslow 1980, 1987, Clark and Clark 1987). Seed size, germination rates, and establishment strategies among tropical trees are diverse (Ng 1978, Whitmore 1983, Foster and Janson 1985, Foster 1986, Swaine and Whitmore 1988, Garwood 1989). "Pioneer" (sensu Swaine and Whitmore 1988), or gap-dependent species, such as *Cecropia* spp. (Cecropiaceae), *Ochroma lagopus* Swartz. (Bombacaceae), and *Heliocarpus appendiculatus* Turcz. (Tiliaceae), have small seeds with extended dormancy and rapid germination and growth in response to increasing light levels (Vázquez-Yánes 1974, Moreno-Casasola 1976, Holthaijzen and Boerboom 1982, Núñez-Farfán and Dirzo 1988). "Climax" or "non-pioneer" species (sensu Swaine and Whitmore 1988), on the other hand, tend to have larger seeds with little dormancy, and rapid germination following dispersal (Foster 1986). Many tree species fall between these limits, combining rapid germination and some shade tolerance with rapid growth responses following canopy opening (Clark and Clark 1992).

Data on seed and seedling ecology of species not encompassed by the pioneer and climax categories are scant, however. In common usage, these categories have been applied only to canopy or emergent trees, and consequently do not include the diversity of plant types that make up any forest. In particular, understory species, shrubs and small treelets, are ubiquitous in tropical forests, can inhibit regeneration of canopy trees (Brokaw 1983, Raich and Gong 1990, Denslow et al. 1991), and yet have been studied rarely relative to canopy trees. Detailed studies of early life history properties, such as germination, establishment, and seedling growth of understory species are therefore needed to complement the relative wealth of comparable information available for canopy tree species, and to permit more reliable predictions of regeneration dynamics in wet tropical forests.

Combinations of early life history characteristics in understory species may differ from those outlined above for rain forest pioneer and climax canopy trees. For example, Vázquez-Yánes and Orózco-Segovia (1984) found that although seeds of many understory species exhibit enforced dormancy and require gaps for germination, others have rapid postdispersal germination and no dormancy regardless of light environments. With regard to germination and seedling establishment, it has been suggested that understory species have a wider ecological amplitude (e.g., Lebrón 1979) and are less dependent on gaps than are canopy trees (Hartshorn 1978, Lebrón 1979, Brokaw 1985). Understory species are likely to recruit into new gaps either from sup-

pressed seedlings or as seeds dispersed into gaps following gap creation (Garwood 1983, Lawton and Putz 1988, Levey 1988a), but appear to not require gap formation to germinate. This is because understory species often produce fewer seeds, and their seeds are less abundant in the seed bank than are seeds of pioneer trees (Vázquez-Yánes 1974, Uhl and Clark 1983, Whitmore 1983, de Foresta and Prevost 1986, Garwood 1989; but see Alvaraz-Buylla and García-Barríos 1991).

In contrast, survival and growth of seedlings and older plants may be influenced more strongly by gap environments than is seedling germination. Growth of understory species is generally highest in gaps relative to other environments (Denslow et al. 1990), and shrubs flower and fruit more abundantly in gaps (Croat 1975, Stiles 1975, Levey 1988a). This concentration of fruits in gaps has led Levey (1990) to conclude that gaps may be "keystone habitats" for frugivores in tropical rain forests.

Gaps (sensu Brokaw 1982) themselves are not homogeneous, but encompass substantial variation in light, temperature, moisture, soil, and nutrient properties (Putz 1983, Núñez-Farfán and Dirzo 1988, Poulson and Platt 1989, Peterson et al. 1990). If understory species are not strictly dependent on gaps for successful recruitment (Hartshorn 1978, Lebrón 1979, Brokaw 1985), then seed germination may be less sensitive to microenvironmental variation within a gap. That is, we would not expect great intraspecific variation in germination and establishment in different parts of a treefall gap.

Later seedling growth, however, should be influenced more strongly by gap microsite, but data addressing this prediction are rare. Denslow et al. (1990, and *unpublished manuscript*) found significant responses to within- and between-gap variation in light availability, but not nutrients, among rooted cuttings of several species in the Melastomataceae and the Piperaceae. As a complement to these long-term studies of the responses of understory species to treefall gaps (Denslow et al. 1990, Denslow et al., *unpublished manuscript*), we examined in detail the ecology of seeds and seedlings of a number of melastome species in and around gaps, and in controlled light environments. We asked seven specific questions concerning the early life histories of these species:

1. What are the germination time courses of newly dispersed melastome seeds?
2. Does passage through birds affect germination?
3. How is the frequency of successful seedling establishment in the field affected by gap microsite?
4. Are melastome seedlings more common in gaps or in surrounding forest?
5. What is the degree of intra- and interspecific variation in distribution and abundance patterns of these seedlings within treefall gaps?

6. How do light conditions, representative of intact forest, gap edges, and gap centers, affect early seedling growth?
7. What is the interspecific variation in these life history parameters, and how does this variation relate to plant life-form and adult distribution?

#### STUDY SITE

All field work was conducted at the La Selva Biological Station (10°28' N, 83°59' W) of the Organization for Tropical Studies. This is a reserve of premontane wet tropical forest (*sensu* Holdridge et al. 1971) in the Atlantic lowlands of Costa Rica (see Hartshorn 1983 for a more detailed description). Average annual rainfall is  $\approx 4000$  mm, with a less rainy season from January through April, when average monthly rainfall is  $< 200$  mm. The soils at La Selva are derived from volcanic parent material (Sancho and Mata 1987, Sollins et al., *in press*) and are high in available nitrogen but low in phosphorus and other nutrients (Vitousek and Denslow 1986, Denslow et al. 1987, Sancho and Mata 1987). Availability of photosynthetically active radiation (PAR) under intact canopy at La Selva is between 1 and 2% of full sunlight (Chazdon and Fetcher 1984). The estimated canopy turnover time (time between treefalls in a single location) at La Selva is  $118 \pm 27$  yr (Hartshorn 1978). Most gaps at La Selva are small ( $88\% < 300$  m<sup>2</sup>; Sanford et al. 1986) with incident PAR levels of  $\approx 9$ – $20\%$  of full sunlight at their centers (Chazdon and Fetcher 1984, Denslow et al. 1990). Available PAR in large gaps (400 m<sup>2</sup>–600 m<sup>2</sup>) is  $\approx 20$ – $35\%$  of full sunlight (Chazdon and Fetcher 1984, Denslow et al. 1990).

#### STUDY SPECIES

The Melastomataceae (henceforth, melastomes) are one of the most species-rich tropical plant families, comprising  $\approx 190$  genera and 4800 species (F. Almeda, *personal communication*). Melastomes are primarily a neotropical group; more than two-thirds of the species occur in Central and South America. All common perennial life-forms, i.e., herbs, small shrubs, subcanopy and canopy trees, lianas, and epiphytes, are represented within the melastomes, although the majority of species are understory shrubs. In the understory at La Selva, the melastomes are the most speciose shrub family (Hammel 1990).

In total, 22 melastome species were used in the laboratory and field experiments in germination, establishment, and seedling growth (Appendix 1). Seeds of all of these species are very small (100–1000  $\mu\text{g}$ ; A. M. Ellison, *unpublished data*). The majority of these species (16 of 22) were shrubs, 5 were treelets or subcanopy trees, one was an herb (Appendix 1). Adult individuals of each of these species are found most commonly in habitats ranging from abandoned pastures to undis-

turbed forest, as well as in swamps and along river banks (Appendix 1; J. S. Denslow and A. M. Ellison, *unpublished manuscript*). We assigned the species' light requirements listed in Appendix 1 based on observed patterns of adult distribution patterns (J. S. Denslow and A. M. Ellison, *unpublished manuscript*) and independent observations of seedling distribution patterns (A. M. Ellison and D. Brenés M., *unpublished data*). *Miconia nervosa* has been considered a "high-light" species in other studies at La Selva (e.g., Denslow et al. 1990); we consider it a "low-light" species here because it has a much broader distribution with respect to ambient light conditions than the other high-light species in Appendix 1. All of the species listed in Appendix 1 were used to study time courses of seed germination *in vitro*. Subsets of these species were used in the experiments examining the effect of dispersal by birds on germination, experiments on field establishment, and studies of early seedling growth. For these latter experiments, we selected species representative of the different life-forms and adult habitats, and for which we had sufficient numbers of seeds or seedlings.

Our selection of species for the experiments was biased in two ways. Availability of fresh fruits was the primary constraint. Of the  $\approx 77$  melastome species at La Selva (F. Almeda, *personal communication*), we encountered fruits on only the 22 species listed in Appendix 1. Second, we wished to compare our data with results obtained from studies of rooted cuttings in tree-fall gaps at La Selva (Denslow et al. 1990, and *unpublished manuscript*). These studies have focused on six common melastomes: *Miconia affinis*, *M. barbinervis*, *M. gracilis*, *M. multispicata*, *M. nervosa*, and *M. simplex*. These species were included in our experiments whenever possible. *M. gracilis* did not germinate reliably *in vitro* or in the field, and was not used in the seedling growth studies. *M. barbinervis*, *M. multispicata*, and *M. simplex* seeds were not available in sufficient quantity for use in the establishment studies in the field.

#### PATTERNS OF GERMINATION: IN VITRO GERMINATION STUDIES

##### *Methods*

We examined the germination rates of fresh melastome seeds *in vitro* (question 1, see *Introduction*). Five to 20 fruits of each of 22 common melastome species were collected from multiple plants at various locations within La Selva. Ripe berries of these species were crushed, and the seeds separated from the pulp in a cup of water. The water and pulp were decanted and the seeds were air dried (20°C) for 72 h and then stored dry at 20°C until used (1–3 mo). *Nepsera aquatica* produces dry, dehiscent capsules, and the seeds were easily shaken out of the capsules. Although we do not know the physiological effects of storing these seeds before use, the rates and total numbers of stored seeds that

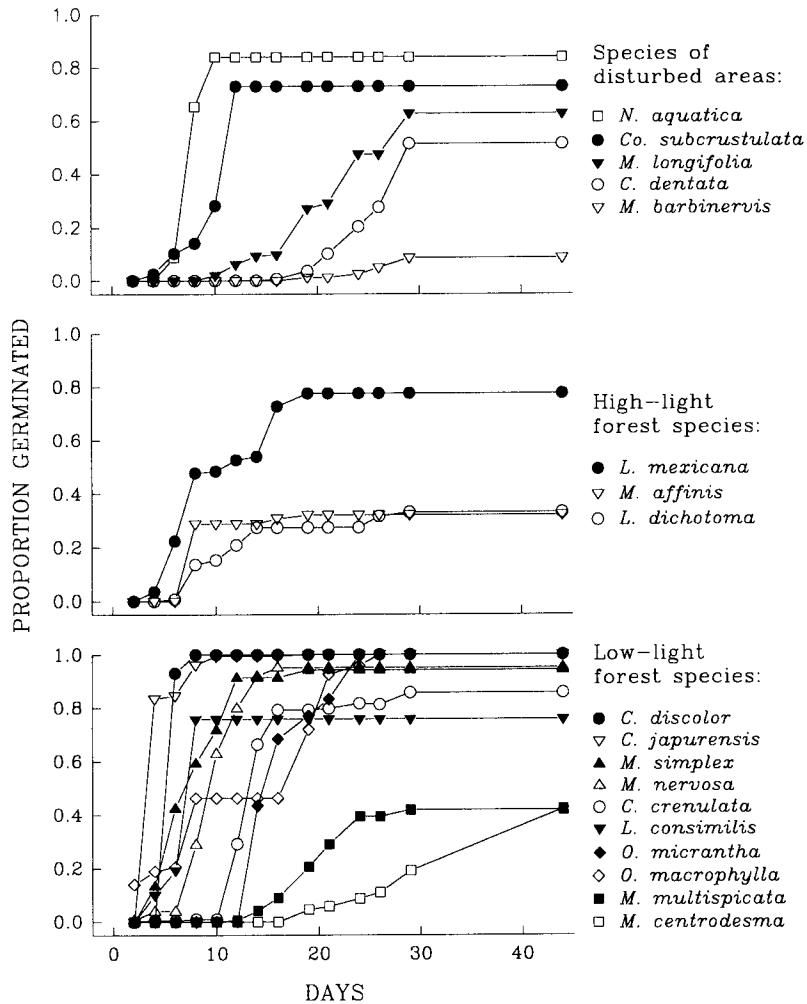


FIG. 1. Germination percentage over time of melastome seeds in petri dishes.

germinated did not differ markedly from seeds planted immediately after collection (for those five species also tested in the experiments with birds described below, and one additional species [*Miconia multispicata*] examined by González J. 1991).

One hundred seeds of each species were placed on saturated filter paper in each of two replicate 10 cm diameter petri plates (except 50 seeds/dish of *M. barbinervis* and *C. subcrustulata*). Petri plates were then placed 20 cm beneath full-spectrum fluorescent lights ( $\approx 250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) on a 12:12 light:dark photoperiod. Temperature was not regulated; ambient daytime temperature at La Selva was  $\approx 25^\circ\text{C}$  throughout the experiment, and plate temperature did not appear to be increased significantly by the lights. Every 48 h, 0.5 mL of distilled water was added to the petri dishes to prevent desiccation. Every 2–3 d for 29 d we examined the seeds, counted all germinants with visible radicles, and removed any seeds that had become infected with fungi (in all cases  $< 5\%$ ). It appeared that germination had ceased after 1 mo, but we maintained

the plates for an additional 15 d to ensure that no late germinants were missed.

### Results

Seeds of most species germinated within 10–12 d of sowing (Fig. 1), and little to no change in cumulative germination frequency was observed after 3 wk. Germination rates of shade-tolerant species were variable (Fig. 1). *Clidemia discolor*, *C. japurensis*, *Leandra consimilis*, *Miconia nervosa*, and *M. simplex*, germinated rapidly, with cumulative frequencies quickly approaching 100%. *Clidemia crenulata*, *Miconia centrodesma*, *M. multispicata*, *Ossaea macrophylla*, and *O. micrantha* germinated more slowly and with variable success. *Clidemia densiflora*, *Miconia dorsiloba*, *M. gracilis*, and *M. grayumii* did not germinate at all (Fig. 1) although few ( $< 5\%$ ) of the seeds were infected by fungi. The remaining species, common to more disturbed areas (3 species) and abandoned pastures (5 species), all germinated with high frequency, with the

exceptions of *Leandra dichotoma* and *Miconia barbivervis* (Fig. 1), of which <20% of the seeds germinated.

To examine statistically the differences in germination rates between species common to abandoned pastures, high-light species of the forest, and shade-tolerant species (Fig. 1), we divided each of these species groups into two sub-groups: those with time to 50% germination <10 d; and those with time to 50% germination >10 d. There were no significant differences in germination times among the three groups of species ( $X_2^2 = 1.30$ ;  $P > .50$ ,  $G$  test).

#### PATTERNS OF GERMINATION: EFFECTS OF BIRDS ON SEED GERMINATION

##### *Methods*

Many melastome fruits are eaten by birds, which also disperse their seeds (Denslow et al. 1986, Levey 1988a, b, 1990, Denslow and Gomez-Diaz 1990, Loiselle and Blake 1990). Passage through birds has been thought to enhance seed germination, but experimental studies have produced mixed results (Izhaki and Safriel 1990). We therefore also investigated the effects of fruit consumption by birds on seed germination rates (question 2, see *Introduction*). We collected additional fruits of *Clidemia densiflora*, *Conostegia subcrustulata*, *Miconia affinis*, *M. simplex*, and *Ossaea macrophylla*, five species that had exhibited disparate responses in the germination experiments in vitro.

In those experiments, *Conostegia subcrustulata* and *M. simplex* had germinated readily and rapidly, with total cumulative germination approaching 100%. We therefore hypothesized that passage through birds would not enhance further, or might even inhibit germination of these two species. *M. affinis* and *O. macrophylla* germinated more slowly and less reliably in the in vitro trials, and for these two species we hypothesized that passage through birds could marginally enhance germination. *Clidemia densiflora* did not germinate at all in the in vitro trials, and we predicted that bird consumption would dramatically enhance germination frequency and rate of *C. densiflora* seeds.

Fruits of each species were fed to Red-capped Manakins (*Pipra mentalis*) caught in mist nets (Loiselle and Blake 1991). Seeds were then separated from fresh droppings and placed into petri dishes on moistened filter paper. For controls, seeds were handled as in the in vitro germination experiments. Individual petri dishes contained either the seeds from one dropping (1–7 replicates), or the seeds from one intact fruit (controls, 2–3 replicates). Germination was scored daily for 6 wk, with the exception of *C. densiflora* which was followed for 16 wk.

We plotted the mean cumulative proportion (over all replicates of each species) of seeds that germinated after consumption by birds on the abscissa, and the mean cumulative proportion of control seeds that germinated on the ordinate. Each point of the plot rep-

resents a successive day, with time proceeding from the bottom left corner to the top right corner of each plot. We used a least squares linear regression model to fit a line through these points. If the slope of this line was not significantly different from 1, then we concluded that there was no difference in cumulative germination frequency between treatments at any given time. Significant deviations from a slope of 1 indicated that the cumulative germination frequency of seeds from fruits consumed by birds increased more rapidly (slope  $\gg 1$ ) or less rapidly (slope  $\ll 1$ ) than that of control seeds. If the data were better fit by a polynomial (quadratic or cubic) regression model than a linear one, then we inferred that there were also differences in the time of onset of germination between control seeds and seeds from bird droppings. All regressions were forced through the origin, because at time = 0, cumulative germination frequency for both treatments = 0.

##### *Results*

Consumption by birds affected the rate and frequency of seed germination, but not precisely as we had hypothesized (Fig. 2). Consistent with our hypothesis, *Clidemia densiflora* seeds from fruits fed to birds germinated significantly earlier and more rapidly than corresponding controls (best fit curve was cubic, with all coefficients >1). However, the total percentage of *C. densiflora* seeds that did germinate was much lower than any other species in this experiment. Also as hypothesized, there was no significant difference in germination rate of *Conostegia subcrustulata* seeds that had passed through birds relative to controls (linear, with slope = 1).

Consonant with our predictions, *Miconia simplex* seeds that had not passed through birds began germinating sooner than seeds of these species that had passed through birds. Contrary to prediction, cumulative germination frequency of seeds from bird droppings increased more rapidly than the corresponding controls (cubic regression, third-order polynomial-term coefficient >1). Also consistent with our hypothesis, seeds of *M. affinis* from bird droppings began germinating earlier than control seeds. However, cumulative germination frequency of control seeds increased at a significantly more rapid rate once germination had commenced (quadratic regression, polynomial-term coefficient >1). The germination behavior of *Ossaea macrophylla* was similar in all respects to that of *M. simplex*.

#### GERMINATION AND ESTABLISHMENT IN THE FIELD

##### *Methods*

Our results from the above studies indicated that germination potential of melastome seeds was relatively high. We therefore investigated the correspondence of these results with seed germination and es-

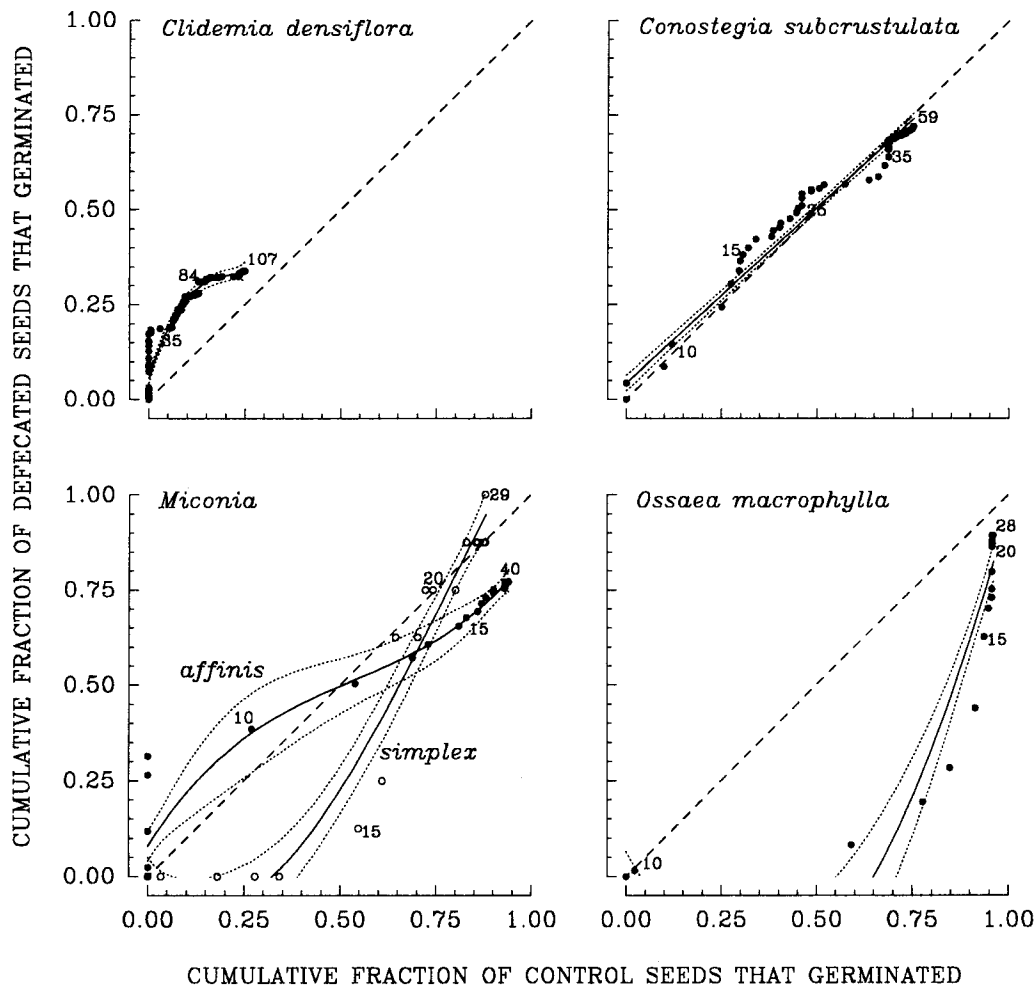


FIG. 2. Comparison of cumulative germination through time of melastome seeds passed through birds relative to paired controls. Each point represents a single day; for clarity, numbers indicate particular days after the start of the germination trials. The best-fit regression line through the points is plotted (—) along with its 95% confidence interval (·····). The dashed line (slope = 1) is provided for reference. See *Patterns of germination: effects of birds . . . : Methods* for interpretation and statistical discussion.

establishment in the field, and examined the effects of different light environments on seedling emergence in gaps (question 3, see *Introduction*).

Seeds of *Miconia affinis*, *M. gracilis*, and *M. nervosa* were extracted from fruits as in the *in vitro* germination experiments, but instead of being stored dry, were planted within 2 d of collection directly into recent gaps (< 1 yr old) created by the fall of single trees. Three "replicate" gaps were used in this experiment, all on the same soil type (Jaguar consociation; Sancho and Mata 1987) on ridge tops. Three light treatments (plots) were established within each gap. In the center of each gap, vegetation < 2 m tall was cleared from a 5 × 5 m plot to create the high-light treatment. In the mid-light treatment, seeds were planted in a 5 × 5 m plot within the gap where the low vegetation was left intact. The low-light treatment seeds were planted into 5 × 5 m plots in the adjacent forest understory. In each plot,

we established three 100 × 75 cm quadrats. In each quadrat we removed the litter and planted 25 seeds of each species ≈ 2 mm beneath the soil. Seeds were planted 3 cm apart in three rows separated by 20 cm. In total, we planted 675 seeds of each species: 75 seeds (three replicate quadrats) of each species in each light treatment in each site. Seeds were sown in September 1988, and quadrats were sampled once every 2 wk for 1 yr. At each sampling date, all seedlings that emerged (cotyledons visible above the soil) were noted and marked with a small plastic stake adjacent to the seedling. Height (± 1 mm) and number of leaves were recorded. Plots were weeded once every 2 wk.

Annual incident direct and indirect sunlight at 50 cm above each quadrat was estimated from hemispherical canopy photographs (Rich 1988, 1989) taken with a 7.5 mm fisheye Minolta lens. Photographs were taken 1 wk after the seeds were sown. Negatives were

TABLE 1. Seedling emergence and survival of *Miconia affinis*, *M. gracilis*, and *M. nervosa* sown into gaps and understory sites.

| Species            | Within gaps               |    |                             |                       |    |                             | In forest understory |   |                             |
|--------------------|---------------------------|----|-----------------------------|-----------------------|----|-----------------------------|----------------------|---|-----------------------------|
|                    | Vegetation removed to 2 m |    |                             | Low vegetation intact |    |                             | Vegetation intact    |   |                             |
|                    | Emerging                  |    | Number surviving after 1 yr | Emerging              |    | Number surviving after 1 yr | Emerging             |   | Number surviving after 1 yr |
|                    | No.                       | %  |                             | No.                   | %  |                             | No.                  | % |                             |
| <i>M. affinis</i>  | 9                         | 12 | 0                           | 6                     | 8  | 0                           | 7                    | 9 | 1                           |
| <i>M. gracilis</i> | 21                        | 28 | 1                           | 14                    | 19 | 0                           | 6                    | 8 | 0                           |
| <i>M. nervosa</i>  | 19                        | 25 | 3                           | 5                     | 7  | 0                           | 3                    | 4 | 0                           |

digitized and analyzed for estimated annual direct site factor (DSF) (direct beam radiation) and indirect site factor (ISF) (reflected skylight) as a proportion of total incident sunlight using software developed by Rich (1989, Rich et al. 1993). The global site factor (GSF; equivalent to the total site factor of Anderson 1964) is a weighted sum of DSF and ISF ( $0.45 \cdot \text{DSF} + 0.55 \cdot \text{ISF}$ ; Rich et al. 1993). These measures of light availability are strongly correlated with available photosynthetically active radiation (PAR) and/or photosynthetic photon flux density (PPFD) as measured with quantum sensors (Rich et al. 1993).

### Results

The light environments in each treatment were similar in each of the three sites into which *Miconia* seeds were sown. GSF was  $0.10 \pm 0.009$  (mean  $\pm$  1 SE,  $n = 3$ ) in the high-light treatment,  $0.05 \pm 0.029$  in the mid-light treatment, and  $0.006 \pm 0.003$  in the low-light treatment. Emergence of seedlings in the three light treatments was low relative to the number of seeds sown (Table 1). Cumulative emergence after 1 yr of all species was highest in the high-light treatments (second-growth vegetation removed) and lowest in the understory (Table 1), and there were no between-species differences in emergence with respect to the three light environments ( $\chi^2_4 = 6.85$ ,  $.5 > P > .1$ ). Overall, total emergence (pooled over the three species) increased with increasing light ( $\chi^2_2 = 19.39$ ,  $P < .001$ ).

In total, only five seedlings remained alive after 1 yr (Table 1). Results are pooled for the three sites in Table 1. All were  $\leq 20$  mm tall after 1 yr of growth and the few leaves were all  $< 1$  cm<sup>2</sup> in area. Many seedlings appeared to have been browsed, but we have no quantitative data on herbivory for these seedlings.

### PATTERNS OF DISTRIBUTION AND ABUNDANCE OF ESTABLISHED SEEDINGS

#### Methods

We sampled the natural distribution and abundance of melastome seedlings in gaps and in the undisturbed forest at La Selva to determine whether the composition and abundance of melastome species differed between gaps and understory forest, or among microsites within gaps and understory light environments (ques-

tions 4 and 5, see *Introduction*). We defined seedlings as plants  $< 15$  cm tall, lacking woody stems, and not sprouts attached to larger plants.

In areas considered primary or secondary forest we sampled seedling distribution in 10 naturally occurring single-tree treefall gaps ( $< 300$  m<sup>2</sup>) that we estimated ranged in age from 6 to 30 mo since treefall (D. Brenés M. and A. M. Ellison, *personal observations*), and in 10 paired understory sites. Understory sites were located between 30 m and 50 m of the gap edge (sensu Brokaw 1982). These understory sites included a fallen trunk, approximately the same length as that of the paired gap's "gap-maker," that was surrounded and overtopped by low ( $\approx 2$  m) vegetation. Such sites could represent old gaps or understory trees that had fallen without disturbing the forest canopy, and contained microsites such as root pits, root mounds, and fallen boles that in gaps were known to affect seedling distribution (e.g., Putz 1983). Site locations and characteristics of gaps and paired understory sites are given in Appendix 2.

In each gap and paired understory site, we counted melastome seedlings in the root pit, on the root mound, on top of the fallen bole itself, and in three 1 m wide transects parallel to the bole at 1 m, 5 m, and 10 m distance from the fallen bole. Each transect was as long as the length of the fallen bole measured from its base to the first main branch. Our sampling convention assumed the fallen bole to be in the gap center; transects  $\pm 1$  m from the bole therefore were near the gap center, while transects  $\pm 10$  m from the bole were nearer the gap edge. We also used the convention that transects labelled +1, +5, and +10 m were to the right of the bole (looking up the trunk), and -1, -5, and -10 m transects were to the left. Seedlings were identified based on comparisons with seedling vouchers (Denslow and Gomez Diaz 1990). Seedlings that were not identifiable from vouchers were collected and grown in shade houses at La Selva until large enough to identify.

In each gap and control site, hemispherical canopy photographs were taken once, in April 1990, to provide a measure of light environment. Photographs were taken 50 cm above ground level in the center of the root pit, on the bole at its center, and in the center of the +1, +5, and +10 m transects. Only one photograph (on the bole) was taken in each understory site, as canopy

TABLE 2. Total number (with % of total) of Melastomataceae seedlings found in natural treefall gaps and understory control sites.

| Species  | In gaps |      | In understory |      |
|--|---------|------|---------------|------|
|  | No.     | %    | No.           | %    |
| <i>Adelobotrys adscendens</i> (SW.) Triana   | 0       | 0.0  | 1             | 4.8  |
| <i>Clidemia discolor</i> (Triana) Cogn.  | 5       | 1.4  | 0             | 0.0  |
| <i>Clidemia ephiphytica</i> (Triana) Cogn. var. <i>trichocalyx</i> (Blake) Wurdack | 7       | 1.9  | 0             | 0.0  |
| <i>Conostegia setosa</i> Triana  | 10      | 2.7  | 4             | 1.6  |
| <i>Henriettea tuberculosa</i> (Donn. Sm.) L. O. Wms.                               | 1       | 0.3  | 0             | 0.0  |
| <i>Leandra dichotoma</i> (D. Don) Cogn.  | 21      | 5.7  | 2             | 8.0  |
| <i>Leandra granatensis</i> Gleason   | 4       | 1.1  | 0             | 0.0  |
| <i>Miconia affinis</i> DC.   | 41      | 11.1 | 5             | 23.8 |
| <i>Miconia appendiculata</i> Triana  | 0       | 0.0  | 1             | 4.8  |
| <i>Miconia centrodesma</i> Naud.   | 0       | 0.0  | 1             | 4.8  |
| <i>Miconia gracilis</i> Triana   | 15      | 4.1  | 1             | 4.8  |
| <i>Miconia multispicata</i> Naud.  | 168     | 45.7 | 3             | 14.3 |
| <i>Miconia nervosa</i> (J. E. Smith) Triana  | 34      | 9.2  | 1             | 4.8  |
| <i>Miconia punctata</i> (Desr.) D. Don ex DC.                                      | 0       | 0.0  | 1             | 4.8  |
| <i>Miconia serrulata</i> (DC.) Naud.   | 4       | 1.1  | 0             | 0.0  |
| <i>Miconia simplex</i> Triana  | 42      | 11.4 | 0             | 0.0  |
| <i>Miconia stevensiana</i> Almeda  | 2       | 0.5  | 0             | 0.0  |
| <i>Ossaea macrophylla</i> (Benth.) Cogn.   | 0       | 0.0  | 1             | 4.8  |
| <i>Triolena hirsuta</i> (Benth.) Triana  | 14      | 3.8  | 0             | 0.0  |
| Total  | 368     |      | 21            |      |

cover was not assumed to vary as widely in the understory. Photographs were analyzed as described in the field germination experiment (see *Germination and establishment in the field: Methods*).

### Results

Overall, melastome seedlings were 20-fold more abundant in gaps than in corresponding understory sites (Table 2). Of those species considered high-light-demanding (Appendix 1), only *Miconia affinis* and *Leandra dichotoma* occurred in the gaps that we sampled. The other high-light species listed in Appendix 1 are more typical of highly disturbed areas (abandoned pastures and riverbanks), and are not common in small gaps within the forest. In total, 368 seedlings were found in the 10 gap sites ( $24.9 \pm 9.89$  seedlings/m<sup>2</sup> [ $\bar{X} \pm 1$  SE] over all gap sites), while only 21 total seedlings were found in the 10 paired understory sites ( $1.1 \pm 0.27$  seedlings/m<sup>2</sup> over all control sites) ( $t_9 = 2.32$ ,  $P = .045$ , paired  $t$  test). Of the 19 species encountered, 14 were more common in gaps than in the understory. The other five species each were represented by only a single individual. Among the seven gaps in which melastome seedlings occurred, the number of seedlings increased significantly with gap age ( $r^2 = 0.69$ ,  $F_{1,6} = 13.15$ ,  $P = .01$ ).

In these sites, we examined in more detail the seedling distribution patterns of the more common species whose abundance permitted detailed statistical analysis: *Leandra dichotoma*, *Miconia affinis*, *M. gracilis*, *M. multispicata*, *M. nervosa*, and *M. simplex*. All species except *M. gracilis* were significantly more common in treefall gaps than in the forest understory (Fig. 3, Table 3). To examine differences in seedling abun-

dances among gap microsites, we analyzed within-gap abundance patterns using  $G$  tests on two-way contingency tables, where the six rows were location within gap (pit, mound, bole, and transects at  $\pm 1$  m,  $\pm 5$  m, and  $\pm 10$  m) and the columns were  $\log_2$  seedlings/m<sup>2</sup>. Degrees of freedom for each  $G$  test are given by (row 1)  $\times$  (column 1), where (row 1) = 5, and (column 1) varies between 1 and 3, depending on the actual number of non-zero seedling categories. Mean ( $\pm 1$  SE) number of seedlings in each within-gap sampling location are shown in Fig. 3.

All six of these species were more abundant in root pits and mounds than elsewhere within gaps. These differences were significant in the cases of *M. affinis* ( $X^2 = 23.15$ ,  $df = 10$ ,  $P = .01$ ), *M. multispicata* ( $X^2 = 31.38$ ,  $df = 15$ ,  $P = .008$ ), and *M. nervosa* ( $X^2 = 15.12$ ,  $df = 5$ ,  $P = .009$ ). The other species showed a tendency towards greater abundance in root pits and on root mounds (*M. gracilis*:  $X^2 = 17.98$ ,  $df = 10$ ,  $P = .06$ ; *L. dichotoma*:  $X^2 = 10.11$ ,  $df = 5$ ,  $P = .07$ ; *M. simplex*:  $X^2 = 8.08$ ,  $df = 5$ ,  $P = .15$ ).

Overall, seedlings were not distributed randomly within gaps. Location within gap (i.e., in the root pit, on the root mound, on the bole, or at varying distances from the bole) had a significant effect on seedling density (Table 4, Fig. 3). Tukey's a posteriori multiple range test indicated that significantly more ( $P < .05$ ) seedlings were found in root pits or on root mounds than in any other location. Seedling densities in root pits and root mounds, however, did not differ significantly from each other ( $P > .05$ , Tukey's multiple range test). Similarly, comparisons between seedling densities in the other locations within gaps and understory controls did not reveal significant differences ( $P > .05$ ).



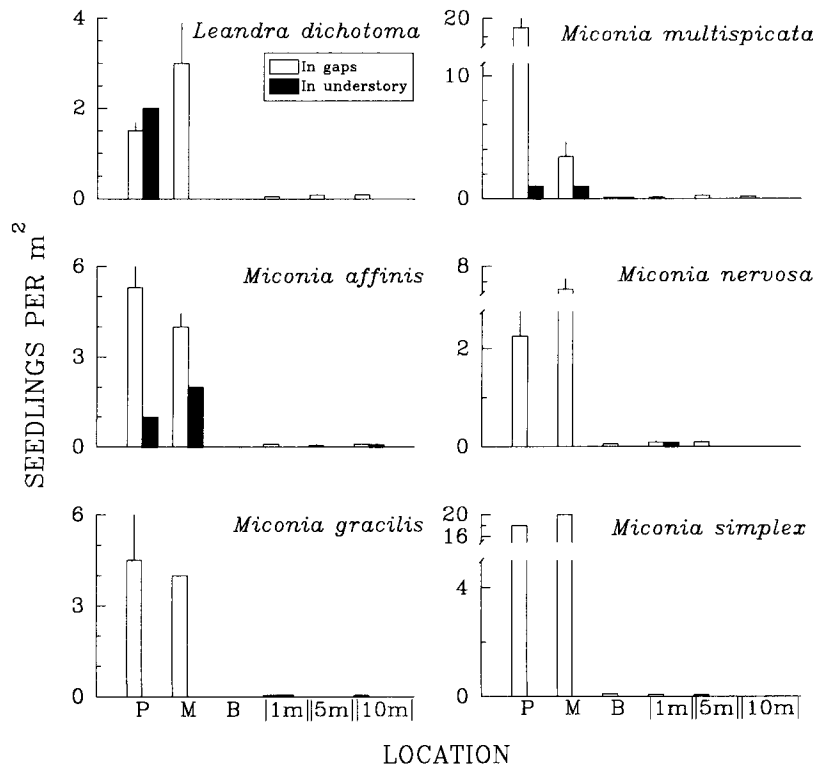


FIG. 3. Seedling density of six most common melastome species in the 10 gaps and paired understory sites. Locations are: P, root pit; M, on root mound; B, on root bole; |1m|, in transects ± 1 m from bole; |5m|, in transects ± 5 m from bole; |10m|, in transects ± 10 m from bole. Data are means and 1 SE.

ANOVA also indicated that variation in seedling abundance among within-gap sites differed between younger and older alluvial soil types (interaction term in Table 4). In gaps on younger alluvial soils, seedlings were less abundant in root pits or root mounds relative to other sites within these gaps. In gaps on weathered alluvium (Arboleda consociation), seedlings were always much more abundant in root pits and on root mounds.

In all gap sites, light level (estimated as GSF) was highest atop the bole, and declined steeply towards the gap edge (Fig. 5). Light levels atop fallen trunks in understory sites were lower than light levels at gap edges (Fig. 5). Because of shading effects by the root mound, light levels in the root pit were comparable to those found between 1 and 5 m away from the fallen bole (Fig. 5). There were significant differences between locations within gaps ( $P < .001$ , ANOVA; Fig. 5), as well as significant differences between gaps in all three light measures ( $P = .001$ , ANOVA; data not shown).

Location within a gap was a stronger determinant of seedling abundance than was variation in light availability within gaps (Fig. 5). Average seedling density was two orders of magnitude greater within root pits than in any other location within gaps, although light levels within root pits were intermediate relative to other positions within the gaps (Fig. 5). ANOVA indicated that overall, only location within gap had a

significant effect on seedling abundance (Table 4); the addition of any measure of light availability, global site factor, direct site factor, indirect site factor, or unweighted openness, as a covariate in the ANOVA did not improve the fit of the model.

SEEDLING GROWTH IN CONTROLLED LIGHT ENVIRONMENTS

Methods

Although previous field and shade-house studies indicated that all melastome cuttings responded positively to some increase in light availability (Denslow

TABLE 3. Results of Wilcoxon's matched-pairs signed-ranks tests contrasting seedling densities in and out of gaps for the six most common species.

| Light requirement* | Species                     | Z-score | Two-tailed P |
|--------------------|-----------------------------|---------|--------------|
| High               | <i>Leandra dichotoma</i>    | 3.06    | .002         |
| High               | <i>Miconia affinis</i>      | 2.35    | .019         |
| Low                | <i>Miconia multispicata</i> | 4.84    | .0001        |
| Low                | <i>Miconia nervosa</i>      | 3.35    | .0008        |
| Low                | <i>Miconia gracilis</i>     | 1.57    | .116         |
| Low                | <i>Miconia simplex</i>      | 2.20    | .028         |

\* Light requirement: Low, some degree of shade tolerance; High, high-light-demanding.

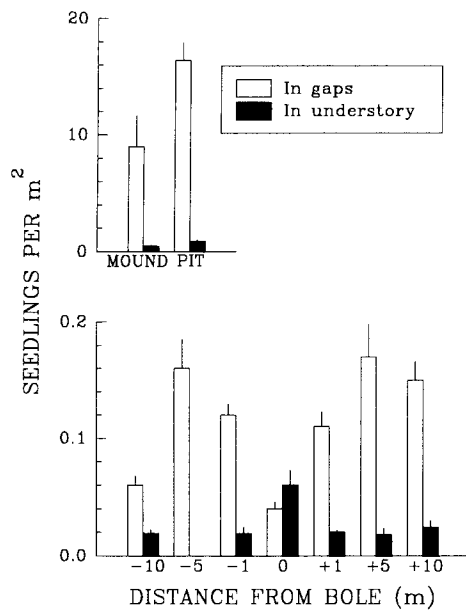


FIG. 4. Density of melastome seedlings away from the gapmaker bole and in tip-up pits and mounds within 10 gaps and paired understorey sites.

et al. 1990, and unpublished manuscript), response patterns of melastome seedlings were undocumented. We examined seedling growth of eight species of melastome under three different controlled light levels in shade-houses at La Selva (question 6, see Introduction). Newly germinated seedlings of *Conostegia subcrustulata*, *Miconia affinis*, *M. barbinervis*, *M. longifolia*, *M. multispicata*, *M. nervosa*, *M. simplex* and *Nepsera aquatica* were transplanted into 50 × 25 × 6 cm plastic flats of heat-sterilized alluvial sand from the banks of the Rio Puerto Viejo. After 8 wk growing in ≈20% of full sunlight, the seedlings developed one pair of true leaves and were transplanted into flats of sterile sand and alluvial soil (50:50). Clear plastic sheeting was placed 1 m above the flats to prevent rain drops from uprooting seedlings. The plastic uniformly reduced ambient light by ≈5%.

Twelve weeks later (two pairs of true leaves, ≈10 mm tall), each seedling was transplanted into the center of a 300 mL, 6 cm diameter plastic cup filled with a 50:50 sand: soil mixture. This mixture was not sterilized. All of these species are mycorrhizal (J. S. Denslow and A. M. Ellison, unpublished manuscript), and although we did not deliberately infect the soil, fresh

TABLE 4. Results of ANOVA testing effects of location within gap and soil type on seedling density.

| Source        | ss     | df | ms    | F     | P     |
|---------------|--------|----|-------|-------|-------|
| Location (L)  | 96.95  | 5  | 19.39 | 21.25 | <.001 |
| Soil type (S) | 5.96   | 3  | 1.99  | 2.18  | .099  |
| L × S         | 28.84  | 14 | 2.06  | 2.26  | .014  |
| Residual      | 59.30  | 65 | 0.91  |       |       |
| Total         | 191.05 | 87 | 2.21  |       |       |

TABLE 5. Survivorship from final transplant to harvest (10 wk) of melastome seedlings in three different light levels.

| Light requirement* | Species                         | Light level (% of full sunlight) |     |     |
|--------------------|---------------------------------|----------------------------------|-----|-----|
|                    |                                 | 2%                               | 20% | 40% |
| High               | <i>Conostegia subcrustulata</i> | 100                              | 100 | 100 |
| High               | <i>Nepsera aquatica</i>         | 100                              | 60  | 100 |
| High               | <i>Miconia longifolia</i>       | 100                              | 95  | 85  |
| High               | <i>Miconia barbinervis</i>      | 100                              | 100 | 100 |
| High               | <i>Miconia affinis</i>          | 90                               | 100 | 80  |
| Low                | <i>Miconia multispicata</i>     | 80                               | 95  | 100 |
| Low                | <i>Miconia nervosa</i>          | 95                               | 90  | 75  |
| Low                | <i>Miconia simplex</i>          | 65                               | 70  | 30  |

\* Light requirement: Low, some degree of shade tolerance; High, high-light-demanding.

soil is likely to have mycorrhizae present. Sixty seedlings of each species (except 20 each of *M. barbinervis* and *C. subcrustulata*) were assigned randomly to three light treatments: 2%, 20%, and 40% of full sun (20 seedlings/treatment). These light levels were similar to those measured in the rain forest understorey, small (<300 m<sup>2</sup>) treefall gaps, and large (>400 m<sup>2</sup>) treefall gaps (Chazdon and Fetcher 1984, Denslow et al. 1990).

Every week we measured total stem length as the height of the plant from soil level to base of top-most leaf pair on the main stem plus the length of any lateral branches. After 10 wk, all surviving plants were harvested and separated into leaves, stems, and roots. Total leaf area of each seedling was measured with a LICOR leaf area meter. To assess changes in biomass allocation patterns over the three light treatments, we separately dried (50°C, 40 h) and weighed (±0.0001 g) leaves, stems, and roots.

Results

Seedling survivorship in shade-houses was generally >80% in all light levels (Table 5), except for *M. sim-*

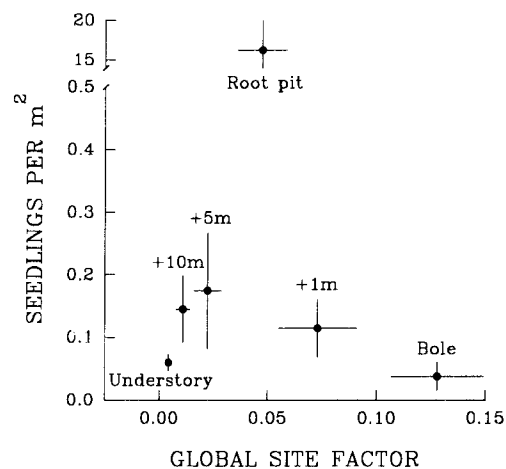


FIG. 5. Relationship between seedling density and global site factor (GSF) at five locations within gaps and in the adjacent forest understorey. Values shown are means ± 1 SE.

TABLE 6. Mass (g) at final harvest of melastome seedlings in the three different light conditions ( $n$  = sample size). Intraspecific differences ( $P < .05$ , Tukey's HSD test for multiple comparisons among means) across light treatments between final biomasses are indicated by differing superscripted letters.

| Light require-ment* | Life-form* | Species                         | Light level (% of full sunlight) |     |                            |     |                             |     |
|---------------------|------------|---------------------------------|----------------------------------|-----|----------------------------|-----|-----------------------------|-----|
|                     |            |                                 | 2%                               |     | 20%                        |     | 40%                         |     |
|                     |            |                                 | $\bar{X} \pm 1 \text{ SE}$       | $n$ | $\bar{X} \pm 1 \text{ SE}$ | $n$ | $\bar{X} \pm 1 \text{ SE}$  | $n$ |
| High                | S          | <i>Conostegia subcrustulata</i> | 0.017 ± 0.009 <sup>a</sup>       | 7   | 0.811 ± 0.185 <sup>b</sup> | 7   | 0.889 ± 0.115 <sup>b</sup>  | 6   |
| High                | S          | <i>Miconia longifolia</i>       | 10.009 ± 0.001 <sup>a</sup>      | 20  | 0.105 ± 0.020 <sup>b</sup> | 19  | 0.109 ± 0.038 <sup>b</sup>  | 17  |
| High                | H          | <i>Nepsera aquatica</i>         | 0.013 ± 0.002 <sup>a</sup>       | 20  | 0.083 ± 0.029 <sup>a</sup> | 12  | 0.325 ± 0.105 <sup>b</sup>  | 20  |
| High                | S          | <i>Miconia barbinervis</i>      | 0.004 ± 0.0004 <sup>a</sup>      | 6   | 0.061 ± 0.041 <sup>a</sup> | 7   | 0.055 ± 0.0 <sup>ab</sup>   | 7   |
| High                | T          | <i>Miconia affinis</i>          | 0.008 ± 0.001 <sup>a</sup>       | 18  | 0.031 ± 0.008 <sup>a</sup> | 20  | 0.029 ± 0.010 <sup>ab</sup> | 16  |
| Low                 | T          | <i>Miconia multispicata</i>     | 0.013 ± 0.002 <sup>a</sup>       | 16  | 0.082 ± 0.014 <sup>b</sup> | 19  | 0.080 ± 0.020 <sup>b</sup>  | 20  |
| Low                 | S          | <i>Miconia nervosa</i>          | 0.004 ± 0.0002 <sup>a</sup>      | 19  | 0.089 ± 0.023 <sup>b</sup> | 18  | 0.028 ± 0.005 <sup>a</sup>  | 15  |
| Low                 | S          | <i>Miconia simplex</i>          | 0.003 ± 0.0002 <sup>a</sup>      | 13  | 0.008 ± 0.002 <sup>b</sup> | 14  | 0.008 ± 0.001 <sup>b</sup>  | 6   |

\* See Appendix 1 for definition of light requirement and life-form.

plex, a shade-tolerant species of the forest understory, in which survivorship declined dramatically with increasing light level. Survivorship of the other species did not vary with light level (Table 5).

All species were substantially heavier at harvest in the 20% light treatment relative to the mass of their conspecifics grown in the 2% light treatment (Table 6). Only the biomass of *Nepsera aquatica*, a high-light species common to riverbanks, increased further between 20% and 40% sunlight (Table 6). Harvest biomass of *Miconia nervosa* was greater at 20% light (Table 6). Differences in growth rate among species and treatment parallel those in final biomass (data not shown).

Leaf area and specific leaf mass were often higher at 20% or 40% of full sunlight than at the 2% levels typical of forest understory, although the patterns were not

consistent within high-light-demanding or shade-tolerant groups (Table 7). Relative allocation to shoots and roots did not differ consistently among light treatments (Table 7).

DISCUSSION

Early life history characteristics, patterns of germination, establishment, and early seedling growth, differed among the melastomes that we studied. Their seeds' responses to passage through birds, likelihood of establishment, and seedling growth responses to varying light conditions varied with life-form and adult habitat. In addition, suites of these characteristics did not co-occur in the same combinations that have been found for pioneer or climax canopy tree species. In closing, we discuss patterns of interspecific variation in these characters that we observed among mela-

TABLE 7. Morphological characteristics at final harvest of melastome seedlings in the three different light conditions (% of full sunlight). Intraspecific differences ( $P < .05$ , Tukey's HSD test for multiple comparisons among means) across light treatments between final biomasses are indicated by differing superscripted letters. Sample sizes as in Table 6.

| Light require-ment* | Species                         | Statis-tic | Leaf area (cm <sup>2</sup> ) |                    |                   | Specific leaf mass (g/cm <sup>2</sup> ) |                   |                   | Root : shoot ratio (g/g) |                  |                   |
|---------------------|---------------------------------|------------|------------------------------|--------------------|-------------------|---|-------------------|-------------------|--------------------------|------------------|-------------------|
|                     |                                 |            | 2%                           | 20%                | 40%               | 2%                                      | 20%               | 40%               | 2%                       | 20%              | 40%               |
|                     |                                 |            | $\bar{X}$                    | $\bar{X}$          | $\bar{X}$         | $\bar{X}$                               | $\bar{X}$         | $\bar{X}$         | $\bar{X}$                | $\bar{X}$        | $\bar{X}$         |
| High                | <i>Conostegia subcrustulata</i> | $\bar{X}$  | 6.8 <sup>a</sup>             | 127.6 <sup>b</sup> | 130 <sup>b</sup>  | 1.3 <sup>a</sup>                        | 2 <sup>b</sup>    | 2.7 <sup>c</sup>  | 0.9 <sup>a</sup>         | 1.3 <sup>a</sup> | 1.1 <sup>a</sup>  |
|                     |                                 | SE         | 3.89                         | 16.68              | 12.89             | 0.19                                    | 0.12              | 0.16              | 0.15                     | 0.25             | 0.10              |
| High                | <i>Miconia longifolia</i>       | $\bar{X}$  | 1.8 <sup>a</sup>             | 23.6 <sup>b</sup>  | 13.9 <sup>b</sup> | 2.6 <sup>a</sup>                        | 2.6 <sup>a</sup>  | 4.5 <sup>b</sup>  | 0.5 <sup>a</sup>         | 0.3 <sup>b</sup> | 0.4 <sup>ab</sup> |
|                     |                                 | SE         | 0.31                         | 4.42               | 4.27              | 0.11                                    | 0.09              | 0.46              | 0.03                     | 0.03             | 0.05              |
| High                | <i>Nepsera aquatica</i>         | $\bar{X}$  | 7.0 <sup>a</sup>             | 27.3 <sup>ab</sup> | 60.6 <sup>b</sup> | 0.8 <sup>a</sup>                        | 1.1 <sup>a</sup>  | 2.1 <sup>b</sup>  | 0.4 <sup>a</sup>         | 0.7 <sup>b</sup> | 0.5 <sup>a</sup>  |
|                     |                                 | SE         | 1.34                         | 8.71               | 15.98             | 0.09                                    | 0.16              | 0.25              | 0.04                     | 0.11             | 0.10              |
| High                | <i>Miconia barbinervis</i>      | $\bar{X}$  | 0.9 <sup>a</sup>             | 14.5 <sup>a</sup>  | 8.5 <sup>a</sup>  | 2.1 <sup>a</sup>                        | 1.9 <sup>a</sup>  | 4.0 <sup>a</sup>  | 1 <sup>a</sup>           | 0.9 <sup>a</sup> | 0.4 <sup>a</sup>  |
|                     |                                 | SE         | 0.25                         | 9.43               | 0                 | 0.58                                    | 0.23              | 0                 | 0.51                     | 0.23             | 0                 |
| High                | <i>Miconia affinis</i>          | $\bar{X}$  | 1.7 <sup>a</sup>             | 7.3 <sup>b</sup>   | 5.9 <sup>a</sup>  | 2.4 <sup>a</sup>                        | 2.7 <sup>ab</sup> | 3.7 <sup>b</sup>  | 0.7 <sup>a</sup>         | 0.4 <sup>a</sup> | 0.5 <sup>a</sup>  |
|                     |                                 | SE         | 0.24                         | 1.94               | 1.99              | 0.3                                     | 0.40              | 0.57              | 0.15                     | 0.06             | 0.11              |
| Low                 | <i>Miconia multispicata</i>     | $\bar{X}$  | 3.5 <sup>a</sup>             | 20.8 <sup>a</sup>  | 13.1 <sup>a</sup> | 1.9 <sup>a</sup>                        | 2.2 <sup>ab</sup> | 4.3 <sup>b</sup>  | 0.7 <sup>a</sup>         | 0.7 <sup>a</sup> | 0.7 <sup>a</sup>  |
|                     |                                 | SE         | 0.82                         | 4.32               | 3.08              | 0.15                                    | 0.09              | 0.98              | 0.08                     | 0.11             | 0.06              |
| Low                 | <i>Miconia nervosa</i>          | $\bar{X}$  | 1.1 <sup>a</sup>             | 21.4 <sup>b</sup>  | 7.7 <sup>ab</sup> | 1.6 <sup>a</sup>                        | 2.6 <sup>b</sup>  | 3.3 <sup>b</sup>  | 0.8 <sup>a</sup>         | 0.7 <sup>a</sup> | 0.4 <sup>a</sup>  |
|                     |                                 | SE         | 0.12                         | 5.56               | 1.96              | 0.16                                    | 0.11              | 0.41              | 0.23                     | 0.17             | 0.04              |
| Low                 | <i>Miconia simplex</i>          | $\bar{X}$  | 0.4 <sup>a</sup>             | 1.2 <sup>a</sup>   | 0.3 <sup>a</sup>  | 4.5 <sup>a</sup>                        | 16.8 <sup>a</sup> | 13.4 <sup>a</sup> | 0.7 <sup>a</sup>         | 0.8 <sup>a</sup> | 0.6 <sup>a</sup>  |
|                     |                                 | SE         | 0.11                         | 0.38               | 0.12              | 1.04                                    | 5.32              | 3.84              | 0.10                     | 0.1              | 0.10              |

\* Light requirement: Low, some degree of shade tolerance; High, high-light-demanding.

stomes, and speculate on the relationship of this variation to plant life form and adult distribution (question 7, see *Introduction*).

#### Germination

All the melastomes examined produce very small seeds. The germination trials in vitro indicated some degree of induced dormancy among at least 18 of the 22 melastomes, whose adult habitats range from open pastures to forest understory. We base this conclusion on these species' responses to germination following manual extraction and prolonged cool, dry storage. However, we have little basis for speculation about dormancy capacity or germination requirements under field conditions. Among canopy trees, only pioneer species characteristic of disturbed habitats have been found to have extended dormancy (Vázquez-Yáñez 1974, Moreno-Casasola 1976, Holthaijzen and Boerboom 1982, Vázquez-Yáñez and Orózco-Segovia 1984, Foster 1986, Núñez-Farfán and Dirzo 1988). The four species that did not germinate in the in vitro trials, *Clidemia densiflora*, *Miconia dorsiloba*, *M. gracilis*, and *M. grayumii*, are all understory species common in the dense shade of the undisturbed forest at La Selva. On the basis of trials in vitro, we cannot draw any conclusions about dormancy in these four species.

We had hypothesized that passage through birds would significantly enhance germination of species that had responded poorly in the in vitro trials. This hypothesis was supported for *Clidemia densiflora*, the only species tested of the four that had not germinated in the in vitro trials. Mayer and Poljakoff-Mayber (1975) suggested that passage through birds and defecation of pulp-free seeds generally should enhance germination of fleshy fruited species. However, other studies have suggested that germination of such species should be more variable (Izhaki and Safriel 1990 and references therein), and that less predictable or asynchronous germination should be favored evolutionarily (e.g., Murray 1988). We examined germination responses after passage through only one bird, *Pipra mentalis*. Other birds feed on melastome fruits (Denslow et al. 1986, Levey 1988b, 1990), and results of identical experiments with different birds could yield results different from ours. In particular, *Pipra*, like most frugivorous species, lacks a grinding gizzard that could abrade seed coats. Additional experiments with other germination conditions or bird species could be used to examine critically our observations that germination patterns are variable within life-form or adult habitat among these melastomes.

#### Establishment

Establishment probabilities (on the order of  $1 \times 10^{-3}$  for *M. affinis*, *M. gracilis*, and *M. nervosa* across all habitats) were low but similar to those observed for other small-seeded species, e.g., *Cecropia obtusifolia* at Los Tuxtlas, Mexico (Alvarez-Buylla and García-Ba-

rríos 1991), and much less than those observed for large-seeded species (e.g., Augspurger 1984, Howe 1990). Establishment of melastome seedlings, like other small-seeded species, was low in forest understory environments. In field experiments, emergence and survival were highest in the high-light environments of treefall gaps for all species planted. Naturally established melastome seedlings also were more common in gaps than in the forest understory.

Seedlings of seven melastome species, *Clidemia discolor*, *Leandra dichotoma*, *Miconia affinis*, *M. gracilis*, *M. multispicata*, *M. nervosa*, and *M. simplex*, were all found more commonly in treefall gaps than in nearby understory. Reproductively mature individuals of two of these species, *C. discolor* and *M. gracilis*, were not restricted to gaps, and in fact are common in the understory at La Selva (J. S. Denslow and A. M. Ellison, *unpublished manuscript*). The other five species appear to be dependent on gaps for fruiting and flowering (Levey 1988a, 1990). Species that were found uncommonly in our search for established seedlings are also found rarely as mature adults at La Selva (J. S. Denslow and A. M. Ellison, *unpublished manuscript*). However, seedlings of two of these species, *Conostegia setosa*, *Henriettea tuberculosa*, were more common in gaps than in the understory, while the rest tended to occur more frequently in the understory.

Field contrasts between gaps and understory illustrated apparent gap-dependence of many melastomes for successful establishment; this result is evidence of a strong light effect on seedling establishment. Within gaps, seedling distributions were not related to estimated light availability; seedlings were most abundant in root pits and on root mounds although light availability was significantly lower in root pits than in gap centers. However, quantitative measures of light within gap microsites were not related significantly to seedling distribution within gaps, and higher light levels have been often cited as one of the main reasons that tree seedlings and saplings grow better in gaps (e.g., Frankie et al. 1974, Denslow 1980, Putz 1983, Augspurger 1984, Fetcher et al. 1987). Putz (1983) found that pioneer tree seedlings colonized pits and mounds at Barro Colorado Island, Panama. He attributed these findings to improved conditions for germination found within these microsites, including the exposure of mineral soil. Tiny roots of lilliputian seedlings are able to immediately penetrate the soil unimpeded by the presence of litter or a dense root mat. However, nutrient availability (extractable P, N mineralization) is lower in the root throw zones of gaps at La Selva (Vitousek and Denslow 1986).

Other workers have described differential species establishment responses to within-gap microsites (Bratton 1976, Núñez-Farfán and Dirzo 1988, Peterson et al. 1990). Both the higher light conditions in treefall gaps and the presence of exposed mineral soil appear to enhance seedling establishment in high-light-de-

manding and shade-tolerant melastome species. Working in temperate forests, Peterson et al. (1990) found that species with different growth forms colonized different microsites within gaps. In particular, small-seeded, wind-dispersed species were more common in pits and mounds, while large-seeded, animal-dispersed species and species that rely more heavily on vegetative reproduction were more common in less disturbed microsites.

Differential seed rain may contribute to this pattern as well. Although no quantitative data are available, seed rain may be higher in gaps than in the forest understory. Fruit production in shade-tolerant as well as high-light-demanding species is higher in gaps (Denslow et al. 1986, Levey 1988a, 1990). Increased activity of frugivorous birds and higher rates of fruit removal (Levey 1988a, b) also may produce higher rates of seed rain. Levey (1988a, 1990) also has suggested that seeds may be dispersed differentially to gap edges where birds perch following feeding. Since root pits often define one edge of a gap, differential dispersal may also contribute to the higher density of seedlings in root throw zones.

#### *Seedling growth in different light environments*

Higher light levels have been cited as a primary cause of more rapid growth of tree seedlings and saplings in gaps (e.g., Frankie et al. 1974, Denslow 1980, Putz 1983, Augspurger 1984, Fetcher et al. 1987). Although the patterns of light intensity and wavelength composition differ between shade-house and natural gap environments, our shade-house results are consistent with field experiments on some of the same species (Denslow et al. 1990). Growth responses vary between the two extremes classically described for photosynthetic responses: growth rates of high-light-demanding species continue to increase at high-light levels, whereas the growth of shade tolerant species plateaus at lower light levels. Among the species we studied, both high-light-demanding (*N. aquatica*, *Co. subcrustulata*) and shade-tolerant (*M. simplex*) exhibited the expected patterns. Between these extremes, however, we found no consistent patterns in seedling growth rates to distinguish among species with different adult habitat distributions. Species rankings based on mass at harvest were similar at 2% and 20% of full sunlight. These growth patterns reflect the light environments typical of a gap-understory mosaic: deeply shaded forest understory (light levels at 1–3% of full sunlight; Chazdon and Fetcher 1984) punctuated by occasional small gaps (light levels at 10–20% of full sunlight; Denslow et al. 1990). Species persisting in this heterogeneous environment might be expected to exhibit considerable shade tolerance as well as some plasticity of growth response in the presence of the enhanced light levels associated with canopy disturbance.

Similarly, comparisons of allocation patterns between species within light treatments did not reveal

any suite of responses common to species from particular habitats. For example, *Conostegia subcrustulata*, found only in abandoned pastures and along roadsides, and the shade-tolerant *Miconia simplex* had similar biomass allocation patterns to leaves, stems, and roots at all light levels. However, total leaf area and specific leaf mass of these two species differed in each light environment. *Conostegia subcrustulata* had significantly greater leaf area but lower specific leaf mass than *M. simplex* in each of the three light environments. The other six species, adults of which were found in habitats ranging from abandoned pastures to forest understory (Appendix 1) showed more similar biomass allocation responses to each other than to either *C. subcrustulata* or *M. simplex* in each light environment. As with germination and establishment patterns, therefore, patterns of early seedling growth in these species did not reflect differences in adult distributions.

#### CONCLUDING REMARKS

Among La Selva melastomes, variation in seed germination, seedling establishment, and seedling distribution was not consistent among species from similar habitats. It may not be possible to generalize broadly from regeneration categories derived from studies of canopy trees (e.g., pioneer vs. climax: Swaine and Whitmore 1988, Whitmore 1989) and based on correlated germination, establishment and growth characteristics of species from different plant families (cf. Martínez-Ramos et al. 1989). Our data from a single plant family suggest that phylogenetic constraints importantly influence some life history traits and that the suites of characteristics often used to describe life history strategies may be decoupled where phylogenetic constraints are strong. For example, the speciose genera *Miconia*, *Clidemia*, *Conostegia*, and *Ossaea* all produce small, watery berries containing large numbers of very small seeds, traits often ascribed to pioneer or colonizing species. Species in these genera, however, occur in a wide variety of habitats including sites heavily disturbed by human activity and intact tropical rain forest understory. In addition this study has shown that germination and seedling growth rates of these species are similar and that even species characterized a priori as highly shade tolerant appear to require gaps and disturbed soil for germination and establishment.

However, none of the species that we characterized as high-light-demanding were found as seedlings in either gap or understory environments in the rain forest at La Selva. In a separate study of seed rain into four gaps in this forest (Denslow and Gomez Diaz 1990), 122 seeds of 20 melastome species were collected over 1 yr. None of the species characterized here as high-light-demanding occurred in those collections (J. S. Denslow and A. E. Gomez-Diaz, unpublished data). Lack of an effective seed rain may thus account for the absence of seedlings of these species in gaps, although

our data indicate that such seedlings should be able to survive initially following germination. Low adult growth rates and perhaps survival in light environments characteristic of this forest (Denslow et al. 1990) apparently account for both the observed distributions of adults and the lack of seed sources for gap colonization. Species lacking an appreciable level of shade tolerance as adults may be unable to survive extended periods of time in the forest understory between canopy opening events. The combined effects of inadequate seed rain and low probability of adult survival in low-light environments may thus produce restricted adult distributions although seed and seedling traits are similar to those of more widely distributed species.

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## APPENDIX 1

Melastomataceae used in germination and seedling growth experiments. All collection locations refer to La Selva Biological Station. All collection dates are in 1988.

| Species   | Life-form* | Habitat† | Light requirement‡ |
|---|------------|----------|--------------------|
| <i>Clidemia crenulata</i> Gleason§                              | S          | P/S      | L                  |
| <i>C. densiflora</i> (Standl.) Gleason§                         | S          | P        | L                  |
| <i>C. dentata</i> D. Don.§                                      | S          | S/O      | H                  |
| <i>C. discolor</i> (Triana) Cogn.§                              | S          | S        | L                  |
| <i>C. japurensis</i> DC. var. <i>heterobasis</i> (DC.) Wurdack§ | S          | R/Sw     | L                  |
| <i>Conostegia subcrustulata</i> (Beurl.) Triana                 | S          | O        | H                  |
| <i>Leandra consimilis</i> Gleason§                              | S          | P/S      | L                  |
| <i>L. dichotoma</i> (D. Don.) Cogn.§                            | S          | S/O      | H                  |
| <i>L. mexicana</i> (Naud.) Cogn.§                               | S          | S/O      | H                  |
| <i>Miconia affinis</i> DC.                                      | T          | S/O      | H                  |
| <i>M. barbinervis</i> (Benth.) Triana                           | S          | O        | H                  |
| <i>M. centrodesma</i> Naud.§                                    | S/T        | P        | L                  |
| <i>M. dorsiloba</i> Gleason§                                    | T          | P        | L                  |
| <i>M. gracilis</i> Triana§                                      | S          | P        | L                  |
| <i>M. grayumii</i> Almeda§                                      | S          | P        | L                  |
| <i>M. longifolia</i> (Aubl.) DC.                                | S          | O        | H                  |
| <i>M. multispicata</i> Naud.                                    | T          | S        | L                  |
| <i>M. nervosa</i> (J.E. Smith) Triana                           | S          | P/S      | L                  |
| <i>M. simplex</i> Triana  | S          | P        | L                  |
| <i>Nepsera aquatica</i> (Aubl.) Naud.                           | H          | R/Sw     | H                  |
| <i>Ossaea macrophylla</i> (Benth.) Cogn.§                       | S          | P/S      | L                  |
| <i>O. micrantha</i> (Sw.) Macf. ex Cogn.§                       | T          | P/S      | L                  |

\* Life-forms: H, herb; S, shrub (multiple trunks, little secondary wood on main stem); T, tree (single trunk, much secondary wood on main stem).

† Habitat where collected: P, primary forest; S, secondary forest; O, abandoned pasture; R, river banks; Sw, swamps.

‡ Light requirement: L, some degree of shade tolerance; H, high-light-demanding.

§ Used in germination study only.



## APPENDIX 2

Description of sites sampled for Melastomataceae seedlings. The location given is the nearest trail, the distance along that trail, and the direction (degrees E of magnetic N) from the trail. The orientation of the fallen bole is given as degrees E of magnetic N.

| Site |            | Bole species   | Location       | Orienta-<br>tion (°E) | Approximate<br>age (mo) | Soil<br>consociation* |
|------|------------|--|----------------|-----------------------|-------------------------|-----------------------|
|      |            |  | Trail (m) °E   |                       |                         |                       |
| 1    | Gap        | <i>Cespedesia macrophylla</i> Seem.<br>(Ochnaceae)               | CCC 575, 160°  | 225°                  | 24                      | Arboleda              |
|      | Understory | <i>Pentaclethra macroloba</i> (Willd.) O.<br>Ktze (Mimosaceae)   | CCC 550, 140°  | 260°                  | ...                     | Arboleda              |
| 2    | Gap        | <i>P. macroloba</i>  | CCC 650, 305°  | 300°                  | 12                      | Arboleda              |
|      | Understory | <i>P. macroloba</i>  | CCC 620, 325°  | 325°                  | ...                     | Arboleda              |
| 3    | Gap        | unidentified   | CCC 685, 140°  | 140°                  | 30                      | Arboleda              |
|      | Understory | <i>P. macroloba</i>  | CCC 720, 140°  | 200°                  | ...                     | Arboleda              |
| 4    | Gap        | <i>P. macroloba</i>  | SSO 150, 80°   | 229°                  | 18                      | Arboleda              |
|      | Understory | <i>P. macroloba</i>  | SSO 150, 80°   | 330°                  | ...                     | Arboleda              |
| 5    | Gap        | <i>Pterocarpus rohrii</i> Vahl<br>(Papilionaceae)                | SURA 250, 240° | 155°                  | 7                       | La Selva              |
|      | Understory | <i>Dipteryx panamensis</i> (Pittier) Record<br>(Papilionaceae)   | SURA 200, 154° | 154°                  | ...                     | La Selva              |
| 6    | Gap        | <i>Pentaclethra macroloba</i>                                    | CEN 640, 130°  | 305°                  | 3                       | Chanchera             |
|      | Understory | <i>P. macroloba</i>  | CEN 650, 340°  | 161°                  | ...                     | Chanchera             |
| 7    | Gap        | <i>Hymenolobium mesoamericanum</i><br>Lima (Papilionaceae)       | CEN 690, 248°  | 201°                  | 27                      | Chanchera             |
|      | Understory | <i>P. macroloba</i>  | CEN 700, 60°   | 139°                  | ...                     | Chanchera             |
| 8    | Gap        | <i>P. macroloba</i>  | SSO 750, 140°  | 230°                  | 24                      | Arboleda              |
|      | Understory | <i>P. macroloba</i>  | SSO 760, 140°  | 220°                  | ...                     | Arboleda              |
| 9    | Gap        | <i>Dussia macrophyllata</i> (Donn. Sm.)<br>Harms (Papilionaceae) | CCL 200, 240°  | 170°                  | 21                      | Holdridge             |
|      | Understory | <i>P. macroloba</i>  | CCL 270, 130°  | 165°                  | ...                     | Holdridge             |
| 10   | Gap        | <i>Inga</i> sp. (Mimosaceae)                                     | CCL 650, 292°  | 251°                  | 10                      | Holdridge             |
|      | Understory | <i>P. macroloba</i>  | CCL 725, 168°  | 310°                  | ...                     | Holdridge             |

\* Soil taxonomy follows Sancho and Mata (1987) and Sollins et al. (*in press*). The Arboleda consociation is a weathered alluvial soil, the Chanchera and La Selva consociations are alluvial soils from the middle trace of the Rio Sarapiquí, and the Holdridge consociation is an alluvial soil from the middle terrace of the Rio Puerto Viejo.