

Seed germination, seedling growth and habitat partitioning in two morphotypes of the tropical pioneer tree *Trema micrantha* in a seasonal forest in Panama

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Abstract: We examined the distribution, germination, growth and photosynthetic characteristics of two co-existing morphotypes of the pioneer tree *Trema micrantha* at the Barro Colorado Nature Monument (BCNM), Panama. Morphotypes differed significantly in distribution and in seed characteristics. A ‘large’-seeded morphotype (endocarp mass = 3.83 mg) was associated with treefall gaps in the forest interior, whereas a ‘small’-seeded morphotype (endocarp mass = 1.38 mg) was found predominantly on landslides on the margins of Lake Gatun. Seeds of the small-seeded morphotype germinated faster than seeds of the large-seeded morphotype, with seedlings of the small-seeded morphotype showing both a higher Unit Leaf Rate (ULR) and a lower Specific Leaf Area (SLA). Differences in photosynthetic rates reflected differences in SLA; the small-seeded morphotype had a higher rate on a leaf area basis, while the large-seeded morphotype had a higher rate on a leaf mass basis. Although allocation patterns between morphotypes varied in a way consistent with known interspecific differences between ‘sun’ and ‘shade’ plants, relative growth rates (RGR) of the morphotypes were similar across different light conditions suggesting that factors other than light, such as water uptake efficiency, soil nutrient requirements, and perhaps seed dispersal characters may explain the habitat partitioning of morphotypes.

Key Words: allocation patterns, Barro Colorado Nature Monument, habitat partitioning, seed size, *Trema micrantha*

INTRODUCTION

Variation in habitat requirements may be one of the principal factors explaining the maintenance of species diversity. In plant communities, most evidence suggests that patterns of distribution and abundance are determined early in life history (Harms *et al.* 2000, Hubbell *et al.* 1999, Silman 1996, Uhl *et al.* 1988, Webb & Peart 1999), and that therefore seed and seedling characteristics are particularly important determinants of regeneration requirements (Davies 1998, Grubb 1977). Studies of co-existing tropical pioneers have revealed strong evidence for habitat partitioning among species with broadly similar regeneration needs (high light conditions resulting from canopy openings). Habitat partitioning among pioneers is manifested as variable recruitment among microsites within gaps (Brandani *et al.* 1988, Orians 1982, Riera 1985), or along a gap size gradient (Brokaw 1985a,

b. 1987; Denslow 1980, 1987) depending on the abundance of species in the forest (Kennedy & Swaine 1992). The mechanistic basis for habitat partitioning among ecologically similar species, however, remains poorly understood.

In this study we examine the seed and seedling ecology of two distinct morphotypes of the fast-growing pioneer tree *Trema micrantha* (L.) Blume at the Barro Colorado Nature Monument (BCNM) in Central Panama. Initial observations indicated that these two morphotypes have different habitat requirements. One morphotype is found on the shoreline of the Panama Canal in very high light conditions and growing on exposed mineral soil on landslides. The other morphotype predominates in treefall gaps in the interior of both young and old secondary forest. We predict that these differences in habitat requirements may be associated with different sets of early life-history traits and morphological and physiological seedling characters. Preliminary work (Parrish and Garwood, unpubl. data) using cpDNA sequences, allozymes and morphology suggests that the small-seeded morphotype represents a previously unrecognized species of *Trema*.

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Differences in dispersal requirements to landslides and treefall gaps may influence seed characteristics. Recruitment in gaps on BCNM occurs primarily from the soil seed bank (e.g. Dalling *et al.* 1997, 1998; Dalling & Hubbell, unpubl. data), selecting for seed dormancy, seed persistence and germination cued by canopy disturbance. In contrast, landslides have greatly impoverished seed banks (Dalling 1992, Guariguata 1990). Successful recruitment on landslides may therefore depend on effective dispersal and rapid seed germination.

Differences in the soil conditions, exposure to wind, and light availability between treefall gaps and landslides may also affect allocation patterns, photosynthetic rates and growth rates of pioneer seedlings (Cordero 1999, Fetcher *et al.* 1996). To test the extent to which variation in seed and seedling characteristics of *Trema* morphotypes might explain differences in their distribution, we compared seed germination patterns in a growing house, and seedling growth and allocation patterns in a pot experiment under a range of light conditions simulating canopy openings of different sizes.

METHODS

Site and study species

This study was carried out in a seasonally moist lowland tropical forest on Barro Colorado Nature Monument (BCNM), in Central Panama (9°10'N, 70°51'W). Rainfall averages 2600 mm y⁻¹, with a pronounced dry season from January until April (Rand & Rand 1982). The flora and vegetation have been described by Croat (1978) and by Foster & Brokaw (1982). Geology and hydrology have been described by Dietrich *et al.* (1982).

Trema micrantha is a pioneer species widely distributed through the neotropics and subtropics from Florida to northern Argentina, and grows in a variety of habitat types, ranging from dry forest to wet and montane forest up to 2500 m in elevation (M. Nee and N. Garwood, pers. comm.). *Trema* fruits all year round and produces single-seeded fruits from axillary inflorescences. Fruits are drupes consisting of a hard endocarp surrounded by fleshy orange mesocarp tissue. At BCNM, *Trema* seeds are primarily bird-dispersed.

Trema recruits from soil seed banks after canopy disturbances and is often abundant in large treefall gaps and openings created by logging or following agricultural abandonment (Brokaw 1987, Uhl *et al.* 1981, 1982). *Trema micrantha* is morphologically highly variable. No varieties or subspecies are currently recognized across most of its range, except in Veracruz, Mexico, where two varieties var. *micrantha* and var. *floridana* (Britt.) Standl. & Steyerf. are distinguished based on leaf shape and pubescence (Nee 1984).

In central Panama we recognize two morphotypes of

Table 1. General characteristics of the two morphotypes of *Trema micrantha* at BCNM. Reproductive dbh is the smallest-sized individual observed in fruit.

	Large-seeded	Small-seeded
Fruit mass (mg)	16 (± 2.37)	8.6 (± 0.40)
Endocarp mass (mg) ¹	3.83 (± 0.22)	1.38 (± 0.13)
Mesocarp mass ^{1,2} (%)	74 (± 0.05)	84 (± 0.01)
Endocarp colour	Black	Brown
Endocarp surface	Sculptured	Smooth
Distribution	Forest interior	Lake shore
Reproductive dbh (cm)	< 1	> 6

¹Air dried mass (± 1 SE); n = 50 seeds from each of 5 trees.

²Mesocarp as per cent total fresh fruit mass (± 1 SE).

Trema based on differences in seed size, and by the colour and sculpturing of the endocarp (Table 1). Henceforth we refer to these as 'large'- and 'small'-seeded morphotypes. Although morphotypic variation in endocarp characteristics occurs throughout the range of *Trema micrantha* (N. Garwood, unpubl. data), it has not been used as a taxonomic character (M. Nee, pers. comm.). After collecting seeds from > 100 trees from across Panama we have not encountered intermediate forms between the morphotypes we describe. Appropriate tests of compatibility between morphotypes, however, have not yet been made.

Local distribution of *Trema* morphotypes at BCNM

Preliminary observations suggested that morphotypes of *Trema* differ in local distribution. We therefore carried out a census of *Trema* abundance and distribution by marking trees visible from trails on Barro Colorado Island (BCI), and by boat from the lakeshore of BCI and adjacent islands and peninsulas of BCNM. Differences in seed characteristics provided the clearest distinction between the two morphotypes, with consistent differences in seed size, endocarp coloration and sculpturing (Table 1). Using these differences, we could only determine the morphotype of each tree by either collecting ripe fruits, or in the case of large, isolated non-reproductive trees in the forest interior, by collecting and sieving seeds out of soil samples taken from directly beneath the tree crown.

Seed mass and seed germination characteristics

Fresh fruit, endocarp and mesocarp masses were measured from 50 fruits collected from each of five trees per morphotype. Additional ripe fruits (between 500–930) were obtained from three trees of each morphotype and seeds were sown onto germination flats containing 1:2 mixture of sand and sieved forest soil (free of additional *Trema* seeds). Germination flats were placed in 50% full sun in a growing house, and watered daily for 20 wk. For the large-seeded morphotype we also determined the germination rate for 10 wk of seeds in the soil seed bank, by collecting two 500-ml (0–3 cm depth) soil samples

from below the crown of each of two isolated large trees. Samples were spread out on a 1-cm-deep layer of sand in germination flats at the same conditions.

Seedling growth and allocation patterns

A pot experiment simulating gaps of different sizes was used to determine whether the two morphotypes show different growth and allocation responses to light. Simulated gaps were created by suspending tree pots within growing frames aligned in a north–south direction. The frames were draped with one layer of black plastic neutral shade cloth (70% light interception), and one layer of a dye-impregnated energy film (Gold Point ST7 SLT-60; R:FR transmittance = 0.15), used both to reduce total irradiance incident on the plants and to reduce the red:far red light ratio to simulate transmission through a forest canopy. Different light treatments were created by varying the width of a central open aperture in the roof of the bench, which exposed seedlings to variable periods of direct radiation (range 4.8–26.2 mol m⁻² d⁻¹ maximal photosynthetically active radiation (PAR) on clear days). Assuming a circular gap, and a 30-m-tall canopy, we calculated that our six light treatments correspond to gaps of 25, 50, 100, 200, 400 and 800 m², respectively. Additional details on the construction of benches and the irradiance regime are provided in Dalling *et al.* (1999).

Seeds from three trees of each morphotype were germinated in a greenhouse and seedlings were grown under 50% full sun until they had produced three true leaves. An initial harvest was made at this time and remaining seedlings were transplanted singly into 8-litre pots containing a 70:30 mixture of sieved forest soil and sand. Two seedlings of each morphotype were placed in each of four replicate benches of each of the six light treatments. Plants received natural rainfall, supplemented by hand watering during dry periods (> 2 d without rain). Plant pots remained at ambient temperatures (28–32 °C) throughout the day, as air could circulate freely from the base of the benches up through the central aperture. Plants were harvested 68 d (small-seeded morphotype) and 60 d (large-seeded morphotype) after transplanting, when the largest plants reached approximately 200 cm² of leaf area. Relative growth rate (RGR; dry weight increase per unit of biomass per unit of time) was calculated as the slope of the relationship between the natural log of whole-plant biomass and time between transplantation and harvest for each morphotype in each gap treatment. Unit leaf rate (ULR; increase in plant dry mass per unit of leaf area and unit of time) was calculated according to the following equation:

$$\text{ULR} = ((W_f - W_i)/(t)) / ((A_f - A_i)/(\ln A_f - \ln A_i))$$

Where W_f and W_i are the final and initial dry mass (g), respectively, A_f and A_i are the final and initial leaf area

(m²), respectively, and t is the duration of the experiment (d). Specific Leaf Area (SLA; leaf area per unit of leaf mass), Leaf Area Ratio (LAR; leaf area per unit of whole plant mass), Leaf Weight Ratio (LWR; leaf weight per unit of whole plant mass) and Root Weight Ratio (RWR; root weight per unit of whole plant mass) were calculated from the final harvest data. Although SLA may be influenced by structural characteristics other than leaf thickness, we assume here that variation in SLA within and between these two morphotypes is largely due to differences in leaf thickness.

Photosynthetic characteristics of the two morphotypes

To measure the photosynthetic characteristics of the morphotypes, we conducted a separate experiment. Seeds were germinated at 50% full sun and grown in a greenhouse in two treatments; partial shade (maximum of 400 μmol m⁻² s⁻¹ PAR), and sun conditions (maximum of 1500 μmol m⁻² s⁻¹ PAR). Light-saturated photosynthetic rates (A_{max}) were measured 18 wk post-germination using an infra-red gas analyser (Model CI-301, CID Inc, Vancouver WA, USA). Measurements were conducted in a closed system and maximum photosynthesis was measured utilizing the range at which CO₂ decreases in the system and the leaf equilibrates. Leaves were harvested immediately after measurement, leaf area was measured with a leaf area meter, and Specific Leaf Area was calculated from harvest data.

Data analysis

We tested for differences in endocarp mass and proportional mesocarp mass between morphotypes using a single-factor analysis of variance (ANOVA) performed on the mean endocarp and fruit mass for each parent tree. The proportion of total fruit mass that corresponded to mesocarp was arcsine transformed prior to analysis. We used a one-way analysis of variance (ANOVA) to test for differences between sun and shade conditions performed on the mean values of SLA and net CO₂ assimilation rates (A_{max}) between morphotypes. We also performed a Tukey's post-hoc probability test for making pairwise comparison among means of the different groups for sun and shade conditions of the different morphotypes. Effects of gap size and morphotype on allocational patterns and growth rates were analysed using a split-plot ANOVA with the morphotype effect nested within the plot term (Multivariate General Linear Hypothesis procedure, SYSTAT 5.2) (Wilkinson *et al.* 1992). Analyses were performed using the means of the two seedlings of each morphotype grown in each simulated gap. Regressions were performed on the mean values of seedling attributes against log (gap size).

RESULTS

Distribution and phenology of *Trema* morphotypes at BCNM

The two *Trema* morphotypes showed clear differences in their local distribution at BCNM. We found 37 *Trema* trees in the forest interior of BCI, of which 29 either bore ripe fruit or had high densities of seeds in the soil beneath their crowns. All 29 trees were of the large-seeded morphotype. In contrast, 29 out of 30 fruiting individuals visited on the lakeshore around BCNM belonged to the small-seeded morphotype. Individuals of both morphotypes could be found in fruit throughout the year, however, the diameter size at which individuals become reproductive appears to be smaller for the large-seeded morphotype (Table 1).

Seed mass and seed germination

Morphotypes differed significantly in their endocarp masses ($df = 1,8$; $F = 93.0$; $P < 0.001$; Table 1); the endocarp mass of the large-seeded morphotype was almost three times greater than that of the small-seeded morphotype. The small-seeded morphotype, however, tended to have a proportionately higher investment of total fresh fruit mass in mesocarp tissue compared with the large-seeded morphotype ($df = 1,8$; $F = 5.1$; $P = 0.06$; Table 1).

Fresh seeds of the small-seeded morphotype mostly germinated within 10 wk, however, the total proportion of seeds germinating varied between 27 and 70% (Table 2). In contrast, fresh seeds of only one of the three parent trees of the large-seeded morphotype showed appreciable seed germination over the 20-wk period, reaching peak germination 16 wk after sowing (Table 2). The poor germination of fresh seeds of the large-seeded morphotype may be indicative of innate seed dormancy (*sensu* Harper 1977) and perhaps deep physiological dormancy (*sensu* Baskin & Baskin 1998), since seeds sieved from the soil

Table 2. Seed germination of the two morphotypes of *Trema micrantha* at BCNM. Seeds of three trees of the small-seeded morphotype: S1, S2, S3. Seeds of three trees of the large-seeded morphotype: L1, L2, L3.

	Number of seeds germinated	Total germination (%)	Maximum germination (wk)
S1 (n = 930)	433	46.56	9
S2 (n = 930)	649	69.78	10
S3 (n = 915)	251	27.43	9
L1 (n = 525)	251	47.81	16
L2 (n = 500)	2	0.40	0
L3 (n = 525)	2	0.38	0
soil 1 (n = ?) ¹	79	not determined	4
soil 2 (n = ?) ¹	152	not determined	4

¹Soil samples collected under the crown of isolated large-seeded morphotype trees.

Number of seeds per samples was not determined.

reached a peak in germination rate after only 4 wk (Table 2).

Seedling growth in simulated gaps

Both morphotypes of *Trema* showed strong plastic responses in growth and allocation to differences in the size of the simulated gaps (Figure 1). In common with other pioneer species we have examined (Dalling *et al.* 1999, 2001), plants responded most strongly in terms of allocation patterns within leaves (SLA and LAR; Figures 1a, b; Table 3) rather than allocation to roots vs. shoots (LWR and RWR; Figures 1c, d; Table 3). The small-seeded morphotype had both lower SLA (Figure 1a) and greater responsiveness of SLA to variation in light availability (gap \times morphotype interaction; Table 3) than did the large-seeded morphotype. In contrast, the large-seeded morphotype had a higher LAR (Figure 1b) despite a similar biomass allocation to leaf tissue (LWR not significantly different; Table 3). The small-seeded morphotype had a higher growth rate per unit leaf area (ULR; Figure 1e; Table 3). However, overall RGR between the two morphotypes was not significantly different (Figure 1f; Table 3).

Photosynthetic carbon gain

The separate study of light effects on leaf structure and photosynthesis gave results that were consistent with findings of the growth analyses of both morphotypes across a light gradient. Specific leaf area (SLA) was consistently higher in the large-seeded morphotype under conditions of sun and shade. Both morphotypes showed a decrease in SLA with an increase in irradiance (Table 4). The light-saturated photosynthetic rate on a leaf mass basis decreased with an increase in irradiance. The large-seeded morphotype had the highest A_{max} under both light treatments (Table 4). On a leaf area basis, A_{max} was similar for both morphotypes in low light and increased with irradiance for both morphotypes. This area-based increase in A_{max} was greatest for the small-seeded morphotype (Table 4).

DISCUSSION

Seed characteristics and the distribution of *Trema* morphotypes at BCNM

The two morphotypes show clear differences in their local distribution at BCNM. The small-seeded morphotype is found almost exclusively on landslides along the shore of Lake Gatun, whereas we only found the large-seeded morphotype growing in treefall gaps in old-growth and secondary forest on BCI. Apparent differences in morphotype distribution are unlikely to be the result of

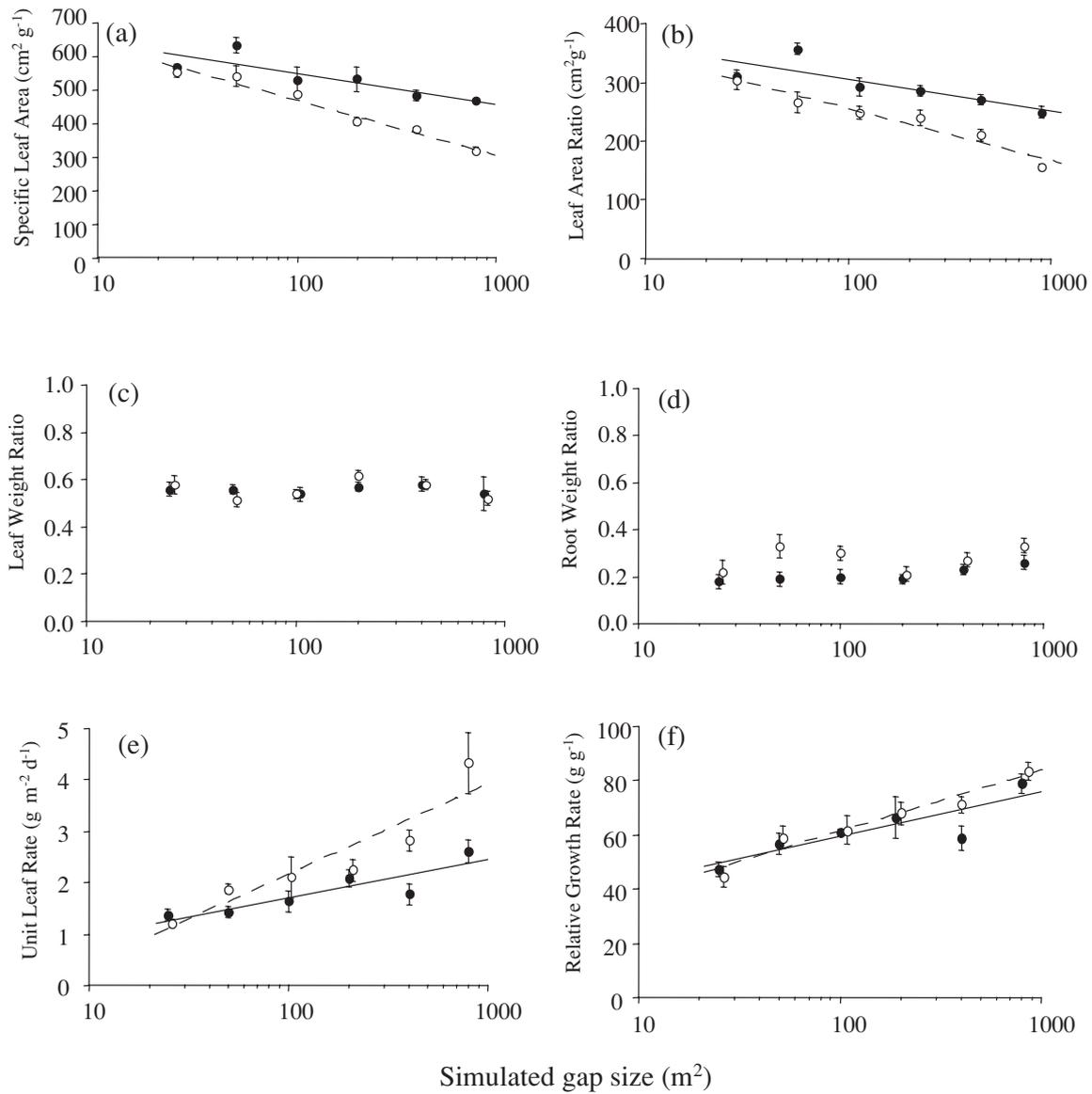


Figure 1. (a) Specific Leaf Area (SLA), (b) Leaf Area Ratio (LAR), (c) Leaf Weight Ratio (LWR), (d) Root Weight Ratio (RWR), (e) Unit Leaf Ratio (ULR), (f) Relative Growth Rate (RGR) of two morphotypes of *Trema micrantha* grown in each of six simulated gap sizes. Seedlings of the large-seeded morphotype: closed circles and solid regression line. Seedlings of the small-seeded morphotype: open circles and dashed regression line. Note: logarithmic scale on x -axis.

Table 3. F-values from split-plot ANOVA conducted on the mean values from two seedlings of each morphotype grown within each simulated gap. Degrees of freedom (df) for growth and morphology measurements: Morphotype = 1,13; Gap = 5,13; Morph \times Gap = 5,13. * $P < 0.05$, *** $P < 0.001$.

Attribute	Morph		Gap		Morph \times Gap	
Leaf Mass Ratio	0.5		1.8		1.1	
Root Mass Ratio	37.9	***	2.7		2.2	
Specific Leaf Area ($\text{cm}^2 \text{g}^{-1}$)	61.4	***	16.5	***	4.6	*
Leaf Area Ratio ($\text{cm}^2 \text{g}^{-1}$)	48.1	***	23.8	***	2.8	
Unit Leaf Rate ($\text{g m}^{-2} \text{d}^{-1}$)	17.3	***	40.9	***	2.3	
Relative Growth Rate ($\text{g g}^{-1} \text{d}^{-1}$)	1.8		16.4	***	0.6	

Table 4. Specific Leaf Area (SLA) and net CO₂ assimilation rates (A_{\max}) of *Trema* seedlings grown for 18 wk in high and low light. Same superscript letters indicates no significant differences between groups ($P < 0.05$).

	Large-seeded morphotype		Small-seeded morphotype	
	Sun	Shade	Sun	Shade
SLA (cm ² g ⁻¹)	352.1 ± 19.1 ^a	709.2 ± 35.3 ^b	223.7 ± 9.6 ^c	561.8 ± 47.3 ^d
A_{\max} (nmol CO ₂ g ⁻¹ s ⁻¹)	341.2 ± 68.4 ^a	367.1 ± 29.9 ^b	265.7 ± 30.4 ^c	309.6 ± 37.6 ^a
A_{\max} (μmol CO ₂ m ⁻² s ⁻¹)	8.7 ± 1.9 ^a	5.2 ± 0.4 ^b	11.9 ± 1.3 ^c	5.5 ± 0.6 ^b

phenotypic plasticity. Recent analysis of chloroplast DNA sequences indicates consistent and substantial sequence differences between morphotypes similar in magnitude to those between *Trema micrantha* and the long-recognized Caribbean species *Trema lamarckiana* (Roem. & Schult.) Blume (Parrish and Garwood, unpubl. data).

As yet, we lack information on the reproductive allocation and frugivore visitation rates to these morphotypes. However, we might speculate that a smaller endocarp mass might provide a dispersal advantage through higher fecundity (Fenner 1985, Salisbury 1973, Westoby *et al.* 1992). This may provide greater opportunities for the small-seeded morphotype to colonize infrequent landslides that lack a soil seed bank. Dispersal limitation may therefore potentially help explain the absence of the large-seeded morphotype on landslides, but seems unlikely to explain the absence of the small-seeded morphotype from nearby treefall gaps.

Seed germination

The different germination characteristics of the two morphotypes may also be associated with differences in recruitment sites. The poor germination of fresh seeds of the large-seeded morphotype as compared with seeds sieved from the soil indicates deep dormancy. Vázquez-Yanes & Smith (1977) found that the seeds of *Trema guineensis* (Schum. & Thonn.) Ficalho from the Ivory Coast required 6 mo of storage at room temperature to reach maximum seed germination, with only 1% seed germination after 1 mo. Coombe (1960), however, found that intermittent germination of *Trema guineensis* seeds began in about 6 wk. Dalling *et al.* (1997) found that both morphotypes are capable of long-term seed dormancy (> 1 y) and suggested that physical dormancy found in some pioneers on BCNM may result from hard seed coats that protect seeds against attack from pathogens and seed predators active at the soil surface. Attempts, however, to induce germination of fresh seeds of the large-seeded morphotype, using either hot-water treatments or acid scarification, have been unsuccessful (K. Silvera, unpubl. data). These results suggest physiological rather than physical dormancy (*sensu* Baskin & Baskin 1998). Vázquez-Yanes & Smith (1977) found evidence for the presence of an endogenous germination inhibitor in the seeds

of *Trema guineensis*. This inhibitor may also be present in the seeds of the large-seeded morphotype of *Trema micrantha*.

Seedling growth and allocation patterns

Overall we find both convergence and divergence in how the two morphotypes responded to contrasting light environments. Morphotypes were similar in overall proportional above- and below-ground biomass allocation, but differed in leaf-level allocation patterns. The small-seeded morphotype produced thicker leaves (lower SLA), and in consequence a lower LAR than the large-seeded morphotype. Low-SLA leaves presumably contained more photosynthetic tissue per unit leaf area, resulting in a higher per area maximal carbon assimilation rate in the sun, and a higher ULR. In contrast, the large-seeded morphotype produced the thinnest (highest SLA) leaves among 13 pioneer species on BCNM (J. Dalling, unpublished data). High SLA, high LAR and high carbon assimilation rate on a per unit leaf mass basis resulted in seedling growth rates (RGR) that almost exactly matched those of the small-seeded morphotype.

These differences in leaf morphology between morphotypes provide an interesting parallel with interspecific variation in morphological traits exhibited by early successional 'sun species' and late-successional 'shade species' (Foster & Janson 1985, Ng 1980, Osunkoya *et al.* 1994, Popma *et al.* 1992, Strauss-Debenedetti & Bazzaz 1991). Differences in SLA for plants in high- and low-light habitats are thought to represent adaptive adjustments in leaf morphology for maximizing light interception in the shade and minimizing water loss in the sun (Lambers *et al.* 1998, Larcher 1983). Indeed, our findings for differences between the two morphotypes in distribution, seed size, leaf morphology, photosynthetic plasticity and the components of relative growth rate are all consistent with the notion that the large-seeded morphotype represents a more shade-adapted later-successional ecotype, while the small-seeded morphotype is better adapted to a high-light, early successional growth habitat. These two morphotypes, however, represent one extreme in the continuum of shade tolerance; the large-seeded *Trema* morphotype has among the highest growth rates of any tree species at BCNM and is known to require large gaps for

successful regeneration (Brokaw 1987, Condit *et al.* 1983).

Alternative axes of variation among morphotypes

Habitat partitioning by *Trema* morphotypes may result from variation in seedling traits that were not considered in this study. Differences in soil fertility between landslides and treefall gaps may strongly influence recruitment success if morphotypes differ in their tolerance to low nutrient supply. Large treefall gaps may have relatively high nutrient availability because of reduced root competition and high initial litter inputs (Denslow *et al.* 1998). Landslide soils, by contrast, lack organic matter and tend to be nitrogen deficient (Dalling & Tanner 1995, Guariguata 1990). Clear differences have already been reported in nutrient requirements of old world *Trema* species. *Trema orientalis* (Blume) Linn. in India is reported to be nodulated by nitrogen-fixing rhizobia and grows rapidly on soils deficient of nitrogen (Samantaray *et al.* 1995), whereas *Trema tomentosa* (Roxb.) Hara is relatively sensitive to nutrient supply (Turner 1991). Future research will determine whether similar differences exist among morphotypes of *Trema micrantha*.

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