

Interactions of gap size and herbivory on establishment, growth and survival of three species of neotropical pioneer trees

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Summary

1 The difference in gap size requirements observed for neotropical pioneer species is a classic example of habitat partitioning among tropical tree species. Previous research has shown that the three species *Miconia argentea*, *Cecropia insignis* and *Trema micrantha* differ in the minimum gap size that they occupy as adult plants in semi-deciduous tropical forest in Panamá. Here we test whether these differences result from variation in seed germination and seedling establishment requirements, or from differences in susceptibility to herbivores.

2 We planted seeds of *Miconia argentea* and *Trema micrantha* into artificially created small (25 m²), medium (64 m²) and large (225 m²) gaps in secondary forest, and transplanted seedlings of all three species into small and large gaps inside and outside mesh cages that excluded invertebrate herbivores.

3 *Miconia* seedlings emerged and established successfully across a broad range of gap sizes, and transplanted seedlings grew slowly but survived well in all gap sizes. By contrast, emergence and survival of *Trema* seedlings occurred only in the large gaps and transplants died in small gaps. Survival of *Cecropia* seedlings was intermediate between *Trema* and *Miconia* in the small gaps and growth was greater than either species in the large gaps.

4 Herbivore exclosures reduced foliar herbivory on all three species. The median lifespan of *Trema* seedlings in small gaps was reduced when the seedlings were exposed to herbivores, but survival of the other species was not affected by the exclosure treatment in either gap size. The growth of *Miconia* seedlings was lower outside exclosures in both gap sizes.

5 Differences in germination and establishment could generate the contrasting gap size distributions observed between *Miconia* and *Trema*, but they are partially offset by measured differences in seed bank density. However, patterns of seedling growth and survival reinforce differences among species at the establishment phase and provide a mechanism for the observed differences in gap size distribution at the sapling stage. ‘Cross-overs’ in species growth rates result in specialization to different environments and reduce their survival in unfavourable conditions. We found no evidence for a definitive influence of herbivory as a mechanism driving differences in gap size distribution among species.

Key-words: Barro Colorado Island, germination, niche partitioning, seedling, tropical forest regeneration

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Introduction

A prominent and long-established hypothesis for the maintenance of diversity in tropical forests is that trees are narrowly specialized along gradients of resource availability correlated with gap size (Denslow 1980). However, surprisingly little work has been done to test this hypothesis (Hubbell *et al.* 1999), despite its continuing influence on tropical forest ecology (Denslow 1987; Brokaw & Busing 2000; Burslem & Swaine 2002; Wright 2002). In this study we use an experimental approach to examine the mechanistic basis for the classic example of species-specific gap size requirements described for pioneer species growing on Barro Colorado Island (BCI), Panamá by Brokaw (1987). A more complete understanding of how tree species potentially partition resources is needed to determine how particular life-history and physiological characteristics of trees might contribute to stabilizing coexistence. Brokaw (1987) observed regeneration of three pioneer species in natural treefall gaps on BCI. He found that *Trema micrantha* established only in the first year after gap creation, grew at a faster maximum rate than the other species and only persisted in the largest gaps (> 376 m²). *Miconia argentea*, in contrast, recruited up to 7 years after initial gap formation and had the lowest maximal growth rates but persisted in all gaps in excess of 102 m². *Cecropia insignis* was intermediate in every respect.

Differences in the distribution of these pioneers could arise during recruitment as a result of differential germination and establishment responses to environmental conditions. Pearson *et al.* (2002) showed that small-seeded (< 1.5 mg fresh mass) neotropical pioneer species including *Miconia* and *Cecropia* require light to stimulate germination, while germination of larger-seeded pioneers (with masses overlapping *Trema*) occurred in the dark, and in some cases required a high magnitude of temperature fluctuation. As light and temperature conditions vary substantially within and between gaps, and in relation to gap size (Brown 1993; Pearson *et al.* 2002), it is possible that the distribution of adult plants may be determined entirely by the availability of different germination cues and by subsequent early establishment success.

Alternatively, gap size preferences of pioneers may be primarily determined later in ontogeny. Interspecific variation in growth and survival under differing conditions of resource availability could drive habitat specialization. Species may differ in the irradiance that maximizes growth because the physiological and morphological traits that confer shade-tolerance (e.g. a low dark respiration rate and a low maximum assimilation rate) necessarily constrain a plant to slow growth at high irradiance relative to a high-light specialized species (Walter 1973; Bazzaz 1979; Givnish 1988; Walters & Reich 1996; Thomas & Bazzaz 1999). As a consequence of this constraint, the rank order of species' growth rates are predicted to change from low

to high light environments. This mechanism would be supported if *Trema* is unable to maintain a positive carbon balance at low irradiance because it has a high minimum respiration rate, whilst *Miconia* is able to grow at lower irradiance but is unable to increase its growth rate sufficiently to be compete successfully with its neighbours at very high irradiance.

Interactions with herbivores may provide an additional mechanistic explanation for differences among species in their gap size differentiation. Plants with low maximum growth rates are known to invest more resources in defence and possess less palatable leaves and higher concentrations of chemical defences than faster growing species (Coley *et al.* 1985). It is argued that a slow-growing plant is unable to sustain the same rate of tissue loss to herbivores as a plant growing quickly because its potential for tissue replacement is constrained by its low assimilation rate (Coley *et al.* 1985). Selection for increased concentrations of defences in slow-growing species generates the prediction that the faster-growing species should be more susceptible to herbivore attack, especially in lower light environments where there is a lower potential for investment in carbon-based defences and where low resource availability constrains tissue replacement (Shure & Wilson 1993).

We test two predictions that will allow us to distinguish among the various hypotheses considered above. First, we use a seed addition experiment to test whether emergence and establishment of one of the small gap species (*Miconia argentea*) occurs successfully in smaller gaps than the large gap species (*Trema micrantha*). Secondly, for all three species, we use a seedling transplant experiment combined with herbivore enclosure treatments to test whether species distributions in relation to gap size are determined by the greater susceptibility to herbivory of the seedlings of fast-growing species, leading to high rates of mortality for these species in small gaps.

Materials and methods

STUDY SITE AND SPECIES

The study was conducted on the Buena Vista (BV) peninsula within the Barro Colorado Nature Monument (BCNM) in the Republic of Panamá, Central America. The BCNM has a mean annual rainfall of 2700 mm and a pronounced 4-month dry season from January to April (Rand & Rand 1982). The primary forest vegetation is semi-deciduous tropical lowland rain forest (Croft 1978). Buena Vista peninsula is an area of 40-year-old secondary forest contiguous with the Soberania National Park. Average canopy height on BV is 20 m, with emergent individuals exceeding this height. The canopy is dominated by a diverse assemblage of pioneer tree species, and has a high abundance of palms.

The three study species (*Miconia argentea*, *Cecropia insignis* and *Trema micrantha*) are pioneers *sensu* Swaine

Table 1 Mean seed mass (mg), minimum gap size for sapling survival (m^2), and the toughness (N) and concentrations of N (% dry mass) and phenols (mg g^{-1} dry mass) of young and old leaves of *Miconia argentea*, *Cecropia insignis* and *Trema micrantha* growing on Barro Colorado Island, Panamá

	Seed mass* (mg)	Minimum gap size for survival† (m^2)	Leaf age	Toughness‡ (N)	N‡ (% dry mass)	Phenols‡ (mg g^{-1} dry mass)
<i>Miconia argentea</i>	0.04	> 102	Young	3.14	2.07	77.5
			Mature	3.84	1.67	31.2
<i>Cecropia insignis</i>	0.62	> 215	Young	4.53	2.41	130.8
			Mature	5.79	2.08	85.6
<i>Trema micrantha</i>	3.90	> 376	Young	2.17	3.09	101.7
			Mature	2.51	2.89	56.0

*Pearson *et al.* (2002); †Brokaw (1987); ‡Coley (1983a).

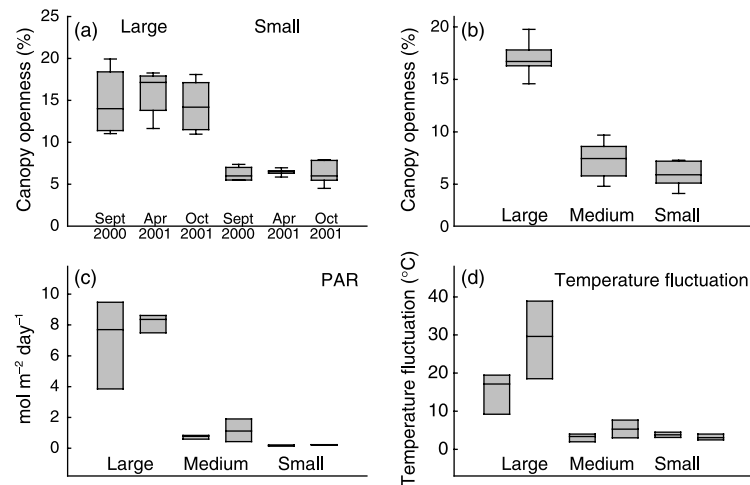


Fig. 1 Box plots of (a) canopy openness in the centres of gaps of the two sizes used in the seedling study for September 2000 (wet season), April 2001 (dry season) and October 2001 (wet season), (b) canopy openness at the edges of gaps of the three sizes used in the seed addition study, (c) PAR calculated across 96 hours in the edges of two gaps of each of the three sizes, and (d) amplitude of diel temperature fluctuation calculated across 96 hours in the edges of two gaps of each of the three sizes. Boundary of the boxes indicates the 25th and 75th percentiles, the line dissecting the box marks the median and the whiskers above and below the boxes mark the 10th and 90th percentiles.

& Whitmore (1988) and are described in Table 1. They are very common as adults and in the seed bank in BCNM, except *Cecropia insignis*, which is the dominant pioneer species on Barro Colorado Island but rare or absent on BV (other *Cecropia* species are common on BV). The distributions of these species in relation to canopy gap size were examined extensively on Barro Colorado Island by Brokaw (1987), who showed that the minimum gap size for sapling survival increased along the series *Miconia* < *Cecropia* < *Trema* (Table 1). Throughout the paper the species will be referred to by their genus names.

GAP CREATION

In April 2000 22 artificial gaps were created within a plateau area of approximately 12 ha on the western half of BV. Six gaps measured 15×15 m on the ground, five measured 8×8 m and 11 measured 5×5 m. Individual gaps were spaced between 20 and 50 m apart. All gaps were originally covered by intact secondary forest. Gaps were created by cutting down and removing all standing trees, shrubs, saplings and seedlings. Resprouts were cut back after 1, 3, 5, 8 and 12 months.

The light environment in gaps was characterized using hemispherical photographs at 1 m above ground level in September 2000, April 2001 and October 2001 in the centre of each gap using a Nikon Coolpix 950 digital camera and a 8-mm fish-eye lens (Nikon, New York, USA). Hemispherical photographs were analysed to obtain canopy openness and global site factors (Hemiview, Delta-T Devices, Cambridge, UK). Global site factor in the large gaps ranged from 0.27 to 0.53 (mean 0.36) and in the small gaps from 0.10 to 0.17 (mean 0.13). Canopy openness did not change significantly with time (Fig. 1a), which suggests that the initial differences between gap size classes were maintained; median canopy openness was elevated at the April 2001 measurement across all gap sizes because some large deciduous canopy trees had lost their leaves during the dry season.

Mean daily photosynthetically active radiation (PAR) was measured over 5 days in each of four large and small gaps using PAR sensors (SKP 215) attached to data loggers (Skye Instruments, Powys, UK) and compared with values for full daylight obtained from an additional sensor recording in a large clearing.

Mean PAR in the large gaps was $26.9\% \pm 5.0$ of full daylight PAR (mean \pm SEM) and in the small gaps $2.83\% \pm 0.94$ of full daylight PAR.

EFFECTS OF GAP SIZE ON SEEDLING EMERGENCE

For each of two species (*Miconia* and *Trema*) two plots of 48×72 cm were established on the edge of nine gaps (three of 15×15 m, three of 8×8 m and three of 5×5 m). *Cecropia* was not used in this study due to limited seed supply. Plots were located beneath the projected canopy gaps but were not in the centre of the gaps because these were occupied by other studies. The 54 plots were kept free of litter throughout the study period. Hemispherical photographs were taken above each gap-edge plot in October 2001 and analysed as above (Fig. 1). PAR and soil surface temperature (2 mm) were recorded over a 5-day period, in the centre of the array of plots, in six of the nine gaps (two of each size) using PAR sensors (SKP 215) and thermistors attached to data loggers (Skye Instruments, Powys, UK). Median canopy openness was highest for the large gaps and lowest for the small gaps, although the small and medium gaps overlapped (Fig. 1b). The PAR at ground level was lower for the small gaps than the medium gaps and greatest in the large gaps (Fig. 1c), although the mean diel amplitude of temperature fluctuation was elevated only for the large gaps (Fig. 1d).

Fresh seeds of *Trema* possess a dormancy mechanism, so soil seed bank samples were used instead. In September 2001 soil from 0 to 15 cm was collected from beneath three large adult *Trema* individuals (> 25 cm d.b.h.) and mixed thoroughly inside black plastic bags (to avoid exposure to light). One litre of this soil was added to the surface of two randomly selected plots per gap, gently pressed down and watered. One litre of soil gave a soil depth of approximately 3 mm across the plot, which results in a maximum burial depth for *Trema* seeds of 1.2 mm (seed diameter 1.8 mm). Similarly, 200 fresh seeds of *Miconia* were scattered on the soil surface of two different plots per gap and the plots watered with a fine spray. In addition three identical replicates of each of the *Trema* seed bank samples and 200 *Miconia* seed samples were put out on trays in a growing house on BCI to determine maximum potential germination under optimum conditions. The trays were watered daily and examined every 5 days until emergence had ceased.

All plots were examined for emerged seedlings of *Trema* and *Miconia* and mortality of previously emerged seedlings every 5 days for 10 weeks. Emerged seedlings were marked with coloured toothpicks, which were later removed if the seedling died. An unmanipulated control plot was established for each treatment plot in each gap and these were also monitored to determine natural emergence from freshly dispersed seeds or from the seed bank. Emergence in treatment plots was expressed as a percentage of total emergence in the

growing house minus the number that emerged in the unmanipulated control plots in the gaps.

EFFECTS OF SEED BANK DENSITY AND PROBABILITIES OF EMERGENCE AND MORTALITY ON SEEDLING RECRUITMENT

Miconia and *Trema* differ by two orders of magnitude in seed mass and by one order of magnitude in seed bank density on the BV peninsula (Table 1, Dalling & Hubbell 2002). Therefore, differences in seed germination and seedling mortality in different gap sizes may have little impact on seedling recruitment and gap size partitioning unless they are of sufficient magnitude to offset the much greater initial abundance of *Miconia*. In order to evaluate this prediction, we simulated seed bank size and the density and mortality of emergents for each species in each gap size by: (a) selecting a random initial seed bank density from a normal distribution with a mean and variance identical to those observed for *Trema* and *Miconia* on BV by Dalling & Hubbell (2002); (b) generating an emergent density by reducing the initial seed bank density by a random emergence probability obtained from a normal distribution with the mean and variance observed in the experiment in the section above; and (c) generating seedling densities at 11 and 22 weeks post-emergence using an analogous procedure to (b) but based on the observed distribution of mortality rates over these intervals. We conducted 1000 simulations for each species per gap size combination and plotted the data to examine differences in density at each stage (initial post-emergence, and after 11 and 22 weeks of subsequent mortality) using the distributions of 1000 values.

EFFECTS OF GAP SIZE AND HERBIVORY ON SEEDLING GROWTH AND SURVIVAL

In July 2000, six seedlings of each of the three species (*Miconia*, *Cecropia* and *Trema*) were transplanted into six small (5×5 m) and six large (15×15 m) artificial gaps on BV peninsula. The seedlings had been grown, from seeds collected on BCI, for 6 months (*Miconia*), 4 months (*Cecropia*) or 2 months (*Trema*), but they all had approximately 10 cm^2 of leaf area at the time of transplantation. A random selection of three seedlings per species per gap was immediately enclosed in individual mesh cages (1×1 mm mesh size) of 40×40 cm and 45 cm height. Similar mesh enclosures used by Sagers & Coley (1995) have been shown to decrease herbivory on seedlings. A single layer of identical mesh was suspended horizontally 45 cm above all remaining seedlings in order to reduce the difference in light conditions between seedlings inside and outside enclosures (no significant difference, $P > 0.05$). The cages were replaced if they were damaged and were extended as the plants grew in height.

The plants were examined monthly for mortality and herbivory (see below). Leaf area was estimated

every second month from measurements of leaf length converted to areas using regression equations obtained from a sample of 50 leaves per species (r^2 for the one-parameter models varied from 0.992 to 0.997). Heights were measured to the apex every second month from February to August 2001 but only for seedlings of *Miconia* and *Cecropia*, as those of *Trema* had mostly died in small gaps. The amount and rate of herbivory was estimated every month. Three individuals per species per gap size treatment and exclosure treatment were selected at random and examined for total percentage leaf area missing (on the entire plant) using a clear plastic grid over the leaf (25 squares/cm²). A new selection of plants was made at each monthly census. Other signs of herbivory (boring, browsing, galls and scales) present anywhere on the plant were also noted at each census.

For *Cecropia* and *Trema* the experiment ended in August 2001 after 13 months growth (when the plants in the large gaps were too big to maintain enclosed), and for *Miconia* the experiment ended in October 2001 after 15 months.

STATISTICAL ANALYSES

Emergence, and the mortality of emergents, are binary response variables and were analysed using logistic regression with species, gap size and the interaction between species and gap size as predictor variables. Relative growth rates of leaf area (RGR_{LA}) were calculated as follows (Evans 1972): $RGR_{LA} = [\log_e(L_2) - \log_e(L_1)] / (t_2 - t_1)$, where L_2 and L_1 are leaf areas at time t_2 and t_1 , respectively. The time series for RGR_{LA} and percentage herbivory were partitioned into two intervals for analysis because of the high mortality of *Trema* seedlings. The first analysis (September 2000 to April 2001) included data for all three species, while the second analysis (April to August 2001) included the data for *Cecropia* and *Miconia* only. The time series for leaf area, RGR_{LA} and percentage herbivory were

analysed by repeated measures analyses of variance using the MANOVA procedure in MINITAB 12 (Minitab Inc., State College, PA, USA) and employing the Pillai Trace as the test statistic as recommended by Tabachnik & Fidell (2001). The effects of species, gap size and their interaction on RGR_{LA} were analysed using a nested MANOVA model (gaps nested within the gap size factor) (Tabachnik & Fiddell 2001). As plants assessed for standing amounts of herbivory were selected at random from all gaps of a particular size the gap factor was excluded from the MANOVA model for these analyses. The percentage herbivory values were transformed ($\log_e(1000x + 1)$) prior to analysis in order to normalize the distribution of residuals.

Rates of mortality were analysed by survival analysis to compare between gap sizes, species and exclosure treatments using the Wilcoxon Statistic implemented by the Life Tables function in SPSS 10.0 (SPSS Inc., Chicago, USA).

Results

EFFECTS OF GAP SIZE ON SEEDLING EMERGENCE AND MORTALITY

There was no emergence of *Trema* seedlings in the unmanipulated control plots that lacked seed addition regardless of gap size, while emergence of *Miconia* seedlings in these plots ranged from zero to four seedlings per plot and was unrelated to gap size. Emergence of seedlings in plots to which seeds had been added increased significantly with increasing gap size ($P < 0.001$), but the interaction between species and gap size was also significant ($P < 0.001$, Fig. 2a,b). The emergence of *Miconia* was $> 17\%$ across all gaps and did not differ significantly between the three gap size classes, while emergence of *Trema* was very low (3%) in the smallest gaps and increased with each increase in gap size class. The growing house replicates produced germination percentages equal to between 112

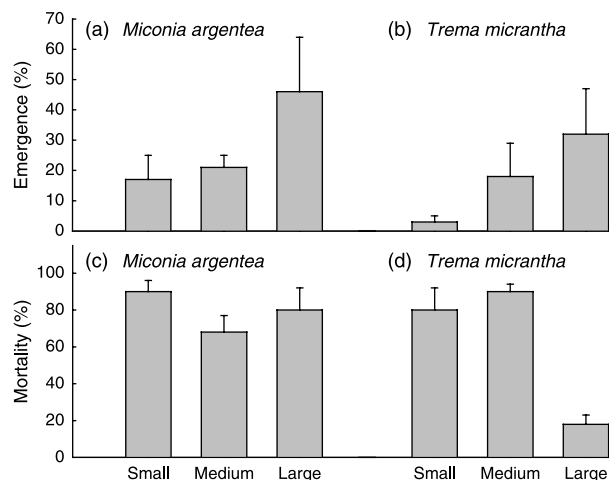


Fig. 2 Mean and standard error emergence (a,b) and seedling mortality after 10 weeks (c,d) of *Miconia* (a,c) and *Trema* (b,d) sown into small, medium and large gaps on Buena Vista Peninsula, Panamá.

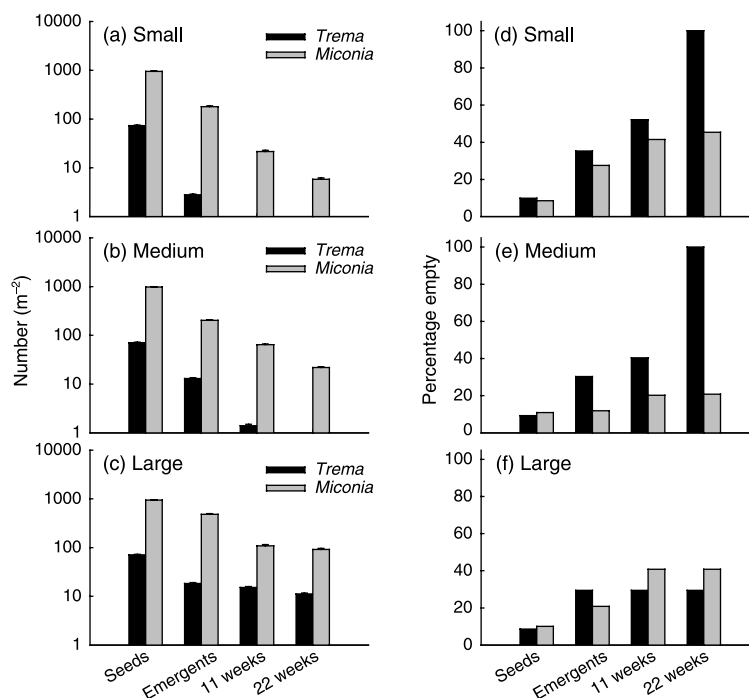


Fig. 3 Projected mean (and standard error) density (a–c) and percentage of sample plots with no individuals present (d–f) for *Trema* and *Miconia* in small (a,d), medium (b,e) and large (c,f) gaps for seeds in the seed bank, emergents, and seedlings after 11 and 22 weeks post-emergence. Values are derived from 1000 simulations based on observed seed bank densities (from Dalling & Hubbell 2002) modified by emergence and mortality probabilities derived from this study.

and 139% of the maximum values for emergence in the field for *Trema*, and between 226 and 252% for *Miconia*.

Mortality of emergents over 10 weeks was significantly lower in the largest gaps and in *Trema* compared with *Miconia* (Fig. 2c,d). However, the mortality of *Miconia* was high (68–90%) regardless of gap size, while high mortality of *Trema* (80–90%) occurred only in the small and medium sized gaps, and dropped to 18% in the large gaps (Fig. 2c,d).

Estimates of the density of emergent seedlings and of surviving seedlings after 11 and 22 weeks based on projections of actual seed bank density and observed probabilities of emergence and mortality emphasize the differences between the two species. In small gaps only a small proportion of the potential *Trema* in the seed bank would emerge and those that did emerge would die before 11 weeks had passed (Fig. 3a). In the largest gaps a very much greater proportion would emerge and very little mortality would occur, even up to 22 weeks post-emergence (Fig. 3c). In contrast, high numbers of *Miconia* would emerge across all light environments (Fig. 3) and, though proportional survival would be higher in larger gaps, individuals would persist through 22 weeks in the small gaps.

In all light environments, fewer than 50% of plots lacked *Miconia* seedlings, even after 22 weeks in all light environments. In contrast, no plots in small and medium gaps would contain *Trema* seedlings after 22 weeks. However, after the same interval *Trema*

seedlings would be absent from a smaller proportion of plots in the largest gaps than would *Miconia* seedlings (Fig. 3f), although *Miconia* would retain an absolute numerical advantage, reflecting its greater abundance in the soil seed bank.

EFFECTS OF GAP SIZE AND SPECIES ON HERBIVORY

Exclosures significantly reduced the amount of herbivory in both the small and the large gaps (Fig. 4, Table 2). Each of the three species showed a reduction in percentage of leaf area missing inside compared with outside exclosures, with a greater reduction in *Miconia* and *Trema* than in *Cecropia*. The effect of exclosures was greatest in the large gaps where growth rates were highest and mortality rates lowest.

Percentage leaf area missing was significantly greater in large than small gaps. However, species showed contrasting outcomes in relation to gap size (Fig. 4); *Miconia* showed evidence of greater herbivory in large than small gaps, and *Trema* and *Cecropia* the opposite.

During the experiment apical damage by shoot borers and browsers occurred in 50% of *Trema* plants outside the protection of exclosures, and was absent from the protected plants. Sixty-three per cent of the damaged plants died within 2 months. Similar damage to *Miconia* and *Cecropia* was absent during the study period. Other forms of herbivory (e.g. galls, scale insects) were too rare to identify patterns.

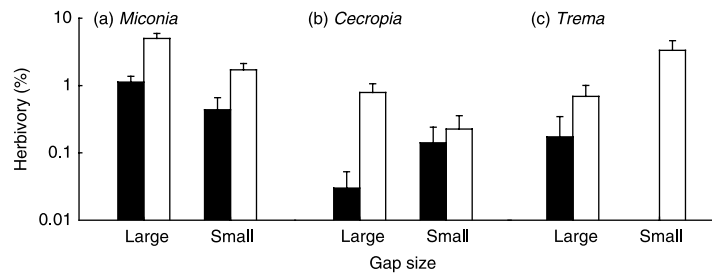


Fig. 4 Mean and standard error percentage herbivory for seedlings of (a) *Miconia*, (b) *Cecropia* and (c) *Trema* inside (closed bars) or outside (open bars) enclosures in large and small gaps. Herbivory values are the means of measurements from 12 months. There was no herbivory on *Trema* inside enclosures in the small gaps.

Table 2 Degrees of freedom, variance ratios (from Pillai statistic) and degrees of significance from multivariate analyses of variance to determine effects of treatments and their interactions on the standing herbivory (%) and the relative growth rates of leaf area (RGR_{LA}) for seedlings of three neotropical pioneers. Degree of significance indicated as follows: NS = not significant; *** $P = 0.001$; ** $P = 0.01$; * $P = 0.05$

	Total herbivory (%)						RGR_{LA} ($g\ g^{-1}\ day^{-1}$)					
	All species (September to April)			<i>Cecropia</i> and <i>Miconia</i> (April to October)			All species (September to April)			<i>Cecropia</i> and <i>Miconia</i> (April to October)		
	d.f.	<i>F</i>		d.f.	<i>F</i>		d.f.	<i>F</i>		d.f.	<i>FF</i>	
Enclosure	7,18	12.24	***	12,5	121	***	4116	0.918	NS	6,84	1.59	NS
Species	14,38	6.50	***	12,5	61.2	***	8234	11.5	***	6,84	18.2	***
Gap size	7,18	9.43	***	12,5	6.63	*	4116	62.7	***	6,84	79.8	***
Gap (gap size)	—	—	—	—	—	—	36 476	3.41	***	54 534	2.99	***
Enclosure \times gap size	7,18	3.73	**	12,5	13.3	**	4116	1.20	NS	6,84	0.761	NS
Species \times gap size	14,38	7.44	***	12,5	3.96	NS	8234	5.76	***	6,84	8.79	***
Enclosure \times species	8234	4.01	***	12,5	5.60	*	8234	1.03	NS	6,84	1.83	NS
Enclosure \times species \times gap size	8234	2.78	**	12,5	8.26	*	8234	2.06	*	6,84	2.59	*

EFFECTS OF GAP SIZE, ENCLOSURE AND SPECIES ON SEEDLING SURVIVAL AND GROWTH

Survival was significantly lower for all species in the small gaps than in the large gaps, but the relative decrease in survival differed among the three species (Fig. 5, Table 3). Relative to the other species survival of *Trema* was low in all sizes of gap regardless of enclosure treatment (large gaps, 61%; small gaps, 3%). Survival of *Cecropia* and *Miconia* was 30% and 75%, respectively, in small gaps but 94% (in both species) in large gaps (Fig. 5a,b). *Trema* was the only species to show a significant increase in survivorship in enclosures and the effect was only significant in the small gaps (Table 3). In the large gaps the survival of protected *Trema* plants was 72% and for unprotected plants survival was 50%, but this difference was not significant (Life Table, $P > 0.05$).

Mean leaf area in August 2001 (the last interval at which all species were censused) was an order of magnitude greater in the large gaps ($3511\ cm^2$), than in the small gaps ($136\ cm^2$). Protection from herbivores increased the leaf area of *Trema* in the large gaps and of *Miconia* in both large and small gaps, but had no significant effects on *Cecropia*. Univariate analyses of variance indicated that the significant effects of

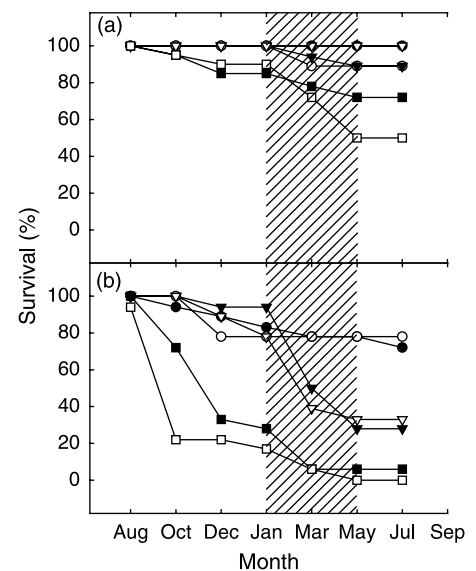


Fig. 5 Percentage survival over time in large (a) and small (b) gaps for seedlings of *Miconia* inside (●) or outside (○) enclosures, *Cecropia* inside (▼) or outside (▽) enclosures, and *Trema* inside (■) or outside (□) enclosures. Hashed box indicates dry season.

enclosure on leaf area development emerged very much earlier in *Trema* (3 months after transplantation) than in *Miconia* (13 months after transplantation) (Fig. 6).

Table 3 Median survival times (months) and degrees of significance for testing effects of exclosures in large and small gaps, gap size inside and outside exclosures and the difference between the species in large and small gaps. > 12 indicates that median survival time was greater than the 12-month duration of this experiment. Degree of significance indicated as follows: NS = not significant; ****P* < 0.001; ***P* < 0.01; **P* < 0.05

		Median survival time (months)		Effect of exclosure		Effect of gap size	
		Large	Small	Large	Small	Exclosure	Open
<i>Miconia argentea</i>	Exclosure	> 12	> 12	NS	NS	*	NS
	Open	> 12	> 12				
<i>Cecropia insignis</i>	Exclosure	> 12	10.0	NS	NS	***	***
	Open	> 12	8.71				
<i>Trema micrantha</i>	Exclosure	> 12	4.57	NS	*	***	***
	Open	> 12	2.62				
		Difference between species					
		<i>Miconia</i>	<i>Cecropia</i>	<i>Trema</i>			
<i>Miconia argentea</i>	Large		NS	***			
	Small		**	***			
<i>Cecropia insignis</i>	Large	NS		***			
	Small	**		***			
<i>Trema micrantha</i>	Large	***	***				
	Small	***	***				

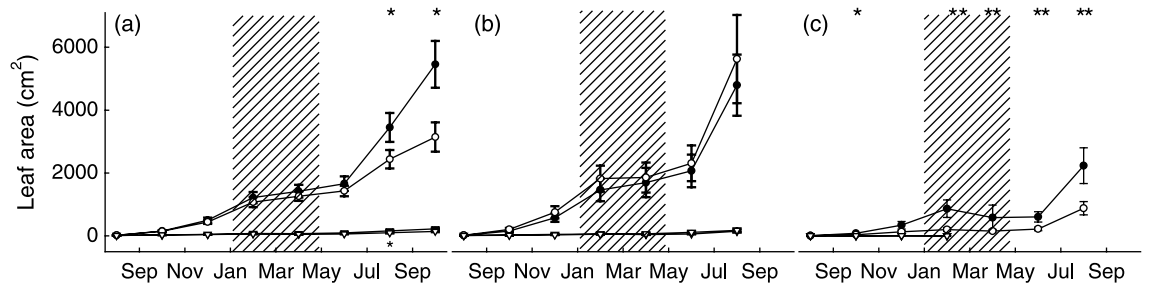


Fig. 6 Mean and standard error leaf area (cm²) for seedlings of (a) *Miconia*, (b) *Cecropia* and (c) *Trema* in large gaps inside (●) and outside exclosures (○) and in small gaps inside (▲) and outside exclosures (△). Hashed box indicates dry season, and degrees of significance from univariate analyses of variance comparing the effect of exclosure treatments at each census are indicated as follows: ***P* = 0.01; **P* = 0.05.

Relative growth rate of leaf area (RGR_{LA}) was significantly higher in large than small gaps (Fig. 7, Table 2). Although the main effect of exclosure was not significant in the MANOVA, there was a significant interaction between exclosure treatment, species and gap size. Protection from herbivores increased RGR_{LA} for *Miconia* and *Trema* seedlings (Fig. 7a); univariate analyses (not shown) suggested that the interaction between species and exclosure treatment was significant for the census interval April–June 2001 and that the exclosure treatment was significant for the census interval June–August 2001. Relative growth rates declined in the dry season but subsequently recovered (Fig. 7b).

There was no evidence that rank hierarchies of species' growth rates were maintained across gap sizes (Table 2, Fig. 8). For example, *Cecropia* had the highest RGR_{LA} in large gaps and *Miconia* had the highest RGR_{LA} in the small gaps regardless of exclosure treatment. *Trema* was unable to maintain positive growth rates in the small gaps and showed the steepest change in RGR_{LA} between small and large gaps. Protection

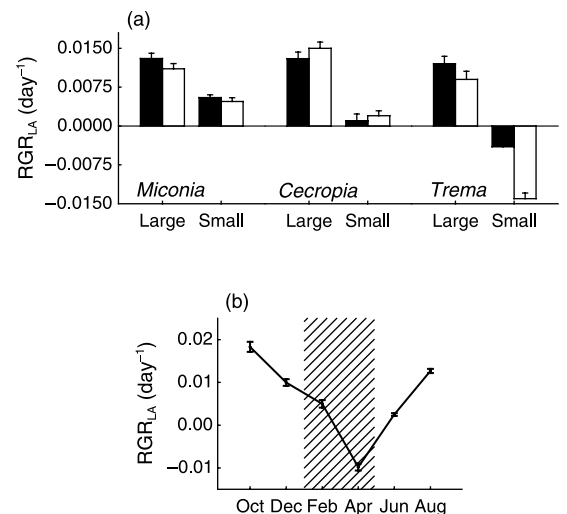


Fig. 7 Mean and standard error RGR_{LA} (g g⁻¹ day⁻¹) for seedlings of (a) *Miconia*, *Cecropia* and *Trema* inside (closed bars) or outside (open bars) exclosures in large and small gaps, and (b) RGR_{LA} averaged across species and gap size treatments through time. Hashed box indicates dry season.

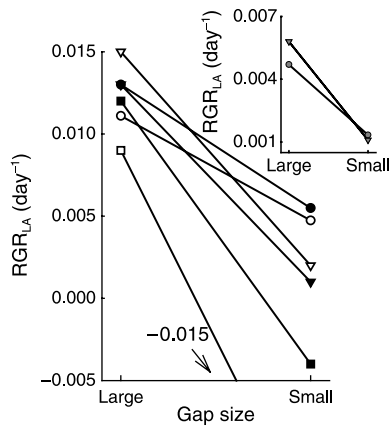


Fig. 8 Schematic illustration of the change in ranks of species RGR_{LA} across gap sizes for the growth interval July 2000 to August 2001. ● = exclosed *Miconia*, ○ = unexclosed *Miconia*, ▼ = exclosed *Cecropia*, ▽ = unexclosed *Cecropia*, ■ = exclosed *Trema*, □ = unexclosed *Trema* and (inset) change in rank of species RGR_{HT} across gap sizes for *Miconia* and *Cecropia* over the growth interval February to August 2001.

from herbivores allowed *Trema* to exceed the RGR_{LA} of unprotected *Miconia* plants in the large gaps. Comparisons of RGR_{HT} for *Cecropia* and *Miconia* over a shorter interval yielded a similar conclusion (Fig. 8 inset).

Discussion

EFFECTS OF GAP SIZE ON SEEDLING EMERGENCE AND EARLY SURVIVAL

The percentage of *Miconia* seeds that emerged was 2.7 times greater in the largest gaps than in the smallest gaps, while the equivalent factor for *Trema* was 10.7. Mortality of *Miconia* emergents was high regardless of light environment. In contrast, the survival of *Trema* was greatly enhanced (by > 60%) in the largest gaps vs. the other gap sizes. The sum of these processes would result in a greater abundance of *Miconia* seedlings than *Trema* seedlings regenerating in small gaps, as found by Brokaw (1987). Simulations demonstrated that whilst high seed bank densities would deliver higher numbers of *Miconia* seedlings across all light environments, higher survival of *Trema* than *Miconia* in high-light environments would result in a higher frequency of plots occupied by *Trema* seedlings after 22 weeks. These findings suggest that differences in emergence success, and in mortality of recent emergents, might contribute to the observed distributions of adult plants.

The basis for the difference in emergence between gap sizes might be that the two species respond differently in their germination to environmental conditions associated with gap formation. Pearson *et al.* (2002) showed that smaller-seeded (< 1.5 mg fresh mass) neotropical pioneer species (including *Miconia argentea*) require an irradiance cue to stimulate germination, whilst larger seeded pioneers (of a range of masses overlapping that of *Trema*) do not respond to irradiance but

do, in many cases, respond positively to a high magnitude of diel temperature fluctuation. Light can be used as a cue to gap presence across all scales of canopy openness, while temperature fluctuations sufficient to initiate high germination occur only in large gaps (Pearson *et al.* 2002).

de Souza & Válio (2001) showed that four photoblastic neotropical tree species germinated to a similar extent on a forest edge and in the understorey (like the *Miconia* in our study) and that germinants had a high mortality in low-light environments. We interpret these findings as showing that the lack of resources and the relatively thin seed coats of small-seeded species precludes their persistence in the seed bank and imposes selection for seeds to germinate rapidly when located at the soil surface (Pearson *et al.* 2003).

The contrasting distributions generated at the emergence phase may be reinforced by frequent superficial drought. Engelbrecht *et al.* (2001) showed that short dry spells during the wet season in central Panamá are sufficient to cause high mortality among the germinants of pioneer species. Very small-seeded species, such as *Miconia*, are particularly susceptible in large gaps where surface soils dry out quickly (B. Murray *et al.*, unpublished data), because the low root growth rates of small-seeded species are not sufficient to keep up with the drying front that descends the soil profile as a soil water deficit develops (C. Ballard *et al.*, unpublished data). Consequently, Dalling and Hubbell (2002) showed higher probabilities of seedling emergence and establishment with increased seed size for 15 neotropical pioneer species establishing from the seed bank.

The outcome of the processes described above is that a larger seed size promotes establishment in hotter and drier environments as well as greater precision in the timing of germination and emergence. The impact of the high mortality of *Miconia* across all conditions, which is a consequence of the lack of seed resources, is reduced by high seed production in this species. In five soil samples taken from between 0 and 6 cm on Buena Vista Peninsula, Dalling & Hubbell (2002) found an average of more than 900 *Miconia argentea* seeds m^{-2} , compared with only 70 seeds m^{-2} of *Trema micrantha*. Therefore, despite the very high mortality of *Miconia* emergents, significant numbers of seedlings will become established in all environments. This seed size/seed number contrast between *Miconia* and *Trema* provides an illustration of how the competition-colonization trade-off might promote species coexistence (Skellam 1951; Dalling & Hubbell 2002).

Projections of the density of emergents and seedlings at 11 and 22 weeks post-emergence based on actual seed bank densities supported the conclusion that *Trema* would be absent from low-light environments but persistent in large gaps. *Miconia* suffered high mortality in all environments but the very high initial densities permitted persistence in all conditions and numerical dominance over *Trema* at 22 weeks post-emergence. Therefore when actual seed bank densities

are considered, the partitioning of species according to gap size, described by Brokaw (1987), can only partially be explained by the very early processes of establishment and initial survival.

EFFECTS OF GAP SIZE AND HERBIVORY ON SEEDLING GROWTH AND SURVIVAL

Protecting seedlings inside mesh exclosures reduced the amount of herbivory and increased the leaf area and relative growth rates of seedlings of *Trema* and *Miconia*. Mortality rates were unaffected by the exclosure treatment in *Miconia* and *Cecropia*, but were greater for *Trema* seedlings outside exclosures, particularly in small gaps. However, very few *Trema* seedlings survived to the end of the experiment in small gaps in either treatment; the effect of exclosures was to decrease the rate of mortality. Marquis (1984) also showed that herbivory can directly decrease the growth rates of the tropical understorey species *Piper arieanianum*, while Sagers & Coley (1995) found that a reduction in herbivory led to an increase in growth rates of the understorey shrub species *Psychotria horizontalis*.

Herbivory rates for our focal species were also recorded by Coley (1983a). She found greater amounts of herbivory on *Trema* and *Cecropia* than on *Miconia*, in contrast to our observation of herbivory decreasing along the series *Miconia* > *Trema* > *Cecropia*. Potential explanations for this discrepancy lie in the differences in forest type sampled, temporal variation, or the contrasting methods used for estimating herbivory. However, it is unlikely that differences in forest type account for the contrasting outcomes, because Coley's (1983a) sample site (BCI) contains secondary forest similar to the forest on BV peninsula, and the invertebrate herbivore communities are likely to be very similar for these sites, which are separated by only 800 m (Coley 1983b). However, it is possible that interannual variation in herbivore densities or contrasting methods of expressing herbivory are important. Coley (1983a) and many subsequent authors have used repeat censuses of marked leaves to calculate a grazing rate per unit time as a measure of herbivory. This method requires the user to assume that leaves that are lost entirely between censuses have either been eaten by herbivores, in which case their area is incorporated into the herbivory estimate (e.g. Coley 1983a), or that they have abscised naturally and can be ignored for estimating herbivory. Either assumption will lead to biased estimates of rates of tissue loss to herbivores, and to difficulties of comparison between species or treatments if leaf life spans differ. Our own data (T. R. H. Pearson, unpublished data) show that when protected from herbivory leaves of *Trema*, and to a lesser extent *Cecropia*, have inherently shorter life spans than *Miconia*. Measurements of rates of leaf area loss on marked leaves that account for inherent differences in leaf life span have confirmed that the greater amount of herbivory on leaves of *Miconia* are not the result of

their slower leaf turnover (unpublished data). However, in practice, many of the differences in herbivory rates reported in the literature might be caused by the biases inherent in the marked leaf method. The marked leaf method is commonly used because it enables estimates of temporal variation in herbivory (Lowman 1984). However, the problem of contrasting leaf life span between species is important, especially for pioneers that replace their leaves rapidly and continuously.

Our measure of herbivory takes no account of tissue or mass loss to sap sucking or root herbivores, and it is unknown to what extent our manipulation of foliar herbivory would have influenced these processes. Here foliar herbivory is considered to be a proxy for all types of damage. However, the presence of other above-ground pests was recorded and was rare, though it is impossible to know the strength of below-ground effects or how these pests vary with species or gap size.

Negative effects on the growth and survival of unprotected *Trema* seedlings in this study were largely caused by damage to the apical meristem. Apical meristem damage has been reported in many studies of tropical woody plants. For example, Janzen (1971) illustrated the negative effects of apical damage on a Costa Rican liana, and Dalling & Hubbell (2002) showed how apical damage altered the composition of pioneers regenerating from the seed bank at the same study site as we used. These authors recorded that > 60% of individuals of five species, including *Trema micrantha*, suffered apical damage. Although Dalling & Hubbell (2002) reported that 88% of individuals of *Cecropia peltata* suffered apical damage, we found that no *Cecropia insignis* individuals were damaged in this manner. Why different *Cecropia* species are favoured in different environments is the subject of an ongoing study.

Brokaw (1987) first illustrated the differences in distribution among the three species used in this study. He also showed that *Miconia* was able to survive in the smallest gaps and that *Cecropia* became successful in gaps > 215 m², which is similar to the large gaps (225 m²) used in this study. *Trema* required gaps > 376 m² to survive and grow to maturity and grew 50% faster than *Cecropia* in these very large gaps. Although the gaps we created on Buena Vista Peninsula would have had a greater effective size than gaps of equal dimensions on BCI (because of the lower canopy height and absence of an understorey on BV), it may be that the gaps in our study were not large enough for *Trema* to achieve its maximum potential growth and survival rates.

This study illustrates changes in species rank order of relative growth rates of leaf area across light environments. *Miconia* maintained the highest rates of leaf area growth in the small gaps, whilst *Cecropia* showed the highest growth rates in the large gaps. *Trema* had negative growth rates in the small gaps and it is likely that it would be the fastest growing species in gaps larger than the maximum used in this study (Brokaw

1987). Our measure of growth rate was estimated from changes in leaf area per plant and our comparisons might yield different outcomes to those based on whole plant growth if plant architecture or allocation to roots or structural tissues differed significantly between species or gap sizes. Moreover, Montgomery & Chazdon (2002) found that the resolution of cross-overs in growth rates among seedlings of tropical trees across a short understorey light gradient was greater for growth rates of total biomass and root growth than for stem extension or diameter growth. If similar trends are manifested among pioneer species growing in gaps, then our analysis based on one measure of above-ground growth might have underestimated the importance of cross-overs in comparisons of seedling growth. Although we made no measurements of interspecific differences in mass allocation or plant architecture, our interpretation based on leaf area growth rates is supported by measurements of height growth for two species over a shorter time period.

We interpret these results as support for the hypothesis that growth rates of pioneer trees cross-over across light environments (e.g. Givnish 1988). Sack & Grubb (2001) have suggested that maintenance of the rank order of growth rates of species across light environments in some experiments might be an artefact of relatively short study periods. A small-seeded light-demanding species will have a high initial RGR across all light environments because of its high leaf area ratio, but over time the residual seed size effect on relative growth rate will diminish and the light-demander will be out-ranked in the shade by a shade-tolerator. The 15-month growth interval we used was sufficient to eliminate seed size differences among our study species, and changes in the rank order of species' growth rates across light environments were evident.

Conclusions

This study illustrates the potential mechanisms driving the coexistence of three ecologically similar species in a species-rich plant community. *Miconia* germinated and emerged across a wide range of light environments, and would persist despite its high mortality because of its high density in the soil seed bank. In contrast, *Trema* emerged and survived in significant numbers only in higher light environments.

These species, and *Cecropia insignis*, also differed in their onward growth and adult distribution: *Trema* occurs in the largest gaps, *Miconia* across all gap sizes and *Cecropia* is intermediate (Brokaw 1987). The mechanistic basis for these contrasting distributions is that the species 'cross-over' in growth rates across light environments, with the most light-demanding species (*Trema*) unable to maintain a positive carbon balance in small gaps and the most shade-tolerant species (*Miconia*) unable to elevate its RGR_{LA} sufficiently to compete with its faster-growing neighbours in the largest gaps. Herbivory interacts with growth rates to

accelerate mortality of plants with a marginal carbon balance, and to decrease growth rates of *Miconia* and *Trema* in situations where they have a positive carbon balance. Although herbivory played a role in decreasing the survivorship of one species, we found no evidence for herbivory as a driving force in maintaining differences in habitat occupancy between species.

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