

T. R. H. Pearson · D. F. R. P. Burslem · R. E. Goeriz ·  
J. W. Dalling

## Regeneration niche partitioning in neotropical pioneers: effects of gap size, seasonal drought and herbivory on growth and survival

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**Abstract** Adaptive trade-offs underlie the specialisation that permits habitat partitioning in species rich plant communities. We investigated the influence of the trade-offs that determine differences in growth and survival among six species of neotropical pioneer trees in gaps in semideciduous forest in Panama. Seedlings of *Miconia argentea*, *Cecropia insignis*, *Luehea seemannii*, *Trema micrantha*, *Ochroma pyramidale* and *Croton bilbergianus* were planted into artificial small (25 m<sup>2</sup>), medium (64 m<sup>2</sup>) and large (225 m<sup>2</sup>) gaps in secondary forest in the Barro Colorado Nature Monument. *Trema* and *Ochroma* suffered  $\geq 50\%$  mortality across all gap sizes, while *Cecropia* had high mortality only during the dry season and in the small gaps, and *Miconia* and *Croton* suffered low to zero mortality across all environments. The highest growth rates in large gaps were attained by *Cecropia* seedlings and in the smaller gaps by *Miconia* seedlings, although there were indications that *Trema* and *Ochroma* required gaps that were larger than any used in this study. Variation in growth and mortality could not be attributed to differences in foliar herbivore damage. Instead, there was strong evidence of a trade-off between maximum growth in the wet season and the ability to survive

seasonal drought, particularly in small gaps. We conclude that variation in allocation in response to multiple limiting resources may be as important as allocation to growth and defence in determining the habitat preferences of neotropical pioneers.

**Keywords** Panama · Seedling · Species richness · Trade-off · Tropical forest

### Introduction

Niche specialisation along gradients of resource availability is a potential mechanism for the coexistence of species in plant communities (Grubb 1977; Grime 1979; Crawley 1990). However, for specialisation to facilitate coexistence it is necessary to invoke the existence of adaptive trade-offs that prevent dominance of a species across the entire range of conditions in which it can survive (Darwin 1859; Clements 1916; Clements et al. 1929). An improved understanding of the multiple overlapping trade-offs that influence plant responses to the environment should therefore help to resolve the ongoing debate on the maintenance of tree species richness in tropical forests (Grubb 1996; Hubbell 2001; Wright 2002).

The availability of light is a fundamental determinant of tree seedling growth and survival in forests (Chazdon 1988). Numerous studies have investigated the traits characteristic of plants specialised to grow at high irradiance in canopy gaps and at low irradiance in the forest understorey (Bazzaz 1979; Bazzaz and Pickett 1980; Peace and Grubb 1982; Canham et al. 1996; Grubb et al. 1996; Walters and Reich 1996). For example, Walters and Reich (1996) showed that generally the same morphological adaptations existed for rapid growth of seedlings of five deciduous tree species in high and low light conditions [a high specific leaf area (SLA), a high net assimilation rate (NAR), and a high relative allocation to leaf mass and leaf area]. Equally in a pot experiment with 11 species of temperate trees and shrubs, allocation to

T. R. H. Pearson (✉) · D. F. R. P. Burslem  
Department of Plant and Soil Science,  
University of Aberdeen,  
Cruickshank Building, St Machar Drive, Aberdeen,  
AB24 3UU, UK  
e-mail: tpearson@winrock.org

R. E. Goeriz · J. W. Dalling  
STRI, Unit 0948,  
APO,  
AA, 34002-0948, USA

J. W. Dalling  
Department of Plant Biology,  
University of Illinois,  
Urbana, IL 61801, USA

#### Present address:

T. R. H. Pearson, Winrock International,  
1621 North Kent Street, Suite 1200, Arlington, VA 22209, USA

roots and leaf thickness were lower, and leaf mass ratio greater, in deep shade (0.3–1.6% of full daylight) than at higher light treatments (Grubb et al. 1996). However, in order for these morphological traits to promote species coexistence, plants adapted to low irradiance sites must be at a competitive disadvantage at high irradiance, and vice versa (Bazzaz 1979; Bazzaz and Pickett 1980; Huston and Smith 1987). Evidence of this trade-off would be provided by ‘cross-overs’ in physiological processes (e.g. net carbon assimilation rates) and growth among species specialised to different light conditions when compared along a light gradient (Givnish 1988; Walters and Reich 1996; Kobe 1999; Thomas and Bazzaz 1999).

Specialisation to light environments might also be manifested as a negative relationship between growth rates at high irradiance and mortality in the shade for comparisons across species. This has been observed when tree species differing widely in shade tolerance have been compared in both temperate (Kobe et al. 1995) and tropical (Hubbell and Foster 1992) tree floras. The relationship is consistent with ‘cross-overs’ in photosynthetic rates in response to variation in irradiance if the high mortality of potentially fast-growing species in the shade is driven by their inability to maintain a positive carbon balance at low irradiance (Givnish 1988). However, an alternative hypothesis proposes that the rank order of species’ growth rates is maintained across irradiance conditions (Kitajima 1994, 1996; Poorter 1999). According to this hypothesis the high mortality of potentially fast-growing species at low irradiance is associated with low investment in morphological and biochemical characteristics that confer defence against herbivores and pathogens, such as thicker, more lignified leaves and the production of secondary chemicals (Kitajima 1994; Cornelissen et al. 1998; Poorter 1999). For example, Coley et al. (1985) argued that slower-growing species with longer lived leaves have an increased investment in anti-herbivore defences, while faster-growing species rely on their ability to replace rapidly tissue removed by herbivores to maintain a high photosynthetic area, and consequently a high growth rate. At low irradiance, fast-growing species are unable to replace tissue lost to herbivores because high respiration rates result in net photosynthetic rates that are not sufficient to maintain a positive carbon balance (Loach 1967; Boardman 1977; Coley et al. 1985; Kitajima 1994).

Although the trade-offs discussed above have been proposed independently to facilitate the understanding of life history differences and coexistence among species, the responses of plants growing in the field should reflect their adaptations to multiple interacting factors (Peace and Grubb 1982; Huston and Smith 1987; Smith and Huston 1989; Canham et al. 1996; Grubb et al. 1996). For example, allometric constraints prevent morphological specialisation to tolerance of low nutrient supply combined with low irradiance (Peace and Grubb 1982). However, plants that are tolerant of both low irradiance and low nutrient supply might lack an ability to grow fast when neither resource is limiting (Huston and Smith

1987). The evidence for interactions between co-limiting factors is provided by pot experiments; for example, the temperate herb *Impatiens parviflora* has a higher differential in growth rates in response to increased nutrient availability when grown at high than low irradiance (Peace and Grubb 1982). The evidence for an interaction between irradiance and water availability on plant growth and survival is less conclusive. Plants grown at low irradiance have increased allocation above ground to maximise light interception, which might reduce their survival under drought conditions, if maximising root surface area increases survival (Smith and Huston 1989). A study of the temperate tree *Liriodendron tulipifera* (Holmgren 2000) found no support for a negative interaction between irradiance and water supply, because shade had a positive effect on growth and survival under dry conditions. Seasonally dry tropical forests provide an appropriate environment to examine this trade-off because dry season reductions in soil water potential imposes water shortage across all forest light environments (Wright and Cornejo 1990; Wright 1991). Pioneer species provide a particularly suitable study system because they respond rapidly in terms of growth and mortality to resource availability.

In this paper we examine growth and survival in relation to biotic and abiotic factors among six species of gap-demanding neotropical pioneer tree species with contrasting seed sizes, growth rates and susceptibilities to herbivory. We address the following questions:

1. Are reversals in the rank order of species’ growth rates apparent across irradiance conditions?
2. Is there a trade-off among species between growth rate in high irradiance and mortality in the shade?
3. Does the amount of herbivore damage affect the rank order of species’ mortality and growth across light environments?
4. How does seasonal drought influence the rank order of mortality and growth across species?

## Materials and methods

### Study site and species

The study was conducted on Buena Vista peninsula (BV) which is an area of 40-year old secondary forest within the Barro Colorado Nature Monument (BCNM), Panama (9°05’N, 79°45’W). The primary vegetation of the BCNM is semi-deciduous tropical forest (Croat 1978). On BV the canopy comprises a community dominated by approximately 30 pioneer species with an average height of 20 m. The BCNM has a mean annual rainfall of 2,700 mm and a pronounced dry season between January and April each year (Rand and Rand 1982).

The species selected for this study were *Miconia argentea*, *Cecropia insignis*, *Trema micrantha*, *Luehea seemannii*, *Ochroma pyramidale* and *Croton bilbergianus* (Table 1, Croat 1978). These species are pioneers sensu Swaine and Whitmore (1988) and are common gap-demanding components of the primary forest flora of the BCNM (Croat 1978). The species were selected on the basis of their frequency at the study site and the availability of seeds, and to present a wide range of seed sizes and growth rates (Table 1). The

**Table 1** Family, mean seed mass, and the toughness, and concentrations of N and phenols in mature and immature leaves of seedlings of the six study species growing on Barro Colorado Island, Panama

Species	Family	Seed mass <sup>a</sup> (mg)	Toughness <sup>b</sup> (N)	Phenols <sup>b</sup> (mg g <sup>-1</sup> dry mass)	N <sup>b</sup> (% dry mass)
<i>Miconia argentea</i>	Melastomat-aceae	0.08	a. 3.8 b. 3.1	31 78	1.7 2.1
<i>Cecropia insignis</i>	Cecropiaceae	0.62	a. 5.8 c. 4.5	86 131	2.1 2.4
<i>Luehea seemannii</i>	Tiliaceae	1.70	a. 3.0 b. 1.6	60 107	2.6 3.2
<i>Trema micrantha</i>	Ulmaceae	3.90	a. 2.5 b. 2.2	56 102	2.9 3.1
<i>Ochroma pyramidale</i>	Bombacaceae	6.10	a. 3.1 b. 1.9	194 219	2.2 2.5
<i>Croton bilbergianus</i>	Euphorbiaceae	24.0	a. 4.0 b. 2.7	41 33	2.7 4.5

<sup>a</sup> Pearson et al. 2002; Dalling et al. 1997

<sup>b</sup> Coley 1983

species will be referred to by their genus names throughout the paper.

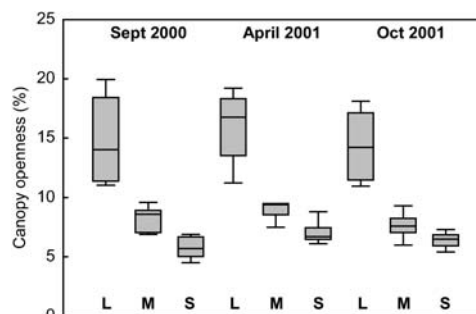
#### Experimental methods

In April 2000, 16 artificial gaps were created within an approximately 12 ha plateau area on the western half of BV. Six gaps measured 15×15 m on the ground, five measured 8×8 m and five measured 5×5 m. All gaps were originally covered by intact secondary forest. The gaps were created by felling and removing all vegetation from the study area. Resprouts were cut back after 1, 3, 5, 9, and 12 months and the study plots were kept free of vegetation.

The light environment in the gaps was characterised using hemispherical photographs at 1 m above ground level. A single photograph was taken in the centre of each gap in September 2000, and April and October 2001 using a Nikon Coolpix 950 digital camera and an 8 mm fish-eye lens (Nikon, N.Y., USA). Hemispherical photographs were analysed to obtain canopy openness (Hemiview, Delta-T, Cambridge, UK) which is illustrated in Fig. 1. Mean daily photosynthetically active radiation (PAR) as a percentage of full daylight was calculated over 5 days in October 2000 in four gaps of each size using PAR sensors (SKP 215) attached to data loggers (Skye Instruments, Powys, UK). An additional sensor recorded concurrently in a large clearing. Mean ( $\pm$  SEM) PAR as a percentage of full daylight was 26.4%  $\pm$  4.1 in the large gaps, 14.1%  $\pm$  6.3 in medium gaps and 3.32%  $\pm$  0.54 in the small gaps.

In July 2000, four seedlings per species were planted 80 cm apart in a random arrangement in square plots in the centre of each gap. At the time of planting each seedling had a total leaf area of approximately 10 cm<sup>2</sup> but seedlings of different species varied in age from 2 to 11 months. The seedlings of four species were obtained from seeds collected on BCI and grown up in a growing house (25% full daylight irradiance) for 6 months (*Miconia*), 4 months (*Cecropia*), 3 months (*Luehea*) or 2 months (*Ochroma*). Seedlings of *Trema* were obtained as germinants that emerged when soil from beneath two adult *Trema* trees was spread out in seed trays in a growing house (25% full daylight irradiance) and were 2 months old at transplantation. Young *Croton* seedlings were collected from seedling clumps in natural gaps on BCI and were transferred directly to the artificial gaps on BV, at which point they were approximately 11 months old.

The seedlings were censused monthly for mortality, leaf turnover and herbivory from August 2000 until December 2001. Leaf area was estimated every second month from measurements of leaf length (or width in the case of *Croton*) converted to area using



**Fig. 1** Box plots of canopy openness (%) calculated from hemispherical photographs for large (L,  $n=6$ ), medium (M,  $n=5$ ) and small (S,  $n=5$ ) gaps in secondary forest in Panama, for photographs taken in September 2000, and April and October 2001. The boundary of the box indicates the 25th and 75th percentiles, the line within the box marks the median, and the whiskers above and below the box mark the 10th and 90th percentiles

regression equations obtained from a sample of 50 leaves per species ( $r^2$  for the one-parameter models varied from 0.973 to 0.997). Relative growth rates of leaf area ( $RGR_{LA}$ ) were calculated from the following formula (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. Plant height was measured at the end of the experiment in December 2001.

To estimate foliar herbivory damage to seedlings we measured the percent leaf area missing at each monthly census using a plastic grid placed over all leaves of three randomly selected individuals for each species and gap size. Two important caveats to the interpretation of the single census damage estimates used in this study need to be taken into account. Firstly, single census estimates may underestimate actual damage if the consumption of entire leaves is undetected, and secondly, damage may be correlated with leaf longevity if damage accumulates steadily through the leaf life-span. To counter the first problem, an estimate of a missing leaf's area was added to the estimate of herbivory whenever a petiole fragment was encountered, indicating consumption of a whole leaf. To determine whether differences in leaf longevity could have biased our herbivory estimates we measured leaf life-span using monthly censuses of marked leaves over 15 months. We found that mean leaf life-spans ranged between 2.4 (*Trema* seedlings in small gaps) and 6.7 months (*Miconia* seedlings in large gaps) and did not correlate with gap size or amount of herbivory between species.

Finally, we made separate measurements of daily herbivory rates using monthly censuses of marked leaves (T. Pearson, unpublished data) and these data support the conclusions based on the standing herbivory estimates presented here.

### Statistical analyses

The time series of  $RGR_{LA}$  and herbivory data were analysed using multivariate analysis of variance (MANOVA) to determine the effects of species, gap size and their interaction on growth rates over all census intervals. The MANOVA model for  $RGR_{LA}$  reflected the nested design of the experiment [the gap factor nested within gap size—represented as  $gap(size)$ ], but the random selection of individuals for estimation of herbivory rates avoided the necessity for a nested model for analysis of herbivory. The herbivory data ( $x$ ) were  $\log_e(1,000x+1)$  transformed prior to analysis in order to normalise the distribution of residuals.

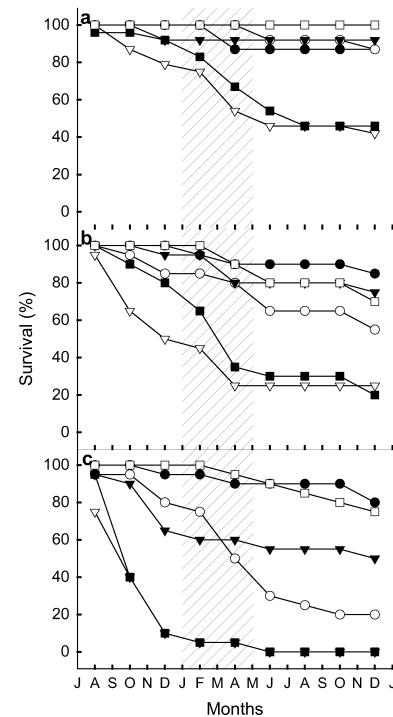
Separate analyses were conducted for the censuses spanning the first wet season (August–December 2000), the dry season (January–April 2001), the second wet season (May–December 2001) and the total period (August 2000–December 2001). The first two of these analyses included all available data, while the second two included data from the medium and large gaps only, because of the high mortality of some species in small gaps.

Survival was analysed using the Life Table function of SPSS 10.0 (SPSS, Chicago, USA) in which comparison of median survival times between gap sizes and species is made using the Wilcoxon statistic.

## Results

### Mortality

All species except *Miconia* had a significantly greater median survival time in large gaps than small gaps and intermediate values in medium gaps, although in many cases median survival time was greater than the 18 month duration of this experiment (Table 2). The effect of reduced gap size was most marked in *Trema* and *Ochroma*, which also had the shortest median survival times in the large gaps. Therefore there was no evidence of a change in the rank order of species' median survival times with gap size in this experiment. The rate of seedling mortality increased in the dry season for *Miconia* in the large gaps, for *Croton*, *Luehea*, *Cecropia*, *Trema* and *Ochroma* in medium gaps and for *Cecropia* in the small gaps (Fig. 2). It would not have been possible to detect an increase in mortality rate in the small gaps for



**Fig. 2** Time course of percentage survival in **a** large, **b** medium and **c** small gaps for seedlings of *Miconia*, black circle; *Cecropia*, clear circle; *Luehea*, black inverted triangle; *Trema*, clear inverted triangle; *Ochroma*, black square; and *Croton*, clear square, growing in secondary forest in Panama. Hatched box indicates dry season

*Trema* and *Ochroma* because few individuals survived to the start of the dry season.

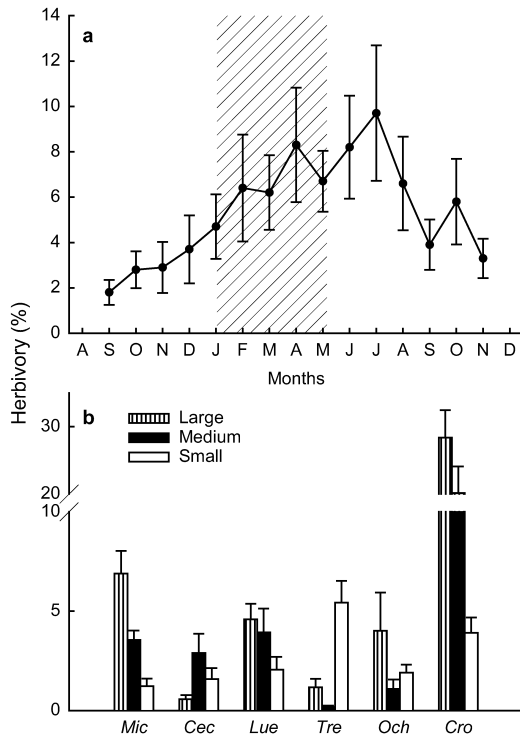
### Herbivory

The mean percentage leaf area missing increased nearly five-fold over time (Fig. 3a), from 1.8% 1 month into the study to a maximum of 9.7% 2 months after the end of the dry season. The effects of species, gap size and the interaction between these two factors were significant from the beginning of the dry season onwards (Table 3, Fig. 3b). *Croton* had a high percentage of leaf area

**Table 2** Median survival time (months) and percentage remaining alive after 18 months for seedlings of six pioneer species planted into large (L), medium (M) and small (S) gaps in secondary forest in Panama. >18 indicates that median survival time was greater than

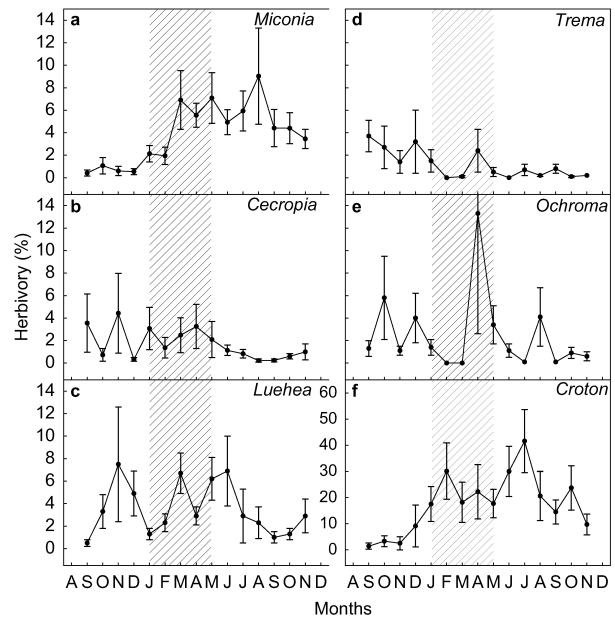
	Median survival times			Percentage remaining alive			Differences between gap sizes			
	Large	Medium	Small	Large	Medium	Small				
<i>Miconia</i>	>18	A	>18	a	>18	a	88	85	80	L=M=S
<i>Cecropia</i>	>18	A	>18	b	11.0	b	88	55	20	L>M>S
<i>Luehea</i>	>18	a	>18	a	>18	b	92	75	50	L=M>S
<i>Trema</i>	11.5	b	7.0	c	3.7	c	42	25	0	L>M>S
<i>Ochroma</i>	13.5	b	9.5	c	3.8	c	46	20	0	L>M>S
<i>Croton</i>	>18	a	>18	ab	>18	a	100	70	75	L>M=S

the 18 month duration of this study. Within a gap size class, median values not sharing a lower case letter are significantly different ( $P<0.05$ ). The significance of differences between gap sizes within a species ( $P<0.05$ ) is shown in the final column



**Fig. 3** Mean and standard error percentage leaf area missing (herbivory) on seedlings of six species of gap-demanding trees growing in secondary forest in Panama: **a** time course over 17 months (*hatched box* indicates dry season), **b** differences between large (*hatched bars*), medium (*open bars*) and small (*closed bars*) gaps for each species

missing relative to the other species in the large and medium gaps, but similar values to other species in the small gaps. Most species showed a trend to a lower percentage of leaf area missing in smaller gaps, but *Cecropia* and *Trema* showed the opposite trend: *Trema* had the second lowest mean percent of leaf area missing in the large gaps but the highest mean value in the small gaps (Fig. 3b).



**Fig. 4** Time course of % herbivory in **a** *Miconia*, **b** *Cecropia*, **c** *Luehea*, **d** *Trema*, **e** *Ochroma* and **f** *Croton* growing in secondary forest in Panama with all gap sizes pooled. Mean  $\pm$  SEM. *Hatched area* indicates dry season

Leaf area missing increased during the dry season and stayed high thereafter in *Miconia* and *Croton*, but declined over time in *Cecropia* and *Trema* (Fig. 4). There were no systematic trends over time in the percentage of leaf area missing on *Ochroma* and *Luehea* (Fig. 4).

**Growth**

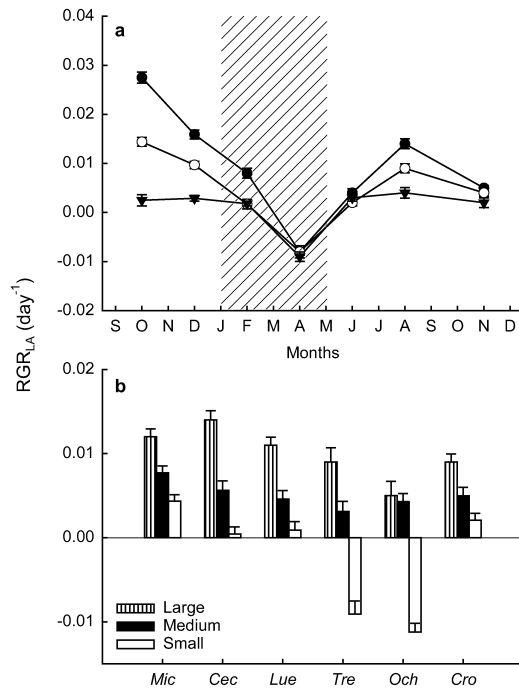
In December 2001, at the end of the study, seedling height in large gaps was 1,151 $\pm$ 63 mm (mean  $\pm$  SEM, range 58–3,600 mm), 473 $\pm$ 43 mm in medium gaps (94–1,724 mm) and 173 $\pm$ 11 mm in small gaps (25–377 mm). In the large and medium gaps RGR<sub>LA</sub> declined from the start of the

**Table 3** Degrees of freedom, *F*-values (derived from the Pillai Trace statistic) and degree of significance from multivariate analyses of variance on amounts of herbivory and relative growth rates of leaf area (RGR<sub>LA</sub>) for the first wet season (August–

December 2000), the dry season (January–April 2001), the second wet season (May–December 2001) and the entire study period. \*\*\*, *P*  $\leq$  0.001; \*\*, *P*  $\leq$  0.01; \*, *P*  $\leq$  0.05

	2000 wet season			2001 dry season			2001 wet season <sup>1</sup>			Entire study period <sup>a</sup>		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
<b>Herbivory</b>												
Species	20, 144	1.33	NS	15, 108	3.10	***	35, 110	2.44	***	75, 70	1.68	*
Gap Size	8, 68	0.45	NS	6, 70	2.52	*	7, 18	5.44	**	15, 10	5.41	**
Species $\times$ Gap size	40, 144	1.78	**	30, 108	1.60	*	35, 110	1.72	*	75, 70	1.57	*
<b>RGR<sub>LA</sub></b>												
Species	10, 584	6.94	***	10, 450	12.6	***	10, 324	7.10	***	30, 805	6.47	***
Gap size	4, 584	56.9	***	4, 450	20.1	***	2, 161	8.82	***	6, 157	23.1	***
Gap (size)	26, 584	6.48	***	26, 450	3.25	***	18, 324	1.95	**	54, 972	3.35	***
Species $\times$ Gap size	20, 584	1.78	*	20, 450	3.08	***	10, 324	1.13	NS	30, 805	1.24	NS

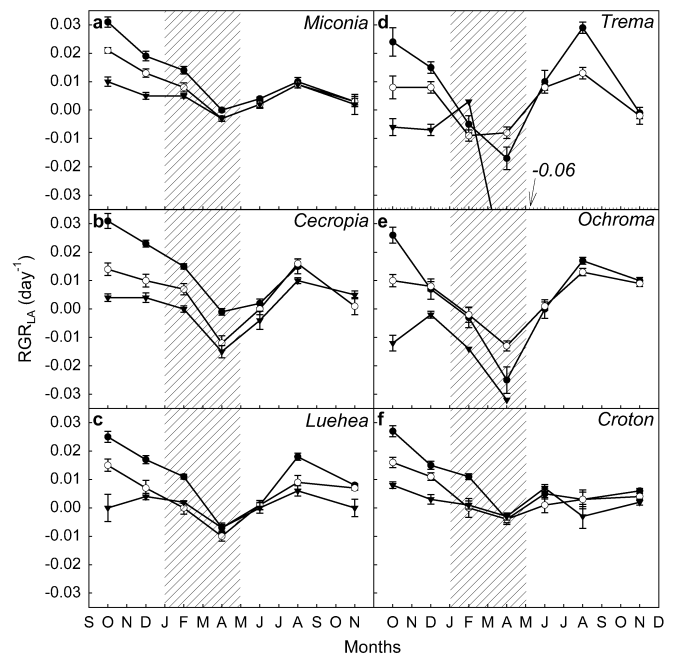
<sup>a</sup> Analyses of data from medium and large gaps only because of high mortality in small gaps



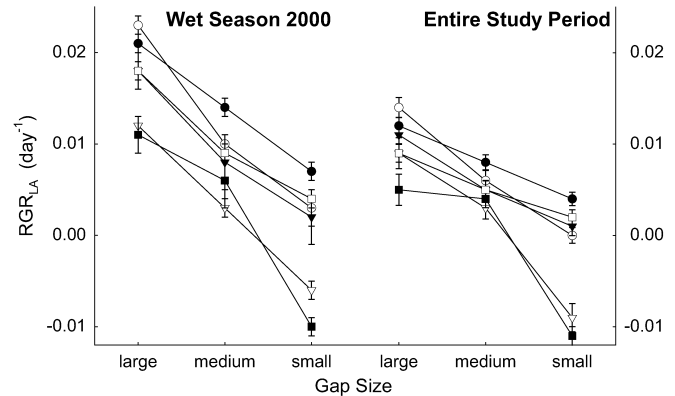
**Fig. 5a, b** Mean and standard error  $RGR_{LA}$  of seedlings of six species of gap-demanding trees growing in secondary forest in Panama. **a** Time course over 15 months; large gaps, black circle; medium-sized gaps, clear circle; small gaps, black inverted triangle. Hatched area indicates dry season. **b** differences between large (hatched bars), medium (open bars) and small (closed bars) gaps for each species

experiment throughout the first wet season and dipped to negative mean values in the dry season (Fig. 5). Maximum values of mean  $RGR_{LA}$  in large and medium gaps were lower in the second wet season than the first, and lower in medium than large gaps. Mean  $RGR_{LA}$  in small gaps was constant and marginally positive in both wet seasons, but declined to negative values similar to those of seedlings in the larger gaps in the dry season (Fig. 5a). The dry season decline in  $RGR_{LA}$  was expressed to varying degrees by the six species (Fig. 6): *Ochroma* and *Trema* declined to the greatest extent, but their mean  $RGR_{LA}$  recovered to values as high as those attained during the first wet season in the medium and large gaps, while *Miconia* and *Croton* declined to less negative values of  $RGR_{LA}$  in the dry season, and growth rates in the second wet season did not rise as high as in the first.

Mean  $RGR_{LA}$  differed significantly among species and gap sizes across the study period (Fig. 5b). The interaction between these factors was significant in the first wet season and in the dry season but the reduced data set available for analysis of  $RGR_{LA}$  in the second wet season (i.e. excluding small gaps) suggested that the interspecific differences in response to medium and large gap sizes had disappeared (Table 3). When measured across the entire study period, the variance in  $RGR_{LA}$  among species was much greater in small gaps than medium or large gaps. There was no evidence that rank hierarchies of  $RGR_{LA}$  were maintained across gap sizes (Fig. 7), for example,



**Fig. 6** Time course of mean ( $\pm$  SEM)  $RGR_{LA}$  for seedlings of **a** *Miconia*, **b** *Cecropia*, **c** *Luehea*, **d** *Trema*, **e** *Ochroma* and **f** *Croton* growing in secondary forest in Panama in large gaps (black circle); medium-sized gaps (clear circle); or small gaps (inverted black triangle). Hatched area indicates dry season



**Fig. 7** Mean and standard error relative growth rates of leaf area ( $RGR_{LA}$ ) of six species of gap-demanding tree species growing in secondary forest in Panama during the first wet season (August–December 2000) and over the entire study period (August 2000–December 2001). Over the entire period the data for *Trema* and *Ochroma* growing in small gaps were obtained for the period August 2000 to April 2001, after which all seedlings had died. *Miconia*, black circle; *Cecropia*, clear circle; *Luehea*, black inverted triangle; *Trema*, clear inverted triangle; *Ochroma*, black square; *Croton*, clear square. x-axis labels are categorical and spacing is arbitrary

the fastest growing species in large gaps (*Cecropia*) was one of the slowest growing in small gaps. The loss of consistency in the rank of  $RGR_{LA}$  between gap sizes was accentuated over time, as the two species that were incapable of achieving a positive  $RGR_{LA}$  in small gaps at any time during the experiment (*Trema* and *Ochroma*)

grew faster relative to the other species in the second than the first wet season.

Among-species relationships between herbivory, mortality and growth

Over the first wet season after planting  $RGR_{LA}$  in large gaps was positively related to  $RGR_{LA}$  in small gaps (Pearson's  $r=0.90$ ,  $n=6$ ,  $P=0.014$ ). However, for growth over the second wet season no relationship existed for  $RGR_{LA}$  in large and small gaps among the four species that had survived in small gaps ( $r=0.68$ ,  $n=4$ ,  $P=0.32$ ). Growth rate in large gaps in the second wet season was negatively related to survival in small gaps throughout the experiment ( $r=-0.87$ ,  $n=6$ ,  $P=0.026$ ) and to mean percentage foliar herbivory across all light environments over the same period ( $r=-0.84$ ,  $n=6$ ,  $P=0.036$ ). There was a trend for  $RGR_{LA}$  in large gaps during the second wet season to be negatively related to survival in small gaps during the dry season ( $r=-0.75$ ,  $n=6$ ,  $P=0.088$ ).

## Discussion

Trade-off in growth rate in high and low light

Relative growth rate of leaf area ( $RGR_{LA}$ ) increased with increasing canopy openness for all six species, but there was no evidence that the rank order of species' relative growth rates was maintained across gap sizes when growth rates were measured over the entire study period. *Cecropia* was the fastest growing species in the large gaps, while *Miconia* grew fastest in the medium and small gaps. *Trema* and *Ochroma* were expected to have the fastest growth rates in the largest gaps, as these species have been shown previously to grow fast at high irradiance (Coley 1983; Brokaw 1987; Dalling et al. 1999). Three factors might contribute to the low growth rates we observed in these species. The first is that the long-term average growth rates include the dry season during which growth rates of these species declined more than the other species. Secondly, the largest gaps in the experiment (225 m<sup>2</sup>) were considerably smaller than the minimum gap size that was required for *Trema* to grow to maturity on BCI in Brokaw's (1987) study (376 m<sup>2</sup>). Therefore, it is possible that growth rates of *Trema* and *Ochroma* would exceed that of the other species in this experiment later in ontogeny and in larger gaps. Finally, our recent work (Dalling et al, unpublished data) suggests that *Ochroma* has a high demand for nutrients, and it is possible either that the soils of Buena Vista are impoverished in the major limiting nutrients, or that larger gaps are required for release from root competition.

Cross-overs in species relative growth rate across four irradiance treatments were observed by Kobe (1999) in a field experiment with four tree species in Costa Rica, and are a prediction of the contrasting photosynthetic light response curves frequently reported for coexisting trop-

ical tree species (e.g. Bazzaz 1979; Chazdon 1988; Zipperlen and Press 1997). Short-term experiments with seedlings in pots have frequently failed to detect cross-overs in species' RGR across irradiance treatments (Kitajima 1994, 1996; Poorter 1999), possibly because the primary determinant of RGR differences between species in these experiments was residual seed size effects (Sack and Grubb 2001). During the first 5 months of this experiment the rank of species' relative growth rate was maintained, but in the second wet season cross-overs in relative growth rate emerged.

In this experiment growth rates were calculated from leaf area changes and comparisons would be distorted if shedding of leaves during the dry season accounted for the fall in growth rates at this time. However, none of the species we used is deciduous, and our conclusions based on leaf area growth are supported by measurements of height growth (unpublished data).

Trade-off between growth rate in high light and mortality in low light

Mortality varied significantly between species, from *Trema* and *Ochroma* which had >50% mortality across all gap sizes and 100% mortality in the smallest gaps, to *Miconia* which had <20% mortality across all gap sizes. *Cecropia* and *Croton* had lower survival in the medium gaps than the large gaps and *Cecropia* and *Luehea* had lower survival in the small than medium gaps.

Therefore, with the exception of *Trema* and *Ochroma*, which may have been light-limited even in the largest gaps (see above), the species in this experiment displayed a negative relationship between mortality in the small gaps and growth rate in the large gaps. This relationship is consistent with the trade-off between growth in high light and survival in low light, which has been observed in recent studies of both temperate and tropical trees (Kitajima 1994; Kobe et al. 1995; Walters and Reich 1996; Kobe 1999). For example, for ten temperate tree species Kobe et al. (1995) found a continuum of growth rate and mortality across a light gradient, but as survival under low light increased, growth under high light decreased.

There is no evidence that the differences among species in mortality in the small gaps was caused by differences in either the amount of herbivory they sustained or in the components of defence reported for these species by Coley (1983, Table 1). *Cecropia* and *Ochroma* had high mortality in small gaps but were subjected to low herbivory in this environment, possibly because they had effective chemical defences (Table 1). *Cecropia* saplings and trees are often occupied by aggressive *Azteca* spp. (Formicidae) ants but we only found ants in the last four months of the study, and then only on the largest seedlings present in the largest gaps. *Trema* is relatively poorly defended against herbivores (Table 1, Coley 1983) and did sustain greater amounts of herbivory in small gaps, but an enclosure study has

demonstrated that protection from herbivores slows down rather than prevents the mortality of *Trema* seedlings in small gaps (Pearson 2002). We conclude that the trade-off between growth rate in high light and survival in low light was not maintained by differential herbivore-induced mortality of poorly defended fast-growing species in low light.

#### Trade-off between growth rate and susceptibility to herbivory

The percentage of leaf area missing through herbivore damage was greater, overall, in the largest gaps, although variation between the species and through time was high. The species with the highest rates of growth in the large gaps (*Cecropia*) and the species anticipated to have the highest growth rates in even larger gaps (*Trema* and *Ochroma*) had the lowest amounts of leaf area missing, which led to a significant negative relationship between growth rate and amount of herbivory.

Therefore we find no evidence in support of the hypothesis that susceptibility to herbivore attack is positively related to a species' ability to grow fast in high light (Coley et al. 1985). However, our study contained only six species, all of them pioneers, and so did not include shade tolerant species that may show contrary effects. Rates of herbivory may also vary greatly from year to year (Filip et al. 1995), and so an outbreak of one or more specialist herbivore species could have greatly altered the results (Barone 1998).

Defence chemistry was not measured in this study, but values of leaf toughness, foliar phenol and nitrogen concentrations are available for young and old leaves of mature individuals of our test species from Coley (1983). If we assume the same ranking of mean values of these variables for our experiment, then we find no evidence of a relationship between investment in these measures of defence and an ability to survive in a low irradiance environment. For example *Croton* had low mortality in the small gaps and *Cecropia* had very high mortality in the small gaps but Coley's (1983) data on leaf toughness, and foliar concentrations of N and phenols predict greater susceptibility of *Croton* than *Cecropia* to herbivory (Table 1). *Croton* is attended by *Ectatomma ruidum* (Ponerinae) ants which feed on nectaries at the base of the leaves, however these ants will jump from the plant if disturbed and even guard *Thisbe irenea* (Riodinidae) caterpillars feeding on the leaves (personal observation). We conclude that the positive relationship between maximum potential growth rate and susceptibility to herbivory determined for comparisons across functional groups of tropical trees cannot be used for predicting differences between species within a functional group.

Trade-off between potential rates of growth and survival and the ability to tolerate two limiting factors

The dry season coincided with a depression in the growth rates of each of the species in all gap sizes. The depression in growth rates was least in the most shade tolerant species (*Miconia* and *Croton*). The dry season months also coincided with an elevation in the mortality rates of the most shade intolerant species *Trema*, *Ochroma* and *Cecropia*.

Before the start of the dry season *Ochroma* already had almost 100% mortality in the small gaps, but during the dry season monthly mortality rate (Sheil et al. 1995) of *Ochroma* rose from 0.05 to 0.12 month<sup>-1</sup> in medium gaps and from 0.01 to 0.07 month<sup>-1</sup> in the large gaps. *Cecropia* was able to maintain a positive growth rate in the small gaps during the wet season, presumably through high investment in above ground tissue (a high leaf area ratio), but during the dry season growth rates in small gaps became negative and monthly mortality rates rose from 0.04 to 0.14 month<sup>-1</sup>.

Liebig's 'Law of the Minimum' (cf. Chapin et al. 1987; Latham 1992) proposed that the performance of plants is constrained by the single resource that is most limiting. However, it is clear that plants can be limited simultaneously by more than one resource (e.g. Chapin et al. 1987; Kolb et al. 1990; Canham et al. 1996; Grubb et al. 1996). Plants have evolved to maximise their growth and survival in high and low irradiance conditions in the context of co-limitation by nutrients and/or water with light when they grow in shade. Therefore, although survival at low irradiance might be assured by a high relative dry mass allocation to leaves (a high leaf mass ratio, LMR), if water or nutrients are simultaneously limiting then dry mass allocation to light interception may incur a cost in terms of reduced access to water and nutrients. For example in our study *Cecropia* survived and grew fast in the wet season but suffered high mortality in the dry season, especially in the small gaps. In a pot experiment (Dalling, unpublished data), in which 11 pioneer species were grown at relatively low irradiance [10.5% full daylight PAR], *Cecropia* had the highest LMR (mean 0.70) and the lowest root mass ratio (root mass ratio, RMR; mean 0.14). These data anticipate our finding that *Cecropia* has a relatively high survival at low irradiance if supplied with ample water, but a low tolerance of seasonal drought.

Smith and Huston (1989) suggested that simultaneous limitation by light and water should be prevalent and important among plants. Canham et al. (1996) showed an effect on shoot growth of this simultaneous limitation for a pot experiment on four temperate tree species. The authors found an interaction between irradiance and water supply on shoot growth and allocation, but indicated that a limitation of water supply was less significant than nutrient limitation for growth and allocation. Holmgren (2000) failed to find support for a proposed negative interaction between shade and drought on the growth of seedlings of the temperate tree, tulip poplar (*Liriodendron*



*tulipifera*) in pots, and indeed showed positive effects of shading on carbon gain under dry conditions. However, the interpretation of pot experiments on the interaction of shade and drought is limited by higher evaporative water loss from plants and soil at high irradiance (Kolb et al. 1990; Burslem 1996; Holmgren 2000). In addition, larger plants grown at high irradiance may have greater absolute and relative access to water because they possess larger roots and a greater RMR. We find evidence in support of Smith and Huston (1989) that the ability of a species to survive and grow at different minimum light conditions is dependent on moisture availability, and that tolerance to co-limitation by low irradiance and water shortage is negatively related to maximum potential growth rate.

## Conclusions

These data allow us to infer a mechanistic basis for the contrasting gap size preferences for *Cecropia*, *Miconia* and *Trema* that were detected in a classic study on BCI by Brokaw (1987). He found that *Trema* grew to maturity only in the largest gaps (over 376 m<sup>2</sup>), while *Cecropia* survived and matured in gaps of over 215 m<sup>2</sup> and *Miconia* was able to survive in all gaps greater than 102 m<sup>2</sup>. These distribution patterns are predicted by the trade-offs found in this study. *Miconia*, *Cecropia* and *Trema* switch ranks of growth rate across irradiance environments and trade-off growth at high irradiance and mortality at low irradiance. However, in contrast to earlier studies that have emphasised the importance of herbivores and pathogens as mediators of this trade-off (Kitajima 1994; Dalling and Hubbell 2002), we found that the negative relationship between wet season growth and dry season mortality could also generate this pattern. Our data suggest that high mortality in shade may be caused by a plant's inability to maintain a positive net carbon gain at low irradiance under any circumstance, as in *Trema* and *Ochroma*, or as in the case of *Cecropia*, when low irradiance is combined with low water supply. Here we found no evidence for the alternative hypothesis that mortality at low irradiance is a result of insufficient investment in structural and biochemical defences against herbivores and pathogens. Instead, our data suggest that the risk of mortality in the shade is positively associated with the low growth rates of seedlings that precede death.

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