Effects of topographic position, leaf litter and seed size on seedling demography in a semi-deciduous tropical forest in Panamá

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Abstract

This study examined whether topography-induced gradients in water potential and leaf litter depth contribute to species coexistence in tropical forests through species-specific effects on seedling emergence and mortality. Seedling emergence and mortality were followed for a period of 12 months in 36 (1 × 2 m) plots on Barro Colorado Island (BCI), Panamá. Plots with and without litter were distributed on slope and plateau sites in three catchments. In the absence of manipulations, the lower litter depth on slopes resulted in approximately four times as many emergent seedlings than on plateau sites. However, litter depth had little effect on seedling community composition. By the end of the first dry-season, post-emergence, there were no significant differences in surviving seedling numbers between any treatments. There were differences in the emergent seedling community between slope and plateau sites within the same catchment as well as differences in composition between catchments, suggesting that both niche partitioning and dispersal limitation might play a role in structuring seedling community composition. During the wet-season seedling mortality was highest on slope sites although this pattern was reversed during the dry-season. In both seasons mortality was higher for small-seeded species. These results demonstrate that gradients in water potential related to topography impact on patterns of seedling emergence and mortality although processes in the first year after emergence may be insufficient to explain observed habitat preferences of adult plants.

Introduction

Many mechanisms have been proposed to account for tree species coexistence in species-rich tropical forests. Some of these have focused on niche differences expressed during regeneration (Grubb 1977) and include differences in seed germination responses to environmental variation (Daws et al. 2002a; Pearson et al. 2002) and differential seedling responses to a heterogeneous light environment (Ricklefs 1977; Denslow 1980; Kobe 1999; Dalling et al. 2004). Although considerable attention has been given to seedling responses to irradiance, these alone are insufficient to explain

species coexistence, since most tropical tree species are shade-tolerant and exhibit little evidence for partitioning of the light environment (Hubbell 1998; Bloor and Grubb 2003). However, the role of other potential differences between species remains insufficiently examined.

Variation in topography is a further source of heterogeneity in tropical forests and some shade-tolerant species have their adult distribution significantly biased towards certain topographic positions (e.g. Condit et al. 1996; Svenning 1999; Debski et al. 2000; Harms et al. 2001; Segura et al. 2003). Factors related to topographic position that potentially affect species distributions include gap formation rates (Poorter et al. 1994), soil water availability (Becker et al. 1988; Daws et al. 2002b), leaf litter depth (Becker et al. 1988), canopy height (Clark et al. 1996) and pH and cation exchange capacity (Silver et al. 1994).

Various authors have suggested that the reported distribution patterns related to topography reflect species-specific plant responses to water potential gradients associated with topographic variation (e.g. Becker et al. 1988; Gibbons and Newbery 2003). Furthermore, slopes of the 50 ha Forest Dynamics Plot on Barro Colorado Island (BCI) have 30–50% more species than adjacent plateau sites (Hubbell and Foster 1983) and Hubbell (1998) suggested this results from the presence of moisture-demanding species and drought-tolerant species on slopes: only drought-tolerant species occur on plateau sites. However, there is little direct evidence that species whose adult distribution is biased towards slopes (hereafter known as slope specialists) are less drought tolerant than widely distributed species. Thus, Condit et al. (1995) found that a severe drought on BCI did not increase the mortality of slope specialists more than other plant functional groups. In a further study of the same drought, Condit et al. (1996) also found that slope specialists had similar rates of decline on both slope and plateau sites. However, both of these studies involved following the demography of established individuals with a diameter at breast height in excess of 10 mm, rather than seedlings.

Seedling emergence and establishment is a high-risk stage in the plant life-cycle (Harper 1977). Thus, differences in the way species respond to the environment may be most apparent at this stage. Therefore, one possible explanation for the higher

species richness on slopes is that seedling survival, particularly during the first dry-season *post*-emergence, will be greater on slopes since they maintain a higher dry-season soil water potential (Becker et al. 1988; Daws et al. 2002b). This may be most apparent for small-seeded species since their small size, and related slow root growth rates (Daws et al. 2003) will reduce survival during dry-spells. This is also likely to be reflected in selection for emergence early in the wet-season to enable seedlings to reach as large a size as possible prior to the dry-season, since dry-season survival may be correlated with seedling size (Poorter and Hayashida-Oliver 2000).

A number of slope specialists on BCI belong to families such as the Melastomataceae, Piperaceae and Rubiaceae (Condit et al. 1996). Species in these families typically have small (< 10 mg) seeds (Foster 1982), which suggests that differential seedling survival, based on seed size, in relation to water potential gradients may contribute to observed plant distribution patterns. However, this remains to be tested.

Leaf litter can have a greater inhibitory effect on the emergence of small- than large-seeded species (Molofsky and Augspurger 1992; Metcalfe and Grubb 1997). Becker et al. (1988) suggested that the depth of leaf litter on BCI is thinner on slope than plateau sites. Consequently, an alternative mechanism for any bias in the distribution of small-seeded species to slopes is that a lower litter depth would favour establishment.

In this study we investigate the effects of topographic position on seedling emergence and mortality in the semi-deciduous forest on BCI. This was achieved by following natural seedling emergence and mortality on slope and plateau sites, with and without leaf litter, over a 12 month period. The specific hypotheses and predictions tested were firstly that topographic variation influences litter depth which in turn impacts on seedling recruitment. We predicted that deeper litter on plateau sites reduces the numbers of emerging seedlings and affects seedling composition by predominantly reducing the emergence of small-seeded species. Secondly, topographic variation influences emergent seedling survival. We predicted higher survival of small-seeded species on slope than plateau sites. Thirdly, the timing of seedling emergence influences seedling establishment. We predicted that seedlings emerging early in the

wet-season are more likely to survive the following dry-season than late-emerging seedlings.

Methods

Study site

The study was conducted in the semi-deciduous forest of BCI, Republic of Panamá (9°10′ N, 79°51′ W), which is described in detail elsewhere (Leigh et al. 1982; Leigh 1999). Rainfall on BCI averages 2600 mm yr^{-1}, with a pronounced dry-season between January and April (Dietrich et al. 1982). The flora is described by Croat (1978) and Foster and Brokaw (1982); in the present paper nomenclature follows Croat (1978). Considerable variation in topography occurs on BCI, with a series of narrow ridges and deep ravines radiating out in all directions from the central basaltic hill-top (Dietrich et al. 1982). Here we define slopes as sites with an upslope area that could contribute drainage while plateau sites had no upslope area (Daws et al. 2002b).

Measurements of leaf litter

Leaf litter depth was measured across the dry- to wet-season transition in 1999. Sites were sampled five times between February 21 and July 12 (Julian day 52–193). For both plateau and slope sites the number of fallen, dead leaves intersecting a knife-point at 1 m intervals along each of three 100 m transects was measured in undisturbed forest understorey (methods follow Molofsky and Augspurger 1992). New transects were measured on each occasion to avoid disturbance caused by earlier measurements.

Effect of topographic position and leaf litter on seedling recruitment

Within each of three catchments, twelve 1 × 2 m plots were established in undisturbed forest understorey, prior to the commencement of the 1999 wet-season. The timing of plot establishment ensured no newly emerged seedlings were already present in the plots. The plots were located adjacent to the following trails on BCI (numbers in brackets refer to the distance from the start of the trail in metres): Donato (300), Lathrop (300) and Snyder-Molino (0). Six plots per catchment were located on slope sites, approximately 10–15 m from the slope bottom, and six on adjacent plateau sites. At each site, three plots were randomly assigned to a litter free treatment while the other three had an intact litter layer. Since litter depth on slopes was less than plateau sites (see Figure 1), additional litter was added to ensure slope sites had an equivalent depth of litter. Although adding/removing leaf litter may affect the soil seed bank within the plots, this was minimised by carefully shaking litter, prior to transfer, to remove loose seeds. At each census, litter was removed from the litter free plots and the litter depth on the with litter slope plots maintained at the same depth as on the with litter plateau sites.

All new seedling recruits appearing in the plots were censused every two to four weeks and where possible identified to at least genus level. Plots were censused a total of 29 times over the period 18 April 1999 to 16 June 2000 (Julian day 108–533). To follow survival, seedlings were marked with coloured toothpicks, and their position within the plot mapped.

For six consecutive days in July 1999, photosynthetically active radiation (PAR) was measured adjacent to both the slope and plateau plots in the Lutz catchment using a PAR sensor (SKP 215, Skye Instruments, Llandrindod Wells, UK) connected to a data logger (Datahog, Skye Instruments). Measurements were recorded every 10 s
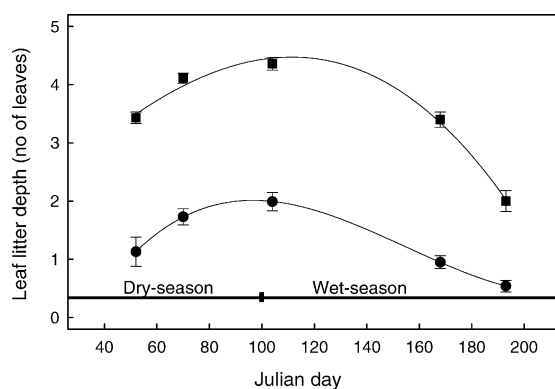

Figure 1. Mean ±1 standard error leaf litter depth across the dry- to wet-season transition in 1999 for plateau sites (■) and slope sites (●) on BCI.

and integrated over 10 min intervals for the entire 6-day-period.

Statistical methods

Since for each sampling time the location of transects was different, and thus statistically independent, the effects of time and topographic position on leaf litter depth were tested using two-way ANOVA implemented in Genstat 5 (4th Edition, Lawes Agricultural Trust, IACR Rothamsted).

The effect of topographic position and litter on the total number of seedlings to emerge and the final number to survive at the end of the first dry-season, was tested on $\ln(x + 1)$ transformed seedling counts using split-plot ANOVA in Genstat 5 with topographic position (slope or plateau) as the 'plot' unit replicated across three catchments. With and without litter treatments were arranged within each plot and treated as the 'within-plot' units.

Mantel tests were used to test for a correlation between geographic distance (Euclidian distance) between topographic positions, within and between catchments, and seedling composition. In addition, partial Mantel tests were used to investigate correlations between topographic position and seedling composition while accounting for the spatial separation of plots or the presence/absence of litter. Similar analyses were also conducted for the effect of litter. Dissimilarity matrices were created for the 36 plots based on species abundance data using the Sørenson coefficient of dissimilarity, the two treatments (litter or topographic position) and geographic distance. Subsequently, the (partial) Mantel correlation coefficients (r) were calculated using XLSTAT version 6.1.9 (Addinsoft, Brooklyn, NY, USA) with the significance of r tested by comparison to a reference distribution obtained under the null hypothesis of no partial correlation between the two matrices. This distribution was obtained by permuting the arrangement of the elements of matrix 1 10,000 times, each time computing the Mantel statistic. The significance of the observed Mantel value was assessed by comparison to the number of times the permuted values were smaller than, equal to, or greater than the Mantel statistic for the actual data (Fortin and Gurevitch 2001).

Mean seedling mortality rates for each seedling plot were calculated for each census interval using the equation:

$$m = 1 - [1 - (N_0 - N_1)/N_0]^{1/t} \qquad (1)$$

where N_0 and N_1 refer to seedling counts at the beginning and end of the census interval and t is the length of the census interval in days (Sheil et al. 1995). Subsequently the mean mortality rate was calculated for both the wet- (defined as 10 April 1999 to 9 January 2000, Julian day 100–374) and dry-seasons (defined as 10 January to 19 April 2000 Julian day 375–475) and compared using Wilcoxon's signed-ranks test (Sokal and Rohlf 1995).

For each seedling, that could be identified to at least genus level (see Appendix 1 for species list), the probability of mortality by the end of the first wet-season (assumed to be Julian day 365) was examined with respect to (1) site (six categories, 1–6) to account for any potential site specific effects on seedling survival, (2) topographic position (two categories; slope or plateau), (3) leaf litter treatment (two categories; plus or minus), (4) seed mass (seven categories, representing seed mass values on a –[$\log_{10}$] scale from 0.01–0.1 mg to 10–100 g with 1 representing seeds of mass 10–100 g and 7 seeds of mass 0.01–0.1 mg, see Appendix 1), (5) con-generic or con-specific seedling density at the time of emergence, and (6) emergence date (three categories; early- (1; Julian day 132–210), mid- (2; Julian day 211–288) and late- (3; Julian day 289–365) wet-season) using the binary logistic regression analysis procedure of Minitab 13 (Minitab Inc., PA, USA). All identifiable seedlings that either died by the end of the wet-season (959) or survived to the end of the wet-season (364) were included in the analysis. The seed mass scale was derived from Foster (1982) and seed mass values were collated from various sources (Foster 1982; N.C. Garwood pers comm; Augspurger 1984; Harms and Dalling 1997; Tweddle et al. 2003). Masses were available for all identifiable taxa, except *Hirtella* spp., *Hura crepitans*, and *Pachyptera kerere*. This totalled three individuals (Appendix 1) which were excluded from the analysis. The probability of mortality during the dry-season (assumed to be Julian days 366–486) was also examined with respect to the above factors. This analysis included 185 individuals that died during the dry-season and 177 individuals that

survived to the end of the dry-season. To evaluate the contribution of each main factor to the full logistic model containing all six terms, the logistic regression analysis was repeated for all possible five-term reduced models followed by likelihood ratio tests, where $G = 2[\log L_{full} - \log L_{reduced}]$, and G is distributed as χ^2 with 1 d.f., to determine the significance of the change in log-likelihood after removal of each term (Tabachnick and Fidell 2001). To assess the contribution of two-way interactions to explaining seedling mortality, a full model containing all the significant main effect terms and all possible two-way interactions using these terms was compared with all possible reduced models from which one interaction term was removed, using likelihood ratio tests as above.

Results

Irradiance and leaf litter measurements

Measurements of PAR over the course of six days in July 1999 for the slope and plateau sites in the Lutz catchment revealed that irradiance was similar between sites: PAR (± 1 standard deviation) was 1.95 ± 3.27 and $1.95 \pm 3.77\%$ of full irradiance on the slope and plateau sites, respectively.

As the dry-season progressed (to approximately Julian day 120) leaf litter depth increased and then decreased steadily after the onset of the wet-season (approximately post-day 120) on both plateau and slope sites. There was always significantly more litter on plateau than slope sites (two-way ANOVA, $F_{1,2996} = 494.87$, $p < 0.001$; Figure 1). The percentage of sampling points without any leaf litter was greater on slope than plateau sites and followed the same seasonal trend as leaf litter depth. At the end of the dry-season (day 120) 20% of sampling points on slopes had no leaf litter compared to 0% on plateau sites. As the wet-season progressed to day 193, 50% of sampling points on slopes had no leaf litter compared to only 9% on plateau sites.

Seedling emergence and cohort composition

A total of 1857 seedlings were censused as emergents in the plots. Of these, 1323 seedlings from 59 taxa were identified to at least genus level. The

majority of identifiable taxa were trees or shrubs (46), followed by lianas and vines (11) and herbs (2). Seedling emergence commenced within 18 days of the start of the experiment and emergence rates were initially high, but declined to almost zero towards the end of the wet-season (Figure 2a). However, with the commencement of the second wet-season, seedling emergence rapidly increased again (Figure 2a). The majority (15 of 20) of the most abundant species in the plots exhibited maximum emergence within the first 60 days of the wet-season (i.e. Julian day 132–192) although for several species the peak of emergence occurred later (Figure 3). For example, *Randia*
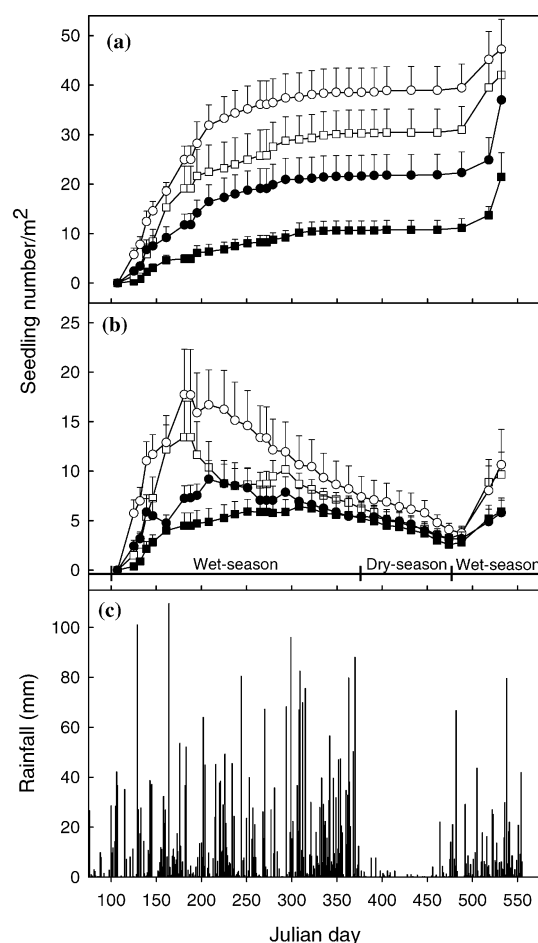

Figure 2. Mean ± 1 standard error for (a) cumulative seedling emergence, (b) total number of surviving seedlings from Julian day 108 (18 April 1999) to day 533 (16 June 2000) on plateau sites (■ and □) and slope sites (● and ○); open symbols are minus leaf litter and solid symbols plus leaf litter treatments and (c) daily rainfall on BCI for the same interval.

armata (Rubiaceae) had a mean emergence date between Julian days 310 and 330, which is close to the end of the wet-season.

Over 50 weeks, cumulative seedling emergence was significantly lower on plateau sites than slopes and in the presence of leaf litter (Figure 2a, split-plot ANOVA, $F_{1,2} = 33.27$, $p = 0.029$ and $F_{1,4} = 36.83, p = 0.004$ for topographic and litter effects, respectively). There was no statistically significant interaction between topographic position and leaf litter (split-plot ANOVA, $F_{1,4} = 0.13, p = 0.79$).

Seedling composition was correlated with both geographical distance between sites (Mantel test, $r = 0.36$, $p < 0.001$) and topographic position (whilst holding either the effect of litter or geographic distance constant) (Partial Mantel test, $r = 0.19$, $p < 0.001$ and $r = 0.17$, $p = 0.002$, holding litter and geographic distance constant, respectively). There was no correlation between composition and presence/absence of litter while holding the effects of topography or geographic distance constant (Partial Mantel test, $r = 0.04$, $p = 0.16$ and $r = 0.05$, $p = 0.10$ holding topographic position and distance constant, respectively).

Seedling mortality

By the end of the first wet-season 72% of emergent seedlings had died, and a further 17% had died by the end of the dry-season. Final mortality was highest on slopes in the absence of litter and lowest on plateau sites with litter (Figure 2b). There were
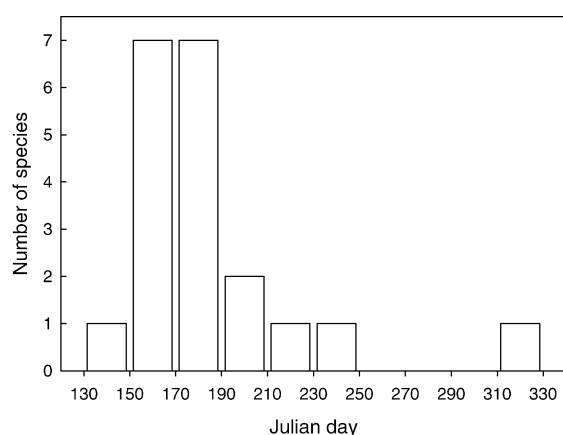

Figure 3. Frequency distribution of mean emergence date for the 20 most abundant, identifiable taxa.

no significant differences in surviving seedling counts at the end of the dry-season either between slopes and plateau sites or between plus and minus litter (split-plot ANOVA, $F_{1,2} = 0.01$, $p = 0.946$ and $F_{1,4} = 0.093$, $p = 0.308$, for topographic position and leaf litter respectively). Seedlings were most likely to die shortly after emergence, with 50% of all seedlings that died doing so within six weeks of emerging. Mean seedling mortality rates for the 36 plots were significantly higher during the wet- than dry-season (0.011 compared to 0.006 d^{-1}; Wilcoxon's signed-ranks test $T_s = 59$, $p < 0.005$).

Binary logistic regression indicated that the best model for predicting the probability of seedling mortality during the wet-season included topographic position, leaf litter and seed mass (Table 1):

$$\text{logit(probability of mortality)}$$
$$= -1.8771 + 0.9796(a) - 0.3964(b)$$
$$+ 0.5922(c) \tag{2}$$

where a is topographic position (0 plateau, 1 slope), b is leaf litter (0 minus litter, 1 plus litter) and c is seed mass class (2–7). Thus, the probability of mortality was lower in the presence of leaf litter, for seedlings on plateau sites and for larger seeded species and genera (Figure 4a).

The best model for predicting dry-season mortality included the effects of topographic position, emergence date and seed mass (Table 1):

$$\text{logit(probability of mortality)}$$
$$= -0.3399 - 1.3379(a) + 0.2975(c)$$
$$+ 0.4598(d) \tag{3}$$

where a is topographic position (0 plateau, 1 slope), c is seed mass class (2–7) and d is emergence interval (1 early-, 2 mid- and 3 late-wet season). Thus, the probability of mortality was lower on slopes and for large seeded species (Figure 4b) as well as for seedlings that emerged earlier in the wet-season (Figure 5).

Discussion

Seedling emergence and composition

In this study, the mean number of seedlings to emerge was 26 m^{-2}. Similarly, Garwood (1983)

Table 1. Log likelihood ratio test for each five parameter reduced logistic model compared to the full six parameter model for wet- and dry-season mortality. Subsequently, reduced models from which each of the possible two-way interactions were removed in turn, were compared to a full model, which included all terms except location, emergence date and seedling density. Values for the log-likelihood test are presented for each reduced model, compared to the full model, in addition to the associated *p*-value for χ^2 with d.f. = 1.

| Term removed from full model	Log-likelihood		2[log L_{full} − log $L_{reduced}$]	
	Wet-season	Dry-season	Wet-season	Dry-season
None	−722.837	−234.057	−	−
Location	−723.022	−234.848	0.370	1.582
Topographic position	−725.619	−236.333	5.564*	4.552*
Leaf litter	−725.655	−234.188	5.636*	0.262
Emergence date	−723.796	−236.953	1.918	5.792*
Seed mass	−731.549	−236.187	17.424**	4.260*
Seedling density	−723.904	−237.712	2.134	2.864
None	−730.797	−232.384	−	−
Topographic position* litter	−730.937	−232.500	0.280	0.232
Topographic position * seed mass	−731.089	−233.353	0.584	1.938
Leaf litter * seed mass	−731.301	−233.439	1.008	2.110

* $p < 0.05$; ** $p < 0.001$.
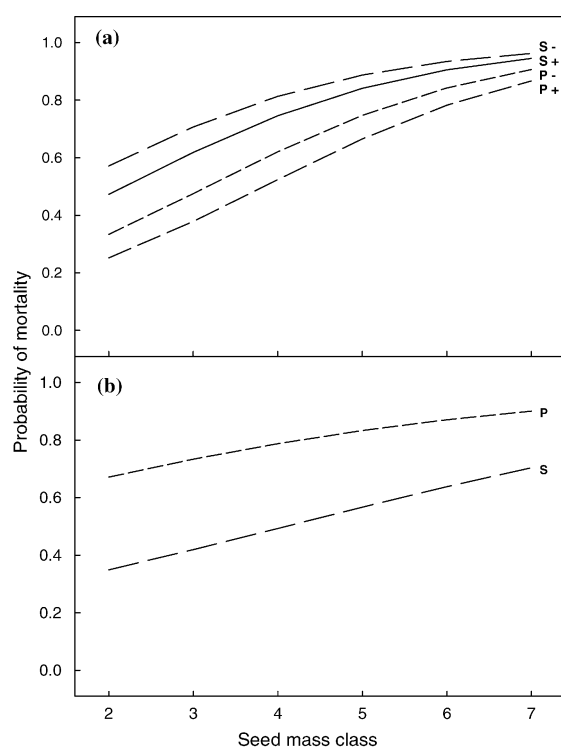
Figure 4. (a) The effect of leaf litter, topographic position and seed size on the probability of seedling mortality during the wet-season and (b) the effect of seed size class [with 2 referring to the largest seeds and 7 the smallest: see Materials and methods] and topographic position on seedling mortality during the dry-season for seedlings that emerged early in the wet-season. P +, P −, S + and S − refer to plateau plus litter, plateau minus litter, slope plus litter and slope minus litter, respectively.

recorded an average number of emergents on BCI of 29 m^{-2}. Seedling emergence peaked early in the wet-season with several species emerging later in the wet-season; a pattern also observed by Garwood (1983). Daubenmire (1972) suggested that early emergence will maximise the length of the first growing season and allow the development of a potentially large root system, which may increase seedling survival during the first dry-season. Although we found that later emerging seedlings were less likely to survive the ensuing
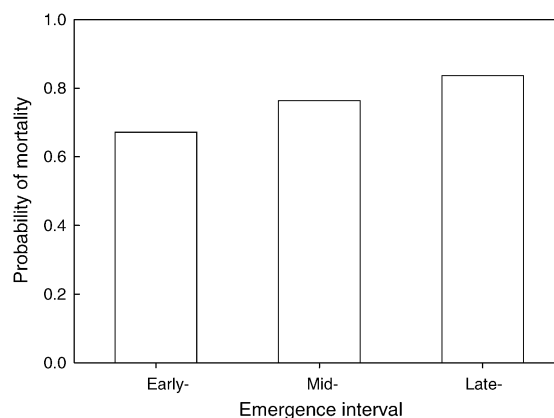

Figure 5. The effect of timing of seedling emergence, during the wet-season (early-, mid- or late-wet season), on the probability of mortality during the following dry-season for species in seed mass class 2 on plateau sites.

dry-season, several species (in particular *Randia armata*) exhibited a peak in emergence late in the wet-season, This suggests that attaining as large a size as possible prior to the dry-season is not the only factor determining the timing of emergence. In support of this proposition Garwood (1983) found that later emerging seedlings were not initially larger at germination than those that emerged early in the wet-season. Consequently, the observed spread of emergence times may reflect opposing selection for early emergence, to increase dry-season survival, and selection for late emergence, to reduce inter-seedling competition for resources.

For many tropical tree species, seedling emergence is higher under high than low light conditions (Raich and Khoon 1990). However, since differences in light levels between positions were negligible (see Results) this phenomenon is unlikely to have caused the observed differences in seedling numbers between topographic positions. Instead differences in seedling numbers may have been caused by a higher soil water potential on slopes (Daws et al. 2002b) which would result in more rapid germination and a higher percentage germination of seeds in the seed bank (Daws et al. 2002a). A second contributory factor may also be the higher density of trees and shrubs and a greater seed rain on slopes (Harms 1997).

In accordance with various studies in tropical forests (for example, Harms 1997; Svenning 1999; Debski et al. 2000; Harms et al. 2001; Segura et al. 2003) we found that species composition differed between slope and plateau sites. However, there were also differences in composition between catchments which correlated with the geographic separation of the study sites, suggesting that both niche partitioning and dispersal limitation contribute to structuring seedling community composition.

For both topographic positions, litter reduced emergence by approximately 50%, presumably by acting as a physical barrier to seedlings (Molofsky and Augspurger 1992) and preventing germination of photoblastic species (Vázquez-Yanes et al. 1990). Small-seeded species might be most affected by litter as they lack the resources to emerge through deep litter (Everham et al. 1996; Metcalfe and Turner 1998) and are more likely to require light for germination (Pearson et al. 2002). However, despite reducing seedling numbers, litter had little effect on species composition. Similarly, Dalling and Hubbell (2002) found that in canopy gaps in Panamá litter reduced seedling numbers but had little effect on composition. These observations suggest litter reduces the emergence of all species and that some individuals of small-seeded species (for example *Piper* spp.) are able to emerge despite the presence of litter. Presumably, small-seeded species emerge from gaps in the litter rather than the elongating shoot forcing litter out of the way (Metcalfe and Turner 1998).

Seedling mortality

Mortality over the 12 month study period was high (88.6%) in agreement with other studies, for both tropical (e.g. deSteven 1994; Gilbert et al. 2001) and temperate seedlings (e.g. Silvertown and Dickie 1980). For the BCI 50 ha plot, Harms et al. (2000) reported an annual seed rain of 1970 seeds m^{-2}. Thus, a total emergent density of 25.8 seedlings m^{-2} (this study) corresponds to ca. 98.7% mortality between these stages. Condit et al. (1996) reported a total stem density for stems greater than 1 cm dbh, in the 50 ha plot on BCI of 0.484 m^{-2}, which corresponds to a ca. 98.1% decrease in seedling numbers between emergence and reaching 1 cm dbh. These levels of seed and seedling mortality support the hypothesis that species-specific responses to the environment are most likely to be apparent at these early stages.

The greater mortality rate in the wet-season than following dry-season suggests the wet-season is the greater barrier to seedling establishment. High wet-season mortality rates may result from intense rainfall preventing seedling establishment or reflect higher activity of seedling pathogens resulting from high relative humidity levels (Cook and Papendick 1972). During the wet-season, mortality rates were higher on slope than plateau sites. Seedlings on slopes may be damaged by overland flow during intense rainfall or the wetter water regime may encourage bacterial or fungal attack on seedlings (Cook and Papendick 1972). However, during the dry-season, this pattern was reversed which may reflect the higher soil matric potential on slopes reducing the impact of dry-season drought.

In this study, leaf litter reduced wet-season seedling mortality. Other studies have found that

litter can influence mortality by increasing (Facelli 1994) or decreasing (Benitez-Malvido and Kossmann-Ferraz 1999) arthropod herbivory. Litter can also reduce water loss from the soil surface thereby ameliorating the effect of short dry periods (Myster 1994). However, the lack of a litter effect on dry-season mortality suggests this was unimportant in the current study. The combination of deep litter on plateau sites and shallow litter on slopes creates two strongly contrasting habitats that might be expected to influence seedling emergence. However, the lack of either a statistically significant difference in seedling numbers at the end of the first dry-season or a litter effect on composition, suggests that in this forest, litter is unimportant for structuring community composition.

Seedlings from small seeds always had a higher probability of mortality than those from large seeds, irrespective of season, topographic position or leaf litter. Larger seeds produce bigger seedlings which have a greater chance of survival under unfavourable conditions or in the event of damage caused by pathogens, herbivores or falling debris (Crawley and Nachapong 1985; Armstrong and Westoby 1993; Leishman and Westoby 1994; Harms and Dalling 1997; Leishman et al. 2000). In addition, seedlings from small seeds have lower root growth rates than those from larger seeds (Daws et al. 2003), which may increase their susceptibility to dry periods, including short dry spells in the wet-season. The advantages of large seed size were maintained for a number of months after germination and were still apparent into the dry-season.

We failed to detect an effect of con-specific seedling density on mortality, although Harms et al. (2000) reported that density dependent mortality is a pervasive process on BCI. The absence of a density effect in our study suggests that, for small seedlings, the main causes of mortality are density independent. Alternatively, 2 m^2 plots may not provide a measure of con-specific seedling density at an appropriate scale for testing density effects.

Implications for species coexistence

Seedlings of species in all seed size classes were more likely to survive dry-season drought on slope than plateau sites, which suggests that slopes may provide 'safe sites' for dry-season survival. However, this positive effect was negated by elevated wet-season mortality on slopes. Consequently these two contrasting pressures resulted in similar overall seedling numbers in plots on the two topographic positions at the end of the first dry-season *post-*emergence. As wet-season mortality of small-seeded species was very high ($>80\%$) on all sites, the positive effect of slopes on dry-season survival may be particularly important for these species. Nonetheless, based on this study, differences in seedling mortality related to seed mass and water potential gradients do not provide a complete explanation for the observation that on BCI, a number of species with small seeds are restricted as adults to slope sites (e.g. Condit et al. 1996).

There is some evidence of the role of 'wet' micro-sites in facilitating seedling survival of small-seeded species in other tropical forests. For example, a study in the Bolivian Andes has shown that Melastomataceae seedlings (typically with seeds in seed mass class 7) are restricted to wet, moss covered micro-sites (Kessler 2000). However, there are also some small-seeded tropical forest species, in particular pioneers (*sensu* Swaine and Whitmore 1988) that are not restricted to 'wet' micro-sites and instead occur in canopy gaps (e.g. *Miconia argentea* with mean seed mass 0.08 mg; M.I. Daws unpublished data) where soil drying will occur rapidly (Becker et al. 1988). For small-seeded pioneers, the risk of high seedling mortality in dry micro-sites is possibly outweighed by the benefit of higher probabilities of dispersal to rare micro-sites (in this case canopy gaps) associated with small seed size. However, even among the pioneer functional group there is some evidence that small-seeded species are restricted to smaller sizes of canopy gap, where soil drying will occur more slowly (Dalling et al. 2004). Consequently more detailed studies on the role of water availability, seed size and establishment success are worth pursuing for tropical forest species.

Based on this study, differences in seedling mortality in relation to topography appear insufficient to explain the observed adult plant habitat associations on BCI and elsewhere. Nonetheless, this study demonstrates that topographic position

does impact on emergence and survival patterns and that leaf litter has limited effect on seedling community structure. Further work is needed to understand more fully the mechanisms that result in topographically induced plant distribution patterns. In particular, observations of seedlings over multiple seasons or during extreme events, such as those associated with El Niño events, may clarify the mechanisms that result in the differentiation of some species across the topographic gradient.

Appendix

Appendix 1. Taxa for which seedlings were identifiable. Also included is seed size class and the number of individuals emerging for each taxa.

Species	Family	Total number of emergents	Seed size class
Acalypha diversifolia	Euphorbiaceae	2	6
Alseis blackiana	Rubiaceae	2	6
Anacardium excelsum	Anacardiaceae	12	3
Annona acuminata	Annonaceae	6	4
Apeiba membranaceae	Tiliaceae	9	4
Aristolochia spp.	Aristolochiaceae	12	4
Arrabidaea spp.	Bignoniaceae	7	4
Astronium graveolens	Anacardiaceae	1	4
Beilschmiedia pendula	Lauraceae	8	2
Brosimum alicastrum	Moraceae	1	3
Casearia arborea	Flacourtiaceae	1	5
Cecropia spp.	Cecropiaceae	108	6
Cissus spp.	Vitaceae	2	4
Coccoloba parimensis	Polygonaceae	1	4
Commelina erecta	Commelinaceae	1	4
Cordia bicolor	Boraginaceae	1	5
Costus spp.	Zingiberaceae	1	4
Coussarea curvigemmia	Rubiaceae	45	5
Crysophyllum panamense	Sapotaceae	1	4
Dalechampia dioscoreifolia	Euphorbiaceae	23	3[a]
Davilla multiflora	Dilleniaceae	27	4
Doliocarpus olivaceus	Dilleniaceae	16	3
Faramea occidentalis	Rubiaceae	4	3
Ficus spp.	Moracaeae	28	5
Guapira standleyanum	Nyctaginacea	1	4
Guarea glabra	Meliaceae	1	3
Gustavia superba	Lecythidacae	4	2
Hasseltia floribunda	Flacourtiaceae	125	4
Heisteria concinna	Olacaceae	8	3
Hippocratea volubilis	Hippocrateaceae	18	4
Hirtella spp.	Chrysobalanaceae	1	4
Hura crepitans	Euphorbiaceae	1	4
Hybanthus prunifolius	Violaceae	73	4
Jacaranda copaia	Bignoniaceae	32	5
Lacmellea panamensis	Apocynaceae	29	3
Luehea seemannii	Tiliaceae	2	5
Mascagnia hippocrateoides	Malphigiaceae	43	5
Miconia spp.	Melastomataceae	39	7

Appendix 1. Continued.

Species	Family	Total number of emergents	Seed size class
Mouriri myrtilloides	Melastomataceae	18	4
Pachyptera kerere	Bignoniaceae	1	4
Palicourea guianensis	Rubiaceae	8	4
Passiflora spp.	Passifloraceae	4	5
Piper spp.	Piperaceae	336	5
Platypodium elegans	Leguminosae	1	3
Poulsenia armata	Moraceae	1	4
Protium panamense	Burseraceae	3	4
Pseudobombax septanatum	Bombacaceae	1	3
Psychotria spp.	Rubiaceae	190	4
Randia armata	Rubiaceae	7	4
Serjania spp.	Sapindaceae	11	4
Simarouba amara	Simaroubaceae	1	4
Solanum spp.	Solanaceae	14	5
Spondias mombin	Anacardiaceae	1	4
Tachigalia versicolor	Leguminosae	1	3
Terminalia amazonica	Combretaceae	6	5
Tetragastris panamensis	Burseraceae	3	3
Trattinnickia aspera	Burseraceae	10	4
Virola surinamensis	Myristicaceae	2	2
Zanthoxylum spp.	Rutaceae	5	5

[a]N Garwood pers comm.

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