

Bettina M. J. Engelbrecht · James W. Dalling
Timothy R. H. Pearson · Robert L. Wolf
David A. Gálvez · Tobias Koehler · Melvin T. Tyree
Thomas A. Kursar

Short dry spells in the wet season increase mortality of tropical pioneer seedlings

Received: 7 May 2005 / Accepted: 17 November 2005
© Springer-Verlag 2006

Abstract Variation in plant species performance in response to water availability offers a potential axis for temporal and spatial habitat partitioning and may therefore affect community composition in tropical forests. We hypothesized that short dry spells during the wet season are a significant source of mortality for the newly emerging seedlings of pioneer species that recruit in treefall gaps in tropical forests. An analysis of a 49-year rainfall record for three forests across a rainfall gradient in central Panama confirmed that dry spells of

≥10 days during the wet season occur on average once a year in a deciduous forest, and once every other year in a semi-deciduous moist and an evergreen wet forest. The effect of wet season dry spells on the recruitment of pioneers was investigated by comparing seedling survival in rain-protected dry plots and irrigated control plots in four large artificially created treefall gaps in a semi-deciduous tropical forest. In rain-protected plots surface soil layers dried rapidly, leading to a strong gradient in water potential within the upper 10 cm of soil. Seedling survival for six pioneer species was significantly lower in rain-protected than in irrigated control plots after only 4 days. The strength of the irrigation effect differed among species, and first became apparent 3–10 days after treatments started. Root allocation patterns were significantly, or marginally significantly, different between species and between two groups of larger and smaller seeded species. However, they were not correlated with seedling drought sensitivity, suggesting allocation is not a key trait for drought sensitivity in pioneer seedlings. Our data provide strong evidence that short dry spells in the wet season differentially affect seedling survivorship of pioneer species, and may therefore have important implications to seedling demography and community dynamics.

Communicated by Jim Ehleringer

B. M. J. Engelbrecht (✉) · R. L. Wolf · J. W. Dalling
T. R. H. Pearson · D. A. Gálvez · T. Koehler
M. T. Tyree · T. A. Kursar
Smithsonian Tropical Research Institute, Gamboa,
P.O. Box 0843-03092, Panamá, Republica de Panamá
E-mail: engelbrb@bci.si.edu

B. M. J. Engelbrecht
Department of Plant Ecology and Systematics,
Technische Universität Kaiserslautern, 67663 Kaiserslautern,
Germany

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

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

Present address: D. A. Gálvez
Departamento de Psicología, Universidad Magna,
77500 Cancún, Quintana Roo, México

Present address: T. Koehler
Department of Botany, University of Hawaii,
Hawaii, HI 96822-2279, USA

M. T. Tyree
USDA Forest Service, P.O. Box 968, Burlington,
VT 05402, USA

T. A. Kursar
Department of Biology, University of Utah,
Salt Lake City, UT 84112, USA

Keywords BCI · Diversity · Drought ·
Gap partitioning · Survival

Introduction

Annual rainfall and dry season length in the tropics have been recognized as important determinants of plant diversity and distribution, as well as of primary productivity (Lieth 1975; Gentry 1988; Veenendaal and Swaine 1998; Hawkins et al. 2003). For tropical regions that experience regular dry seasons, drought periods have been shown to have strong effects on seedling growth and mortality of forest species (e.g., Fisher et al. 1991; Mulkey and Wright 1996; Veenendaal and

Swaine 1998; Poorter and Hayashida-Oliver 2000; Daws et al. 2002; Engelbrecht and Kursar 2003). However, even aseasonal sites may experience dry spells of a few days to several weeks duration (Becker 1992; Burslem et al. 1996; Walsh and Newbery 1999). Such less predictable events have received little attention, but may also influence forest composition, particularly if they occur during seasonal peaks in seedling recruitment.

The initial seedling stages of pioneer species may be especially vulnerable to short dry spells, as most have small seeds (<10 mg; Swaine and Whitmore 1988) and hence small initial seedling size. In many forests, pioneers recruit exclusively in gaps created by treefalls (Swaine and Whitmore 1988; Dalling and Hubbell 2002), which are exposed to high levels of irradiance and consequently show higher air and soil temperature, and lower relative air humidity, than the surrounding understory (Ashton 1992; Brown 1993). Under these conditions, superficial soil layers may dry out quickly, and seedlings recruiting in gaps should show high transpiration rates. Even short rainless periods may induce drought stress and mortality, and may either constrain overall recruitment success or influence species relative abundance.

Previous work provides evidence that pioneer species partition gaps according to size and substrate conditions (Brokaw 1987; Brandani et al. 1988; van der Meer et al. 1998; Dalling et al. 1998). This has been attributed mainly to a trade-off between seedling growth and mortality rates under different light conditions (Dalling et al. 1998; Dalling and Hubbell 2002), with elevated mortality of the fastest growing species apparent in the dry season (Pearson et al. 2003a, b). Sensitivity to drought stress during emergence and establishment may provide an additional mechanism contributing to species coexistence among pioneers. Since small seeded species are only capable of successful emergence from the surface few millimeters of soil (Pearson et al. 2002) we predict that they will be particularly susceptible to surface drying events.

We thus hypothesized that short dry spells in the wet season are a significant source of seedling mortality for pioneers recruiting on exposed soil in gaps in tropical forests, with small seeded and shallow-rooted species most at risk to desiccation. Although circumstantial evidence suggests that dry spells during the rainy seasons are an important cause for pioneer seedling mortality in gaps (e.g., Brown and Whitmore 1992; Dalling and Hubbell 2002), their potential impact on initial pioneer seedling mortality has not yet been addressed.

To determine whether short dry spells could influence pioneer recruitment success we first analyzed the frequency and length of wet season dry spells from 49 years of rainfall records from a rainfall gradient across the Isthmus of Panama. Then, to test our hypotheses that dry spells reduce seedling survivorship, we experimentally enhanced a natural dry spell during the wet season,

and recorded survival of six pioneer species sown into control and irrigated plots in large artificially created gaps. To determine whether these treatments effectively altered soil moisture conditions we tracked soil water potentials through the experiment. Finally, we evaluated whether differences in the allocation patterns among species contributed to variation of drought sensitivity from measurements made on harvested seedlings at the end of the experiment.

Materials and methods

Study site

The study was conducted in Panama at the Barro Colorado Nature Monument (BCNM), a 5,600-ha forested area administered by the Smithsonian Tropical Research Institute, which includes Barro Colorado Island (BCI) in Gatun Lake and the adjacent peninsulas on the mainland. Field experiments in this study were conducted in a semi-deciduous secondary forest (about 60 years old, 20 m canopy height) at the Buena Vista Peninsula, about 1 km north of the BCI. The area has a long-term mean annual rainfall of approximately 2,600 mm (see below for details) with a pronounced dry season from mid-December through mid-April. The wet season receives 90% of the annual rainfall (for details see Leigh 1999).

Study species

We selected six abundant pioneer species for the study: *Apeiba aspera* Spruce ex Benth. (Tiliaceae), *Ochroma pyramidale* (Cav. ex Lam.) Urban (Bombacaceae), *Luehea seemanii* Tr. & Planch. (Tiliaceae), *Miconia argentea* (Sw.) D.C. (Melastomataceae), *Cecropia insignis* Liebm. (Urticaceae) and *Piper marginatum* Jacq. (Piperaceae). The six study species can be divided by seed weight into two groups: *Miconia*, *Piper* and *Cecropia* have significantly smaller seed mass than the larger seeded species *Luehea*, *Ochroma* and *Apeiba* (Table 1, *t*-test on log-transformed data: $t=3.972$, $P<0.05$). All these species are characterized by gap requirement for regeneration, high maximum growth rates and small seeds (Dalling et al. 2004; Daws et al. 2002; B. Engelbrecht, unpublished data and personal observation). Following the opening of a canopy gap, they typically germinate during the early to mid-wet season (Dalling and Hubbell 2002).

Seeds for the field and greenhouse experiments were collected in the BCNM at the end of the dry season (April 2000) from at least three maternal sources for each species. All seeds were cleaned, thoroughly mixed, and dried for storage until the beginning of the experiment. Seeds of *Luehea*, *Ochroma* and *Apeiba* were heat-pretreated immediately before sowing to ensure high germination rates (Table 1).

Table 1 Species, fresh seed mass (+ ISE), mean seedling age at the start of the experiment (days), the number of seeds initially sown into each treatment plot, seed pretreatments used to break

dormancy, date of sowing, and observed gap size requirements (Brokaw 1987; J. W. Dalling, unpublished data; B. Engelbrecht, personal observation)

Species	Seed mass (mg)	Mean seedling age at treatment start	No. of seeds sown per plot	Pretreatment of seeds	Date of sowing	Gap size requirements
<i>Miconia</i>	0.063 ± 0.002	15.9 ± 3.1	600	–	6/02/2000	Small
<i>Piper</i>	0.164 ± 0.006	9.1 ± 2.4	750	–	5/28/2000	Clearings
<i>Cecropia</i>	0.484 ± 0.015	14.1 ± 1.7	300	–	6/05/2000	Medium
<i>Luehea</i>	1.667 ± 0.114	17.9 ± 3.4	100	In 70°C water, 2 min	6/11/2000	Small
<i>Ochroma</i>	5.638 ± 0.076	14.2 ± 5.7	250	In 100°C water, 30 s	6/11/2000	Large
<i>Apeiba</i>	14.072 ± 1.123	9.0 ± 2.4	100	In 70°C water, 2 min	6/09/2000	Small

Frequency of dry spells in the wet season

To evaluate the potential importance of wet season dry spells on seedling survival, we analyzed the frequency and length of dry periods from a 49-year rainfall record (1953–2002) for three sites along a north–south rainfall gradient across the Isthmus of Panama. The sites were Balboa Heights on the drier Pacific site of the Isthmus (supporting deciduous dry forest, long-term average rainfall 1,800 ± 266 mm, average ± SD over 94 years), BCI (semi-deciduous moist forest, 2,578 ± 497 mm, 74 years) and Gatun on the wet Caribbean side of the Isthmus (evergreen wet forest, 3,016 ± 541 mm, 95 years). Rainfall data were provided by the Terrestrial-Environmental Sciences Program of the Smithsonian Tropical Research Institute (T-ESP) and by the Meteorology and Hydrology Branch of the Panama Canal Authority, Republic of Panama (ESP 2005). In this study, dry days were defined as days in which rainfall was less than evapotranspiration. Average daily evapotranspiration in the wet season on BCI is 2.8 mm (May–November, 1993–2000, ESP 2005). Since no further evapotranspiration data are available from the Isthmus, we assumed equal evapotranspiration across the Isthmus. Dates for the beginning and end of the wet season were adopted from the Panama Canal Authority (ESP 2005). They used a metric that tracks 11 variables (ESP 2005), among them measures of rainfall, windspeed and direction, air humidity and evaporation. These data are available since 1953. We generated frequency histograms of the length of dry spells in the wet season for the three sites using the program RAIN (M.T. Tyree, unpublished) for the period 1953–2002.

Experimental study of drought survival in the field

To study the effect of short dry spells on wet season seedling mortality, we established 32 seedling plots in four 15 × 15 m² gaps on the Buena Vista Peninsula, BCNM. Gaps in the forest were created by felling and removing all vegetation, including the sparsely developed understory. Eight 1.30 × 0.80 m² plots were established at least 1 m apart along the north and west sides of these gaps to ensure maximum daily sun exposure. All

plots were kept free of litter for the duration of the experiment. Litter was removed to maximize germination of light sensitive seeds (Vazquez-Yanes et al. 1990; Pearson et al. 2003c). A prior study conducted at the same site indicated that litter removal does not affect post-establishment mortality of pioneers species (Dalling and Hubbell 2002). We systematically assigned alternating plots to two treatments: dry (sheltered) or wet (irrigated and sheltered); for details see below.

Seeds were sown in at the beginning of the wet season in May/June 2000 (after a period of high rainfall), with seeds of all species spread evenly through all the plots. Seeds of the six pioneer species were sown into the plots in sequence (Table 1), to allow for approximately synchronous germination. The number of seeds sown was based on germination success in greenhouse trials, and was chosen to obtain a minimum of 30 emergent seedlings of each species per plot. The emergence and mortality of individual seedlings was monitored within a grid of 0.10 × 0.10 m² quadrats at 3- to 5-day intervals starting in mid-June for 4 weeks before the treatments were started. To facilitate tracking the fate of individuals, seedlings were tagged with color-coded toothpicks according to species and emergence date.

The treatments were started on 10 July 2000 (day 0), 1 day after the beginning of a natural dry spell, after almost 8,500 seedlings had emerged. All plots were covered with transparent plastic sheets, 60-cm high at the highest point, and extending 20 cm past the edge of the plots to minimize effects of rain splash or lateral soil water movement. The irrigation plots were hand watered daily to receive 18 mm of water (equivalent to 540 mm monthly rainfall). Water was rain-water collected in the gaps, or water from nearby Gatun Lake, which is extremely nutrient poor (Yavitt and Wright 2001).

After the treatments were started, mortality of all seedlings was censused daily in the mornings, except on one day with heavy morning rain. Seedlings were recorded as dead if they had no living above-ground tissue (including stems), or if they had disappeared. Parallel studies in the growing house confirmed that apparently dead seedlings were unable to recover following rewetting (B. Engelbrecht, unpublished data). New seedling emergence was no longer followed once treatments began; seedlings that emerged directly next to existing ones were removed to avoid confusion.

Microclimatic and environmental conditions in the plots

Light conditions in the plots were assessed using hemispherical photographs taken directly over the middle of each plot with a digital camera and fisheye lens (Model Coolpix-950, Nikon, Melville, NY, USA). Photographs were analyzed using Hemiview 2.1 (Delta-T Devices, Cambridge, UK), yielding an estimate of the global site factor (GSF), the percentage of total photosynthetic photon flux density (PPFD) incident above the canopy that reached the gap surface. GSF was calculated under the assumption that in July on BCI direct and indirect light contribute 32 and 68% of the total light, respectively (calculated from Becker 1987 and ESP 2005). Average GSF for all four gaps was $26 \pm 3\%$ (18 ± 1 , 22 ± 1 , 29 ± 2 and $33 \pm 3\%$ in the individual gaps, $n=8$, mean \pm SE). Additionally, PPFD was measured directly during the study using a quantum sensor and datalogger SKP216 and Datalog (Skye Instruments, Llandrindod Wells, UK) located in the center of the largest gap (Fig. 1c). Illustrative soil surface temperatures (2 mm depth) were taken next to the PPFD sensor using a bead thermistor attached to the same data logger (Fig. 1b). Daily rainfall during the study was monitored in the lab clearing on BCI (Fig. 1a, data from ESP 2005).

PPFD during the experiment was similar to the preceding and following periods, i.e., PPFD values measured on top of a canopy tower on BCI during the experiment (ESP 2005) were not different from that for June, the remaining days of July, or August (t -test: $P=0.33$). To quantify the effect of the plastic covers on microclimate, we measured PPFD and soil surface temperature below the plastic cover and next to it in the open for 1 week, directly before the start of the experiment. Conditions under the plastic covers compared to the open were subject to short-term variation, with an overall average reduction of daytime PPFD (0600–1830 hours) by $18.5 \pm 19.5\%$ and a reduction of temperatures at the soil surface by $0.7 \pm 1.9^\circ\text{C}$ (average \pm SD). Temperature reductions were most pronounced during temperature peaks so that the maximum measured temperature in the open was 54.2°C , whereas under the plastic cover it was 42.3°C during this interval.

After the treatments were started, soil water potentials were measured daily (except on day 5) at a random location in each plot. Soil samples of approximately 0.5-ml volume were collected at noon (1130–1230 hours, local time) from 0.5–1 cm depth, and immediately placed in psychrometer chambers (leaf cutter psychrometers, Merrill Specialty Equipment, Logan, Utah). Chambers were allowed to equilibrate for 3.5 h to room temperature (approximately 23°C), and water potentials determined after 15 and 45 s cooling time (CR7, Campbell Scientific Equipment, Logan, Utah, USA). We used temperature corrected measurements with 15 s cooling time for measurements above -2.5 MPa, and 45 s cooling time for measurements below -2.5 MPa, using appropriate calibration curves. Additionally, after

8 days of treatment, we measured soil water potential profiles of the upper 10 cm of soil for one non-irrigated plot in each gap. Directly adjacent to the plots and under the plastic cover, a hole about 15 cm deep was excavated with one smooth vertical wall. Within 10 min after opening the hole, soil samples were removed with a spatula at five assigned depths (0–0.5, 0.5–1, 1.5–2, 4–4.5 and 9.5–10 cm, measured with a ruler), removing and discarding the air-exposed outer 5 mm, and immediately placed in the psychrometer chambers. Water potential measurements were taken as described above.

Allocation patterns

At the end of the experiment, 7–13 individuals of each species were harvested from the irrigated plots and their

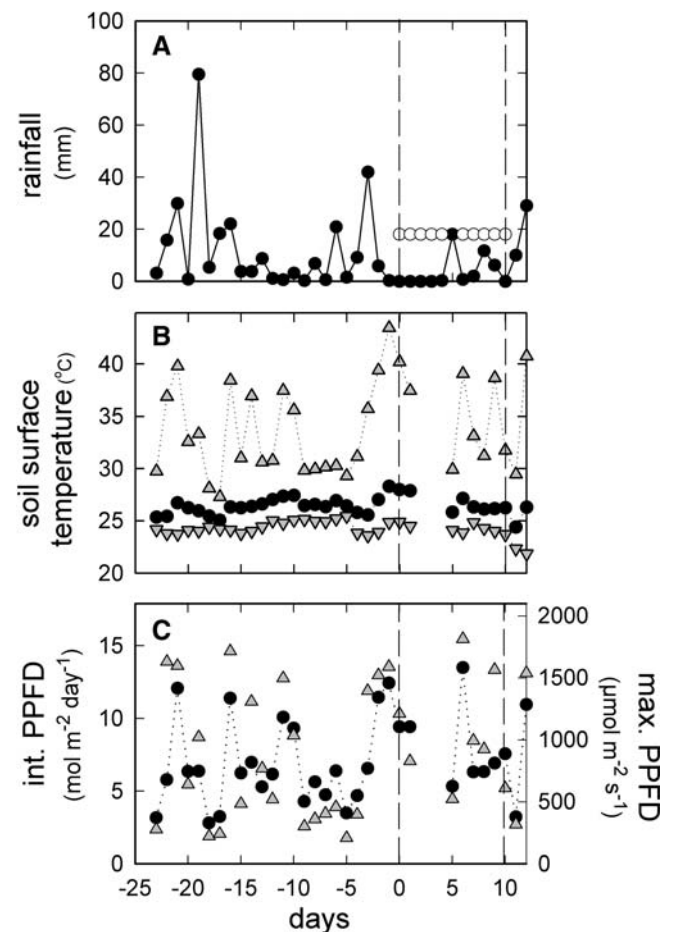


Fig. 1 Rainfall (a), soil surface temperatures (b), and light conditions (c) before and during the drought experiment at Buena Vista, Panama. The dashed vertical lines mark the beginning and the end of the experiment (with day 0 as the first treatment day). Rainfall is for the laboratory clearing on BCI, the open symbols give the amount of water added in the irrigation treatments. Soil surface temperatures are average (filled circle), minimum (inverted open triangle) and maximum (open triangle) temperatures exemplarily measured in the most open gap. Light conditions are integrated (filled circle) and maximum PPFD (open triangle). Data for days 2–5 are missing due to technical difficulties

allocation patterns determined. The individuals were chosen to represent the available age range for each species, but were selected randomly with respect to size. The plants were extracted in the field with their rooted soil volume intact, and were washed and processed in the laboratory. Leaf areas were calculated from measurements of leaf lengths and widths, using the regression of leaf area on length \times width for each species. Leaf area measurements were taken by scanning leaves and analyzing them with Delta-T Scan (Delta-T Devices). The regressions were derived from the measurements of at least ten leaves and ten cotyledons per species. All R^2 values were >0.9 . As a measure of rooting depth, the maximum extension parallel to the direction of the stem was measured on roots suspended in a water-filled clear-bottom tray. Dry weights of leaves, shoots and roots of each plant were determined separately on a 6-figure balance, after drying in an oven at 70°C for 48 h. From these measurements, we calculated total biomass, root mass fraction (root mass divided by whole plant biomass) and the rooting depth per leaf area for each individual.

Data analysis

Seedling survivorship was analyzed as a nested repeated measures ANOVA (Table 2) using PROC MIXED in SAS (SAS Institute, Cary, N.C., USA). Analysis of variance rather than survival analysis was appropriate as the fate of a single cohort of seedlings present when treatments were initiated was tracked over time. The dependent variable was the arcsin-transformed proportion of the initial cohort of seedlings surviving of each species in each plot repeated for each day. We analyzed proportional data because the plots had different numbers of initial germinants. The mean age of seedlings

Table 2 Nested repeated measures analysis of variance performed on arcsine-transformed survival data using PROC MIXED in SAS for six pioneer species grown in irrigated and dry plots in four artificial treefall gaps

Effect	<i>df</i>	<i>F</i>	<i>P</i>
Irrigation	1, 3.38	15.91	0.022
Species	5, 173	7.75	<0.0001
Day	9, 237	23.27	<0.0001
Irrigation \times species	5, 174	1.15	0.337
Irrigation \times day	9, 237	7.16	<0.0001
Irrigation \times species \times day	90, 237	0.85	0.814
Tests of irrigation effect by species			
<i>Miconia</i>	1, 45	3.68	0.061
<i>Piper</i>	1, 45	1.50	0.228
<i>Cecropia</i>	1, 45	2.25	0.140
<i>Luehea</i>	1, 49.4	0.71	0.403
<i>Ochroma</i>	1, 67.3	12.29	<0.001
<i>Apeiba</i>	1, 62.1	4.33	0.042

Degrees of freedom are Satterthwaite-adjusted for heterogeneous error variance. Tests of the overall effect of the irrigation treatment on survival for each species (from the species \times irrigation interaction) are shown separately

for each plot \times species combination when treatments were initiated was used as a covariate, but did not explain significant variation in seedling survival and was dropped from the model. After model simplification and tests of normality and homogeneity of variance, post hoc comparisons were made for each species \times treatment \times day to determine after how many days survivorship diverged significantly between irrigated and dry plots (Table 3, Fig. 4).

The strength of treatment effects on seedling survival at the end of the experiment (using data from day 10) was assessed in two ways: first, we calculated species drought sensitivity index (DS), a measure of species susceptibility to drought, defined as the reduction in survival in the dry compared to the irrigated treatment relative to the survival in the irrigated treatment [$DS = (S_{\text{irrigated}} - S_{\text{dry}}) \times (S_{\text{irrigated}})^{-1}$, where S_{dry} and $S_{\text{irrigated}}$ are the % survival (S) in the dry and irrigated treatment, respectively]. Second, we calculated species drought importance index (DI), a measure of the proportion of mortality in the dry treatment that is directly attributable to drought, as opposed to other factors responsible for mortality in both treatments [$DI = (S_{\text{irrigated}} - S_{\text{dry}}) \times (100 - S_{\text{dry}})^{-1}$, compare Engelbrecht et al. 2005].

Allocation differences among species were analyzed in an ANOVA on log-transformed data, with a Scheffe post hoc test for differences between individual species (STATISTICA, StatSoft, Tulsa, Okla., USA). Differences between the three larger and three smaller seeded species were analyzed in *t*-tests using species averages as individual data points. The relation between allocation and survival parameters across species was analyzed using Pearson product-moment correlations. When necessary, data were log transformed to meet the requirements of normal distributions and equal variance. The squared values of the correlation coefficient (r^2) are presented here. The correlation coefficient provides a better indication of the strength of the relationship between variables than does the *P*-value, given the small samples size (number of species) in this experiment (Draper and Smith 1998; Dytham 1999). *P*-values, as well as significance after sequential Bonferroni adjustment within groups of tests (Rice 1989), are also given.

Results

Frequency of dry spells

Analyses of 49 years of rainfall data from across the Isthmus of Panama showed that short dry spells occur frequently, even in the wet season (Fig. 2), with the frequency of dry spells declining exponentially with increasing length. The probability of dry spells was highest at Balboa Heights, on the drier Pacific side of the Isthmus of Panama, and was similar at BCI in the center of the Isthmus and at Gatun on the wet

Table 3 Seedling survival to the end of the experiment in both treatments (S_{dry} and $S_{\text{irrigated}}$, % from beginning), the time until a significant treatment effect was observed (at $P < 0.05$), drought sensitivity (DS) and the importance of drought for their total dry spell mortality (DI) for six pioneer species

	Species	S_{dry}	$S_{\text{irrigated}}$	Days to significant effect	DS	DI
Smaller seeded	<i>Miconia</i>	56.5	86.4	9	0.35	0.69
	<i>Piper</i>	67.4	92.5	10	0.27	0.77
	<i>Cecropia</i>	64.4	89.8	8	0.28	0.71
Larger seeded	<i>Luehea</i>	79.1	91.3	NS	0.13	0.58
	<i>Ochroma</i>	64.7	94.1	3	0.31	0.83
	<i>Apeiba</i>	56.0	74.8	3	0.25	0.43

For calculations of DS and DI see Materials and methods. All t -tests comparing smaller and larger-seeded species were $P > 0.05$

Caribbean side. For example, a dry spell of at least 6 days duration occurred on average five times a year in Balboa, and about 2.5 times a year at BCI and Gatun. About every other year a dry spell of at least 10 days duration, comparable to that imposed in this study, occurred at Gatun and BCI, and nearly every year at Balboa. Even 30-day dry spells have occurred in the last 49 years in the wet season at BCI and Gatun.

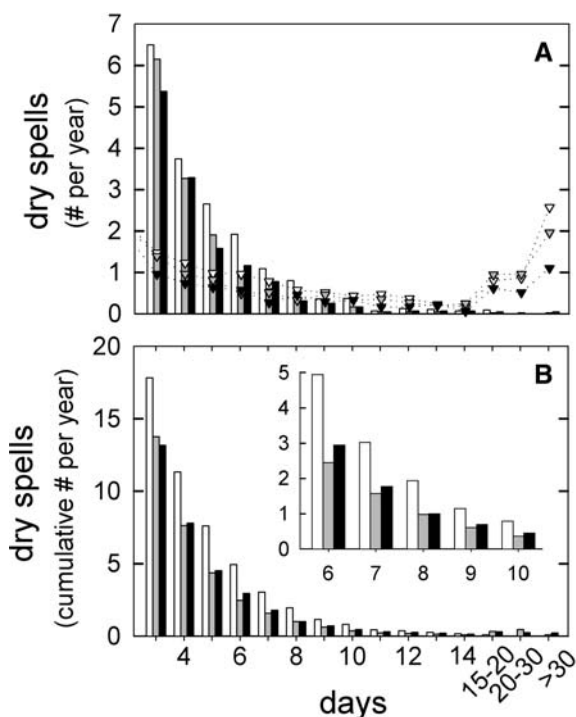


Fig. 2 Frequency of dry spells over 49 years for Balboa Heights on the Pacific side (open), BCI in the center (gray) and Gatun on the Atlantic side (black) of the Isthmus of Panama. **a** Frequency histogram of the absolute occurrence of dry spells of a given length per year in the wet season (bars). For comparison, dry season frequency is also given (triangles). **b** Cumulative frequency histogram giving the occurrence of dry spells in the wet season of $\geq x$ days per year. The inset (same axes as B) shows the cumulative frequency of dry spells 6–10 days long, which is the duration relevant for the field experiment in this study. Dry spells were defined as periods during which rainfall was less than evapotranspiration, for details see Materials and methods

Soil water potentials in artificial gaps

The water potential of soil just below the surface (0.5–1.0 cm) decreased rapidly in the experimental dry treatment, but generally remained above -0.5 MPa in the irrigated treatment (Fig. 3a, b). In the experimental dry treatment, minimum values after only 3 days of drought were at -3 MPa, and minimum water potential over the course of the experiment reached extremely low values of less than -5 MPa. After 8 days of experimentally enhanced drought, soil water potentials showed a very pronounced increase with depth (Fig. 3c). Whereas water potentials at the soil surface (0–0.5 cm) averaged about -1 MPa, with minimum values below -5 MPa, potentials remained above -0.5 MPa at depths below 1.5 cm.

Pioneer seedling survivorship under dry and irrigated conditions

Seedling survivorship varied significantly across irrigation treatments, over time and among species (Table 2). Overall, seedling survivorship was significantly higher in the irrigated than the dry plots (Table 2), with a treatment effect apparent as soon as 4 days after the treatments commenced ($t = 3.30$, $P = 0.028$). Differences in the survivorship between treatments increased over time (treatment \times day interaction; Table 2, Fig. 4). The repeated measures ANOVA indicated that overall species responded rather similarly to the irrigation treatment (no species \times treatment interaction, Table 2), with only *Ochroma* and *Apeiba* showing a significant treatment effect in this analysis.

However, the strength of species responses to the treatments manifested itself as the experiment progressed and soil water potentials between treatments diverged. For the larger-seeded species *Ochroma* and *Apeiba* significant differences between treatments emerged after 3 days, while the small-seeded species *Miconia*, *Cecropia* and *Piper* showed significant treatment effects after 8, 9 and 10 days, respectively (Table 3, Fig. 4). For the larger-seeded species, the relative difference in survival between treatments tended to be maintained over time rather than increase over the

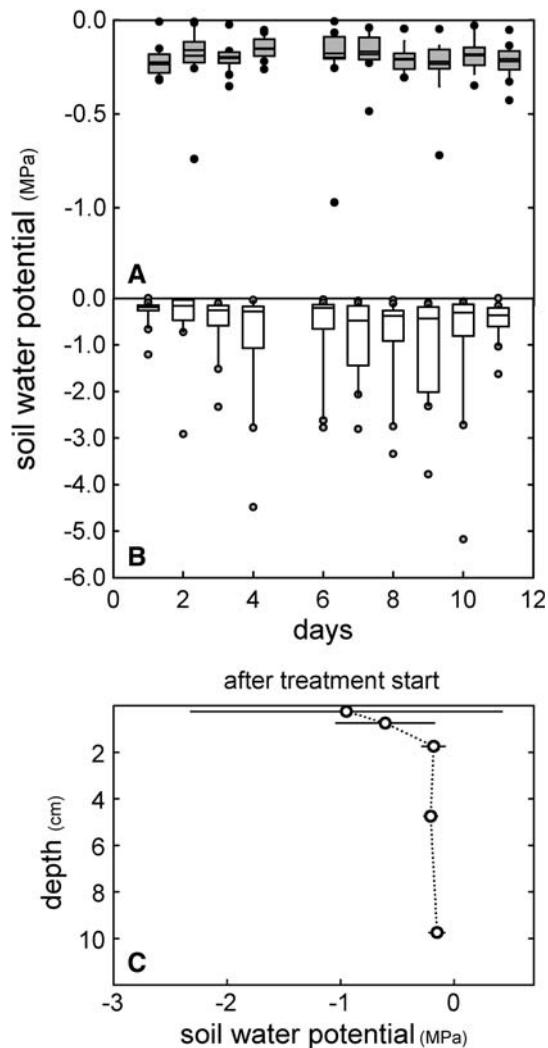


Fig. 3 Soil water potentials (0.5–1 cm depth) in artificial gaps over the course of the experiment in the irrigated (a) and the dry treatment (b). One sample was taken at a random location in each plot every day. Data are the median (horizontal line), the 25th and 75th percentiles (box), the 10th and 90th percentiles (ends of vertical lines), and outliers (circles). c Profile of soil water potentials with depth on day 8 in the dry treatment of the experiment. Data are average \pm SD; $n=4$ soil profiles from four gaps

duration of the experiment. By the end of the experiment all species except *Luehea* had significantly higher survival in the irrigated than in the dry treatment ($P < 0.05$; Fig. 4). Drought sensitivity (DS), a measure of susceptibility to drought mortality, varied among species from 0.13 to 0.35 (Table 3). Variation in the strength of treatment effects among species was uncorrelated with mean seedling age (Pearson $r^2 = 0.03$, $F = 0.13$, $P = 0.74$), even though species differed by more than a week in mean age at the start of the experiment (Table 1).

Many individuals in the dry treatment clearly died of drought stress manifested as wilting followed by shriveling and obvious drying out. Other causes of death were herbivory and trampling or digging by animals. Many of the seedlings simply disappeared and the cause of death

(or disappearance) could not be determined. The importance of other factors—besides drought—leading to seedling mortality in the dry spell is evident from the occurrence of up to 22% mortality even in the irrigated treatment (*Apeiba*). Comparison of survival in the irrigated versus the dry treatment allows an assessment of the relative drought importance (DI) for total seedling mortality in the dry spell. It was high in all species, ranging from 0.43 to 0.83 (Table 3).

Species differed significantly in rooting depth, root biomass, total plant biomass, and leaf area (Table 4, Fig. 5). Larger seeded species had higher root and plant biomass but a lower rooting depth per unit leaf area than smaller seeded species (Table 4). Seed mass was significantly positively correlated with root biomass, plant biomass and rooting depth, and negatively correlated with rooting depth per unit leaf area, while root mass fraction did not correlate with seed size (log–log correlations; Table 5). Neither root mass fraction nor rooting depth per unit leaf area scaled with total plant biomass. The correlations of all of the biomass and allocation parameters with survival, drought sensitivity (DS), or the importance of drought for total mortality (DI, Table 5) were weak ($r^2 < 0.25$) and not significant. Smaller seeded species did not have lower survival in either treatment, were not more drought sensitive, and drought was not more important for overall mortality than in larger-seeded species (Tables 3, 4).

Discussion

Periodic and prolonged dry spells are a frequent phenomenon in central Panama. Dry spells of more than 10 days duration occurred during the wet season at least every other year at three sites spanning a rainfall gradient across the Isthmus of Panama. In this study we show that an experimental 10-day dry spell in the wet season led to a pronounced and significant decrease in survivorship of newly emerged seedlings of five of six pioneer species in large gaps (Fig. 4), suggesting that seedling recruitment can be strongly affected by such events.

Drought in tropical forests

Pronounced dry seasons occur regularly once or twice a year throughout most of the tropics (Walsh and Newbery 1999). Dry season drought has been shown to be a significant source of mortality for seedlings of tropical woody plants, with species exhibiting a wide range of sensitivity to drought conditions (Mulkey and Wright 1996; Engelbrecht and Kursar 2003; Pearson et al. 2003b). However, significant effects found in these studies were only observed after several weeks of dry season drought. Severe droughts associated with El Niño Southern Oscillation events have also been shown to increase mortality of juveniles and adults in many

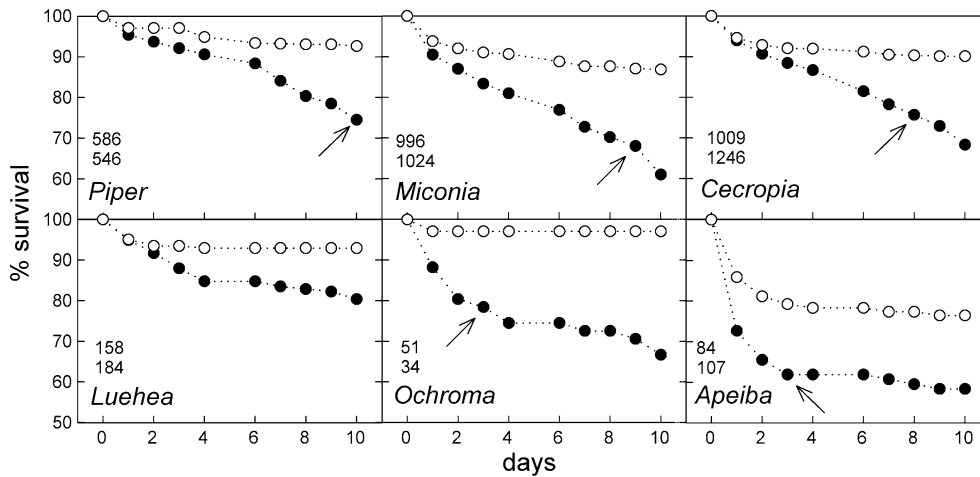


Fig. 4 Survival of seedlings of six pioneer species in dry and irrigated treatment plots in artificial gaps relative to the number of seedlings at treatment start (day 0). Data are pooled for all plots and gaps. Closed symbols dry treatment, open symbols irrigated

treatment. Arrows indicate first day for which irrigated and dry treatments differ (compare Table 3). Additionally, the number of individuals of each species at treatment start in the irrigated (first number) and dry treatment (second number) are given

tropical tree species (e.g., Condit et al. 1995; Delissio and Primack 2003; Potts 2003).

Here, we show that even short duration dry spells can have a strong effect on soil moisture availability. We found that for large gaps exposed to direct solar radiation, soil water potentials at the soil surface decreased rapidly within only 4 days, and a strong gradient developed, from very low values at the soil surface (minimum of -5 MPa) to considerably higher water potentials at 2 cm soil depth (Fig. 3). Low water potentials can be explained by high soil surface temperatures (up to $>40^{\circ}\text{C}$; Fig. 1; Pearson et al. 2002) that develop in sun-exposed gaps. High temperatures lead to steep vapor pressure deficit gradients between the air and the soil, causing high evaporative water loss from the soil surface. The steep decrease in soil water potential at the soil surface, together with high surface air temperatures (Ashton 1992), lead to severe drought stress in gaps, particularly for small, newly emerged pioneer seedlings with shallow root systems.

These effects observed at the soil surface are in marked contrast to studies that frequently show that at deeper soil layers (~ 20 cm) moisture is higher in gaps than in the understory (Becker et al. 1988; Healey 1990; Veenendaal et al. 1995). Such differences in deeper soil layers can be ascribed to lower root density in gaps, and may be responsible for higher dry season survival of established seedlings in gaps than in the understory (Fisher et al. 1991; Veenendaal et al. 1995; Poorter and Hayashida-Oliver 2000).

The effects of dry spells on pioneer seedling recruitment

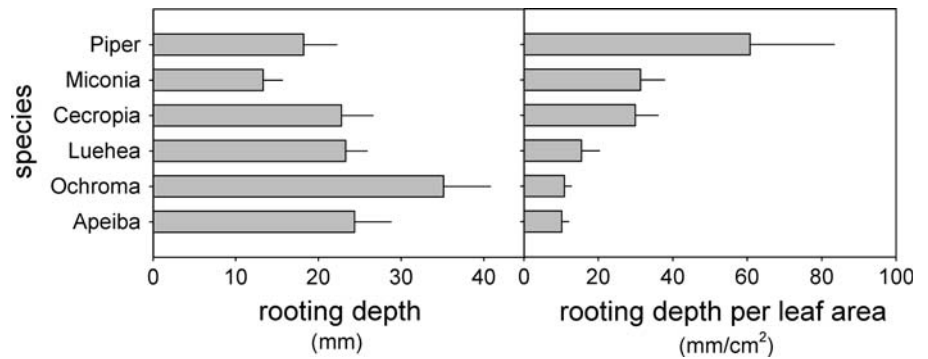
Results from this study showed that, for all six study species, seedling survivorship was lower under dry spell conditions than in the irrigated treatment, with a significant treatment effect in five out of the six species. The strength and timing of the drought effect on post-emergence seedling survivorship varied among species.

Table 4 Biomass and allocation characteristics of the species in the field in irrigated plots

	Species	<i>n</i>	Rooting depth (mm)	Root biomass (g)	Plant biomass (g)	Leaf area (cm^2)	Rooting depth per leaf area (mm cm^{-2})	Root mass fraction (g g^{-1})
Smaller seeded	<i>Miconia</i>	10	$13.30 \pm 2.35^{\text{b}}$	$0.0006 \pm 0.0003^{\text{b}}$	$0.0015 \pm 0.0005^{\text{b}}$	0.71 ± 0.18	31.35 ± 6.44	0.366 ± 0.056
	<i>Piper</i>	10	$18.20 \pm 4.03^{\text{b}}$	$0.0010 \pm 0.0004^{\text{b}}$	$0.0036 \pm 0.0014^{\text{b}}$	2.62 ± 1.10	60.77 ± 22.58	0.370 ± 0.050
	<i>Cecropia</i>	13	$22.77 \pm 3.81^{\text{b}}$	$0.0009 \pm 0.0002^{\text{ab}}$	$0.0037 \pm 0.0008^{\text{ab}}$	1.97 ± 0.55	29.91 ± 6.10	0.297 ± 0.031
Larger seeded	<i>Luehea</i>	10	$23.30 \pm 2.60^{\text{a}}$	$0.0017 \pm 0.0003^{\text{a}}$	$0.0071 \pm 0.0014^{\text{a}}$	2.80 ± 0.63	15.46 ± 4.80	0.249 ± 0.020
	<i>Ochroma</i>	7	$35.14 \pm 5.65^{\text{a}}$	$0.0025 \pm 0.0006^{\text{a}}$	$0.0120 \pm 0.0021^{\text{a}}$	3.83 ± 0.73	10.90 ± 1.80	0.235 ± 0.053
	<i>Apeiba</i>	8	$24.38 \pm 4.39^{\text{a}}$	$0.0029 \pm 0.0004^{\text{a}}$	$0.0094 \pm 0.0016^{\text{a}}$	2.59 ± 0.40	10.15 ± 1.85	0.311 ± 0.021
ANOVA	<i>F</i>		44.862	14.152	6.585	3.328	2.304	2.161
	<i>P</i>		<0.0001	<0.0001	<0.0001	<0.05	0.058	0.073
<i>t</i> test	<i>P</i>		0.102	<0.05	<0.05	0.178	<0.05	0.178

The plants were harvested at the end of the experiment, and were between 17 and 44 days old. Age distribution was the same in the sample of all species. Values are averages \pm SE. *F* and *P* values for tests of species differences in an ANOVA are given ($df=5$). Species with different superscripts differed at the 0.05 level in a pair-wise Scheffe post hoc test. *t*-tests are for comparisons of smaller versus larger-seeded species. All data were log transformed prior to analysis

Fig. 5 Rooting depth and 'rooting depth per leaf area' for seedlings of six pioneer species at the end of the experiment. Seedlings were between 17 and 44 days old. The data in the graph are averages \pm SE



The results from our experiment thus suggest that dry spells in the wet season may strongly and differentially affect pioneer recruitment success in tropical forests.

The observed treatment effects on species survivorship at the end of the experimental dry spell were independent of seed mass. In contrast, the timing of drought effects on seedling survivorship differed between small and large-seeded pioneers, suggesting different mechanisms of drought effects. The progressive drying out of the superficial soil layers over time led to the eventual desiccation and death of seedlings of the smaller seeded species. However, for the larger-seeded species, we suspect that the timing and magnitude of drought effects may have been influenced by using pre-scarified seeds, resulting in frequent seed germination at the soil surface. During the experiment, we observed that seeds that germinated on top of the soil surface, and whose roots were associated with loose superficial

soil aggregates died rapidly, whereas individuals with root systems well established in the continuous soil matrix were much less affected by the drought. Under natural conditions, seeds of our study species are dispersed in the late dry season, several months before our experiment began, and in the case of the larger-seeded species, remain unable to germinate for several months after dispersal (Dalling et al. 1997). Over this period, seeds gradually become buried in the soil, or are removed from the soil surface by secondary dispersers. Germination at the soil surface might therefore have enhanced the effect of drought in large-seeded species in the experiment. Such an experimental artifact was unforeseen when the experiment was run and highlights the importance of simulating the natural distribution of seeds in the soil when running manipulative experiments. To conclusively evaluate seed size effects on susceptibility to drought a revised experimental design

Table 5 Squares of Pearson correlation coefficients for correlations among biomass, allocation parameters, seedling survival (S), and the importance of drought for total mortality (DI), and drought sensitivity (DS)

Square of rank correlation coefficients (r^2)										
Log root biomass	Log plant biomass	Root mass fraction	Log rooting depth	Log rooting depth per leaf area	Survival overall	Survival dry	Survival irrigated	DI	DS	
Biomass and allocation parameters										
Log seed mass	0.95*** ^a (+)	0.89** (+)	0.49 (-)	0.70* (+)	0.79* (-)	0.03	0.00	0.14	0.19 (-)	0.12
Log root biomass		0.94*** ^a (+)	0.44 (-)	0.69* (+)	0.70* (-)	0.01	0.01	0.09	0.14	0.14
Log plant biomass			0.61 (-)	0.86** (+)	0.60 (-)	0.02	0.07	0.01	0.04	0.18 (-)
Root mass fraction				0.74* (-)	0.56 (+)	0.18 (-)	0.24 (-)	0.07	0.00	0.20 (+)
Log rooting depth					0.48 (-)	0.05	0.07	0.02	0.01	0.06
Log rooting depth per leaf area						0.05	0.00	0.14	0.19 (+)	0.06
Survival and drought importance parameters										
Survival overall						0.85** (+)	0.78** (+)	0.28 (+)	0.23 (-)	
Survival dry (S_{dry})							0.40 (+)	0.03	0.62 (-)	
Survival irrigated ($S_{irrigated}$)								0.75* (+)	0.00	
Drought importance (DI)										0.23 (+)

See Materials and methods for more detailed explanations. The direction of the trend is given for those correlations with $r^2 > 0.15$, with (+) indicating a positive, and (-) indicating a negative trend. Additionally, significance based on P values is given as * $P < 0.05$ and ** $P < 0.01$. Two of the correlations, indicated by^a, are significant after sequential Bonferroni adjustment (Rice 1989) within groups of tests (within biomass and allocation parameters, 15 tests; biomass and allocation versus survival and drought importance parameters, 30 tests; within survival and drought importance parameters, 10 tests)

would be required that included burying seeds at different depths in the soil.

Although seed size effects on drought sensitivity were not detected in this study, a comparable field experiment that tracked both the emergence and the initial survival of pioneer seedlings at the same study site found lower survivorship of small-seeded species (Dalling and Hubbell 2002). We suggest that drought might contribute to such size-dependent seedling mortality in pioneer seedlings, since the maximum soil depth from which successful seedling emergence can take place is strongly correlated with seed mass (Bond et al. 1999; Pearson et al. 2002). Consequently, the very smallest-seeded pioneers such as *M. argentea* (0.063 mg) are only able to emerge through a few millimeters of soil (Pearson et al. 2002), which exhibit the most severe drought conditions. Such seedlings are therefore likely to be more vulnerable to drought and to remain susceptible for a longer period post-emergence relative to larger seeded species.

This study focused on initial post-emergence seedling survivorship, and showed strong effects even of short dry spells. Additionally, dry periods during the rainy season may influence recruitment patterns in gaps through effects on seed germination and initial seedling emergence. Soil water potentials that are similar to or higher than those measured in this experiment are sufficient to significantly reduce seed germination rates in pioneer species (Evans and Etherington 1990; Daws et al. 2002), and germination sensitivity to soil water potentials shows strong interspecific variation (Daws et al. 2002). We expect that the vulnerability of pioneer seedlings to wet-season drought decreases once they have made it through the initial tiny stages, and have developed a root system extending to soil layers not affected by superficial drying processes (Fig. 3c). Nevertheless, even for the sapling stage increased mortality and reduced growth during the dry season have been observed for several pioneer species at our study site (Pearson et al. 2003a, b).

The effects of resource allocation on seedling survivorship

We hypothesized that the development of deep root systems that reach soil layers of higher soil water potential would be crucial for plant survival during dry spells. Both rooting depth, and biomass allocation to roots have been correlated with species drought sensitivity (Reader et al. 1992; Lloret et al. 1999), while theoretical models predict a correlation between drought sensitivity and the ratio of root area to leaf area (Sperry et al. 1998). We investigated whether rooting depth (determining the access to soil water), the ratio of (absorbing) rooting depth to (transpiring) leaf area (determining plant water balance and thus plant water potentials), or biomass allocation to roots explained species drought sensitivity in the field. Seedlings harvested from irrigated plots at the end of the experiment showed that species differed significantly in

key parameters of biomass and allocation (Table 4). Nevertheless, none of the measured variables were correlated with the strength of drought treatment effects (Table 5). Our data suggest they do not play a key role in explaining drought sensitivity in the initial seedling stages of pioneer species, although the sample size of six species does not allow us to conclusively reject the possibility that size or biomass allocation affect the drought sensitivity of pioneer species.

Physiological traits at the cell level allowing for the tolerance of low water potentials may be more important for drought survival in seedlings of tropical pioneer species than desiccation avoidance through different biomass allocation patterns. In seedlings of tropical non-pioneer species, lethal leaf water potentials have been shown to be highly correlated with drought survival (Tyree et al. 2003). For 3-week-old *Ochroma* seedlings surprisingly low lethal water potentials of -5 MPa were reported (Tyree and Zimmermann 2002), and preliminary data suggest that lethal water potentials for our remaining species are at a similarly low range (B. Engelbrecht, unpublished data).

Dry spell effects on treefall gap species composition

Dry periods during the rainy season lead to both temporal and spatial variation of soil moisture conditions, which through their differential effects on pioneer species recruitment, may influence species composition in gaps. Successful recruitment is dependent upon germination from a soil seed bank during a relatively short period after the formation of a canopy gap (Swaine and Whitmore 1988; Garwood 1982), with germination induced by changes in red:far-red ratios, temperature fluctuations or increased nitrate concentrations (e.g., Vásquez-Yanes and Smith 1982; Daws et al. 2002; Pearson et al. 2002). Depending on the precipitation regime during the initial phase after the opening of a canopy gap, species regeneration success may vary. If a dry spell follows gap formation, decreased seed germination and increased seedling mortality are likely to occur, with differential effects on different species. Thus, short dry spells may result in high variation among gaps in species-specific germination success and seedling survivorship depending on the timing of gap formation in relation to dry spells and the distribution of seeds in the soil. In contrast, gaps forming in the dry season are unlikely to be suitable for germination and establishment of pioneer seedlings. Shade tolerant species already present in the seedling layer in these gaps may have an advantage over pioneers in such situations.

Among pioneers, there is strong evidence that species are associated to particular gap sizes and positions within gaps (Brokaw 1987; van der Meer et al. 1998; Dalling et al. 1999). Microclimatic and soil conditions in gaps depend on their size (Brown 1993). While seedling studies have commonly focused on the light environ-

ment within gaps (Augsburger 1984; van der Meer et al. 1998; but see Pearson et al. 2003a, b), higher light exposure in larger gaps also leads to higher soil surface temperatures (Pearson et al. 2003a), inducing lower soil water potentials at the soil surface, and therefore leading to more extreme drought conditions. Variation of the severity of drought conditions developing during dry spells within and among gaps may lead to spatial variation of species-specific germination and survival and represent a further mechanism how dry spells can affect community composition in gaps.

Hence, soil moisture variation combined with differential seedling drought sensitivity offer an additional potential axis for temporal and spatial gap partitioning among pioneer species. Dry spells may therefore contribute to the maintenance of diversity in species-rich tropical forests.

Acknowledgements We thank Maria Pickering, Amy Faivre, Lauren Schachner and Didimo Moran for assistance with the field experiment, and Susanne Aref, Rachel Gallery and David Moore for statistical advice. We also thank all the BCI residents for their timely help in preparing seeds, for their willingness to spend evenings sorting toothpicks, as well as for moral support. The Smithsonian Tropical Research Institute provided excellent logistical support. Rainfall data were provided by the Terrestrial-Environmental Sciences Program of the Smithsonian Tropical Research Institute and by the Meteorology and Hydrology Branch of the Panama Canal Authority, Republic of Panama. The project was funded by the University of Utah, the USDA Forest Service, The Andrew W. Mellon Foundation and The Leverhulme Trust.

References

- Ashton PMS (1992) Some measurements of the microclimate within a Sri-Lankan tropical rainforest. *Agr For Meteorol* 59:217–235
- Augsburger CK (1984) Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *J Ecol* 72:777–795
- Becker P (1987) Monthly average solar radiation in Panama—daily and hourly relations between direct and global insolation. *Solar Energy* 39:445–453
- Becker P (1992) Seasonality of rainfall and drought in Brunei Darussalam. *Brunei Mus J* 7:99–109
- Becker P, Rabenold PE, Idol JR, Smith AP (1988) Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. *J Trop Ecol* 4:173–184
- Bond WJ, Honig M, Maze KE (1999) Seed size and seedling emergence: an allometric relationship and some ecological implications. *Oecologia* 120:132–136
- Brandani A, Hartshorn GS, Orians GH (1988) Internal heterogeneity of gaps and species richness in Costa Rican tropical wet forest. *J Trop Ecol* 4:99–109
- Brokaw NVL (1987) Gap-phase regeneration of three pioneer tree species in a tropical forest. *J Ecol* 75:9–19
- Brown ND (1993) The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rainforest. *J Trop Ecol* 9:153–168
- Brown ND, Whitmore TC (1992) Do dipterocarp seedlings really partition tropical rain forest gaps? *Philos Trans R Soc Lond B* 335:369–378
- Burslem DFRP, Grubb PJ, Turner IM (1996) Responses to simulated drought and elevated nutrient supply among shade-tolerant tree seedlings of lowland tropical forest in Singapore. *Biotropica* 28:636–646
- Condit R, Hubbell SP, Foster RB (1995) Mortality rates of 205 neotropical tree and shrub species and the impact of severe drought. *Ecol Monogr* 65:419–439
- Dalling JW, Hubbell SP (2002) Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *J Ecol* 90:557–568
- Dalling JW, Swaine MD, Garwood NC (1997) Soil seed bank community dynamics in seasonally moist lowland forest, Panama. *J Trop Ecol* 13:659–680
- Dalling JW, Hubbell SP, Silvera K (1998) Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *J Ecol* 86:674–689
- Dalling JW, Lovelock CE, Hubbell SP (1999) Growth responses of seedlings of two neotropical pioneer species to simulated forest gap environments. *J Trop Ecol* 15:827–839
- Dalling JW, Hubbell SP, Winter K (2004) Variation in growth responses of neotropical pioneers to simulated forest gaps. *Funct Ecol* 18:725–736
- Daws MI, Burslem DFRP, Crabtree LM, Kirkman P, Mullins CE, Dalling JW (2002) Differences in seed germination responses may promote coexistence of four sympatric *Piper* species. *Funct Ecol* 16:258–267
- Delisio LJ, Primack RB (2003) The impact of drought on the population dynamics of canopy-tree seedlings in an aseasonal Malaysian rain forest. *J Trop Ecol* 19:489–500
- Draper NR, Smith H (1998) Applied regression analysis, 3rd edn. Wiley, New York
- Dytham C (1999) Choosing and using statistics. A biologist's guide. Blackwell, Oxford
- Engelbrecht BMJ, Kursar TA (2003) Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. *Oecologia* 136:383–393
- Engelbrecht BMJ, Kursar TA, Tyree MT (2005) Drought effects on seedling survival in a tropical moist forest trees. *Trees Struct Funct* 19:312–321
- ESP (2005) Environmental Science Program of the Smithsonian Tropical Research Institute. <http://www.striweb.si.edu/esp/>. Cited March 2005
- Evans CE, Etherington JR (1990) The effect of soil water potential on seed germination of some British plants. *New Phytol* 115:539–548
- Fisher BL, Howe HF, Wright SJ (1991) Survival and growth of *Virola surinamensis* yearlings: water augmentation in gap and understory. *Oecologia* 86:292–297
- Garwood NC (1982) Seasonal rhythm of seed germination in a semideciduous tropical forest. In: Leigh Jr EG, Rand AS, Windsor DM (eds) The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, pp 173–199
- Gentry AH (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann Mo Bot Gard* 75:1–34
- Hawkins BA, Field R, Cornell HV, Currie DJ, Guegan J-F, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JR (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117
- Healey JR (1990) Regeneration in a Jamaican montane tropical rain forest. PhD Dissertation, University of Cambridge
- Leigh EG Jr (1999) Tropical forest ecology. A view from Barro Colorado Island. Oxford University Press, Oxford
- Lieth H (1975) Primary production of the major vegetation units of the world. In: Lieth H, Whittaker RH (eds) Primary productivity of the biosphere. Springer, Berlin Heidelberg New York, pp 203–231
- Lloret F, Casanovas C, Penuelas J (1999) Seedling survival of Mediterranean shrubland species in relation to root:shoot ratio, seed size and water and nitrogen use. *Funct Ecol* 13:210–216
- Mulkey SS, Wright SJ (1996) Influence of seasonal drought on the carbon balance of tropical forest plants. In: Smith AP, Mulkey SS, Chazdon RL (eds) Tropical forest plant ecophysiology. Chapman and Hall, New York, pp 187–216

- Pearson TRH, Burslem DFRP, Mullins CE, Dalling JW (2002) Germination ecology of neotropical pioneers: interacting effects of environmental conditions and seed size. *Ecology* 83:2798–2807
- Pearson TRH, Burslem DFRP, Goeriz RE, Dalling JW (2003a) Interactions of gap size and herbivory on establishment, growth and survival of three species of neotropical pioneer trees. *J Ecol* 91:785–796
- Pearson TRH, Burslem DFRP, Goeriz RE, Dalling JW (2003b) Regeneration niche partitioning in neotropical pioneers: effects of gap size, seasonal drought and herbivory on growth and survival. *Oecologia* 137:456–465
- Pearson TRH, Burslem DFRP, Mullins CE, Dalling JW (2003c) Functional significance of photoblastic germination in neotropical pioneer trees: a seed's eye view. *Funct Ecol* 17:394–402
- Poorter L, Hayashida-Oliver Y (2000) Effects of seasonal drought on gap and understory seedlings in a Bolivian moist forest. *J Trop Ecol* 16:481–498
- Potts MD (2003) Drought in a Bornean everwet rain forest. *J Ecol* 91:467–474
- Reader R, Jalili A, Grime JP, Spencer RE, Matthews N (1992) A comparative study of plasticity in seedling rooting depth in drying soil. *J Ecol* 81:543–550
- Rice WR (1989) Analyzing tables of statistical tests. *Evolution* 43:223–225
- Sperry JS, Adler FR, Campbell GS, Comstock J (1998) Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant Cell Environ* 21:347–359
- Swaine MD, Whitmore TC (1988) On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75:81–86
- Tyree MT, Zimmermann MH (2002) Xylem structure and the ascent of sap. Springer, Berlin Heidelberg New York
- Tyree MT, Engelbrecht BMJ, Vargas G, Kursar TA (2003) Desiccation tolerance of five tropical seedlings in Panama: relationship to a field assessment of drought-performance. *Plant Physiol* 132:1439–1447
- van der Meer PJ, Sterck FJ, Bongers F (1998) Tree seedling performance in canopy gaps in a tropical rainforest at Nouragues, French Guiana. *J Trop Ecol* 14:119–137
- Vásquez-Yanes C, Smith H (1982) Phytochrome control of seed germination in the tropical rain forest pioneer trees *Cecropia obtusifolia* and *Piper auritum* and its ecological significance. *New Phytol* 92:477–485
- Vazquez-Yanes C, Orozco-Segovia A, Rincon E, Sanchez-Coronado ME, Huante P, Toledo JR, Barradas VL (1990) Light beneath the litter in a tropical forest: effect on seed germination. *Ecology* 71:1952–1958
- Veenendaal EM, Swaine MD (1998) Limits to tree species distributions in lowland tropical rainforests. In: Newbery DM, Prins HHT, Brown ND (eds) *Dynamics of tropical communities*. Blackwell, Oxford, pp 163–191
- Veenendaal EM, Swaine MD, Agyeman VK, Blay D, Abebrese IK, Mullins CE (1995) Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. *J Ecol* 83:83–90
- Walsh RPD, Newbery DM (1999) The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. *Philos Trans R Soc Lond B* 354:1391–1405
- Yavitt JB, Wright SJ (2001) Drought and irrigation effects on fine root dynamics in a tropical moist forest, Panama. *Biotropica* 33:421–434