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Survival and ecophysiology of tree seedlings during El Niño drought in a tropical moist forest in Panama

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ABSTRACT. In tropical forests, severe droughts caused by El Niño events may strongly influence the water relations of tree seedlings and thereby increase their mortality. Data on known-aged seedlings of three common shade-tolerant canopy tree species (*Trichilia tuberculata*, *Tetragastris panamensis* and *Quararibea asterolepis*) in a Panamanian moist forest are presented. Seedling survival during a severe El Niño dry season (1997–98) was compared with prior long-term survival data, and levels of drought stress were assessed by measuring plant water potentials and gas exchange characteristics. Contrary to prediction, dry-season seedling survival was not dramatically reduced in any species compared with that expected in 'normal' years. In *Trichilia* and *Quararibea*, pre-dawn water potentials averaged −2 MPa and midday water potentials about −3 MPa. Stomatal conductances were very low, averaging 26 mmol m^{-2} s^{-1} for *Tetragastris* and 11–13 mmol m^{-2} s^{-1} for *Trichilia* and *Quararibea*. Photosynthetic rates also were very low but consistently positive, averaging 0.8–1.1 µmol m^{-2} s^{-1}. The findings suggest that, once established, seedlings of common tree species in this semi-deciduous forest may be tolerant of drought events.

KEY WORDS: El Niño Southern Oscillation, tropical forest, Panama, *Quararibea asterolepis*, seedling survival, stomatal conductance, *Tetragastris panamensis*, *Trichilia tuberculata*, water relations

INTRODUCTION

Tropical forests occur over a wide range of rainfall regimes that vary both in total precipitation and in seasonality. Both length and intensity of dry seasons can have important ecological consequences for tropical plants. In a neotropical

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semi-deciduous forest, it has been shown that soil moisture and soil water potential decrease considerably during the dry season (Becker *et al.* 1988, Windsor 1990); therefore, understorey plants in these forests regularly experience moderate to severe dry-season water stress (Mulkey & Wright 1996, Tobin *et al.* 1999). Superimposed on the seasonal patterns, El Niño Southern Oscillation (ENSO) events can cause severe droughts in the neotropics, with potentially long-lasting impacts on population structure and community dynamics (see Whitmore 1998), such as pronounced shifts in fruit and seed production and strong increases in plant mortality (Condit *et al.* 1995, Gilbert *et al.* 2001, Wright *et al.* 1999).

Tree seedlings should be especially prone to dry-season stress, and younger seedlings should suffer most, as they have had less time to develop extensive and deep root systems (Poorter & Hayashida-Oliver 2000). Stress should be especially severe during El Niño droughts and should result in higher seedling mortality than in ‘normal’ years. Few studies of tropical tree seedlings have combined analysis of dry-season mortality and physiology to test these expectations (Veenendaal *et al.* 1995), particularly during strong ENSO events. Here, we present data on mortality and physiology of seedlings of three common shade-tolerant tropical tree species during a severe El Niño drought in central Panama. We compared dry-season survival during a severe El Niño with dry-season survival estimated from prior long-term annual survival for known-aged seedlings ranging in age from 0–10 y. We also assessed levels of drought stress by measuring plant water potential and gas exchange characteristics. We predicted that: (1) dry-season mortality would be high and would be greater in younger seedlings than in older seedlings, (2) seedlings would show evidence of physiological stress, and (3) younger seedlings would show greater stress than older seedlings.

METHODS

Study site and climate

Barro Colorado Island (BCI), Republic of Panama (9°09′N, 79°51′W) harbours 1600 ha of tropical moist forest. Annual rainfall averages 2600 mm, with a pronounced 4–5 mo dry season from mid-December through April (Windsor 1990). During the dry season, soil water content and water potentials decline steadily (to as low as −1.5 to −2.3 MPa at 20 cm depth; Becker *et al.* 1988), and they increase only after heavy rains (Windsor 1990). Our study was conducted during the 1997–98 dry season, which coincided with a severe El Niño event. Total precipitation in 1997 (1703 mm) was the lowest ever recorded on BCI since 1925 (S. Paton, pers. comm.). The dry season (defined by meteorological parameters for the Panama Canal watershed; unpublished Panama Canal Commission records) started earlier and lasted > 1 mo longer than in average years (171 instead of 137 d). Rainfall between November 1997 and January

1998 was lower than in average years, which resulted in an early drop of gravimetric soil moisture to below-average levels (Figure 1).

Study species

The species studied were *Trichilia tuberculata* (Triana & Planch.) C. DC. (Meliaceae), *Tetragastris panamensis* (Engl.) Kuntze (Burseraceae) and *Quararibea*

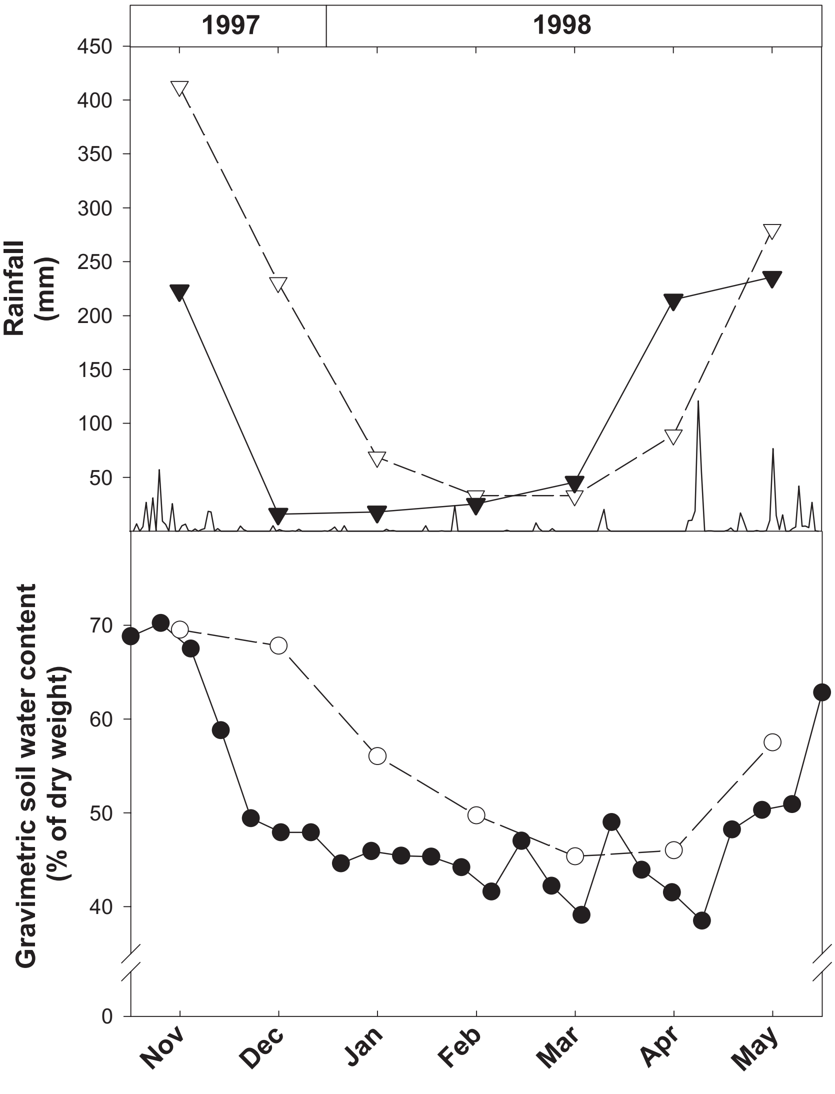

Figure 1. Monthly rainfall and gravimetric soil moisture content on BCI in the 1997–98 dry season (closed symbols) compared with long-term averages (open symbols). A line profile of the daily rainfall is also shown; note that greater-than-average April precipitation resulted from only two days of intense rainfall (*c.* 100 mm d^{-1}) and did not signal the end of the dry season. Long-term averages are from 1929–1998 for rainfall, and from 1971–1998 for soil moisture. Ticks mark the middle of each month. Data from S. Paton, Smithsonian Environmental Sciences Program.

asterolepis Pitt. (Bombacaceae). They are common canopy species, ranking among the 10 most abundant tree species in a 50-ha mapped plot on BCI (Hubbell & Foster 1990). They differ in seed size, initial seedling size and germination phenology. *Trichilia* has smaller seeds and initial seedling height than the other two species (mean seed dry mass and median seedling height = 149 mg and 8 cm for *Trichilia*, 335 mg and 11 cm for *Quararibea*, and 399 mg and 14 cm for *Tetragastris*; Wright, unpubl. data, and De Steven 1994). *Tetragastris* seedlings emerge in mid-wet season and may be 5–6 mo old at the start of the dry season, whereas *Quararibea* and *Trichilia* emerge at the end of the wet season and are 1–3 mo old when the dry season starts (De Steven 1994). The species also differ in ecological amplitude with respect to moisture. *Quararibea* has the narrowest described climatic range, being found only in tropical moist forests and in premontane wet forests, whereas *Tetragastris* has the widest ecological amplitude, ranging from tropical dry forests to tropical wet and premontane wet forests (Holdridge system; Croat 1978). All three species are shade tolerant, with annual survival rates of older seedlings ranging from 80–90% y^{-1}, and are widely distributed independently of known differences in soil moisture availability within the 50-ha plot (De Steven 1994).

Survival measures and analysis

A long-term study of seedling dynamics of these three species was conducted from 1987–1997 in permanent 4-m × 16-m transects established at focal adult trees (details in De Steven 1994). At the end of December in each year, newly germinated seedlings in the transects were mapped and marked with numbered plastic bands. Annual survival thereafter was measured from the start of one dry season to the start of the next. By the December 1997 census, when the long-term study ended, there were surviving seedlings from up to 11 cohorts.

Dry-season survival during the 1997–98 El Niño (from December 1997 to the end of the 1998 dry season) was determined by a re-census of all seedlings after the onset of rains. For logistical reasons, newly recruited seedlings (age = 0) were re-censused in early May (4 mo after the 1997 census), and seedlings aged ≥ 1 y were re-censused in early June (5 mo after the 1997 census). 'Actual' dry-season survival was calculated for each seedling cohort as the fraction of n seedlings alive in December 1997 that survived to the re-census in 1998.

Because we had data on dry-season survival only for the 1998 dry season but yearly values of annual (12 mo) seedling survival for the prior years of 1987–97, we used an indirect approach to interpret the El Niño dry-season mortality. Multiple known-age cohorts had been monitored yearly (De Steven 1994 and unpubl. data), so there were 3–9 estimates of annual survival for seedlings of different age classes. Using these annual survival rates, we estimated the dry-season survival 'expected' (predicted) for each age class and census year according to the formula of Sheil *et al.* (1995), which assumes constant within-year survival:

$$\text{predicted dry season survival} = (\text{annual survival})^{m/12}$$

where m is the number of months after initial re-census (4 mo for age 0 seedlings, and 5 mo for seedlings age $\geq$ 1 y). We then evaluated whether actual dry-season survival in 1998 fell within the 95% confidence limits for the mean predicted dry-season survival of each seedling age class, with the expectation that significantly lower survival compared to the predicted values would indicate a possible impact of the severe dry season.

Assuming constant within-year survival introduced a possible bias. For example, if dry-season survival tends to be lower than wet-season survival during 'normal' years, expected survival values would be biased upwards. However, of the few studies that have examined drought effects on seedling survival in wet tropical forests, none provides the data needed to evaluate whether this bias is real or significant. Depending upon the species, survival through a seedling's first dry season has been shown to be higher, as well as lower, than in the previous wet season when seedlings emerged (Garwood 1982, Poorter & Hayashida-Oliver 2000, Turner 1990, Veenendaal *et al.* 1995), and it is not known whether mortality differs between subsequent dry and wet seasons. Thus, our assumption was a reasonable starting point for analysis.

Physiological measures and analysis

To measure physiological parameters, we selected a subsample of marked seedlings from the December 1997 census in six age categories: newly recruited seedlings (age 0) and seedlings aged 1, 2, 3–4, 5–6 and 7–10 y. Older age categories included multiple years because the number of surviving seedlings declines with increasing age of a cohort, and thus fewer older plants were available. For each species, we selected at least four seedlings in each age category. We chose plants based on location and site accessibility but at random with respect to any plant trait other than age. For each species, the chosen seedlings were distributed across study transects at three or four adult trees that were distributed widely through the BCI forest, so that measurements were not conducted on plants at only one site. Seedling height ranges in the sample were 14–44 cm, 7–20 cm and 10–31 cm for *Tetragastris*, *Trichilia* and *Quararibea*, respectively.

Physiological measurements were made in mid-dry season, on 13 and 20 March 1998, when gravimetric soil moisture was close to its minimum (Figure 1). Leaf water potentials were measured with a portable pressure chamber (PMS Instruments, Model 1000, Corvallis, OR, USA), following the recommendations of Koide *et al.* (1989). Pre-dawn and mid-day measurements were taken between 04h30 and 06h30, and between 11h30 and 13h30, respectively. Because *Tetragastris* proved to have a resinous sap that interfered with measurement, we were able to obtain leaf water potentials only for *Quararibea* and *Trichilia*. Leaf photosynthesis and stomatal conductances were measured in all three species with a portable infrared gas analyser (Li-COR, Model 6400, Lincoln, NE, USA). Measurements were made between 09h30 and 11h30 at ambient temperatures (31.6 ± 0.1 °C, average ± SE, n = 45), and humidities (75.3 ± 0.3%), resulting in leaf to air VPDs of 0.92 ± 0.02 kPa. A light-emitting diode (LED; Li-COR, Model 6400-02, Lincoln, NE, USA) provided a constant photosynthetic photon flux density (PPFD) of 20 µmol m^{-2} s^{-1}, comparable to the average ambient PPFD of 28.2 ± 9.4 µmol m^{-2} s^{-1}. Taking into account the increased CO_2 concentrations at the forest floor (Sternberg *et al.* 1989), CO_2 in the sample chamber was held at about 400 ppm, and the flow rate was set to 250 ml s^{-1}. Leaf gas exchange was measured for up to 5 min to obtain stable stomatal conductances.

Because some seedlings were relatively small and had very small leaves, it was occasionally necessary to sacrifice whole plants to obtain water potentials. If we could not make all measurements on a single plant, matched pairs of seedlings of the same age, location and approximate size were used to obtain complementary data. Since we could not obtain a complete set of measurements on every seedling, our data represent a composite picture of physiological characteristics.

The effects of species and seedling age on physiological parameters were evaluated by analysis of covariance (ANCOVA), with species as a fixed main effect and seedling age category as a covariate. ANCOVAs were performed on the dependent variables of pre-dawn leaf water potential, mid-day leaf water potential, stomatal conductance and photosynthetic rate. Based on residuals diagnostics, we used untransformed values of water potential and photosynthesis, and logarithmic transformations of conductance. The assumption of homogeneous slopes was satisfied for all dependent variables (see Neter *et al.* 1990), so the ANCOVA models tested the species effect and the seedling age effect. We also performed ANCOVAs using seedling height, a measure of plant size, as a covariate rather than age. However, seedling age and height were strongly correlated in all three species (Pearson's r = 0.81, 0.82, 0.64 and n = 21, 26, 26 for *Tetragastris*, *Trichilia*, and *Quararibea*, respectively, all $P < 0.001$), and the results were not different from tests using seedling age. Therefore, only the tests for age effect are presented. Analyses were performed using SYSTAT® Version 9 (SPSS Inc. 1999).

RESULTS AND DISCUSSION

Contrary to expectation, survival through the severe El Niño dry season was relatively high for all three species and in all age classes. Generally, 80–95% of the seedlings alive in December 1997 survived to the end of the dry season. In *Trichilia* and *Tetragastris*, actual dry-season survival was within the confidence limits of predicted mean values and was often higher than the mean (Figure 2). Only *Quararibea*, a species restricted to relatively humid forest types, showed evidence of poorer survival in some (but not all) age classes, with values lower

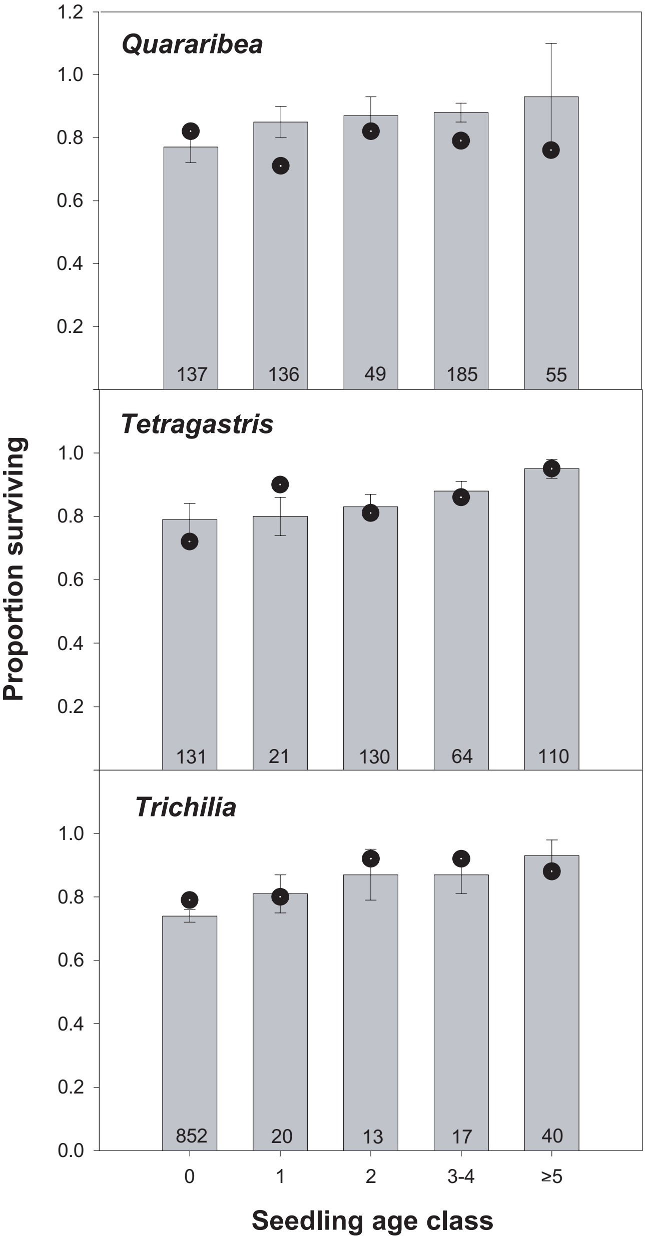

Figure 2. Expected and actual dry-season survival of different age classes of *Tetragastris*, *Trichilia* and *Quararibea* seedlings. The expected values (bars) and their 95% confidence limits (vertical lines) are over a 4-mo interval for the age 0 cohort, and over a 5-mo interval for seedlings ⩾ 1 y. Expected values are derived from n = 3–9 annual estimates, depending upon cohort age (see Methods). Actual survival rates (circles) were those observed in the 1997–98 dry season. Numbers at the base of each bar indicate the number of seedlings re-censused for actual dry-season survival in each age class.

than the confidence limits of the predicted mean. Given that the expected dry-season survival values were potentially biased upwards, these results support the conclusion that the 1998 drought did not dramatically elevate seedling mortality compared to 'normal' years.

There was no strong evidence that younger seedlings were more sensitive to El Niño conditions than older ones, because actual survival of younger seedlings was not consistently at the lower end of the confidence limits compared to survival of older seedlings (Figure 2). In general, annual survivorship increases with age over the first few years of seedling life (De Steven 1994 and unpubl. data). Of the three species, only *Quararibea* did not show a general increase in actual dry-season survival with age class (Figure 2), again indicating somewhat greater drought sensitivity than the other two species.

Physiological measurements also suggested that the seedlings experienced less severe stress than expected. Pre-dawn xylem water potentials averaged about −2 MPa in both *Trichilia* and *Quararibea* (Table 1). Mid-day water potentials were reduced compared with pre-dawn water potentials, averaging about −3 MPa. The two species did not differ in either parameter (Table 1). These water potentials were well above the lowest dry-season values observed for understorey plants on BCI (−3.5 MPa and −4.5 MPa, respectively; Robichaux *et al.* 1984, Tobin *et al.* 1999). They were also higher than values measured for *Trichilia* saplings and trees in previous El Niño dry seasons on BCI (−2.6 to −3.2 MPa and −3.8 MPa for pre-dawn and mid-day values, respectively; Fetcher 1979, Robichaux *et al.* 1984), and were only slightly lower than values found in saplings and trees of both species at the end of 'normal' dry seasons (Becker *et al.* 1988, Rundel & Becker 1987, Wright & Cornejo 1990). Although average mid-day water potentials of these species were close to their turgor loss point of about −3.2 MPa (determined by Robichaux *et al.* 1984, Rundel & Becker 1987), the seedlings were not visibly wilted at the time of measurement. In

Table 1. Water potential and gas exchange characteristics of *Tetragastris*, *Trichilia* and *Quararibea* seedlings in the middle of the 1998 dry season. Data are means ± SE, pooled over all age classes. F-value is the ANCOVA test for between-species differences, where: ** $P \leq 0.01$, n.s. = not significant. Values with the same superscript do not differ in Scheffe pairwise tests at $P \leq 0.05$, n.a. = data not available.

			Species		
Variable	F	P	*Tetragastris*	*Trichilia*	*Quararibea*
Pre-dawn water potential (MPa)	1.0	n.s.	n.a.	−1.97 ± 0.08	−2.12 ± 0.12
Midday water potential (MPa)	1.5	n.s.	n.a.	−3.12 ± 0.16	−2.88 ± 0.13
Stomatal conductance (mmol m^{-2} s^{-1})	10.6	**	25.8 ± 4.0 ^{a}	12.9 ± 2.2 ^{b}	11.2 ± 1.2 ^{b}
Photosynthesis (µmol m^{-2} s^{-1})	5.6	**	1.11 ± 0.04 ^{a}	0.76 ± 0.09 ^{b}	0.81 ± 0.07 ^{b}
n (pre-dawn, midday)			–	22, 11	20, 21
n (others)			19	8	16

greenhouse conditions, plants of all three species showed wilting when subjected to extreme drought (Engelbrecht, *pers. obs.*). Lack of apparent wilt in the field suggests that the seedlings had not reached critical drought stress, because drought-induced mortality consistently occurs only well after the wilting point is reached (Engelbrecht, unpubl. data).

We had predicted that younger seedlings would be more stressed by drought than older ones, since little-developed and/or shallow root systems would limit the water available to smaller seedlings (Poorter & Hayashida-Oliver 2000). However, there was no significant relationship of water potential to seedling age (pre-dawn $F = 0.3$, $df = 1, 39$; midday $F = 0.7$, $df = 1, 29$; both $P > 0.10$), perhaps because the sampled seedlings did not vary widely in height despite nearly 10 y difference in age. Alternatively, neither age nor height may be a good correlate of root volume or depth in these species.

Neither stomatal conductance nor photosynthesis was influenced by seedling age (F values = 0.2–2.4; all $df = 1, 39$; all $P > 0.10$); however, the two parameters did differ among species (Table 1). Conductance was extremely low in all species, but was higher in *Tetragastris* (mean: 26 mmol m^{-2} s^{-1}) than in *Trichilia* and *Quararibea* (mean: 11–13 mmol m^{-2} s^{-1}). All plants showed low but consistently positive photosynthetic rates, which were again greatest for *Tetragastris*, and indistinguishable between *Quararibea* and *Trichilia*. Whether photosynthetic rates were limited by low stomatal conductance, or by low light conditions, or both, is uncertain. Even under very low light, unstressed tropical plants in the understorey show stomatal conductances from 30 up to 350 mmol m^{-2} s^{-1} (Pearcy & Calkin 1983, Poorter & Oberbauer 1993, Roberts *et al.* 1990). Very low conductances comparable with those in our study (< 50 mmol m^{-2} s^{-1}) were consistently observed in plants exposed to severe drought (Reekie & Wayne 1992, Veenendaal *et al.* 1995, Wright *et al.* 1992). Early reduction of stomatal conductance, leading to extremely low transpiration rates under forest understorey conditions, may allow these seedlings to minimize direct drought damage.

Our findings suggest that established seedlings of common shade-tolerant tree species in this semi-deciduous forest may be tolerant of severe drought events. We cannot exclude the possibility that dry-season effects were expressed later, i.e. that seedlings weakened by stress died later in the rainy season as light became more limiting. But clearly any effects of drought on survival were not immediate. These seedlings experience drought each year as surface soils dry out. Even during severe droughts, their physiological and morphological characteristics, and their position in the shaded understorey may allow them to be less susceptible to drought than larger plants with exposed canopies (see Condit *et al.* 1995). Despite a large amount of literature on physiological consequences of drought on seedlings of tropical woody plants (see Mulkey & Wright 1996), few empirical data are available on the survival consequences (Fisher *et al.* 1991, Garwood 1982, Gilbert *et al.* 2001, Poorter &

Hayashida-Oliver 2000, Turner 1990, Veenendaal *et al.* 1995). Our study shows that the effect of increased dry-season severity can differ from expected, which highlights the need for more observational and experimental studies on the ecological effects of drought on tropical plants. Such studies will be important for understanding the role of climatic factors in shaping tropical forests and the consequences of past and future global climate change (Whitmore 1998).

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