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ORIGINAL ARTICLE

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Drought effects on seedling survival in a tropical moist forest

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Abstract The amount and seasonality of rainfall varies strongly in the tropics, and plant species abundance, distribution and diversity are correlated with rainfall. Drought periods leading to plant stress occur not only in dry forests, but also in moist and even wet forests. We quantified experimentally the effect of drought on survival of first year seedlings of 28 co-occurring tropical woody plant species in the understory of a tropical moist forest. The seedlings were transplanted to plots and subjected to a drought and an irrigation treatment for 22 weeks during the dry season. Drought effects on mortality and wilting behavior varied greatly among species, so that relative survival in the dry treatment ranged from 0% to about 100% of that in the irrigated treatment. Drought stress was the main factor in mortality, causing about 90% (median) of the total mortality observed in the dry treatment. In almost half of the species, the difference in survival between treatments was not significant even after 22 weeks, implying that many of the species are well adapted to drought in this forest. Relative drought survival was significantly higher in species associated with dry habitats than in those associated with wet habitats, and in species with higher abundance on the dry side of the Isthmus of Panama, than in those more abundant on the wet side. These data show that differential species survival in response to drought, combined with variation in soil moisture availability, may be important for species distribution at the local and regional scale in many tropical forests.

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Introduction

Annual rainfall in tropical forests varies from about 800 mm to more than 10,000 mm (Richards 1998). In dry tropical forests and savannas, drought is a very obvious ecological factor, and plants show many characters that have clearly evolved in response to drought (Medina 1983; Holbrook et al. 1995; Borchert 1998). In contrast, the importance of drought in moist and wet tropical forests for plant phenology, growth and survival, for life history and life form distributions, and for plant community composition is far less obvious, and has therefore received less attention. However, in most tropical forests—including moist and wet forests—rainfall is seasonal, with one or two dry seasons per year (Windsor 1990; Walsh and Newbery 1999), and even in many aseasonal equatorial forests dry periods of more than 2 weeks occur at least every other year (Burslem et al. 1996; Becker 1992; Walsh and Newbery 1999). Especially severe droughts occur in many tropical regions in association with El Niño climatic events (e.g., Toma et al. 2000; Walsh and Newbery 1999).

Forest formations, plant diversity, and the distribution of species as well as functional groups, vary strongly with annual rainfall and/or dry season length in the tropics (e.g., Medina 1983; Gentry 1988; Swaine 1996; Bongers et al. 1999; Reich 1995). At the same time, soil moisture variation may underlie plant associations with topography (e.g., ridge, slope; Webb and Peart 2000; Harms et al. 2001; Chuyong et al. 2003; Guntilleke et al. 2003; Johns and Dattaraja 2003). During the dry season, plants in moist and wet tropical forests can be exposed to considerable drought stress, indicated by low leaf water potentials and wilting (e.g., Chiarello et al. 1987; Veenendaal et al. 1995; Tobin et al. 1999; B.M.J. Engelbrecht, personal observations), and drought has been associated with increased mortality in tropical plants (e.g., Fisher et al. 1991; Turner 1990; Veenendaal et al. 1995; Condit et al. 1995; Gilbert et al.

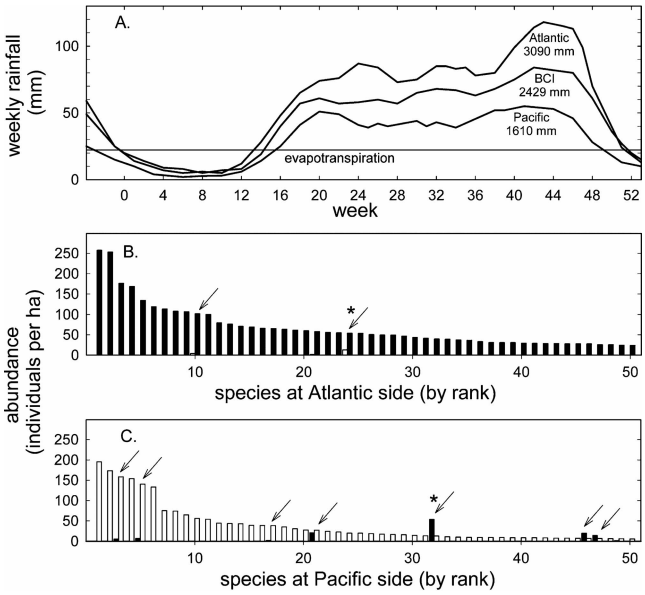

Fig. 1a–c Rainfall gradient and species abundances across the Isthmus of Panama—a distance of approximately 65 km. **a** Weekly rainfall for three sites across the Isthmus of Panama. *Solid lines* Running averages for 27 years, *insets* average annual rainfall (redrawn from Condit 1998). *BCI* Barro Colorado Island. **b** *Black bars* Abundance of stems of 1 cm dbh and larger of the 50 most abundant species on the wet Atlantic side, *open bars* (highlighted by *arrows*) abundance of the same 50 species on the dry Pacific side. **c** *Open bars* Abundance of stems of 1 cm dbh and larger of the 50 most abundant species on the Pacific side, *black bars* (*arrows*) abundance of the same 50 species on the wet Atlantic side. The single *asterisk* in **b** and **c** marks the only species overlapping between the two data sets, *Thevetia ahouai*. Data in **b** and **c** are from Condit et al. 2004

2001). Thus species-specific differences in the ability to survive drought may be a major factor influencing forest species distributions in the tropics. However, rigorous comparative assessmentss of the effects of drought on plant survival are largely missing.

Across the Isthmus of Panama, there is a pronounced gradient of annual rainfall and dry season length over a distance of only 65 km (Fig. 1a). A nearly continuous band of forest stretches along the Panama Canal, with dry forest species dominating the Pacific side and moist or wet forest species on the Atlantic side (Fig. 1b and c; Condit 1998; Pyke et al. 2001). At a smaller landscape scale, factors such as topography are indicative of soil water availability (Becker et al. 1988), and habitat associations have been shown for about 50% of the species in a 50 ha forest dynamics plot on Barro Colorado Island (BCI; Harms et al. 2001). The strong gradients of rainfall and species distribution that occur in Panama provide an ideal opportunity to link tropical plant species survival under drought with plant distribution and diversity gradients at different scales.

Our main hypothesis is that differences in species drought performance, i.e., ability to survive drought, together with spatial variation in soil moisture availability, lead to differential abundance, distribution and diversity across moisture gradients. Our objective for this study was to quantify drought performance for a large number of species, thereby permitting a quantitative test of our main hypothesis. Such assessments also provide a baseline for quantitative evaluations of the relative importance of the different underlying mechanisms for plant mortality under drought (Tyree et al. 2002, 2003).

In this study we specifically pursued the following questions: to what extent does drought performance vary between co-occurring species? What is the importance of drought stress relative to other factors leading to mortality? If we define drought performance as the difference in survival in wet versus dry plots, can we use drought performance to predict species distributions along moisture gradients?

We quantified the drought effect on first-year seedlings of 28 species of tropical woody plants in a natural setting in a tropical moist forest by comparing species performance under dry relative to wet treatments. Young seedlings in their first year of growth are likely to be the life stage most sensitive to drought in many species (e.g., Marod et al. 2002; Gerhardt 1996), because plants are small and have limited root systems, and thus do not have access to lower soil layers with higher water potentials. In drought periods, seedling mortality in the natural habitat may be influenced by drought stress, but also by non-drought stressors (e.g., light, nutrients, pathogens, and herbivore damage; e.g., Augspurger 1984a, b; Howe 1990), as well as their interactions. In this report we focus on survival in irrigated vs. dry plots, allowing us to assess the relative importance of drought effects compared to other factors influencing seedling mortality. We linked the processes observed on the population level to known community composition patterns.

Materials and methods

The experiment was conducted in Panama at the Buena Vista Peninsula, which is part of the Barro Colorado Nature Monument (BCNM). Average annual rainfall is approximately 2,600 mm with a pronounced 4-month dry season from about mid-December through mid-April (Windsor 1990).

We worked with seedlings of 28 woody plant species with diverse phylogenetic backgrounds that all co-occur within BCNM (Table 1). Seeds were collected in the year 2000 in BCNM and germinated in the greenhouse under moderately low light. Seedlings were transplanted to 60 experimental plots (0.8 m × 1.0 m) in the forest understory in September through November 2000. For all seedlings, the dry season 2000/2001 was the first dry season they experienced. According to time of fruiting and germination, the seedlings were between 2 and 9 months old at the onset of their first dry season, and seedling heights and leaf areas varied.

One seedling of each species was transplanted to each plot. Seedlings were exposed to two treatments, dry and irrigated (30 plots of each), for 22 weeks in the dry season (18 December 2000–12 June 2001). Dry plots were covered with transparent rain-out shelters, irrigated plots were watered regularly, approximating monthly precipitation of 220 mm. Dry plots were not trenched, allowing natural

Table 1 Study species, family and order, leaf phenology, life form and seed size. Species names, authorities and families are according to the VAST Nomenclatural Database of the Missouri Botanical Garden (2003). The assignment to order is based on APG (1998)

Species	Species code	Family	Order	*N* wet	*N* dry	Seed size[a]	Life form[a]	Leaf phenology[a]
Andira inermis (W. Wright) Kunth ex. DC	AND	Fabaceae	Fabales	30	29	1	2	1
Beilschmiedia pendula (Sw.) Hemsl.	BEI	Lauraceae	Laurales	30	30	1	1	1
Calophyllum longifolium Willd.	CAL	Clusiaceae	Malpighiales	30	30	1	1	1
Cordia alliodora (Ruiz & Pav.) Oken	COR	Boraginaceae	Solanales	28	26	3	1	2
Cupania sylvatica Seem.	CUP	Sapindaceae	Sapindales	30	31	3	2	1
Dipteryx panamensis (Pittier) Record & Mell	DIP	Fabaceae	Fabales	30	30	1	1	2
Garcinia intermedia (Pittier) Hammel	GAR	Clusiaceae	Malpighiales	30	30	3	2	1
Hybanthus prunifolius (Humb. & Bonpl. ex Roem.& Schult.) Schulze-Menz	HYB	Violaceae	Malpighiales	30	31	3	3	1
Hymenaea courbaril L.	HYM	Fabaceae	Fabales	30	30	1	1	1
Inga multijuga Benth.	ING	Fabaceae	Fabales	30	30	2	1	1
Lacistema aggregatum (P. J. Bergius) Rusby	LAI	Lacistemataceae	Malpighiales	30	30	3	2	1
Lacmellea panamensis (Woodson) Markgr.	LAC	Apocynaceae	Gentianales	30	30	2	1	1
Licania platypus (Hemsl) Fritsch	LIC	Chrysobalanaceae	Malpighiales	30	30	1	1	1
Ouratea lucens (Kunth) Engl.	OUR	Ochnaceae	Malpighiales	30	30	2	2	1
Picramnia latifolia Tul.	PIC	Simaroubaceae	Sapindales	30	30	2	3	1
Piper trigonum C. DC.	PTRI	Piperaceae	Piperales	30	30	3	3	1
Pouteria unilocularis (Donn. Sm.) Baehni	POU	Sapotaceae	Ericales	30	30	3	1	1
Pseudobombax septenatum (Jacq.) Dugand	PSE	Malvaceae	Malvales	30	30	3	1	2
Psychotria horizontalis Sw.	HOR	Rubiaceae	Gentianales	30	29	3	3	1
Pterocarpus rohrii Vahl	PTE	Fabaceae	Fabales	26	24	1	3	2
Swartzia simplex (Sw.) Spreng.[b]	SWA	Fabaceae	Fabales	30	30	2	2	1
Sorocea affinis Hemsl.	SOR	Moraceae	Rosales	30	30	3	2	1
Tabebuia rosea (Bertol.) A. DC.	TAB	Bignonaceae	Lamiales	30	30	3	1	2
Thevetia ahouai (L.) A. DC.	THE	Apocynaceae	Gentianales	30	29	2	3	1
Trichilia tuberculata (Triana & Planch.) C. DC.	TRC	Meliaceae	Sapindales	30	29	2	1	1
Virola surinamensis (Rol. ex Rottb.) Warb.	VIR	Myristicaceae	Magnoliales	30	30	2	1	1
Xylopia macrantha Triana& Planch.	XYL	Annonaceae	Magnoliales	24	25	3	2	1
Xylosma chlorantha Donn. Sm.	XYO	Flacourtiaceae	Malpighiales	27	25	3	3	1

[a]Classifications: seed size: *1* large (greatest expansion >30 mm), *2* medium (10–30 mm), *3* small (<10 mm); life form: *1* tree, *2* sub tree, *3* shrub; leaf phenology: *1* evergreen, *2* deciduous

[b]Referred to as "var. grandiflora" on Barro Colorado Island (BCI; see Croat 1978)

draw-down of soil water by larger trees. Light intensities over the plots were 4.5–9.5% of the incident PPFD above the forest canopy in the dry plots, and 5.8–12.6% in the wet plots (for details, see Engelbrecht and Kursar 2003). All plots were caged with wire mesh to exclude vertebrate herbivores, and to avoid damage through leaf, twig- and branch-fall (Clark and Clark 1989; Howe 1990). However, results from subsequent years suggest that the exclosures did not increase seedling survival, i.e., large herbivore and physical damage were not important (unpublished data).

Censuses of gravimetric soil water content, seedling survival and plant wilting state were conducted regularly throughout the experiment over 22 weeks. Gravimetric soil water content (based on soil dry weight at 105°C) was determined in each census for the upper 10 cm of soil at a random position in each plot. Gravimetric soil water contents immediately adjacent to each plot were additionally followed throughout the subsequent dry season (2002) under unmanipulated conditions, and compared with the 2000–2001 experimental data. After 17 weeks of experimental treatment, when gravimetric soil water content was at its minimum, we measured profiles of soil water potentials down to 30 cm depth in seven dry and two wet plots using psychrometers (for details, see Engelbrecht and Kursar 2003).

The wilting state of each leaf was evaluated (not wilted, slightly wilted, wilted, severely wilted; Tyree et al. 2002, 2003) and whole plant wilting state was scored as the wilting state of the most wilted leaf on the plant. Additional categories were living seedlings without leaves ("nearly dead"), and "dead" seedlings. Seedling survival was scored according to living above-ground tissues (i.e., color and elasticity of the stem). Plant survivorship or death was confirmed in the field after rewetting of soils with the start of the wet season.

We calculated % survival (S) and % mortality (M) over 22 weeks as

$$S = \frac{N_{22}}{N_0} \times 100, \quad (1)$$

and

$$M = \frac{N_0 - N_{22}}{N_0} \times 100, \text{ so that } M + S = 100, \qquad (2)$$

where N_0 is the sample size at the beginning (see Table 1) and N_{22} is the number of individuals surviving after 22 weeks.

Results and discussion

Soil water, wilting, and survival during the dry season

In the drought experiment, gravimetric soil water content was significantly lower in the dry than in the irrigated treatment (Fig. 2a). Minimum soil water contents in the dry treatment were slightly but not significantly lower, and remained low for a longer time, than under unmanipulated conditions in a "normal" dry season (2001/2002, Fig. 2a). Soil water potentials and their vertical profiles differed strongly between treatments, with soil water potentials as low as −6 MPa at the soil surface and a strong exponential increase toward lower soil layers in the dry treatment (Fig. 2b).

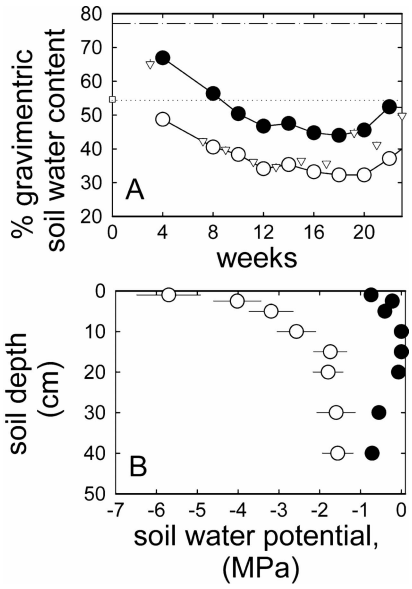

Fig. 2a and b Soil moisture in dry and irrigated treatments. **a** Percent gravimetric soil water content [100× g water (g dry soil)$^{-1}$] in the upper 10 cm soil in the experimental plots during 2000–2001, with *weeks* indicating the number of weeks after initiating the experiment on 18 December 2000 (*open circles* dry treatment, *filled circles* irrigated treatment; n=30; ANOVA: P<0.0001 for treatment, time, and their interaction; data from Engelbrecht and Kursar 2003). For comparison, gravimetric soil water contents under unmanipulated conditions in the dry season of 2001–2002 are given for 60 sites directly adjacent to the plots (*open triangles*). *Horizontal lines* Gravimetric water content at field capacity (*dash-dot*) and average gravimetric water content for the wet season of 2001 (*dotted*). SE are smaller than the symbols. **b** Soil water potential profiles measured on week 17 when soil water content was at a minimum (symbols as in **a**; dry treatment $n = 7$, averages ± SE, irrigated treatment $n = 2$, averages; data from Engelbrecht and Kursar 2003)

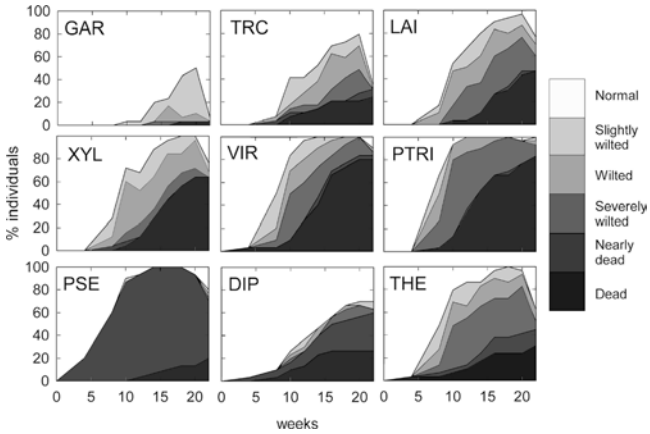

Fig. 3 Wilting states and mortality in the dry treatment. Non-deciduous species: *GAR* Garcinia, *TRC* Trichilia, *LAI* Lacistema, *XYL* Xylopia, *VIR* Virola, *PTRI* Piper. Three species that were deciduous during the experiment: *PSE* Pseudobombax, *DIP* Dipteryx, *THE* Thevetia. *Weeks and Symbols* as indicated in Fig. 2

In most species, the dry treatment caused wilting and mortality. The effects of drought differed strongly between species. As examples, Figs. 3 and 4 show the wilting behavior and mortality of nine species in the dry treatment over time. In some species [e.g., Garcinia (GAR)] few plants showed visible signs of drought stress throughout the experiment, and mortality was extremely low. At the other extreme, wilting started very early in the experiment, plants went quickly through all wilting states, and most individuals died [Virola (VIR), Piper (PTRI)]. Between these extremes was a continuum of reactions with different combinations of wilting behavior and mortality. As is well known for adult trees, and as we found for seedlings, Pseudobombax (PSE) was deciduous, with plants shedding their leaves but experiencing low mortality. Several species not recorded as deciduous showed intermediate seedling deciduousness along with low mortality [e.g., Dipteryx (DIP) and Thevetia (THE)].

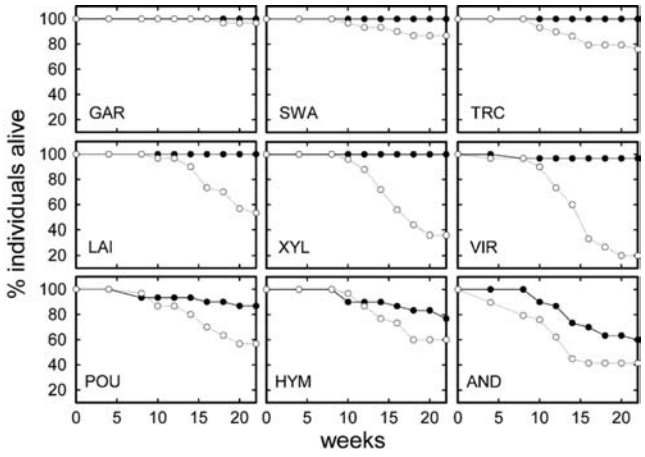

Fig. 4 Survival in the dry and the irrigated treatment. Six species without any mortality in the irrigated treatment are shown as examples: *GAR*, Swartzia (*SWA*), *TRC*, *LAI*, *XYL*, *VIR*. Three species with pronounced mortality in the irrigated treatment: Pouteria (*POU*), Hymenaea (*HYM*), and Andira (*AND*). *Weeks* and symbols as indicated in Fig. 2

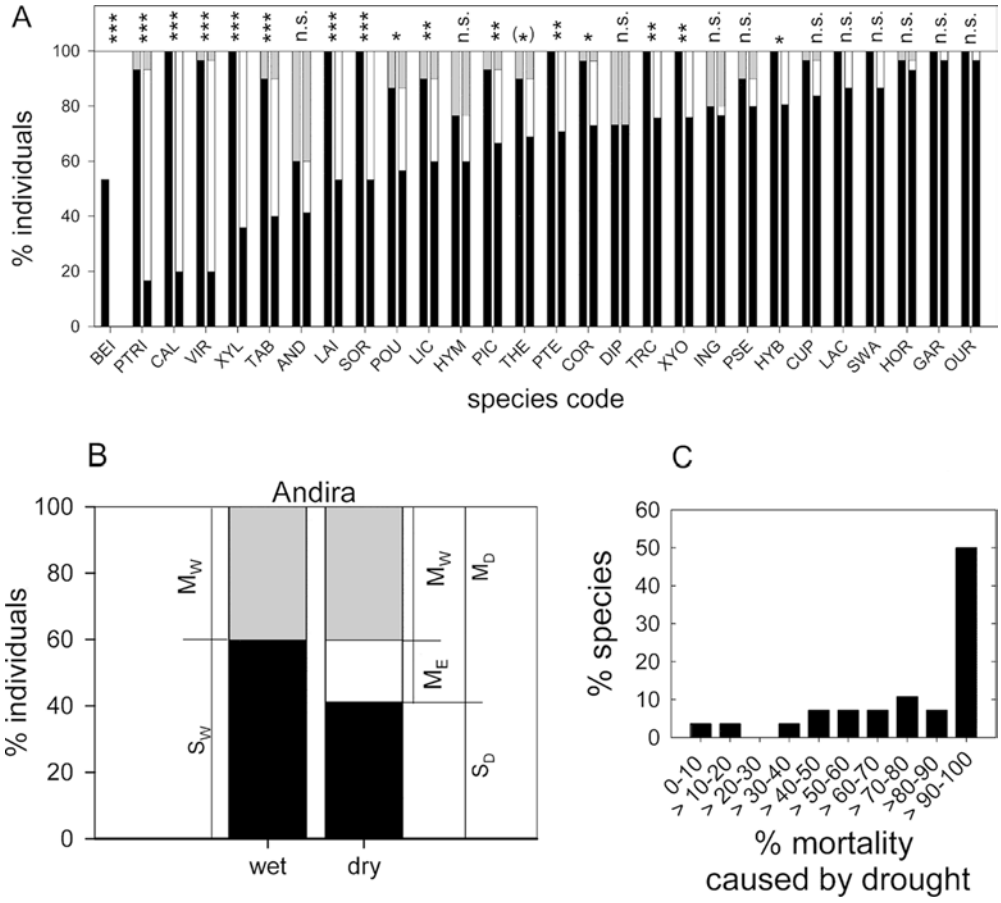

Fig. 5 **a** Percent of individuals alive (*open and grey bars*) or dead (*black bars*) at the end of the experiment (22 weeks) for seedlings of 28 species in the irrigated treatment (*first bar*) and the dry treatment (*second bar*). The causes of mortality (white and grey) are indicated in b. The causes of mortality could not be distinguished for Beilschmiedia. Results of Fisher's exact test for treatment effects on survival within each species: ***$P<0.0001$, **$P<0.005$, *$P<0.05$, (*) $P=0.05$, n.s. $P>0.05$. Species codes are given in Table 1. **b** The effects of drought and non-drought factors on survival of Andira in the irrigation experiment. For the irrigated (*wet*) treatment, mortality is only due to non-drought factors (M_W, grey), resulting in a survival rate of S_w (*black*). Under the non-irrigated treatment, the same non-drought factors are present, and lead to mortality (M_W). Additionally, excess mortality, or M_E (white), is due to drought and to interactions of drought with the non-drought factors. Given M_W plus M_E, the resultant survival rate in the non-irrigated treatment equals S_D (*black*). **c** The importance of drought as a cause of mortality in 27 species. Frequency *histogram* for percent mortality due to drought relative to total mortality in the dry treatment ($100\times I$; see Eq. 3). Beilschmiedia was excluded from this analysis

Survival curves of nine species for ten censuses during the experiment (Fig. 4) and the survival and mortality at the end of the experiment illustrate the varied treatment responses of the study species (Fig. 5a). In the irrigated treatment survival exceeded 90% for 22 species at the end of the 22 week experiment (Fig. 5a). In the other six species [Beilschmiedia (BEI), Andira (AND), DIP, Hymenaea (HYM), Inga (ING), Pouteria (POU)], several individuals died even in the irrigated treatment. In BEI, severe wilting was observed in the irrigated treatment, and mortality even in the irrigated treatment may have been caused by drought. In none of the other species did wilting occur in the irrigated treatment, indicating that factors other than drought caused the death of these individuals.

Under the dry treatment, mortality was higher and differed more among species, ranging from 5% to 100% (Fig. 5a). This is exemplified by the continuum from GAR, with virtually no mortality, to VIR with very high mortality (>80%) after 22 weeks in the dry treatment (Fig. 4). Only one species, DIP, had higher survival (ns) in the dry as compared to wet treatment. After 22 weeks of drought, the dry treatment reduced survival in 16 species but the treatment effect was not significant in the other 12 species.

Drought as the cause of seedling mortality

Seedling death during drought can occur both as a direct result of water stress, or because drought can exacerbate the effects of non-drought factors such as pathogens, herbivores, competitors or light (e.g., Augspurger 1984a, b). For example, low light or herbivores can weaken plants and predispose them to an early death under drought stress (Schoeneweiss 1986; Howe 1990; Gerhardt 1996). In our experiment, we asked to what extent seedling death was caused by drought and its interactions. To quantify this, we assumed that all non-drought causes of mortality act equivalently between treatments, i.e., in the absence of drought

the same proportion of plants would die in both treatments. Thus, except for Beilschmiedia (see above), all excess mortality in the dry treatment can be ascribed to drought, either directly or through interactions (Fig. 5a and b).

Under the assumptions that (1) drought was not a cause of mortality in the irrigated treatment, and (2) non-drought factors act equivalently on both treatments, we calculated the relative importance of drought as a cause of seedling mortality in the field (I) as

$$I = \frac{M_D - M_W}{M_D} = \frac{M_E}{M_E + M_W} \quad (3)$$

where M_W = mortality in the wet plots, M_D = mortality in the dry plots, M_E, is extra mortality in the dry plot ($M_D - M_W$). M_E, and hence I, includes direct drought effects and may include mortality due to interactions between drought and other stresses (Fig. 5c). Referring to the open bars in Fig. 5a and comparing mortality in the dry and irrigated treatments, shows that I ranged from 0 for DIP to nearly 1.0 for Xylopia [XYL], Lacistema [LAI] and others. For 28 species, the median of the relative importance of drought, I, was 0.89. In only 5 out of 27 species (18.5%) was more than 50% of the mortality due to reasons other than drought stress (i.e., $I<0.5$). Hence, drought effects were the main reason for mortality in the dry treatment (Fig. 5c).

Because non-drought factors, especially light and herbivore or pathogen pressure, may (co-) vary with drought (e.g., Wright 1996; Wolda 1988), distinguishing between non-drought and drought factors requires experiments in the natural habitat. One must directly compare performance under dry and wet (irrigated) treatments, where we can make the assumption that any non-drought stressor causes equal mortality under both treatments (M_W in Eq. 3). The need to directly compare dry and irrigated treatments is exemplified by our results, as several of the species showed pronounced mortality for irrigated plants (e.g., high M_W as for AND, DIP; Figs. 4 and 5a). In fact, in the irrigated treatment herbivores and pathogens were the main reasons for seedling mortality (pers. observation). For example, the high mortality in AND in both treatments was due to herbivory by a beetle (*Diabrotica* sp., Chrysomelideae; D. Windsor, personal communication). In these examples, the importance of drought stress leading to seedling mortality would have been overestimated if all mortality had been ascribed to drought effects.

To our knowledge, only four studies have been conducted in tropical forests in which survival (or mortality) during the dry season was directly compared to an irrigation treatment, thus allowing assessment of the role of drought stress in seedling mortality (Fisher et al. 1991; Mulkey and Wright 1996; Poorter and Hayashida-Oliver 2000; Cabin et al. 2002). However, each of these studies included only a small number of species, and the applied drought levels varied. Direct comparisons among them, as well as to our study, are therefore not possible.

Quantifying drought performance

In this paper we have focused on relative survival in dry plots (S_D) compared to watered plots (S_W) as a crucial component of drought performance. We calculated drought performance (D_p) as:

$$D_p = \frac{S_D}{S_W} \times 100 = 100 - \frac{S_W - S_D}{S_W} \times 100 \quad (4)$$

where S_W and S_D are the survival over 22 weeks in the wet and the dry treatment, respectively. Referring to the solid bars in Fig. 5a and comparing survival in the dry and irrigated treatments, Fig. 6a shows that D_p ranged from 0 to 100% among 28 species.

Our approach of quantifying D_p allows for a ranking of the effect of drought stress on survival among species. Ranking of species did not significantly change over time in this experiment (data not shown). Hence the relative D_p for a particular species, as measured experimentally, should be similar to the relative drought performance found in a natural dry season with naturally occurring seedlings. Thus, relative drought performance provides a powerful, quantitative tool for examining the importance of drought for species distribution patterns (see below). The actual mortality in our experiment cannot necessarily be directly compared to the natural dry seasons because drought performance depends on experimental levels, i.e., length and intensity of the drought. However, gravimetric water contents in the subsequent dry season matched those in our experiment very closely (Fig. 2), suggesting that our experimental treatment was a realistic one.

The drought performance parameter, D_p, reflects the interactions of drought stress with other factors as well as 'innate plant drought-resistance', a function of morphological, physiological, and molecular mechanisms of desiccation-tolerance and desiccation-delay. Adaptations to drought, allowing high survival rates even under considerable drought stress, are advantageous for plants in areas exposed to annual pronounced dry seasons as well as occasional severe dry seasons associated with El Niño events. Adaptations include physiological and morphological mechanisms of desiccation delay (e.g., early stomatal closure, low cuticular conductance, extended root systems), and mechanisms of desiccation tolerance (e.g., ability of cells to survive at low water potentials, low xylem vulnerability to embolism, osmotic adjustment). In moist tropical forests, mechanisms of desiccation tolerance are of major importance for seedling survival through a dry season (Tyree et al. 2003).

Drought-resistance can be evaluated only under strictly controlled conditions, where drought is the only stressor, while all other abiotic factors are held constant and all biotic effects on plant water relations (e.g., mycorrhizae, pathogens, or competitors, reviewed in Lösch and Gansert 2002) are excluded. While such an approach might be preferable for identifying and evaluating mechanisms of desiccation tolerance and desiccation delay (Tyree et al. 2002, 2003), it may be of limited value for assessing the

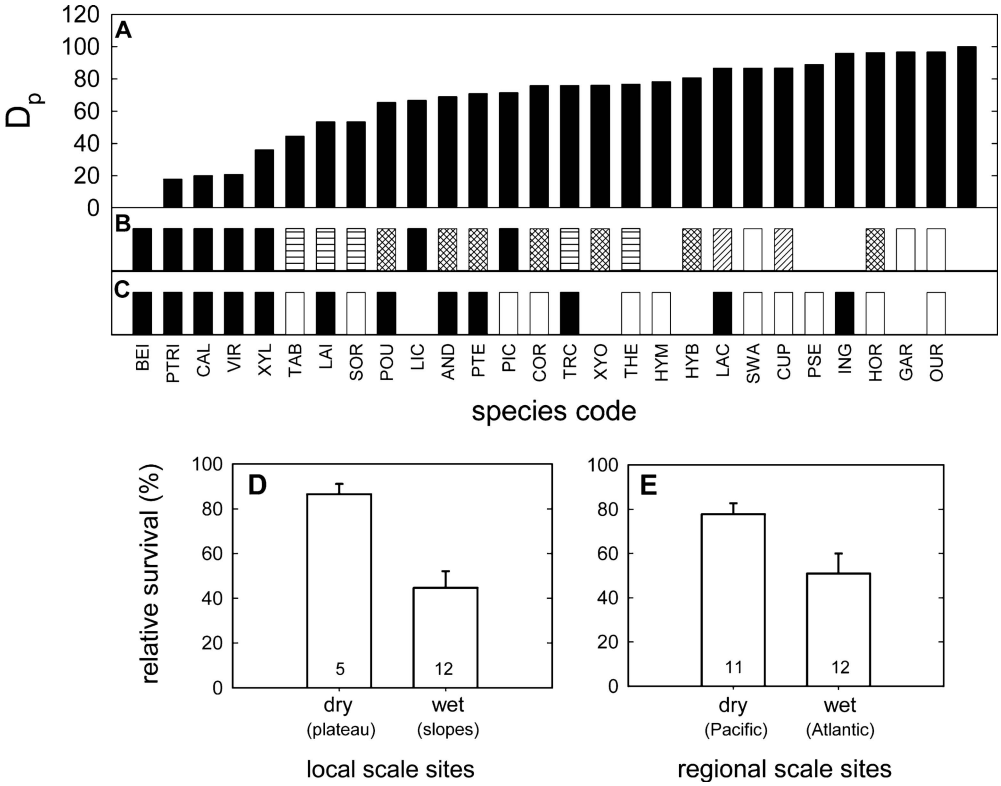

Fig. 6 **a** Relative survival in the dry treatment compared to the irrigated treatment or drought performance (D_p in Eq. 4) for 28 species. Species codes as in Table 1. **b** Habitat associations in the 50 ha plot on BCI to topographically defined units indicative of soil moisture. Only significant associations based on torus translations are given. *Black* Positive association to wet habitats (slopes and or streams), *horizontally hatched* negative association to dry habitats (low and/or dry plateau), *cross hatched* no association, *diagonally hatched* negative association to wet habitats, *open* positive association dry habitats. Species for which no information was available are left blank. **c** Abundance on the wet Atlantic and on the dry Pacific side of the Isthmus of Panama. *Black* Abundance higher at the Atlantic than at the Pacific side, *open* abundance higher at the Pacific side. **d** Comparison of relative drought survival (D_p) for species associated with dry or wet habitats (*dry* positive association with plateau or negative with slopes, *wet* positive associations with slopes or negative with plateau, see **b**). **e** Comparison of D_p for species with higher abundance at the dry or wet side of the Isthmus of Panama (see **c**). Data are average ± SE, *n* are given in the columns. Distributions are based on Harms et al. 2001, Condit et al. (2004)

ecological importance of drought. Thus our measure of D_p, by quantifying the drought performance of plants under actual field conditions and by distinguishing mortality due to drought from non-drought factors, provides an ecologically relevant measure of this trait.

Drought performance may determine species distributions in tropical forests

There were dramatic differences among species in D_p, with values from 0 to 100%. Because dry season soil moisture contents and dynamics of soil water depletion vary spatially at the microsite, landscape and regional scale (e.g., Becker et al. 1988; Engelbrecht 1998; B.M.J. Engelbrecht et al. unpublished data), we hypothesized that differences in D_p would influence plant distributions. Our results strongly suggest that seedlings of a wide range of species in tropical moist forests suffer drought-induced mortality during the dry season, especially in severe dry seasons. Pronounced mortality was already evident half-way through the experiment (Fig. 3), implying that even dry seasons of below average duration are sufficient to induce mortality in many species. Hence drought should be a strong selective agent in the moist tropical forest of our study site. In fact, under natural conditions, lower seedling survival in the dry than in the wet season has been shown in dry, moist and even wet tropical lowland forests (dry: Gerhardt 1996; Marod et al. 2002; moist: Howe 1990; Turner 1990; Garwood 1982; Poorter and Hayashida-Oliver 2000; wet: Green and Newbery 2002). Thus, species with low drought performance should be at a disadvantage under dry conditions.

On the other hand, for more than one-third of the species in this study, the drought effect was not significant. In a study of naturally established seedlings of three common shade-tolerant tree species on BCI (among them *Trichilia tuberculata* [TRC], a species we found to have intermediate D_p; Fig. 5a) survival was not lower in a severe El Niño dry season compared to normal years (Engelbrecht et al. 2002). These observations indicate that a large proportion of the common species in the moist forest at our study site may be well adapted to drought, and survive even severe dry seasons or in dry microsites.

We also find that D_p is a strong determinant of plant distributions across microsites and regions that differ in water availability. Species associations with dry or wet

habitats have been calculated for the 50 ha forest dynamics plot on BCI (Harms et al. 2001) and we compared these with D_p. In those species associated with dry habitats in the 50 ha plot (e.g., plateau), D_p was significantly higher than in the species associated with wet habitats (e.g., slopes; Fig. 6b,d; *t*-test: $P<0.0005$). Consistent with our results, a number of studies have shown that variables that are indicative of rhizosphere water availability at the microsite level correlate with the habitat associations of tropical forest plants worldwide (e.g., Webb and Peart 2000; Harms et al. 2001; Chuyong et al. 2003; Gunatilleke et al. 2003; Johns and Dattaraja 2003).

With respect to distribution on a regional scale, we assessed species differences along the rainfall gradient across the Isthmus of Panama. Our analysis was based on two forest dynamics plots: 4 ha at Cocoli on the dry side of the Isthmus and 5.96 ha at Sherman on the wet side of the Isthmus (see Condit et al. 2004, for data and details on the plots). We found that D_p was significantly higher in species with higher abundance on the dry side of the Isthmus of Panama than in those more abundant on the wet side (Fig. 6c,e; *t*-test: $P<0.05$). On the regional scale, water availability has long been considered one of the main factors limiting species distribution in lowland tropical forests (reviewed in Veenendaal and Swaine 1998), and an increasing amount of correlative evidence links rainfall with the distributions of tropical forest species (Swaine 1996; Condit 1998; Bongers et al. 1999; Pyke et al. 2001). However, mechanisms leading to the observed patterns both at the local and regional scale are poorly studied (but see Veenendaal and Swaine 1998), and therefore remain largely unresolved. Nevertheless, further studies of drought performance may provide mechanistic insights.

We focused on D_p in seedlings because recruitment may be the key life history stage that is influenced by drought. In our experiment, drought stress affected survival and wilting behaviour of seedlings of the study species to very different extents (Figs. 3, 4 and 5a), likely resulting in differential consequences of drought for species recruitment patterns. With respect to seasonal and interannual variation in water availability, recruitment of the most drought-sensitive species will be affected even by moderate drought, restricting successful recruitment of these species to exceptionally wet years, whereas recruitment of those species with high relative drought survival will not be affected by dry season drought. We also hypothesize that seedlings of species typically found in dry sites will show a lower impact of drought on recruitment than species typically found in wetter sites. Therefore drought effects on recruitment may be an important mechanism for constraining species distributions. In fact, the change in the composition of species along the rainfall gradient across the Isthmus of Panama is dramatic (Fig. 1b and c). Only 2 of the 50 most abundant species at the wet Atlantic side occur also at the dry side, and 7 of the 50 most abundant species on the dry side occur also on the wet side. Furthermore, only one species (*Thevetia ahouai*) overlaps among the most abundant species at the Atlantic and the Pacific side. The extent to which the effect of drought on recruitment is one of the mechanisms responsible for this pattern remains to be determined.

To our knowledge, only one study has accumulated direct experimental evidence that links the processes observed on the population level to community composition (Veenendaal and Swaine 1998). They showed that species extending into drier forests had much lower mortality (<10%) under experimental drought than species native to evergreen wet forest (30–80%). The importance of drought for species distribution was further supported by a transplant experiment, which showed consistently higher mortality in moist than in wet forest. Despite this clear pattern, there were prominent—and yet unexplained—exceptions both in their study and in the study presented here; for example we found Tabebuia to be rather drought sensitive, although it is a typical dry forest species. These exceptions point out the importance of other mechanisms besides drought for determining species distribution along rainfall gradients.

With global climate change, shifts in rainfall patterns together with an increase in the frequency of El Niño events are expected for the tropics (Hulme and Viner 1998; Timmermann et al. 1999). Variation in forest composition along rainfall gradients suggests that changes in rainfall will have profound impacts on tropical forest communities (Condit 1998). Quantitative assessments of the differential abilities of species to survive drought will permit us to rigorously test to what extent species drought performance influences plant distributions. A knowledge of drought performance will therefore contribute to our understanding of the processes that determine tropical forest community composition, such as coexistence in highly diverse communities and gradients of species diversity (cf. Givnish 1999; Hubbell 2001; Wright 2002), as well as to predicting climate-induced changes in tropical forest communities.

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