

Diversity of Tropical Tree Seedling Responses to Drought

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ABSTRACT

Drought is an important seedling mortality agent in dry and moist tropical forests, and more severe and frequent droughts are predicted in the future. The effect of drought on leaf gas exchange and seedling survival was tested in a dry-down experiment with four tree species from dry and moist forests in Bolivia. Seedlings were droughted and wilting stage and gas exchange were monitored. Drought led to a gradual reduction of photosynthesis and stomatal conductance over time, whereas respiration and photosynthetic water-use efficiency initially increased with drought and then declined. Seedlings gradually went through the different wilting stages, until they eventually died, but the trajectory differed for the four species. The strong relationship between wilting stage and photosynthesis means that simple field observations can provide valuable information on plant physiological performance. Three different drought strategies were identified. Dry forest species *Ceiba samauma* shed its leaves and survived. The moist forest species *Cariniana ianeirensis* postponed drought stress by having low rates of transpiration and high water-use efficiency. Dry forest *Astronium urundeuva* and moist forest *Triplaris americana* followed an opportunistic strategy; they are early successional species that can quickly grow to maturity but periodic drought can be lethal. Strikingly, dry and moist forest species did not differ clearly in their drought tolerance strategies.

Abstract in Spanish is available at <http://blackwell-synergy.com/loi/btp>.

Key words: *Astronium urundeuva*; Bolivia; *Cariniana ianeirensis*; *Ceiba samauma*; drought stress; gas exchange; *Triplaris americana*; tropical dry forest; tropical moist forest; wilting stages.

GRADIENTS OF DISTRIBUTION AND DIVERSITY of tropical forest species are strongly associated with gradients in annual rainfall and soil moisture availability (e.g., Gentry 1988, Swaine 1996, Bongers *et al.* 1999, Poorter *et al.* 2004). Forests at the dry end of the continuum experience strong annual droughts, but moist tropical forests halfway along the continuum also experience seasonal dry periods, albeit less frequently and less severe (Becker *et al.* 1988, Windsor 1990, Meinzer *et al.* 1995). During a prolonged dry season, moist forest plants may be deprived of rainfall for up to 3 mo after reaching their permanent wilting point (Veenendaal *et al.* 1996). Such prolonged dry periods are often associated with El Niño Southern Oscillation (ENSO) events (Timmermann *et al.* 1999, Nakagawa *et al.* 2000). Seedlings are especially prone to dry season stress as young plants have had little time to develop extensive root systems (Condit *et al.* 1995, Poorter & Hayashida-Oliver 2000). Indeed, drought has been associated with increased mortality and decreased growth rates in seedlings of tropical plants (e.g., Mulkey & Wright 1996, Veenendaal *et al.* 1996, Engelbrecht & Kursar 2003, Poorter 2005). The ability of seedlings to survive periodic drought is thus a major factor influencing seedling growth and consequently species composition in dry and humid forests (Mulkey & Wright 1996, Khurana & Singh 2001).

There are two mechanisms of drought resistance—desiccation delay and desiccation tolerance. Plants may delay desiccation by increasing access to water and by reducing water loss. This may be

achieved by morphological or physiological adaptations to drought or a combination of both. Examples of morphological adaptations are having a deep root system, being able to store water in organs, having small and compound leaves to reduce transpirational water loss, or shedding leaves when the plant can no longer maintain a positive carbon balance (Levitt 1980, Davis & Mooney 1986, Pallardy & Rhodes 1993, Grubb 1998). Physiological adaptations include reduction of stomatal conductance upon drought and having low cuticular conductance. Desiccation tolerance is achieved through osmotic adjustment and stomatal control, which allow gas exchange and water transport to take place at low water potential and by traits that increase resistance to xylem embolism (Jones & Sutherland 1991; Tyree *et al.* 2002, 2003; Engelbrecht & Kursar 2003).

Understanding how successful different drought resistance strategies are for species originating from different positions along the water availability continuum is important for predicting the consequences of climatic change on species performance and composition. During the last decades, tropical forests have experienced more frequent and more severe droughts (Malhi & Wright 2004) and this trend is expected to continue (Timmermann *et al.* 1999). If plant survival during drought can be related to the position on the rainfall gradient of the forest the species originates from and/or to their physiological and morphological responses to drought, we would have a tool to predict future forest composition under different drought regimes. This knowledge would become especially useful if visual indicators could be correlated with plant physiological performance.

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TABLE 1. Species included in the study, their origin ('Dry': dry deciduous forest, Inpa; 'Moist': semi-evergreen moist forest, La Chonta), the density at which the species occur in Inpa and La Chonta, their deciduousness, their root water content (root WC), and specific root length (SRL) at the start of the experiment.*

Species	Family	Origin	Density (per ha)		Deciduousness		Root WC (%)	SRL (m/g)
			Inpa	La Chonta	Seedling	Adult		
<i>Astronium urundeuva</i> (Allemão) Engl.	Anacardiaceae	Dry	1.34	0	No	Yes	66.1 ^{ab}	22.0 ^a
<i>Ceiba samauma</i> (Mart.) K. Schum	Bombacaceae	Dry	0.34	0.19	Yes	Yes	84.5 ^c	7.0 ^a
<i>Triplaris americana</i> L.	Polygonaceae	Moist	0	0.17	No	No	62.0 ^a	108.1 ^b
<i>Cariniana ianeirensis</i> R. Knuth	Lecythidaceae	Moist	0.88	3.21	Yes	Yes	69.9 ^b	5.2 ^a

*Values in the same column followed by a different letter are significantly different ($P < 0.05$; one-way ANOVA with LSD post hoc tests).

In a dry-down experiment we determined the physiological responses to drought of first-year seedlings of four Bolivian tropical tree species. Species were selected from two forest types differing in soil water availability, to capture a range of positions along the water availability continuum, and hence, a potential range in drought strategies. The following questions were addressed: (1) How do seedlings respond to sudden drought in terms of gas exchange and survival? (2) Do species that originate from different positions along a water availability continuum follow different trajectories of physiological change during progressive drought? (3) Are visual wilting stages good indicators of physiological performance of plants at different moments during the process of desiccation?

METHODS

PLANT MATERIAL.—Four tree species were selected from two types of Bolivian lowland forest that differ in water availability (Table 1). *Astronium urundeuva* Engl. occurs only in dry forest and *Ceiba samauma* K. Schum. occurs predominantly in dry forests, but at low density in moist forest as well; *Triplaris americana* L. only occurs in moist forest and *Cariniana ianeirensis* Knuth occurs predominantly in moist forests, but can be found at humid places in dry forest as well (L. Poorter, pers. obs.). The selected species thus occupy different positions along the rainfall continuum. *Cariniana ianeirensis* is a partial shade-tolerant species, whereas the other species are long-lived pioneers. Henceforth, the species will be referred to by their genus name only.

Seeds were collected from a dry deciduous forest (Inpa) and from a semi-evergreen moist forest (La Chonta). Inpa (16°6' S, 61°42' W), a dry deciduous forest, has an annual rainfall of 1160 mm with a distinct dry period (potential evapotranspiration > precipitation) of 3 mo and a lowest dry season gravimetric soil water content of 4.6 percent (± 0.4 SE; L. Poorter, pers. obs.). La Chonta (15°47' S, 62°55' W), a moist semi-evergreen forest, has an annual rainfall of 1580 mm with a distinct dry period of 1 mo and a lowest dry season gravimetric soil water content of 11.9 percent (± 1.4 SE; L. Poorter, pers. obs.). Seeds were germinated in a nursery shade house in Santa Cruz, Bolivia (16°30' S, 68°10' W) at ca 15 percent of full sunlight in trays with a 50:50 mixture of river sand and organic soil. The recently germinated seedlings were transplanted to individual 200-mL tubes (3-cm wide \times 12-cm long) filled with 50 percent river sand, 25 percent soil from the top layer of the

moist forest, and 25 percent soil from the top layer of the dry forest. From each species, 25 individuals were grown at 10 percent of full sunlight, in a neutral-density shade house that was established at the Instituto Boliviano de Investigación Forestal.

DROUGHT EXPERIMENT.—When the seedlings were ca 15-cm tall and had developed on average seven leaves, five plants per species were harvested to determine specific root length (SRL) and root water content at the start of the experiment. The roots were weighted and placed in a transparent tray with water on top of an A4-sized paper with a 2 \times 2 cm grid and the intersections of roots with gridlines were counted. Root length was estimated using $R = \frac{\pi \cdot N \cdot A}{2H}$ (Newman 1966), where R is the total length of the root, N is the number of intersections between root and gridlines, A is the area of the rectangle, and H is the total length of the straight lines of the grid. After oven drying for at least 48 h at 70°C, dry mass of the plant parts was measured with a microbalance. The leaf and root water content at the start of the experiment were calculated as $100 \times \frac{(\text{freshmass} - \text{drymass})}{\text{drymass}}$ (%) and SRL was calculated as root length over root dry mass (m/g).

Ten plants per species were randomly allocated to a drought treatment in which they were no longer watered, or to a control treatment, in which case they continued receiving water every day. The experiment was conducted in the dry season, in August 2004. In this dry-down experiment, we were interested in short-term responses of seedlings to sudden drought, as short dry spells have been shown to affect survival of tropical tree seedlings in the field within a few days (Engelbrecht *et al.* 2006). The experiment thus presented a worst-case scenario in which seedlings restricted by a limited pot volume were exposed to sudden drought.

The effect of the drought treatment was assessed every morning by assigning each seedling to one of five visual wilting stages (Table 2; Engelbrecht & Kursar 2003) based on easily perceptible characteristics, such as the leaf angle and necrosis. The classification was later compared with the photosynthetic performance (see below) of the same plants at given wilting stages to assess the accuracy of visual wilting stages in assessing seedling performance.

GAS EXCHANGE MEASUREMENTS.—The photosynthetic capacity of leaves under saturating light (A_{MAX} ; $\mu\text{mol CO}_2$ taken up/m² leaf area/sec) can be used to assess the potential carbon uptake of plants. Together with measurements of dark respiration (R_{DARK} ; $\mu\text{mol CO}_2$ released in the dark/m² leaf area/sec), this gives a good

TABLE 2. *Wilting stages and the visual characteristics on which they were based (after Engelbrecht & Kursar 2003)*

Wilting Stage	Characteristics
0 Normal	No sign of water stress. All leaves green and with full turgor
1 Slightly wilted	Slight leaf angle changes. Some leaves losing turgor
2 Wilted	Leaves start to 'hang' and have lost turgor
3 Severely wilted	Leaves are hanging. Beginning leaf necrosis
4 Nearly dead	All leaves dead. Stem alive, as distinguished by color and elasticity
5 Dead	All above ground parts dead

indication of a plant's performance in terms of their carbon balance. The intrinsic photosynthetic water-use efficiency (WUE ; $\mu\text{mol CO}_2$ taken up/ $\mu\text{mol H}_2\text{O}$ used) was calculated as $A_{\text{MAX}}/\text{stomatal conductance } (G_S)$; Osmond *et al.* 1980, Farquhar *et al.* 1989).

Gas exchange parameters were measured every second day from the start of the experiment (no measurements could be made on day 4 because of technical problems). Measurements were made on five plants per species per treatment. In principle, the same individuals were used, unless plants died; those were replaced by other plants of the same treatment until, eventually, most plants died and the number dropped below five. Measurements were taken at 0800–1130 h to avoid potentially confounding effects by mid-day depression of photosynthesis. Measurements were made on attached, fully expanded leaves using a CIRAS-1 portable infrared gas analyzer (PP-Systems, Amesbury, MA, U.S.A.) operating in open flow mode and fitted with a Parkinson leaf cuvette that included 2.5 cm² leaf area. The CO₂ concentration of the reference air was maintained at 360–380 ppm by a CO₂ control module and all measurements were performed at a relative humidity of 75 percent, typical conditions for shade houses the plants were grown in.

Preceding the measurements of A_{MAX} , several photosynthesis light response curves were made for each species. From these light response curves, the photosynthetic photon flux density (PAR, photosynthetic active radiation; $\mu\text{mol quanta/m}^2/\text{sec}$) at light saturation was determined. Based on these measurements, the saturating light intensity for further measurements was set at 800 $\mu\text{mol quanta m}^2/\text{sec}$ for all species. Readings were taken once a stable output was obtained.

Dark respiration was measured on leaves that were pre-darkened with dark cloth for at least 30 min. As the leaf cuvette could not be temperature regulated, the measurements were performed at different temperatures. To correct for this, the temperature sensitivity of respiration (Q_{10} : the proportional increase in R_{DARK} with a 10°C increase in temperature) was assumed to be 2.0 and, based on this assumption, all R_{DARK} values were standardized to a temperature of 25°C. The Q_{10} is not 2.0 for all species under all conditions (Atkin & Tjoelker 2003) and particularly the Q_{10} of plants under stress may deviate from 2.0 (M. Slot, pers. obs.). For this study it was, however, sufficiently accurate to assume a Q_{10}

of 2.0, as the majority of the R_{DARK} measurements could be made within a small temperature range (range over experimental period: 20–30°C; mean: 24°C; maximum range on single day: 5°C).

STATISTICAL ANALYSES.—Biomass allocation data and physiological parameter data at $t = 0$ were normally distributed (Kolmogorov–Smirnov tests, all P values > 0.05), so differences of these initial values between species were determined with one-way analysis of variances (ANOVAs) with least significant difference (LSD) *post hoc* tests. Differences in parameter values during the progressive drought were analyzed with 2-sample t -tests ($N = 5$) by comparing the parameter value of the measuring date with the parameter value at $t = 0$. The differences of A_{MAX} and WUE measured on plants that had been assigned to different wilting stages were analyzed with Kruskal–Wallis tests. All statistical analyses were performed using SPSS 12.01 (SPSS, Inc. Chicago, IL, U.S.A.).

RESULTS

EFFECT OF DROUGHT ON WILTING, MORTALITY, AND GAS EXCHANGE.—No control plants showed signs of wilting and gas exchange parameter values never differed significantly from those at $t = 0$. All measurements of droughted plants were therefore compared to $t = 0$ values of the same plants rather than to values of control plants and only drought treatment values are shown in tables and figures.

The first signs of droughting were visible within 5 d when, for all four species, 60–100 percent of the individuals were (slightly) wilted (Fig. 1). All *Astronium* and *Triplaris* plants moved rapidly through the wilting stages and died by day 9. *Ceiba* and *Cariniana*, in contrast, did not enter the 'nearly dead' or 'dead' stages until day 10. *Ceiba* was the only species for which all plants survived until the end of the experiment (day 12). In fact, after 5 mo of droughting, most *Ceiba* plants were still alive, as distinguished by color and elasticity of the stems (L. Poorter, pers. obs.).

The maximum photosynthetic rate (A_{MAX}) dropped in all species after initiation of the drought treatment (Fig. 2A). Already on day 2, the start of a downward trend in photosynthesis was observed, and on day 6, the photosynthetic rates were significantly lower than the rates at day 0 for all species (2-sample t -test, $P < 0.05$). The values continued to drop as drought progressed until the plants were 'nearly dead' and A_{MAX} values did not differ significantly from zero. For all species but *Astronium*, dark respiration rates (R_{DARK}) showed an initial significant increase after which they declined and approached zero when plants were nearly dead (Fig. 2B). Stomatal conductance (G_S) changed over time (Fig. 2C). Starting with values of 40–80 mmol/m²/sec, drought treatment soon caused conductance to drop and, by day 6, G_S had already reached near-zero values for all species but *Astronium*. Upon initiation of drought, WUE increased significantly for all species except *Triplaris* (Fig. 2D). In *Ceiba* and *Cariniana*, WUE reached higher values, but as with *Astronium* and *Triplaris*, WUE dropped to near-zero values toward the end of the experiment when A_{MAX} had strongly decreased.

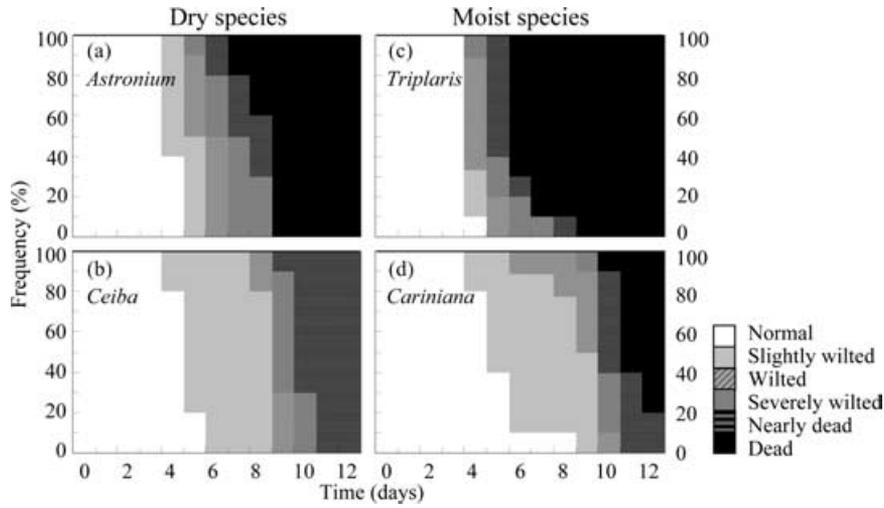


FIGURE 1. Relative frequencies of wilting stages and mortality of seedlings ($N = 10$) of two dry forest species (A, B) and two moist forest species (C, D) during progressive drought.

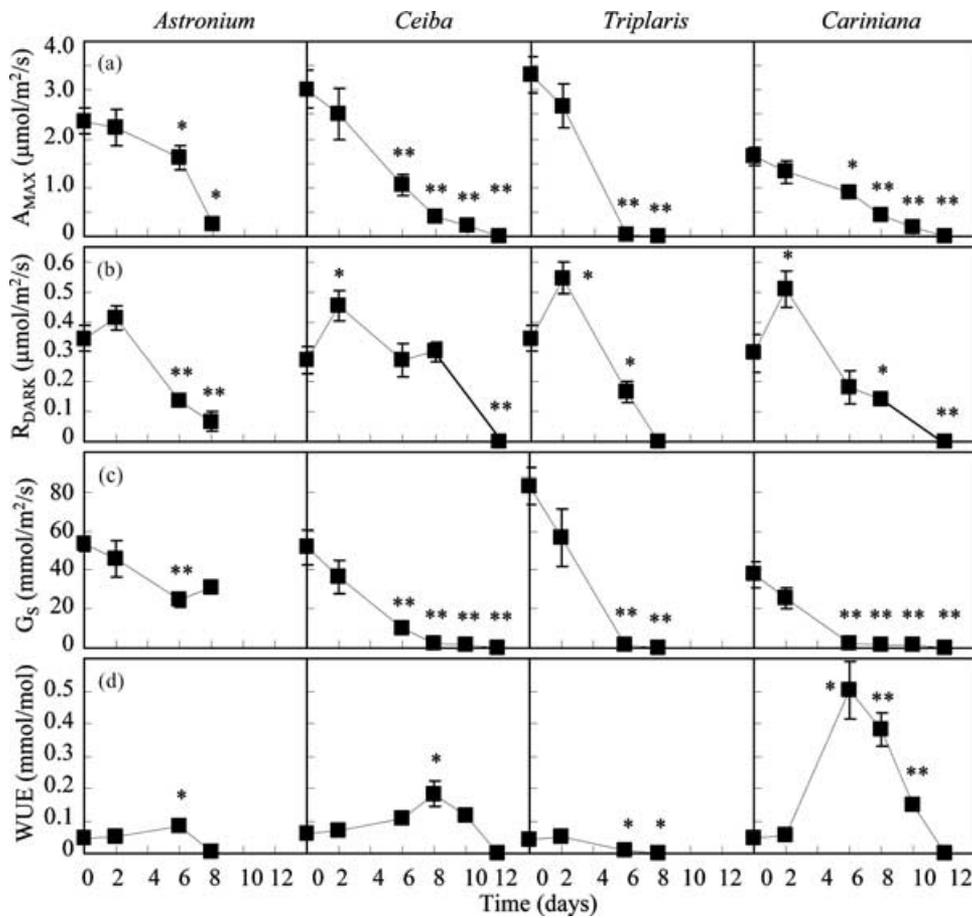


FIGURE 2. (A) Maximum photosynthetic capacity (A_{MAX}), (B) leaf dark respiration (R_{DARK}), (C) stomatal conductance (G_S), (D) and intrinsic water-use efficiency (WUE) of seedlings of four tropical tree species during progressive drought. Error bars represent 1 SE; values significantly different from the value at $t = 0$ (2-sample t -test) are indicated with one ($P = 0.05$) or two ($P = 0.01$) asterisks.

TABLE 3. Initial values of physiological parameters of seedlings of four tropical tree species ± 1 SE of the mean ($N = 10$ per species).*

	A_{MAX} ($\mu\text{mol}/\text{m}^2/\text{sec}$)	R_{DARK} ($\mu\text{mol}/\text{m}^2/\text{sec}$)	G_5 ($\text{mmol}/\text{m}^2/\text{sec}$)	WUE (mmol/mol)
<i>Astronium</i>	$2.52^b \pm 0.25$	$0.32^a \pm 0.03$	$50.1^b \pm 3.1$	$0.05^a \pm 0.003$
<i>Ceiba</i>	$2.69^b \pm 0.25$	$0.27^a \pm 0.02$	$42.5^b \pm 5.4$	$0.066^b \pm 0.003$
<i>Triplaris</i>	$3.45^c \pm 0.20$	$0.27^a \pm 0.03$	$81.3^c \pm 5.5$	$0.043^a \pm 0.003$
<i>Cariniana</i>	$1.51^a \pm 0.13$	$0.25^a \pm 0.04$	$27.6^a \pm 3.7$	$0.059^{ab} \pm 0.006$

*Values in the same column followed by a different letter are significantly different ($P < 0.05$; one-way ANOVA with LSD post hoc tests).

INTERSPECIFIC VARIATION IN DROUGHT RESPONSES.—Species differed markedly in initial parameter values (Figs. 1 and 2; Tables 1 and 3). A_{MAX} at $t = 0$ differed significantly between the species (one-way ANOVA; $F = 13.9$, $P < 0.01$; Table 3), with *Cariniana* having the lowest and *Triplaris* having the highest A_{MAX} . The same species difference was found for G_5 while for WUE , only *Ceiba* stands out with a significantly higher initial value than the other species. Such initial differences may be important as they could shed light on the species' growth strategy under nonlimiting conditions. The pretreatment values also set a baseline by which treatment effects could be compared. Root water content at $t = 0$ was highest in *Ceiba* seedlings and lowest in *Triplaris* seedlings (Table 1). SRL on the other hand, was by far the greatest in *Triplaris* plants, with no differences among the other species.

The species from drier origin followed comparable trends in drought response for all gas exchange parameters, but *Astronium* seedlings reached photosynthetic and respirational inactivity much earlier than *Ceiba* seedlings (Fig. 2A–D). Similarly, the moist forest species differed primarily in the timing of termination of photosynthetic and respirational activity. An apparent difference between the moist forest species was the vast increase in WUE in *Cariniana* against no increase in *Triplaris* followed by a decrease relative to $t = 0$ (2-sample t -test, $P < 0.05$).

RELATIONSHIP BETWEEN WILTING STAGE AND GAS EXCHANGE.—Are wilting stages good indicators of physiological performance of plants at different moments during the process of desiccation? There is a strong negative relation between wilting stage and A_{MAX} (Fig. 3A). The relationship between WUE and wilting stage is less straightforward (Fig. 3B). For *Ceiba* and *Cariniana*, the WUE is highest at intermediate wilting stages, whereas no clear patterns can be identified for *Astronium* and *Triplaris*.

DISCUSSION

EFFECT OF DROUGHT ON WILTING, MORTALITY, AND GAS EXCHANGE.—Drought clearly had a strong effect on seedlings in the worst-case scenario presented here. During the first few days, plants remained visibly unaffected, but soon showed signs of wilting

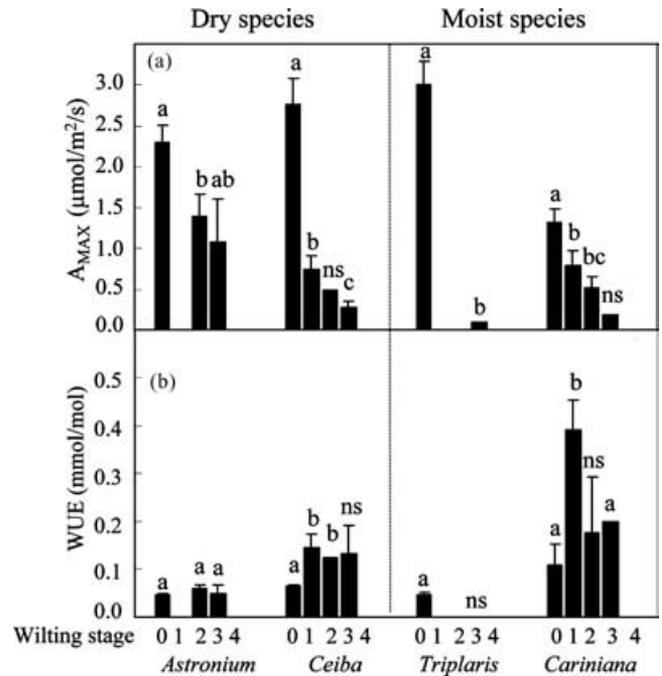


FIGURE 3. (A) Mean (± 1 SE) photosynthetic capacity (A_{MAX}) and (B) mean (± 1 SE) intrinsic water-use efficiency (WUE) per wilting stage for seedlings of four tropical tree species exposed to drought. Bars within species followed by a different letter are significantly different (one-way ANOVA, $P < 0.05$).

and eventually most died. Desiccation can cause membrane rupture and consequently leakage in plant cells (Hinch *et al.* 1987, Smirnov 1993) and, in the long run, a significant decrease in photosynthetic rates limits the photosynthates available for maintenance and repair, leading to the death of the plants. Drought is known to be an important cause of seedling mortality (Fisher *et al.* 1991, Lieberman & Li 1992, Veenendaal *et al.* 1996, Engelbrecht & Kursar 2003) and even short dry spells may lead to increased mortality (Engelbrecht *et al.* 2006). This sensitivity of seedlings to drought is confirmed by our data, though the short duration of the drying down process excludes depletion of photosynthates as a cause of mortality.

Because of the short duration of drying down of the plants, the strategies we have observed are based on the short-term effects of drought on leaf gas exchange. Important longer-term adaptations to drought include plasticity of rooting depth (Reader *et al.* 1993), changes in biomass allocation toward increased root growth (Poorter & Nagel 2000), and stomatal adjustment (*e.g.*, Escalona *et al.* 1999, Bonal & Guehl 2001).

INTERSPECIFIC VARIATION IN DROUGHT RESPONSES.—The species studied varied substantially in their response to experimental dry-down and there was little similarity in wilting patterns among species from nearby positions along the water availability continuum. Seedlings of dry forest species *Astronium* went through all wilting stages and died early (Fig. 1A), while dry forest species *Ceiba* stayed longer in the 'slightly wilted' stage before rapidly becoming

'nearly dead' at the end of the experiment (Fig. 1B). The moist forest species *Triplaris* moved quickly through the wilting stages and died early in the experiment (Fig. 1C), whereas *Cariniana* moved gradually through the wilting stages before dying late in the experiment (Fig. 1D). *Cariniana* is a moist forest species that performed relatively successfully during this drought experiment. This species does also occur in dry forests (Table 1), but only at wet sites, such as near streams (L. Poorter, pers. obs.).

The differences in success between the species appear to be linked to species-specific characteristics rather than to species origin per se. *Ceiba* and *Cariniana* survived the longest time under drought conditions. These species clearly have an advantage over the others: first, they have greater water storage capacity in their roots (Table 1); second, they have a larger root dry mass (data not shown), which when combined yields a higher potential water storage capacity; and third, they have a higher *WUE*, suggesting that the plant uses the water more efficiently (Table 3). Interestingly, these species had very low SRL (Table 1). In this dry-down experiment, the availability of water stored in the roots proved more advantageous than having a large network of fine roots to extract water from the drying soil (having a high SRL, like *Triplaris* has; Table 1), as soil water was rapidly depleted from the relatively small tubes.

Cariniana also had a significantly lower A_{MAX} at the start of the experiment, and the control plants had low rates of A_{MAX} until the end of the experiment. This low rate came with a very low stomatal conductance and high *WUE*. Because R_{DARK} was not different from other species the photosynthetic gain was relatively low. Consequently, the water requirement for this species was low, while the high *WUE* minimized the water loss. This allowed the plants to delay significant reduction of photosynthesis, which was also expressed by their wilting stages.

RELATIONSHIP BETWEEN WILTING STAGE AND GAS EXCHANGE.—All species showed signs of wilting when drought progressed (Fig. 1). These visual wilting stages related very well with A_{MAX} (Fig. 3). For all species, A_{MAX} was significantly lower for plants at higher wilting stages than for those with little or no signs of wilting. Each step to a higher wilting stage was accompanied by a decrease in A_{MAX} . This means that the visual wilting stages allow us to compare the photosynthetic fitness of individuals of a certain species and rank them accordingly, using the simple visual signs of wilting on which the stages are based. Also, in multispecies surveys, one can get a fairly good impression of the photosynthetic performance by using wilting stages. Visual wilting stages have been shown to correlate strongly with leaf water content of a tropical tree species *Licania platypus* (Hemsl.) Fritsch (Tyree *et al.* 2002), suggesting that they can indicate both leaf morphological and physiological condition.

There appears to be a curvilinear relationship between wilting stage and *WUE* (Fig. 3). In the early stage of drought and wilting, stomata close (G_S declines) and, consequently, *WUE* increases. This is in accordance with previous works (*e.g.*, Li 2000, Adams & Kolb 2004). When drought progresses, A_{MAX} drops to such low levels that *WUE* approaches zero. At intermediate wilting stages, the leaves, especially of *Cariniana*, thus use water most efficiently, but the relationship is weak and insufficient for use in field monitor-

ing of species performance. Valladares and Sánchez-Gómez (2006) suggest that there is a biphasic response in *WUE* during drought, analogous to that found in respiration (*e.g.*, Flexas *et al.* 2005) and triggered by the increased maintenance component of respiration at severe water stress. In our experiment, however, R_{DARK} had dropped considerably by the time *WUE* increased (Fig. 2). Brodrribb (1996) also found a biphasic response during drought in a study of changes in intercellular CO_2 concentration (c_i), a parameter that is related to *WUE* (Brodrribb 1996, Brodrribb & Hill 1998). After an initial stomatal control phase, with a reduction in c_i as G_S decreased, there followed a nonstomatal limitation phase as G_S approached a minimum, causing c_i to increase. This process might have taken place in the *Ceiba* and *Cariniana* plants in our study but this cannot be inferred from our data with certainty.

DROUGHT STRATEGIES.—Within the relatively short experimental period, the plants cannot have benefited from enhanced root growth or long-term osmotic adjustment. However, we can identify different drought strategies among the species in our experiment. *Ceiba* is able to shed its leaves during prolonged drought, a morphological desiccation delay strategy. In this worst-case scenario experiment, this proved to be a life-saving strategy. However, shedding leaves means that new leaves need to be produced later. Perhaps, its high photosynthetic rate allows *Ceiba* to store sufficient carbon and flush again at the onset of the wet season. *Cariniana*, on the other hand, was successful in postponing negative effects of drought by having a slow metabolism, a purely physiological strategy.

Astronium and *Triplaris* share a similar strategy. Both are early successional fast-growing species (M. Slot, pers. obs.) with relatively high photosynthetic rates. Especially, *Triplaris* invests little in below ground resource capture but instead focuses on height growth (M. Slot, pers. obs.). The small root system in combination with high water requirements for high photosynthetic rates, and a low *WUE* cause this species to lose turgor faster than any other species. The species dies almost instantaneously after soil drying, which explains its riverine distribution in dry forests. This species follows an opportunistic growth strategy in which periodic drought could be lethal, but the species can quickly grow to maturity if no severe drought takes place.

Astronium is a fast-growing, opportunistic species like *Triplaris*. It regenerates in high light conditions where it realizes fast growth rates and attains a large size before the onset of the dry season. Such large plants survive the dry season successfully because of their extensive and deep root system (Poorter & Hayashida-Oliver 2000, Poorter 2005).

The current experiment represented a worst-case scenario of plants growing in relatively small tubes that resulted in rapid mortality of the opportunistic species. Yet, an equally quick response to drought in terms of mortality was found in a field study by Engelbrecht *et al.* (2006) in which the effect of dry spells on tropical pioneer species in Panama was studied, while other studies report on much slower droughting of tropical saplings (*e.g.*, Bonal & Guehl 2001). It has been suggested that drought strategies of individual species may be linked with successional status (Veenendaal & Swaine 1998). Engelbrecht *et al.* (2006), however, found large interspecific

variation in drought responses among pioneer species, which suggests that it is difficult to identify such clear-cut differentiation in (the success of) drought strategies in relation to successional status.

With the presented data, we could identify species-specific variation in strategies to cope with drought stress. In order to identify a relation between species origin, drought avoidance strategy, and physiological performance during drought, future research should focus on the identification of functional groups of tropical forest tree species based on drought stress responses, and how the relative abundance of these groups varies along the rainfall gradient. The strong relationship between visual wilting stages and photosynthetic capacity suggests that the former is a promising tool with which to monitor plant responses to drought.

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