

Drought resistance in early and late secondary successional species from a tropical dry forest: the interplay between xylem resistance to embolism, sapwood water storage and leaf shedding

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ABSTRACT

The mechanisms of drought resistance that allow plants to successfully establish at different stages of secondary succession in tropical dry forests are not well understood. We characterized mechanisms of drought resistance in early and late-successional species and tested whether risk of drought differs across sites at different successional stages, and whether early and late-successional species differ in resistance to experimentally imposed soil drought. The microenvironment in early successional sites was warmer and drier than in mature forest. Nevertheless, successional groups did not differ in resistance to soil drought. Late-successional species resisted drought through two independent mechanisms: high resistance of xylem to embolism, or reliance on high stem water storage capacity. High sapwood water reserves delayed the effects of soil drying by transiently decoupling plant and soil water status. Resistance to soil drought resulted from the interplay between variations in xylem vulnerability to embolism, reliance on sapwood water reserves and leaf area reduction, leading to a tradeoff of avoidance against tolerance of soil drought, along which successional groups were not differentiated. Overall, our data suggest that ranking species' performance under soil drought based solely on xylem resistance to embolism may be misleading, especially for species with high sapwood water storage capacity.

Key-words: drought avoidance; drought tolerance; evolutionary trade-off; hydraulic architecture; secondary succession; soil drought; stem water storage capacity.

INTRODUCTION

Tropical landscapes in many areas of the world are a mosaic of active agricultural lands, secondary woody vegetation and patches of mature forest (Chazdon 2003). Dramatic differences in the microenvironments experienced by early

and late successional woody species raise questions concerning the functional attributes that allow certain species to establish and persist in the early secondary forest patches. The strong gradients in conditions and resources created during secondary succession offer a unique opportunity to explore physiological and ecological mechanisms associated with adaptations of species to given environments while controlling for geographic locality. The conventional wisdom derived from studies in wet regions is that in recently opened habitats, fast-growing, light-demanding species prosper and are filtered out as vegetation cover develops, producing shadier habitats where shade-tolerant species prevail (Bazzaz & Pickett 1980; Guariguata & Ostertag 2001). However, it is less clear whether drought risk changes during secondary succession and thus physiological strategies for dealing with drought (Fetcher, Oberbauer & Strain 1985; Guariguata & Ostertag 2001; Vieira & Scariot 2006). In recently abandoned agricultural lands where soil properties are degraded (Ellingson *et al.* 2000), elevated temperature and vapour pressure deficit (VPD) (Camargo & Kapos 1995) and lower soil water holding capacity are expected (Cotler & Ortega-Larrocea 2006), but soil water availability may depend on the soil evaporation/vegetation transpiration balance (Kapos 1989; Marthews *et al.* 2008). The potential relevance of this gradient of drought risk along secondary succession in abandoned agricultural lands should be greater in tropical dry regions with their low rainfall, high seasonality of rainfall and slow vegetation recovery (Lebrija-Trejos *et al.* 2011). Surprisingly, descriptions of environmental gradients along secondary succession in the dry tropics are uncommon. One report from Lebrija-Trejos *et al.* (2011) indicates that in a region of tropical dry forest, the early successional stages experience higher loads of direct radiation during the rainy season, making the environment warmer, with lower air humidity and reduced water content in the soil. These gradients of drought risk could be exacerbated during the onset of the dry season and by periods of short drought (of several weeks duration) that commonly occur during the rainy season (García-Oliva, Ezcurra & Galicia 1991; Páramo-Pérez 2009). Community studies in tropical dry

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forest regions suggest that dominant tree species and their leaf and stem morphological traits change as secondary succession progresses towards decreasing severity of temperature and drought stress (Lebrija-Trejos *et al.* 2010; Maza-Villalobos, Balvanera & Martínez-Ramos 2011). Overall, these results suggest that the physiological mechanisms contributing to growth and survival under drought may be important determinants of species abundance and composition at different stages of secondary succession (Vieira & Scariot 2006).

Plants can maintain physiological functioning during drought by two mechanisms: desiccation avoidance and desiccation tolerance (Larcher 2003; Tyree *et al.* 2003). Desiccation avoidance involves traits that increase access to water or reduce the water loss, such as deep roots, water storage in stems and roots, stomatal restriction of transpiration, and leaf shedding. Desiccation tolerance is attained by traits that allow plants to function in spite of low soil and plant water potentials. Previous studies have found that in seasonal tropical forests, seedling survival under severe drought is mostly determined by resistance of xylem to embolism formation (Tyree *et al.* 2003), and that the degree of embolism resistance varies widely among tropical tree species (Brodribb *et al.* 2003; Choat *et al.* 2003; Tyree *et al.* 2003; Lopez *et al.* 2005; Markesteijn *et al.* 2010). A large variation in speed of leaf shedding in response to drought has been observed among species of seasonal tropical forests (Bullock & Solis-Magallanes 1990; Borchert 1994; Pineda-García, Paz & Tinoco-Ojanguren 2011). However, the extent to which this mechanism contributes to maintenance of xylem hydraulic integrity and thus to interspecific differences in the ability to withstand drought is still poorly known (Engelbrecht & Kursar 2003; Slot & Poorter 2007; Méndez-Alonzo *et al.* 2012). If maintaining xylem function during drought periods is critical for seedling survival, we might expect a tradeoff between xylem resistance to embolism and the speed of leaf area reduction to avoid severe hydraulic failure. Such a tradeoff has been suggested by previous studies in tropical dry forests, but the evidence is not conclusive (Sobrado 1993; Méndez-Alonzo *et al.* 2012, but see Sobrado 1996; Markesteijn *et al.* 2010 for negative evidence). The ambiguity concerning the role of leaf shedding might be the result of not assessing leaf area reduction as a continuous response to drought (Méndez-Alonzo *et al.* 2012) and instead basing comparisons on gross phenological groups (i.e. evergreen versus deciduous). Overall, the potential role of a tradeoff of xylem embolism resistance against the sensitivity of leaf shedding in species habitat partitioning along the gradients of drought risk that occur during secondary succession in tropical dry forests, remains to be explored.

Tree taxa with succulent stems are abundant in tropical dry forests, suggesting that the capacity to store water in sapwood might be of special importance as a drought avoidance mechanism (Borchert 1994). For adult trees, sapwood water storage has been linked with water demands for reproduction and leaf flushing at the end of the dry season (Reich & Borchert 1984; Borchert 1994; Chapotin,

Razanameharizaka & Holbrook 2005). Transient use of water stored in stems of seasonal tropical forest trees has also been shown to reduce daily fluctuations in transpiration-induced tension that could generate xylem embolism (Goldstein *et al.* 1998; Scholz *et al.* 2007, 2011; Meinzer *et al.* 2008). By this mechanism, trees transiently buffer daily fluctuations in plant water status and extend carbon gain on a daily basis. The selective value of sapwood water reserves in seedlings may be high because at this stage of development, plant rooting depth and capacity to explore the soil for water are limited, and plants are not subject to selective pressures of water demands for reproduction. To date, the role of sapwood water storage in allowing seedlings to withstand dry spells has not been addressed. Finally, because high sapwood water storage capacity appears to be positively correlated with xylem vulnerability to embolism among species (Scholz *et al.* 2011), it is possible that stem water storage mediates a tradeoff between resistance to embolism and its avoidance by shedding leaves.

In the present study, we assessed responses of seedlings of early and late successional species from the tropical dry forest to a simulated short drought event, and explored mechanisms responsible for variation in plant performance among species and successional groups. We firstly characterized key environmental variables along a gradient of secondary succession in the field to test whether seedlings are potentially exposed to higher risk of drought at early successional stages. Secondly, using potted seedlings we tested whether early and late successional species differed in drought resistance, that is, whether at a given soil water deficit their physiological function differed. Thirdly, by monitoring loss of photosynthetic rate, leaf area and stem conductivity, along with both soil and plant water deficits for a range of species varying in maximum sapwood water content, we were able to explore the interplay between xylem resistance to embolism, leaf area loss and sapwood water storage as mechanisms for coping with soil drought. In particular we asked: (1) How do mechanisms of drought tolerance and avoidance vary among successional groups and species?; (2) How do physiological performance and mechanisms for withstanding drought vary with stem water storage capacity?; (3) What is the role of stem water storage in response to short periods of soil drought?; (4) Are there tradeoffs between drought resistance and avoidance strategies in ensuring xylem safety?; and (5) Do early and late successional groups differentiate along such a tradeoff?

METHODS

Study system

This study was conducted on greenhouse-grown seedlings of 12 tree species common in the tropical dry forest of Chamela, Jalisco, México, located at 19°30' N, 105°03' W on the Pacific Coast. This plant community experiences a markedly seasonal precipitation regime, with most of the 748 mm mean annual precipitation falling from July to

Table 1. Study species representative of early and late successional sites in the tropical dry forest of Chamela, Jalisco, Mexico

Early successional	Late successional
<i>Mimosa arenosa</i>	<i>Caesalpinia coriaria</i>
<i>Senna atomaria</i>	<i>Lonchocarpus constrictus</i>
<i>Piptadenia constricta</i>	<i>Ipomea wolcottiana</i>
<i>Caesalpinia eriostachys</i>	<i>Aoplanesia paniculata</i>
<i>Cordia eleagnoides</i>	<i>Ceiba grandiflora</i>
<i>Gliricidia sepium</i>	<i>Ceiba aesculifolia</i>

Note: Early successional species are those specialized a colonizing early secondary sites, plus those species that successfully establish in the early habitats but are also abundant at the late successional stages. Late successional species are those species mostly restricted from the late successional to old growth forests sites.

October (Lott, Bullock & Solis-Magallanes 1987). The seasonality of water available for plants is exacerbated by the predominance of shallow soils (10–45 cm depth; Galicia *et al.* 1999). The great majority of species at Chamela lose their leaves in response to drought, remaining leafless during 5 to 7 months, and flushing back at the onset of the rainy season (Bullock & Solis-Magallanes 1990). Leaf shedding and flushing events are also commonly observed in response to episodic dry spells during the rainy season (Páramo-Pérez 2009). The landscape around Chamela consists of patches with mature intact forest, and patches with different age of abandonment after human-related activities, resulting in a mosaic of vegetation patches with different ages of recovery. The vegetation across chronosequences ranging from 0 to 12 years after abandonment, as well as the mature forest, have been censused during 6 years in permanent plots (Maza-Villalobos *et al.* 2011; Ramos-López 2012). Based on this information, we selected 12 tree species differing in their successional status to study performance under drought and drought resistance strategies at the seedling stage (Table 1). Because we were interested in discerning traits that enable or impede establishment and persistence in the early successional sites, we selected two groups of six species each: (1) 'early successional species', comprising specialists (pioneers) largely restricted to early successional stages, plus generalists that appear during early stages of succession, but also remain abundant across different successional stages; and (2) 'late successional species', comprising taxa that successfully establish in late to old growth forest, but not in early sites.

Environmental variation along an axis of vegetation recovery

A static picture of environmental gradients potentially experienced by seedlings across early phases of secondary succession and in the mature forest was obtained in the lands surrounding Chamela during three clear-sky days at the onset of the dry season. Physical variables, including canopy openness, soil volumetric water content, air

temperature, relative humidity and soil temperature were measured in eight plots differing in fallow age (*0 years fallow*: recently abandoned pastures with no time of recovery; *early fallow*: 3–5 years of recovery; and *mid fallow*: 8–12 years of recovery) and in two mature forest plots. These 10 plots belong to a larger permanent study that evaluates the dynamic changes of vegetation along secondary succession in the Chamela region (see Maza-Villalobos *et al.* 2011 for a complete site and plot description). In each site, 12 to 33 sampling points were randomly selected. Percent canopy openness was extracted from Maza-Villalobos *et al.* (2011). Gravimetric water content of the upper 10 cm of soil was obtained from ~100 mL soil cores sampled in the early morning. Samples were first weighed fresh, then oven dried for 5 d at 100 °C to determine gravimetric water content as: (soil fresh mass – soil dry mass) / dry mass × 100. In each plot, air temperature (to 0.1 °C) and relative humidity were recorded at 20 cm above the forest floor every 5 min between 1200 and 1400 h using automated sensors and data loggers (HOBO Pro2, Onset, Cape Cod, MA, USA). Temperature and humidity data were used for calculating the VPD (kPa). Temperature at the soil surface (to 0.1 °C) was also measured every 5 min between 1200 and 1400 h using an infrared thermometer (OS530HR, Omega, Stamford, CT, USA). Because we were unable to place sensors in all plots simultaneously, to control for the day-to-day variation we grouped sites based on their age of abandonment so that on each day we sampled three to four sites representing the four stages of vegetation recovery described above. Using this approach, the data collection was completed within 3 d.

Experimental procedures

We collected seeds of each of the 12 species from at least 10 individuals during the peak of fruit production. Early successional species were collected from individuals growing in the early fallow sites, while late successional species were collected in late successional sites and in the mature forest within the boundaries of Chamela Biological Station. A greenhouse experiment was established to evaluate responses of 1-year-old seedlings to progressive soil drought. Seeds were placed in wet sand beds in a greenhouse for germination. Fifteen days after the radicle emerged, when the first pair of leaves was fully expanded, we randomly chose 56 seedlings per species and transplanted them to ca. 6-l (14 cm diameter × 40 cm tall) pots with basal drainage (one seedling per pot) containing river sand. Initially, each pot received a dose of controlled-release fertilizer (14.61 g of Multicote 8: 18N – 6P – 12K + 2MgO + ME; Haifa Chemicals, Haifa Bay, Israel). The pot position was assigned in a randomized block design to statistically control for solar radiation and temperature variation in the greenhouse. Plants were grown for a 12-month period at low soil water deficit (soil water potential between –0.05 and –0.22 MPa). The average greenhouse conditions were: air temperature 21.5 °C (48.0 to 7.6 °C), relative humidity 60% (85–41%) and a daily average of photosynthetic photon flux (PPF) of 745 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (max. 917 $\mu\text{mol m}^{-2} \text{s}^{-1}$). At 12 months, six

blocks, containing ~10 plants per species, were subjected to progressive soil desiccation by cessation of watering, simulating rates of decline in soil water potential (Ψ_{soil}) from -0.5 to -5 MPa in 27 d, a rate similar within the range of values observed in the field in the Chamela region (Páramo-Pérez 2009).

Physiological and morphological traits prior to imposition of drought

Before imposing a progressive drought treatment on the greenhouse-grown seedlings, we measured leaf gas exchange, stem hydraulic conductivity and stem water content at full hydration. The initial photosynthetic capacity (A_{ini} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured in four seedlings of each species. Measurements were made between 0800 and 1100 h with a portable gas exchange system (Li-Cor 6400, Lincoln, NE, USA) on two young, fully expanded leaves per seedling. Air CO_2 concentration and PPF were maintained at $\sim 400 \mu\text{mol mol}^{-1}$ and at $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. We measured the stem hydraulic conductivity in five seedlings per species. For each plant, the stem was cut at the base under water and immediately transported to the laboratory where a second cut was made under water with a razor blade to remove possible vessel obstructions. Stem sections ranged between 10 and 14 cm long, and when present, leaves were removed and scars were sealed with parafilm. The stem section was connected to a reservoir containing a degassed and filtered ($0.2 \mu\text{m}$) 10 mM KCl solution providing a hydraulic head of ~ 3 kPa. With the stem section attached to the reservoir and after a 15 min period of stabilization, we quantified the water flow (mass per 10 s; g s^{-1}) passing through the stem section. Three consecutive measurements were taken to assure that water flow had reached a steady state. The hydraulic conductivity (k_h) was calculated as the ratio between the water flow (F) passing through the stem section and the pressure gradient (dP/dx) (Tyree & Ewers 1991). The total length and diameter of each stem were measured to 0.01 mm. The stem-specific hydraulic conductivity (k_s) sensu Tyree & Ewers (1991) was then calculated as $k_s = (k_h / \text{xylem cross-sectional area}) \times \text{stem length}$. Sample collections and measurements were made prior to dawn to obtain the maximum native conductivity. Finally, we measured wood density (WD; g cm^{-3}) in five individuals per species, following Pineda-García *et al.* (2011), and calculated saturated sapwood water content (SWC) by applying the equation proposed by Simpson (1993). The seedlings sacrificed for hydraulic measurements were used to obtain total mass before drought imposition. The mean mass of 12-month-old seedlings ranged from 2.32 to 23.80 g, and in no case was the sand matrix observed to contain a high root density, indicating the likely absence of severe pot effects on availability of soil resources for plant growth.

Monitoring of progressive soil drought

The time course of soil volumetric water content was continuously monitored for each experimental pot using a

theta probe soil moisture sensor -ML2x, and a HH2 reader (Delta-T Devices, Cambridge, UK), inserted laterally to the pot at 10 and 20 cm depth. Volumetric water content was later converted to soil water potential using a soil water release curve constructed with a dew point potentiometer (WP4-T, Decagon Devices Inc., Pullman, WA, USA) for the sand used as the growth medium.

Loss of photosynthetic capacity, leaf area, plant water status and stem conductivity

Photosynthetic CO_2 assimilation rates were monitored on 26 randomly selected seedlings of each species during the desiccation trial. The measurement protocol was the same as that used prior to imposition of drought. Measurements were done in young, fully developed healthy leaves, and restricted to the remaining non-wilted leaves as wilting progressed. The photosynthetic rate was transformed to percentage loss (PLA) relative to the maximum value registered before the beginning of the experimental drought by applying the formula: $\text{PLA} = 100 \times ((A_{\text{ini}} - A) / A_{\text{ini}})$. The same group of plants was used for monitoring percentage loss of initial leaf area (PLLA) by applying $\text{PLLA} = 100 \times ((LA_{\text{ini}} - LA) / LA_{\text{ini}})$. Percentage loss at any census was visually assessed by comparing the living leaf area to a photograph of the initial condition. The total number of censuses of both variables ranged between 10 and 50, depending on the species. Plant water status and stem hydraulic conductivity were monitored during the desiccation trial by collecting plants representing a wide range of visible wilting conditions. Sample sizes ranged from 8 to 20 depending on the species. Each plant was collected at predawn for measuring leaf water content, leaf water potential (Ψ_L), and stem k_s . Before the hydraulic conductivity determinations and to obtain leaf water content, one leaf was excised and used to extract one disc of 1 cm^2 that was immediately weighed and then oven dried for 42 h at 70°C . A second leaf or a distal shoot tip (depending on the species) was then immediately excised and used for Ψ_L measurements using a pressure chamber. Finally, plants were cut under water at the stem base and kept submerged inside a black plastic bag for laboratory measurements of stem k_s a few minutes later. The main stem was recut under water and used for measuring k_s , following the procedures described previously. Maximum conductivity (k_{smax}) of each stem was then obtained after flushing out emboli by applying a 100 kPa pressure head during 10 min, and re-measuring water flow. Per each stem, we quantified the percentage loss of hydraulic conductivity (PLC) as: $\text{PLC} = 100 \times ((k_{\text{smax}} - k_s) / k_{\text{smax}})$. We also tracked plant water status in those seedlings used for monitoring photosynthesis and leaf area loss, by inferring water potential from leaf water content. At every census, 1 cm^2 leaf disc was collected between 0800 and 1100 h, immediately wrapped in aluminium foil, bagged and a few minutes later processed using the protocols previously described for obtaining leaf water content. Leaf samples were always taken from the least wilted tissues available in each plant. The data

obtained by destructive sampling prior to stem hydraulic conductivity determination were used to derive relationships between leaf water potential and leaf water content per species. Strong relationships detected between water potential measured directly and water potential derived from leaf disks ($r^2 > 0.67$) allowed us to use minimally destructive sampling to analyse loss of photosynthesis and leaf area with plant water status.

Statistical analysis

Environmental conditions along a successional gradient

Microenvironmental changes during secondary succession were analysed by regressing mean values of soil and air temperature, relative humidity, soil water content, and the VPD against canopy openness. Special attention was given to canopy openness as it is recognized that vegetation development is the causal factor for changes in microenvironment during secondary succession (Guariguata & Ostertag 2001; Lebrija-Trejos *et al.* 2010, 2011). Also, we decided to use canopy openness as an explanatory variable because there was uncertainty in the determination of the time elapsed since abandonment of each of the plots (Maza-Villalobos *et al.* 2011).

Drought performance among species and successional groups

Patterns of percentage loss of physiological performance (PLA, PLLA and PLC) for each species during soil desiccation were analysed by plotting dependent variables against soil water potential, and fitting a non-linear Weibull four-parameter model. The Weibull model was used because its flexibility allowed for properly fitting the different shapes of the loss of physiological performance among the species studied (Lopez *et al.* 2005). To characterize species performance during soil desiccation, we derived thresholds of Ψ_{soil} at which plants lost 20% ($\Psi_{\text{soil}20}$), 50% ($\Psi_{\text{soil}50}$) and 80% ($\Psi_{\text{soil}80}$) of each of the three physiological performance variables defined previously. Analogous curves describing the loss of function were obtained by taking the plant water potential as a reference. From these curves, we derived thresholds of Ψ_{plant} at which species lost 20% ($\Psi_{\text{plant}20}$), 50% ($\Psi_{\text{plant}50}$) and 80% ($\Psi_{\text{plant}80}$), of physiological function. However, we were not able to derive Ψ_{soil} and Ψ_{plant} values for 80% loss of hydraulic conductivity for *Ceiba grandiflora* because this species dropped all of its leaves before reaching a higher level of hydraulic loss. The hypothesis that early and late successional species differed in their loss of function during drought was tested by *t*-test using the threshold values of Ψ_{soil} for 20, 50 and 80% loss of photosynthetic capacity (PLA), leaf area (PLLA) and hydraulic conductivity (PLC) as data points. Secondly, to examine how mechanisms for maintaining physiological function under drought varied among successional groups and species, we compared early versus late successional

species by using *t*-tests based on species-specific thresholds of Ψ_{plant} for PLA, PLC and PLLA. Finally, we assessed patterns of coordination between loss of function in response to soil water deficit, and in response to plant water deficit. To do so, we calculated Pearson correlation coefficients between Ψ_{soil} and Ψ_{plant} at 20, 50 and 80% loss of initial photosynthesis, leaf area and stem conductivity. In this analysis, a positive 1:1 correlation would indicate that plants respond to soil desiccation as simple osmometers.

To address the role of sapwood water storage in species' ability to avoid or tolerate soil drought, we firstly regressed values of Ψ_{plant} and Ψ_{soil} at 20, 50 and 80% loss of photosynthesis, leaf area and stem conductivity, against values of stem water content at full hydration for each species. Secondly, we calculated the difference between the plant predawn water potential and the soil water potential ($\Psi_{\text{plant}} - \Psi_{\text{soil}}$) at the three thresholds of loss of stem conductivity, as a measure of plant decoupling from soil desiccation, and we regressed this variable against stem water content at full hydration (soil and plant predawn values were only obtained for PLC). Finally, to detect the existence of a tradeoff between drought avoidance through leaf area loss and xylem resistance to embolism, we performed Pearson correlation analyses between PLLA and PLC at 20, 50 and 80% loss when referenced to soil and plant water potentials.

RESULTS

Environmental conditions along a successional gradient

Recently abandoned sites exhibited higher soil and air temperature, lower relative humidity and higher VPD, which changed monotonically with canopy closure (Fig. 1a–d, respectively) as expected. The soil water content decreased exponentially with increasing canopy openness, reaching an asymptote at about 30% canopy openness (Fig. 1e).

Drought performance among species and successional groups

For all species the photosynthetic rate, leaf area and stem specific conductivity decreased during soil drying, following non-linear trends that varied widely in shape among species (Supporting Information Fig. S1). Of the three functional traits evaluated, the photosynthetic rate was the most sensitive to soil drought, whereas the stem hydraulic conductivity was affected only at much more negative water potentials (Fig. 2a–c). For example, the 12 species lost 50% of their initial photosynthetic rate at a relatively high mean soil water potential of -0.58 MPa (Fig. 2a), whereas 50% loss of hydraulic conductivity occurred at a mean Ψ_{soil} of -4.86 MPa (Fig. 2c). Soil water potential at 20, 50 and 80% loss of hydraulic conductivity exhibited the greatest variation among species, with Ψ_{soil} at 50 PLC ranging from -1.64 MPa in *Cordia eleagnoides* to -7.0 MPa in *Ipomea wolcottiana* (Fig. 2c). However, early and late successional

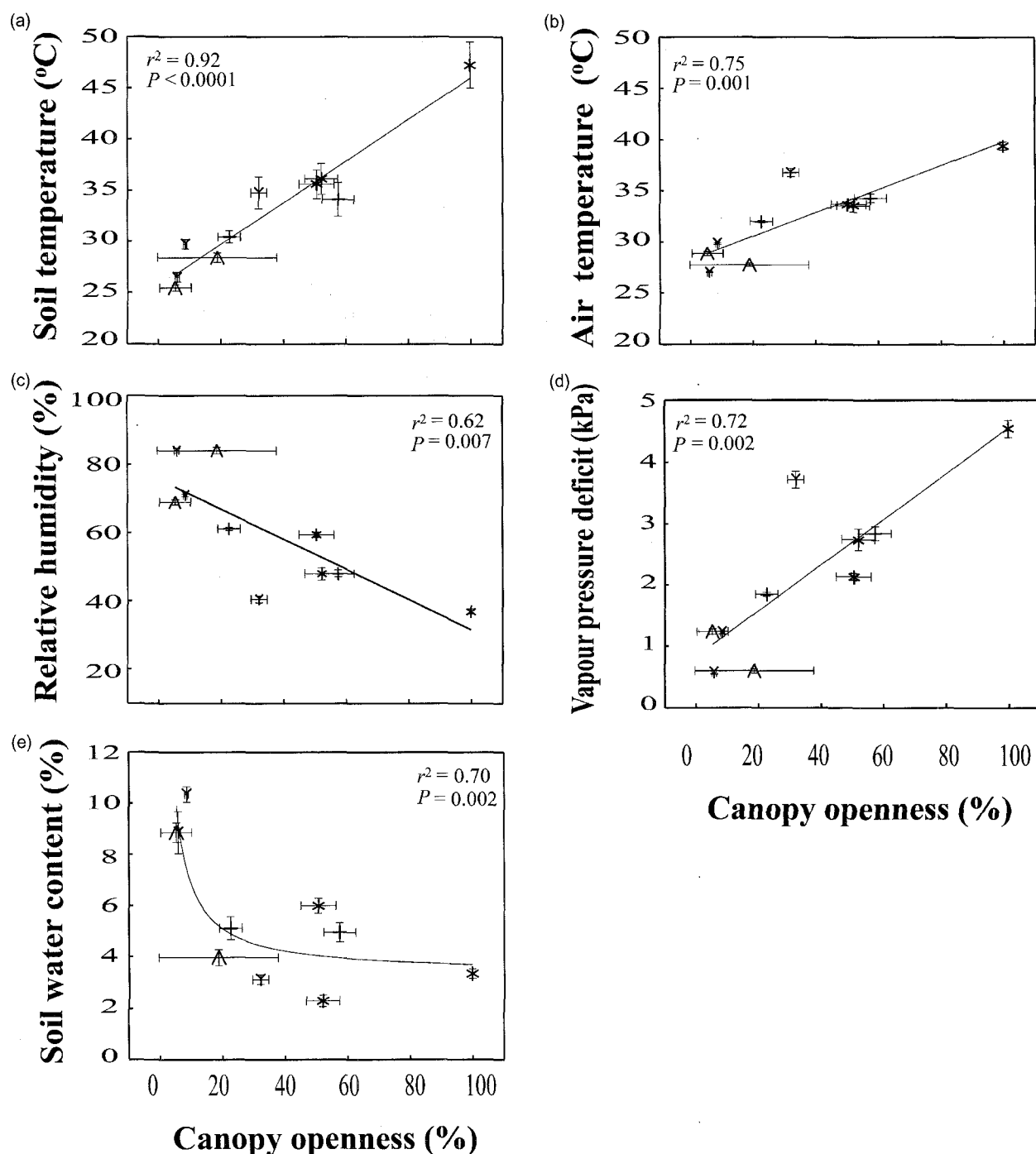


Figure 1. Environmental variation along a gradient of canopy openness in early successional and mature forest plots with different disturbance histories in a tropical dry forest region in Chamela, Jalisco, Mexico. (a) soil temperature; (b) air temperature; (c) relative humidity; (d) vapour pressure deficit; and (e) soil water content. Symbols: (*) 0 years fallow: recently abandoned pastures; (+) early fallow: 3–5 years after abandonment; (Y) mid fallow: 8–12 years after abandonment; (Δ) mature forest. Standard error bars are shown.

species did not differ significantly with respect to values of Ψ_{soil} corresponding to 20, 50 and 80% loss of photosynthetic rate, leaf area and stem hydraulic conductivity (data not shown; Fig. 2a–c).

Three patterns arose when evaluating functional response to drought in relation to plant water potential.

Firstly, as with Ψ_{soil} , there was high variation among species in the Ψ_{plant} at which the loss of functions occurred (Supporting Information Fig. S2), with loss of photosynthetic activity occurring most rapidly and showing the least variability across species, and stem conductivity showing the opposite pattern (Fig. 2d–f). Secondly, losses of function in

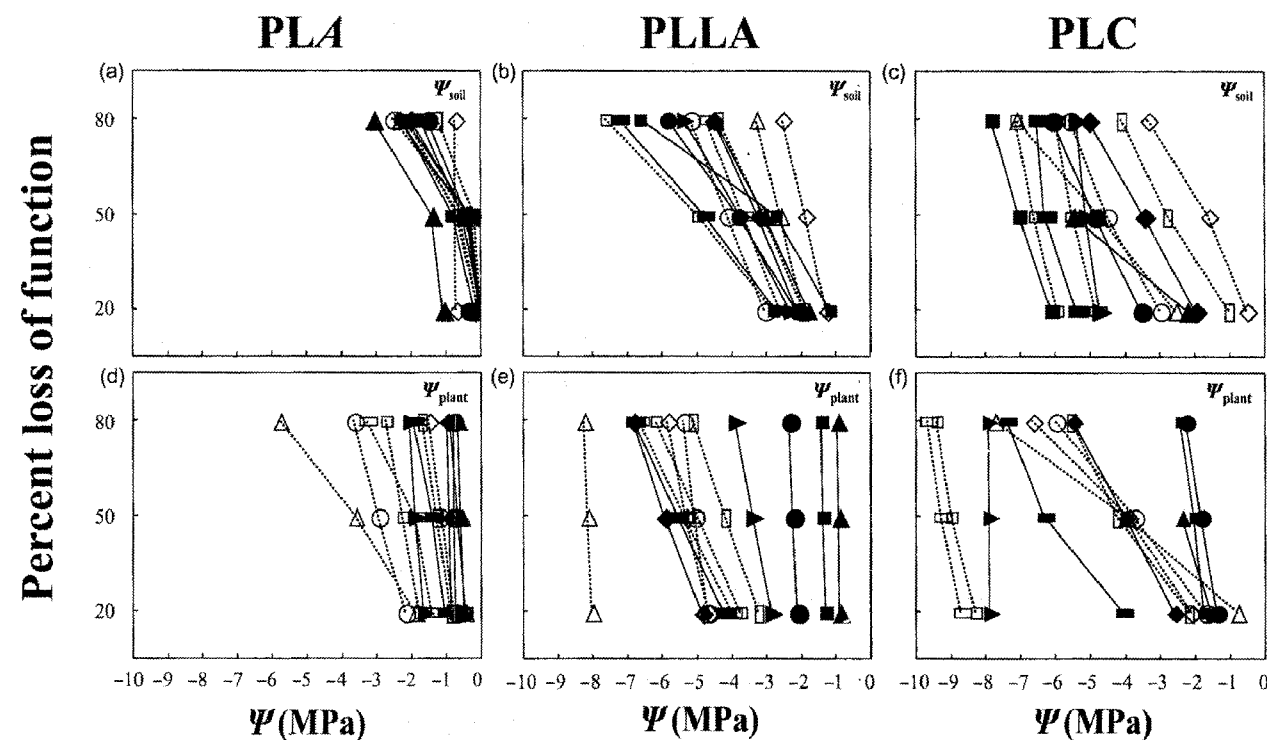


Figure 2. Trajectories of loss of plant function in relation to soil and plant water deficit during a progressive soil drought event for seedlings of 12 tropical dry forest tree species. Data points represent soil and plant water potential values (Ψ_{soil} , Ψ_{plant}) at 20, 50 and 80% loss of photosynthetic rate (PLA) (a and d), leaf area (PLLA) (b and e) and stem hydraulic conductivity (PLC) (c and f). Closed symbols indicate late successional species and open symbols represent early successional species. *Caesalpinia eriostachys* □, *Cordia eleagnoides* ◇, *Gliricidia sepium* △, *Senna atomaria* ▢, *Piptadenia constricta* ▣, *Mimosa arenosa* ○, *Apoplanesia paniculata* ◆, *Caesalpinia coriaria* ■, *Ceiba aesculifolia* ●, *Ceiba grandiflora* ▲, *Ipomea wolcottiana* ■, *Lonchocarpus constrictus* ►. Ψ values at 80 PLC for ▲ *C. grandiflora* were not obtained (see Methods section).

relation to drought followed different trajectories when expressed in relation to Ψ_{plant} , resulting in changes in the rankings of species according to their apparent sensitivities to drought (Fig. 2d–f). This was indicated by the lack of significant correlation between values of Ψ_{plant} and Ψ_{soil} at which given losses of function occurred ($P > 0.08$ for all correlations). Thirdly, unlike results based on Ψ_{soil} ,

successional groups did differ in sensitivity to changes in Ψ_{plant} ; in particular regarding photosynthesis and marginally in loss of leaf area, but not in loss of stem conductivity (Table 2). Early successional species lost 50 and 80% of photosynthesis and leaf area at more negative plant water potentials, than did late successional species (Fig. 2d).

Trait	Late successional species	Early successional species	t-Test	
	Mean $\Psi \pm \text{SE}$	Mean $\Psi \pm \text{SE}$	t	P
PLA $\Psi_{\text{plant } 20}$	-0.89 $\pm$ 0.18	-1.52 $\pm$ 0.23	-2.12	0.06
PLA $\Psi_{\text{plant } 50}$	-1.06 $\pm$ 0.21	-2.22 $\pm$ 0.39	-2.61	0.03
PLA $\Psi_{\text{plant } 80}$	-1.25 $\pm$ 0.25	-3.13 $\pm$ 0.64	-2.75	0.02
PLLA $\Psi_{\text{plant } 20}$	-2.74 $\pm$ 0.65	-4.76 $\pm$ 0.70	-2.12	0.06
PLLA $\Psi_{\text{plant } 50}$	-3.27 $\pm$ 0.87	-5.55 $\pm$ 0.55	-2.22	>0.05
PLLA $\Psi_{\text{plant } 80}$	-3.74 $\pm$ 1.07	-6.27 $\pm$ 0.46	-2.18	>0.05
PLC $\Psi_{\text{plant } 20}$	-3.23 $\pm$ 1.02	-4.00 $\pm$ 1.45	-0.43	0.68
PLC $\Psi_{\text{plant } 50}$	-4.11 $\pm$ 1.03	-5.72 $\pm$ 1.09	-1.08	0.31
PLC $\Psi_{\text{plant } 80}$	-5.13 $\pm$ 1.19	-7.53 $\pm$ 0.71	-1.80	0.11

Note: All tests considered 12 species, except PLC₈₀, where $n = 11$ (see Methods section). Significant differences are shown in bold ($P \leq 0.05$).

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Table 2. Thresholds of plant water potential (Ψ) for 20, 50 and 80% loss of photosynthetic rate (PLA), leaf area (PLLA) and stem hydraulic conductivity (PLC) for seedlings of early and late successional tropical dry forest species

Table 3. Relationships between stem water storage capacity and threshold values of soil and plant Ψ for 20, 50 and 80% loss of photosynthetic rate (PLA), leaf area (PLLA) and stem hydraulic conductivity (PLC), during progressive soil drought

		r^2	P
Soil water potential	PLA $\Psi_{\text{soil } 20}$	0.13	0.25
	PLA $\Psi_{\text{soil } 50}$	0.12	0.26
	PLA $\Psi_{\text{soil } 80}$	0.02	0.68
	PLLA $\Psi_{\text{soil } 20}$	0.59	0.003
	PLLA $\Psi_{\text{soil } 50}$	0.37	0.04
	PLLA $\Psi_{\text{soil } 80}$	0.05	0.49
	PLC $\Psi_{\text{soil } 20}$	0.01	0.71
	PLC $\Psi_{\text{soil } 50}$	0.05	0.45
	PLC $\Psi_{\text{soil } 80}$	0.13	0.27
Plant water potential	PLA $\Psi_{\text{plant } 20}$	0.46	0.01
	PLA $\Psi_{\text{plant } 50}$	0.32	0.05
	PLA $\Psi_{\text{plant } 80}$	0.25	0.10
	PLLA $\Psi_{\text{plant } 20}$	0.39	0.03
	PLLA $\Psi_{\text{plant } 50}$	0.50	0.01
	PLLA $\Psi_{\text{plant } 80}$	0.56	0.005
	PLC $\Psi_{\text{plant } 20}$	0.35	0.04
	PLC $\Psi_{\text{plant } 50}$	0.62	0.002
	PLC $\Psi_{\text{plant } 80}$	0.60	0.003

Note: All tests considered 12 species, except PLC₈₀, where $n = 11$ (see Methods section).

Regression summary statistics are shown. Significant differences are shown in bold ($P \leq 0.05$).

Correlates of maximum water storage capacity

Saturated sapwood water storage capacity (SWC) of species was positively related to the plant Ψ at which 20, 50 or 80% loss of performance (PLA, PLLA and PLC) occurred (Table 3, Fig. 3). In contrast, these correlations tended to weaken or disappear when performance was related to soil Ψ . On the other hand, SWC was positively associated with our measure of the degree of decoupling between plant and soil ($\Psi_{\text{plant}} - \Psi_{\text{soil}}$). Species with a high SWC were able to maintain their Ψ above that of the soil during drought (Fig. 4). In contrast, the Ψ of the species with the lowest stem SWC remained below that of the soil during the entire drying cycle. As the soil drought intensified only the species with the highest stem water storage capacity maintained plant water potential above that of the highly desiccated soil (Fig. 4b,c).

Drought resistance and avoidance through reduction of leaf area

There were significant positive correlations between thresholds of Ψ_{plant} and Ψ_{soil} for leaf area loss (avoidance) and the corresponding thresholds for loss of stem hydraulic conductivity (resistance). However, these trends were significant only at elevated levels of water stress (80% loss of plant function, Fig. 5a). Thus, species that lost 80% of initial stem conductivity at high water potentials also lost 80% of initial leaf area at high water potentials when considering both soil and plant water status (Fig. 5). Early and late

successional species were not clearly separated along relationships between PLLA and PLC neither at the soil nor at the plant water status level.

DISCUSSION

Early successional sites are drier and warmer both above and below ground, compared with mature forest sites

As expected, our results suggest that secondary succession in tropical dry forests imposes a gradient of drought risk for seedlings, which peaks at the early stages and dramatically decreases with canopy development. Concurrent reductions in VPD and air temperature, and increases in soil water content with increasing canopy cover, suggest that such a gradient of drought risk occurs both above and below ground, likely because a reduction of initial high radiation loads and consequent evaporative water losses from the upper soil layers decline as the canopy develops. Our findings agree with those of previous studies reporting that during the onset of the dry season, superficial soil water content increases and VPD and air temperature decrease with seral stage development in other tropical dry forests (Hasselquist, Allen & Santiago 2010; Lebrija-Trejos *et al.* 2011). Together, these results suggest firstly that drought episodes during the rainy season may be stronger and/or longer in early successional sites than in mature forest sites. Secondly, the ways plants use water and respond to droughts may be important sources of species habitat partitioning, particularly for the early stages of plant development.

High variation in physiological performance among tropical dry forest species during periods of drought

In tropical dry forests, plants are subject to drought both due to seasonality of rainfall and to the occurrence of drought spells during the rainy season (García-Oliva *et al.* 1991; Páramo-Pérez 2009). Under this scenario, species success may largely be determined firstly by the ability of plants to continue growing particularly during drought periods, and secondly by avoiding hydraulic failure and thus death. Finally, successful species would be the ones that are preconditioned for rapid recovery of growth when drought ends (Sobrado 1993; Pineda-García *et al.* 2011). Our results suggest that tropical dry forest species vary widely in their capacity to maintain function during soil droughts. The amplitude of variation in drought performance depended upon the physiological response and the level of soil drought being considered. In our study, the wide variation among species in trajectories for loss of stem conductivity across all levels of Ψ_{soil} suggests that species' ability to maintain the hydraulic capacity of stems may be a major axis of species differentiation in response to soil drought in tropical dry forests. In contrast, the rapid decline in photosynthetic rates and loss of leaf area during the early stages of

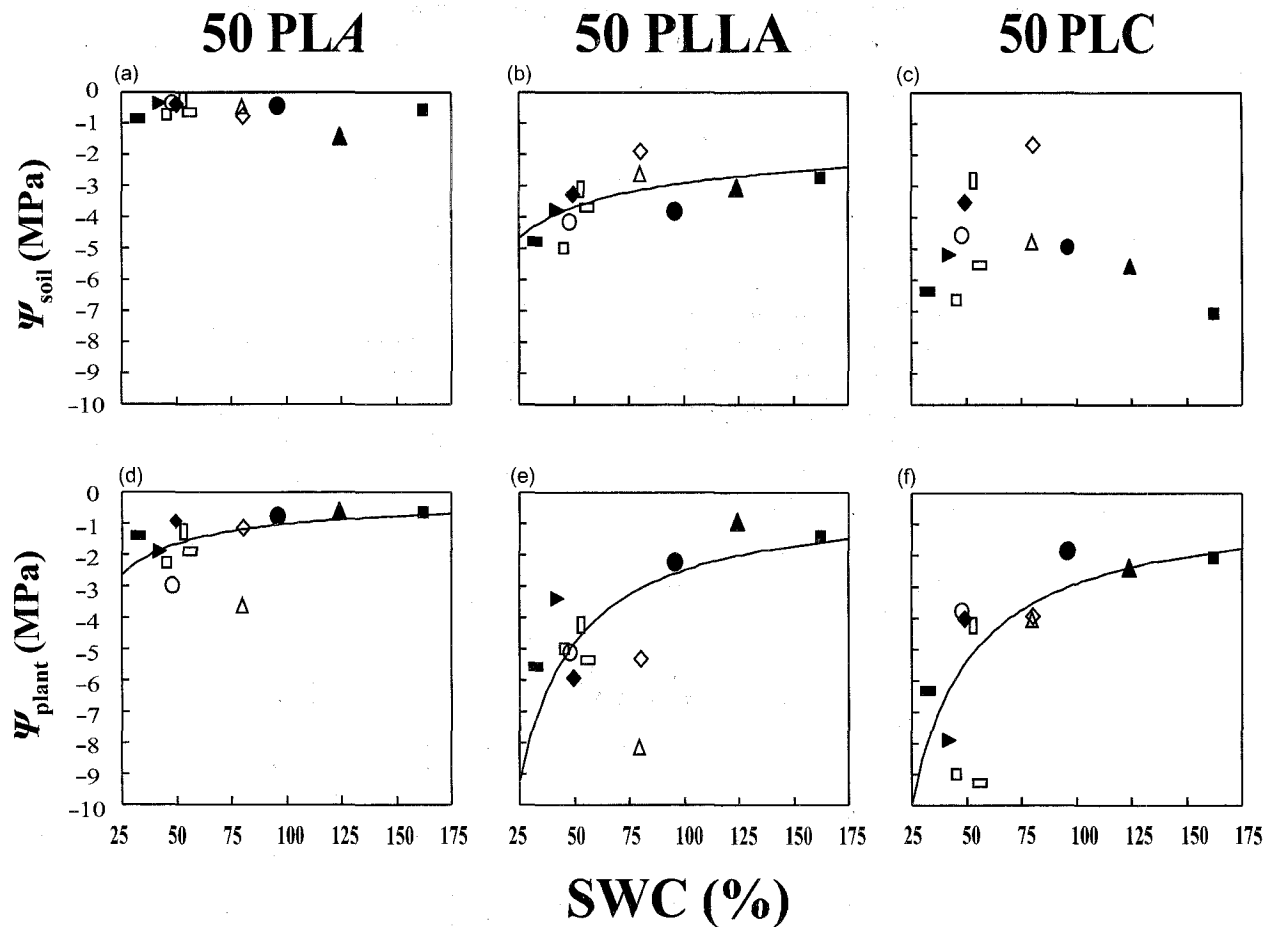


Figure 3. Relationships between maximum sapwood water content (SWC) and soil and plant water potentials (Ψ_{soil} , Ψ_{plant}) at 50% loss of photosynthetic rate (PLA) (a and d), leaf area (PLLA) (b and e) and stem hydraulic conductivity (PLC) (c and f) among seedlings of 12 tropical dry forest species. Species symbols as in Fig. 2. See Table 3 for summary statistics.

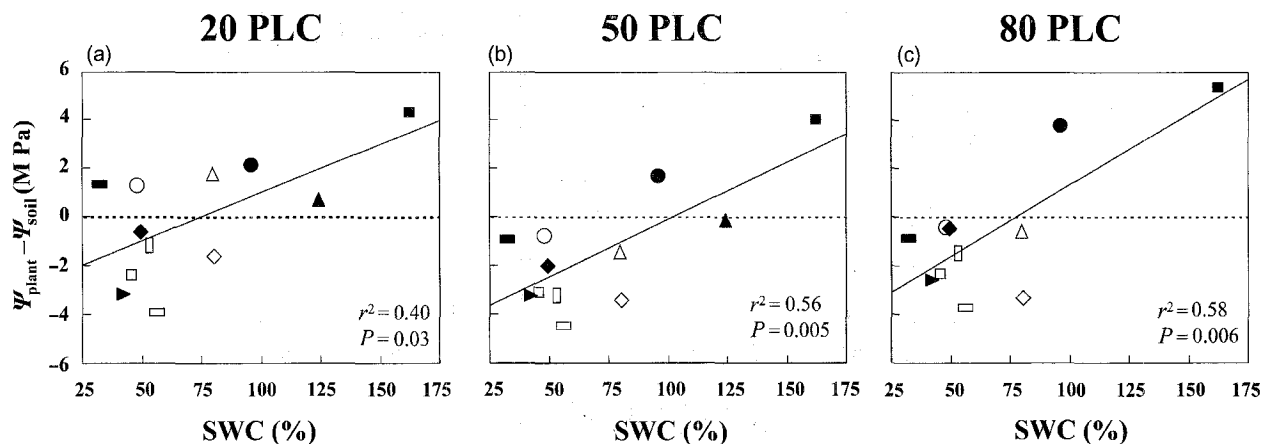


Figure 4. Predawn disequilibrium between plant and soil water potential ($\Psi_{\text{plant}} - \Psi_{\text{soil}}$) at different thresholds of percent loss of stem conductivity (PLC) in relation to stem water storage capacity (SWC). Species symbols as in Fig. 2. Ψ values at 80 PLC for *C. grandiflora* were not obtained (see Methods section). Dotted line represents equilibrium between the plant and soil Ψ . (a) 20 PLC; (b) 50 PLC; (c) 80 PLC.

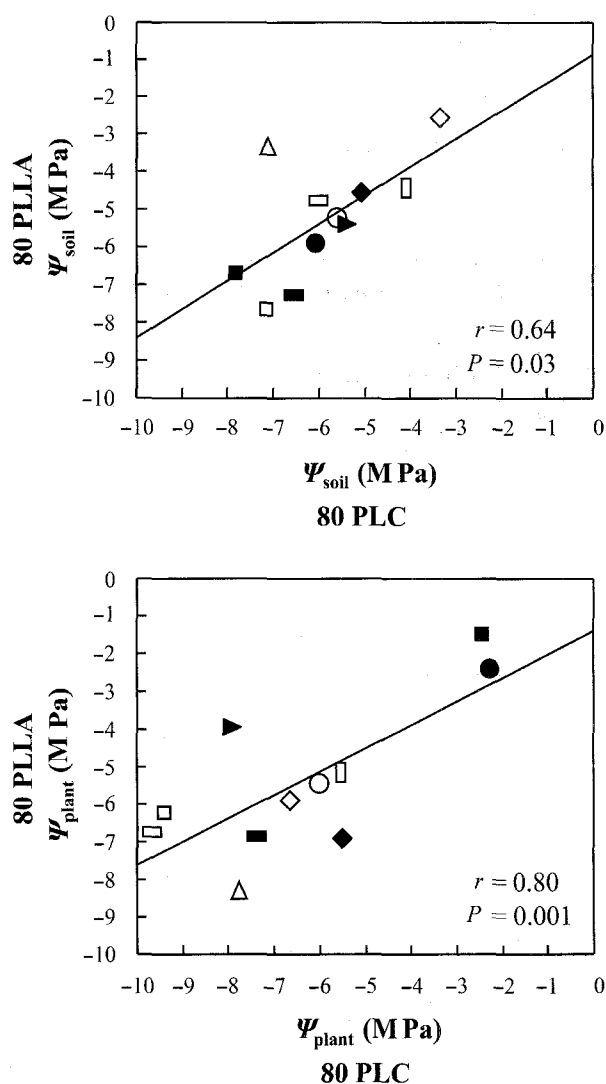


Figure 5. Correlations between water potentials at 80% loss of stem conductivity (80 PLC) and 80% loss of leaf area (80 PLLA) among seedlings of 11 tropical dry forest tree species. Thresholds referenced to soil (upper), and plant (lower) Ψ . Species symbols as in Fig. 2. Value of 80 PLC for $\blacktriangle$ *C. grandiflora* was not obtained (see Methods section).

drought seem to be generalized responses among the species studied. In principle, these results can be expected among species belonging to a drought-deciduous community. However, this pattern did not persist at later stages of soil drought when species varied widely in their ability to retain 20% of their leaf area. Because the remaining leaves had negligible rates of net photosynthesis at the highest levels of soil drought, the functional significance of retaining a larger fraction of leaves may not be related to maintenance of growth during drought, but rather to maintaining the potential for a fast recovery when drought ends. This potential advantage may be especially important when responding to repeated short droughts occurring during the rainy season. In tropical seasonal forests, drought spells are pervasive events (Borchert, Rivera & Hagnauer 2002; Peña

& Douglas 2002; Ichie *et al.* 2004; Engelbrecht *et al.* 2006; Páramo-Pérez 2009), which in Chamela can last between 7 and 30 d, reducing soil water content to as low as 3% (García-Oliva *et al.* 1991; Páramo-Pérez 2009).

Early and late successional species did not differ in resistance to soil drought

Overall, our results suggest that the successional groups did not differ in terms of resistance to soil drought; rather, a large variation in all responses was clear within each group, particularly for the early successional species. Species capable of establishing during early successional stages maintained 20% of hydraulic conductivity and leaf area at low, intermediate or high levels of soil drought, as was the case with *C. eleagnoides*, *Mimosa arenosa* and *Caesalpinia eriostachys*, respectively. The ability of the species that were more sensitive to soil drought to successfully establish in the drought-prone early-successional habitats seems puzzling.

One potential explanation is that seedlings of these species may escape from the microenvironment very early during drought periods, either by rapidly accessing deeper root soil zones after they emerged or by rapidly reducing leaf area and thus water loss. The lack of soil moisture data at greater depths in Chamela prevents us from determining whether the detected differences in soil water content at 10 cm between early successional and late successional forest, persist with soil depth. Overall, the importance of rapid root elongation to seedling success in the early secondary sites remains to be elucidated. Escaping from soil drought through leaf shedding may be an important adaptation for species with xylem that is highly vulnerable to cavitation (Sobrado 1993; Holbrook, Whitbeck & Mooney 1995; Choat *et al.* 2005), particularly if plants are restricted to using water from shallow soil layers (Jackson *et al.* 1995; Meinzer *et al.* 1999), as is the case for seedlings. In our system, the faster loss of leaf area and stem conductivity among some early successional species at elevated levels of soil drought suggests that rapid drought escape through leaf area reduction is a strategy for preventing massive hydraulic failure, allowing survival during prolonged droughts in the first seral stages of the secondary succession. This seems to be the case for early successional specialists such as *M. arenosa* and *Senna attomaria*. In Chamela, a negative correlation between vegetation leaf litter production and rainfall in early secondary plots (Arreola-Villa 2012) is consistent with this idea, though this hypothesis remains to be tested experimentally. Future comparative studies evaluating plant performance and survival in relation to speed of leaf shedding during drought in sites undergoing secondary succession may resolve this question. On the other hand, our data suggest that high resistance to soil drought based on high resistance of xylem to embolism may be common among generalist species capable of establishing themselves during early stages of secondary succession. Such is the case with *C. eriostachys* and *Piptadenia constricta*.

The inclusion of a larger number of species, as well as more detailed understanding of species distributions and ecology, may be necessary to determine the extent to which successional groups differ in their physiological resistance to soil drought.

Sapwood water storage decouples plant and soil water status, allowing species with contrasting physiological tolerances to perform similarly at a given level of soil water deficit

The joint analysis of species' responses to water deficit at both the soil and plant level revealed a poor correspondence, suggesting that inherent tolerances of tissues (xylem or leaf) to dehydration are insufficient to explain species rankings according to their ability to maintain physiological functions during soil drying. This was indicated by the lack of significant correlations between thresholds of plant and soil water potentials for losses of stem conductivity, leaf area and photosynthetic activity.

In addition, our data suggest that more than one physiological trait was responsible for maintaining a given level of performance as the soil dried. In particular, the relationships involving maximum stem water storage suggest that this variable played an important role in decoupling plant water status from soil water status, allowing those species with more vulnerable xylem to maintain function at higher levels of soil desiccation. Species with higher water storage capacity were more vulnerable to xylem embolism and lost leaf area and photosynthetic activity more rapidly as drought intensified. A positive association between xylem capacitance and vulnerability to embolism has been noted in numerous woody species representative of a broad range of communities (Meinzer *et al.* 2008, 2009; Scholz *et al.* 2011), including the tropical dry forest (Méndez-Alonso *et al.* 2012). This pattern may result from physical constraints on xylem structure–function relationships. In a given xylem volume, more space for storing water may imply a reduction of mass invested in xylem structural reinforcements that contribute to embolism and implosion resistance (Jacobsen *et al.* 2005; Pratt *et al.* 2007). On the other hand, the rapid loss of photosynthesis and leaf area with increasing plant water deficit observed among species with high internal water storage capacity may be a mechanism to reduce water loss and delay the occurrence of massive hydraulic failure (Brodribb & Holbrook 2003; Bucci *et al.* 2005). Contrary to our predictions, species such as *Ceiba aesculifolia*, *Ceiba grandiflora* and *Ipomea wolcottiana* with high sapwood water storage capacity and thus with highly vulnerable xylem were less responsive to progressive soil drought than some species with greater resistance to embolism. This result suggests that even in small plants with low absolute water storage capacity, water storage can facilitate decoupling of plant water status from that of the soil. The potential buffering role of water storage during prolonged soil drought was confirmed by the relationship between the wood saturated water content and the disequilibrium between plant and soil water potential

observed even at higher levels of water stress. In other words, species with greater stem water storage capacity were able to maintain their water potential above soil as drought intensified. Previous studies in tropical seasonal communities have recognized the sapwood as a transitory water source to extend daily carbon gain and to dampen fluctuations in xylem tension that could potentially produce runaway embolism (Stratton, Goldstein & Meinzer 2000; Scholz *et al.* 2007, 2011; Meinzer *et al.* 2008), but there is a relative scarcity of data on the specific role of stem water storage in allowing woody plants to survive droughts that run for weeks. This role may be especially important for seedlings with a limited capacity for soil exploration, thus relying on their water reserves during prolonged drought. For the tropical dry forest species studied here, the maintenance of physiological function under soil drought appeared to result either from having xylem with low vulnerability to embolism, or from having xylem with high capacity to store water. The decoupling between plant and soil water status by reliance on stored water may explain why early and late successional species differ in terms of their mean tolerance of plant water deficits, but did not differ in tolerance of soil drought. Previous evidence from tropical dry forest trees shows that among adult trees, water stored in stems is mostly used for reproduction and leaf flushing at the end of the dry season (Reich & Borchert 1984; Borchert 1994; Chapotin *et al.* 2005). A shift in the role of sapwood water storage with ontogeny is a hypothesis that remains to be tested.

Overall, our results suggest that ranking species according to their expected performance under soil drought solely on the basis of xylem resistance to embolism may be misleading, especially for those species with high capacity to store water in their stems.

Responses of tropical dry forest species to severe soil drought are segregated along an axis of resistance to avoidance

Maintaining xylem capacity to supply water during intense drought has been proposed as a key strategy related to survival of individuals because disruption of xylem water transport is likely to result in massive tissue death by dehydration (Tyree *et al.* 2003). Repeated measurements of physiological responses to progressive soil drought suggested that a tradeoff between the capacity to maintain xylem functionality at low soil water potentials and avoidance of soil drought existed among the tropical dry forest species studied. This tradeoff, which constrained species' behaviour during severe drought periods, was expressed in two different ways. Firstly and most obvious, there was a negative association between xylem resistance to embolism and the speed of leaf area loss to reduce transpiration as a means of delaying the onset of severe plant water deficits. This was indicated by a strong positive correlation between PLC and PLLA detected only at high levels of plant water deficit. Species with vulnerable xylem tended to exhibit a more pronounced drought avoidance behaviour. Secondly,

as previously discussed, under conditions of severe soil drought, species with vulnerable xylem relied on stem water storage to decouple plant water status from that of the soil, thereby delaying the onset of tension-induced xylem embolism. In other words, our results suggest that two mechanisms of avoidance, leaf loss and use of stored water, are traded off against xylem resistance to embolism, resulting in a continuum of plant strategies for coping with soil drought. The lack of a clear segregation of ecological groups along the resistance versus avoidance tradeoff in our study (Fig. 5, top) suggests that more than one physiological mechanism may enable seedlings to prevail against soil drought in open early and late successional forest habitats. It is important to note that while drought-resistant species with both high and low vulnerability to cavitation coexist across successional habitats, those species with large sapwood water storage capacity do not seem to be prevalent in the early successional forest. This observation is consistent with extensive field surveys (Maza-Villalobos 2012; Ramos-López 2012). However, it remains to be investigated whether an avoidance strategy involving water storage is specifically selected against in open early successional forest areas.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Functional responses of tropical dry forest tree seedlings during an experimental soil drought: (a) percentage loss of photosynthetic rate; (b) percentage loss of leaf

area; and (c) percentage loss of stem hydraulic conductivity as a function of soil water potential. Vertical line represents the soil water potential at which 80% of the function was lost. Closed symbols indicate late successional species and open symbols represent early successional species. *Caesalpinia eriostachys* □, *Cordia eleagnoides* ◇, *Gliricidia sepium* △, *Senna atomaria* ▢, *Piptadenia constricta* □, *Mimosa arenosa* ○, *Apoplanesia paniculata* ◆, *Caesalpinia coriaria* ■, *Ceiba aesculifolia* ●, *Ceiba grandiflora* ▲, *Ipomea wolcottiana* ■, *Lonchocarpus constrictus* ►.

Figure S2. Functional responses of tropical dry forest tree seedlings during an experimental soil drought: (a)

percentage loss of photosynthetic rate; (b) percentage loss of leaf area; and (c) percentage loss of stem hydraulic conductivity as a function of plant water potential. Vertical line represents the plant water potential at which 80% of the function was lost. Closed symbols indicate late successional species and open symbols represent early successional species. *Caesalpinia eriostachys* □, *Cordia eleagnoides* ◇, *Gliricidia sepium* △, *Senna atomaria* ▢, *Piptadenia constricta* □, *Mimosa arenosa* ○, *Apoplanesia paniculata* ◆, *Caesalpinia coriaria* ■, *Ceiba aesculifolia* ●, *Ceiba grandiflora* ▲, *Ipomea wolcottiana* ■, *Lonchocarpus constrictus* ►.