

# Leaf phenology is associated with soil water availability and xylem traits in a tropical dry forest

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**Abstract** In tropical dry forests, spatial heterogeneity in soil water availability is thought to determine interspecific differences in key components of resource use strategies, such as leaf phenology and xylem function. To understand the environmental drivers of variation in leaf phenology and xylem function, we explored the relation of soil water potential to topographic metrics derived from a digital elevation model. Subsequently, we compared nine xylem hydraulic, mechanical and storage traits in 18 species in three phenological classes (readily deciduous, tardily deciduous, and evergreen) in the dry tropical forest of Chamela, Mexico. Soil water potential was negatively correlated with elevation, insolation and water flow

accumulation. Evergreen species characterized low-elevation moist sites, whereas deciduous species dominated hills and dry sites. Overall, evergreen species had lower xylem specific conductivity than deciduous species, and tardily deciduous species were different from readily deciduous and evergreen species in five of eight xylem traits. In dry tropical forests, water availability promotes divergence in leaf phenology and xylem traits, ranging from low wood density, evergreen species in moist sites to a combination of low wood density, readily deciduous species plus high wood density, tardily deciduous species in dry sites.

**Keywords** Biomechanics · Leaf deciduousness · Soil water potential · Topography · Wood density · Xylem hydraulic conductivity

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## Introduction

Temporal and spatial variation in water availability is certainly one of the main drivers of ecological diversification in seasonally dry tropical forests (hereafter SDTF) (Engelbrecht et al. 2007; Sterck et al. 2011; Toledo et al. 2012). In SDTF, the abundance and distribution of tree species, both regionally and locally, is predicted well by the sensitivity of species to water deficits (Eamus and Prior 2001; Engelbrecht et al. 2007; Pennington et al. 2009). At regional scales, species turnover is associated with annual precipitation, which is positively correlated with species richness (Gentry 1995; Engelbrecht et al. 2007). At local scales, topography is the main factor determining the habitat of species (Webb and Peart 2000; Harms et al. 2001; Balvanera et al. 2002; Segura et al. 2003; Pineda-García et al. 2011). Indeed, because it affects drainage patterns and accumulation of soil water and nutrients,

micro-topography has been proposed as a factor that contributes to the local non-random distribution of species (Clark et al. 1999; John et al. 2007). Micro-topography is, therefore, a good candidate for being a determinant of the high diversity of tree species in the tropics, via niche specialization to differential water distribution (Wright 2002; Valencia et al. 2004). One way in which tree species cope with water limitation in SDTF is by modulating leaf phenology, avoiding transpiration during the most water-stressed times of the year (Borchert 1994). Leaf phenology is also correlated with leaf and xylem traits that likely allow species to range along a continuum of resource exploiting strategies (Fu et al. 2012; Méndez-Alonzo et al. 2012), from slow to fast resource exploiters with nearly equivalent carbon gain (Sterck et al. 2011).

In the SDTF, trees face the opposing selective demands of surviving the evaporative demand of the dry season while maximizing their water acquisition and transpiration during rainy season (Eamus 1999). One of the most recurrent strategies to cope with drought in SDTF is leaf shedding at the onset of the dry season. This drought-avoidance strategy allows plants to survive the dry season without compromising their hydraulic pathway and ultimately their fitness (Borchert 1994; Givnish 2002). An understanding of hydraulic design has proven critical in identifying the mechanisms that determine leaf phenology in SDTF (Eamus and Prior 2001). In SDTF, tree species seem to be arranged on a continuum between two extreme resource exploitation strategies (Chen et al. 2009; Sterck et al. 2011; Fu et al. 2012): an acquisitive strategy, characteristic of drought-avoider species, which generally have fugaciously deciduous leaves of short leaf lifespan and wood with high hydraulic conductivity, low resistance to cavitation and low density, versus a conservative strategy, which is characterized by species with tardily deciduous leaves of long leaf lifespan and wood with low hydraulic conductivity, high resistance to cavitation and high density (Méndez-Alonzo et al. 2012). Although this scheme is useful to understand the continuous variation in leaf shedding in dry tropical forests, there is still little known about the environmental and physiological factors that promote divergence between evergreen and deciduous species in the SDTF. For example, several studies have found that deciduous species are more hydraulically efficient and more vulnerable to embolism than evergreen species (Sobrado 1993; Choat et al. 2005; Chen et al. 2009), but other studies have reported higher efficiency in hydraulic conductivity and gas exchange in evergreens (Goldstein et al. 1989; Zhang et al. 2007; Hasselquist et al. 2010), and still other reports have not found significant differences in hydraulic efficiency or safety between leaf habits (Sobrado 1997; Brodribb et al. 2002; Ishida et al. 2010; Markesteijn et al. 2011a; Markesteijn et al. 2011b). Therefore, the hydraulic basis of the

dichotomy in leaf phenology of dry tropical forest trees is still an open question.

To understand the array of leaf phenologies in SDTF, it is necessary to explore water-use physiology (Borchert 1994; Brodribb et al. 2002), and to study variation in abiotic factors (Givnish 2002; Williams et al. 2008; Pringle et al. 2011). Here, we explore how differences in leaf phenology are associated with variation in soil water availability (estimated by soil water potential) and landscape topography, and in xylem traits reflecting water use in the dry tropical forest of Chamela, Mexico. We expected that the species that are found on drier parts of the landscape and retain their foliage well into the dry season should be selected toward a conservative strategy of resource use, investing in xylem traits that increase drought tolerance at the expense of conductive efficiency. Evergreen riparian species should show a contrasting xylem syndrome with low drought tolerance, but high efficiency. Water storing, fugaciously deciduous species in dry sites have been predicted to resemble evergreen species in their cavitationally vulnerable, efficiently conducting xylem (Olson and Carlquist 2001; Méndez-Alonzo et al. 2012). Shedding leaves readily at the beginning of the dry season would not only avoid extensive xylem cavitation, but confine most conduction to periods of abundant water. As a result, selection would likely favor efficient water conduction during the rainy season by increasing vessel diameter and length, and maximizing relative growth rates (Chabot and Hicks 1982; Givnish 2002; Kondoh et al. 2006). This would imply that species that avoid seasonal drought by readily shedding their foliage should converge with species of moist sites on xylem traits that confer high water transport efficiency. Based on 18 species of a dry tropical forest in Chamela, Mexico, we examined the expectations that (1) soil water availability would predict the distribution across the landscape of leaf habits. In other words, evergreen species should preferentially grow in areas of higher soil water availability, and drought-deciduous species at sites with lower soil water content; (2) among the drought-deciduous species, we expected to find the most highly drought resistant species in the driest areas of the landscape; and (3) xylem drought resistance should be correlated with leaf phenology, ranging from evergreen drought sensitive species to readily deciduous species to tardily deciduous but highly drought resistant species.

## Methods

### Study site

The Chamela-Cuixmala Biosphere Reserve, on the Pacific coast of Jalisco, Mexico (19°29'N, 105°02'W), includes

two types of vegetation: low-stature dry tropical forests that are characterized by trees less than 10 m tall on average and nearly exclusively dry season deciduous, and medium stature tropical forests characterized by tree species between 10 and 30 m tall that are a mixture of brevi-deciduous to evergreen species (Lott et al. 1987). Mean annual temperature is 24.9 °C and ranges from 14.8 to 32 °C (Bullock 1986). Average annual rainfall is  $752 \pm 256$  mm, and occurs from June to October. The highest rainfall probability occurs from July to September, when 50 % of the total annual precipitation falls in six or seven events (Bullock 1986). Leaf flushing is rapid after the first 100 mm of rainfall (Bullock and Solis-Magallanes 1990).

#### Soil water potential

We marked six individuals per 18 species, widely ranging in phylogenetic affinity and phenology (Figure S1). Four soil samples were taken next to each trunk at 10 cm deep. Samples were obtained on 6 November 2008, 60 days after the last rain, a time of the year when plants commonly experience drought stress and when spatial heterogeneity in soil water availability peaks (Méndez-Alonzo, unpublished data). For each tree, four soil samples were collected in cardinal positions located within 0.5 m of the trunk, using a 10 cm diameter core. Soil was collected in 20 ml plastic vials, and immediately sealed with parafilm (Pechiney Plastic Co, Chicago, USA) and transported to the laboratory, where soil water potential was measured to 0.1 MPa using a dew point potentiometer (Model WP4-T, Decagon Devices, Inc. Pullman WA 99163 USA).

#### Digital elevation model and topographic metrics

We recorded the geographical coordinates and elevation of each individual (Fig. 1). These data were entered into a geographic information system (GIS; Arc View 3.2 ESRI Inc.) that mapped the Estación de Biología Tropical Chamela of the Instituto de Biología, UNAM. The GIS also included a digital elevation model (DEM) of the Station, which was produced using the information available from INEGI, <http://mapserver.inegi.org.mx/DescargaMDEWeb/>. The DEM was produced using the digitized 1:50000 maps covering Mexico in 2003. From the geometric characterization of the terrain in the DEM, we calculated the following metrics: insolation, defined as the solar incidence per pixel per year, transformed to meters ( $\text{W m}^{-2}$ ) and flow accumulation (%), defined as the total number of pixels that drain into a pixel divided by the total number of pixels. Flow accumulation measures the potential runoff per unit area.

#### Leaf retention census and phenological syndromes

We conducted eight leaf censuses, starting on 15 October 2008, 30 days after the last rain, and concluding 15 March 2009, during the late dry season. During this period, we marked three terminal sun branches on each of our six adult individuals per species and recorded the number of leaves or leaflets lost. Selected individuals were representative of species height and diameter (from 5 to 10 m in species on hills and from 10 to 20 m in species in valleys), and the selected branches were laterals 2–3 m long.

For deciduous species, we determined two main syndromes of phenology-xylem behavior, based on the relationship between days since the beginning of the dry season (days after the last 10 mm rain) and the percentage of leaves retained. In this way, species that lost > 50 % of their leaves within 60 days since the last rain were termed *readily deciduous*; in contrast, species that retained > 50 % of their leaves more than 60 days since the last rain event were categorized as *tardily deciduous*. Finally, we termed *evergreen* species that did not reach 50 % leaf loss during the period studied (Table S1).

#### Xylem anatomical traits

Anatomical traits were measured from the same six individuals per species used to calculate leaf retention time. We sampled a  $1 \text{ cm}^3$  block of wood from the basal part of sun-exposed terminal branches (one branch per individual) with diameters of at least 1 cm and lengths of approximately 2 m. The block was fixed in FAA and dehydrated in successive ethanol baths and finally embedded in epoxy resin. Ten cross-sections were obtained using a sliding microtome and sections were stained with safranin. Subsequently, we measured the following xylem anatomical traits from a minimum of 25 adjacent pairs of vessels per cross-section: tangential and radial diameter, vessel wall thickness, vessel area and vessel density (vessels/ $\text{mm}^2$ ), giving a total of 250 measurements per individual. We calculated per species the hydraulically weighted vessel diameter ( $D_h$ ), as

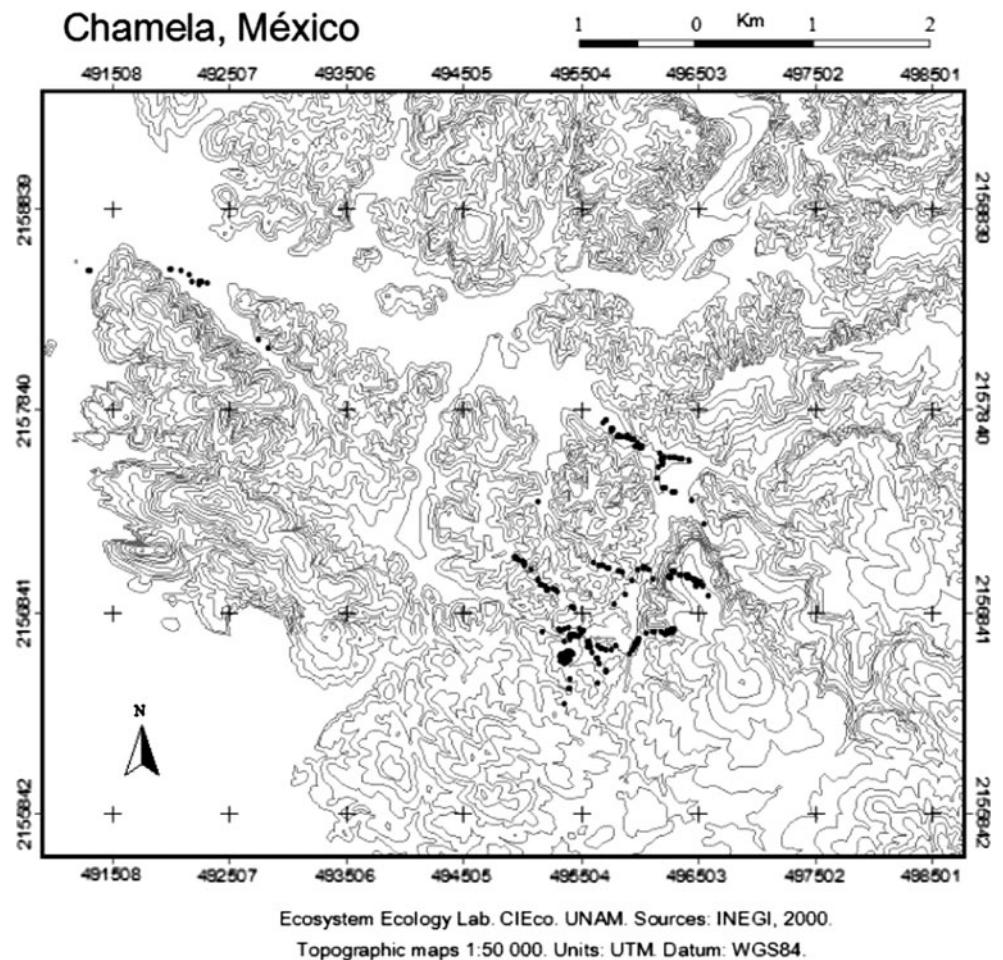
$$D_h = \left[ \left( \frac{1}{n} \right) \sum_{i=1}^n d^4 \right]^{\frac{1}{4}},$$

where  $d$  is mean vessel diameter (Poorter et al. 2010); and the potential conductivity,  $K_p$ , which was calculated with the following formula based on the Hagen–Poiseuille law, under the assumption that species have nearly equivalent vessel and conductive path lengths:

$$K_p = \left( \frac{\pi \rho_w}{128n} \right) VD,$$

where  $\rho_w$  and  $n$  are the density and viscosity of water at 20 °C (Poorter et al. 2010). For conduit pairs, we also

**Fig. 1** Topographic map showing the distribution of the studied individuals in the Chamela Tropical Biology Station, Jalisco, Mexico. *Black circles* represent individuals. *Contour intervals* 40 m



measured the index of resistance to implosion  $(t/b)^2$ , an anatomical proxy for cavitation resistance (Hacke et al. 2001; Jacobsen et al. 2005), where  $t$  is the thickness of the wall of two adjacent vessels, and  $b$  is the side of a square with area equal to the average lumen diameter of vessels (Hacke et al. 2001).

#### Xylem morphological and physiological traits

We also measured the following morphological and physiological traits in the same branches used for measuring the anatomical traits: xylem water content (Cornelissen et al. 2003), stem specific density (Cornelissen et al. 2003), specific hydraulic conductivity ( $K_s$ ) (Sperry et al. 1988) and xylem modulus of elasticity (Niklas 1992).

To measure xylem water content, we debarked and removed the pith from a 1 cm<sup>3</sup> segment adjacent to the area sampled for anatomical measurements. The segments were weighed and soaked in tap water for 24 h, reweighed, and oven-dried at 70 °C for 3 days. Xylem water content was calculated as dry weight/fresh weight. Stem specific density was measured by the ratio of dry weight/volume, calculated by immersion (Cornelissen et al. 2003).

Specific hydraulic conductivity was measured on the same six branches sampled for anatomical and morphological traits at the onset of the dry season. Branches >1 m in length and >1 cm in diameter were collected on mornings in November 2010, approximately a month after the last rains. After collection, branches were immediately wrapped in black plastic bags and transported to the lab, where we removed the leaves and selected straight segments approximately 50 cm long. We removed native embolism by applying a 100 kPa flush for 10 min with an air compressor, using a 10 mM KCl solution that was filtered (0.2 μm) and degassed overnight. We repeated the flushing until no obvious increase in bulk conductivity ( $K_h$ ) was observed, which occurred normally after two flushes. After embolism removal, we forced the KCl solution through the stems by applying a pressure head of 10 kPa, using a Sperry apparatus (Sperry et al. 1988). We collected water in vials filled with absorbent paper that were weighed after one to 2 min to record bulk flow ( $K_b$ ). Finally, we divided bulk flow by xylem transectional area to estimate specific hydraulic conductivity ( $K_s$ ) (Pockman and Sperry 2000).

Finally, we measured the xylem elastic modulus (MOE) and the modulus of rupture (MOR), two indices of



mechanical resistance, on six 40-cm long straight segments adjacent to those used to measure hydraulic conductivity per species, maintaining a 20:1 length to diameter ratio. Segments were wrapped in plastic and refrigerated until measurement. After debarking, segment diameter was calculated as the mean of the basal and apical diameters. Segments were tested in three-point bending with an Instron 3345 mechanical testing machine with a 5-kN load cell (Instron Corporation, Canton, MA, USA; Gere and Timoshenko 1999). MOE and  $F_{\max}$ , the maximum stress at the moment of breakage, were calculated with SYSTEM IX/S INSTRON software (Instron Corporation, Canton MA, USA), and MOR was calculated as  $(F_{\max} \times L \times R)/4I$ , where  $L$  is the tested length,  $R$  is the radius and  $I$  is the second moment of area of a circular section:  $I = (\pi/4) \times r^4$  (Gere and Timoshenko 1999).

### Statistical analyses

To test how landscape determines soil water availability, we correlated the following GIS-based metrics with soil water potential: elevation (m), insolation ( $\text{W m}^{-2}$ ) and flow accumulation (% , calculated as the sum of all the pixels that drain into the selected pixel/total number of pixels), using Pearson correlation analysis.

Leaf retention time (LRT) was calculated for each species as the date on which 50 % of leaf loss had occurred by fitting a sigmoidal three parameter model to the plot of date as the independent variable and percentage leaf loss as the dependent variable (Méndez-Alonzo et al. 2012, SigmaPlot 10.0, Systat, Inc.). LRT allowed us to classify our species in three phenological syndromes (evergreen, tardily deciduous, readily deciduous, Table S1). We compared xylem traits among syndromes by Kruskal–Wallis tests, followed by non-parametric post hoc Behrens–Fisher tests (Munzel and Hothorn 2001). We also explored xylem differences between phenological syndromes taking into account phylogenetic relationships using a phylogenetic ANOVA (Garland et al. 1993). We reconstructed phylogenetic relationships between sampled species using the Angiosperm Phylogeny Website (Stevens 2008) and set branch lengths to one (Figure S1). All analyses were performed in R using the npmc (Munzel and Hothorn 2001) and geiger (Harmon et al. 2008) packages.

## Results

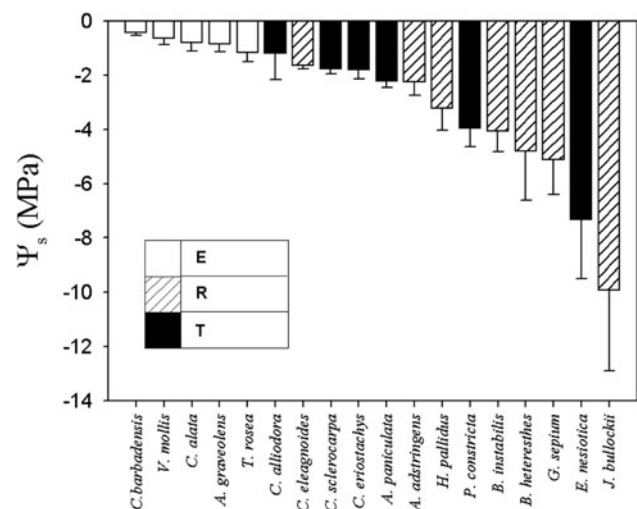
### Soil water potential and topography

Soil water potential beneath our study trees showed wide variation, ranging from  $-0.42$  MPa in *Coccoloba barbadensis* to  $-7.31$  MPa in *Esenbeckia nesiotica*. Evergreen

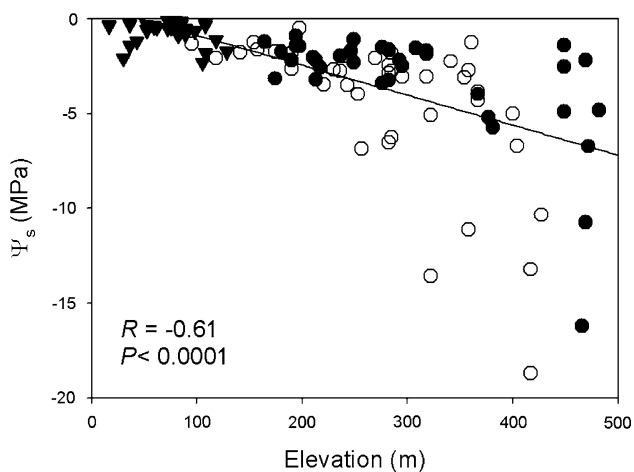
species were restricted to sites with values of soil water potential higher than  $-1.2$  MPa, whereas deciduous species occupied soils with potentials between  $-1.2$  and  $-7.3$  MPa. Within deciduous species no trend was observed with respect to soil water potential between readily and tardily deciduous species (Fig. 2). Soil water potential reflected local topography, being negatively correlated with elevation ( $R = -0.61$ ,  $P < 0.0001$ ; Fig. 3), less strongly so with solar insolation ( $R = -0.35$ ,  $P < 0.0001$ ) and flow accumulation ( $R = -0.27$ ,  $P < 0.0001$ ).

### Xylem characteristics between phenological syndromes

Most xylem traits studied showed significant differences between phenological syndromes based on Kruskal–Wallis comparisons (Table 1). In general, xylem traits of evergreen species were more similar to traits of readily deciduous species than to those of tardily deciduous ones. Indeed, water content of the xylem, modulus of elasticity, wood density, potential hydraulic conductivity and the index of resistance to implosion, did not show significant differences between evergreen species and readily deciduous species. In contrast, xylem specific hydraulic conductivity was lower for evergreen species than for readily deciduous and tardily deciduous species (Fig. 3). The  $P$  value of the comparisons taking into account phylogenetic relationships agreed in general with the conclusions of Kruskal–Wallis comparisons, except for potential and specific hydraulic conductivity, for which no differences were detected (Table 1; Fig. 4).



**Fig. 2** Values for water potential of soil at 10 cm depth under six individuals of 18 species of the dry forest of Chamela, Mexico. Soil was collected on November 6th, 2008. Deciduous species were found in sites with significantly lower soil water potentials than evergreen species ( $F = 4.39$ ,  $P = 0.03$ ), but no difference in soil water potential was found between readily and tardily deciduous species. *E* Evergreen species, *R* readily deciduous species, *T* tardily deciduous species



**Fig. 3** Soil water potential was negatively correlated with elevation (meters above sea level) in the dry forest of Chamela, Mexico. Evergreen species (*filled triangles*) were absent from elevated sites and mostly occupied low riparian sites. Readily deciduous (*open circles*) and tardily deciduous (*filled circles*) were found on dry hills

## Discussion

In SDTF, the distribution of phenological guilds across the landscape was a function of soil water availability, with evergreen species dominating the wetter valleys and readily and tardily deciduous species coexisting on dry slopes and hilltops. Our results suggest a convergent suite of xylem traits between evergreen and readily deciduous species. In contrast, xylem of tardily deciduous species was conspicuously different. Our study agrees with the notion that leaf habit is a product of the selective pressures imposed by the environment in tandem with stem hydraulic characteristics (Chabot and Hicks 1982). In our study system, it appears that high water availability, whether seasonal or permanent, may drive convergence between

evergreen and fugaciously deciduous categories in xylem hydraulic design.

### Topography effects on soil water availability

We found marked differences in soil water potential between valleys and hills. At low-elevation sites, water potentials were between  $-0.41$  and  $-1.2$  MPa. In contrast, water potentials dropped below  $-9.0$  MPa on ridges and slopes, and were highly variable across species. Our results show that the use of landscape metrics can help explain the variation in soil water availability within SDTF. As expected, valleys had the lowest insolation and highest water flow accumulation, achieving greater soil water content through the year in comparison with slopes and hills (Galicia et al. 1999; Dawns et al. 2002; Barij et al. 2007; Markesteijn et al. 2010). Our soil water potential measurements were highly variable across sites and underneath each individual, probably because superficial soils are subject to more intense dehydration than deeper soil layers (Bucci et al. 2009; Markesteijn et al. 2010). Nevertheless, our soil water potential data reflected the distribution of the sampled species across the landscape based on their phenology.

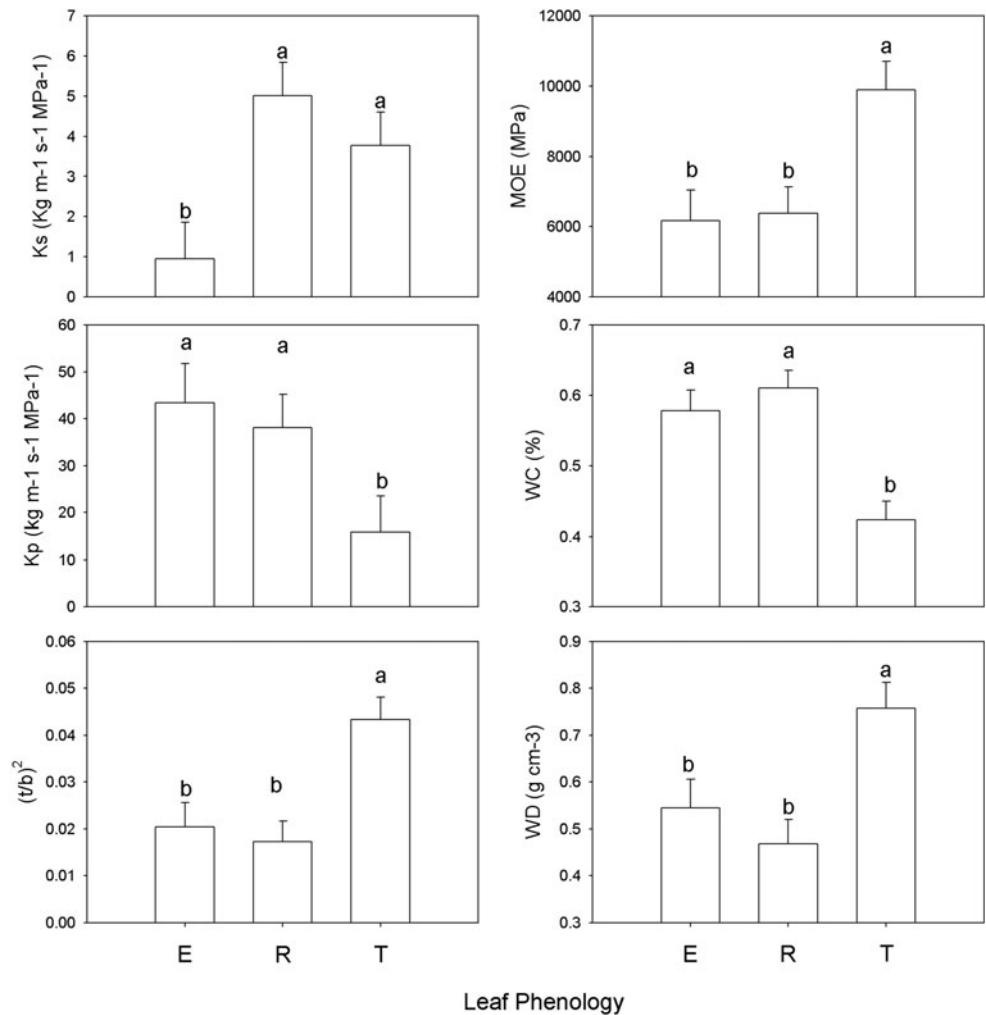
Our results show that variation in leaf habit is associated with water availability as a function of topography. Evergreen species were not found on hills and sites with soil water potentials below  $-1.2$  MPa, and, by contrast, deciduous species were mostly absent from moist valleys. At Chamela, evergreen species likely tap permanent sources of water, allowing the maintenance of leaves throughout the year (Hasselquist et al. 2010). With increasing elevation, soil water availability was less and we observed greater variation in xylem hydraulic conductivity and mechanical resistance. In other ecosystems, such as

**Table 1** Comparisons of xylem morphological, physiological, and anatomical traits between leaf phenology syndromes: evergreen (E), readily deciduous (R) and tardily deciduous (T)

Variable	KW	P value KW	P value PA	Leaf Phenology		
				E	R	T
Vessel area	4.045	0.132	0.261	–	–	–
Vessel diameter	3.432	0.180	0.268	–	–	–
Vessel density	0.898	0.638	0.855	–	–	–
Vessel resistance to implosion	9.159	0.010	0.012	A	A	B
Potential conductivity	6.934	0.031	0.193	A	A	B
Wood density	9.921	0.007	0.022	A	A	B
Xylem water content	11.516	0.003	0.005	A	A	B
Specific xylem conductivity	6.871	0.032	0.066	A	B	B
Modulus of elasticity	7.907	0.019	0.036	A	A	B

Groups were compared through Kruskal–Wallis tests (KW) and phylogenetic ANOVAS (PA). For variables with differences between syndromes, leaf phenology homogeneous groups resulting from non-parametric post hoc tests are reported

**Fig. 4** Functional xylem trait differences between phenological syndromes in the dry tropical forest of Chamela, Mexico.  $K_s$  specific hydraulic conductivity,  $K_p$  potential hydraulic conductivity  $(t/b)^2$  resistance to implosion,  $WD$  xylem density,  $WC$  xylem water content,  $MOE$  modulus of elasticity,  $E$  evergreen species,  $R$  readily deciduous species,  $T$  tardily deciduous species



Mediterranean woodlands, the reduction of soil water availability at higher elevations is associated with increases in wood density and mechanical resistance (Barij et al. 2007). At our study site, apparently there is no single optimal strategy, but a mixture of strategies that cope with seasonal drought. At Chamela, water-use strategies involve coordinated suites of xylem structural features and leaf phenology. The functional differences between these different syndromes seem likely associated with variation in the distribution of species between dry slopes and shady valleys.

In the context of this heterogeneous distribution of strategies across our topographic gradient, our results help illustrate that species with markedly different xylem traits and phenologies coexist. Species with traits suggesting increased resistance to drought co-occur with species with a drought-avoidance strategy. For example, soil water potentials near *Esenbeckia nesiotica*, a dense wooded species that is only tardily deciduous, was  $-8.0$  MPa. Soil water potential was  $-9.0$  MPa for *Jatropha bullockii*, a readily deciduous species that drops its leaves very early in

the dry season, long before *E. nesiotica*. The differences in hydraulic design in the xylem are likely associated with other ecological differences, such as assimilation rates, as has been found in other studies (Ishida et al. 2008; Fu et al. 2012). It would appear that, in the drier parts of the landscape, species bearing traits that determine two contrasting resource use strategies coexist.

#### Xylem functional traits of evergreen versus deciduous species

We found marked differences in the xylem construction of tardily deciduous species versus evergreen and readily deciduous species. The tardily deciduous species were characterized by a suite of xylem traits that suggest a conservative strategy of resource exploitation, including high-density wood, thicker vessel walls, lower xylem water content and lower potential conductivity. In contrast, readily deciduous and evergreen species had a suite of traits that correspond to a lower level of drought tolerance, including lower density wood, thinner vessel walls, higher

xylem water content and higher potential conductivity. With their efficient hydraulic systems, readily deciduous species maximize water transport during the rainy season. During the dry season, their massive stem water storage and deciduousness likely allow them to avoid highly negative water potentials (Olson and Carlquist 2001). Evergreens, by dominating moist sites, are able to maximize their water transport throughout the year. The evergreens and readily deciduous species converge in xylem traits that allow efficient water transport, maximizing water transport at either the periods or sites of high water availability. In other dry tropical forests (such as Santa Rosa, Costa Rica, which has a relatively high annual rainfall of 1,500 mm per year), evergreens include species with high-density wood, low hydraulic conductivity and high resistance to embolism and are found on the driest parts of the landscape (Brodribb et al. 2002; Choat et al. 2005; Zhang et al. 2007; Markesteijn et al. 2011b; Fu et al. 2012). At much drier Chamela, true evergreen species on dry hills would face catastrophic cavitation during the driest season of the year, and being outcompeted by the more hydraulically efficient readily deciduous species. Evergreen species at Chamela are located in areas that offer a constant supply of water through the year, satisfying their water demand even during the dry season (Goldstein et al. 1989; Hasselquist et al. 2010).

Intriguingly, we found that specific hydraulic conductivity was lower in evergreen than in deciduous species. This is in agreement with previous reports that found a higher specific conductivity in deciduous species (Brodribb et al. 2002). Although our data did not allow us to examine the mechanistic basis for this difference in  $K_s$ , a combination of a reduction in vessel length, total pit area and in the proportion of fibers versus parenchyma might be responsible for the increasing resistance to flow in the evergreen species (Comstock and Sperry 2000; Poorter et al. 2010). The lower specific hydraulic conductivity in the evergreen species we studied might be associated with lower leaf hydraulic conductivities and lower photosynthetic rates, allowing a slower growth rate that is sustained through the year and that might be associated with increased foliar longevity (Farmer 1918; Brodribb and Field 2000; Miyazawa and Kikuzawa 2005; Fan et al. 2012). There is also evidence that the traits related with stem economy (such as wood density and moisture content) are decoupled with those related with leaf economy (as SLA, chlorophyll content, nutrient stoichiometry) in trees of tropical rain forests, as a consequence of the diminished importance of drought tolerance in relation to other stressors, such as nutrient limitation and herbivory (Baraloto et al. 2010). In Chamela, deciduous trees are subject to a strong and seasonally water-stressed environment and include a wide range of hydraulically contrasting wood

strategies able to predict phenologic variation (Méndez-Alonzo et al. 2012), but evergreen trees, which occupy an environment more similar to rainforest, might allow a more complex set of hydraulic strategies between the leaf and stem hydraulic traits.

Species in moist sites possessed a range of traits shared in part with species from tropical rainforests, both in the xylem and in the leaves (Pringle et al. 2011; Méndez-Alonzo et al. 2012). Morphological features of members of the lineages that donate species to SDF are likely an important factor in the structuring of SDF communities. Species that evolved in moist tropical forests would require fewer morphological and physiological adaptations to the moist sites within dry forests, with traits such as shade tolerance, allowing them outcompete readily deciduous species in moist areas. A way to test the relative importance of “rainforest immigration” versus the invasion of lineages evolved in dry tropical forests in the structuring of moist communities at Chamela would be the comparison of the phylogenetic patterns of ancestry in habitat types to infer the likely routes of invasion of the Chamela moist forest patches (Pennington et al. 2006).

Conclusion: a note on assembly rules of tree communities in a SDF

A fundamental goal of plant community ecology is to discover the routes by which species occupy a given space, thus making up a community (Keddy and Weiher 1999). Plant species distribution, either locally or regionally, is influenced by species resistance to drought (Engelbrecht et al. 2007; Toledo et al. 2012). In our study area, beta-diversity was highly influenced by water availability, which depends on landscape configuration (Balvanera et al. 2002; Segura et al. 2003). Water availability gradients, therefore, determine to a large extent the non-random occurrence of species, which in turn reflect the adaptive evolution of species in response to such environmental stresses (Harms et al. 2001; Valencia et al. 2004). In the SDF of Chamela, the occurrence of two phenologically contrasting vegetation units can be explained by variations in the water availability in each unit. In SDF, the driest sites have a wider spectrum of leaf and stem strategies than moist sites. This wide set of apparently functionally equivalent strategies permits coexistence of a large number of species with presumably more or less equivalent carbon acquisition rates (Pineda-García et al. 2011; Sterck et al. 2011). Moist sites have a narrower spectrum of strategies in the traits that we measured, and given their different selective pressures, should certainly show strong variation in other functional traits associated with herbivory, height competition, and light harvesting (Poorter et al. 2010; Pringle et al. 2011). SDF are strongly spatially structured



communities, in which water distribution conditions the diversity of functional strategies and species.

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