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Wood anatomy of dominant species with contrasting ecological performance in tropical dry forest succession

Eunice Romero[a,c] (iD), Edgar J. González[a] (iD), Jorge A. Meave[a] (iD) and Teresa Terrazas[b] (iD)

[a]Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria, Mexico City, Mexico; [b]Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Mexico City, Mexico; [c]Posgrado en Ciencias Biológicas, Unidad de Posgrado, Circuito de Posgrados, Ciudad Universitaria, Mexico City, Mexico

ABSTRACT
Environmental restrictions faced by successional species (those occurring in recovering vegetation) change gradually between early and late succession. In tropical dry forest (TDF), legume species dominate early succession, that is, accumulate more biomass than coexisting species, but later are gradually replaced by late successional species. Stem anatomical traits are involved in water conduction efficiency and safety, and thus biomass accumulation. We hypothesized that anatomical characteristics of dominant species may explain their status in their respective successional community. We analyzed the wood anatomy of TDF dominant successional species: *Mimosa eurycarpa* and *M. tenuiflora* (early successional), *Lysiloma divaricatum* (late successional), and *Euphorbia schlechtendalii* (successionally ambiguous). Anatomical variables and indices were estimated and compared between species through linear modeling. Unexpectedly, *Mimosa* species differed in porosity type, which is one characteristic linked to water stress tolerance. *M. eurycarpa* and *L. divaricatum* are ring-porous (an uncommon feature in tropical species), whereas *M. tenuiflora* and *E. schlechtendalii* displayed diffuse porosity. *M. eurycarpa* had the lowest vulnerability index (VI) and the highest relative hydraulic conductivity. Within-individual differences in relative water conduction in ring-porous species, driven by high vessel density in earlywood and low VI in latewood, likely represent a highly advantageous strategy in water-stressed successional environments.

Introduction

When a site that underwent severe anthropogenic modifications is abandoned, the plant community can recover through secondary succession (Drury and Nisbet 1973; Pickett 1976). As this process unfolds vegetation cover and biomass increase, and species turnover takes place. In advanced successional stages, some communities attain attributes similar to those existing in the pre-disturbance condition (Whittaker 1953; Finegan 1996). Tropical dry forest (TDF) occurs in tropical regions with a well-marked dry season lasting up to seven months, which may result in high water stress for plants (Brown and Lugo 1990). Deforestation for agriculture or livestock ranching enhances such regional climatic constraints, as sites devoid of vegetation cover are subjected to high temperatures and solar irradiance (Lebrija-Trejos et al. 2011; Pineda-García et al. 2013). Thus, species occurring in recovering communities face continuous changes in resource availability and environmental conditions, such as water, space and light, which in turn are driven by the development of plant community structure (Lebrija-Trejos et al. 2010b).

Temporal changes in species composition largely reflect contrasting performances among species, because not all of them are able to survive, grow and reproduce under these changing conditions in a successional community (Connell and Slatyer 1977; Pineda-García et al. 2016). Particularly, early secondary TDF vegetation across large areas in the Neotropics consists of a thorny low forest dominated by different species of *Acacia* and *Mimosa*, which are prevalent in the forest for at least 20 years, but often persist in it for several more decades (Burgos and Maass 2004; Lebrija-Trejos et al. 2010a). With time, these legume species are gradually replaced by late successional or typical mature forest species (Lebrija-Trejos et al. 2010a).

Also, species replacements are largely associated with the different functional traits they have, among which anatomical features can be important. Plants interact with their environment and uptake resources through their roots, stems and leaves (Durante et al. 2011), and these organs' traits determine their functions (Carlquist 2001). Given the underlying link between structure and function, the wood anatomical features of the stem affect the amount of biomass accumulated by a plant (Craven et al. 2013), its growth speed (Hoeber et al. 2014), as well as water conduction efficiency and safety (Pratt et al. 2007; Lens et al. 2013). Three

basic cell types make up the wood in angiosperm stems, namely fibers, vessel elements and parenchyma cells, with each of these bearing different functions and production costs. Lignin accumulation in the secondary walls of fibers is directly related to cell diameter and cell wall thickness; such accumulation results in wood that is hard and more resistant to mechanical damage, although these two latter properties require larger biomass investments (Larjavaara and Muller-Landau 2010). Vessel lumen diameter is associated with wood hydraulic properties, as wider vessels conduct more water (Zimmermann 1983). However, a mechanical trade-off is also implied, as the risk of embolism heightens with an increase in vessel lumen diameter if soil water is limited (Cochard 2006). Vessel density and distribution also influence water conductance safety (Ewers et al. 2007; Zanne et al. 2010; von Arx et al. 2013). Redundancy in the hydraulic architecture of a tree is given by a large density of vessels along with an increased level of vessel grouping. A potential consequence of redundancy is that if one vessel is blocked, water could continue its movement to adjacent vessels through their contiguous walls (Tyree et al. 1994; Cruiziat et al. 2002). When water is scarce, some vessels may become inoperative due to air embolism, and in these cases redundancy may be useful to maintain water transport through alternative routes (Ewers et al. 2007). Parenchyma spatial arrangement has been associated with maintenance of water transport through refilling of embolized conduits and with embolism prevention by conferring high hydraulic capacitance (Morris et al. 2016). Also it has been found that angiosperm species with large vessels tend to have axial parenchyma packed around them, suggesting an important role in long-distance xylem water transport (Morris et al. 2018). Water availability at the time of conduit development is closely linked to final cell size, and thus, it affects conduit diameter size (Gartner et al. 1990). In some species classified as ring-porous, large differences in vessel diameter and fiber wall thickness between the early and late phases of the wood growing period allows the distinction between earlywood (produced early in the season) from latewood (produced later in it). In contrast, in species with diffuse porosity latewood may be sometimes recognized exclusively by few layers of more lignified fibers or by marginal parenchyma (Tarelkin et al. 2016). In ring-porous species, earlywood vessels with large diameters display different efficiency and vulnerability hydraulic properties that differ from latewood vessels with small diameters, and this has been interpreted as one of the major adaptations among temperate trees (IAWA 1989; Woodcock 1994; Domec and Gartner 2002).

Species occurring in recovering vegetation (which can be collectively referred to as successional species) face environmental restrictions that gradually change in nature and intensity between early and late successional stages. We hypothesized that, among these successional species, the dominant ones, which make the largest contribution in biomass to a successional community, display important anatomical characteristics that may explain their status in the community. Specifically, we expected dominant species at early stages to have wood anatomical features associated

with low hydraulic vulnerability, which ultimately enhances their ability to withstand water stress. Similarly, we expected dominant species at late successional stages to display anatomical features associated with an efficient resource uptake that enhances growth rates, biomass accumulation, and mechanical support. To test this hypothesis, for every dominant species in the early and late communities of a tropical dry forest, we: (1) quantified various anatomical traits, including vessel and fiber dimensions, and vessel distribution; (2) estimated their relative hydraulic conductivity and the vulnerability index; and (3) compared these variables between species.

Material and methods

Study area

The study was conducted in Nizanda, Oaxaca, southern Mexico (16° 39′ 30″ N, 95° 00′ 40″ W). Although mature TDF still covers large areas in the region, agriculture has been practiced there for a very long time, which explains the numerous secondary vegetation patches of different ages across the region (Gallardo-Cruz et al. 2012). Mean annual temperature is 27.6 °C and average total annual rainfall is 902.6 ± 355.4 mm (±SD), with 90% of it falling during the rainy season; in addition to the strong seasonality, annual precipitation is highly unpredictable, as indicated by the coefficient of variation (39.7%; CICESE 2015).

Secondary succession in the study area and species selection

The abandonment of agricultural fields triggers a secondary succession process that has been studied extensively in the region (Lebrija-Trejos et al. 2008; Brienen et al. 2009; Lebrija-Trejos et al 2010a, 2010b, 2011). Regarding TDF successional environmental gradient characterization, forest structure changes significantly with time shaping the local environment (basal area from 0 to 25 m²/ha and total crown cover from 0 to 7.2 m; Lebrija-Trejos et al. 2008, 2010b). During wet season, soil water availability and relative humidity are greater in late-successional sites than early ones (soil water potential changed significantly from −45 to −18 kPa and relative humidity from 67 to 74%), while vapor pressure deficit decreased around 0.5 kPa from early to old sites; light as well as air and soil temperatures decrease with plant community development (75–15% of open-sky radiation, 31.7 to 29.3 °C and +2.5 °C to −0.5 °C relative to ambient, respectively), which makes early-successional sites sunny, hot, and dry (Lebrija-Trejos et al. 2010b, 2011).

For this study, we selected the dominant species based on previous knowledge about their ecological performance (i.e., presence and abundance along the successional gradient; Pérez-García et al. 2001; Gallardo-Cruz et al. 2005; Lebrija-Trejos et al. 2010a; Pérez-García et al. 2010; Romero-Pérez 2014; Romero et al. submitted). Only three species stand out as being dominant in the secondary vegetation of Nizanda (i.e., they attain high basal area and high density of

individuals in comparison with other species also present in the recovering vegetation: *Mimosa eurycarpa* Robinson, *Mimosa tenuiflora* (Willd.) Poir in early successional plots, and *Lysiloma divaricatum* (Jacq.) J.F. Macbr. (Fabaceae) in late successional plots.

In Nizanda, recovering tropical dry forest is a diverse community, with the presence of at least 57 woody species (Lebrija-Trejos et al. 2010a). The majority of these successional species (50) have been also recorded in mature tropical dry forest stands of the region and are considered typical of it (Pérez-García et al. 2010). For this study, we selected two of the seven successional species absent in the mature forest, namely *M. eurycarpa* and *M. tenuiflora*. We also selected two species from the large group occurring in secondary forests, having different abundance patterns along the successional gradient (Romero-Pérez 2014), and also occurring in mature forest stands, namely *L. divaricatum* (present from early to late successional plots, it attains higher basal area values in late successional plots and also in mature forest plots), and *Euphorbia schlechtendalii* Boiss. (Euphorbiaceae, present from middle to late successional plots and also present in mature forest of the study region).

Regarding dominance patterns of the selected species, the two *Mimosa* are notorious for their dominance at early stages of succession, although *M. eurycarpa* is more frequent than *M. tenuiflora*. Both *Mimosa* species are still dominant during the subsequent four decades of succession, after which they gradually lose dominance. These *Mimosa* species can persist as big trees (up to ca. 9 m tall and 18 cm DBH [diameter at 1.30 m]) in successional stands as old as 60 years or more, but with very low frequencies. In contrast, *Lysiloma divaricatum* (up to 11 m tall and 27.3 cm DBH in successional stands) is a nonthorny Fabaceae that occurs in stands as young as two years old, where it has a low frequency, although it gradually becomes the only dominant species in late successional stages.

The reason to include *Euphorbia schlechtendalii* in the study was somewhat different. Unlike the aforementioned legumes, this species does not attain dominance at any stage of the successional gradient. However, there is an interesting ecological ambiguity related to it: in the TDF of Nizanda this is a relatively common mature forest species (Gallardo-Cruz et al. 2005), as well as a successional species, as its presence has been recorded in secondary stands as young as 25 years of age (Romero-Pérez 2014). Yet, *E. schlechtendalii* has been reported as an early dominant species in secondary TDF stands in other regions of Mexico differing in latitude and precipitation (Trejo-Vázquez 1998). We expected that the comparative analysis of its wood anatomy would be useful as a first insight into explaining its successional ambiguity.

Sample collection

Three adult healthy-looking individuals with straight stems of each species were selected in the field (see Appendix 1 in Supplementary material). A wood sample was collected with a saw from the main stem of each individual, and

immediately fixed in a glycerin–ethanol–water solution (1:1:1), in which they remained for three months until sectioning. Transverse, tangential and radial sections (20 μm thick) were cut with a sliding microtome (Leica 2000 R, Wetzlar, Germany). The sections were dehydrated with ethanol (50%, 70%, and 96%), stained with safranin-fast green, and mounted with synthetic resin.

Anatomical description and measurements

Wood anatomical traits were described following IAWA recommendations (IAWA 1989) with an optical Olympus microscope. All vessel and fiber variables were measured with Image Pro v. 6.1. We measured the tangential vessel diameter of 45 vessels per individual of diffuse-porous species, and 90 vessels per individual in ring-porous species (45 earlywood and 45 latewood vessels), as we distinguished differences within the same growth ring. For each individual, in 10 optical microscopic fields at 4X zoom (area in one optical field = 3 mm^2), we counted the number of vessels, the number of vessel groups, and the number of vessels per group. In the case of fibers, tangential diameter and lumen diameter we measured 50 cells per individual.

Statistical analyses

Generalized linear mixed-effects models (GLMM) were constructed to describe and compare mean anatomical traits among species (Appendix 2 in Supplementary material). For every response variable (vessel tangential diameter, number of vessels/3 mm^2, number of vessels per group, fiber diameter, and fiber lumen) we constructed two basic models: a model assuming differences in the estimated means between species, and a model that did not assume this (null model). Further models were constructed to examine the influence of explanatory variables: porosity type, earlywood vs latewood, family, and dominance in early succession (see Appendix 2 in Supplementary material). Model selection for each response anatomical variable was performed using the sample-corrected Akaike Information Criterion (AICc; Burnham and Anderson 2003). Model fitting was performed in R (R Core Team 2015), using the lme4 package (Bates et al. 2015).

We explored two appropriate probability error distributions for each anatomical response variable (Appendix 2 in Supplementary material): for positive continuous variables (i.e., vessel diameter, fiber diameter, and fiber lumen), we used the log-normal and gamma distribution; for the number of vessels per 3 mm^2, models assumed either a Poisson or a negative binomial distribution; and for the number of vessels per group, the error distribution was either a one-inflated Poisson or a one-inflated negative binomial. One-inflated distributions were used because of the large number of solitary vessels (which were taken as groups containing one vessel element only).

All derived variables (i.e., not measured directly in the wood sample) were not modeled but calculated from the means estimated from the above-mentioned models. We calculated mean number of vessels per mm^2 as:

mean number of vessels per 3 mm^2/3,

mean fiber wall thickness was calculated as:

(mean fiber diameter – mean fiber lumen)/2,

and the mean Runkel ratio as:

2 × (mean fiber wall thickness/mean fiber lumen).

Finally, for each species, we calculated the relative hydraulic conductivity (RHC; Fahn et al. 1986) as:

r^4 × number of vessels/mm^2,

where *r* is vessel radius, and the vulnerability index (VI; Carlquist 1977) as:

vessel tangential diameter/number of vessels per mm^2

Results

General wood features

Growth rings were typically delimited by radially flattened latewood fibers, which were associated with marginal parenchyma in the three legumes (Figures 1, 2). *L. divaricatum* and *M. eurycarpa* had ring-porous wood, whereas *E. schlechtendalii* and *M. tenuiflora* presented diffuse-porous wood. In all four species, most vessels were solitary or in small groups, although clusters up to seven vessels were observed in *M. tenuiflora* and up to eight in *E. schlechtendalii*. Vessel elements had simple perforation plates and alternate intervascular pits. Distribution of axial parenchyma was apotracheal and paratracheal; in particular, it was apotracheal reticulate in *E. schlechtendalii* (Figure 2(D)), vasicentric to confluent in *L. divaricatum* and in *M. eurycarpa* (Figure 2(A,C)), and aliform to confluent bands in *M. tenuiflora* (Figures 1(B)). Regarding cell contents, starch grains were common (Figure 2(B)), and the legumes showed abundant crystalliferous strands. In all four species, fibers had very small simple pits and abundant gelatinous fibers in bands, mostly in the latewood. Rays were heterogeneous uni-, bi- to 4-seriate, with laticifers in *E. schlechtendalii* and homogeneous bi- to 3-seriate in *M. eurycarpa* and *L. divaricatum* but uni to bi-seriate in *M. tenuiflora* (Figure 1(E–H)).

Among species comparison of anatomical features

Quantitative features describing the wood of the four successional tree species are shown in Appendix 3 (vessel dimensions and vessel distribution estimated means), Appendix 4 (fiber estimated dimensions), and Appendix 5 (RHC and VI), in Supplementary material. Some differences between species were observed regarding vessel diameter. Ring-porous wood species (*L. divaricatum* and *M. eurycarpa*) had smaller vessel diameters than diffuse-porous species (*E. schlechtendalii* and *M. tenuiflora* (Appendix 2 shows that "earlywood vs latewood" model had the lowest AICc, indicating differences in vessel diameter; Figure 3(A, C, D) and Appendix 3 shows which estimated means differ between them: see confidence intervals around each mean; any overlaping of upper or lower limits indicate no significant differences). When the

wood of ring-porous species was divided into earlywood and latewood, vessel dimensions of species with diffuse porosity (whole-wood) turned out to be equal to those of the earlywood vessels produced by ring-porous species (Figure 3(B)). The vessel diameter model that included porosity type (which establishes that mean vessel diameter differs between diffuse- and ring-porous species) was the best supported (Appendix 2 in Supplementary material), showing that mean vessel diameter in latewood was smaller than mean vessel diameter in earlywood, and also smaller than in whole wood (Figure 3(B)). Among the four species, *M. eurycarpa* had considerably greater number of vessels per mm^2 (Figure 4(A)), whereas vessel abundance did not differ between the other species.

Although *E. schlechtendalii* had on average more vessels per group than the other species (Figure 4(B); Appendix 3 in Supplementary material), data produced insufficient evidence to conclude that the number of vessels per group differs between species (i.e., null model and species model were equally supported; Appendix 2). On average, all species had 1.56 vessels per group (Appendix 3 in Supplementary material). However, the confidence interval around the estimated mean for *E. schlechtendalii* (as many as 2.88 vessels per group) was broader than for the other species (Figure 4(B)). Mean fiber diameters differed between diffuse- and ring-porous species, as the porosity-type model had the lowest AICc among all models considered (Appendix 2 in Supplementary material). Mean fiber diameter did not differ statistically between *E. schlechtendalii* and *M. tenuiflora*, and neither did it differ between *L. divaricatum* and *M. eurycarpa* (Figure 4(C)). Fiber lumina was larger for *E. schlechtendalii* (family model was the best supported model, Appendix 2; Appendix 4), and Runkel ratio was lower than that for the legume species (Figures 4(D), 5; Appendix 5 in Supplementary Materials). Fiber wall thickness differed among all species, with *M. tenuiflora* having the thickest fiber walls, and *E. schlechtendalii* the thinnest ones (Figures 4(E), 5).

Figure 6 shows the comparisons of RHC and VI among species. RHC did not differ between the earlywood of *M. eurycarpa* and the whole-wood of *M. tenuiflora*, although it was more variable in the former. The whole-wood of *M. tenuiflora* and *E. schlechtendalii*, and the earlywood of *L. divaricatum* shared equally high VI and equally low RHC values; in contrast, the latewood of both *L. divaricatum* and *M. eurycarpa* had equally low values for RHC.

Discussion

In this study, we hypothesized that xylem anatomical traits of dominant early and late successional species could explain, at least partially, their dominance in their respective communities during secondary succession. We found that the two main dominant successional species, namely *Mimosa eurycarpa* (in early succession) and *Lysiloma divaricatum* (in more advanced stages; see Methods), are ring-porous, an anatomical feature that may confer on them the expected hydraulic properties; apparently, *M. eurycarpa* shows low
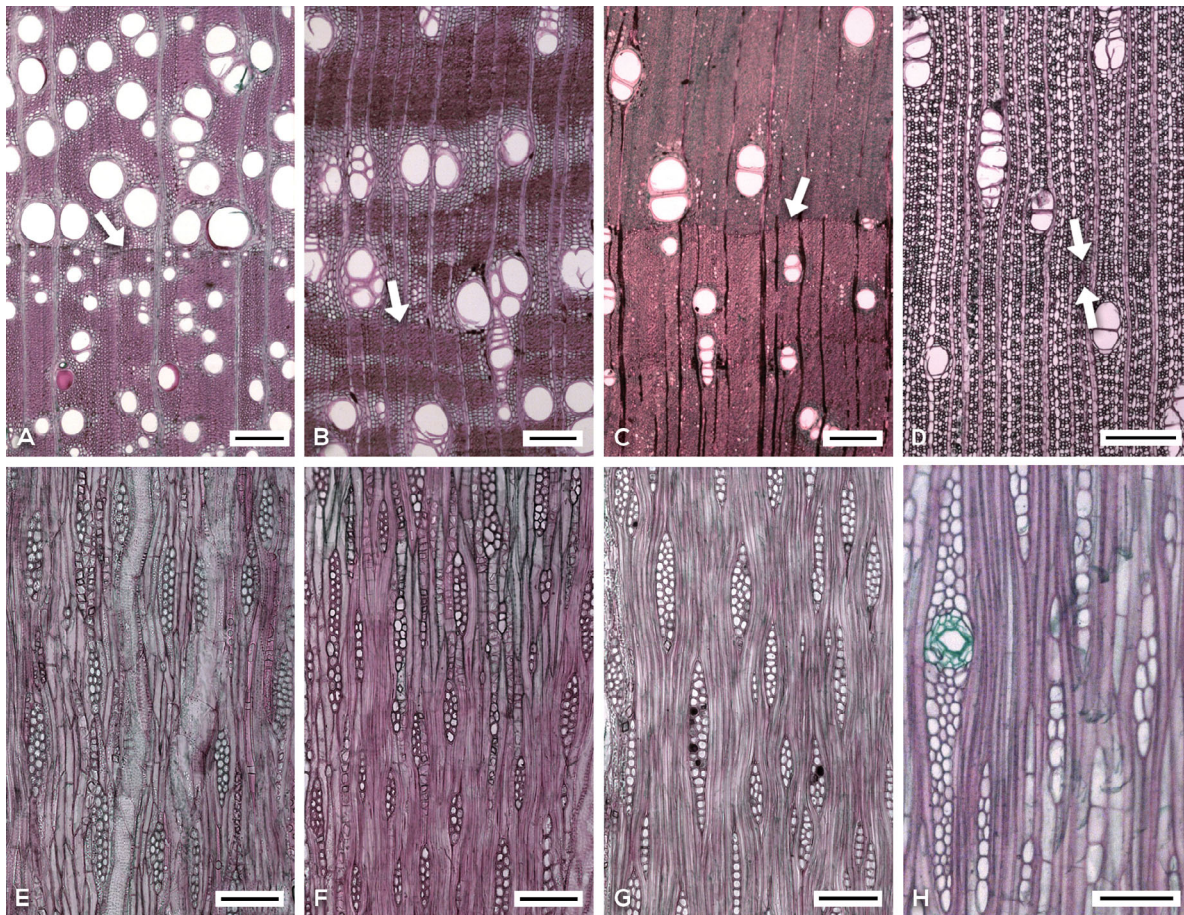
Figure 1. Anatomical comparison of four important successional tree species in a tropical dry forest. (A–D) Transverse sections; growth mark boundary is highlighted with an *arrow*. (E–H) Tangential sections showing rays. (A, E) *Mimosa eurycarpa*. (B, F) *Mimosa tenuiflora*. (C, G) *Lysiloma divaricatum*. (D, H) *Euphorbia schlechtendalii*. Bar is 200 μm in A-C, 100 μm in E–H; 300 μm in D.

hydraulic vulnerability in the dry season, whereas *L. divaricatum* displays an efficient water uptake in the rainy season. Surprisingly, we did not observe the expected similarities between the two early successional dominant species, with the most striking difference being related to porosity type.

L. divaricatum, the only dominant late successional species, also occurs in early successional sites; we thus foresaw the presence of certain characteristics in its wood that could somehow allow this species to withstand the limiting water conditions prevailing in those sites. In consistency with this expectation, we found evidence suggesting that its latewood is hydraulically safe, while the RHC of its earlywood is virtually the same as that recorded for the whole-wood of *M. eurycarpa*. Although no differences were found for vessel diameter in the latewood of these two species, the lower vessel density in *L. divaricatum* likely imposes a limit to its performance in early succession, as it cannot attain high water conduction. Moreover, its earlywood has high VI values, which implies that *L. divaricatum* may not be able to recover readily after the severe water stress experienced under these conditions. In both ring-porous species, there are probably variable degrees of hydraulic efficiency and security in their wood, as indicated by the differences between earlywood and latewood; such within-stem functional differentiation has been observed for several temperate forest species (Woodcock 1994; Domec and Gartner

2002), as well as in some tropical taxa from very dry regions (Fichtler and Worbes 2012). The ring-porous species studied by us seem to have an efficient water uptake in the rainy season, while the features of the vascular tissue produced in the dry season may be rather associated with hydraulic safety (Domec and Gartner 2002). Notoriously, earlywood vessels observed in the different species resemble each other more closely than the vessels of earlywood and latewood produced by the same species (Figure 3(B)). The high variability between early- and latewood emerges as a potentially important feature associated with their dominance.

Vessel density and degree of vessel grouping (number of vessels per group) are variables associated to the maintenance of the hydraulic function under drought stress, with vessel redundancy being the underlying mechanism (Ewers et al. 2007). Our results showed that vessel grouping did not differ significantly among the four species, so probably this feature does not play a functional role as important as previously thought (Halis et al. 2014; Ayup et al. 2015) or it can be related to the occurrence of paratracheal parenchyma. Yet, further studies are needed to confirm these possibilities.

Regarding RHC, the two early dominant species (*M. eurycarpa* and *M. tenuiflora*) appear to have a greater capacity to conduct water than the dominant species in more advanced stages (*L. divaricatum*), with *M. eurycarpa* being the species that attains the highest mean value and variability in its
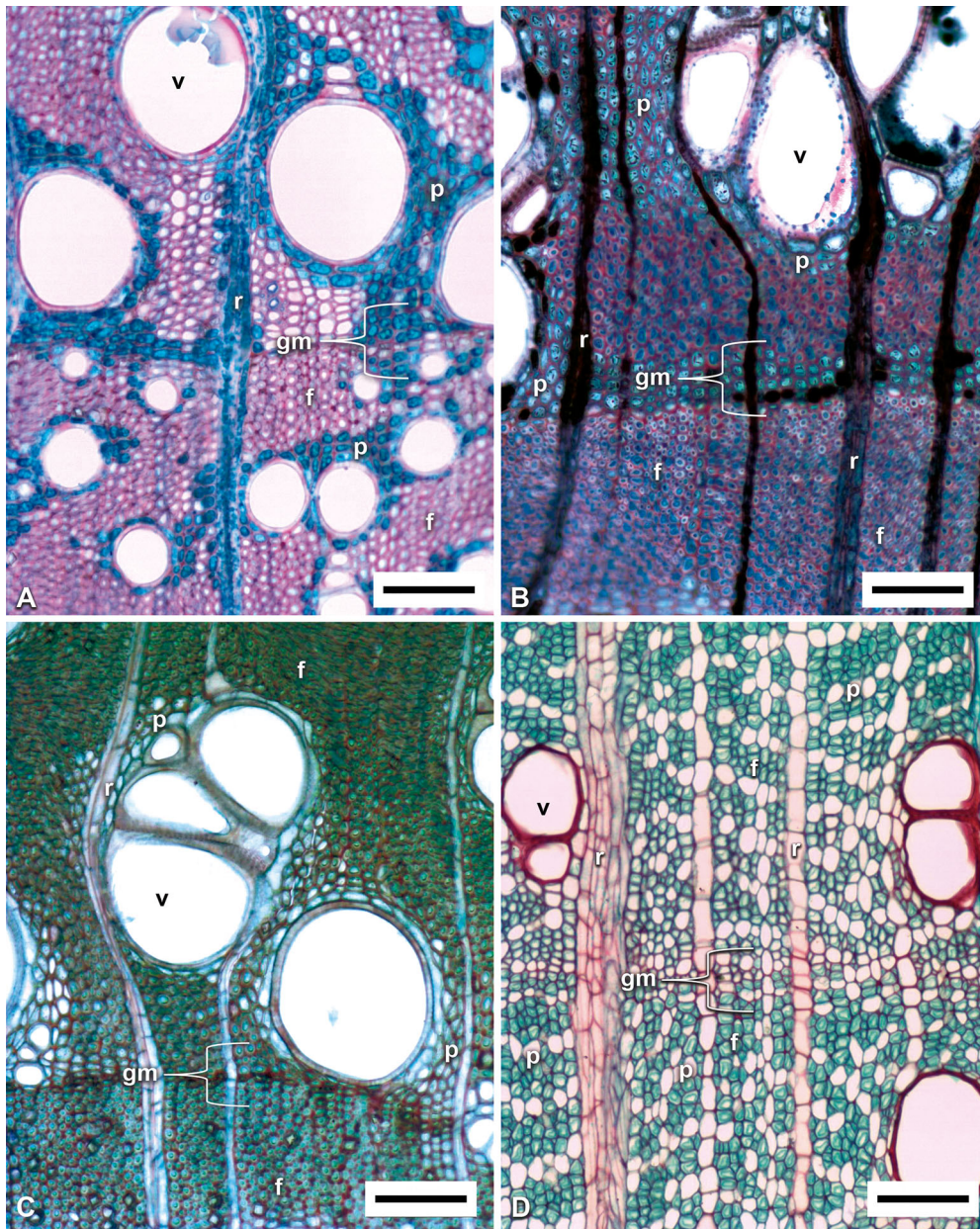
Figure 2. Detail of anatomical cell types view in transverse sections. (A) *Mimosa eurycarpa*. (B) *Mimosa tenuiflora*. (C) *Lysiloma divaricatum*. (D) *Euphorbia schlechtendalii*. Bar is 100 μm. f = fiber, gm = growth mark, p = axial parenchyma, r = ray, v = vessel.

earlywood. In *M. tenuiflora*, whole-wood RHC was undistinguishable from earlywood RHC in *M. eurycarpa*, although this lack of difference was mostly due to the large variation in vessel diameter and distribution in *M. eurycarpa*. It is likely that this variation allows for rapid adjustments in *M. eurycarpa* to changes in water availability throughout the year (Fichtler and Worbes 2012).

    E. schlechtendalii and, unexpectedly, *M. tenuiflora* showed high VI. This result was expected for *E. schlechtendalii* given its absence in the early-successional water-stressed environment, but not for *M. tenuiflora*, given its dominance in some early stands. The banded paratracheal parenchyma in *M. tenuiflora* may be associated with its ability to cope with hydraulic vulnerability, as parenchyma cells surrounding the vessels can store water, thus protecting them from hydraulic failure (Taneda and Sperry 2008; Zheng and Martínez-

Cabrera 2013; Trifilò et al. 2014; Carlquist 2015). *M. tenuiflora* has nearly as much mean percentage of parenchyma per 2 mm^2 (24.6% = 5% radial plus 19.6% axial) as *E. schlechtendalii* (31.5% = 19.8% radial + 11.7% axial) and more than *M. eurycarpa* (14.5% = 3.8% radial + 10.7% axial) and *L. divaricatum* (21.5% = 8.2% radial + 13.3% axial). Moreover, *M. tenuiflora* also seems to have the highest amount of axial parenchyma of the four species (19.6%; unpublished data) which may increase the probability of connection with vessels, thus influencing water transport maintenance. This parenchyma feature may be associated with the persistence of the leaves in *M. tenuiflora*, as this species retains its foliage for a longer time than *M. eurycarpa* (Maldonado-Romo 2014). Moreover, we also observed in *M. tenuiflora* a RHC similar to the most dominant successful species (*M. eurycarpa*, Figure 6(A)); together with the above-described parenchyma
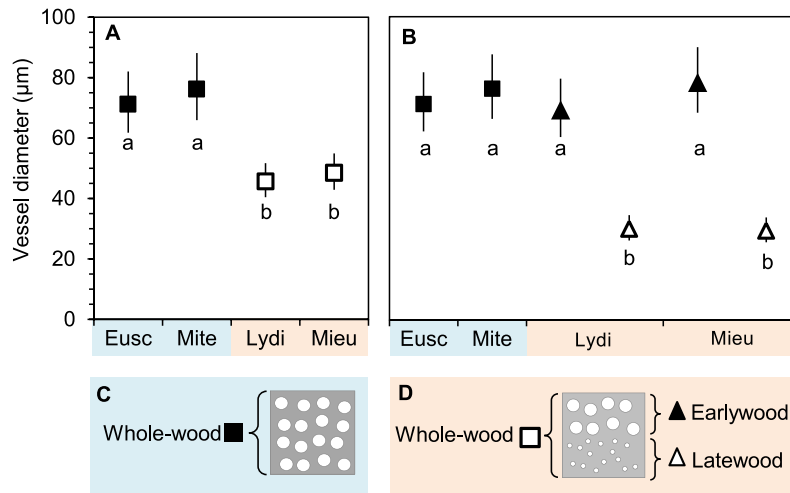
Figure 3. Anatomical comparison of vessel diameter estimated means of four successional tree species in a tropical dry forest. Different letters indicate significant differences. Eusc, *Euphorbia schlechtendalii*; Mite, *Mimosa tenuiflora*; Lydi, *Lysiloma divaricatum*; Mieu, *Mimosa eurycarpa*. (A) Species model; estimated means between species are different. (B) wood zone model; estimated means between wood zones are different. (C) diffuse-porous wood scheme; open circles represent vessels. (D) ring-porous wood scheme; tissue produced during rainy season (closed triangle, earlywood) can be clearly distinguished from tissue produced later during growth season (open triangle, latewood). Confidence intervals are shown. Model comparison was made with AICc.
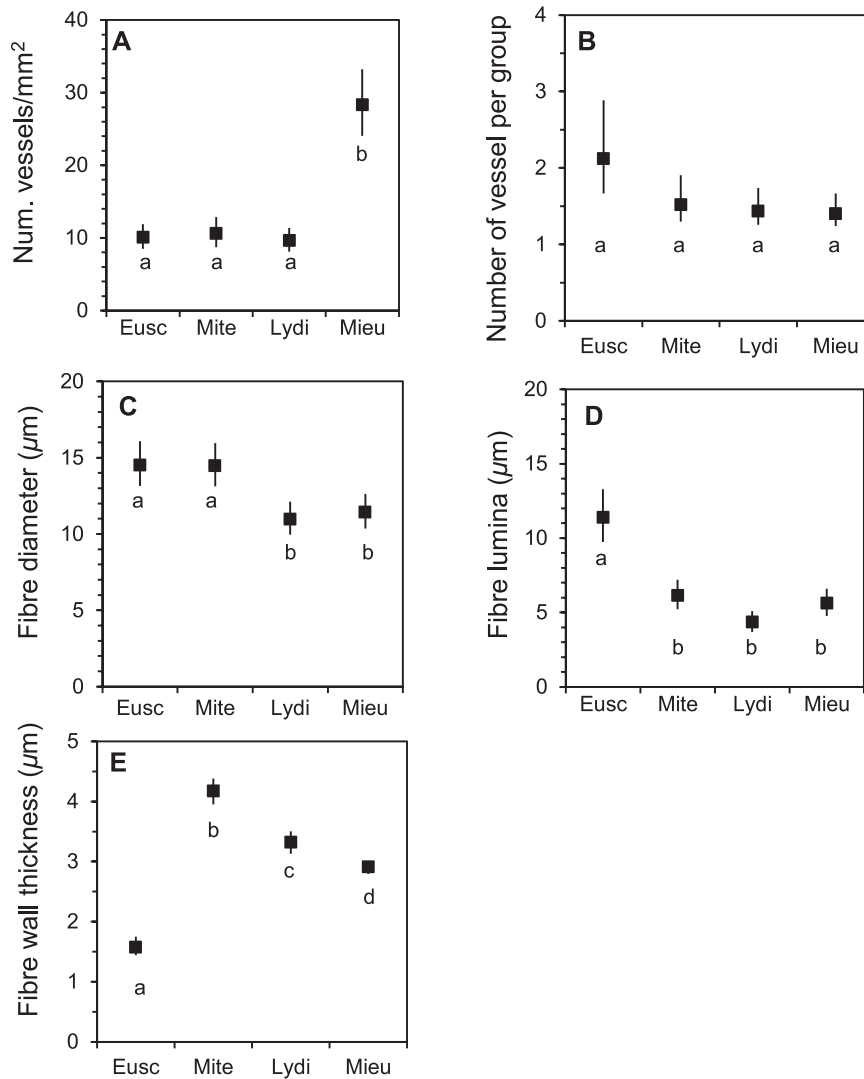

Figure 4. Comparison of anatomical features among four important successional tree species in a tropical dry forest. Different letters indicate significant differences. Eusc, *Euphorbia schlechtendalii*; Mite, *Mimosa tenuiflora*; Lyd, *Lysiloma divaricatum*; and Mieu, *Mimosa eurycarpa*. (A) Number of vessels per mm²; (B) number of vessel per group; (C) fiber diameter; (D) fiber lumina diameter; (E) fiber wall thickness.
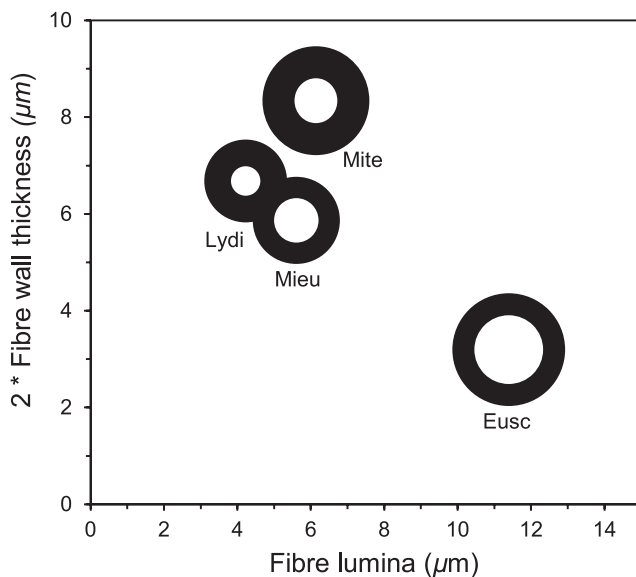
Figure 5. Runkel ratio of four important successional tree species. Open black dots represent estimated mean fiber dimensions (wall thickness, lumen width, and cell width). Eusc, *Euphorbia schlechtendalii*; Mite, *Mimosa tenuiflora*; Lydi, *Lysiloma divaricatum*; Mieu; *Mimosa eurycarpa*.
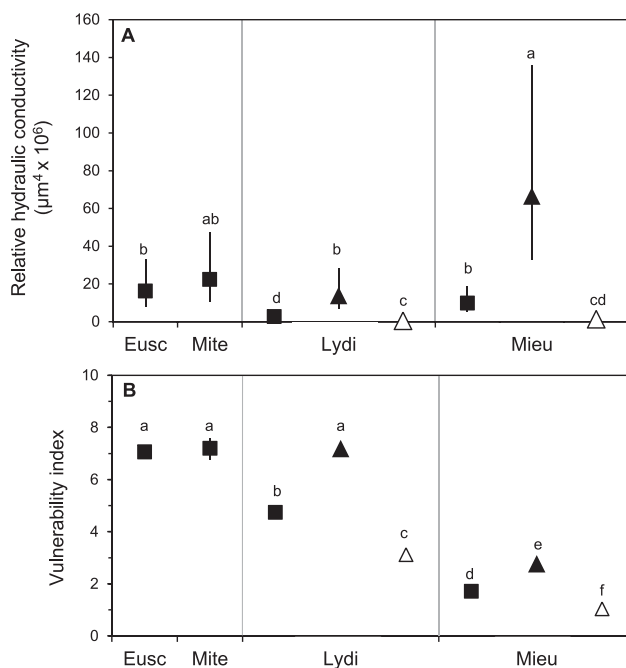

Figure 6. Relative hydraulic conductivity (**A**) and vulnerability index (**B**) for four important successional tree species in a tropical dry forest. Eusc, *Euphorbia schlechtendalii*; Mite, *Mimosa tenuiflora*; Lydi, *Lysiloma divaricatum*; Mieu, *Mimosa eurycarpa*. Whole-wood variables of *L. divaricatum* and *Mimosa eurycarpa* were divided in latewood, and earlywood. Closed squares, whole-wood; closed triangles, earlywood; open triangles, latewood.

feature, such high RHC seems to be advantageous for fast biomass production. The combination of these two traits may explain why *M. tenuiflora* can grow successfully in harsh early successional environments. Fiber lumen area, fiber wall fraction, and fiber wall to lumen ratio can explain wood density, which is an important physical property that has been linked with mechanical strength and with a growth-mortality tradeoff (Poorter et al. 2008; Osazuwa-Peters et al. 2017). Thus, regarding biomass production costs Runkel ratio

may indicate how is the trade-off between abundance and lumen vs wall thickness when having similar density.

We anticipated that *E. schlechtendalii* would differ from the three legumes studied both in fiber and vessel dimensions, as well as parenchyma distribution, partly because of its different familial affiliation (Euphorbiaceae). Indeed, their values of fiber diameter, lumina and wall thickness were different from those recorded in the legumes. Nonetheless, its vessel features and associated emergent properties (i.e. RHC and VI) were remarkably similar to those of *M. tenuiflora*. The anatomical features observed in *E. schlechtendalii* (vessel diameter size and distribution, and parenchyma distribution) do not confer hydraulic safety, which is one reasonable explanation for its absence in early successional stages. Future studies on the hydraulic architecture of *E. schlechtendalii* individuals growing in different communities may support this possibility. It is likely that tree height plasticity may explain the ecological success of this species in early stages of other TDFs; the species has been reported to grow as a shrub (I. Trejo-Vázquez pers. comm.), while in our study site, it is a tree as tall as 8 m. Thus, it seems that in Nizanda the height of this species promotes a high hydraulic conductivity, rather than minimizing the risk of xylem hydraulic damage associated with drought, as reported for other tropical species (Rowland et al. 2015; Zach et al. 2010).

Competitive advantages of the most successful early dominant species

Notwithstanding the strong water-related environmental filters operating in early succession, *M. eurycarpa* is remarkable, as it reaches considerably higher basal area values (a common structural variable interpreted as a proxy of biomass production) than any other successional species in early stands, including its congeneric *M. tenuiflora* (Lebrija-Trejos et al. 2011; Romero et al. unpublished). For this reason, we predicted that *M. tenuiflora* would depart from the others in certain anatomical features that would guarantee its success in early succession. In consistency with this idea, *M. eurycarpa* showed the lowest vulnerability index of all species examined, especially for its latewood, so probably this species conducts water even at the end of the growing season.

Our results for *M. eurycarpa* whole-wood suggest that this species does not face the expected trade-off between high efficiency in water conduction at the cost of low water security (Sperry et al. 2008; Gleason et al. 2016); hydraulic safety in this species is likely possible not only due to small vessel diameter, but also to a large investment in large numbers of vessels. The anatomical characteristics of *M. eurycarpa* probably ensure highly efficient water conduction when water is available, while they may reduce its hydraulic vulnerability when this resource is scarce; similar patterns have been reported for other species growing in environments with unpredictable water availability (De Micco et al. 2008). Initially, we anticipated a low RHC for this species. This was true only when the analysis was conducted at the whole-wood level. Conversely, when the analysis was dissected by earlywood and latewood, *M. eurycarpa* turned out to have

the highest RHC in its earlywood among the four species. Such a high RHC is an outcome from its considerably high frequency and diameter of vessels.

One important expectation in our study was that the wood of the two early dominant species, namely *M. eurycarpa* and *M. tenuiflora*, would largely resemble to each other due to their congeneric status (although they are not so closely related phylogenetically; Simon et al. 2011). Surprisingly, our results revealed large differences in their anatomical features, the most important of which are porosity type and vessel density, specially ring porosity, which is a rare trait in Mimosoideae (Evans et al. 2006).

Although the two early congeneric dominant species (*M. eurycarpa* and *M. tenuiflora*) have similar ecological behaviors (Lebrija-Trejos et al. 2008; Romero et al. submitted; see Methods), *M. tenuiflora* does not make a structural contribution to successional forests as high as that of *M. eurycarpa*. The diffuse porosity of *M. tenuiflora* probably enables this species to attain a high hydraulic efficiency in the rainy season, and thus to accumulate biomass rapidly; however, such vessel features may also entail high costs in hydraulic safety during the dry season. Considering vessel diameter, we may conclude, in agreement with Montaño-Arias et al. (2013), that *M. tenuiflora* is vulnerable to hydraulic stress. This may well be an explanatory factor of the comparatively lesser dominance of *M. tenuiflora* in the regional TDF secondary succession.

Considerations on the statistical analysis

Anatomical variation among and within species is high, and there is a large variety of procedures to quantify it (Scholz et al. 2013). At present, there is a strong need for standardized statistical analysis of anatomical features (Ewers and Fisher 1989; Mencuccini et al. 2010; von Arx et al. 2013; Wegner et al. 2013). In fact, some wood anatomical studies have overlooked statistical issues (Montaño-Arias et al. 2013). For example, since multiple measurements are usually performed in a single individual, no independence can be assumed among them, and thus pseudoreplication becomes a problem when making inferences (Hurlbert 1984; Lazic 2010). A solution is to average over all measurements done on the same individual (Hurlbert 1984; Kroodsma et al. 2001); however, this procedure largely reduces sample size, which can strongly affect statistical power (Schank and Koehnle 2009). A better option is the use of mixed models, which account for both the within- and between-individual variation, providing more accurate estimates than those obtained assuming independence (Lazic 2010). This is the statistical approach we used in this study. Furthermore, an additional consideration is the error distribution we assume on the response variable. Given that such distribution is not known *a priori*, the exploration of alternative distributions is advisable (Dick 2004). We suggest that our analytical approach be routinely applied in the study of many anatomical variables often measured repeatedly on a single individual.

Concluding remarks

Our results suggest that the two early dominant species display different strategies to cope with drought stress in early successional stages. By examining earlywood and latewood separately, which has commonly been done for temperate species (Woodcock 1994; Domec and Gartner 2002) but infrequently for tropical trees, we were able to observe differences in RHC and VI within a single individual. Such variation, along with a high vessel density, could be the key to the ecological success of the pioneer *M. eurycarpa*, as this combination of anatomical characteristics seems to be advantageous. Among the four studied species, *M. eurycarpa* is apparently characterized by the lowest VI during the dry season and the highest RHC during the rainy season. New studies are needed to further support this conclusion. Within-individual differences in relative water conduction in successional ring-porous species, driven by high vessel density and diameter in earlywood and low VI in latewood, seems to represent a highly advantageous strategy in water-stressed successional environments.

Disclosure statement

No potential conflict of interest was reported by the authors.

ORCID

Eunice Romero 🆔 http://orcid.org/0000-0002-8282-3005
Edgar J. González 🆔 http://orcid.org/0000-0001-9113-1070
Jorge A. Meave 🆔 http://orcid.org/0000-0002-6241-8803
Teresa Terrazas 🆔 http://orcid.org/0000-0001-7749-5126

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