Physiology / Fisiología

STUDIES OF PLANT HYDRAULICS AND WATER RELATIONS IN MEXICAN ENVIRONMENTS: ADAPTATION, PHYSIOLOGY, AND APPLICATIONS

ESTUDIOS SOBRE HIDRÁULICA Y RELACIONES HÍDRICAS DE PLANTAS EN AMBIENTES MEXICANOS: ADAPTACIONES, FISIOLOGÍA Y APLICACIONES

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Abstract
Given the outstanding global progress of research on the hydraulic pathway in plants, and its important role as an indicator of plant mortality risk, we reviewed: (1) the adaptive basis of hydraulic traits and their importance for overall plant function; (2) the number of primary scientific articles on plant hydraulics that have been produced in Mexico in the last 40 years, (3) research related to specific environments in Mexico, and (4) the possible applications of plant hydraulics to natural resource management. Our systematic review included 83 articles. The number of publications per year steadily increased over time, reaching its maximum in 2021. Veracruz and Yucatán are the states where the majority of scientific articles on plant hydraulics have been produced, but for most states less than two publications on this subject appeared in ca. 40 years, and none was found for Oaxaca and Chiapas, the most biodiverse states. In plant hydraulics, the most studied biome in Mexico was the tropical dry forest, followed by crops; trees were the most studied growth-form, followed by herbaceous crops and epiphytes. We point to the need of enhancing research in the interface between plant hydraulic function and remote sensing, as well as developing applications in adaptive forest management and ecological restoration. We hope that this review may ignite a national collaborative effort to quantify critical traits that could inform the hydraulic functioning of Mexican ecosystems, particularly in the underrepresented and highly diverse states of Mexico.
Keywords: adaptation, drought vulnerability, ecophysiology, plant water relations, systematic review.

Resumen
Debido al impactante progreso mundial de la investigación sobre el transporte hidráulico como indicador del riesgo de mortalidad en plantas, revisamos (1) las bases adaptativas de los caracteres hidráulicos y su importancia para la función sistémica de las plantas; (2) los artículos científicos primarios producidos en México relacionados con hidráulica de plantas en los últimos 40 años, (3) la investigación relacionada con ambientes o formas de vida específicas dentro de México, y (4) las posibles aplicaciones prácticas de la hidráulica de plantas al manejo de los recursos naturales. Nuestra revisión sistemática incluyó 83 artículos. El número de publicaciones por año incrementó constantemente a través de los años, alcanzando su máximo en 2021. Veracruz y Yucatán son los estados con la mayoría de publicaciones en hidráulica de plantas. En contraste, para casi todos los estados del país se encontraron menos de dos publicaciones y no se encontró ninguna para Oaxaca y Chiapas, los estados más diversos. El bioma más estudiado en México en hidráulica de plantas es la selva baja caducifolia, seguido de los cultivos; los árboles son la forma de vida más estudiada, seguida de cultivos herbáceos y epífitas. Proponemos estimular la investigación en la interfaz entre la función hidráulica de las plantas y la percepción remota, así como desarrollar aplicaciones en manejo forestal adaptativo y restauración ecológica. Es necesario detonar un esfuerzo colaborativo nacional para cuantificar caracteres críticos sobre la función hidráulica de los ecosistemas mexicanos, particularmente en los estados más diversos y menos estudiados.
Palabras clave: Adaptación, ecofisiología, relaciones hídricas de plantas, revisión sistemática, vulnerabilidad a la sequía.

Plants face a daily trade-off involving carbon dioxide (CO_2) absorption versus losing water through stomata. This is inevitable because when leaves open their stomata to take up CO_2 from the atmosphere, they expose the wet surfaces of the inner leaf to a dry atmosphere, leading to an approximate exchange of 400 H_2O units lost for every one CO_2 unit gained (Nobel 1999, Taiz & Zeiger 2010). This trade-off originates due to the low concentration of CO_2 within the stomatal chambers and the relatively lower vapor pressure deficit in the surrounding atmosphere. In consequence, the plant faces the dilemma of losing too much water and risking hydraulic failure, or instead capturing too little atmospheric carbon and "starving" because of the depletion of essential non-structural carbohydrates (McDowell *et al.* 2008). This trade-off generates a systemic response of events that impacts not only leaves, but also stems, roots, and even reproductive organs. The most common process of water transport in plants follows what has been called a transpiration chain, and the mechanism involved is generally known as the tension-cohesion theory (Dixon & Joly 1895). The driving force of the tension created by the transpiration from open stomata promotes the generally unidirectional movement of water in the soil-root-stem-leaf-atmosphere direction (Sperry *et al.* 2003).

The continuum of water transport is a consequence of the interaction between non-covalent molecular forces that bind the water molecules together and that also cause the adhesion of the water to the inner walls of conduits (vessels or tracheids) in the wood of plants (*i.e.*, xylem). The force that generates the initial impulse to this transport is the desiccation caused by the release of water from the mesophyll of the leaves (Nobel 1999, Taiz & Zeiger 2010). Gas exchange (involving water release for the uptake of CO_2) through the stomatal pores on the leaf surfaces causes a water potential gradient. This negative water potential gradient prompts water to move from the root boundary with the soil to the stomata, where transpiration occurs (Evert 2006). When the level of relative water saturation in the surrounding air decreases, vapor pressure deficit and leaf desiccation increase, resulting in higher transpiration per unit leaf area, which in turn depends on the size and density of stomata and vein network conductance (Nobel 1999). Leaves are both the main bottleneck to the flow of water within this complex system (Sack & Holbrook 2006), and at the same time, it is the organ mainly involved in maximizing light interception and photochemical energy transduction via photosynthesis, causing morphological and physiological modifications, both at the acclimation and adaptive levels (Smith *et al.* 1997, Scoffoni *et al.* 2014). This transport mechanism can be quantified by means of the water potential (Ψ), which is the comparison of the free energy of any solution with respect to pure water (Dixon & Joly 1895, Scholander *et al.* 1965, Tyree & Ewers 1991, Tyree & Zimmermann 2013).

Ψ reflects the ability of water to move from a solution from one compartment to another, and in plants, it can be used to compare the amount of water that can be mobilized from the compartment with the highest Ψ ($\Psi = 0$ for pure water) toward that of lower Ψ through a water concentration gradient, wherein the case of plants, $\Psi_{plant} < \Psi_{soil}$ is a necessary condition for water movement (Kramer & Boyer 1995, Nobel 1999). This analogy of hydraulic potentials with respect to electrical and chemical systems allows making relative comparisons of the state of water stress experienced by different species of plants, plant varieties or experimental treatments within the same species. Maintaining an intact conductive stream within a plant requires a balance between the tension in the water column inside the xylem, the water-conducting tissue, and the cohesion between water molecules.

However, this system is delicate and the negative pressure of this water column (expressed by its water potential Ψ) presents daily and seasonal variability. When plants transpire through the leaves but have a Ψ that does not allow the extraction of water from the soil ($\Psi_{plant} > \Psi_{soil}$), high tensions can occur inside the xylem resulting in cavitation events, which produce xylem embolisms. Xylem embolisms are air bubbles that block the flow of water, reducing hydraulic conductivity (Sperry & Tyree 1988, Tyree & Sperry 1988). Plants can avoid water loss, and extreme xylem tensions, through stomatal closure, but if drought is persistent and hydraulic dysfunction is sustained over time, the plant depletes its carbon reserves and is more susceptible to attack by pathogens (Anderegg *et al.* 2012, 2015). At the same time, hydraulic collapse might be magnified by the loss of water via plant cuticles (Duursma *et al.* 2019), which are plant surfaces covered with waxes that evolved to produce a nearly impermeable transportation system (Fernández *et al.* 2017). The interactive effects of plant hydraulic collapse

plus the loss of productivity and biotic attacks induce plant mortality (McDowell *et al.* 2008, McDowell 2011). Given that hydraulic collapse is the main physiological mechanism responsible for triggering plant mortality (Rowland *et al.* 2015, Adams *et al.* 2017, Brodribb *et al.* 2020), causing massive tree mortality in both young and adult growth phases, and that irrigation to maintain the favorable water status of plants is commonly one of the main limits to expand the productivity of crops, it is critical to understand the relative susceptibility of the biota to drought.

To better predict the response of vegetation to drought, it is essential to connect specific physiological responses with differing levels of vulnerability. When the water potential drops to extreme stress during a drought event, xylem embolisms block conduits and lower water conductivity (frequently noted as Ψ_{50}, *i.e.*, the water potential at which plants lose 50 % of their hydraulic conductivity, assuming that 100 % conductivity is reached at $\Psi = 0$, or close to a species-specific optimum), which can be so severe as to cause interruption of the water supply essential for survival ('hydraulic failure', empirically considered at Ψ inducing 88 % loss of conductivity). Nowadays, there is consensus on the main role of hydraulic failure in plant mortality, with numerous studies showing that drought-induced hydraulic damage drives tree mortality and species distributional shifts (Choat *et al.* 2012, Anderegg *et al.* 2015, Trueba *et al.* 2017, Choat *et al.* 2018).

Given the often-catastrophic consequences of hydraulic failure, it is no surprise that natural selection has shaped plant hydraulic systems in ways that make them resistant to it. A multitude of features of the xylem are clear adaptations to withstand water stress. A few examples include the following:

(1) Trees move water in narrow, membrane-bounded conduits, which are much shorter than the length of a tree. Embolisms usually are stopped by the lateral pit membranes that surround conduits (Li *et al.* 2016, Trueba *et al.* 2019), so the relatively short lengths of conduits means that when any one conduit embolizes, the blockage is confined to one relatively small part of a plant.

(2) The number of conduits, and how they are grouped, suggests that redundancy in the hydraulic network is persistent across plant lineages and life and growth-forms. Per unit leaf area, plants have a very large number of conduits in their secondary xylem. It would be much less costly in terms of carbon for plants to build just one large conduit, but this does not happen. Instead, selection seems to favor a great deal of redundancy, with many narrow conduits operating in parallel. In such highly redundant systems, when a single conduit is embolized, there are still many functional conduits operative, and water can still reach the leaves. There is practically no theory available to predict how conduit lengths should be distributed in a plant (Comstock & Sperry 2000), and none at all regarding how many conduits there should be per unit leaf area.

(3) Conduit diameter and conduit wall thickness vary according to water availability in the environment. A great deal of comparative evidence suggests that wider conduits are more vulnerable to drought-induced embolism formation than narrow ones (Olson 2020, Anfodillo & Olson 2021). There is still no consensus regarding a physiological mechanism that would lead to a vulnerability-diameter link, but the comparative trends are very clear. For example, dryland plants tend to have narrower conduits than similar-sized plants in moist areas, and plants in saline drylands even more so (Olson *et al.* 2020a), exactly what would be expected if narrower conduits conferred greater resistance to drought-induced embolism. Along these lines, conduit wall thickness also is clearly acted on by selection in the context of vulnerability to drought, with, for a given conduit diameter, species more subject to drought having thicker conduit walls.

(4) Communicating pits between conduits. A final set of traits we will mention are the characteristics of the pits that communicate adjacent conduits. In plants exposed to highly negative xylem pressures, these pits are invariably tiny; in plants in which pressures are never as negative, they can be much larger, suggesting that small pits contribute to resisting passage of embolisms between conduits (Carlquist 2001). Between different plant phyla, conifers have valve-like structures between communicating tracheids (torus and margo) that allow confinement of emboli. These structures are rarely present in Anthophyta, and comparative reviews of the resistance to hydraulic failure across plant lineages point toward increasing resistance in conifers over angiosperms (Maherali *et al.* 2004, Pitterman *et al.* 2005, Choat *et al.* 2012).

Why might Mexican ecosystems be the best natural laboratory for studies of plant hydraulic architecture?

Owing to its complex geology and physical geography, Mexico is one of the most biodiverse countries on Earth. With its diversity of phylogenetic lineages, plant growth forms, and habitats, Mexico is the country that best represents plant diversity on Earth. It is, moreover, the country that has given more useful domesticated plants than any other. As such, Mexico is home to *ca.* 2,400 genera and *ca.* 24,000 species of vascular plants, making this country the fourth or fifth most biodiverse political entity globally (Villaseñor 2016). A typical scenario of Mexican geography is the myriad of different micro-environments across its territory. The combination of complex topography, its geographical position amidst the boundary between the Nearctic and Neotropical biogeographic realms, and its subtropical and tropical position allows Mexico to encompass most terrestrial biomes of Earth within its territory. The overall replacement of species across territorial units (Morrone 2019) makes it complicated to delimit only by the calculation of species richness the set of regions most suitable for species conservation at the national scale. Moreover, the high species richness in Mexico makes calculating environmental services, such as carbon storage and productivity, daunting. Within this country, the most common hydrological regime is seasonal, and this seasonality, coupled with high species diversity, leads to morphological and physiological diversity, such that there is high variation across ecosystems in plant species shape, size, morphology, and function.

In addition to the heterogeneity in plant structure and function due to evolutionary history in the context of environmental variability, current climatic changes are disrupting terrestrial ecosystems at the global level, and given that Mexico encompasses both tropical, subtropical, and arid latitudinal belts, we expect drought to be a prime climatic threat to plant diversity. Drought is a complex phenomenon that can be understood using meteorological, hydrological, agronomic, and eco-physiological techniques (Dai 2013), and is expected to increase with climate change, as forecasts imply decreasing precipitation and increasing temperatures within Mexico (Cavazos *et al.* 2013, Colorado-Ruiz *et al.* 2018).

Therefore, it is critical to study the mechanisms of water transport to evaluate the risk of drought failure in plants and their cascade of functional changes in forests (Adams *et al.* 2009, Anderegg *et al.* 2012; Jump *et al.* 2017). At the level sensed by the individual plant, climate change can induce increases in vapor pressure deficit (VPD) leading to aridification (Berdugo *et al.* 2020). Increased aridity and VPD raise the pressure on the hydraulic and photosynthetic systems of plants (Choat *et al.* 2018, Trueba *et al.* 2019, Grossiord *et al.* 2020, Olson *et al.* 2020b, López et al. 2021). Despite the physiological adjustments of plants in the face of water stress, the drought tolerance thresholds of many plant species are currently exceeded, resulting in massive mortality events (Hartmann *et al.* 2015).

Although forest dieback occurs on a global scale, this phenomenon is still poorly understood in many parts of the world, and we consider critical for the management of Mexican forest resources to deploy academic and institutional efforts toward comprehending the risk of massive forest mortality within the Mexican biomes. Collecting this information is therefore essential in order to gain a broader view of the mechanisms leading to the decline and shifts of Mexican vegetation in the current context of climate change and increasing aridification.

Given the outstanding plant richness in Mexico, we aim to review the quantity and location of scientific articles analyzing plant hydraulic traits (PHT) within Mexico. As stressed before, drought can seriously threaten plant survival and the function of whole ecosystems. Because PHTs may inform natural resource managers regarding the threats faced by ecosystems within the expected climate alterations facing the 21st century, we aim this review to inform priority areas where further efforts should be taken to improve knowledge regarding the functioning of our biota, and their inherent risks of mortality or dysfunction. Given the covariation between traits commonly quantified in functional plant ecology and plant hydraulics, we also present a rationale to select key traits that might be useful to represent the functionality of the vegetation at the regional and national scales, being suitable to be included in surveys by the national agencies describing the geographical distribution of the biota and management of forest resources (*i.e.*, the National Institute of Statistics, Geography and Informatics, INEGI, and the National Forest Commission, CONAFOR, for Mexico). Finally, we reviewed the state-of-the-art of plant hydraulics within important biomes or plant functional groups in Mexico, including deserts, tropical dry forests, and CAM plants, which are highly

diverse in Mexican ecosystems. Further, we present future challenges in applied ecology employing functional ecology and ecophysiological methods. In summary, our objectives are: (1) to present to the Mexican readership a brief review of the mechanisms of water transport in plants, including their relevance as adaptations and their implications for inferring ecosystem structure and function; (2) to identify in which biomes and states within Mexico PHTs have been quantified and to identify critical areas in terms of biodiversity or functional diversity lacking this knowledge; and (3) to recommend guidelines to expand our comprehension of the variability in PHTs within Mexico and present possible applications of PHTs in managing natural ecosystems and agroecosystems.

A systematic review of plant hydraulic studies in Mexico

To explore the development of published research on plant water relations conducted in Mexico, we performed a systematic review of the primary literature covering *ca*. 40 years, based on the criteria of the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) protocols (Page *et al.* 2021). Between November 30th, 2021, and December 3rd, 2021, using the *Clarivate Web of Science* database, we performed searches using the following terms: Mexico hydraul*, Mexico water-use, and Mexico water relations. The initial display of results offered 2,551, 1,311, and 1,744 entries, respectively. From this total, we filtered the articles of the following disciplines: biology, agronomy, ecology, plant sciences, forestry, and biological conservation. This filter yielded 262, 377, and 420 entries. Subsequently, we reviewed the titles and abstracts and excluded secondary literature (reviews and comments) and articles not related to plant water transport (918 exclusions) (Figure 1).

From this filtered dataset (141 articles), we reviewed the methods to exclude works that were not performed within Mexico. From this further exclusion, we obtained 83 entries (Figure 1). These were reviewed and the following information was extracted: location and state where the research was mainly conducted, the vegetation type according to Rzedowski (2006), the growth-form investigated, and finally, the plant genera studied. We correlated time vs the number of publications, and integrated the information of the frequency of occurrence of genera within scientific publications using a semantic cloud generator (wordcloud.cs.arizona.edu). Figures and analyses were performed in SigmaPlot 11.0 (Systat Software Inc. Chicago IL, U.S.A.). For the relation between number of publications per year, the normality of data was tested using Shapiro-Wilks test. As the dataset did not fulfill the normal distribution, a nonparametric Spearman correlation analysis was performed using SigmaPlot 11.0.

Geographic and ecological patterns in the study of plant hydraulics in Mexico

We found a positive trend of increase in the number of research articles related to plant hydraulics or including PHTs from 1985 to 2021 (r_S = 0.82, P < 0.001), reaching its maximum during 2021 with seven articles (Figure 2). The Mexican states with the highest number of publications were Veracruz and Yucatán, followed by Jalisco (Table 1). We could not find any scientific publication for 13 states, and just 1-2 for nine states out of the 32 states that conform to the political and geographical organization of the country (Table 1). Surprisingly, there were no publications from the most biodiverse states of Mexico: Oaxaca and Chiapas, nor for some of the most important agronomic areas of Mexico, such as Chihuahua and Sinaloa (Table 1).

The biome (vegetation type) with the highest number of scientific publications related to plant hydraulics was the Tropical Dry Forest, with 20 records, followed by Xerophytic Scrub and Crops with 17 records each (Figure 3A). The growth-form most frequently studied were trees, with 36 records, followed by crops (herbaceous) with 15, and epiphytes with 12 (Figure 3B). Few records were found for Tropical Rainforests, although this vegetation type is among the most species-rich in our country. Other relevant vegetation types lacking research are fir forests (*Abies*) and high-altitude grasslands, which may be presently disturbed by climatic change modifications. Among growth-forms, there is little research on some of the most charismatic species of Mexico, such as *Agave* (with exception of *Agave tequilana*), as well as important genera in Cactaceae, such as columnar and barrel cacti (*Pachycereus, Carnegiea, Echinocactus, Ferocactus, Neobuxbaumia,* amongst other cacti genera). The semantic cloud showed

Identification of studies via databases and registers

Identification

Records identified from*:
Databases (n = 3)
Registers (n = 5,606)

→ Records removed *before screening*:
Records removed for corresponding to non-biological disciplines (n = 4,547)

Screening

Records screened
(n = 1,059)

→ Records excluded (secondary literature, not related articles)
(n = 918)

Reports sought for retrieval
(n = 141)

→ Reports not retrieved
(n = 0)

Reports assessed for eligibility
(n = 141)

→ Reports excluded because the studies were not performed in Mexico (n = 57)

Included

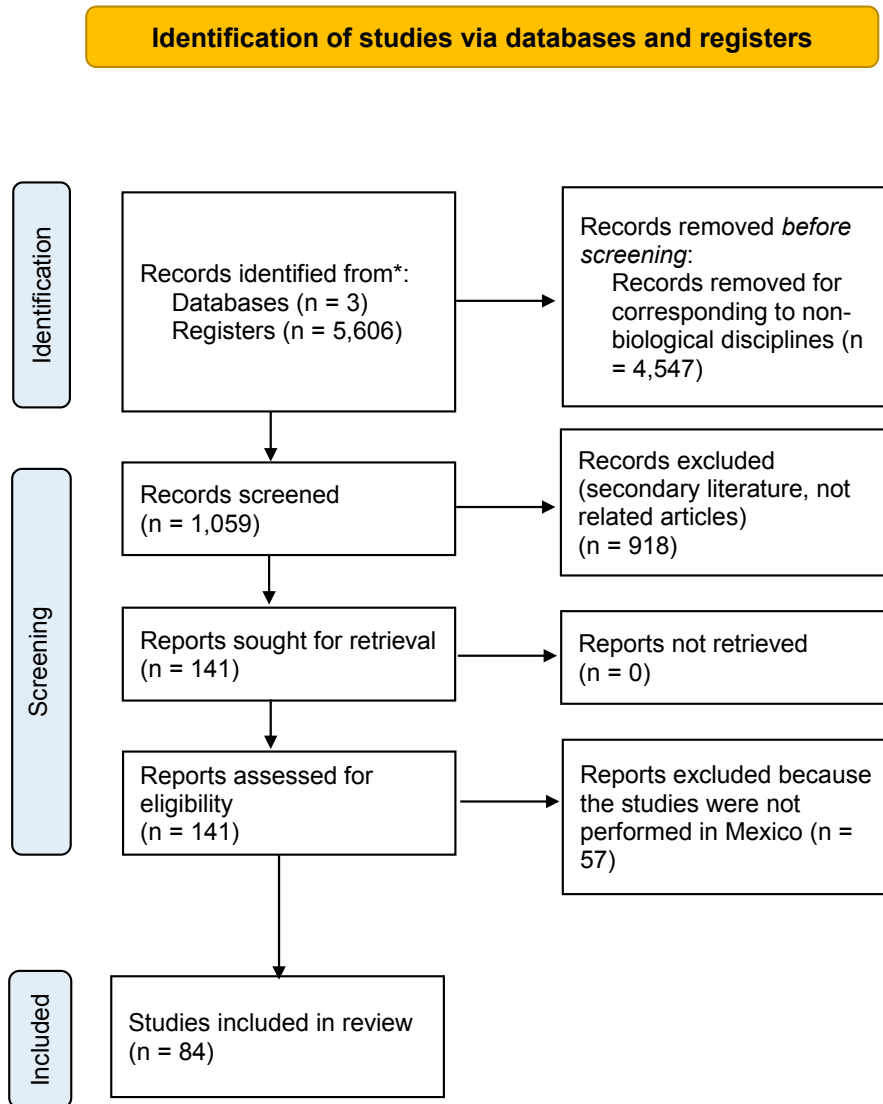Studies included in review
(n = 84)

Figure 1. Flowchart based on the PRISMA protocols (Page *et al.* 2021) to discriminate the scientific publications on plant water relations from studies conducted in Mexico in the 1985-2021 period.

that *Quercus* is the most studied tree genus in our dataset, *Tillandsia* the most studied epiphytic genus and *Capsicum* the most studied crop genus ([Figure 4](#)). Most of the studied species appear only in one study. With exception of *Manilkara*, four of the five most speciose tree genera in Mexico (Cavender-Bares 2019) are represented at least two times (*Quercus, Pinus, Bursera,* and *Lysiloma*). Limited research on plant hydraulics has been performed for the most conspicuous crops in our country, namely maize and beans, and nearly none in squash, edible fruits, and other economically important crops ([Figure 4](#)).

Selected case studies of plant hydraulics in Mexican environments

PHTs in young plants of tropical deciduous forests. Seedlings are highly sensitive to changes in water availability due to their small amounts of resource reserves and limited development of radicular systems. In seasonal ecosystems, both high rates of mortality and growth are typically observed in response to drought or pulses of rain (Engelbrecht

et al. 2007). This has led ecologists to the premise that community assembly largely occurs at the seedling stage (Comita & Engelbrecht 2014), and that natural selection might strongly shape the ways seedlings use water and respond to drought (Paz *et al.* 2015). In this context, studying the diversity of adaptations of seedlings becomes key to predicting responses of individual species to current and future environmental scenarios, as well as to scale up to understand species coexistence and to design plant communities in ecological restoration.

Here we pinpoint some interesting findings of the research performed with seedlings of Tropical Dry Forest trees in Mexico. The Tropical Dry Forest is one of those terrestrial ecosystems where the variability of water availability rules over community structure and ecosystem functioning. There, plants are subject to seasonal drought, and dry spells during the rainy season whose frequency and duration vary erratically among years (Maass *et al.* 2018). Under this scenario, an overarching hydraulic hypothesis is that the ability of plants to tolerate drought compromises their ability to acquire and use water to maximize growth when water is available (Méndez-Alonzo *et al.* 2012, Paz *et al.* 2015).

Pineda-García *et al.* (2016) did an elegant test of this hypothesis by comparing actual physiological rates of plants subject to high water availability and to progressive soil drought. They found that xylem water conductivity, photosynthetic rates, and growth rates under no water limitation were negatively correlated to the level of dehydration at which xylem water conductivity and photosynthesis decrease 50 % due to drought, *i.e.*, to their drought tolerance. The universality of this hydraulic efficiency-safety trade-off has been challenged given the inconclusive results among studies with adult trees from other seasonal ecosystems (Gleason *et al.* 2016). However, the consistent morphological, anatomical, and physiological evidence from Tropical Dry Forest species, among seedlings, saplings, and adults (Engelbrecht & Kursar 2003, Markesteijn *et al.* 2011, Méndez-Alonzo *et al.* 2012, Paz *et al.* 2015, Pineda-García *et al.* 2016; among others), strongly suggests that the high heterogeneity of water regimes in this ecosystem may select for tight hydraulic coordination.

Experiments with young plants have allowed the understanding of functional coordination above and belowground, and their interplay with leaf phenology. Common garden experiments have shown that a continuum of plant strategies to deal with drought, from tolerance to avoidance, is defined by the coordination of multiple traits at the xylem, root, leaf, and overall whole plant levels. Species with very tolerant xylem also have dense tissues with low water reserves, deep roots, and retain leaves for long periods during drought. In turn, species with intolerant xylems have soft tissues full of water, and shallow roots and are rapidly deciduous (Paz *et al.* 2015, Pineda-García *et al.* 2016).

Interestingly, because non-tolerant species rapidly reduce water loss and use water storage to maintain water potential, both drought tolerant and drought avoiders exhibit high survival under soil drought (Pineda-García *et al.* 2016). Amazingly, fast-growing species with intermediate xylem traits that do not invest much in dense tissues or storage, but that do so in new leaves, also coexist in the dry forest (Paz *et al.* 2015). How come drought tolerant, drought avoiders and water exploiter tree species coexist in this ecosystem is really intriguing.

Overall, the tight coordination of hydraulic, water use, allocation and phenological traits, suggest that a few easy-to-measure traits can be proxies to select species for restoring open degraded areas, where the risk of drought is augmented. For example, tolerant species with dense stems and leaves, or avoiding species with soft, succulent tissues may be good candidates to conform to the initial stages of restoration systems, while intermediate density species may be selected to speed up productivity and biodiversity recovery (H. Paz, unpublished). How functional coordination varies among communities with different water regimes, and thus how general are proxies for plant water use strategies are still open questions. With no doubt, water acquisition and hydraulics at the root level are still much the hidden half. In this respect, young plants are great models to do experiments and gain insights.

Hydraulic traits, phenology, and resources acquisition in desert trees. Mexico harbors the richest desert flora in the world, yet the ecophysiology and hydraulic features of this widespread Mexican environment have been poorly studied. Desert environments are characterized by low and unpredictable precipitation. Under these extreme conditions, water stress is a dominant selective pressure that may act in different directions, resulting in a diversity of plant
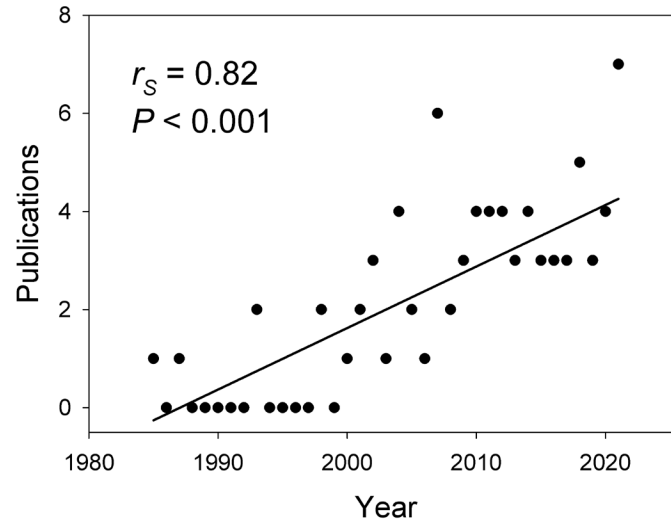
Figure 2. Increase in the number of scientific publications per year in Mexico related to plant water relations in the 1985-2021 period. Reports were extracted from the Clarivate ® Web of Science database.

structural and functional attributes that allow plant survival. For desert plants, the study of plant hydraulic traits, and their relationship with resource use, are important to identify different strategies displayed by individual plants to enhance survival or reproduction. The fast-slow plant economics spectrum is a general frame that allows determining the use of resources by plants based on the relative carbon costs of tissues and organs (Reich 2014). In this spectrum, the central concept is that plants face a trade-off between productivity and persistence.

This tradeoff contrasts, on the one hand, fast resource use plants defined by fast growth, cheap organs (low leaf mass per area [LMA], and low specific stem density [SSD], short-leaf lifespan), and fast return of carbon and nutrients investment (high photosynthetic [A] and transpiration rates [T]); and, on the other hand, slow resource use plants that are characterized by slow growth, expensive organs, long-lived leaves (with high LMA, low A and T) and high SSD. Unfortunately, few studies have explored plant hydraulics and resource use in Mexican deserts, which make up a vast and diverse system to identify important plant strategies in surviving water stress.

Here we describe the diversity of water use strategies in response to drought in ten tree species of the Sonoran Desert with different leaf phenology, based on González-Rebeles *et al.* (2021). Leaf phenology was determined by measuring leaf life span and canopy leaf duration (FD), which varied among tree species in a range from 30 to more than 365 days, revealing a high variation within the groups usually classified by leaf habit as evergreen and deciduous. Predawn (Ψ_{pd}) and midday water potentials (Ψ_{md}) were measured during the hydrological year in the area and used to determine hydroscape area (HA), a parameter that quantifies water status regulation through stomata and classifies species along an iso-anisohydric continuum (Meinzer *et al.* 2016).

Sonoran Desert trees showed high variation in HA, moreover, FD and HA were correlated, indicating a diversity of strategies, implying that the control of plant water potential is linked to phenology. More isohydric species maintain high water potentials through the day and the favorable season, but they close stomata and drop their leaves to reduce transpiration at different times, as soil water potential decreases at the end of the season.

Evergreen species were more anisohydric, with large decreases in daily and seasonal water potentials, and low stomatal conductance (gs). FD and HA showed high correlations with hydraulic and economic attributes, linking phenology and physiology at the whole-tree (canopy) scale. HA and FD were positively correlated with leaf mass per area (LMA), a trait related to mechanical strength and resource assimilation of leaves, and specific stem density (SSD), a trait indicating wood capacitance (water storage capacity) and mechanical strength; HA was also correlated with hydraulic attributes such as hydraulically weighted vessel diameter of the leaf, a measurement that represents

the relative conductance of each vessel, considering its relation to its diameter raised to its fourth power (Coomes *et al.* 2008).

HA and FD correlations with hydraulic and economic features suggest that water stress as a selective pressure may link the iso/anisohydry and fast-slow resource use strategies (Chave *et al.* 2009). Furthermore, this study shows that HA, FD, LMA, and SSD are functional traits that may describe several hydraulic and economic attributes to characterize species and their responses to water availability.

In summary, this study differentiated species along a continuum of hydraulic and economic strategies, based on the covariance of functional traits. At one extreme, fast resource use species take advantage of the favorable season, increasing acquisitive functional traits like high water transport and gas exchange capacities, but are very sensitive to soil desiccation, dropping leaves in the dry season. In contrast, slow resource-use species cope with low resource availability during the dry season, increasing drought tolerant and conservative traits. These traits, however, limit their capacity to exploit resources more efficiently during the favorable season.

CAM hydraulics. Crassulacean acid metabolism (CAM) represents a metabolic pathway in which additional steps are added to the typical C_3 photosynthesis, resulting in plants that have the highest water use efficiency among vascular plants (Borland 2018). Mexico, having extensive arid and semi-arid ecosystems, has been the center of radiation of plant lineages with a high prevalence of CAM (*e.g.*, Asparagaceae, Bromeliaceae, Cactaceae, Crassulaceae, and Orchidaceae; Espejo-Serna & López-Ferrari 2018, Rodríguez *et al.* 2018); as well as a domestication center for CAM crops (*e.g.*, *Opuntia, Agave,* and *Vanilla*; Andrade *et al.* 2007, Davis *et al.* 2019). Yet, the vast majority of the Mexican CAM species lack hydraulic studies, even when they exhibit some of the most interesting adaptations in water acquisition and use.

In CAM plants, stomata open mainly during the nighttime, when air relative humidity is high and thus transpiration rates are low. Carbon absorbed during the night is stored in acids inside the vacuole and broken down during the day in performance of photosynthesis (Males & Griffiths 2017). Large succulent cells with high vacuole capacity are often associated with the presence of CAM (Silvera *et al.* 2010, Borland *et al.* 2018). Additionally, specialized hydrenchyma is conspicuous in CAM plants due to its role in providing water during prolonged droughts.

The large volumes of succulent tissues of CAM plants present challenges to plant hydraulics. Among these are generating osmotic gradients to direct water transport from the hydrenchyma to the photosynthetic tissue and having special tracheids that withstand large contractions in hydrenchyma volume without loss of conductive function (reviewed in Schulte 2009). Males (2017) found an overinvestment in leaf veins in CAM Bromeliaceae species, compared to C_3 species, and related this to the need to replenish water into succulent tissues. All of these examples of hydrologic adaptations in CAM species warrant further research.

One of the most interesting and understudied hydraulic curiosities in CAM plants is the array of adaptations that these plants exhibit in collecting and using alternative water sources (fog or dew). In Mexican deserts, CAM plants may receive very small amounts of water in the form of rain (*e.g.*, the Sonoran Desert can receive less than 50 mm per year; García 1965, Hernández-Cerda & García 1997). In some cacti, effective dew collection is achieved through the spines, which have low emissivity coefficients that lead to radiative cooling during the night and dew condensation (Ju *et al.* 2012, Malik *et al.* 2015). Microchannels on the spines funnel water toward the spine base, even against gravity, where the water is absorbed by special leaf trichomes (Ju *et al.* 2012, Kim *et al.* 2017). The trichomes absorb liquid water rapidly and store it in mucilage, discouraging evaporation of the condensed liquid (Kim *et al.* 2017).

In a similar adaptation to cacti, epiphytic members of Bromeliaceae have evolved leaves that cool radiatively during the night and condense dew (Chávez-Sahagún *et al.* 2019) or that have small boundary layers that enable the interception of the small water droplets present in fog (termed nebulophytes; Martorell & Ezcurra 2007, Reyes-García *et al.* 2012). These bromeliads have lost most root absorptive capacity (Benzing 2000, Leroy *et al.* 2019) and rely on complex trichomes for water absorption directly into the leaf (Benzing 1976, Pierce *et al.* 2001, Ohrui *et al.* 2007). Recently, these trichomes were found to allow long-distance water transport along the leaf surface (Herppich *et al.* 2019, Ha *et al.* 2021), making up an alternative water transport to xylem. This unique external transport system

Table 1. The number of scientific publications per state of Mexico related to plant water relations during the 1985-2021 period (N = 80, three articles do not indicate the state where research was conducted). No publications have been reported to date in Mexican states without bar charts. Reports were extracted from the Clarivate® Web of Science database.

State	Publications	State	Publications
Veracruz	16	Querétaro	1
Yucatán	15	Tamaulipas	1
Jalisco	8	Zacatecas	1
CDMX	6	Aguascalientes	0
Baja California	4	Campeche	0
Baja California Sur	4	Chihuahua	0
Nuevo León	4	Chiapas	0
San Luis Potosí	4	Colima	0
Sonora	4	Durango	0
Coahuila	3	Guerrero	0
Michoacán	2	Hidalgo	0
Puebla	2	Morelos	0
Tabasco	2	Nayarit	0
Estado de México	1	Oaxaca	0
Guanajuato	1	Sinaloa	0
Quintana Roo	1	Tlaxcala	0

is not susceptible to cavitation or dependent on water potential gradients, contributing to the persistence of epiphytic species in dry environments.

The implications of the use of dew or fog on the overall hydraulic configuration of CAM plants have not been explored. Nevertheless, with relatively large/constant volumes of water being absorbed through the leaf or stem trichomes, transport in these plants often does not follow the traditional soil-plant-atmosphere model. Furthermore, the few studies performed highlight that both water collection and/or transport efficiency are variable depending on each species' morphology and anatomy. Thus, this is a highly unexplored field of research that will surely yield interesting findings in the future.

Applications and new research opportunities in plant hydraulics within Mexico

Currently, several researchers across several Mexican institutions and across a wide number of states within Mexico are quantifying the responses of plants to water stress. We hope that, by reviewing their work, a more consolidated effort to coordinate this research will be stimulated and that both the new generations of plant ecology students and decision-makers will be motivated toward defining novel ways to produce information that leads to improving our forest management in the imminent scenario of climatic modifications. By generating information on critical functional traits, including measurements of community-weighted tree height, height-standardized xylem conduit diameter, stem density, leaf density, area, and mass per area, Mexico would achieve a first inventory of the risk of impacts of recurrent water stress episodes on Mexican vegetation, as well as contributing to enhancing our understanding of the heterogeneity and ecosystem services of our biomes.

We are conscious that such a formidable task involves experts from other areas of knowledge. And in consequence, we would expect that future efforts to quantify the risk of our flora to hydraulic dysfunction would imply a multidisciplinary approach. Along these lines, we can envision that the following recent areas of exploration would be much needed to anticipate the fate of our forests in the 21st century.

Anatomical correlates of vulnerability to drought. Given widespread forest mortality across the world due to climate change induced drought, it is urgent to understand the anatomical correlates of vulnerability to drought. The field of plant hydraulics is largely stalled at this point, exactly when it needs to reach a consensus. Despite abundant comparative evidence that wider conduits are more vulnerable to embolism (Olson 2020, Anfodillo & Olson 2021), there is no clear causal mechanism to connect diameter with vulnerability. There is some evidence that thicker intervessel pit membranes are associated with greater resistance to embolism (Jansen *et al.* 2009, Lens *et al.* 2013, Brodersen *et al.* 2014, Kaack *et al.* 2021). However, the thickness of pit membranes cannot be the main driver of variation in vulnerability to drought induced embolism because angiosperms and conifers show similar patterns of vulnerability to drought, height limitation by water availability, as well as dieback and mortality. Both angiosperms and gymnosperms grow taller in moister situations, and to similar maximum heights. Also, both angiosperms and gymnosperms sacrifice terminal branches and re-sprout shorter when climates become drier (Rood *et al.* 2000, Koch *et al.* 2004, Olson *et al.* 2018, Anfodillo & Olson 2021). But conifers and angiosperms have very different pit membrane structures. Angiosperm pit membranes are homogeneous, with water passing only through micro-pores of complex structure (Kaack *et al.* 2021). Conifer pits, on the other hand, have a torus-margo structure, with water passing through massive spaces in pit margos. Angiosperm pit membranes impede embolism passage by virtue of their narrowness, and probably their surfactant lipids (Schenk *et al.* 2017). Conifer pits impede embolism passage, instead, by acting like tiny valves: upon a pressure differential, the margo allows the torus to seal against the inner surface of the pit chamber of the functional tracheid, thus sealing it off from the embolized tracheid. These modes of embolism confinement are so different that pit membrane structure cannot be the main explanation for the similar patterns of height limitation, drought vulnerability, dieback, and other phenomena that are exhibited in very similar ways by angiosperms and conifers alike. And yet, despite the clearly urgent situation faced by forests worldwide, there is little current clarity regarding the way forward for research on the structural causes of vulnerability to drought-induced embolism.

Surveying key metrics related to tree mortality risk. To enhance our knowledge of the potential risk of hydraulic failure of our vegetation, we require coordinated surveys of key metrics regarding the risk of tree mortality. Despite current knowledge of the mechanisms of response to water stress, no large-scale study has included the interaction of the two types of traits involved in hydraulic failure in drought conditions: (1) hydraulic vulnerability, and (2) stomatal adjustments. Closing stomata prevents water loss during a drought event. However, the plant may continue to lose water through the leaf cuticle as well as through poorly closed stomata (Duursma *et al.* 2019). The rate of this water loss, known as minimum conductance (g_{min}), is still largely neglected despite its importance in understanding the depletion of the last water supply in the plant. Knowledge of "safety margins", representing the water states to which the water and carbon exchanges of the plant are impacted (Trueba *et al.* 2019), is also essential for monitoring the impact of water stress on vegetation. Currently, models based on hydraulic traits such as Ψ_{50}, Ψ_{90}, Ψ_{tlp}, g_s and g_{min}, the former two for stems and leaves and the latter only for leaves, are being developed to predict vegetation dieback (Martin-StPaul *et al.* 2017, Cochard *et al.* 2021). Nevertheless, in Mexico, we lack data on these hydraulic traits for many dominant species and for most regions of the country. Designing research projects aiming to measure key ecophysiological traits in Mexico, and using such traits in predictive models, is therefore a crucial task to understand the fate of Mexican biodiversity under climate change.

Drought resistance of crop species and varieties. Understanding of the hydraulic pathway within plants, accompanied by meteorological forecasts at the short and long term (*i.e.*, yearly to decadal), should provide crucial information regarding the potential resistance of crop species to drought. Phenotyping the variability in hydraulic traits across the most important crops in Mexico should be a research agenda, to facilitate the search for drought-resistant varieties, including intraspecific variability in Mexican-diverse genera such as *Zea, Capsicum, Phaseolus, Cucurbita, Solanum,* and *Physalis*, among other important crop genera. Given their importance as economic crops, fruit trees should also be subject to quantifications of their hydraulic risk. Plant hydraulics can also inform management practices to reduce the hydraulic footprint of crops, by integrating hydraulic information and close-to-the-ground
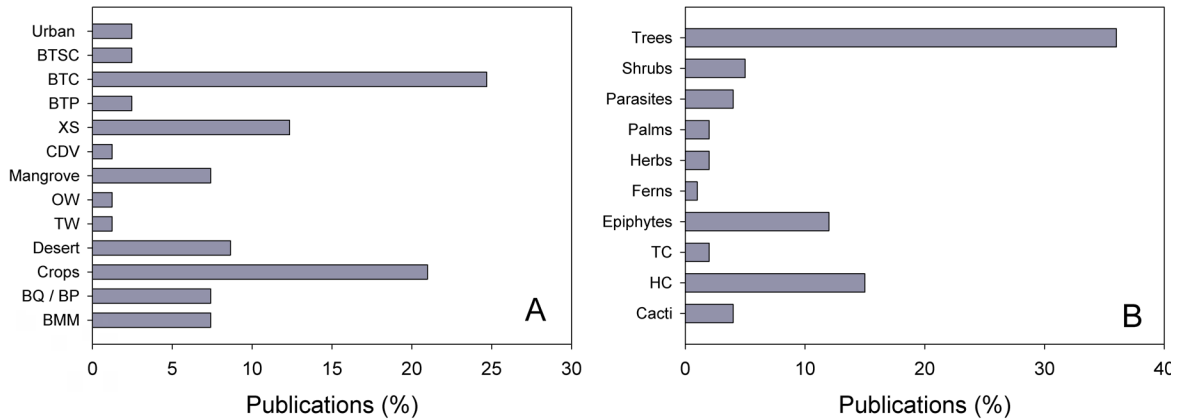
Figure 3. (A) Number of scientific publications per vegetation type ($N = 81$) using Rzedowski's (2006) classification of Mexico's vegetation: BMM = Cloud Forest (*Bosque mesófilo de montaña*), BQ = Oak Forest (*Bosque de Quercus*), BP = Conifer Forest (*Bosque de coníferas*), MX = Xerophytic Scrub (*Matorral xerófilo*), BTP = Tropical Rainforest (*Bosque tropical perennifolio*), BTC: Tropical Dry Forest (*Bosque tropical caducifolio*), BTSC = Tropical Semi-Evergreen Forest (*Bosque tropical subcaducifolio*), TW = Tropical Wetland except mangroves (*Humedales tropicales, excepto manglares*), OW = Other Wetlands (*Humedales de climas no tropicales*), CDV = Coastal Dune Vegetation (*Vegetación de dunas costeras*). (B) Number of scientific publications per plant growth-form or relevant taxa ($N = 83$): TC = Tree crops, HC = Herbaceous crops. Reports were extracted from the *Clarivate® Web of Science* database.

remote sensing, via precision agriculture. Precision agriculture may be a fundamental technique to control spatial and temporal variability within agricultural fields and may offer a way to reduce the irrigation input to agriculture, enhance productivity, and expand the sustainability of crops.

Lidar and hyperspectral imagery of our national forest resources. Currently, CONAFOR, the Mexican authority censusing the state of our forests undertook a stratified sampling to quantify several important metrics of forest extension, physiognomy, and richness (Inventario Nacional Forestal y de Suelos, Mexico, 2022; snmf.cnf.gob.mx/principaleindicadoresforestalesciclo-2015-2020-beta). Although the maps produced can inform the authorities and scientists regarding the distribution and general characteristics of our biomes across the whole territory, they are limited in spatial and temporal extension. In addition, no functional trait indicative of the relative risk of hydraulic dysfunction is presented. Even tree height, a key functional trait, was only rarely measured: the maximum records are of trees 30-45 meters tall, even though much taller trees are common in several Mexican habitats (Martin Ricker, *pers. comm.*, Inventario Nacional Forestal y de Suelos de Mexico 2022). We advocate that future deliveries of the INFS may take advantage of the recent technology to characterize forest vegetation.

Two remote sensing technologies are key to enhancing the resolution of the survey to the scale of the individual tree. (1) Light detection and ranging (LIDAR), a technology using pulsated lasers to create cloud points of the forest canopy, with spatial resolution reaching the centimeter scale (Lefsky *et al.* 2002, Calders *et al.* 2020). This technology is suitable to determine the maximum heights of the tallest individual trees, which coincidentally are the trees most exposed to catastrophic drought (Fajardo *et al.* 2019), and therefore we would be able to determine the areas with a higher risk of drought given the height distribution of the vegetation across our territory. In turn, a canopy height map would allow a better estimation of the carbon budget at a national scale. (2) Hyperspectroscopy, a term that refers to the characterization of the pattern of reflectance/absorbance of light in any particular surface such as plant leaves, by using sensors with a high capacity for discrimination of the light spectrum (usually hundreds of bands, from the UV, 300 nm to the Thermal infrared, ca. 2500 nm), producing a characteristic spectral signature per species (Seeley & Asner 2021). This signature is suitable to be explored at the scale of the plant itself, using hand spectrometers, or using spectrometers within remote platforms, normally airplanes or satellites. In conjunction with LIDAR, hyperspectroscopy may allow quantifying species richness and canopy height for the Mexican territory, and

to estimate biomass, composition and productivity (Meireles *et al.* 2020, Williams *et al.* 2021). Achieving this level of spatial and spectral resolution would be an initial step toward quantifying the potential risk of our biomes to massive tree mortality at the scale of individual localities or municipalities (Jetz *et al.* 2016).

The use of Mexican vegetation as a Nature-based solution to promote the mitigation of cities to climate change. Current strategies for mitigating the negative effects of greenhouse emissions imply the use of vegetation to enhance ecosystem services. For example, vegetation is critical in the achievement of long-term solutions to enhance habitability within urban areas. Urban vegetation faces several environmental conditions not present in non-urban ecosystems, including a disturbed circadian cycle due to artificial light (Bennie *et al.* 2016), pollution, and water scarcity. However, urban trees contribute substantially to human welfare in cities, including non-conventionally measured ecosystem services, such as diminishing the risk of mental affections such as anxiety and depression, as traps to contaminants, and play a critical role in reducing the heat-island effect, which is an increase in the day and night temperatures in cities due to the absorption of heat and sunlight by artificial surfaces such as concrete and asphalt. Given the importance of plants to urban habitability, a further research agenda accompanying the re-greening of Mexican cities is to study the vulnerability of native and alien flora to hydraulic and physiological dysfunction.

Conclusion: Mexico, the country that best represents the world's hydraulic diversity

Mexico offers a privileged scenario to address some of the most urgent issues in current plant hydraulics. At least a substantial amount of the lack of knowledge regarding the causes of vulnerability to drought-induced embolism is due to the limited functional, climatic, and phylogenetic diversity examined in most studies, and it is here where Mexico has a nearly unique opportunity to contribute. Most studies that have attempted to elucidate the structural correlates of vulnerability to drought-induced embolism have examined temperate cold-adapted trees from northern latitudes. These systems are inappropriate starting points precisely because they are adapted not just to drought but to freezing-induced embolism as well. Therefore, it is impossible to know to what degree aspects in these studies reflect adaptation to freezing-induced embolism. Instead, elucidating the structural causes of vulnerability to drought-induced embolism needs to start by examining species that evolved in the context of and are adapted to completely frost-free habitats, both wet and dry. Such habitats abound in Mexico, from the southeastern lowland Tropical Rainforests that almost never experience persistent drought to the vast and diverse Tropical Dry Forests of the Pacific coast and the interior lowland depressions. Selecting this diversity of habitats promises to provide the first truly appropriate and thorough examination of the anatomical features that correlate with vulnerability to drought-induced embolism.

In their search for appropriate samples to represent global diversity, an important question faced by comparative researchers is "which single country best represents the world flora?" Mexico is essentially the only contender, with all other countries falling as distant seconds. Most of the orders of vascular plants grow in Mexico, meaning that it provides very wide phylogenetic coverage. For instance, South Africa and Mexico are the two centers of diversity of cycads, but unlike South Africa, with its very low diversity of conifers, Mexico is one of the centers of global conifer diversity. Practically all the plant growth forms worldwide occur in Mexico, from very tall trees to cushion plants, tiny globular succulents to the world's largest arborescent cacti, plus globally unique life forms such as *Astrophytum caput-medusae*, with its bizarre crown of leaf-like extensions of the stem springing from a small underground tuber. The only angiosperm habits, to our knowledge, absent from Mexico are some of the more unusual *Euphorbia* habits, such as leaf-bearing spiny pachycauls. Virtually all biomes are represented in Mexico, from very high elevation alpine habitats to deserts, tropical dry and rain forests, vast temperate forests, and prairies, to highland cloud forests (Rzedowski 2006). No other country even comes close to this span, even continent-sized ones such as China, the United States, Brazil, or Australia. China and the US have a good representation of temperate originated clades, such as conifers, antique angiosperms, and herbs and shrubs (*e.g.*, *Rhododendron*, *Pedicularis*, *Paeonia*) but lack much diversity of tropical habitats and warm desert habits, including succulent deserts and deciduous tropical forests (Wang *et al.* 2017). The continental US only covers some tropical habitats by virtue of including Florida and Hawaii,

Figure 4. Semantic cloud showing the frequency of occurrence of the most studied genera (only 75 displayed) in 84 scientific publications related to plant water relations produced in Mexico between 1985 and 2021. Larger fonts indicate higher frequency of occurrence across studies. Position indicates the rank, from the most studied genus to the least. Figure produced by term rank frequency following a Jaccard similarity coefficient on http://wordcloud.cs.arizona.edu/cloud.html?id=25852. The use of this algorithm does not allow to use italics.

but these are small and relatively phylogenetically depauperate (Shreve 1917). Brazil is largely lacking in highland habitats, temperate forests, deserts, and is depleted in conifers and cycads (Fiaschi & Pirani 2009). Australia's vegetation is almost entirely evergreen and sclerophyll, with 10% of its flora accounted for by just two genera, *Acacia* and *Eucalyptus*. Most wood density is medium to high. If one knows where to look in Australia, there is some diversity, *e.g.*, in wood density (*Adansonia, Brachychiton, Cochlospermum*, and *Dendrocnide* are relatively low density), and there is an acceptable phylogenetic span (including cycads, some conifers, and reasonable coverage of ordinal-level angiosperm diversity), but in general, the variance in trait diversity is low. Moreover, there is very little representation of habits such as succulents, very little tropical deciduous forest, and no true highlands. No food plants of any significance were domesticated in Australia, and the species that have (pulp *Eucalyptus* for example) are modern domesticates (Barlow 1994). Peru and Ecuador host higher numbers of species than Mexico, and very wide ranges in habitats, but they still are distant seconds to Mexico in terms of global representativity. They lack representation of the vast north temperate broadleaf deciduous forests made up of *Quercus, Acer, Nyssa, Fagus, Tilia, Carya, Betula, Alnus, Carpinus, Ostrya*, and other genera that dominate much of the north temperate zone. These communities are very well represented in Mexico's rich cloud forests. Moreover, South America has no representatives of the conifer lineages so characteristic of the north temperate zone such as *Pinus, Picea, Abies, Pseudotsuga*, and *Taxus*, which are so richly represented in Mexico. Thus, even with their globally unparalleled species richness, the countries of northwestern South America are still markedly less representative of the global flora than Mexico.

Regarding specific trends in hydraulic architecture, for example, current studies of the pit membrane thickness-vessel diameter, have covered relatively narrow ranges of vessel diameter (Lens et al. 2013, Scholz *et al*. 2013). Leaf size correlates with twig vessel diameter, so there is little hope of remedying this situation in the temperate forests of North America and Europe, with their very limited morphological ranges. In contrast, the Tropical Dry Forests in Mexico feature species such as *Aralia mexicana*, and wet forests *Cecropia* and *Gunnera*, both with leaves over one-meter-long and very wide terminal twig vessels and low-density wood. They also include species with very small leaves, such as *Hybanthus* and legumes such as *Caesalpinia* with high-density wood.

This range of terminal twig vessel, leaf size, and wood density far surpasses that of any forest in the north temperate zone. As one of the global epicenters of plant domestication, Mexico is also a center of agrobiodiversity, with dozens of ethnic groups stewarding thousands of years of traditional breeding of corn, beans, squash, avocadoes, vanilla, agaves, prickly pears, Solanaceae crops, and many other plant groups. For coverage representative of the world's floristic and biocultural diversity, and for a morphological range that can provide the statistical power necessary to recover key relationships such as the morphological basis of vulnerability to drought-induced embolism, researchers should converge on Mexico as a model system.

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