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Drought Resistance and Its Relationship with Functional Traits of Tree Species in a Tropical Urban Environment

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Abstract

Despite the progress to understand drought tolerance worldwide, the response of urban trees to the increased frequency and severity of droughts, particularly in tropical regions, remains unclear. Such an evaluation is essential for predicting future urban forest dynamics. The leaf turgor loss point (π_{TLP}), leaf safety margins (SMs) and their relationship with functional traits were measured in ten native tree species during wet and dry seasons in a tropical urban environment. We detected interspecific variation in tree responses related to desiccation tolerance and desiccation avoidance as strategies to resist drought. Desiccation avoidance was linked to lower adjustment of midday water potentials and water-conservative traits such as high wood density, low specific leaf area (SLA), and high leaf dry matter content, while species with more negative π_{TLP} maintained stomatal conductance and growth despite decreasing leaf water potentials. Although the differences between predawn and midday potentials during the dry season suggest that severe drought does not occur, some species showed negative safety margins. This indicates that while some urban trees can tolerate or avoid current dry periods, continued climate change may push certain species beyond their safe operating range, making species selection for urban planning increasingly critical.

Keywords: drought resistance; climate resilience; leaf safety margin; turgor loss point; urban trees

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1. Introduction

Drought resistance has been widely studied through various physiological mechanisms, including the leaf potential at turgor loss point (π_{TLP}), which has proven to be key for characterizing tree responses to water stress at the leaf level [1,2] as the maintenance of cell turgor in leaves is critical for gas exchange and growth [3]. Several studies have examined π_{TLP} in trees across different ecosystems and seasons [4–8]. In general, authors report a consistent positive relationship between π_{TLP} values and water availability, indicating that as the water deficit increases, π_{TLP} becomes more negative, underscoring the adaptive significance of π_{TLP} across environments [1,9,10]. However, high variation has been detected among species within the studied sites, showing a strong relationship between π_{TLP} and drought-induced hydraulic dysfunction [6,11]. Increasing negative leaf π_{TLP} among species served as a proxy for increasing the ability to acquire water to sustain photosynthetic gas exchanges; thus, lower wood density is correlated with higher hydraulic conductivity and lower xylem resistance with drought-induced embolism [8].

As π_{TLP} reflects the leaf potential at which stomatal closure occurs and the operating range of water potentials for controlling leaf water status [12,13] it is more negative in species with greater dehydration tolerance [10]. The midday water potential (Ψmd) is a measure of the minimum water potential experienced by a tree during the day and compared to the predawn water potential (Ψpd), which makes it possible to assess the daily water adjustment capacity of trees [14]. In a meta-analysis conducted by Fu & Meinzer, lower diurnal minimal leaf water potentials were associated with lower π_{TLP} [15]; among seasons, species sensitive to water deficit tend to have minimal changes in their water status, while, in tolerant species, these variations are more marked. Tolerant species also have a greater capacity to regulate water potential throughout the day and to modify it between rainy and dry seasons [16]. The results showed that tree water potentials vary not only when comparing species among gradients of water availability but also within sites [17].

The ability of species to adjust their water status relative to their π_{TLP}, both daily and across seasons, is known as the leaf safety margin (SM), defined as the difference between π_{TLP} and Ψmd, and a larger SM is thought to be associated with the stomatal regulation, which helps to prevent excessive water loss [18]. The strong direct relationship found between midday water potential (Ψmd) and π_{TLP} [15] suggests that the lower the $\pi_{TLP,}$ the higher the dehydration resistance, but leaf safety margins are lower in favor of gas exchange during the growing season. However, Martin-StPaul et al. [19] suggest that drought resistance cannot be predicted solely from π_{TLP} values, as it also depends on the timing stomatal closure. Therefore, general assumptions linking low π_{TLP} and high drought resistance should be interpreted with care. Despite substantial progress in understanding stomatal behavior through diurnal measurements of water potential [7,14] it remains unclear whether daily fluctuations in leaf water potential—from predawn to midday—are consistently related to π_{TLP}, especially in urban environments. Moreover, how these daily dynamics influence the leaf safety margin has not been fully evaluated.

Drought resistance mechanisms have been reported to be influenced by multiple functional traits, ranging from leaf area and mass to leaf osmotic adjustments. For example, some species have thicker cuticles to cope with water stress in arid environments [20]; species with denser wood and lower specific leaf area tend to be more tolerant to water stress-induced mortality [6,21]. Despite these findings, conflicting opinions still exist regarding the relationship between functional traits and drought resistance, as other authors found a decoupling between morphological traits and drought adjustment mechanisms [22]. Therefore, further research integrating physiological mechanisms and functional traits on drought tolerance is needed.

Given the current climate projections, urban environments are expected to experience an increase in the frequency, intensity, and duration of droughts [23], which will exacerbate existing stressors for urban trees. Despite the considerable progress on the understanding of drought resistance, it is still not clear how urban trees, particularly those in tropical regions, adjust their π_{TLP}, and whether they operate within a safe physiological threshold or close to their critical limits due to diurnal changes in water potentials in response to variation in water availability. In this study, we addressed the following research questions: (1) How does drought tolerance as inferred from the π_{TLP} and SM vary seasonally? (2) Which functional traits are associated with drought tolerance? We hypothesized that, at the leaf level, species exhibit distinct mechanisms to cope with drought depending on their water-use strategies. Specifically, acquisitive species, characterized by lower wood density, were expected to display greater adjustments in daily water potentials, more negative π_{TLP} and narrower leaf safety margins, consistent with a drought–tolerance strategy. In contrast, species with higher wood density were expected to show limited adjustments

in daily water potentials due to stronger stomatal control under drought, thereby maintaining wider safety margins indicative of a drought-avoidance mechanism." To test this hypothesis, we evaluated the π_{TLP} and diurnal changes in water potentials (between dawn and midday) during the rainy and dry seasons, as well as several functional traits of 10 morphologically and ecologically different tropical tree species in an urban environment. Answering these questions is essential to advance our understanding of the mechanisms of drought tolerance in tree species; this knowledge will help identify the functional traits that favor such tolerance, as well as guide the selection of suitable tree species for urban areas in the face of climate change. Furthermore, identifying tree functioning thresholds during drought periods and whether trees are operating within a safe water potential threshold, particularity during dry seasons, is crucial for diagnosing the health of urban ecosystems.

2. Materials and Methods

2.1. Study Area and Species Selection

This study was conducted on the campus of Medellín of the Universidad Nacional de Colombia (6°15′44″ N, 75°34′37″ W), located in the center of the urban metropolitan area of the Aburrá Valley, the second largest conurbation of Colombia with almost five million inhabitants. The average annual temperature is 22.9 °C, and the average rainfall is 1776 mm (precipitation data from 2015 to 2024; Figure 1a), according to records from the early warning system for the Aburrá Valley (SIATA). Rainfall is bimodal, with a dry season between December and February, during which less than 100 mm of rain fall per month, and two peaks of rainfall between April and May and October and November. We took our data during the rainy season from October to November 2023, and during the dry season from January to March 2024, which was much drier than the average (Figure 1b)

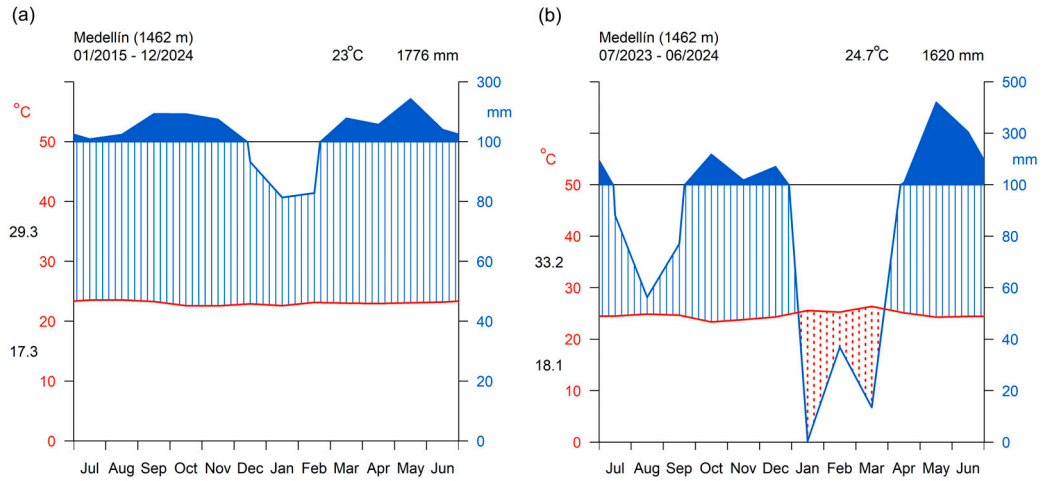

Figure 1. (**a**) Climograph for Medellín city (2015–2024). (**b**) Climograph during the months of the experiment. Mean temperature and precipitation are shown above each climograph.

To select our species, we compiled a list of the most abundant native tree species from the campus arboretum (Figure S1), considering only those with more than five individuals. This list was the cross-referenced with the inventory of the urban tree species across the city to ensure broader representativeness of the urban forest composition. From these comparisons, we obtained a subset of candidate species. Finally, based on the basic wood density gathered from the literature, we selected ten species, including a wide range of WD, to capture a range of ecological and growth strategies. For each species, six healthy, mature individuals were chosen for measurements (Table 1).

Table 1. List and characteristics of the 10 species studied.

Species	ID	Botanical Family	Leaf Phenology	Theoretical Wood Density (g/cm^3) [1]
Erythrina fusca (Lour.)	Ef	Fabaceae	Evergreen	0.29
Annona muricata (L.)	Am	Annonaceae	Evergreen	0.36
Triplaris americana (L.)	Ta	Polygonaceae	Semideciduous	0.49
Guarea guidonia (L.) Sleumer	Gg	Meliaceae	Evergreen	0.60
Coccoloba acuminata (Kunth)	Cc	Polygonaceae	Evergreen	0.58
Swartzia robiniifolia (Vogel)	Sr	Fabaceae	Semideciduous	0.84
Pithecellobium dulce (Roxb.) Benth.	Pd	Fabaceae	Evergreen	0.68
Psidium guajava (L.)	Pg	Myrtaceae	Evergreen	0.65
Hymenaea courbaril (L.)	Hc	Fabaceae	Evergreen	0.79
Bulnesia arborea (Jacq) Engl	Ba	Zygophyllaceae	Evergreen	0.94

[1] Global wood density database [24] and the BIOMASS library of R [25].

2.2. Measurement of Functional Traits of Leaves and Stems

Leaf functional traits were measured in healthy and fully expanded leaves following the standardized protocols of Pérez-Harguindeguy et al. [26]. For each tree, three branches were sampled within the middle third of the crown. From each branch, three mature leaves were selected. All leaf and branch samples for functional traits were collected at the end of the wet and dry seasons, respectively.

Leaf area (LA: cm^2) was determined using a LI-COR 3100C portable meter (LI-COR Inc., Lincoln, NE, USA) in nine leaves from each individual. Leaves were then weighed in an analytical balance to the nearest 0.1 mg and oven-dried for 72 h at 60 °C to determine the dry weight. Leaf thickness (LT; mm) was measured with a digital micrometer at the base, apex, and middle portion, avoiding main and secondary veins. From these data, the specific leaf area (SLA; cm^2/g) was calculated by dividing LA by its dry mass. Leaf tissue density (LD; g/cm^3) was obtained from the inverse of the SLA and the leaf thickness. Finally, leaf dry matter content was calculated from the fresh weight and leaf dry weight (LDMC; dry mass/fresh mass of a saturated leaf; mg/g). Additionally, the leaf relative water content was calculated from 1 cm^2 leaf discs that were weighed fresh, and then rehydrated for 24 h and oven-dried for 72 h at 60 °C (RWC (%) = [(fresh mass − dry mass)/(saturated mass at full turgor − dry mass)] * 100). As an osmotic adjustment mechanism, proline content (µg/mg) was extracted during the wet and dry seasons using the method described by Melgarejo et al. [27].

To characterize the leaf anatomical features, three leaves were taken from every tree, and freehand cross-sections were made in three portions from each. Stomatal density was assessed using impressions with a layer of transparent enamel; these were complemented by paradermal sections on the abaxial side of the leaves for pubescent species. All tissues were decolorized in 2% hypochlorite and then stained with a mixture of astrablue and fuchsin [28]. After staining, the samples were mounted on slides and observed under a microscope at 40× to capture images. Measurements of the parenchyma, epidermis, cuticle, and stomata count were performed using ImageJ software (v2023) [29]. To measure the anatomical features of the xylem, a section was taken from one of the previously used branches, and cuts were made in the transverse and longitudinal planes. To observe the characteristics of the xylem, fuchsin staining was performed, and microscopic photographs were taken at 5×, 40×, and 100×, which allowed for the measurement of the diameter and thickness of pores, fibers, and pits, respectively.

Wood basic density (WD, g/cm^3) was determined in two branches 15–20 cm long and 2 cm in diameter. These segments were cut from the distal portion of the branch and then WD was calculated using the water displacement method to calculate sample volume;

the sample was then oven-dried for 72 h to determine mass. Stem water storage capacity (SWS, %) was measured in five stem sections, each 3 cm long and 1–2 cm in diameter. These sections were hydrated to determine the saturated mass and then oven-dried for 72 h at 60 °C to determine the dry mass: SWS = [(saturated mass − dry mass)/(dry mass)] * 100.

2.3. Leaf Water Potentials

To measure leaf water potentials, five leaves were cut from different branches per individual and immediately stored in Ziplock bags to prevent water loss and transpiration. They were collected between 5 a.m. and 6 a.m. to measure predawn water potential (Ψpd; MPa) and between 12 p.m. and 2 p.m. to obtain midday water potential (Ψmd; MPa). After collection, the samples were taken to the laboratory for immediate measurement using a Scholander pressure chamber (1505D; PMS Instrument Company; Albany, OR, USA).

2.4. Water Potential at Turgor Loss

These measurements were taken with a vapor pressure osmometer (VAPRO 5600; Wescor, Logan, UT, USA) that measures plant tissue osmolality. For each individual, three leaf discs of 6 mm were sampled from fully expanded, mature leaves that had been previously rehydrated in dark, humid conditions to ensure full turgor. The discs were taken from the central portion of the leaf lamina, avoiding major veins, and immediately frozen to preserve tissue integrity until measurement. From this value, the osmotic potential at full turgor was calculated following the protocol and equations described by Maréchaux et al. [2], adapted from the work of Bartlett et al. [30].

$$\pi_{osm} = \frac{2.5}{1000} \times C_0$$

$$\pi_{tlp} = 0.832 \times \pi_{osm} - 0.631$$

where C_0 is the osmolality value measured with the osmometer. To do so, the equipment was programmed in delayed mode, and the value was taken when it reached equilibrium (<5 mmol difference between one reading and the next).

2.5. Leaf Safety Margin and Diurnal Change in Water Potential

The leaf's safety margin, which describes its functional threshold, was calculated from the difference between the midday water potential and the turgor loss point [31].

$$SM = \Psi\text{md} - \pi_{TLP}$$

With the water potential measurements at dawn and midday, a new variable was calculated to indicate the species' water adjustment throughout the day as the absolute difference between these two potentials. This difference was established as a proxy for stomatal behavior.

$$\Delta\Psi_L = |\Psi\text{md} - \Psi\text{pd}|$$

Both variables were calculated from previously measured values of leaf water potential (predawn and midday) and π_{TLP} obtained for each individual tree, as described in the corresponding Methods section.

2.6. Statistical Analysis

To answer the research questions, two-way ANOVAs were conducted, considering species and season as fixed factors and drought adjustment mechanisms as random factors. A post hoc Tukey test was then applied to identify significant differences between species and seasons for each mechanism measured. To assess the variation in drought tolerance

across seasons, robust linear regression models (rlms) were generated to relate each of the mechanisms evaluated (SM and π_{TLP}) to the diurnal change in water potential. Finally, to analyze the mutual relationship and interdependence between physiological variables and functional traits across species, a canonical correlation analysis (CCA) was performed using the R CCA library [32] considering, on the one hand, only the physiological variables collected during the dry season—as this period represents the peak of water stress and thus, provides the most relevant conditions to be evaluated for drought response—and, on the other hand, the morphological and anatomical traits of leaves and stems included in the analysis. Subsequently, to evaluate the redundancy of the analysis and validate the robustness of the results, the Candisc package of the R software (v2023) [33] was used, which allows for verification of how much of the variability in one of the data matrices can be explained by the other. All statistical analyses were performed in R version 4.3.1.

3. Results

3.1. Functional Differences Among Species

Significant differences were found among species in the six most commonly evaluated leaf and stem traits (Figure 2). For example, *Triplaris Americana* (L.) had the highest leaf area (192.6 ± 41 cm^2), in contrast with *Bulnesia arbolea* (Jacq) Engl y *P. dulce*, which had the lowest values (2.4 ± 0.37 cm^2; 5.6 ± 1.44 cm^2, respectively). Leaf dry matter (LDMC) and leaf density (LD) showed a similar pattern among species and opposed to specific leaf area (SLA); for example, *Hymenaea courbaril* (L.) had high values of LDMC and LD and low ones of SLA. On the other hand, wood density (WD) and stem water storage capacity (SWS) exhibited a negative relationship (Figure S4). Species with a higher investment in leaf tissue density also tended to invest more in wood density. An example of this is *B. arborea*, which had the highest wood and leaf density (0.87 ± 0.02 g/cm^3; 0.4 ± 0.05 g/cm^3, respectively), whilst *Erythrina fusca* (Lour.), for example, had the lowest wood and tissue density (0.38 ± 0.03 g/cm^3; 0.24 ± 0.04 g/cm^3).

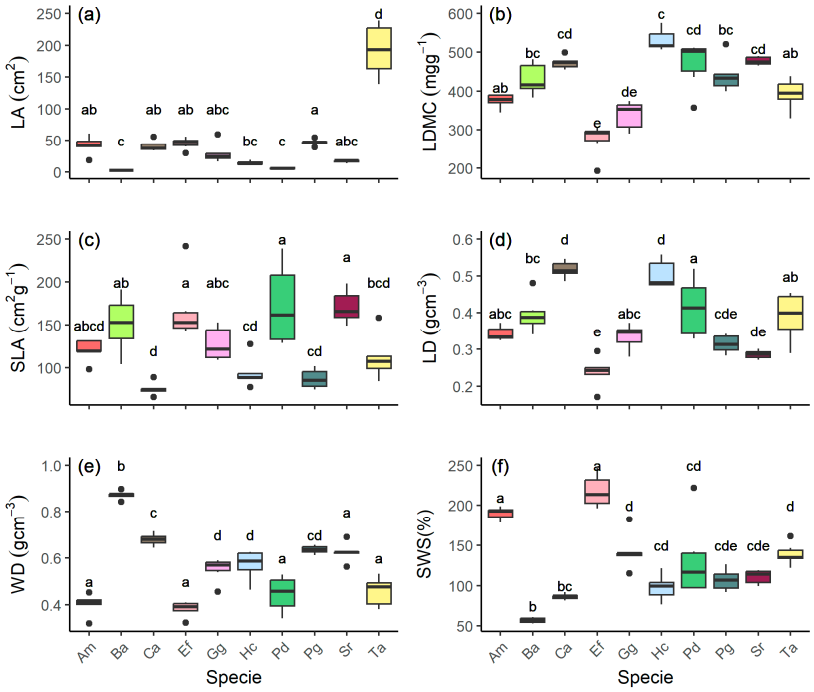

Figure 2. Foliar and stem functional traits for the 10 tree species studied. (**a**) LA: leaf area; (**b**) LDMC: leaf dry matter content; (**c**) SLA: specific leaf area; (**d**) LD: leaf tissue density; (**e**) WD: wood density; (**f**) SWS: stem water storage capacity. Different letters indicate significant differences between species ($p < 0.05$) according to post hoc multiple comparisons.

Additional traits related to drought response were also measured, including relative water content (RWC) and leaf proline concentration (Table S1, Figure S2), and other anatomical functional traits such as stomatal density and mesophyll structure. Although not shown here, these variables are presented in the Supplementary Materials (Figures S3 and S4) and provide further support for the physiological differences observed among species.

3.2. Seasonal Adjustment in Water Relations

π_{TLP} did not differ between seasons for most of the species, except for three of them: *B.arborea*, *H.courbaril*, and *Swartzia robiniifolia* (Vogel) (p-values: <0.0001, 0.009, 0.0003, respectively; Figure 3a). In contrast, and as expected, all species, except *E. fusca* showed an adjustment in daily ΨLeaf between seasons and were significantly lower in the dry season (Figure 3b,c). During the wet season, the predawn water potential ranged from −0.08 MPa in *P. guajava* to −1.3 MPa in *Guarea Guidonia* (L.) Sleumer. In the dry season, the predawn values dropped, reaching values as low as −2 MPa in *T. americana*. At midday, the least negative wet season value was observed in *C. acuminata* (−0.26 MPa), while in the dry season, *B. arborea* exhibited the most negative value (−4.13 MPa). Regarding the leaf safety margin (SM), only the three species with significant π_{TLP} adjustment (*B. arborea*, *H. courbaril*, and *S. robiniifolia*) maintained similar SM values across seasons. For the remaining species, SM decreased significantly in the dry season, approaching zero in several cases (Figure 3d).

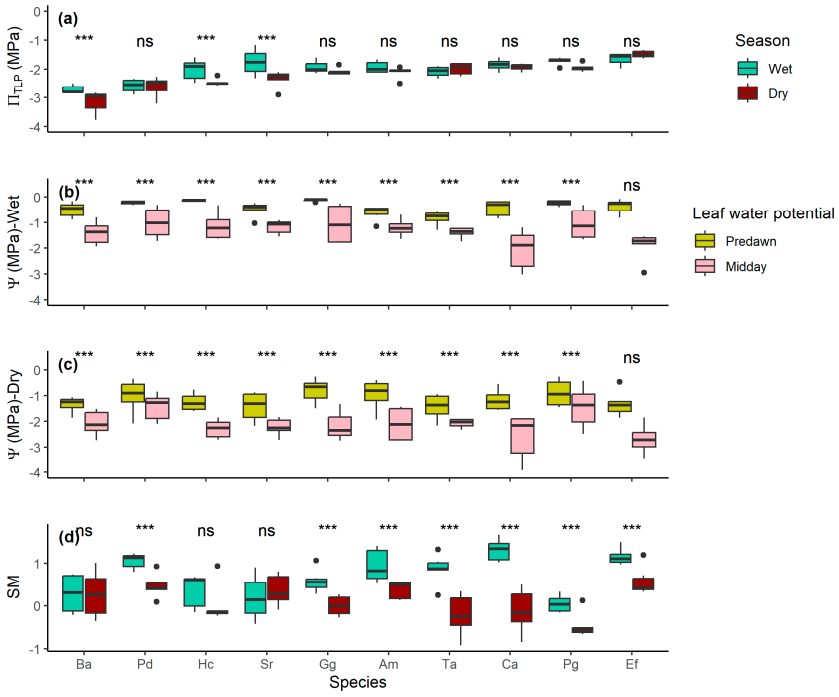

Figure 3. Boxplot showing differences in physiological drought adjustment mechanisms between seasons. (**a**) Water potential at turgor loss point. (**b**) Water potential adjustment in wet season. (**c**) Water potential adjustment in dry season. (**d**) Leaf safety margin. *** Statistical significance: $p < 0.05$, ns = not significant.

3.3. Seasonal Variation in Drought Tolerance

Overall, species that achieved more negative π_{TLP} values had the greater diurnal variation in water potential (Figure 4a,b). In the dry season, a significant relationship was observed between diurnal changes in water potential and π_{TLP} ($\beta = -0.4796$, $p = 8.4 \times 10^{-8}$). This indicates that species capable of adjusting their water potential at midday achieved more negative π_{TLP} values.

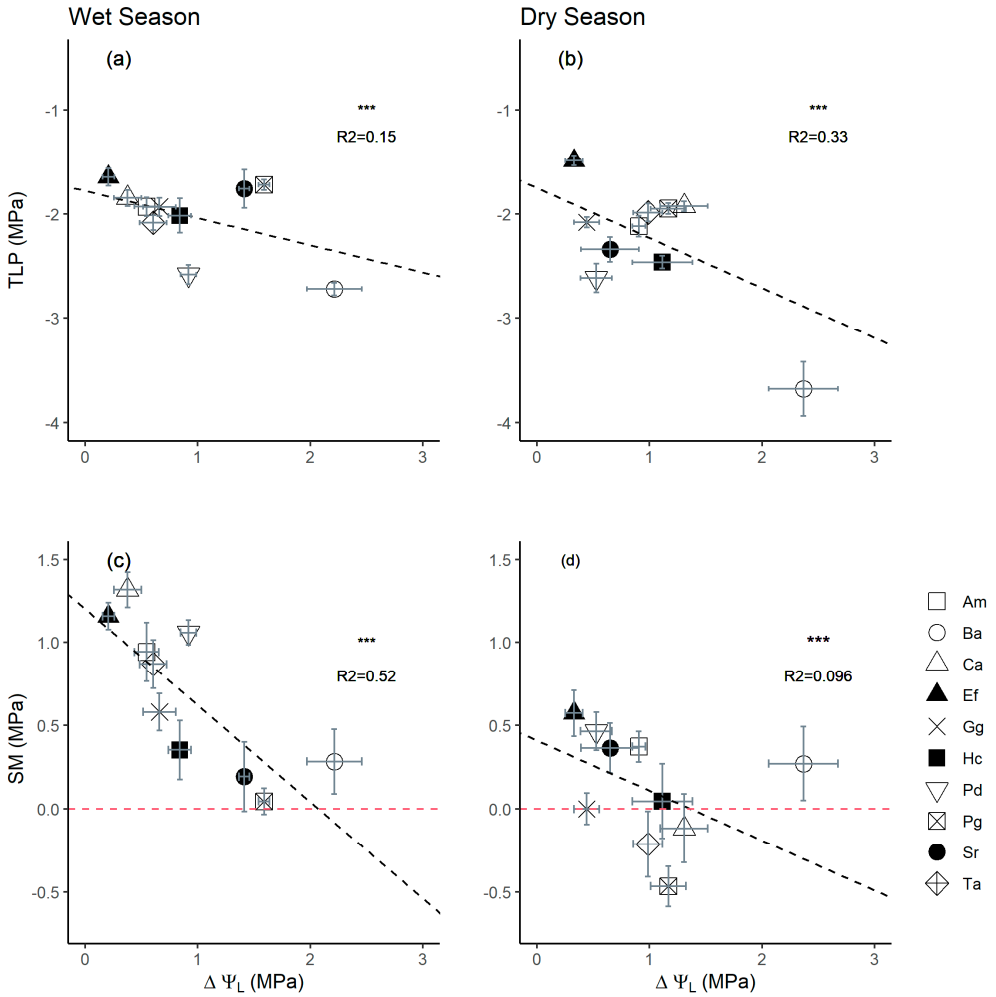

Figure 4. Relationship between the diurnal change in water potential (ΔΨL) and two drought adjustment mechanisms: π_{TLP} (**a**,**b**) and SM (**c**,**d**). The results are shown for the wet season (**a**,**c**) and the dry season (**b**,**d**). Asterisks indicates statistical significance at $p < 0.05$ for the regression model.

The maximum magnitude of the change in water potential between the wet and dry seasons was 2.86 MPa and 3.36 MPa, respectively, achieved in both seasons by *B. arborea*. This species also maintained a positive SM, suggesting a remarkable capacity for physiological adjustment.

For the SM, the relationship was $\beta = -0.3037$, $p = 6 \times 10^{-4}$, suggesting that the turgor safety margin decreased as the diurnal variation in potential increased and as π_{TLP} decreased (Figure 4c,d). For the wet season, the relationships between the mechanisms were similar; there was also a negative relationship between ΔΨL and π_{TLP} ($\beta = -0.2626$, $p = 7 \times 10^{-4}$), and between ΔΨL and SM ($\beta = -0.58$, $p = 1.98 \times 10^{-13}$). These results show that, although all species seem to adjust their turgor safety margin in the dry season, those with greater plasticity in water potential experience a lower or even negative SM in that season. This pattern is explained by the observation that Ψmd decreases significantly in the dry season, while π_{TLP} remained relatively constant across seasons for most species. During drought, these species operate below their turgor threshold, which could compromise their physiological functionality.

3.4. Functional Trait–Drought Tolerance Relationship

The canonical correlation analysis (CCA) relating functional traits to drought adjustment mechanisms between seasons (Figure 5) revealed a strong association, with the first

pair of canonical variates showing a correlation of 0.856. Additionally, 59% of the variance in the physiological variable matrix was explained by the trait matrix.

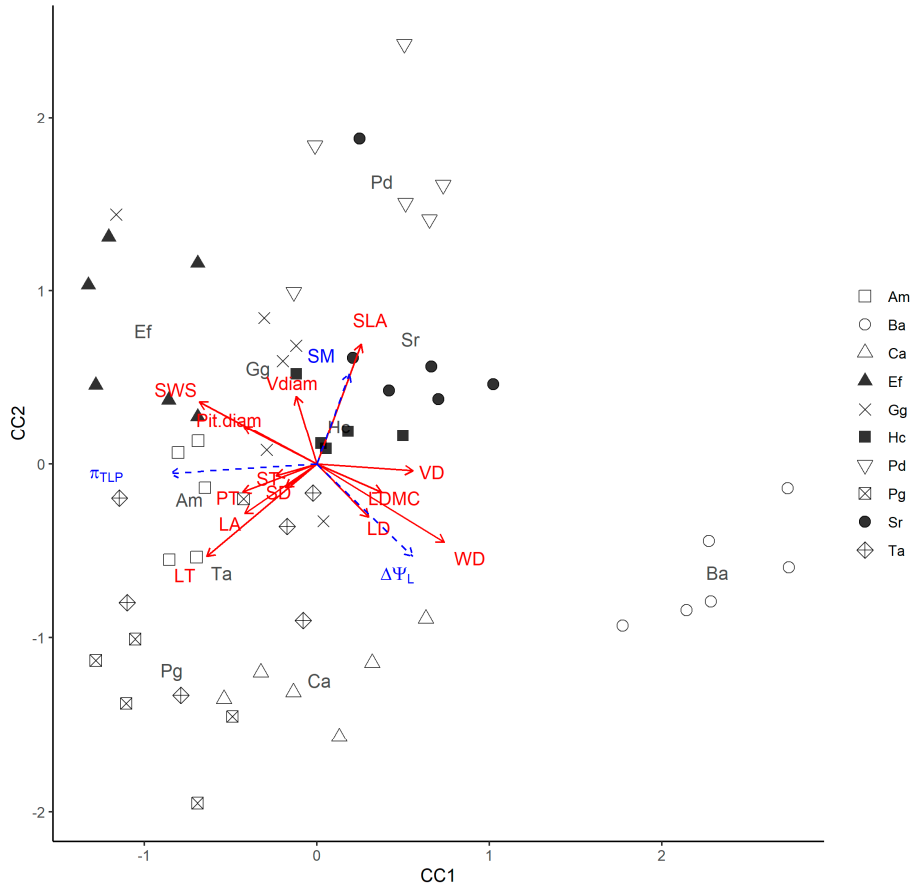

Figure 5. Canonical correlation analysis for leaf and stem functional traits across all species, together with physiological mechanisms. Traits in red: SLA: specific leaf area; SD: stomatal density; LDMC: leaf dry matter content; LD: leaf tissue density; PT: palisade parenchyma; ST: spongy parenchyma; LT: leaf blade thickness; LA: leaf area of the photosynthetic unit; Pit.diam: pit diameter; VD: xylem vessel density; Vdiam: xylem pore diameter; SWS: stem water storage capacity; WD: wood density. Mechanisms in blue: π_{TLP}: water potential at turgor loss point; SM: turgor safety margin; ΔΨL: diurnal change in leaf water potential.

On the first canonical axis (CC1), the most influential traits were wood density (WD, 0.74), leaf thickness (LT, −0.63), and stem water storage capacity (SWS, −0.68). Among the physiological mechanisms, the turgor loss point (π_{TLP}, −0.85) showed the greatest negative contribution, indicating that species with higher wood density and lower leaf thickness were also correlated with the most negative π_{TLP} values. In the second canonical axis (CC2), the functional traits that presented the greatest correlation were specific leaf area (SLA, 0.62), LT (−0.53) and wood density (WD, −0.45), and, among the physiological mechanisms, the turgor safety margin (SM, 0.52) was the variable with the greatest weight in this axis, which suggests a negative relationship between the thickness and density of the leaf tissue and the capacity to maintain an optimal turgor value in the dry season.

4. Discussion

The evaluation of seasonal variation in the turgor loss points and leaf safety margins, and the functional traits associated in ten native tree species located in a tropical urban area support our hypothesis about the occurrence of different strategies to resist drought evaluated at the leaf level, drought tolerance and drought avoidance. The main results of

this study show the following: (1) Most species exhibited significant changes in their water adjustment mechanisms between seasons, but the species that most successfully adjusted their π_{TLP} were those with the narrowest safety margin during both dry and wet season. (2) The drought tolerance strategy was primarily related to conservative traits.

Drought is rarely an isolated stressor in urban ecosystems; trees in cities are also exposed to elevated temperatures due to the urban heat island effect, increased atmospheric pollution, soil compaction, restricted rooting volume, and altered phenological cues due to artificial light and microclimatic variation [34–37]. These factors can interact synergistically with water deficit, amplifying physiological stress and reducing tree resilience. Although our study focuses on seasonal drought responses through hydraulic traits, these findings must be interpreted within this broader urban context. In addition to the complex set of urban stressors, phenology may also modulate tree responses to drought through its influence on seasonal water demand and leaf-level functioning. Although all species in this study are tropical evergreens—and presumed to maintain the foliage over the year—they may still exhibit intra-annual leaf turnover or delayed flushing, which can affect leaf age, gas exchange rates, and, consequently, hydraulic behavior [38]. Recent studies show that drought can also shift the timing and duration of phenological events, with consequences for water use and carbon balance [39,40]. While a diverse pool of species may buffer some of these phenological shifts under climate change [41], species-specific physiological traits remain critical. For example, Kunert et al. demonstrates that π_{TLP} is more variable and ecologically meaningful in evergreen species, as it directly influences their spatial distribution along moisture gradients [42]. Evergreen species, unable to shed their leaves to avoid drought stress, must instead tolerate low water potentials physiologically. This highlights the importance of π_{TLP} as a key trait shaping hydraulic strategy and drought resilience in urban trees. These findings support our species-specific approach but highlight the need to consider phenology as a factor shaping physiological resilience.

4.1. Seasonal Variation in π_{TLP} and SM

Drought tolerance in tree species has been widely assessed through turgor loss point (π_{TLP}), which has been linked to mortality and distribution of woody species along water gradients in different biomes [6,12,42]. In dry ecosystems, π_{TLP} values tend to be more negative and to decrease during periods of drought [43,44]. However, our results indicate that only some species were able to adjust their π_{TLP} during the dry season (e.g., *B. arborea*, *S. robiniifolia*, *H. courbaril*), suggesting that they can continue with their photosynthetic activity even in dry periods [1,45].

In our species, those that exhibited greater diurnal fluctuations in water potential (indicative of anisohydric behavior [14]) also showed lower π_{TLP} values (Figure 3). This is consistent with the work of Johnson et al. who found that anisohydric species, despite operating closer to hydraulic function, often display greater osmotic adjustment capacity, like the accumulation of osmolytes, which lowers osmotic potential (πo) [31]. Also, in anisohydric species, the conversion of starch into osmolytes is key [46]. Although we did not find significant differences in proline accumulation between seasons, a significant negative correlation with π_{TLP} was identified, indicating that species with the lowest values of π_{TLP} accumulate more osmolytes in their tissues, with contribute in drought conditions.

Despite adjustments in π_{TLP}, the leaf safety margin (SM) remained narrow during dry season, suggesting increased vulnerability. Species that reduce their π_{TLP} did not necessarily expand their SMs but maintained them within functional thresholds (above but closer to zero). Species with wider safety margins in the dry season have been reported to exhibit stronger stomatal control, with higher Ψmd [31,47]. Likewise, species with a small hydraulic safety margin have been found to exhibit greater stomatal conductance

and photosynthesis, which allows them to use water more efficiently under favorable conditions, but also exposes them to greater midday water stress due to their increased water consumption [31,48]. In contrast, species with a larger safety margin exhibit lower photosynthesis and transpiration, but, in turn, they reduce the risk of hydraulic failure under severe drought conditions [49]. This aligns with findings by Binks et al., who showed that during a long-term experimental drought (over 12 years), drought-sensitive species exhibited significant osmotic adjustment, while drought-tolerant species showed little or no change in their turgor loss point (π_{TLP}) [50]. These results suggest that tolerant species may already possess constitutive traits that confer drought resistance, making further short-term adjustments unnecessary. In contrast, sensitive species rely more on plastic physiological responses when exposed to prolonged water stress. A drop in turgor pressure can act as a physiological signal, triggering protective responses such as stomatal closure and reduced leaf conductance [51].

4.2. Relationship Between Functional Traits and Drought Tolerance

Wide stem structural and foliar variability was observed among the species studied. Those with greater investment in foliar tissue also showed a high investment in wood construction (represented by high wood density). In accordance to the "fast-slow" continuum [50,51], Oliveira et al. proposed that there is also an equilibrium with the SMs, in which fast-growing plants would have a high return in carbon gain at the cost of riskier behavior [52]. Although growth was not measured in this study, it is observed that species with lower π_{TLP} presented traits associated with slow growth in this continuum and vice versa; for example, high SLA has been associated with less negative π_{TLP} [6,53], although, in this study, SLA was highly correlated with SM during the dry season (Figure 4); when considering safety in water relation, species with lower SLA can exhibit an advantage. On the other hand, Meinzer et al. found that species with higher SMs had higher capacitance in the sapwood [54], which agrees with our results, given that species with greater water storage capacity (SWS) in tissues presented higher safety margins, particularly during the wet season. However, during the dry season, SWS appeared to be independent of safety margins. A similar pattern was observed for relative water content (RWC) but was positively related to SMs in the wet season. This suggests that the buffering capacity for midday water potential does not depends on the amount of water stored in tissues, but, instead, density in tissues confers a certain tolerance regarding a lower π_{TLP} and stable safety margins, because our tolerant species also showed small but positive SMs.

As mentioned above, π_{TLP} is an early indicator of water stress before the occurrence of a significant decrease in stem conductance [11]. Correlations between canonical axes and hydraulic mechanisms reinforce these associations. In CC1, π_{TLP} (contribution of -0.85) and variation in $\Delta\Psi$ (0.56) were the main variables associated with WD, suggesting that species with higher wood density had more negative values of π_{TLP} and greater adjustment in their water potential. Although Maréchaux et al. [22] did not find a strong relationship between π_{TLP} and several functional traits, this study did find a clear trend: species with more conservative traits, such as higher LDMC and WD, were able to reach more negative π_{TLP} values. This is consistent with the findings of Greenwood et al. [21], who also suggested that these species could exhibit lower mortality as drought conditions intensify. Species with lower WD and less capacity for stomatal regulation tend to exhibit higher mortality under severe drought conditions [55]. Therefore, it could be argued that higher wood density and tighter stomatal control could confer greater drought tolerance to species. This is also consistent with the relationship between tolerance and pit diameter, as species with smaller diameters have a greater tolerance based on the π_{TLP} [56]. However, in this study, species with these characteristics showed greater variations in their water

potential, suggesting that they may be adopting short-term adjustment strategies to mitigate water stress.

In CC2, the positive correlation between SLA and SM suggests that species with thinner leaves and higher specific leaf area may be more dependent on soil moisture; also, they would have more control over stomatal closure when soil or atmospheric moisture decreases. In the dry season, the SMs oscillated around zero in all species, but were slightly higher in *B. arborea*, *P. dulce*, *S. robiniifolia*, and *H. courbaril*, species located on the positive side of the axis. Although the leaf economy traits defined by Wright et al. [57] were not analyzed in detail, it is evident that SLA was not coupled with drought tolerance as measured with π_{TLP}, in line with the work of Maréchaux et al. [2]. In contrast, stem structural traits appear to be more determining; Zhu et al. proposed that π_{TLP} can position a species within Reich's fast-slow continuum and found that species with lower π_{TLP} tend to have denser tissues and lower SLA [6]. These findings are consistent with our hypotheses, except for *B. arborea*, which is a unique case within the group of species studied, as it exhibited the greatest diurnal variation in water potential, but it is the only one that remained stable in its SM in both seasons, presenting very similar values. Although this species may exhibit less stomatal control than the others, it has unique characteristics that confer it higher resistance to water dysfunction, such as higher wood density and low SLA.

5. Conclusions

Although the dry season in the study site is usually short and mild, our results suggests that many urban tree species in Medellín operate near their functional safety thresholds, particularly during the dry season. Although several species demonstrated the capacity to adjust their turgor loss point (π_{TLP}), their safety margins (SMs) remained narrow, increasing the risk of hydraulic failure under prolonged drought. Species with more conservative traits—such as higher wood density, low SLA, and higher LDMC—were better able to maintain stable π_{TLP} values and exhibited greater drought resilience. Conversely, species with more acquisitive strategies appeared more vulnerable, especially under intensifying climate extremes. This indicates that while some urban trees can tolerate current dry periods, continued climate change may push certain species beyond their safe operating range, making species selection for urban planning increasingly critical.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f16091493/s1, Figure S1: (a) Climograph for the city of Medellín. (b) Total precipitation during the months of the experiment. (c) Map showing the location of the trees on the El Volador campus; Table S1: Analysis of variance for physiological and biochemical mechanisms (Proline) during the dry and rainy seasons; Figure S2: Relationship between proline content and π_{TLP} (top rows) and relationship between leaf RWC and SM (bottom rows). The results are shown for the wet season (left) and the dry season (right); Figure S3: Correlations among wood traits. All traits included. Ancrad: ray width; Altrad: ray height; Frecrad: ray frequency; Altpunt: pit aperture height; Ancpunt: pit aperture width; Pit.D: pit diameter; Ancfib: fiber width; Anclum: lumen width; Grparfib: fiber wall thickness; VD: vessel density; V.diam: vessel diameter; SWS: stem water storage capacity; WD: wood density; Figure S4: Correlations among foliar traits. All traits included. LA: leaf area; SLA: specific leaf area; LDMC: leaf dry matter content; LT.ap: leaf apex thickness; LT: mid-leaf thickness; LT.Ba: leaf base thickness; LD: leaf tissue density; C.ad: adaxial cuticle; Epi: epidermis; PT: palisade parenchyma; ST: spongy parenchyma; Epi.ab: abaxial epidermis; C.ab: abaxial cuticle; SD: stomatal density.

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