Plant, Cell & Environment

WILEY

Plant, Cell & Environment

ORIGINAL ARTICLE

Seasonal Shifts in Tree Water Use and Non-Structural Carbohydrate Storage in a Tropical Dry Forest

Maria Medeiros[1] | André Luiz Alves de Lima[2] | José Raliuson Inácio Silva[2] | Angela Lucena Nascimento de Jesus[2] | Cynthia L. Wright[3] | Eduardo Soares de Souza[2] | Mauro Guida Santos[1]

[1]Department of Botany, Bioscience Center, Federal University of Pernambuco, Recife, Pernambuco, Brazil | [2]Serra Talhada Academic Unit, Federal Rural University of Pernambuco, Serra Talhada, Pernambuco, Brazil | [3]Southern Research Station, USDA Forest Service, Knoxville, Tennessee, USA

Correspondence: Maria Medeiros (maria.juciclea@ufpe.br)

Received: 26 August 2024 | **Revised:** 17 February 2025 | **Accepted:** 18 February 2025

Funding: This work was supported by FACEPE (Facepe-Pronem-APQ-0336-2.03/14); FACEPE Fellow-IBPG-0330-2.07/21; CAPES/TAMU project (006/2014) and INCT: National Observatory of Water and Carbon Dynamics in the Caatinga Biome – ONDACBC.

Keywords: Caatinga | deciduous | evergreen | NSC | semiarid | stomatal conductance | water potential | wood density

ABSTRACT

Predictions of increased drought frequency and intensity have the potential to threaten to forest globally. The key to trees response to drought is an understanding of tree water use and carbohydrate storage. Our objective was to evaluate sap velocity and dynamics of non-structural carbohydrates (NSC) in native trees of a dry tropical forest, during rainy and drought periods. We evaluated six key species of the Caatinga: three deciduous species with low wood density (WD), two deciduous species with high WD and one evergreen species during the rainy and dry periods. We measured sap velocity, xylem water potential, stomatal conductance, phenology and NSC. We found that the evergreen specie had higher sap velocity and frequent NSC production. While the low deciduous WD species showed low sap velocity, store water and NSC mainly in the stem and roots, and have leaf sprouting and flowering at the end of the dry period. The deciduous high WD also showed low sap velocity, however, with low stored NSC. These results suggest that under longer dry seasons and an irregular rainy seasons, species with low WD that use part of the stored NSC to resprout still during dry season may be the most affected.

1 | Introduction

Increased drought frequency and intensity have emerged as a novel threat to forests globally (Allen et al. 2017; Intergovernmental Panel on Climate Change [IPCC] 2023). In seasonally dry tropical forests (SDTF), drought conditions arise due to irregular rainfall and high evaporative demand. However, prolonged drought conditions are expected under climate change scenarios which alter rainfall regimes or reduced total annual rainfall. These changes, could fundamentally affect vegetation responses and lead to SDTF which are sensitive and vulnerable (Allen et al. 2017). In this context, a broad understanding of plant response and function under drought conditions is needed.

Drought can cause tree hydraulic failure through embolism and cavitation (i.e., interruption of sap velocity in the xylem), and if strong enough, can lead to the death of organs or the entire plant (Scoffoni et al. 2017). In addition to hydraulic failure, drought can also lead to tree mortality due to carbon starvation, in which the tree suffers carbon depletion due to stomatal closure (McDowell et al. 2022). This can occur because, under water limitations, plants tend to close their stomata to avoid excessive water loss. In some case, species which are more sensitive to water deficit may close their stomata earlier, thus reducing the assimilation of CO_2, and consequently affecting carbohydrate reserves (McDowell et al. 2008). Therefore, the effects of long-term drought can shift the dynamics of non-structural carbohydrates (NSC) storage and allocation, functions

which are fundamental to maintaining metabolic, defence or osmoregulation functions (Sevanto et al. 2014; McDowell et al. 2022). Thus, an effective way to assess the impacts of drought stress is by tracking the dynamics of sap velocity together with NSC storage (Granier 1985; Zhang et al. 2015).

The dynamics of sap velocity are related to tree water use, and hence essential to understanding the variation in responses between coexisting tree species in SDTF (Bosch et al. 2014; Wright et al. 2024). Other measures such as water potential, and stomatal conductance form a set of coordinated functional traits that, analyzed with the plant's morphological characteristics, help answer questions about water transport control (Vico et al. 2014).

Similarly, NSC, reflects on plants' ecophysiological responses, since drought progression can influence storage (Zhang et al. 2015). NSC consists of soluble sugar (SS) (sucrose, fructose and glucose), which is responsible for growth, osmoprotection, transport and signalling, and starch that is stored long-term (Hartmann and Trumbore 2016). Drought can influence variation of NSC indifferent organs of the trees; by changing it's allocation and partitioning in thick roots, stems and leaves (Hartmann and Trumbore 2016; Santos et al. 2021). Some studies have shown that seasonal carbohydrate dynamics may differ between coexisting evergreen and deciduous species. For example, according to the findings of Palacio et al. (2018), carbohydrate storage in branches was crucial in evergreen Mediterranean oaks, while it played a minor role in deciduous oaks. However, this relationship in SDTF species is still unclear, and analyzing sap velocity and NSC together can help explain species' different strategies to tolerate drought. In SDTF, tree functional groups can be classified based on morphological, physiological and phenological traits (Lima and Rodal 2010). In the Caatinga SDTF of northeast Brazil specifically, functional groups have been defined based on phenology and wood density (WD) (Lima and Rodal 2010; de Oliveira et al. 2015). These function groups tend to align with hydraulic strategies and drought tolerances (Wright et al. 2021; Brito et al. 2022). Generally, high WD species have greater mechanical stability, which promotes high resistance to cavitation (Markesteijn, Poorter, Paz, et al. 2011). Further, high WD species which are evergreen are characterized by thick-walled xylem, which further promotes cavitation resistance (Markesteijn, Poorter, Paz, et al. 2011; Janssen et al. 2020) and spend the entire year with leaves, allowing for continued rates of CO_2 assimilation and resource acquisition (Souza et al. 2015; Tonet et al. 2024). Moreover, metabolic and xylem hydraulics responses may be associated with WD and leaf phenology, particularly considering that species with high WD have higher leaf life span (Lima et al. 2018; Poorter et al. 2019). In contrast, deciduous low WD species are characterized by wide vessels with thin walls and have a comparatively greater maximum xylem capacitance (Poorter et al. 2010; Pineda-García et al. 2012). Therefore, traits related to WD and stomatal control may indicate the presence of a trade-off, in which some species may invest more in hydraulic safety (more resistant xylem vessels, with greater vessel wall thickness and greater lignification), but have lower carbon assimilation, due to greater stomatal control, consequently, have lower NSC synthesis while other species maximize carbon assimilation and NSC synthesis, however, have lower hydraulic safety due to lower investment in their xylem vessels (Janssen et al. 2020; Tomasella et al. 2020; Oliveira et al. 2021).

Previous work in SDTF found that the relationship between WD and seasonal changes in tree water status can be largely predicted by functional group (Borchert 1994; Lima and Rodal 2010; de Oliveira et al. 2015; Souza et al. 2015). More recently, other studies found that drought tolerance, hydraulic architecture, water use and conductance also generally align with functional type (Wright et al. 2021, 2024; Brito et al. 2022; Medeiros et al. 2024). However, few studies have explored hydraulic and carbon trade-offs in SDTF, and the linkages between other physiological measures, such as sap flow velocity and NSC are needed (Santos et al. 2021; Wright et al. 2024).

Given this context, we ask: (1) How does sap velocity and NSC change between different periods of the year among coexisting species in an SDTF? (2) Is there a water-carbon trade-off revealed by a relationship between hydraulic and carbohydrate storage functional traits? We studied six species that play essential ecological roles in the Caatinga to answer the questions: *Commiphora leptophloeos* (Mart.) J. B. Gillett, *Spondias tuberosa* Arruda, *Amburana cearensis* (Allemao) A.C.Sm. (deciduous with low WD); *Cenostigma pyramidale* (Tul.) Gagnon & G. P. Lewis and *Aspidosperma pyrifolium* Mart. & Zucc (deciduous with high WD); and *Sarcomphalus joazeiro* (Mart.) Hauenshild (evergreen). Although we focus on species-level difference, we used the functional groups framework to hypothesize the following: deciduous species low-wood-density show seasonal differences in sap flow velocity rather than deciduous species high-wood-density, and species evergreen high-wood-density have the highest sap velocity. In addition, deciduous species accumulate more NSC in stems and roots during the dry period, while evergreen species have the highest NSC concentration across leaf, stem and root organs, regardless of period of the year.

The Caatinga is a Brazilian biome that is often overshadowed by the global recognition of the Amazon Rainforest. While the general public associates Brazil or South America with the Amazon, there are other biomes, such as the Caatinga, that offer a completely different but equally important ecological environment. This biome plays a crucial role in maintaining biodiversity and ecosystem services, highlighting the need to understand the strategies of the species that live in it (Santos et al. 2014). This includes trees that can function as important 'carbon sinks', mitigating the effects of climate change (Mendes et al. 2020).

2 | Materials and Methods

2.1 | Study Site

The study site was located at the Fazenda Buenos Aires (07°56′ 50″ S, 38°23′29″ W), outside of the Serra Talhada, PE, Brazil (Figure 1). The Köppen classification BSh which is characterized by the hot semi-arid climate. The average annual rainfall is estimated to be 632 mm. The rainy season, which generally occurs from January to April, accounts for 65% of this average. Monthly average air temperatures range between 23.6°C and 27.7°C, and maximum temperatures exceed 32°C (Pereira et al. 2015).

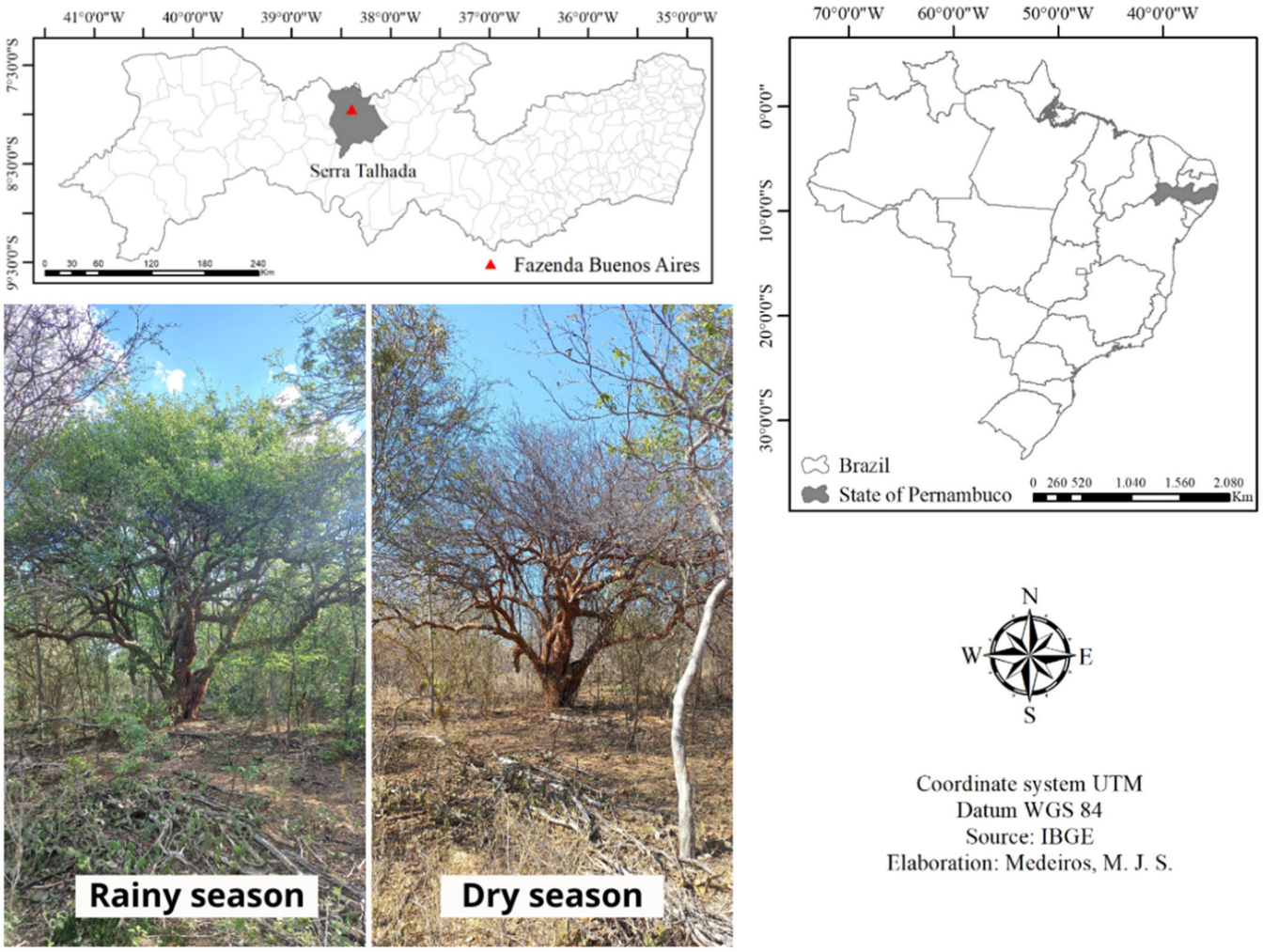

FIGURE 1 | Map of the study area and photos of *Commiphora leptophloeos* taken at Fazenda Buenos Aires Farm, Serra Talhada-PE, Brazil, during the rainy season (left; photo taken in January) and the dry seasons (right; photo taken in September). Photo credit: M. Medeiros.

The soil texture class of the study area was homogeneous and classified as sandy loam (de Alcântara et al. 2021)

In this study, we performed measurements of sap velocity (J_s) in three periods of 2022: rainy period (March–May), transition period (June–July) and the period of the first rains (November–December); and measurements of Xylem water potential (Ψ_{xylem}), Stomatal conductance (g_s) and Concentration of NSC: SS, and starch in March and November 2022.

2.2 | Meteorological Variables

Meteorological data was obtained from a flux tower located on site, and which is part of the AmeriFlux network (BR-CST). It is 11 m high, and 3 m above the forest canopy. Specifically, we obtained rainfall, relative humidity, air temperature and volumetric soil water content. Data from all sensors were measured every 1 min, and mean/sum data were recorded by a data logger (model CR1000, Campbell Scientific Inc., Logan, UT, USA) every 30 min (Silva et al. 2017). Rainfall was measured by a tipping-bucket style rain gauge (model TE 525 WS-L, Texas Electronics, Dallas, TX, USA). Relative humidity and air temperature were measured by (EE181-L, Campbell Scientific) and the volumetric soil water content was measured by TDR type sensor (CS616, Campbell Scientific) at soil depths of 5, 10, 20, 30 and 40 cm. Temperature and relative humidity were used to calculate the vapour pressure deficit (Santos et al. 2024). Volumetric soil water content was used to calculate the change in soil water storage (ΔSWS, in mm) in the top 40 cm.

$$\Delta SWS = \Sigma[(\theta_{t+1} - \theta\_{t})*\Delta z_n], \quad (1)$$

where θ is the volumetric water content of the soil at time t, and the subsequent timestamp, $t + 1$, ΔZ is the soil depth interval, and n is the soil depth interval, aggregated across the five layers. The ΔSWS was then averaged by day and summed by month.

2.3 | Species Selection

We studied six widely distributed tree species from the Caatinga dry forest that varied in their WD from 0.32 to 0.74 g cm^3: *C. leptophloeos* (Mart.) J. B. Gillett, *S. tuberosa* Arruda, *A. cearensis* (Allemao) A.C.Sm., *C. pyramidale* (Tul.) Gagnon & G. P. Lewis

TABLE 1 | Characteristics for the selected species, including stem-specific wood density (WD), diameter close to the ground (D) and tree height (HT).

Species	Family	WD (g cm^{-3})	D (cm)	HT (cm)
Commiphora leptophloeos (Mart.) J. B. Gillett	Burseraceae	0.32 ± 0.06	30.3 ± 9.3	5.46 ± 0.95
Spondias tuberosa Arruda[a]	Anacardiaceae	0.49 ± 0.02[b]	78.9 ± 37.8	5.63 ± 0.95
Amburana cearensis (Allemao) A.C.Sm.	Fabaceae	0.51 ± 0.09	13.84 ± 3.4	4.00 ± 0.90
Sarcomphalus joazeiro (Mart.) Hauenshild[a]	Rhamnaceae	0.62 ± 0.01[b]	21.0 ± 6.4	5.45 ± 0.44
Cenostigma pyramidale (Tul.) Gagnon & G. P. Lewis	Fabaceae	0.69 ± 0.09	12.0 ± 2.0	5.84 ± 1.35
Aspidosperma pyrifolium Mart. & Zucc.	Apocynaceae	0.74 ± 0.04	9.3 ± 2.1	2.90 ± 0.15

[a]Species which we observed to be multi-stemmed.
[b]Values obtained from de Lima et al. (2012).

and *A. pyrifolium* Mart. & Zucc. Which also included an evergreen species: *S. joazeiro* (Mart.) Hauenshild (formerly *Ziziphus joazeiro* Mart.) (Lima and Rodal 2010) (Table 1). These species have great ecological and economic importance, such as timber and medicinal uses for the Caatinga, in addition to providing ecosystem services (Rito et al. 2017; Arnan et al. 2018). For each species, we select three to five individuals to measure the functional traits detailed below.

2.4 | Tree Characteristics

Because tree size and WD may be related to water use and hydraulic strategy (Meinzer et al. 2009; Wright et al. 2021), we measured tree diameter, height and stem-specific WD. Tree diameter was obtained with a measuring tape wrapped around the tree base just above the ground. Tree height was measured with a hypsometer (SNDWAY, SW-1000A). WD was either measured in the field or obtained from de Lima et al. 2012 (i.e., *S. tuberosa* and *S. joazeiro*; Table 1). To measure WD in the field, we collected samples of wood from branches that were approximately 2 mm thick and 2 cm long. Samples were collected from terminal branches approximately 2 m above the ground. After removing the bark, the wood sample was immersed in distilled water for 24 h, until saturated, to determine sample volume (v) according to Archimedes' principle. Afterward, the samples were dried in an oven at a temperature of 70°C for 72 h to obtain the dry mass (m). WD was calculated as $WD = m/v$ (Pérez-Harguindeguy et al. 2013).

2.5 | Sap Velocity

To measure tree water use dynamics, that is, sap velocity, Granier-style thermal dissipation sensors were constructed and installed similar to the modifications in Wright et al. (2024). For each individual, one sensor was installed in the main stem of the tree (at approximately 50 cm height). As in the Granier (1985) original design, the sensor consists of two probes: the upper probe is heated, while the lower probe is not. Thus, the temperature difference between the two probes equates to the heat transfer rate, which is a proxy of the water transfer rate. That is, when the upper probe temperature is close to the lower probe temperature (ΔT is small), sap velocity at the point of measurement is fast, and vice versa. We highlight that the installation of sap flow sensors provided measurements of unidirectional sap velocity and from a single point where the sensor was installed on each tree. Sap velocity was calculated using Grainer's original equations and the average sap velocity, J_s (cm h^{-1}), is calculated as:

$$Js = 119 * 10^{-6} * K^{1.23}; \quad (2)$$

where

$$K = (\Delta T_{Max} - \Delta T)/\Delta T; \quad (3)$$

Here, ΔT_{Max} is the maximum temperature difference between the two probes at zero sap velocity, and ΔT is the difference between the probes when the tree is transpiring. We used the AquaFlux (Speckman et al. 2019) package in R to determine ΔT_{Max}, defined to occur during night-time hours when VPD approaches zero (below 0.3 kPa for at least 1 h). As noted, some species are multi-stemmed individuals, such as *S. joazeiro* and *S. tuberosa*. For these, we considered the main stem to be the central stem with the largest diameter. Because we are more interested in the rates of water use, and due to a limited number of sensors, we made no attempt to upscale transpiration to the individual tree level.

To compare changes in J_s between species, we summarize both the diurnal pattern as well as daily values averaged from the 11:00 to 15:00 time window to capture maximum velocities during three periods: the peak rainy season (19 March to 31 May 2022), the transition to the dry season (1 June to 19 July 2022) and the first rains of the next rainy season (9 November to 31 December 2022). We selected these three periods because sap velocity was perceptible, data gaps and sensor malfunctions were limited, and to relate to other traits as described in the next sections.

2.6 | Phenology

We carried out phenological observations once in the rainy period (25 March 2022) and dry period (3 November 2022), of five phenophases of the species, defined as: (1) Canopy—total number of mature leaves; (2) Leaf fall—yellowing leaves or leafless branches; (3) Budding—leaf shoots; (4) Flowering—presence of flowers; (5) Fruiting—presence of fruit. Based on these observations, Fournier's (1974) Percentage of Intensity

was applied, which estimates the intensity of each phenophase. For field observations, a scale from 0% to 100% was established, based on the intensity of each phenophase. From these observations, Fournier's Percentage of Intensity (Fournier 1974) was applied to evaluate the phenology, in which the intensity of each phenophase is estimated through a semi-quantitative interval scale of five categories (0–4), with intervals of 25% between each of them: 0—absence of phenophase; 1—presence of the phenophase with a magnitude between 1% and 25%; 2—presence of phenophase with magnitude reaching between 26% and 50%; 3—presence of phenophase with magnitude reaching between 51% and 75%; 4—presence of phenophase with magnitude reaching between 76% and 100%.

2.7 | Xylem Water Potential and Stomatal Conductance

We measured xylem water potential (Ψ_{xylem}) in terminal branches once during the rainy period (25 March 2022) and once dry period (3 November 2022), before dawn (4:00–5:00) and at noon (12:00–13:00) using a Scholander-type pressure chamber. We also measured the stomatal conductance (g_s) of fully exposed and sunlight-receiving leaves of terminal branches in the lower stratum of the canopy. To do so, we used a porometer (Decagon Devices Inc., 2365 NE Hopkins Court Pullman WA 99163) on the same days but during different time intervals: 9:00–10:00 AM and 14:00–15:00 PM.

2.8 | Concentration of NSC in Leaves, Stems and Roots

To measure NSC, we collected samples from each biological replicate from three organs: several fully expanded leaves (~800 mg), terminal branches (~5000 mg) and fine roots (~600 mg) (< 2 mm) from the soil sub-surface (< 10 cm depth), which were sorted and stored (Quentin et al. 2015). These samples were collected once in each period: rainy period (9 April 2022), and dry period (19 October 2022). First, we placed the samples in a microwave oven at 700 W for 30 s to stop all enzymatic activity, as per Quentin et al. (2015). After this procedure, samples were stored in paper bags at room temperature for a maximum of 1 month for analysis. To quantify total SS and starch for these samples, we used the methodology of Santana-Vieira et al. (2016), as described below.

We extracted SS from the dry material using 80% ethanolic suspension according to the methodology of Farrar (1995). The samples were ground in a mortar and suspended in 1200 μL of 80% ethanol. After vortexed, the samples were incubated for 90 min in a water bath at 70°C. Subsequently, the material was centrifuged at 15 000*g*-force, and the supernatant was collected. This process was repeated using 600 μL of 80% ethanol for another 30 min. We determined the concentration of SS using the phenol-sulphuric acid method by adding 0.5 mL of 5% phenol and 2.5 mL of sulphuric acid to the extract aliquot. We measured the SS concentration using a dual-beam spectrophotometer at 487 nm (Genesis 10S UV-Vis, Thermo Scientific) (Dubois et al. 1956).

For starch quantification, the pellets were resuspended in 800 μL of 0.2 M KOH solution and vortexed. The supernatant was placed in a water bath at 95°C for 2 h. Then, the samples were adjusted to pH 5.5 with 200 μL of acetic acid and centrifuged at 15 000*g*-force, and the supernatant was then collected. Finally, the samples were hydrolyzed with 10 units of amyloglucosidase (A1602, Sigma-Aldrich) for 1 h in a thermal bath at 55°C to digest the gelatinized starch into glucose. Starch concentrations (measured as glucose equivalents) were measured at 487 nm using a dual-beam spectrophotometer (Dubois et al. 1956). Before conducting the analysis, we conducted a preliminary test to establish the dry weight (mg) for use in the extraction process. This involved measuring the SS content of 10, 20 and 40 mg of dry matter from two randomly selected individuals in each organ of the species. Our objective was to verify if the concentration of SS increased in proportion to the mass of dry matter. This procedure enabled us to assess the saturation level of the extracts. Based on this evaluation, we determined that a dry weight of 20 mg would be appropriate for all organs.

2.9 | Statistical Analysis

To test how sap velocity differs by species and period, we tested several mixed effects models for repeated measures. First, we modeled sap velocity with species as a fixed effects factor, and species replicate as a random effects factor within each period. For this, we created three different models: one for the rainy period, one for the transition period and one for the period with the first rains of the upcoming rainy season. Second, we modeled sap velocity with period as the fixed effects factors and species as a random effects factor. For all mixed effects models, we confirmed homogeneity in the variance of the residuals and used Tukey's post hoc to denote differences between species or period. For NSC, SS and starch, we compared between periods and species using an analysis of variance (ANOVA) since these variables were collected after longer time intervals, and temporal auto correlation can be assumed as null. When there was a significant difference between period or species, the NSC, SS and starch data were compared between periods and species, using Tukey test, at 5% probability. We also performed ANOVA and Tukey test ($p < 0.05$) to verify if there were differences in the means of xylem water potential and stomatal conductance between species. In addition, we also performed a Principal component analysis (PCA) for possible grouping of variables between species. All analyses and graphing were performed using the R v.4.2.0 programming language (R Core Team 2022).

3 | Results

3.1 | Environmental Variables

The total annual rainfall recorded for 2022 was 772 mm (Figure 2), which is higher than the historical average. The rainiest months were March (165 mm), which we considered to be the peak of the rainy season (March–May), and December (122 mm), which we considered to be the start of the next rainy

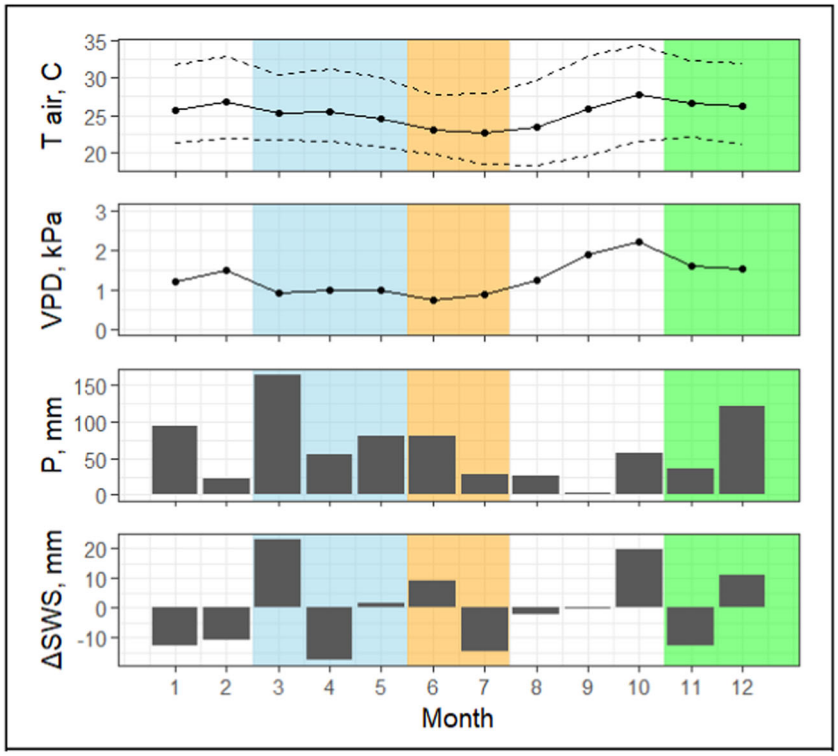

FIGURE 2 | Monthly average air temperature (T air, C) with average daily minimum and maximum (dashed lines), monthly average vapour pressure deficit (VPD, kPa), monthly total change in soil water storage (ΔSWS, mm) in the top 40 cm, and monthly total precipitation (P, mm) from January to December 2022 at Fazenda Buenos Aires near Serra Talhada, PE, Brazil. Periods are denoted as: rainy in blue, transition in orange and first rains in green. [Color figure can be viewed at wileyonlinelibrary.com]

season (November–December). We recorded 56 mm of rainfall in April. However, due to the rain gauge's logger failure from 23 March to 9 April 2022 (39 days), this amount is likely underestimated. The driest month was September, during which no significant rainfall was recorded. A notable dry season rain event occurred on 26 October (53 mm). In November, it rained 37 mm. However, sizeable rain occurred from 28 November to 2 December 2022 (total of 88 mm over 5 days), marking the first events of the next rainy season. The ΔSWS was highest in March, corresponding to the month with the highest rainfall (Figure 2). The VPD was low from January to June, increasing from July to October. Despite the recorded dry season rain, the highest VPD peak occurred in October (2.23 kPa). From November onwards, there was a reduction in VPD (Figure 2).

3.2 | Seasonality of Sap Velocity Between Species

Sap velocity (J_s) differed by species for each period and between the peak rainy season versus first rains (Figure 3; Table S1). Most species showed greater sap velocity during the first rains season (months November–December), especially when compared to the transition period (Figure 3). The evergreen species, *S. joazeiro*, had the highest J_s compared to the species of the other functional groups, regardless of season, reaching an average of 135 $g\,s^{-1}\,m^{-2}$ during the first rains (Figure 3). All species showed an increase in sap velocity after 7:00 AM and a decrease after 15:00 PM regardless of periods (Figures 4 and S1). The timing of peak J_s varied by species and period, ranging from 12:30 to 13:30. Specifically, during the rainy period, J_s peaks in *A. cearensis*, *S. joazeiro* and *C. pyramidale* occurred at 12:30 PM; in *A. pyrifolium* it occurred at 13:00 PM; and in *C. leptophloeos* and *S. tuberosa*, occurred later, at 13:30 PM (Figure 4; Table S2). While in the transition period, only *C. leptophloeos* and *S. tuberosa* showed changes in their J_s peak times. Both species had earlier peaks: *C. leptophloeos* peaked half an hour earlier and *S. tuberosa* peaked an hour earlier. During the first rains, the species exhibited later peaks, from half an hour to an hour later, except *S. joazeiro*, which showed an earlier sap velocity peak (−0.5 h) (Figure 4; Table S2).

3.3 | Phenology

The phenology revealed different intensities in the proportion of phenophases among species (Figure S2). Specifically, observations made on 25 March 2022 show that the intensity of crown coverage was 100% in *A. cearensis*. In contrast, the lowest crown coverage was registered in *C. leptophloeos*, corresponding to 27% of the proportion of its phenophases, However, *C. leptophloeos* presented a higher intensity of sprouting (20%) and fruiting (30%) when compared to the other species (Figure S2a). Flowering was observed only in *C. pyramidale*, corresponding to 38% of its phenophases. As for *A. pyrifolium*, high leaf fall was recorded (33% of the proportion), and the flowering and fruiting phenophases were not observed

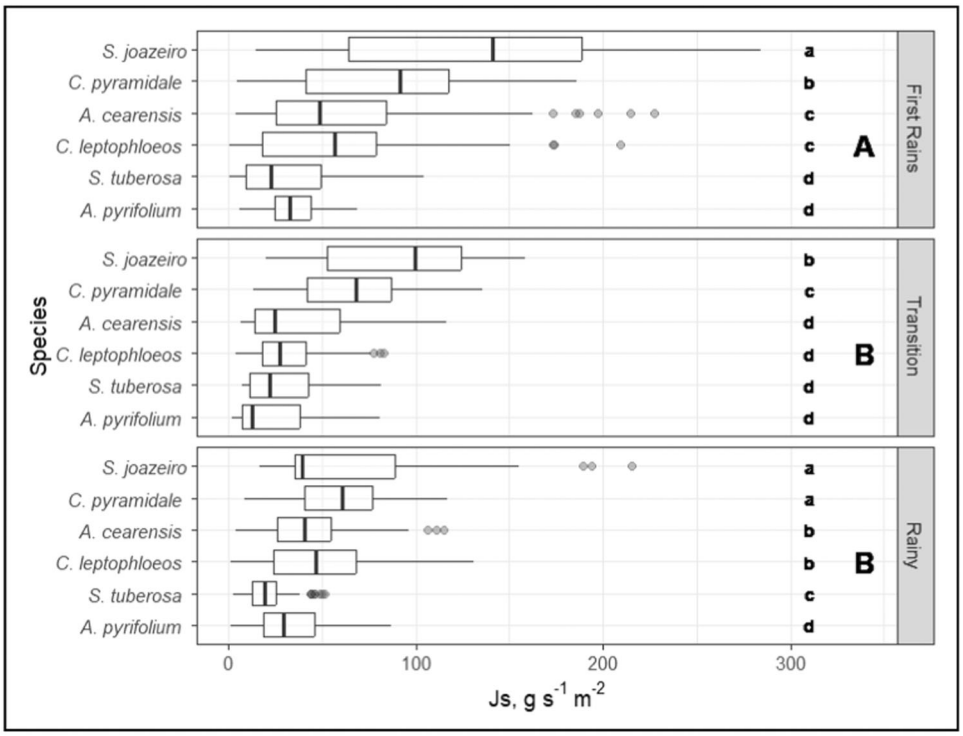

FIGURE 3 | Daily peak average of sap velocity (J_s) from the time window 11:00 to 15:00 in individuals of each species during the periods: rainy (19 March to 31 May 2022), transition to dry season (1 June to 19 July 2022), and the first rains of the next rainy (9 November to 31 December 2022). Significant differences between species within each period are denoted by small. Significant differences between the three periods are denoted by larger letters. Statistical results are summarized in Table S1.

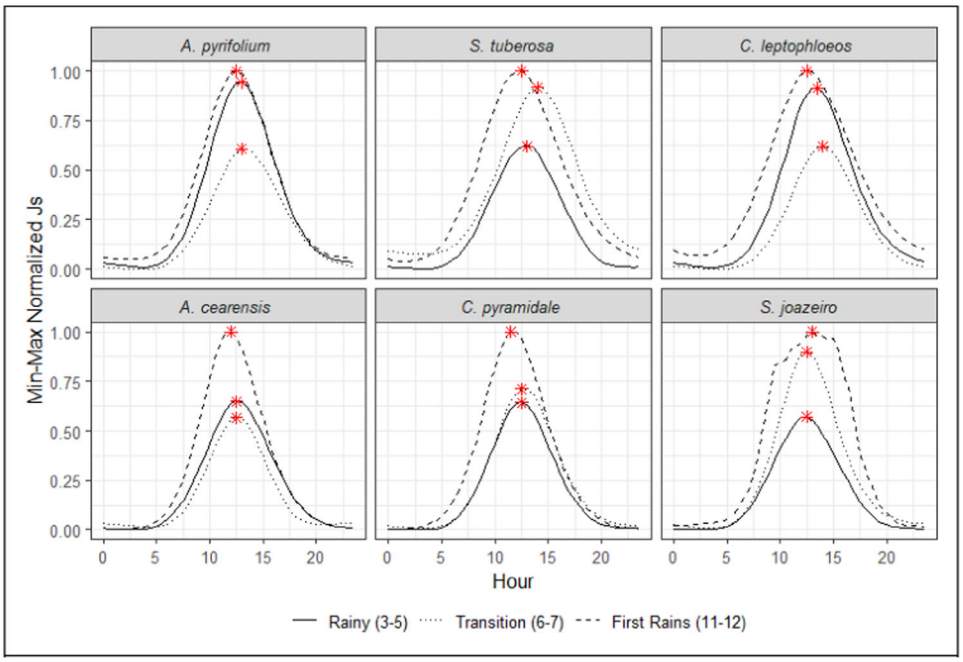

FIGURE 4 | Average diurnal pattern of min-max normalized sap velocity by species during the periods: rainy (19 March to 31 May 2022), transition to dry season (1 June to 19 July 2022), and the first rains of the next rainy (9 November to 31 December 2022). The red star denotes the timing of peak sap velocity, as noted in Table S2. [Color figure can be viewed at wileyonlinelibrary.com]

on the evaluation date (Figure S2a). For observations made on 3 November 2022, the month corresponding to the dry period, *C. leptophloeos* (31%), *S. tuberosa* (33%) and *S. joazeiro* (3%) flowered (Figure S2b). The deciduous species with low WD started to sprout, while the deciduous species with high WD had a higher proportion of sprouting, mainly *C. pyramidale* (45%). The *A. cearensis*, still showed a high proportion of leaf fall (51%) (Figure S2b).

3.4 | Changes in Xylem Water Potential and Stomatal Conductance

During the peak rainy period (March), the xylem water potential (Ψ_{xylem}) was higher in the deciduous with low WD, especially in the predawn, and in *S. tuberosa* (predawn: −0.21 MPa; midday: −0.87 MPa) (Figure 5a). *S. joazeiro* had lower Ψ_{xylem} in the midday (−3.25 MPa), differing significantly from the Ψ_{xylem} of the other species. In the dry period, Ψ_{xylem} did not differ among species during predawn (Figure 5a). However, midday Ψ_{xylem} was significantly higher in *C. leptophloeos* and *A. cearensis*, and significantly lower in *A. pyrifolium* (Figure 5a).

As for stomatal conductance (g_s), there was no statistically significant difference between species or between measurement intervals during the peak rainy period measurement (25 March 2022) (Figure 5b). For the dry period measurement (3 November 2022) g_s was not recorded for *C. leptophloeos*, *A. cearensis* and *S. tuberosa* due to leaf loss (Figure 5b). However, for this measurement, there was a significant difference between the deciduous species with high WD. The g_s was higher in *S. joazeiro*, followed by *A. pyrifolium*, and lower in *C. pyramidale*. Still, there was no difference between the predawn and mid-day intervals of the day for each species (Figure 5b).

3.5 | NSC Concentration in Different Organs

The SS showed significant differences between the rainy and dry periods in some organs for the species, except for *S. joazeiro* (Figure 6a). The deciduous species with low WD showed higher SS concentrations in the leaves in the rainy season: *C. leptophloeos* (309.0 ± 109.7 mg g^{-1} DM), *A. cearensis* (580.5 ± 313.0 mg g^{-1} DM), *S. tuberosa* (383.0 ± 127.7 mg g^{-1} DM) (Figure 6a). The highest concentration of SS was recorded in the leaves of *A. cearensis* (580.4 ± 313.0 mg g^{-1} DM) and the lowest in *A. pyrifolium* (88.8 ± 15.0 mg g^{-1} DM) (Figure 6a). Root SS concentration was higher in the dry period for *C. leptophloeos* (329.1 ± 22.7 mg g^{-1} DM) and *S. tuberosa* (310.0 ± 68.6 mg g^{-1} DM) (Figure 6a).

Starch differed in the leaf and/or root between the seasons for each deciduous species (Figure 6b), while for the evergreen species, the starch only difference in the stem between the periods (Figure 6b). *C. leptophloeos* presented a higher concentration of starch in the leaves than the other species (88.1 ± 18.4 mg g^{-1} DM) (Figure 6b). The lowest concentration of starch in leaves was recorded in *S. tuberosa* in the rainy period (28.7 ± 9.0 mg g^{-1} DM). However, this species had a higher concentration of starch in the root during the dry period (53.7 ± 19.4 mg g^{-1} DM) (Figure 7). In the dry period, only *S.*

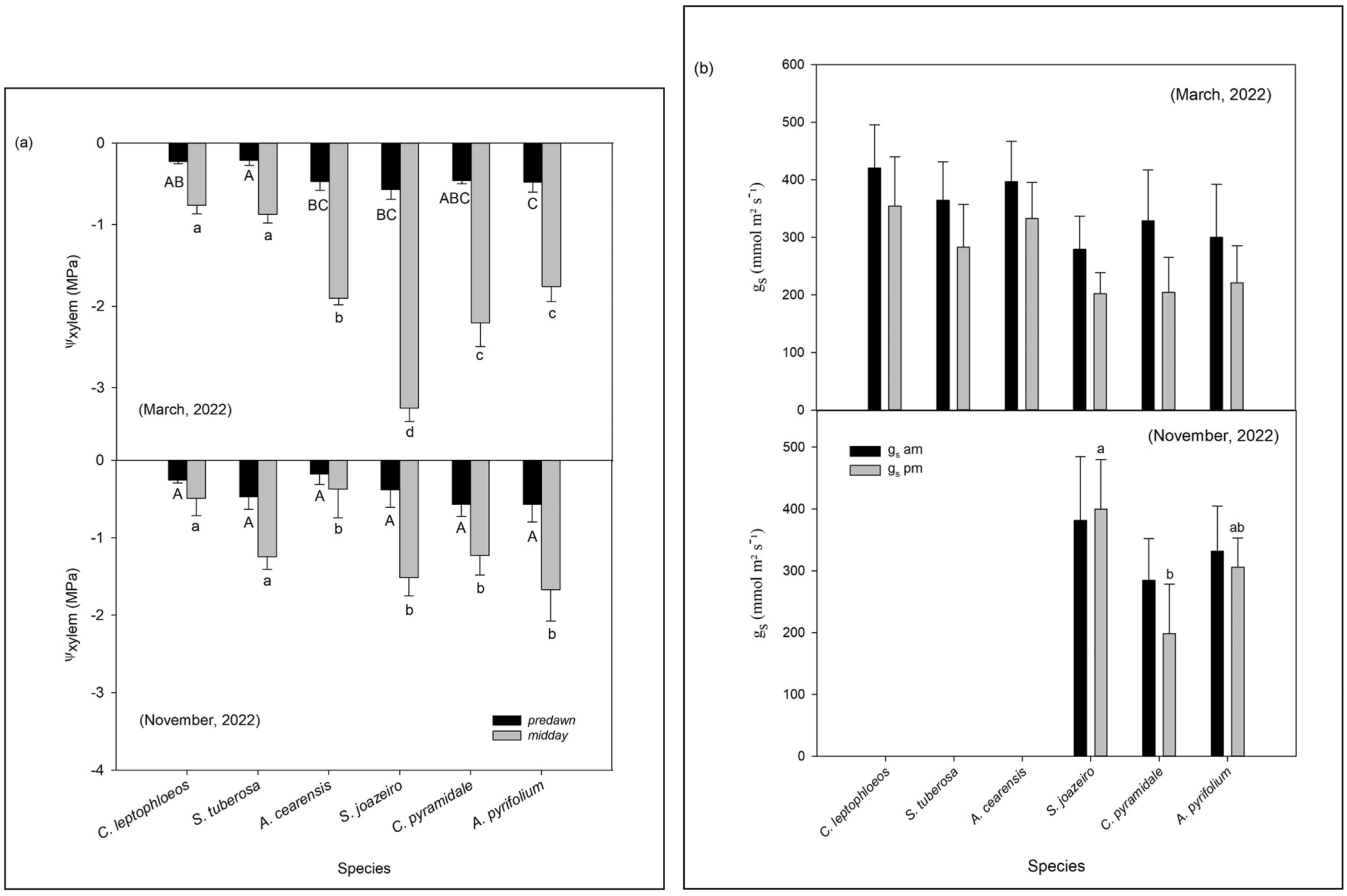

FIGURE 5 | (a) Xylem water potential (Ψ_{xylem}) of species in predawn and midday, and (b) Stomatal conductance (g_s) of the species in the AM (9:00 to 10:00) and PM (14:00 to 15:00) on 25 March 2022 (rainy period) and 3 November 2022 (dry period), 2022, municipality of Serra Talhada-Pernambuco, Brazil. Uppercase letters compare predawn and lowercase letters compare midday values between species, at the 5% level of probability by Tukey's test.

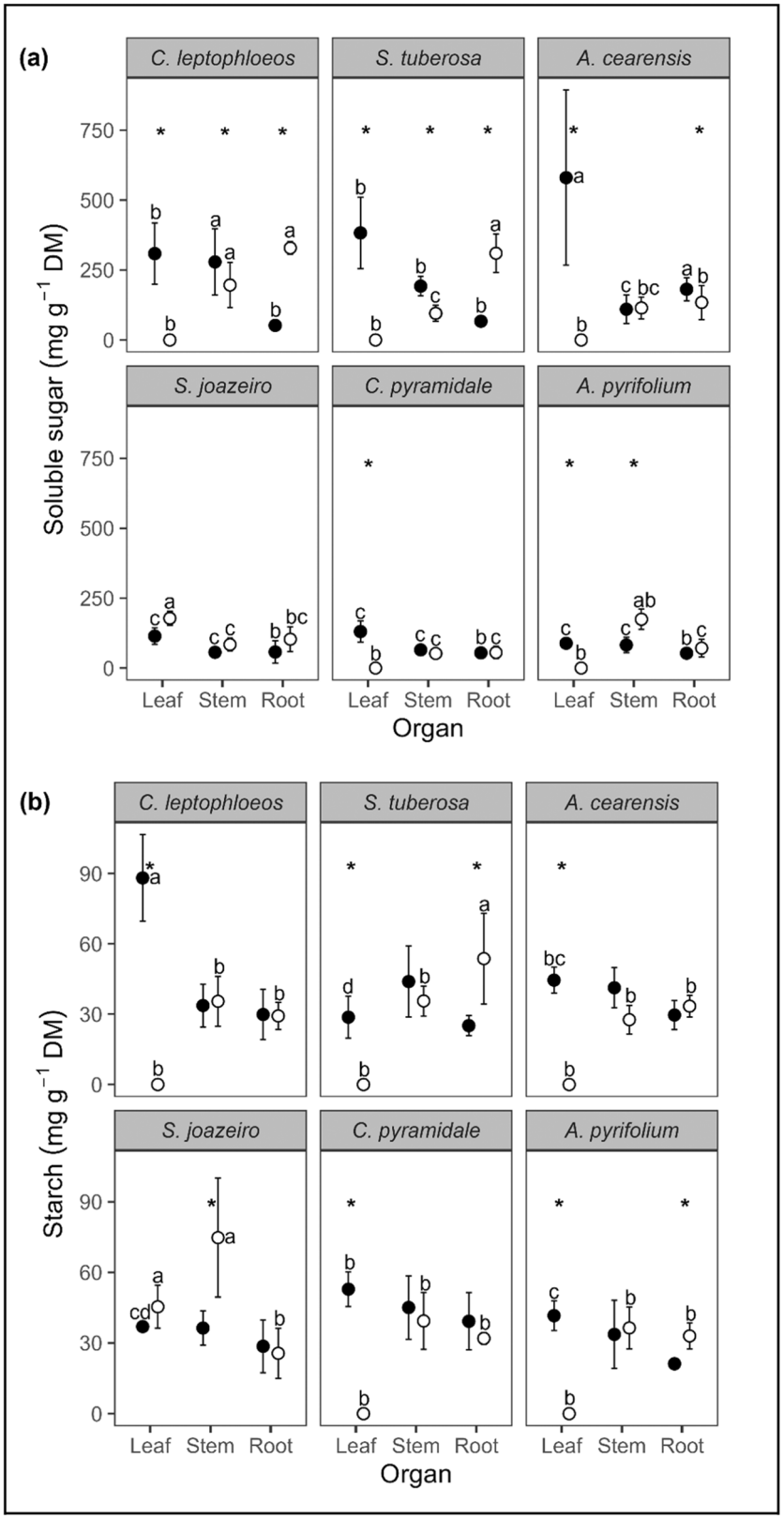

FIGURE 6 | (a) Concentration of soluble sugar (SS), and (b) starch in different plant organs (leaf, stem, root) measured on 9 April 2022 (rainy period) and 19 October 2022 (dry period), in Serra Talhada, State of Pernambuco, Brazil. Filled points represent rainy period and unfilled points represent dry period. *Difference between periods for each species and small letters denotes the difference between species within each organ and in each period by Tukey's test ($p < 0.05$).

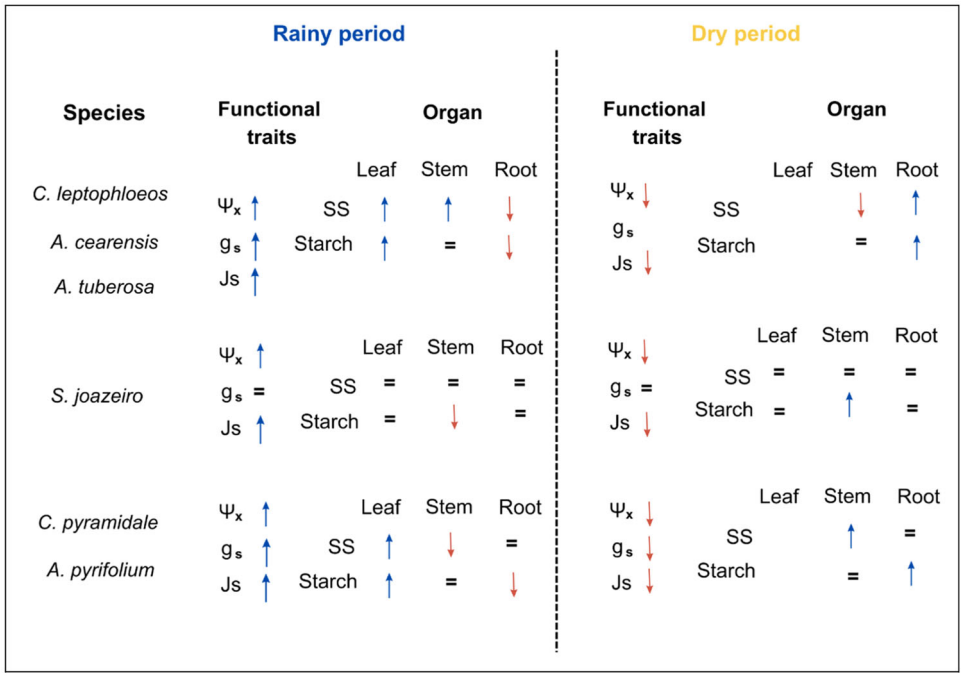

FIGURE 7 | Summary of functional traits in each species and between the rainy and dry periods in the year 2022 in the Caatinga dry forest. Blue arrow pointing up indicates it was higher; red down arrow indicates that it was smaller, and '=' sign indicates that there is no difference between the seasons. Absence of arrow or '=' sign indicates that these traits were not measured in the dry period due to leaf loss. Ψ_x, xylem water potential; g_s, stomatal conductance; J_s, sap velocity; SS, soluble sugar. [Color figure can be viewed at wileyonlinelibrary.com]

joazeiro differed in stem starch, being higher than the other species (74.8 ± 25.3 mg g^{-1} DM) (Figure 7).

When we evaluated the total concentration of NSC in each organ, we found that the species *C. leptophloeos*, *A. cearensis* and *S. tuberosa* presented higher concentrations in the leaves during the rainy period than the other species (Figure S3). During the dry period, only *S. joazeiro* presented leaves for quantification of the NSC concentration, which did not differ between the rainy and dry periods (Figure S3).

3.6 | PCA

The PCA indicates the separation of species by the concentration of NSC in different organs and physiological traits (Figure 8). The PC1 explained 36.7% of the variables and PC2 explained 20.4%. The variables on PC1, PD, gs_am, gs_am, and NSC, SS and starch in different organs (leaf, stem and root), were more related to the species with low WD, *C. leptophloeos*, *A. cearensis* and *S. tuberosa* (Figure 8). For PC2 variables J_s and WD were more related to species with high WD, *C. pyramidale*, *A. pyrifolium* and *S. joazeiro* (Figure 8).

4 | Discussion

Our results show that species had varied J_s and NSC throughout various periods of the year. *C. leptphloeos*, *A. cearensis* and *S. tuberosa* (deciduous species with low WD) present lower J_s and have higher concentrations of NSC, especially SS, in the rain period in leaves, while in the dry period, they present higher amounts of starch in the stem (*C. leptphloeos* and *A. cearensis*) and in the root (*S. tuberosa*). *S. joazeiro* (the evergreen species) presents higher J_s in all periods of the year and frequent synthesis of NSC, in addition to a high concentration of NSC in the stem. The species *C. pyramidale* and *A. pyrifolium* have contrasting J_s and NSC dynamics. *C. pyramidale* had higher J_s throughout the periods. On the other hand, *A. pyrifolium* presents lower J_s throughout the periods. Furthermore, the NSC concentration in the organs of these species is comparatively lower than that *C. leptphloeos*, *A. cearensis*, *S. tuberosa*, and to the starch in the stem of the *S. joazeiro*.

4.1 | Dynamics of Sap Velocity in Response to Seasonality

In the Caatinga, seasonality is well marked, and plants respond to rainfall and VPD (Lima and Rodal 2010; Souza et al. 2015; de Queiroz et al. 2020). Thus, maintaining J_s in the rainy season is essential to carry out their gas exchange and secure resources (Würth et al. 2005; Hartmann and Trumbore 2016; Paloschi et al. 2021). We found that the sap velocity was higher for most species during the two wet period, that is, rainy and first rains, which is not surprising given higher soil water availability. However, there were species-level differences. Sap velocity was highest for *S. joazeiro*, which likely has a deep root system as evidenced by its lower Ψ_{xylem} in midday (de Lima et al. 2012) and seasonal shifts in water isotope signatures (Wright et al. 2021). During the dry period, *S. joazeiro*, *C. pyramidale* and *C. leptophloeos* had higher sap velocity in November. This is possibly because *S. joazeiro* and *C. pyramidale* are species with

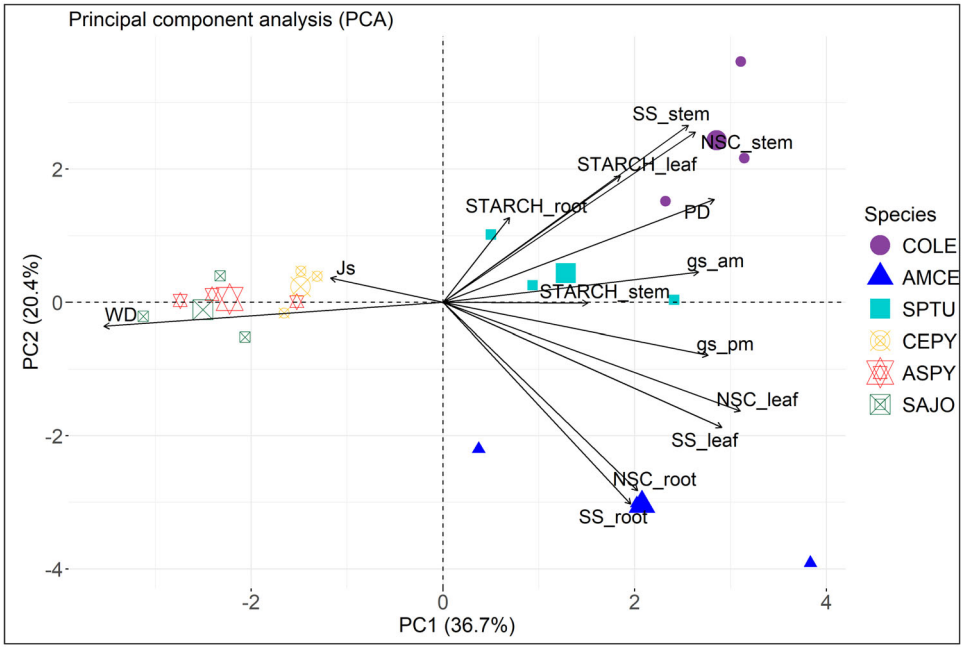

FIGURE 8 | Principal component analysis (PCA) by species: *Commiphora leptophloeos* (COLE), *Amburana cearensis* (AMCE), *Spondias tuberosa* (SPTU), *Cenostigma pyramidale* (CEPY), *Aspidosperma pyrifolium* (ASPY), *Sarcomphalus joazeiro* (SAJO). gs_am, stomatal conductance in the morning; gs_pm, stomatal conductance in the afternoon; J_s, average sap velocity; NSC_leaf, leaf non-structural carbohydrates; NSC_root, root non-structural carbohydrates; NSC_stem, stem non-structural carbohydrates; PD, xylem water potential in predawn; SS_leaf, leaf soluble sugar; SS_root, root soluble sugar; SS_Stem, stem soluble sugar; STARCH_leaf, leaf starch; STARCH_root, root starch.; STARCH_stem, stem starch; WD, wood density. [Color figure can be viewed at wileyonlinelibrary.com]

high WD that can tolerate dry conditions and can still initiating leaf sprouting (Poorter et al. 2010; de Lima et al. 2012). On the other hand, *C. leptophloeos* had a high flower production, which requires internally stored water and NSC for this phenophase (Lima et al. 2021; Resco de Dios and Gessler 2021).

The low hourly J_s of *C. leptphloeos*, *S. tuberosa* and *A. cearensis* can be due stomatal closure and high xylem capacitance resulting from lower WD and large water storage capacity (Yu et al. 2019; Brito et al. 2022). The hourly sap velocity patterns revealed that the species follow similar diurnal behaviour as a response to atmospheric demand. This behaviour was expected since many studies have shown that high VPD reflects low stomatal conductance (Yu et al. 2019; Grossiord et al. 2020). At the same time, transpiration increases in many species, resulting in numerous consequences for species tolerance, such as failure hydraulics or in other species occur reduced photosynthetic rates and risks of carbon depletion due to low stomatal conductance (Piper 2011; Grossiord et al. 2020; McDowell et al. 2022). In SDTF such as the Caatinga, this becomes a serious problem, as it increases water loss by evapotranspiration and thus contributes to severe drought events and water deficit of trees (Grossiord et al. 2017, 2020; McDowell et al. 2022).

We found that the species *C. leptophloeos* maintained the same sap velocity peak observed between 2018 and 2019, while *C. pyramidale* presented a later J_s peak (12:30 PM) in relation to the results obtained by Wright et al. (2024). This change in peak times in different years possibly occurred because in 2022, there was more rainfall, and these conditions favoured transpiration for a longer time in the species *C. pyramidale*.

4.2 | Responses of Species to Water Availability

C. leptphloeos, *S. tuberosa* and *A. cearensis* showed higher Ψ_{xylem} both in predawn and midday during the rainy period, possibly due to greater cell turgidity, that is, greater capacitance, which is often observed in species with relatively lower WD (Borchert and Pockman 2005; Oliva Carrasco et al. 2014). While *S. joazeiro*, *C. pyramidale* and *A. pyrifolium*, which have greater WD, probably have lower capacitance, reflecting their Ψ_{xylem}. Deciduous trees with high WD with low capacitance, such as *C. pyramidale* and *A. pyrifolium*, may be more tolerant to desiccation, as their tissues support low water potential and saturate quickly after water availability (Borchert and Pockman 2005). Similar results for this same study site, although for fewer species, can be found in Brito et al. (2022) and Medeiros et al. (2024). *S. joazeiro* had a lower Ψ_{xylem} in the predawn and sharply reduced in the midday, being the lowest compared to the other species in the rainy period. This behaviour can be supported by a deep root system that helps uptake water in the deepest layers of the soil (Lima and Rodal 2010). In addition, the high density of wood itself helps to withstand very negative pressures and consequently promotes greater resistance to cavitation (Poorter et al. 2010; Markesteijn, Poorter, Paz, et al. 2011; de Lima et al. 2012), factors that favoured high sap velocity for this species during the evaluated period.

Regarding stomatal conductance, there was no significant difference among species or reading intervals for the rainy period. Because there is higher water available in the rainy season, tree may not need to restrict their gas exchange, allowing for generally greater carbon gain (Dalmolin et al. 2015). In the month

representing the dry period, g_s was high in species with high WD and remained similar in the afternoon, especially in *S. joazeiro*. The anomalous rain event in October and November may have promoted gas exchange in species that still had leaf cover (Borchert 1994; Lima et al. 2021). The presence of leaves in the evergreen species during the dry period and the reduction in VPD in November favoured an increase in g_s and, consequently, in J_s (Brodribb et al. 2002; Grossiord et al. 2020).

4.3 | Relationship Among NSC Concentration, Phenology and Sap Velocity

The species with low WD (*C. leptophloeos*, *A. cearensis* and *S. tuberosa*) had a higher concentration of total NSC in the rainy period than the species with high WD (*C. pyramidale*, *A. pyrifolium* and *S. joazeiro*). *C. leptophloeos*, *A. cearensis* and *S. tuberosa* have a drought avoidance mechanism (Blanco-Sánchez et al. 2022), so they lose their leaves earlier to escape excessive water loss by transpiration (Markesteijn, Poorter, Paz, et al. 2011; de Lima et al. 2012; de Souza et al. 2020). Therefore, they need to maximize their CO_2 assimilation when resources are available and store NSC for use during the dry season to maintain their metabolism and translocate C (Würth et al. 2005; Kawai et al. 2022). In addition, there may be an increase in NSC reserves in specific plant organs, such as stems and roots, which are trees main NSC storage organs (Tomasella et al. 2020). During the dry season, trees can mobilize stored carbohydrates to supply the continuous metabolic demand of the plant (Piper 2011). Plants that can maintain high amounts and availability of NSC during drought may be more resilient (Tomasella et al. 2020). There is a connection between the parenchyma cells that contain NSC and the xylem vessels, allowing the exchange of water and solutes between these structures. This exchange plays a key role in regulating the metabolism and efficient transport of NSC through the phloem in plants (Tomasella et al. 2020; Kawai et al. 2022).

The highest concentration of starch in the leaves and stem of *S. joazeiro* was essential to maintain high J_s and g_s during the dry period. The sugars present in the xylem sap can reduce osmotic potential, and this is important for the plant, as the higher concentration of solute in the xylem allows more significant water transport, increasing the flow (O'Brien et al. 2014). Water tends to flow from the soil, with a higher osmotic potential, towards the xylem, where the osmotic potential is lower (O'Brien et al. 2014; Tomasella et al. 2020). Studies have shown that tropical trees with higher concentrations of NSC had higher xylem water potential during the dry period (O'Brien et al. 2014). Furthermore, this higher concentration of NSC and the higher WD of this species may help species in this functional group to withstand negative pressures and have greater resistance to cavitation (Markesteijn, Poorter, Paz, et al. 2011). Since *S. joazeiro* is an evergreen species, this favoured the production of SS found in the leaves and stem, allowing SS to be available for frequent use (Piper 2011; Palacio et al. 2018). This suggests that evergreen species may have greater resistance to cavitation, which maintains J_s and NSC production even in the dry period, which may increase hydraulic security and avoid carbon starvation (Janssen et al. 2020; McDowell et al. 2022), although more representative measurements of various evergreen species are needed to test this.

The species that showed the lowest concentration of NSC was *A. pyrifolium*. This behaviour corresponded to low J_s, which suggests that this species has little NSC production and storage capacity and greater hydraulic control to avoid excessive water loss (Vico et al. 2014; Wang et al. 2016). However, analysis of other traits of this species, such as anatomy and photosynthesis, is necessary for a better understanding of the physiological mechanisms of this species.

The species *C. leptophloeos* showed a high concentration of SS in the stem during the dry period. This suggests that, in addition to a high stem water storage capacity, this species is also able to store large amount of SS in its stem, which can become available for early metabolism (Palacio et al. 2018; Kawai et al. 2022). This finding is unique because it suggests that tree stems play an important role in long and short-term storage of needed resources such as water and SS. Not surprisingly, *S. tuberosa* stored more starch in the root during the drought, which promoting the translocation of sugars necessary for metabolism (Hartmann and Trumbore 2016). It is well-documented that *S. tuberosa* has an extensive resource capacity in the roots, which is essential for flowering and supporting a high yield of fleshy fruits even at the end of the dry season (Lima et al. 2009). Furthermore, starch storage in the root system may play an important role in leaf sprouting in the next season and in recovery from stress after drought (Resco de Dios and Gessler 2021; Santos et al. 2021). Starch is the main long-term storage compound, and deciduous species such as *S. tuberosa* depend on the translocation of stored NSC more so than evergreens like *S. joazeiro*, because deciduous species build a new leaf canopy each season (de Lima et al. 2012; Rosell et al. 2021).

Phenology was a good predictor of sap velocity, as flow responded to phenophase intensities, indicating that phenology responds to seasonality (Lima et al. 2021; da Silva E Teodoro et al. 2022). Due species having more than 50% of crown coverage in most species in the rainy month (March 2022), and *C. leptophloeos* and *S. tuberosa* presenting the budding phenophase, the J_s was high in the species, especially in *S. joazeiro*, which stood out among them. The species *A. pyrifolium* did not present the reproductive phenophases (flowering and fruiting) in March (Figure S2a), (which demand greater flow to the drains), resulting in lower J_s than the other species. Possibly lower J_s also occurred because this species presented high leaf fall, low water potential and low stomatal conductance, more conservative drought tolerance strategies (Markesteijn, Poorter, Bongers, et al. 2011).

Many deciduous species with high WD start sprouting soon after the first rains that mark the end of the dry season. This explains greater sprouting in *C. pyramidale* and *A. pyrifolium* and lower leaf sprouting in deciduous species with low WD (de Lima et al. 2012, 2021). However, *C. leptophloeos* and *S. tuberosa* showed high Fournier intensity in the flowering phenophase, suggesting that greater starch storage in the stem of *C. leptophloeos* and the root of *S. tuberosa* may support the reproductive phenophase of these species (Figure S2b). These species start flowering in the late dry season, regardless of the occurrence of rain (de Lima et al. 2012, 2021). Therefore, long-term stored starch could be translocated to these drains (Piper 2011; Rosell et al. 2021), and the water status in deciduous species with low WD is kept high.

5 | Conclusions

We found that species have varied water use and allocation of NSC. *C. leptphloeos, S. tuberosa* and *A. cearensis* have high stem water storage and NSC storage, and *S. joazeiro* maintains high sap velocity and NSCs production during the wet and dry periods. Considering longer dry periods and irregular rainy periods, deciduous species with low WD that use stored NSC to resprout and flowering during the dry season may be the most affected by drought due to the risk of depletion of their reserves.

Author Contributions

M.M., C.L.W. and M.G.S. conceived the study. M.M., J.R.I.S. and A.L.N.d.J. collected the data. M.M. and C.L.W. analyzed the data. M.M., C.L.W., A.L.A.d.L. and M.G.S. wrote the first draft with edits from all authors. A.L.A.d.L., E.S.d.S. and M.G.S. provided supervision and resources.

Acknowledgements

We would like to thank the students from the Plant Physiology laboratory (Laboratório de Fisiologia Vegetal, LFV), Department of Botany at UFPE, for their assistance with laboratory analyses, the Study Group of Semiarid Ecohydrology, the Centre for Functional Ecology of Plants (Núcleo de Ecologia Funcional de Plantas, NEFPlan), and the Universidade Federal Rural de Pernambuco, Serra Talhada Academic Unit (UFRPE/UAST) for assistance in fieldwork, especially Nielson Brito, Cíntia Amando, and Romário Horas. We also thank the Postgraduate Programme in Plant Production at UFRPE/UAST for the availability of equipment and laboratories. We are grateful to professor Dr. José Romualdo de Sousa Lima from the Federal University of Agreste de Pernambuco (UFAPE) for the Scholander pressure chamber and Senhor Homem Bom Magalhães for access to the field site. This work was financially supported by FACEPE (Facepe-Pronem-APQ-0336-2.03/14). M.M. is funded by (FACEPE Fellow-IBPG-0330-2.07/21). The work was also supported by the CAPES/TAMU project (006/2014) for the measures of sap velocity and by the INCT: National Observatory of Water and Carbon Dynamics in the Caatinga Biome – ONDACBC, contributing with meteorological data.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

de Alcântara, L. R. P., A. P. Coutinho, S. M. D. S. Neto, A. E. C. de Gusmão da Cunha Rabelo, and A. C. D. Antonino. 2021. "Computational Modeling of the Hydrological Processes in Caatinga and Pasture Areas in the Brazilian Semi-Arid." *Water (Switzerland)* 13: 1877.

Allen, K., J. M. Dupuy, M. G. Gei, et al. 2017. "Will Seasonally Dry Tropical Forests be Sensitive or Resistant to Future Changes in Rainfall Regimes?." *Environmental Research Letters* 12: 023001.

Arnan, X., I. R. Leal, M. Tabarelli, et al. 2018. "A Framework for Deriving Measures of Chronic Anthropogenic Disturbance: Surrogate, Direct, Single and Multi-Metric Indices in Brazilian Caatinga." *Ecological Indicators* 94: 274–282.

Blanco-Sánchez, M., M. Ramos-Muñoz, B. Pías, et al. 2022. "Natural Selection Favours Drought Escape and an Acquisitive Resource-Use Strategy in Semi-Arid Mediterranean Shrubs." *Functional Ecology* 36: 2289–2302.

Borchert, R. 1994. "Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees." *Ecology* 75: 1437–1449.

Borchert, R., and W. T. Pockman. 2005. "Water Storage Capacitance and Xylem Tension in Isolated Branches of Temperate and Tropical Trees." *Tree Physiology* 25: 457–466.

Bosch, D. D., L. K. Marshall, and R. Teskey. 2014. "Forest Transpiration From Sap Flux Density Measurements in a Southeastern Coastal Plain Riparian Buffer System." *Agricultural and Forest Meteorology* 187: 72–82.

Brito, N. D. S., M. J. S. Medeiros, E. S. Souza, and A. L. A. Lima. 2022. "Drought Response Strategies for Deciduous Species in the Semiarid Caatinga Derived From the Interdependence of Anatomical, Phenological and Bio-Hydraulic Attributes." *Flora* 288: 152009.

Brodribb, T. J., N. M. Holbrook, and M. V. Gutiérrez. 2002. "Hydraulic and Photosynthetic Co-Ordination in Seasonally Dry Tropical Forest Trees." *Plant, Cell & Environment* 25: 1435–1444.

Dalmolin, Â. C., F. de Almeida Lobo, G. Vourlitis, et al. 2015. "Is the Dry Season an Important Driver of Phenology and Growth for Two Brazilian Savanna Tree Species With Contrasting Leaf Habits?." *Plant Ecology* 216: 407–417.

Dubois, M., K. A. Gilles, J. K. Hamilton, P. A. Rebers, and F. Smith. 1956. "Colorimetric Method for Determination of Sugars and Related Substances." *Analytical Chemistry* 28: 350–356.

Farrar, J. F. 1995. "Carbon Partitioning." In *Photosynthesis and Production in a Changing Environment. A Field and Laboratory Manual*, edited by D. O. Hall et al., 222–246. Chapman and Hall.

Fournier, L. A. 1974. "Un método Cuantitativo Para la Medición de Características Fenológicas en árboles." *Turrialba* 24: 422–423.

Granier, A. 1985. "Une Nouvelle Méthode Pour la Mesure du Flux de Sève Brute Dans le Tronc des Arbres." *Annales des Sciences Forestières* 42: 193–200.

Grossiord, C., T. N. Buckley, L. A. Cernusak, et al. 2020. "Plant Responses to Rising Vapor Pressure Deficit." *New Phytologist* 226: 1550–1566.

Grossiord, C., S. Sevanto, I. Borrego, et al. 2017. "Tree Water Dynamics in a Drying and Warming World." *Plant, Cell & Environment* 40: 1861–1873.

Hartmann, H., and S. Trumbore. 2016. "Understanding the Roles of Nonstructural Carbohydrates in Forest Trees—From What We Can Measure to What We Want to Know." *New Phytologist* 211: 386–403.

Intergovernmental Panel on Climate Change (IPCC). 2023. *Climate Change 2022 – Impacts, Adaptation and Vulnerability*. Cambridge University Press.

Janssen, T. A. J., T. Hölttä, K. Fleischer, K. Naudts, and H. Dolman. 2020. "Wood Allocation Trade-Offs Between Fiber Wall, Fiber Lumen, and Axial Parenchyma Drive Drought Resistance in Neotropical Trees." *Plant, Cell & Environment* 43: 965–980.

Kawai, K., S. Waengsothorn, and A. Ishida. 2022. "Sapwood Density Underlies Xylem Hydraulics and Stored Carbohydrates Across 13 Deciduous Tree Species in a Seasonally Dry Tropical Forest in Thailand." *Trees* 37: 485–495.

Lima, A. L. A., and M. J. N. Rodal. 2010. "Phenology and Wood Density of Plants Growing in the Semi-Arid Region of Northeastern Brazil." *Journal of Arid Environments* 74: 1363–1373.

Lima, A. L. A., M. J. N. Rodal, C. C. Castro, et al. 2021. "Phenology of High- and Low-Density Wood Deciduous Species Responds Differently to Water Supply in Tropical Semiarid Regions." *Journal of Arid Environments* 193: 104594.

de Lima, A. L. A., E. V. de Sá Barretto Sampaio, C. C. de Castro, M. J. N. Rodal, A. C. D. Antonino, and A. L. de Melo. 2012. "Do the Phenology and Functional Stem Attributes of Woody Species Allow for

the Identification of Functional Groups in the Semiarid Region of Brazil?." *Trees* 26: 1605–1616.

Lima Filho, P. J. M., F. Santos, and C. Antônio. 2009. "Avaliações Fenotípicas e Fisiológicas de Espécies de Spondias Tendo Como Porta Enxerto o Umbuzeiro (*Spondias tuberosa* Cam.)." *Revista Caatinga* 22: 59–63.

Lima, T. R. A., E. C. D. Carvalho, F. R. Martins, et al. 2018. "Lignin Composition Is Related to Xylem Embolism Resistance and Leaf Life Span in Trees in a Tropical Semiarid Climate." *New Phytologist* 219: 1252–1262.

Markesteijn, L., L. Poorter, F. Bongers, H. Paz, and L. Sack. 2011. "Hydraulics and Life History of Tropical Dry Forest Tree Species: Coordination of Species' Drought and Shade Tolerance." *New Phytologist* 191: 480–495.

Markesteijn, L., L. Poorter, H. Paz, L. Sack, and F. Bongers. 2011. "Ecological Differentiation in Xylem Cavitation Resistance Is Associated With Stem and Leaf Structural Traits." *Plant, Cell and Environment* 34: 137–148.

McDowell, N., W. T. Pockman, C. D. Allen, et al. 2008. "Mechanisms of Plant Survival and Mortality During Drought: Why Do Some Plants Survive While Others Succumb to Drought?." *New Phytologist* 178: 719–739.

McDowell, N. G., G. Sapes, A. Pivovaroff, et al. 2022. "Mechanisms of Woody-Plant Mortality Under Rising Drought, CO_2 and Vapour Pressure Deficit." *Nature Reviews Earth & Environment* 3: 294–308.

Medeiros, M., C. L. Wright, A. L. A. de Lima, et al. 2024. "Divergent Hydraulic Strategies of Two Deciduous Tree Species to Deal With Drought in the Brazilian Semi-Arid Region." *Trees* 38: 681–694.

Meinzer, F. C., D. M. Johnson, B. Lachenbruch, K. A. McCulloh, and D. R. Woodruff. 2009. "Xylem Hydraulic Safety Margins in Woody Plants: Coordination of Stomatal Control of Xylem Tension With Hydraulic Capacitance." *Functional Ecology* 23: 922–930.

Mendes, K. R., S. Campos, L. L. da Silva, et al. 2020. "Seasonal Variation in Net Ecosystem CO_2 Exchange of a Brazilian Seasonally Dry Tropical Forest." *Scientific Reports* 10: 9454.

O'Brien, M. J., S. Leuzinger, C. D. Philipson, J. Tay, and A. Hector. 2014. "Drought Survival of Tropical Tree Seedlings Enhanced by Non-Structural Carbohydrate Levels." *Nature Climate Change* 4: 710–714.

Oliva Carrasco, L., S. J. Bucci, D. Di Francescantonio, et al. 2014. "Water Storage Dynamics in the Main Stem of Subtropical Tree Species Differing in Wood Density, Growth Rate and Life History Traits." *Tree Physiology* 35: 354–365.

de Oliveira, C. C., R. B. Zandavalli, A. L. A. de Lima, and M. J. N. Rodal. 2015. "Functional Groups of Woody Species in Semi-Arid Regions at Low Latitudes." *Austral Ecology* 40: 40–49.

Oliveira, R. S., C. B. Eller, F. V. Barros, M. Hirota, M. Brum, and P. Bittencourt. 2021. "Linking Plant Hydraulics and the Fast–Slow Continuum to Understand Resilience to Drought in Tropical Ecosystems." *New Phytologist* 230: 904–923.

Palacio, S., J. J. Camarero, M. Maestro, A. Q. Alla, E. Lahoz, and G. Montserrat-Martí. 2018. "Are Storage and Tree Growth Related? Seasonal Nutrient and Carbohydrate Dynamics in Evergreen and Deciduous Mediterranean Oaks." *Trees* 32: 777–790.

Paloschi, R. A., D. M. Ramos, D. J. Ventura, et al. 2021. "Environmental Drivers of Water Use for Caatinga Woody Plant Species: Combining Remote Sensing Phenology and Sap Flow Measurements." *Remote Sensing* 13: 1–18.

Pereira, P. D. C., T. G. F. D. Silva, S. Zolnier, J. E. F. D. Morais, and D. C. D. Santos. 2015. "Morfogênese da Palma Forrageira Irrigada por Gotejamento." *Revista Caatinga* 28: 184–195.

Pérez-Harguindeguy, N., S. Díaz, E. Garnier, et al. 2013. "New Handbook for Standardised Measurement of Plant Functional Traits Worldwide." *Australian Journal of Botany* 61: 167–234.

Pineda-García, F., H. Paz, and F. C. Meinzer. 2012. "Drought Resistance in Early and Late Secondary Successional Species From a Tropical Dry Forest: The Interplay Between Xylem Resistance to Embolism, Sapwood Water Storage and Leaf Shedding." *Plant, Cell and Environment* 36: 405–418.

Piper, F. I. 2011. "Drought Induces Opposite Changes in the Concentration of Non-Structural Carbohydrates of Two Evergreen Nothofagus Species of Differential Drought Resistance." *Annals of Forest Science* 68: 415–424.

Poorter, L., I. McDonald, A. Alarcón, et al. 2010. "The Importance of Wood Traits and Hydraulic Conductance for the Performance and Life History Strategies of 42 Rainforest Tree Species." *New Phytologist* 185: 481–492.

Poorter, L., D. M. A. Rozendaal, F. Bongers, et al. 2019. "Wet and Dry Tropical Forests Show Opposite Successional Pathways in Wood Density but Converge Over Time." *Nature Ecology & Evolution* 3: 928–934.

de Queiroz M. G., T. G. F. da Silva, S. Zolnier, et al. 2020. "Spatial and Temporal Dynamics of Soil Moisture for Surfaces With a Change in Land Use in the Semi-Arid Region of Brazil." *Catena* 188: 104457.

Quentin, A. G., E. A. Pinkard, and M. G. Ryan, et al. 2015. "Non-Structural Carbohydrates in Woody Plants Compared Among Laboratories." *Tree Physiology* 35: 1146–1165.

R Core Team. 2022. *A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria*. https://www.R-project.org/.

Resco de Dios, V., and A. Gessler. 2021. "Sink and Source Co-Limitation in the Response of Stored Non-Structural Carbohydrates to an Intense but Short Drought." *Trees – Structure and Function* 35: 1751–1754.

Rito, K. F., V. Arroyo-Rodríguez, R. T. Queiroz, I. R. Leal, and M. Tabarelli. 2017. "Precipitation Mediates the Effect of Human Disturbance on the Brazilian Caatinga Vegetation." *Journal of Ecology* 105: 828–838.

Rosell, J. A., F. I. Piper, C. Jiménez-Vera, et al. 2021. "Inner Bark as a Crucial Tissue for Non-Structural Carbohydrate Storage Across Three Tropical Woody Plant Communities." *Plant, Cell & Environment* 44: 156–170.

Santana-Vieira, D. D. S., L. Freschi, L. A. H. Almeida, et al. 2016. "Survival Strategies of Citrus Rootstocks Subjected to Drought." *Scientific Reports* 6: 38775.

Santos, M., V. Barros, L. Lima, G. Frosi, and M. G. Santos. 2021. "Whole Plant Water Status and Non-Structural Carbohydrates Under Progressive Drought in a Caatinga Deciduous Woody Species." *Trees* 35: 1257–1266.

Santos, M. G., M. T. Oliveira, K. V. Figueiredo, et al. 2014. "Caatinga, the Brazilian Dry Tropical Forest: Can It Tolerate Climate Changes?." *Theoretical and Experimental Plant Physiology* 26: 83–99.

Santos, W. R., A. M. R. F. Jardim, L. S. B. Souza, et al. 2024. "Can Changes in Land Use in a Semi-Arid Region of Brazil Cause Seasonal Variation in Energy Partitioning and Evapotranspiration?." *Journal of Environmental Management* 367: 121959.

Scoffoni, C., C. Albuquerque, C. R. Brodersen, et al. 2017. "Leaf Vein Xylem Conduit Diameter Influences Susceptibility to Embolism and Hydraulic Decline." *New Phytologist* 213: 1076–1092.

Sevanto, S., N. G. Mcdowell, L. T. Dickman, R. Pangle, and W. T. Pockman. 2014. "How Do Trees Die? A Test of the Hydraulic Failure and Carbon Starvation Hypotheses." *Plant, Cell & Environment* 37: 153–161.

Silva, P. F., J. R. S. Lima, A. C. D. Antonino, et al. 2017. "Seasonal Patterns of Carbon Dioxide, Water and Energy Fluxes Over the Caatinga and Grassland in the Semi-Arid Region of Brazil." *Journal of Arid Environments* 147: 71–82.

da Silva E Teodoro, É. D. M., A. P. A. da Silva Silva, N. D. S. Brito, M. J. N. Rodal, R. A. Shinozaki-Mendes, and A. L. A. de Lima. 2022. "Functional Traits Determine the Vegetative Phenology of Woody Species in Riparian Forest in Semi-Arid Brazil." *Plant Ecology* 223: 1137–1153.

de Souza, B. C., E. C. D. Carvalho, R. S. Oliveira, F. S. de Araujo, A. L. A. de Lima, and M. J. N. Rodal. 2020. "Drought Response Strategies of Deciduous and Evergreen Woody Species in a Seasonally Dry Neotropical Forest." *Oecologia* 194: 221–236.

Souza, B. C., R. S. Oliveira, F. S. Araújo, A. L. A. Lima, and M. J. N. Rodal. 2015. "Divergências funcionais e estratégias de resistência à seca entre espécies decíduas e sempre verdes tropicais." *Rodriguésia* 66: 21–32.

Speckman, H., B. E. Ewers, and D. P. Beverly. 2019. "AquaFlux: Rapid, Transparent and Replicable Analyses of Plant Transpiration." *Methods in Ecology and Evolution* 11: 44–50.

Tomasella, M., E. Petrussa, F. Petruzzellis, A. Nardini, and V. Casolo. 2020. "The Possible Role of Non-Structural Carbohydrates in the Regulation of Tree Hydraulics." *International Journal of Molecular Sciences* 21: 144.

Tonet, V., T. Brodribb, and I. Bourbia. 2024. "Variation in Xylem Vulnerability to Cavitation Shapes the Photosynthetic Legacy of Drought." *Plant, Cell & Environment* 47: 1160–1170.

Vico, G., S. E. Thompson, S. Manzoni, et al. 2014. "Climatic, Ecophysiological, and Phenological Controls on Plant Ecohydrological Strategies in Seasonally Dry Ecosystems." *Ecohydrology* 8: 660–681.

Wang, L., Y. Dai, J. Guo, R. Gao, and X. Wan. 2016. "Interaction of Hydraulic Failure and Carbon Starvation on *Robinia pseudoacacia* Seedlings During Drought." *Linye Kexue/Scientia Silvae Sinicae* 52: 1–9.

Wright, C. L., A. L. A. de Lima, E. S. de Souza, J. B. West, and B. P. Wilcox. 2021. "Plant Functional Types Broadly Describe Water Use Strategies in the Caatinga, a Seasonally Dry Tropical Forest in Northeast Brazil." *Ecology and Evolution* 11: 11808–11825.

Wright, C. L., J. B. West, A. L. A. de Lima, E. S. Souza, M. Medeiros, and B. P. Wilcox. 2024. "Contrasting Water-Use Strategies Revealed by Species-Specific Transpiration Dynamics in the Caatinga Dry Forest." *Tree Physiology* 44: 1–15.

Würth, M. K. R., S. Peláez-Riedl, S. J. Wright, and C. Körner. 2005. "Non-Structural Carbohydrate Pools in a Tropical Forest." *Oecologia* 143: 11–24.

Yu, T., Q. Feng, J. Si, and E. A. Pinkard. 2019. "Coordination of Stomatal Control and Stem Water Storage on Plant Water Use in Desert Riparian Trees." *Trees* 33: 787–801.

Zhang, T., Y. Cao, Y. Chen, and G. Liu. 2015. "Non-Structural Carbohydrate Dynamics in *Robinia pseudoacacia* Saplings Under Three Levels of Continuous Drought Stress." *Trees* 29: 1837–1849.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.