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ORIGINAL ARTICLE

Contrasting diurnal and seasonal root water uptake patterns among different plant life forms in a neotropical dry forest

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Abstract

Key message The woody plant life forms in a tropical dry forest differ largely in their diurnal and seasonal patterns of root water uptake and the related atmospheric and edaphic drivers.

Abstract As a consequence of global climate change, the frequency and intensity of drought events in tropical forest ecosystems is expected to increase. Woody species in tropical dry forests (TDFs) exhibit diverse strategies to withstand drought such as leaf-shedding or stem succulence that have mainly been studied from an aboveground perspective. Much less is known about the functioning of small and fine roots during the dry season and their response to soil re-wetting. We measured sap flux in small-diameter roots (2–6 mm) of four woody Ecuadorian TDF species using calibrated miniature sap flow gauges based on the heat-ratio method to unravel seasonal and diurnal patterns in root water uptake in dependence on phenology, soil moisture, and climatic drivers. Continuous data from 17 months showed that water uptake in the deciduous trees *Eriotheca ruizii*, *Ceiba trischistandra*, and *Vachellia macracantha* was closely linked to leaf phenology, soil moisture, and, in wet soil, vapor pressure deficit (VPD), while the tall, stem-succulent cactus *Armatocereus laetus* revealed a highly opportunistic water uptake pattern with rapid responses to small rainfall amounts in the dry season and decoupling from atmospheric drivers. While root sap flux density was on average highest in *C. trischistandra* with largest foliage area, the cactus roots were able to absorb water all day round without daytime dormancy and thus outperformed the other two species even during wetter periods. Deeper insights into small-root functionality across seasons is essential for a more mechanistic understanding of the water relations of TDF perennials with different drought response strategies.

Keywords Cactus · Diurnal variation · Drought-deciduous trees · Ecuador · Heat-ratio method · Root sap flux

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Introduction

Tropical dry forests (TDFs) once covered large areas in both the Neotropics and the Paleotropics, but their area is rapidly declining due to human activities (Bastin et al. 2017). About half of the current TDF area is located in the Neotropics (Miles et al. 2006; Estrada-Medina et al. 2013; DRYFLOR 2016). TDFs are characterized by a distinct rainfall seasonality with alternating wet and dry seasons (Murphy and Lugo 1986). During the usually four to more than six months long dry season, TDFs experience severe climatic drought and pronounced soil desiccation that strongly hampers soil biological and root activity (Murphy and Lugo 1986; Mooney et al. 1995). Water availability is therefore the key factor limiting plant establishment, growth, and survival in these forests (Maas and Burgos 2011). Despite these environmental constraints, TDFs belong to the most biodiverse ecosystems in the tropics (Murphy and Lugo 1986; Escribano-Avila et al. 2017), which harbor an impressive diversity of plant life forms adapted to water limitation (Medina 1995).

TDF plants do not only have to cope with the long dry season but also with a high interannual variability of rainfall onset, duration, and intensity in the wet season (Murphy and Lugo 1986), which increases the risk of drought damage of the vegetation. Moreover, climate warming will rise the vapor pressure deficit (VPD) of the atmosphere and is predicted to increase the frequency and intensity of droughts in tropical regions in the future (Miles et al. 2006; Malhi et al. 2009; Chadwick et al. 2015; Fang et al. 2022). Thus, the uncertainty in annual rainfall patterns most likely will increase in tropical dry regions in the decades to come (Feng et al. 2013).

In order to adapt to long drought periods and the irregularity of rainfall, TDF tree species have evolved distinct strategies to avoid or tolerate water deficits (Olivares and Medina 1992; Poorter and Markesteijn 2008; Chaturvedi et al. 2021), either through phenological (e.g. timing of leaf shedding and renewal), structural (e.g. stem hydraulic properties, rooting patterns), or physiological modifications (e.g. water relations regulation, cellular desiccation tolerance, photosynthetic pathways) (Holbrook et al. 1995). The broad spectrum of drought response strategies found in TDF trees is well displayed by the co-existence of contrasting leaf phenology types in these biodiverse ecosystems that range from deciduous (drought-avoiding) to evergreen (drought-tolerant) (Borchert 1994; Giraldo and Holbrook 2011).

The dominant strategy in most TDFs is drought-deciduousness (Murphy and Lugo 1986; Mooney et al. 1995), i.e., the shedding of leaves at the onset of the dry period for several months to avoid tissue desiccation through transpiration when soil water supply becomes limited (Borchert 1994; Wolfe et al. 2016). Many obligate deciduous trees, including stem succulents and cacti, are characterized by low wood densities, fairly high water transport capacities, and a high hydraulic capacitance in the stem (Borchert 1994; Bobich and North 2009; Àvila-Lovera and Ezcurra 2016; Alvarado and Terrazas 2023). Semi-evergreen species shed their leaves only for some weeks during the dry season (Eamus 1999). Many deciduous and stem-succulent trees are capable of flushing new leaves and/or flowers within or at the end of the dry season, supported by stored water (Borchert 1994; Chapotin et al. 2006; Wright et al. 2024). In contrast, evergreen trees that maintain their sclerophyllous foliage throughout the dry season, often have higher wood densities and a more embolism-resistant xylem than deciduous trees, but they are typically lacking the capacity to store notable amounts of water in stem tissues (Borchert 1994; Holbrook et al. 1995; Medina 1995; Eamus 1999). In climates with a highly irregular occurrence of severe drought periods, stem-succulent plants with CAM metabolism such as Cactaceae or Euphorbiaceae are promoted (Ellenberg 1981; Lüttge 2008).

While a considerable number of studies have addressed the water relations and drought response strategies of neotropical TDF trees from an aboveground perspective (Sobrado and Cuenca 1979; Sobrado 1986; Hasselquist et al. 2010; Markesteijn et al. 2010; Wu et al. 2019; Wright et al. 2021, 2024), much less attention has been paid to the root systems of dry forest trees and their functionality during dry and wet seasons (Scholz et al. 2002; Hultine et al. 2023). This is unfortunate and hampering a full understanding of the drought response strategies of TDF trees, since root system adaptations to water scarcity are of equal importance for the drought survival of trees as are adaptations at foliage, crown, and stem levels (Sobrado 1986). Roots as the interface between soil and plant, and their distribution in the soil exert a large influence on tree water consumption, and their functioning during soil drought is crucial for the trees' survival and fitness during and after the dry season. In particular, the switch in root functioning between wet and dry seasons and upon rewetting after long drought is not well understood for major TDF tree life forms.

Evergreen dry forest species generally develop deeper root systems that enable them to access water in deeper soil layers when the topsoil dries out (Sobrado and Cuenca 1979; Eamus 1999; Paz et al. 2015). In contrast, (non-succulent and succulent) drought-deciduous species typically build shallower root systems which allow rapid water absorption in the topsoil as soon as rainfall is starting to rewet the soil (Paz et al. 2015). This strategy of a rapid root response to rewetting has been intensively studied in Cactaceae species, which combine stem succulence and the CAM photosynthetic pathway with the development of a far-reaching lateral root system with so-called rain roots in the topsoil that can effectively tap even small and erratic rainfall events (Kluge and Ting 1978; Nobel 1988, 2002; Shiskova et al. 2013; Rodriguez-Alonso et al. 2018). However, their root systems might be less effective in exploiting deep soil water reserves. There is some evidence for a trade-off between rooting depth and stem hydraulic capacitance in tropical dry forest trees (Borchert 1994; Paz et al. 2015).

So far, the water use of TDF trees during the wet and dry season has mostly been investigated via leaf transpiration measurements (Sobrado and Cuenca 1979; Sobrado 1986; Hasselquist et al. 2010; Markesteijn et al. 2010; Wu et al. 2019; Wright et al. 2021, 2024) and sap flow recording in stems (Meinzer et al. 1999; Scholz et al. 2002; Andrade et al. 2005; Butz et al. 2017, 2018; Wright et al. 2024) or larger lateral roots > 10 mm in diameter (Scholz et al. 2002; Hultine et al. 2023) using invasive methods. These and other studies have revealed that tropical dry forest species differ substantially in their hydraulic strategies and seasonal water-use dynamics, indicating functional divergence in drought responses with respect to stem hydraulic architecture and capacitance, and carbon allocation patterns (da Silva Brito et al. 2022; Medeiros et al. 2025). Incorporating belowground sap flux dynamics into this framework may allow to better understand the role of root hydraulics in different drought-response syndromes.

The functioning of small-diameter roots which are close to the root segments that conduct water uptake has, however, received much less attention in dry forest systems and was not studied with non-invasive in situ-measuring techniques. While recording sap flow in roots of 2–6 mm in diameter does not directly capture the process of water uptake, the measuring site is close enough to the terminal root tips to monitor uptake dynamics reliably without the obscuring effect of hydraulic capacitance introduced by larger root segments. Of particular interest is the water uptake activity of the absorbing fine roots of different TDF tree life forms during the dry season and how rapidly these roots are resuming function when the soil starts to rewet. Deeper insights into the seasonal and diurnal dynamics of root water absorption of trees with contrasting drought response strategies would help to better understand how the trees are coping with unpredictable rainfall events and which life forms might be particularly vulnerable to a warming and drying climate.

In this study in a southern Ecuadorian dry forest, we employed miniature sap flow gauges to monitor sap flow in situ in roots of 2–6 mm in diameter that were located close to the water absorbing fine roots, comparing four co-occurring woody species with contrasting leaf phenologies (drought-deciduous to evergreen) and stem water storage capacities (stem- and root-succulent trees, a non-succulent tree, and a tall cactus). Two wet and one dry season were covered by continuous sap flow measurements, and the measured flux density was related to microclimatic and soil moisture data in order to identify the main drivers of sap flux in the different species. The drought response strategies represented in the four studied species were deciduous, stem-succulent trees (*C. trischistandra*), deciduous, root-succulent trees (*E. ruizii*), non-succulent semi-deciduous trees (*V. macracantha*), and tall woody, stem-succulent Cactaceae with CAM metabolism (*A. laetus*). We were especially interested in (i) diurnal water uptake patterns as influenced by the contrasting diel courses of photosynthesis in C_3 and CAM plants, (ii) the contrast between wet and dry season uptake rates, (iii) the velocity at which root water uptake recovers upon soil re-wetting, and (iv) the role of microclimatic variables and soil moisture as drivers of root water uptake in the different species.

Materials and methods

Study site and species selection

The study was conducted in the Laipuna Nature Reserve in the region of Macará in southern Ecuador (4°22´S, 79°90´W) which belongs to the Tumbesian Dry Forest ecoregion in south-western Ecuador and north-western Peru, a biodiversity hotspot rich in endemic plant species (Espinosa et al. 2012; Wurz et al. 2023). The reserve covers an elevational gradient from 600 to 1200 m a.s.l. in the Catamayo River canyon on the lower south-western slopes of the Andean Cordillera in rugged, hilly terrain with mostly northern aspect. Mean annual temperature at 600 m a.s.l. is 23.4 °C and mean annual precipitation is approximately 545 mm, with high interannual variability (Pucha-Cofrep et al. 2015; Spannl et al. 2016). Annual precipitation patterns show a distinct dry season from June to December, when VPD reaches peak values, and a rainy season typically lasting from January to May, when the westerly winds of the Innertropical Convergence Zone (ITCZ) hit the southern Ecuadorian coast and rainfall occurs typically during night (Volland-Voigt et al. 2011; Spannl et al. 2016). However, also in the rainy season, short periods of drought can occur (Fig. 1). The soils are classified as Cambisols (Butz et al. 2018) with a profile depth of > 50 cm.

The natural forest vegetation is a fairly species-rich premontane, seasonal tropical dry forest with an average canopy height of 11–16 m (maximum 20 m) and dominance of drought-deciduous trees (Aguirre et al. 2006; Wurz et al. 2023; Werner and Homeier 2024). In the reserve, roughly 80 tree species have been identified, with Fabaceae being the by far species-richest family. A large variety of tree life-forms exhibiting different drought adaptation strategies is

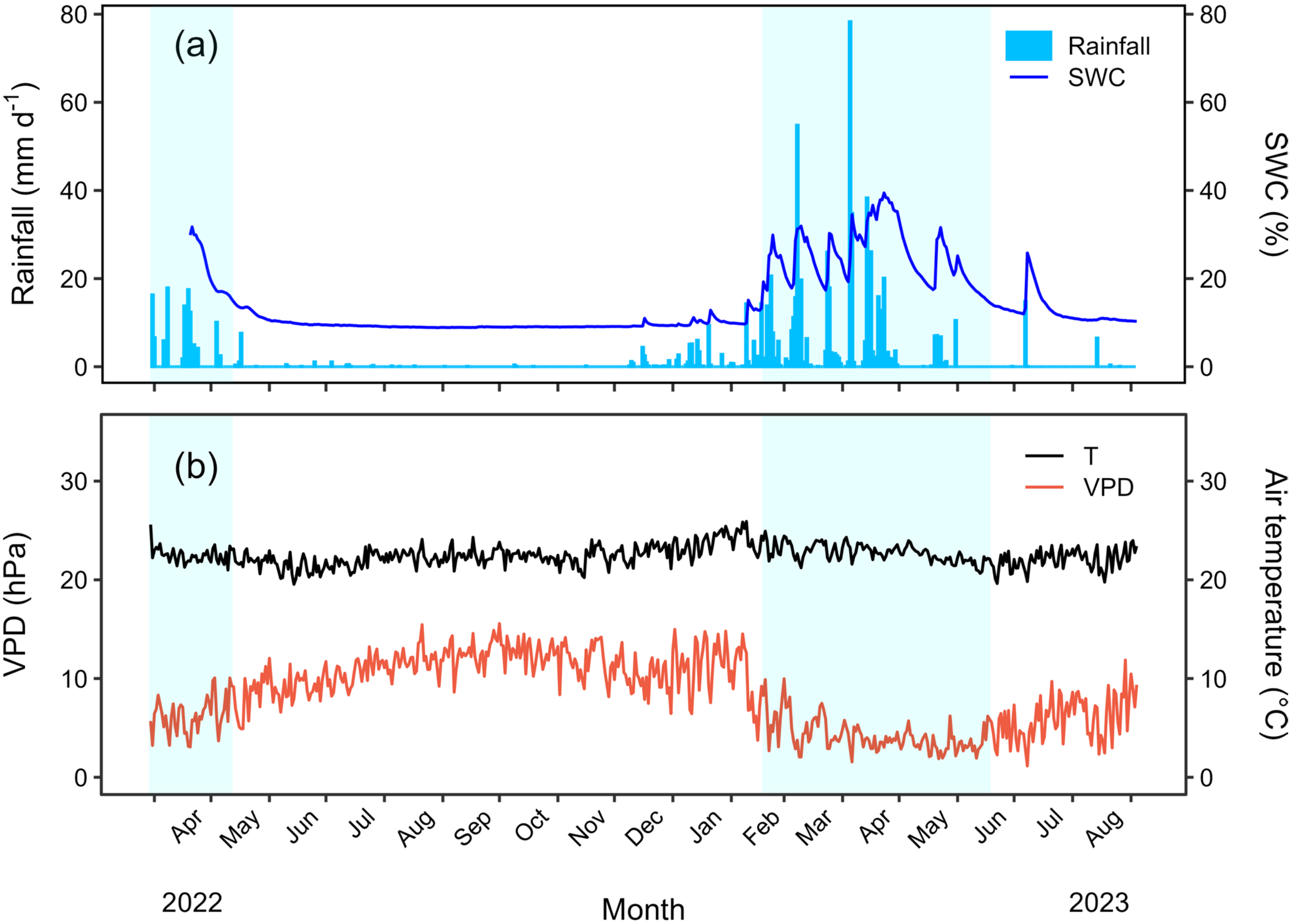

Fig. 1 Seasonal course of (**a**) rainfall and soil water content (SWC), and (**b**) vapor pressure deficit (VPD) and air temperature (daily totals or means) at the study site in the period March 30, 2022 to September 04, 2023. Light blue shading indicates the seasons in which SWC is >15 vol%, which is the definition used here to delineate the rainy season. Note that according to the standard Oceanic Niño Index (ONI) classification, the 2021–2022 period is categorized as a moderate La Niña event (drier than average) and the 2023–2024 period as a strong El Niño event, as reflected in higher than usual rainfall and extension of precipitation into the normal dry season in June and July

Table 1 Some characteristics of the four studied species relating to leaf phenology, water storage organs, wood specific gravity (WSG), maximum tree height (Height$_{max}$), and maximum diameter at breast height (dbh$_{max}$) recorded on individuals in permanent forest plots in the study area

Species	Family	Phenological type	Storage organ	WSG	Height$_{max}$ (m)	dbh$_{max}$ (cm)
Armatocereus laetus	Cactaceae	Evergreen	Stem	-	7	15
Ceiba trischistandra	Malvaceae	Deciduous	Stem	0.21	20	149
Eriotheca ruizii	Malvaceae	Deciduous	Root bulbs	0.47	18.5	75
Vachellia macracantha	Fabaceae	Semi-deciduous	None	0.84	14	43

present, including the dominant drought-deciduous species, as well as evergreen species and stem-, leaf- and root-succulent taxa.

For this study, we chose four woody species from a study plot at 600 m a.s.l., each representing a characteristic life-form in this dry forest ecosystem: *Ceiba trischistandra* (A. Gray) Bakh. (Malvaceae), *Eriotheca ruizii* (K. Schum.) A. Robyns (Malvaceae), *Vachellia macracantha* (Humb. & Bonpl. ex Willd.) Seigler & Ebinger (Fabaceae), and *Armatocereus laetus* (Knuth) Backeb (Cactaceae). The species differ in several aspects, notably in leaf longevity, the capacity for water storage in different organs, and in root system structure, which enables them to pursue different drought survival strategies (Table 1).

The stem-succulent *C. trischistandra* and the root-succulent *E. ruizii* are two of the most abundant deciduous canopy tree species in the forest (Werner and Homeier 2024). While both species shed their leaves simultaneously at the end of the wet season, typically from June onwards, *E. ruizii* builds new foliage only upon soil rewetting usually from January onwards and thereafter. In contrast, *C. trischistandra* is able to flush new leaves already several weeks prior to the start of the rainy season, mobilising water stored in the trunk. Both species form a more superficial root system. The semi-deciduous Fabaceae *V. macracantha* differs in its leaf phenology from these two and other deciduous species, in that it is never completely leafless but continuously exchanges leaves, apparently due to a less drought-sensitive foliage and probably deeper rooting. The fourth species, *A. laetus*, is one of the most common tall evergreen stem-succulent cactus species in the region, which forms a superficial, lateral root system, as is characteristic for many Cactaceae.

Recording of climatic variables and soil moisture

Climatic data were recorded continuously at 30-min intervals from March 30, 2022, onwards on a climate tower installed inside the forest at an elevation of 600 m a.s.l. Air temperature and relative air humidity were measured with a HMP115 temperature and air moisture sensor (Vaisala, Vantaa, Finland) that uses a Pt1000 platinum resistance temperature sensor and a Humicap180R© capacitive thin-film polymer sensor. Atmospheric vapor pressure deficit (VPD) was calculated from temperature and air humidity with the Tetens' formula (Tetens 1930). Rainfall was continuously recorded with tipping bucket rain gauges (Model 52203, R.M. Young Company, Traverse City, Michigan, USA) and expressed as daily or half-hourly totals. Volumetric soil water content (vol%; hereafter soil water content, SWC) was continuously measured from April 20, 2022, onwards with TEROS 12 frequency-capacitance soil moisture sensors (METER Group Inc., Pullman, WA, USA) installed in 5 cm soil depth. Incoming short-wave radiation was measured with a net radiometer (NR01, Hukseflux Thermal Sensors B.V., Delft, The Netherlands). The foliation status of the leaf-bearing trees was monitored at weekly intervals throughout the study period. For the purpose of this study and in line with Butz et al. (2018), we defined the dry season as the period in which SWC fell below 15 vol%, and the rainy season as the period where SWC remained > 15 vol% for at least five consecutive days (Fig. 1).

Measurement of root water uptake

To monitor root water uptake in the four study species under in situ conditions, custom-made miniature sap flow gauges were externally mounted on small-diameter roots (2–6 mm in diameter) of at least three individuals in each of the four species. These root segments belonged in most cases to the 4th, 5th or 6th orders in the hierarchical classification of developmental orders of the distal root system (with the 1st order being the most distal unbranched segment). While these segments primarily served in resource transport, they were close to the sites of root water absorption, which is usually assumed to occur in the 1st and 2nd orders (McCormack et al. 2015). Sensors were mounted to intact, straight root segments of approximately 10 cm length growing in the topsoil (5–10 cm soil depth), which were traced from the stem for species identification. At the gauge installation point, the root surface was carefully cleaned from soil particles and organic material in order to ensure a tight contact between sensor and root. After sensor mounting, the shallow pits in the topsoil were filled again with the removed soil to minimize temperature fluctuations in the root surroundings. Sap flow data were continuously recorded at 30-min intervals from March 30, 2022, until July 10 (*C. trischistandra* and *V. macracantha*), or until September 04 (*A. laetus* and *E. ruizii*), 2023, with a CR1000 data logger extended with a AM16/32 multiplexer (Campbell Scientific, Cambridge, UK).

The sap flow gauges used here were built after the design desribed in Clearwater et al. (2009) with the main difference that cork as backing material was replaced by silicone (Wagnersil 32 N, Wagner Dental, Hückelhoven, Germany) as proposed by Skelton et al. (2013). This led to more stable readings when measuring in damp soil. The sensor gauge (size 7 mm x 7 mm x 20 mm) carried a pair of thermocouples placed at equidistant points 5 mm upstream and downstream of the heating source. A holder of the same material provided fitting notches to align root and sensor gauge. A surrounding clip made of PVC cable duct facilitated installation inside the small soil pit, where the roots were accessed.

The type-T thermocouples were welded with 0.25 mm thermocouple wire. A 47 Ω chip resistor (RMC 1206, 2 mm x 3.6 mm x 2 mm, 0.25 W, True Components, Hirschau, Germany) served as heating element. To provide electrical insulation, thermocouples and heat resistor were dipped in insulation varnish (RS Components Ltd., Corby, UK). For the heater, the 12 V battery voltage was reduced to 5 V with a DC/DC converter resulting in 0.53 W heating power.

The datalogger was programmed to fire a 6-second heat pulse every 30 min and record the appropriate pre- and post-heat pulse temperatures for calculation of sap flow velocity (see below). According to Clearwater et al. (2009), a heat pulse duration of 6 s was considered adequate in terms of ensuring sufficient temperature inflection at the thermocouple position and avoiding root tissue damage due to excessive heat.

In this study, two wiring schemes for the sensor-datalogger connection were applied. Type A wiring followed Clearwater et al. (2019) who used copper wire for the heater and thermocouple extension wire for the thermocouples. The internal temperature sensor of the datalogger was used as reference for the temperature measurements of the thermocouples. Type B wiring used only copper wire and incorporated a thermistor (B57861S, TDK Electronics AG, Munich, Germany) into the sensor-cable junction as the temperature reference. Wiring scheme B was cheaper and easier to handle but yielded less accurate temperature readings, as was revealed by the subsequent analysis of the collected data. We assume that in wiring scheme B, mechanical shortcomings (notably insufficient thermal isolation of the sensors on the small-diameter roots) may have impaired sensor functioning especially during very hot and dry periods, leading to inaccurate reference temperature measurements by the thermistors, especially in the dry season. As a consequence, high-resolution sap flow data (30-min intervals) of sufficient quality were only available for two of the four study species (*A. laetus* and *E. ruizii*) recorded with wiring scheme A. For the remaining two species (*C. trischistandra* and *V. macracantha*), data were recorded with wiring scheme B and were not suitable for analyses requiring high temporal resolution. Therefore, we present in Fig. 3 high-resolution sap flow data and diurnal sap flux patterns (Fig. 3) only for the two species monitored using wiring scheme A, whereas for the other species, only daily flow sums were retrieved which were used to display seasonal trends (Fig. 2).

Due to frequent data gaps during measurement in the highly compacted soil, which caused incomplete daily and seasonal sap flux curves, we present here only the most complete data sets from one root per species.

The physical background and sensor calibration

Externally attached gauges applying the heat-ratio method (HRM) to measure sap flow in plant organs of small diameters, when flow rates are often <2 g h^{-1}, were first designed by Clearwater et al. (2009). They served as models for the gauge design used in this study. With the HRM method, which is based on the seminal work of Marshall (1958), sap flow in either direction can be measured by placing the thermoelements at equal distances upstream and downstream of the heating source. Accordingly, sap flow velocity is calculated from the relation of the temperature rise at the two upstream and downstream measuring points after the heat pulse as:

$$v_h = \frac{k}{x}\ln\left(\frac{\delta\, T_1}{\delta\, T_2}\right) \qquad \left(\mathrm{cm\, s^{-1}}\right)$$

where k is the thermal diffusivity of wet wood (cm^2 s^{-1}), x the distance of the thermocouple locations to the heating source (cm), and δT_1 (downstream) and δT_2 (upstream) the temperature rise (K) at the two measuring points averaged for the interval 55 to 70 s after the heat pulse. Earlier measurements with a variety of small-diameter roots had given this time period as that post-heating time interval, in which the δT_1 - δT_2 difference was maximal. The term ln (δT_1/ δT_2) reflects the heat dissipation in upstream and downstream direction in the root in dependence on sap flow rate and is termed HRM value in the subsequent text.

The small diameter of the roots studied here required fixing the sensor externally to the root surface with the consequence that the heat field between root and sensor cannot be easily calculated or modeled. On the other hand, the small size of roots and sensors enabled direct calibration of the measured water fluxes in the root by volumetry. For more detailed information see the Supplementary Information.

For each root segment and gauge, we obtained the slope of the linear regression between the flow rates (0 to 2 g h^{-1}) and the observed HRM values and calculated sap flow in the unit of g h^{-1} by multiplying the HRM values with the mean slope per species:

$$\text{Sap flow }\left(\mathrm{g\, h^{-1}}\right) = \ln\left(\frac{\delta\, T1}{\delta\, T2}\right) \times \left(slope_{species}\right)$$

Anatomical analysis of the root vascular system

To express the measured root flux per conduit cross-sectional area in the root xylem, we related the flow in g h^{-1} to the cumulative conductive conduit area (A_{lumen} in mm^2) in the root xylem of the measured root segments. To calculate A_{lumen}, root segments of 10 cm length of all measured roots were harvested after sap flow measurements had been completed in September 2023. After completing the calibration runs in the laboratory, segments of 10–20 µm thickness of the root segments were cut with a sliding microtome (G.S.L.1, WSL, Birmensdorf, Switzerland) and stained with safranin (1% in 50% ethanol, Sigma-Aldrich Chemie GmbH, Steinheim, Germany) and alcian blue (1% in 50% ethanol, Carl Roth GmbH + Co.KG, Karlsruhe, Germany). After fixation of the cross-sectional cuts on microscope slides with Euparal (Carl Roth GmbH + Co.KG, Karlsruhe, Germany), they were oven-dried for at least two weeks to obtain dry permanent samples. Photographs of the cuts were taken with a stereo-microscope equipped with a camera (SteREOV20, Carl Zeiss MicroImaging GmbH, Göttingen, Germany) at 125x magnification. Image processing for the cumulative cross-sectional area of the conducting elements was conducted with Adobe Photoshop CS6 (version 13.01.1, Adobe Systems Incorporated, USA) and ImageJ software (version 1.53) using the particle analysis function to estimate A_{lumen}.

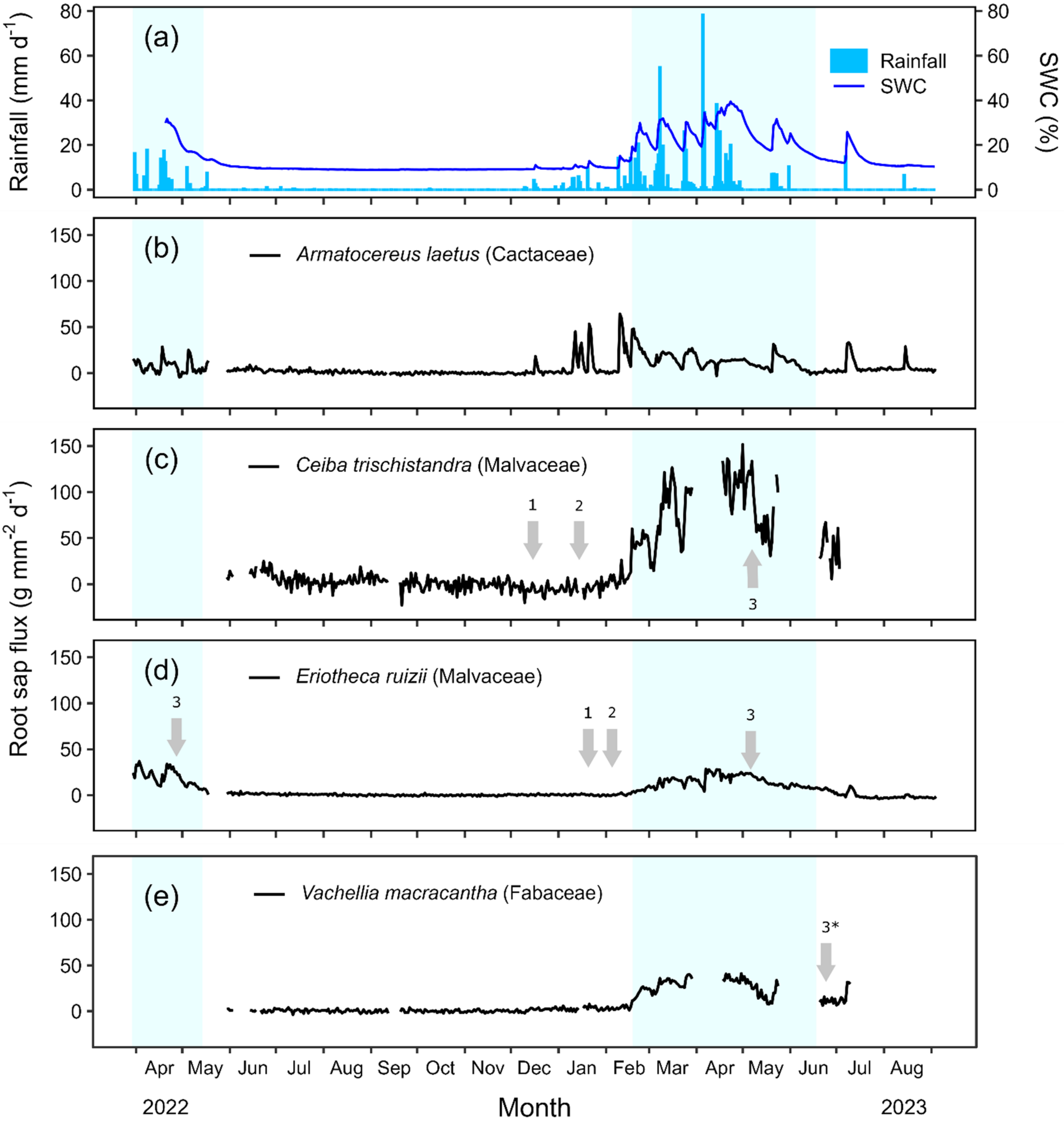

Fig. 2 Seasonal variation in daily sums of root sap flux density across wet and dry seaons in the period from April 2022 – to September 2023 for the four species *Armatocereus laetus* (**b**), *Ceiba trischistandra* (**c**), *Eriotheca ruizii* (**d**), and *Vachellia macracantha* (**e**) in relation to daily rainfall amounts and daily means of soil water content (**a**), SWC, 0–5 cm). Light blue shading indicates the rainy seasons (SWC > 15 vol%). Sap flux density relates to the cross-sectional area of the conducting xylem elements in the root. Data for April/May 2022 are missing for *C. trischistandra* and *V. macrantha*. Displayed are the sap flux density values of one root per species. Grey arrows indicate specific leaf phenological events in the deciduous tree species with 1: start of leaf flushing, 2: completed leaf expansion, and 3: start of leaf shedding (in *C.trischistanra* and *E. ruizii*). Since *V. macracantha* is a semi-deciduous species, the timing of leaf phenological events cannot be precisely given. Only the onset of continuous leaf renewal (indicated by leaf discoloration at the onset of the dry season) can be identified (3*)

Data processing and statistical analyses

To visualize 30-min resolution sap flux data for *E. ruizii* and *A. laetus* (Fig. 3), the data were smoothed with a LOESS function over ten data points (5 h) using the smooth_vec function from the timetk package in R software (version 2.9.0, Dancho and Vaughan 2023). To estimate the effects of SWC and VPD on root sap flux for the species *E. ruizii* and *A. laetus*, multiple regression analysis was employed separately for each species (since we only use data from one replicate per species). In the regressions, we included the variables daytime, radiation intensity and, for the deciduous species *E. ruizii*, crown status (leafless vs. leaf-bearing, dummy-coded) as predictors. The sample analyzed with the models comprised a total of 23,529 measurements for *E.ruizii* and a total of 974 measurements for *A. laetus*, respectively. Since we assumed root sap flux would increase with rising SWC, and that this effect would be strongest under periods of high VPD — typically during daytime in *E. ruizii* and during nighttime in *A. laetus* (stomata closed during daytime), we included an interaction term between SWC and VPD in the models. Prior to fitting the models, we log-transformed (base e) SWC and VPD to achieve a roughly symmetrical distribution and avoid leverage issues and influential cases. We fitted the models in R (version 4.4.2; R Development Core Team, 2023) using the function lm. We modelled the diurnal variation in root sap flux by transforming daytime values into angles (in radians) by first dividing daytime by 24 and then multiplying with 2 * pi, and finally including the sine and cosine of the resulting variable into the models (Stolwijk et al. 1999). A QQ-plot of the residuals and residuals plotted against the fitted values revealed a violation of the assumptions of normally distributed and homogenous residuals of the model fitted for *E. ruizii*. We therefore included modeling the dispersion of root sap flux as a function of the sine and cosine of daytime into the model and then re-fitted it using the function glmmTMB of the eponymous package (version 1.1.10; Brooks

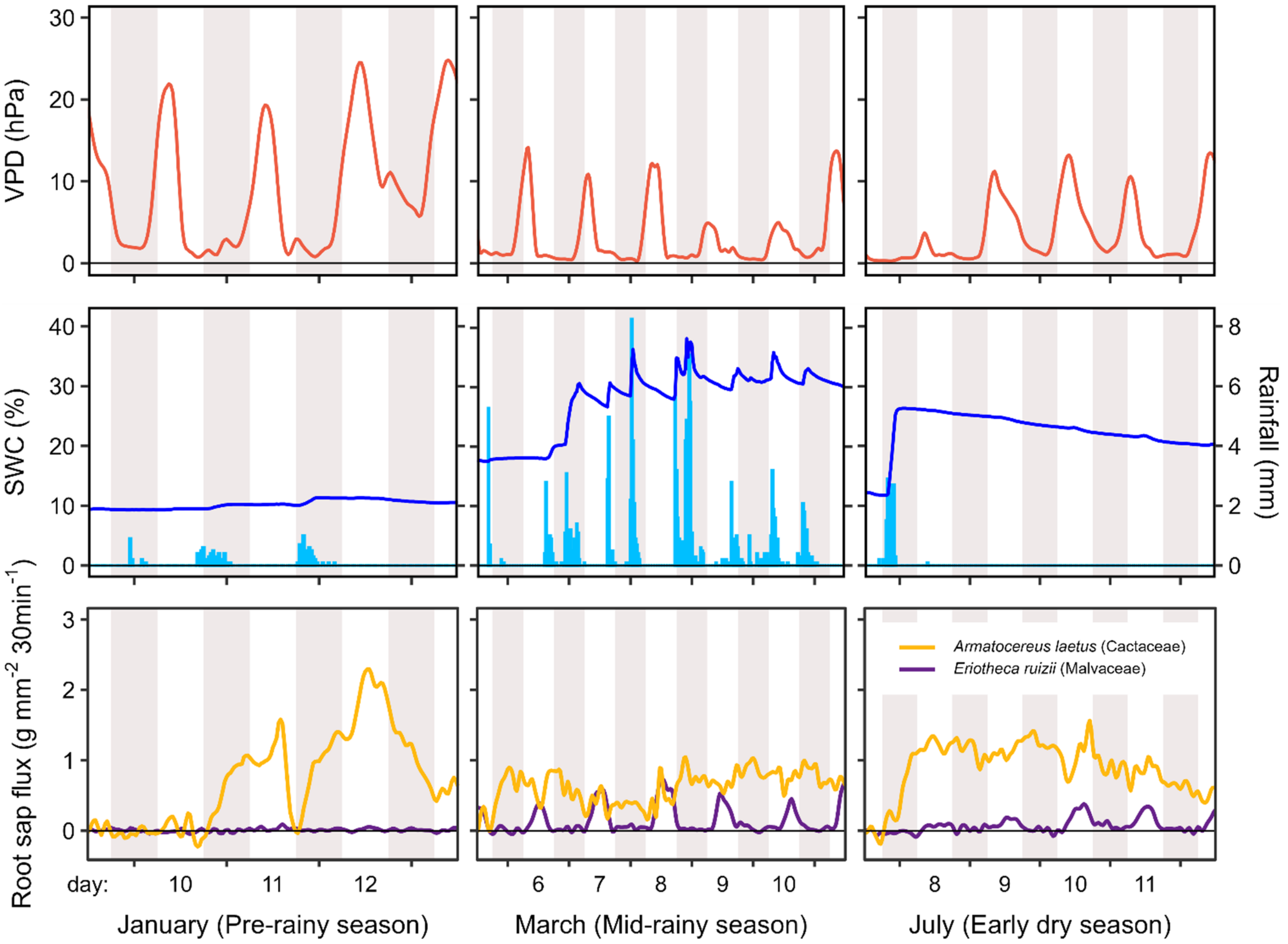

Fig. 3 Diurnal variation in root sap flux density of the dry-deciduous tree *Eriotheca ruizii* (purple line) and the tall cactus *Armatocereus laetus* (yellow line) on each four to six days and nights in the pre-rainy season (January), mid-rainy season (March) and early dry season (July) in 2023 in relation to rainfall amount (blue bars), soil water content (SWC, blue lines), and vapor pressure deficit (VPD, red lines), given as 30-min amounts or means. Nighttime periods are shaded in grey. Ticks on the X-axis mark mid-night

et al. 2017). Hence, the model we fitted was still a multiple regression, but the model also estimated the effect of (the sine and cosine of) daytime on residual standard deviation. In the model fitted for *A. laetus*, a QQ-plot revealed significant temporal autocorrelation. To cope with this, we applied downsampling to two randomly chosen data points (12 h apart) per day. Model stability was assessed in case of the *A. laetus* model by means of DF-beta values (Field 2005). For *E. ruizii*, we determined model stability by dropping individual measurements from the data, one at a time, and comparing the estimates derived from models fitted with the respective subsets with those obtained for the full dataset. The two approaches revealed both models to be of good stability (see Tables 3 and 4). For the *E. ruizii* model, we estimated 95% confidence limits of the model estimates and fitted values by means of a parametric bootstrap ($N = 1000$ bootstraps; function simulate of the package glmmTMB). Since the interaction between SWC and VPD was not significant in the model for *A. laetus*, we fitted the model again without the interaction and yet reported the results of the first model in Table S1. Semi-partial R^2 values (Jaeger et al. 2016) for individual fixed effects of the models were calculated for both *E. ruizii* and *A. laetus*, using the function r2beta from the r2glmm package (version 0.1.3; Jaeger 2025). For more details see the Supplementary Information.

Results

Root water uptake in the wet and dry season

Continuous measurements of root sap flux density (J_s) over a full dry and a full wet season from April 2022 to September 2023 revealed distinct seasonal root water uptake patterns in the four studied species in response to rainfall and soil water availability (Fig. 2). In the three drought-deciduous species *E. ruizii*, *C. trischistandra*, and *V. macracantha*, sap flux density closely followed seasonal SWC variation, with water uptake starting with soil rewetting upon the onset of the rains in February 2023 (Fig. 2). However, a closer look on the development of J_s during the rewetting period revealed differences between these three species: While for *C. trischistandra*, the tallest of the tree species studied, root water uptake was already observed prior to the start of the rainy season from about February 1st onwards, a pronounced increase associated with the onset of the rainy season occurred at approximately the same time in *C. trischistandra* and *V. macrantha*, while *E. ruizii* responded with delay of about two weeks. The patterns of the three species contrasted strikingly with the seasonal J_s course observed in the tall cactus *A. laetus*, which responded with root water uptake already to very small rainfall amounts (< 5 mm d^{-1}) in December and reached fairly high J_s rates in January, when the other species were still inactive. On the other hand, the cactus reached its annual peak in root water uptake already in Febuary 2023, when the soil moisture just began to increase, and it declined toward March, April and May, when soil moisture was highest. *A. laetus* responded with rapid J_s increases also to the two minor rainfall events during July and August in the 2023 dry season. The three deciduous species differed clearly from *A. laetus* in that they increased their J_s rate from February till late April/early May 2023 in response to soil rewetting. The four species further differed with respect to maximum root sap flux density recorded. The J_s peak reached by *C. trischistandra* in April/May 2023 was about three to four times higher than that of *V. macrantha* and *E. ruizii*, and roughly twice as high as that of *A. laetus* (Table 2, Fig. 2).

Diurnal patterns of root water uptake

Diurnal patterns of root sap flux density during a pre-rainy, a rainy and an early dry season are shown in Fig. 3 exemplarily for *E. ruizii*, a drought-deciduous C_3 tree, and *A. laetus*, a stem-succulent tall cactus with CAM metabolism, to visualize influences of soil moisture, VPD and photosynthetic pathway on water uptake activity. While the C_3 plant *E. ruizii* with assumed nighttime stomatal closure showed typical water uptake peaks at noon, when VPD was largest and stomatal conductance likely peaked, J_s revealed no overarching diurnal variation pattern in the CAM plant *A. laetus* (Figs. 3 and 4). During the mid-rainy season with highest soil moisture, a drop in root water uptake was visible in the second half of the daytime period (from 1 p.m. to 7 p.m.), which can be related to stomatal closure. However, in the pre-rainy and the early dry season with reduced soil moisture, the cactus absorbed soil water during day and night and showed a flow peak during daylight hours, similar to the C_3 plant (but with higher nighttime fluxes) (Fig. 4). Interestingly, root water

Table 2 Daily means (and standard error) of root sap flux density (g mm^{-2} 30 min^{-1}) for *Armatocerus laetus*, *Ceiba trischistandra*, *Eriotheca ruizii*, and *Vachellia macracantha* during the rainy season 2023 (February, March, April, May, June)

Species	Feb	Mar	Apr	May	Jun
Armatocereus laetus	1.26 (0.03)	0.69 (0.01)	0.48 (0.02)	0.50 (0.01)	0.25 (0.01)
Ceiba trischistandra	2.00 (0.09)	3.12 (0.09)	4.58 (0.22)	3.52 (0.13)	-
Eriotheca ruizii	0.22 (0.01)	0.60 (0.02)	0.86 (0.02)	0.66 (0.01)	0.40 (0.01)
Vachellia macracantha	0.87 (0.03)	1.26 (0.02)	1.49 (0.04)	0.93 (0.03)	-

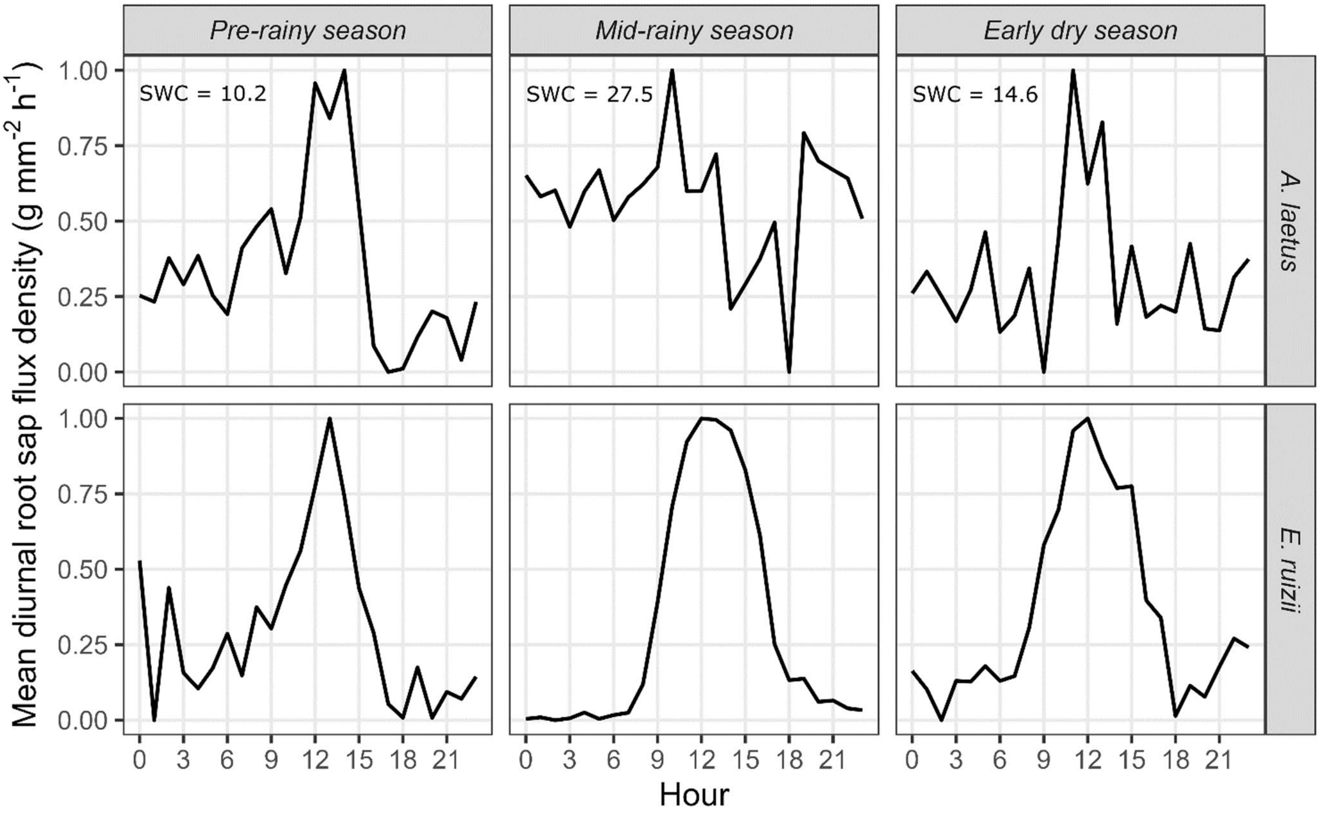

Fig. 4 Mean diurnal curve of root sap flux density (g mm^{-2} h^{-1}) for *Armatocereus laetus* and *Eriotheca ruizii* in the pre-rainy season (January), mid-rainy season (March) and early dry season (July) in 2023 given in relative units (1 = maximum). Mean soil water content (SWC, vol%) is given for the three periods as well

uptake continued during the night in these two periods, even though VPD approached zero (Fig. 3).

The species comparison further demonstrates that root water flux is generally smaller per cross-section (i.e. flow velocity is lower) in *E. ruizii* roots than in the cactus roots, since not only daily peak flux densities were lower, but the flux was usually maintained for only 12 h per day or less, while the cactus roots regularly took up water for almost 24 h (day and night) (Figs. 3 and 4).

Factors controlling root water uptake

The regression models revealed that, in general, there was an effect of VPD and SWC on root sap flux density in *E. ruizii* (full-null model comparison, likelihood ratio test: X^2= 3195, df=3, P<0.001), and the interaction between VPD and SWC was significant (Table 3, Fig. 5). More specifically, a rising VPD caused increased root water uptake especially when SWC was high during the rainy season, as visible during the mid-rainy and early dry season (Figs. 3 and 4, middle and right column). Other significant factors driving J_s of *E. ruizii* were time of day, radiation intensity, and crown status (leafless vs. leaf-bearing) (Table 3, Fig. S1).

In *A. laetus*, in contrast, VPD and SWC had an overall effect on root sap flux in the full-null model comparison ($F_{2,963}$=172.108, P<0.001), but when the predictors were tested individually, our model detected only a marginal influence of VPD on sap flux density (P=0.077; Table 4), and the relationship was negative (Fig. 6). On the other hand, the influence of SWC was significant and positive (Table 4, Fig. 6), and radiation intensity was another significant driver (Table 4, Fig. S2).

Discussion

Our continuous sap flux measurements on small-diameter roots of four characteristic TDF species revealed contrasting seasonal water uptake patterns, in particular during the process of soil re-wetting. The differences were particularly striking between the three deciduous tree species and the cactus species with different photosynthetic pathways (Butz et al. 2018; de Souza et al. 2020). Root sap flux ceased completely in all four studied species in June 2023, three to four weeks after the last larger wet-season rain event, when soil moisture in the topsoil had reached a constant level of about 10 vol%, which seems to represent the moisture

Table 3 Results of the root sap flux model for *Eriotheca ruizii*. Given are estimates, their standard errors, 95% confidence intervals, and results of significance tests for the predictors VPD, SWC, time of day, radiation intensity, crown condition (leafless vs. leaf-bearing), and the VPD x SWC interaction

term	estimate	SE	CI_{lower}	CI_{upper}	X^2	df	*P*	min	max
(Intercept)	0.033	0.001	0.031	0.036				0.054	0.054
VPD (1)	0.013	0.001	0.011	0.014				0.012	0.013
SWC (1)	0.062	0.001	0.060	0.064				0.062	0.062
Sin(daytime) (2)	-0.002	0.001	-0.004	-0.001	20.850	2	**0.007**	-0.002	-0.002
Cos(daytime)	-0.005	0.001	-0.007	-0.003				-0.005	-0.005
Radiation	<0.001	<0.001	<0.001	<0.001	792.928	1	**<0.001**	0.031	0.031
Crown (3)	0.039	0.002	0.035	0.043	357.410	1	**<0.001**	0.039	0.039
VPD x SWC (1)	0.023	0.001	0.022	0.024	1772.652	1	**<0.001**	0.023	0.023

(1) log-transformed and then z-transformed to a mean of 0 and a standard deviation (sd) of 1;

orig. means (sd): natural log. of VPD: 1.727 (0.984) and natural log. of SWC: 2.559 (0.440)

(2) the indicated test refers to the overall effect of daytime

(3) dummy coded factor with levels: leafless (reference level) and leaf-bearing

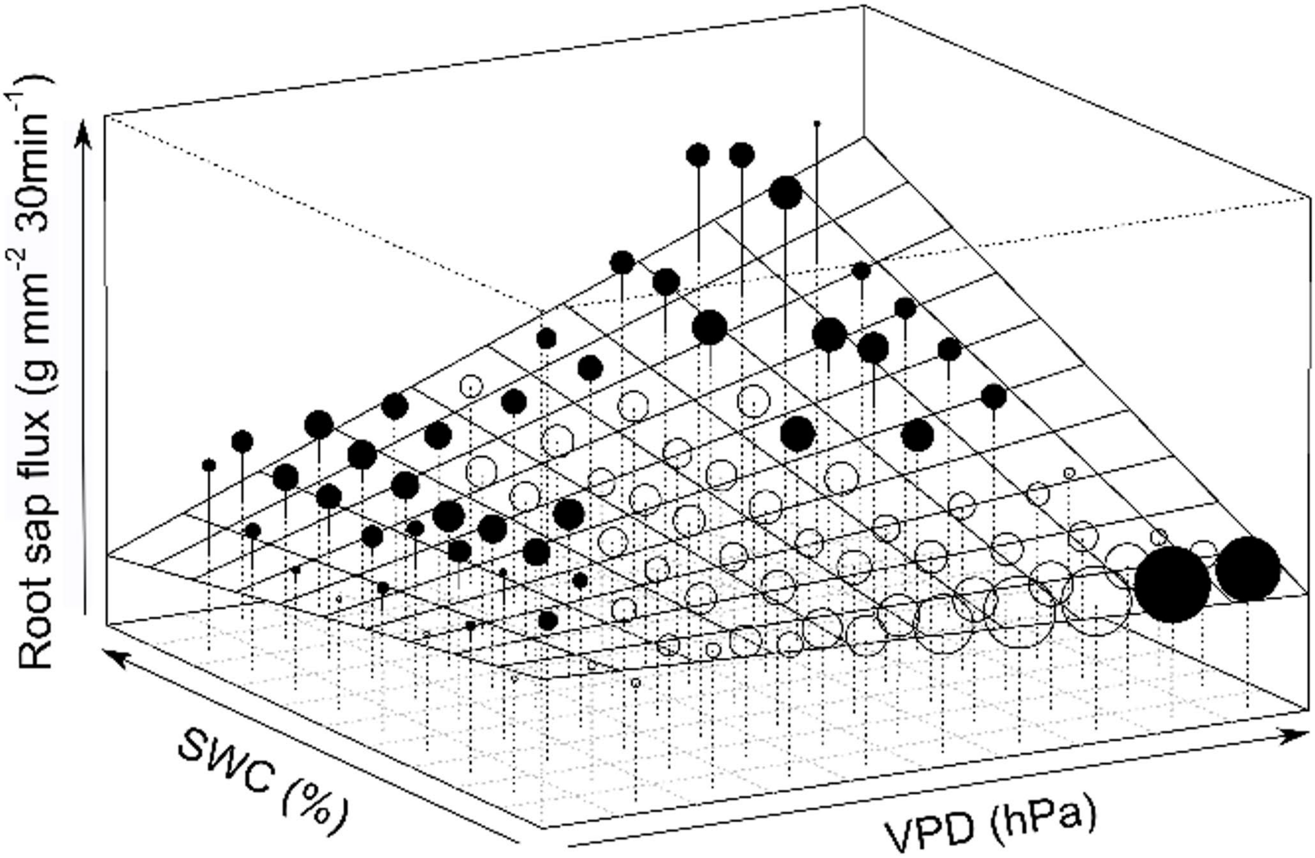

Fig. 5 Effects of SWC and VPD on root sap flux density (surface area) in *Eriotheca ruizii*, for daytime and radiation intensity being at their average (crown status dummy-coded and then centered, $R^2=0.19$, $P<0.001$). Dot volume depicts the number of samples per cell. Values below the fitted model surface are depicted as open, values above the surface as filled dots ($n=23529$). Note that during the rainy season (high SWC values; backside of the 3D plot), VPD had a clear positive effect on root sap flux, whereas during the dry season (low SWC values; frontside of the 3D plot), VPD hardly affected root sap flux

threshold where root water uptake ceases in this silt- and clay-rich soil. The sap flux measurements further demonstrate that all monitored roots of the four species were able to resume water absorption after a dormant period of more than six months with the start of the next rainy season, which indicates that any drought-induced reduction in root functioning (e.g. through drought-induced embolism in the root xylem or lacunae formation in the root cortex; Cuneo et al. 2021) was not permanent and that root water uptake recovered rapidly with the onset of the rainy season. Thus,

Table 4 Results of the root sap flux model for *Amatocereus laetus*. Given are estimates, their standard errors, 95% confidence intervals, and results of significance tests for the factors VPD, SWC, time of day, and radiation intensity. Also given are minimum and maximum values of model estimates obtained by the exclusion of individual sap flux measurements from the model, one at a time

term	estimate	SE	CI_{lower}	CI_{upper}	F	df	*P*	min	max
(Intercept)	-0.784	0.111						-0.813	-0.739
VPD (1)	-0.037	0.021	-0.078	0.004	3.835	1	0.077	-0.045	-0.032
SWC (1)	0.399	0.033	0.334	0.465	140.132	1	**<0.001**	0.390	0.420
Sin(daytime) (2)	0.005	0.021	-0.035	0.045	0.290	2	0.839	<0.001	0.009
Cos(daytime)	0.015	0.026	-0.036	0.066				0.009	0.023
Radiation	<0.001	<0.001	<0.001	<0.001	6.912	1	**<0.001**	<0.001	<0.001

(1) log-transformed

(2) the indicated test refers to the overall effect of daytime

Statistical significance of all predictors was tested using *F*-tests with denominator degrees of freedom of 963

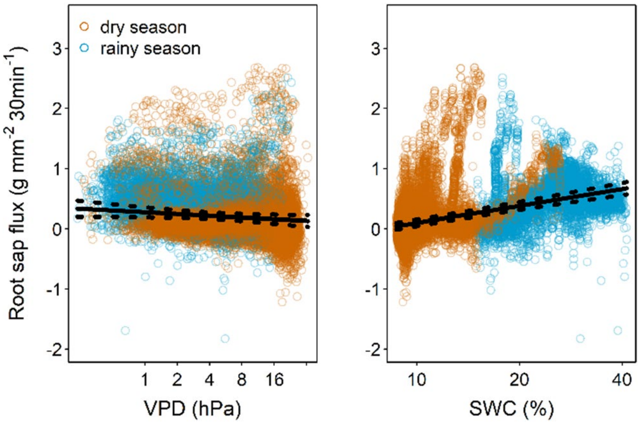

Fig. 6 Root sap flux density in *Amatocereus laetus* as a function of VPD (left, $R^2=0.004$, $P=0.068$) and SWC (right, $R^2=0.13$, $P<0.001$). Lines show the fitted model with all other predictors being at their average (dotted lines: 95% confidence intervals) ($n=974$)

the absorbing roots of these TDF functional types must be well adapted to severe soil desiccation, either through a high drought resistance or by means of partial drought avoidance (shedding of finest rootlets) and the capacity for rapid root tip regrowth, or a combination of both.

A closer look on the root response to the onset of rainfall from December 2022 onwards shows that the tall cactus was able to respond nearly immediately (within roughly 6 h) to the first small rainfall events in mid-December with significant water uptake (peak sap flux densities > 15 g mm^{-2} d^{-1}), when a soil moisture increase was hardly measurable, and long before the three deciduous tree species were responding. Correspondingly, in mid-January, when more continuous rainfall started, *A. laetus* reached already peak water uptake rates of >50 g mm^{-2} d^{-1}, in stark contrast to the three other species. In stem-succulent *C. trischistandra* and semi-deciduous *V. macracantha*, significant root water uptake started only after a delay of about eight weeks in mid-February; in root-succulent *E. ruizii*, water uptake resumed even later around February 20. These contrasts are partly explained by different responses of the species' leaf phenology to soil rewetting (Borchert 1994; Rivera and Borchert 2001; Poorter and Markesteijn 2008; Lohbeck et al. 2015; Butz et al. 2017).

Despite the observation of rapid water uptake recovery with the first rains, the cactus *A. laetus* showed across seasons a fairly low soil moisture influence on water absorption, as demonstrated by the fact that the lowest J_s rates were recorded in the period with elevated soil moirsture (March), while peak rates occurred in a fairly dry period (January). Thus, the root sap flux pattern of the cactus can be characterized as highly opportunistic, with water uptake being closely tied to erratic rainfall events rather than SWC differences between dry and wet seasons. Moreover, the apparent decoupling of uptake from VPD in the mid-rainy and early dry season suggests that changes in plant-internal water potential gradients in the succulent organs are more influential than atmospheric drivers of water flux. The rapid root response to even light rain events during a long drought fits to uptake patterns observed in the leaf-succulent *Agave deserti* (Graham and Nobel 1999). This first amount of water acquired will initially replenish the depleted water storage in the succulent stem.

The high responsiveness of the root water uptake of the cactus to small soil moisture peaks is most plausibly explained by the existence of a shallow, but wide-spreading root system in the topsoil, the capacity to rapidly grow new rootlets after rewetting, and possibly the ability for hydraulic recovery of embolized roots (Kirschner et al. 2021). Desert succulents such as *Ferocactus acanthodes* and *Opuntia* and *Agave* species are able to grow ephemeral rain roots from lateral root buds within a few hours after a rainfall event (Nobel and Sanderson 1984; Nobel 1988, 2002; Palta and Nobel 1989; Snyman 2006; Kirschner et al. 2021). These rain roots possess a higher hydraulic conductivity than the established longer-living roots (Kirschner et al. 2021) and can therefore rapidly take up water from even light rains of only few mm. Thus, dryland succulents combine a number of root morphological and physiological adaptations that may offer them advantages over dry forest trees in terms of the exploitation of small and erratic rainfall events (Nobel 1988; Nobel and Huang 1992; Graham and Nobel 1999; Snyman 2006).

In stark contrast to the cactus, the root-succulent tree *E. ruizii* was unresponsive to small rainfall amounts at the end of the dry season, but the species showed a clear increase in uptake from the drier to the wetter periods. In addition, VPD was an important driver of root water uptake in the mid-rainy and the early dry season with wetter soil, a response not observed in the cactus.

Among the three deciduous tree species, *C. trischistandra* was the only one that flushed new foliage a few weeks prior to the onset of the rainy season, likely enabled by the considerable stem water reserves of this stem-succulent species (Rivera and Borchert 2001; Rivera et al. 2002; Chapotin et al. 2006). However, significant root water uptake started only several weeks later with the first larger rainfall events, suggesting that photosynthesis and transpiration were maintained in that period mostly through stored water (Chapotin et al. 2006). With proceeding soil rewetting, *C. trischistandra* then rapidly increased its root water uptake and reached the highest sap flux densities of all four species, matching the stem sap flux data of Butz et al. (2018) for this species at our study site.

The semi-deciduous *V. macracantha* differed from the other three species in its leaf phenology by never being completely leafless and instead continuously exchanging its leaves (Williams et al. 1997). Despite this behavior, root water uptake was restricted to the rainy season in a similar manner as in *C. trischistandra* and *E. ruizii*. This Fabaceae species possesses a fairly large root system (pers. observ.) and is thought to reach deep soil layers (Cordero et al. 2016), which might well explain the species' ability to maintain its leaves for longer. The higher specific leaf area (SLA) of *C. trischistandra* (154 cm^2/g) and *E. ruizii* (131 cm^2/g) compared to *V. macracantha* (72 cm^2/g) further suggests a longer leaf lifespan of the latter species.

The example of the deciduous tree *E. ruizii* and the cactus *A. laetus* demonstrates the complex interplay of photosynthetic pathway and related stomatal regulation, on the one hand, and of climatic and edaphic drivers, on the other, on the diurnal patterns of root water uptake. Consistent with the typical physiological behavior of a C3 plant, *E. ruizii* closes stomates during the night and thus restricts transpiration and consequently root water uptake to the daylight hours. Root sap flux was mainly driven by variation in both SWC and VPD (and radiation which is linked to VPD), with J_s generally increasing with SWC. Beyond a certain SWC threshold, root sap flux was mainly dependend on VPD: Js increased with VPD at low saturation deficits, but declined again when VPD exceeded about 10 hPa. Since rainfall often occurred during the night at our site, stomatal conductance and water uptake during the day were mainly controlled by VPD and less so by the rewetted soil. Apparently, the corresponding VPD threshold level for transpiration and sap flux varies with soil water content (e.g. Gao et al. 2022), which may explain the interaction between atmospheric and edaphic drivers of root sap flux found in our study.

Contrary to expectation, the cactus took up water during the main part of the rainy season not only during the night but also during daytime without a clear diurnal cycle. Only in periods with high soil moisture, the species showed the expected daytime drop in water uptake due to stomatal closure. The maintenance of positive nocturnal sap flux in the cactus, even during periods of high rainfall, is consistent with CAM physiology, where nocturnal stomatal opening supports CO_2 uptake while minimizing transpiration. In fairly dry soil (during the pre-rainy and early dry season), we measured even higher uptake rates over the day than in the night, which resembles a C_3 species. In fact, in some CAM plants, stomatal opening for CO_2 assimilation during the daylight hours has been observed under well-watered conditions (Hartstock and Nobel 1976; Nobel 1988), as for example in *Opuntia* species (Hanscom and Ting 1978; Acevedo et al. 1983). Yet, our data show this behavior for a fairly dry, and not the wet season. This suggests that the cactus opened its stomates during the day to built a transpiration-driven root-to-plant soil water potential gradient that enables root water uptake, though at the cost of transpiration. Water uptake during daylight hours in the cactus as in the morning during the mid-rainy season could also be driven by plant-internal water redistribution between parenchymatic (water storing) and chlorenchymatic (photosynthesizing) tissues, enabled through nocturnal potential drops in the malate-producing chlorenchyma (Schulte and Nobel 1989; Holbrook 1995; Nobel and Loik 1999; Lüttge 2008), which may build a negative root-to-stem water potential gradient in the cactus at the end of the night. Finally, the very large hydraulic capacitance of the succulent stem will largely decouple root water uptake and transpiration in *A. laetus*, with transpirational water loss easily replenished from internal storage without the need for root water uptake. These mechanisms can plausibly explain water uptake over the full day and night in cacti (Holbrook1995).

On certain occasions, the sap flow sensors recorded reverse flow in the roots of both *E. ruizii* and *A. laetus*. While the flow densities were usually small and may thus partly be attributable to measuring inaccuracies, it is possible that the sap indeed moved temporarily in direction of the root tips, when the water potential gradient reversed during extreme soil desiccation. Further studies have to show whether reverse flow is in fact leading to water losses from the roots, given the specific adaptations that succulent desert plants may possess to prevent water flow from roots to the soil.

Conclusion

Our 17 month-measuring campaign is to our knowledge the first study in a tropical dry forest that has monitored the activity of root segments close to the absorbing 1st-order fine roots in situ. The study revealed contrasting water uptake patterns in four TDF plant life forms differing in phenology, hydraulic capacitance, rooting patterns, and photosynthetic pathway. While the deciduous trees exhibited seasonally varying uptake patterns and root sap flux constrained to periods of higher soil water availability and leaf presence, demonstrating their specific drought-avoidance strategy, the tall cactus *A. laetus* with CAM metabolism displayed a highly opportunistic water uptake pattern, with rapid root sap flux increases after isolated rainfall events even during the dry season and no signs of a drought-induced impairment of root system functionality. Moreover, the expected primarily nocturnal root water uptake was observed in the cactus only during the mid-rainy season but not in periods with drier soil. The direct comparison of the deciduous root-succulent tree *E. ruizii* and the stem-succulent cactus *A. laetus* demonstrates that the cactus is clearly superior in its root water uptake capacity not only in periods with low or erratic rainfall, but also during the wet season, because its roots are active also during the night, thereby more than doubling the amounts of water absorbed in comparison to *E. ruizii*.

Future studies should focus on the vitality, growth and mortality of the fine roots (<2 mm in diameter) of TDF plants during and after the dry season, which is notoriously difficult to achieve in the desiccated and compacted soil. Yet, deepening our understanding of fine root system functioning in TDFs is indispensable for modelling the water fluxes in these systems and for better predicting how vegetation structure and composition might change with advancing climate warming and drying.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00468-026-02784-5.

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Author contributions CL and JH conceived the study idea and developed the study. CL, JH and LW installed the sensors in the field. Sensor construction and calibration, data collection and analysis were performed by LW, HC, RM, JG, DW, KT, SS and JB. The first draft of the manuscript was written by LW and CL; all authors commented on the subsequent versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated and/or analysed during the current study are available in the RESPECT projects' database "FOR816 data warehouse (FOR816dw)", https://vhrz669.hrz.uni-marburg.de/tmf_respect/data_pre.do?cmd=showall, under the dataset ID 2064.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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