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Interaction of rainfall events and atmospheric demand regulates sap velocity in dry-land trees

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Abstract

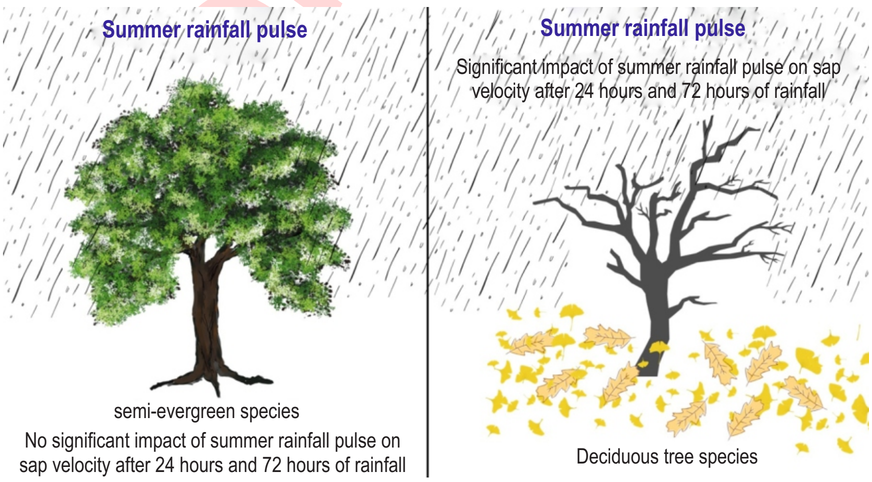
Aim: Understanding how rainfall pulses influence tree water use is essential for interpreting ecohydrological functioning in arid and semi-arid forest ecosystems. This study evaluated summer rain pulse driven changes in sap velocity dynamics of *Anogeissus latifolia* and *Azadirachta indica* tree species.

Methodology: Continuous sap velocity measurements were obtained using thermal sap flow sensors installed on mature trees. Sap velocity responses were analysed for immediate (24 hr) and delayed (72 hr) rainfall phases. Statistical analyses included ANOVA and regression modelling of sap velocity with vapour pressure deficit (VPD).

Results: Summer rain pulses significantly increased sap velocity in *A. latifolia* ($F = 16.78$, $p < 0.001$), with mean sap velocity increasing from 0.47 ± 0.33 to 0.64 ± 0.42 cm hr^{-1}. In contrast, *A. indica* showed no significant response ($F = 0.27$, $p = 0.607$). Vapour pressure deficit (VPD) exhibited a weak positive relationship with sap velocity in both species, although atmospheric coupling was substantially stronger in *A. indica* ($R^2 = 0.161$, $p < 0.001$) than in *A. latifolia* ($R^2 = 0.016$, $p = 0.011$).

Interpretation: Results indicate that phenology and canopy condition strongly regulate tree hydraulic response to rainfall events. Deciduous tree (*A. latifolia*) exhibited stronger rainfall-driven increase in sap velocity, whereas semi evergreen *A. indica* maintained comparatively stable transpiration patterns, indicating contrasting hydraulic regulation strategies.

Key words: Ecohydrology, Rainfall pulse, Sap velocity, Semi-arid forests, Transpiration dynamics



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Introduction

Tree transpiration represents a key component of terrestrial ecohydrological processes, regulating plant water relations, energy balance, and ecosystem carbon-water coupling under changing environmental conditions (Steppe *et al.,* 2010; Nelson *et al.,* 2020). The mechanism of transpiration is extremely complex (Pérez-Anta *et al.,* 2024) and is governed by several environmental and physiological factors, as well as by the interplay of different factors (Chen *et al.,* 2014; Ajjur and Al-Ghamdi, 2021). Relative humidity, air temperature, solar radiation (Keyimu *et al.,* 2017), vapor pressure deficit (VPD) (Wu *et al.,* 2020), wind speed (MacDonald *et al.,* 2018), soil temperature (Keyimu *et al.,* 2017), precipitation (Huang and Zhang, 2016; Wang *et al.,* 2017; Mu *et al.,* 2022; Li *et al.,* 2024) and soil moisture (Yu *et al.,* 2021) are the examples of environmental factors and major external determinants of tree transpiration. Whereas, leaf area index (Sebastiani *et al.,* 2023), different attributes of leaves (leaf size, leaf shape, its orientation) (Kozlowski and Pallardy, 1997), stomata size, stomatal density, the morphology of guard cell (Bertolino *et al.,* 2019), stomatal conductance (Liu *et al.,* 2024) and leaf hydraulic conductance (Li *et al.,* 2021) are among the physical and physiological factors or intrinsic factors of trees that regulate transpiration.

Tree transpiration is measured indirectly through the measurement of sap flow velocity (Wan *et al.,* 2024). Sap flow measurements, particularly those utilizing the heat ratio method (HRM), provide a direct, reliable, and high-resolution approach for quantifying tree water use and transpiration dynamics, including low and reverse flow rates (Burgess *et al.,* 2001). The vegetation-water relations in dry-lands are more complex and unique (Küçük *et al.,* 2022), because, in arid and seasonally dry ecosystems, water availability is highly variable and episodic rainfall events can strongly influence the physiological responses of plants by altering the soil moisture availability and atmospheric demand (Tang *et al.,* 2022). Understanding the way how trees respond to short-term precipitation pulses is, therefore, essential for predicting ecosystem functioning and vegetation resilience under increasing climatic variability (Huxman *et al.,* 2004).

Previous studies have demonstrated that transpiration responses to rainfall are controlled not only by root-zone soil moisture recharge, but also by atmospheric drivers such as VPD and solar radiation (Meinzer *et al.,* 2003; Liu *et al.,* 2017). In semi-arid regions, trees often exhibit contrasting hydraulic strategies depending on their phenological traits. Deciduous species may display reduced transpiration during dry seasons due to leaf shedding and hydraulic limitation, thereby decoupling from atmospheric demand. In contrast, evergreen species maintain physiological activity and canopy conductance even under water stress, resulting in higher sensitivity to VPD and different physiological recovery trajectories following rainfall (Zhang *et al.,* 2022; Tang *et al.,* 2025). Despite increasing ecohydrological attention to rainfall pulse dynamics in water-limited systems, comparative assessments of immediate versus delayed transpiration responses across contrasting functional types remain limited. In particular, very little information is available on short-term sap velocity responses of dominant dry tropical tree species from Indian arid and semi-arid ecosystems under episodic summer rainfall conditions. Furthermore, the relative influence of rainfall pulses and atmospheric demand on transpiration regulation in deciduous and semi-evergreen tree species remains insufficiently understood. The timing and magnitude of sap flow responses following discrete rainfall events can, therefore provide critical insights into hydraulic recovery, stomatal regulation, and species-specific drought adaptation strategies under increasingly variable climatic conditions.

The present study investigates sap velocity dynamics in two contrasting tree species, the deciduous *A. latifolia* and the evergreen (semi-evergreen) *A. indica,* under summer rainfall conditions in arid and semi-arid environments. Using high-resolution HRM sap flow measurements, immediate (24 hr) and delayed (72 hr) responses of sap velocity to rainfall events, species-specific differences in transpiration dynamics, and the influence of atmospheric demand, particularly vapor pressure deficit, on sap flow behavior were evaluated. It is hypothesized that rainfall-induced changes in sap velocity would differ between species due to contrasting phenological strategies, with stronger rainfall sensitivity expected in the deciduous species during periods of reduced canopy activity. However, as the two species were studied under different site conditions, the observed responses may also partially reflect the environmental differences between locations.

Materials and Methods

Study species and experimental sites: Sap flow measurements were conducted in two tree species representing contrasting phenological strategies: *A. latifolia* (deciduous) and *A. indica* (semi-evergreen). The study was primarily conducted at the ICFRE-AFRI Experimental Site, Jodhpur [arid zone; Long: 73°.030'64'', Lat: 26°.230'86''], focusing on *A. indica* and at Sitamata Wildlife Sanctuary, Chittorgarh [semi-arid zone; Long: 74°.49'167'', Lat: 24°.286'94''], focusing on *A. latifolia. A. indica* is generally classified as an evergreen to semi-evergreen species that retains functional canopy cover most of the year, with a brief period of leaf shedding and new leaf emergence during March-April under dry tropical conditions. *A. latifolia* is a deciduous species that exhibits substantial seasonal leaf shedding during dry periods, resulting in reduced canopy activity prior to monsoonal rainfall. During the monitoring period (April-July 2024), prevailing climatic conditions differed notably between the two locations (Table 1).

Sap flow measurements: Sap velocity was monitored using Heat Ratio Method-based sap flow sensors. Within each species, four representative trees were selected based on diameter at breast height (DBH) and designated as the main tree and three replicates (R1, R2, and R3).The DBH ranged from 10.8 to 24.5 cm for *A. latifolia* and from 16.4 to 27.1 cm for *A.indica.* To capture

Table 1: Sap velocity response and peak timing across rainfall phases

Species	Response scale	Sap velocity (cm h^{-1}) (Mean ± SD)	Peak time (hh:mm) (Mean ± SD)
Anogeissus latifolia	Immediate (24 h-BR)	0.47 ± 0.33	14:45 ± 00:57
Anogeissus latifolia	Immediate (24 h-PR)	0.64 ± 0.42	13:08 ± 03:45
Anogeissus latifolia	Delayed (72 h-BR)	0.47 ± 0.33	12:00 ± 04:58
Anogeissus latifolia	Delayed (72 h-PR)	0.63 ± 0.45	14:30 ± 04:02
Azadirachta indica	Immediate (24 h-BR)	5.99 ± 4.57	14:30 ± 01:17
Azadirachta indica	Immediate (24 h-PR)	5.72 ± 4.72	13:15 ± 01:30
Azadirachta indica	Delayed (72 h-BR)	5.74 ± 2.59	10:45 ± 02:13
Azadirachta indica	Delayed (72 h-PR)	5.61 ± 2.53	11:00 ± 01:50

BR-Before rain, PR-Post rain, n=96

radial variations in water transport, the Main tree was equipped with three sap flow meters installed at different radial positions (M1, M2, and M3). Similarly, the replicate trees were equipped with two sap flow meters each (named R11, R12; R21, R22; and R31, R32). Sensors were installed at breast height (1.3 m) following standard installation protocols. To minimize the wounding effect and improve thermal coupling of the needles to the sapwood, inert silicon vacuum grease was applied to drill bits and probes prior to insertion. After careful removal of the bark, the probes were inserted into the xylem. While sensors were capable of multi-depth readings, outer sap velocity measured at a depth of 1.25 cm was used as primary measure of sap velocity for this analysis. Sap velocity (cm hr^{-1}) was logged hourly and values represent direct sensor-based measurements and were not normalized by sapwood area. Sensors malfunctioning or showing unrealistic values were excluded. Continuous sap velocity measurements were conducted from April 2024 to July 2024, focusing on summer rainfall events, with observations recorded hourly. Data were aggregated at tree level by taking the average values from active sensors installed on the same individual.

Environmental measurements: Simultaneous measurements of air temperature (°C), relative humidity (%) and solar radiation were obtained hourly during the monitoring period. Vapor pressure deficit (VPD) was calculated from air temperature and relative humidity using the following standard psychrometric relationship:

$$VPD\ (kPa) = 0.6108 \times \exp[(17.27 \times Ta) / (Ta + 237.3)] \times (1 - RH/100)$$

where, VPD is the Vapour Pressure Deficit (kPa); Ta is the Air temperature (°C) and RH is the Relative humidity (%)

Rainfall event classification: Rainfall events exceeding 1 mm, as recorded by the weather station, were considered for analysis. Sap flow data were categorized relative to rainfall events to assess short-term and delayed physiological responses. Four temporal phases were defined:

- Twenty-four hours before rainfall (immediate pre-rain phase)
- Twenty-four hours after rainfall (immediate response phase)
- Seventy-two hours before rainfall (delayed pre-rain phase)
- Seventy-two hours after rainfall (delayed response phase)

These phases were used to evaluate both immediate and extended responses of tree water use to rainfall events.

Data processing: Raw datasets were cleaned to remove erroneous values and non-functional sensor records. Data were aggregated at tree level by averaging values from active sensors installed on same individual. Peak daily sap velocity timing was determined based on hourly maxima. Sap velocity was selected as the primary response variable for analysis due to its direct representation of sap flow dynamics independent of tree-specific scaling factors.

Statistical analyses: Statistical analyses were performed in R software. Differences in sap velocity between rainfall phases and response scales were assessed using analysis of variance (ANOVA). Species-specific analyses were conducted to evaluate contrasting physiological responses. Linear regression models were used to assess relationships between sap velocity and vapor pressure deficit (VPD).Summary statistics were expressed as mean ± S.D.

Results and Discussion

Sap velocity dynamics differed markedly between *A. latifolia* and *A. indica.* These differences in absolute magnitude and environmental sensitivity likely reflect a combined influence of contrasting species-specific ecohydrological strategies (deciduous vs evergreen) and different site conditions (Jian *et al.,* 2016). The deciduous *A. latifolia* exhibited clear sensitivity to rainfall events, whereas sap velocity in the evergreen *A. indica* remained comparatively stable and appeared primarily influenced by atmospheric drivers. Rainfall pulse responses in dryland ecosystems are frequently characterized by rapid but transient physiological adjustments driven by short-term soil moisture recharge and changes in plant hydraulic status (Ogle and Reynolds, 2004; Feldman *et al.,* 2024). Pulse-reserve theory suggests that episodic rainfall events temporarily alleviate hydraulic constraints, allowing increased transpiration even

Table 2: Statistical analysis of rainfall and atmospheric effects on sap velocity

Species	Analysis	Factor	Statistic	p-value	Result
Anogeissus latifolia	Two-way ANOVA	Rain phase	F = 16.78	<0.001	Significant
Anogeissus latifolia	Two-way ANOVA	Response scale (24h vs 72h)	F = 0.03	0.853	Not significant
Anogeissus latifolia	Linear regression	VPD	R^2 = 0.016	0.011	Weak but significant
Azadirachta indica	Two-way ANOVA	Rain phase	F = 0.27	0.607	Not significant
Azadirachta indica	Two-way ANOVA	Response scale	F = 0.23	0.632	Not significant
Azadirachta indica	Linear regression	VPD	R^2 = 0.161	<0.001	Significant

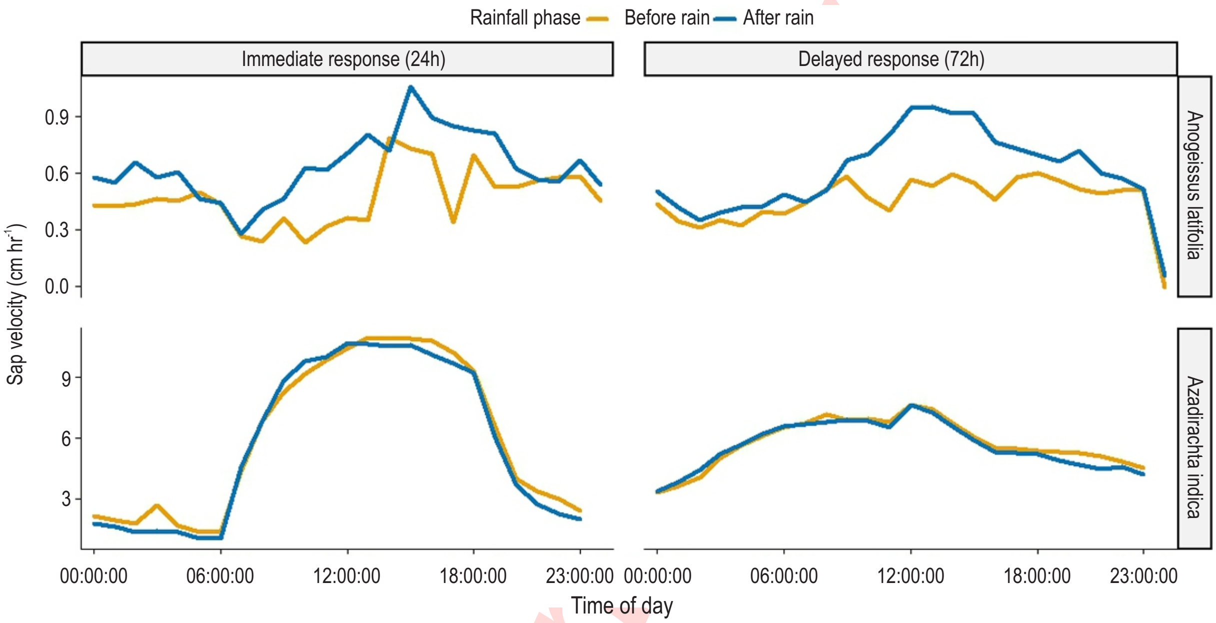

Fig. 1: Diurnal variation in sap velocity of *Anogeissus latifolia* and *Azadirachta indica* under immediate (24 hr) and delayed (72 hr) rainfall response phases. Lines represent mean sap velocity (cm hr^{-1}) across time of day under before-rain (BR) and post-rain (PR) conditions. Panels are separated by species and response scale to illustrate short-term and delayed hydrological responses.

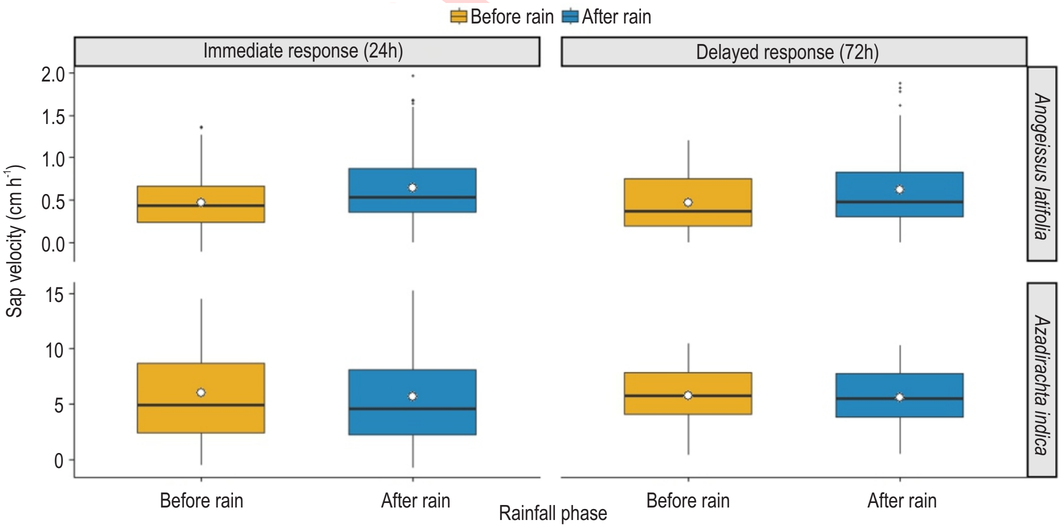

Fig. 2: Comparison of sap velocity distribution between rainfall phases for immediate (24 hr) and delayed (72 hr) response periods. Boxplots show median, interquartile range and variability of sap velocity (cm hr^{-1}) for *Anogeissus latifolia* and *Azadirachta indica* under before-rain (BR) and post-rain (PR) conditions. White points indicate mean values.

Table 3: Linear regression analysis showing relationship between vapour pressure deficit (VPD) and sap velocity in two tree species

Species	Regression equation	Intercept (± SE)	VPD slope (± SE)	R^2	F-value	P-value	Interpretation
Anogeissus latifolia	Sap velocity = 0.344 + 0.114 × VPD	0.344 ± 0.084	0.114 ± 0.045	0.016	6.45	0.011	Weak but significant positive response
Azadirachta indica	Sap velocity = 1.509 + 0.902 × VPD	1.509 ± 0.527	0.902 ± 0.105	0.161	73.25	<0.001	Positive relationship indicating stronger atmospheric sensitivity

under otherwise water-limited conditions (Schwinning and Ehleringer, 2001; Tang *et al.,* 2022; Fang *et al.,* 2023). In such systems, the magnitude and duration of plant responses depend on both rooting depth and canopy phenology, as well as the interaction between soil moisture availability and atmospheric demand (Vico *et al.,* 2015; Wang *et al.,* 2019).

The contrasting patterns observed between *A. latifolia* and *A. indica*, therefore, provide an opportunity to evaluate the manner in which functional traits influence a balance between the soil moisture-driven and atmospheric-driven transpiration controls. While deciduous species often exhibit rapid, but short-lived responses to rainfall pulses due to seasonal reductions in leaf area and hydraulic activity, evergreen species may maintain more stable physiological function, relying less on episodic surface moisture inputs and more on continuous regulation through stomatal sensitivity to environmental drivers (Rocha *et al.,* 2025). Rainfall significantly increased sap velocity in *A. latifolia* (Table 2; Fig. 2). During the immediate response phase (24 hr), the mean sap velocity increased from 0.47 ± 0.33 cm hr^{-1} before rainfall to 0.64 ± 0.42 cm hr^{-1} after rainfall. A comparable increase was observed during the delayed response period (72 hr), rising from 0.47 ± 0.33 cm hr^{-1} to 0.63 ± 0.45 cm hr^{-1}. The increase in sap velocity following rainfall likely reflects transient improvement in plant water status or soil moisture availability. In semi-arid environments, short rainfall pulses can rapidly reduce plant water stress, enhancing hydraulic conductivity and stomatal opening even without major changes in canopy development (Huxman *et al.,* 2004; Huang and Zhang, 2016; Ma *et al.,* 2025).

Given that *A. latifolia* exhibited reduced leaf area during summer period, rainfall-induced increase in sap velocity may represent enhanced stem recharge or temporary increase in the residual transpiration rather than sustained canopy-level activity. Another possible explanation for increased sap velocity following rainfall is enhanced stem capacitance recharge and improved xylem hydraulic conductivity (Zhang *et al.,* 2025). Under prolonged dry conditions, embolism formation and reduced hydraulic efficiency may restrict water transport (Zahedi *et al.,* 2025). Rainfall events may partially restore hydraulic function by increasing soil water potential and reducing xylem tension. Such short-term increases in sap velocity have been reported in pulse-driven systems where trees capitalize on transient resource availability without necessarily increasing long-term transpiration capacity (Schwinning and Ehleringer, 2001; Jian *et al.,* 2016; Li *et al.,* 2024). The relatively modest absolute sap velocity values observed in *A. latifolia* compared to *A. indica* further suggest that hydraulic recovery may operate within constrained canopy demand during the deciduous phase, indicating that rainfall effects reflect physiological adjustment rather than structural increase in transpiring surface area.

Two-way ANOVA confirmed a significant effect of rainfall phase (F = 16.78, $p < 0.001$), indicating that rainfall significantly increased the sap velocity. In contrast, the response scale (24 hr vs 72 hr) was not significant (F = 0.03, p = 0.853), and no significant interaction between rainfall phase and response scale was detected (F = 0.04, p = 0.848; Table 3). The absence of a significant response-scale effect suggests rapid physiological adjustment following rainfall, with increased sap velocity maintained over subsequent days without distinct temporal differentiation between immediate and delayed phases (Schwinning and Ehleringer, 2001; Mu *et al.,* 2022; Tang *et al.,* 2022). In contrast, sap velocity in *A. indica* at Jodhpur site remained relatively stable across rainfall phases, with no significant differences between before- and after-rain periods (F = 0.27, p = 0.607; Table 3). This stability may suggest that sap flow dynamics in this evergreen species were less dependent on short-term rain pulses and may reflect sustained canopy function and reduced reliance on transient rainfall events, consistent with patterns reported for evergreen dryland species (Fang *et al.,* 2023; Tang *et al.,* 2025). The contrasting rainfall responses between species underline the importance of phenological strategy in regulating water-use dynamics (Jian *et al.,* 2016). Deciduous species experiencing seasonal canopy reduction may display pronounced sensitivity to episodic rainfall due to transient alleviation of drought stress, whereas evergreen species may maintain more stable transpiration regimes governed by atmospheric demand.

Distinct diurnal patterns were observed in both species, with sap velocity generally increasing after sunrise, reaching peak values during midday to early afternoon, and declining toward evening (Fig. 1). Peak timing analysis revealed rainfall-associated shifts and substantial daily variability in *A. latifolia*. The mean peak timing shifted from approximately 14:45 ± 00:57 hr before rainfall to 13:08 ± 03:45 hr after rainfall during the immediate response phase, and from 12:00 ± 04:58 hr to 14:30 ± 04:02 hr during the delayed response period (Table 2). The relatively large standard deviations indicate high variability in daily peak timing, suggesting greater variability in diurnal

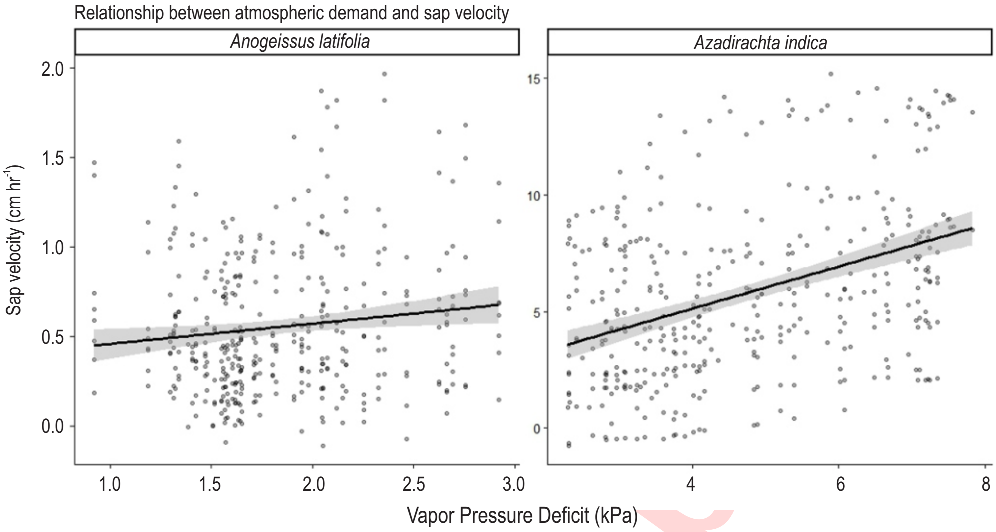

Fig. 3: Relationship between atmospheric demand (vapour pressure deficit; VPD) and sap velocity in two tree species. Scatterplots with fitted linear regression lines showing species-specific responses of sap velocity (cm h^{-1}) to VPD (kPa). Shaded areas represent 95% confidence intervals. For *Anogeissus latifolia*: Sap velocity = 0.344 + 0.114 × VPD (R^2 = 0.016, p = 0.011). For *Azadirachta indica*: Sap velocity = 1.509 + 0.902 × VPD (R^2 = 0.161, p < 0.001).

regulation compared to the more consistent patterns observed in the evergreen species. Such variability may reflect transient adjustments in hydraulic functioning or stomatal behaviour under changing moisture conditions during the deciduous phase (Rocha *et al.,* 2025). In contrast, the peak timing in *A. indica* remained relatively consistent across rainfall phases, indicating stable daily sap flow behaviour. Evergreen species frequently maintain strong coupling between transpiration and atmospheric drivers, resulting in consistent diurnal regulation independent of short rainfall events (Meinzer *et al.,* 2003; Wan *et al.,* 2024; Tang *et al.,* 2025). Together, these findings indicate that short-term sap velocity dynamics were controlled by different drivers in two species, with rainfall pulses dominating in the deciduous species and atmospheric demand exerting stronger control in the evergreen species.

Rainfall-associated shifts in peak sap velocity timing may also indicate changes in stomatal sensitivity and hydraulic coordination between soil water availability and atmospheric demand (Rocha *et al.,* 2025). Earlier peak timing following rainfall in *A. latifolia* suggests that improved plant water status allowed increased sap velocity earlier in the day when radiation and VPD started rising, potentially reflecting reduced hydraulic limitation. Conversely, the relatively stable peak timing in *A. indica* indicates strong stomatal regulation aligned with atmospheric drivers rather than soil moisture pulses. This difference aligns with theoretical frameworks suggesting that evergreen dryland species maintain tighter stomatal control to avoid excessive hydraulic risk under high evaporative demand. Variability in peak timing, therefore, provides additional insight into species-specific regulation strategies beyond changes in mean sap velocity alone (Meinzer *et al.,* 2003; Duan *et al.,* 2026). Vapor pressure deficit (VPD) significantly influenced sap velocity, although species responses differed in strength (Fig. 3). For *A. latifolia*, a weak but statistically significant positive relationship was observed (slope = 0.114 ± 0.045, F = 6.45, p = 0.011), but extremely low explanatory power (R^2 = 0.016) indicates that atmospheric demand explained only a small proportion of variance in sap velocity during the study period. This suggests that rainfall pulses and transient hydraulic recovery contributed more strongly to variations in sap velocity in this deciduous species than atmospheric drivers. Conversely, *A. indica* exhibited a statistically significant but modest positive relationship between sap velocity and VPD (slope = 0.902 ± 0.105, F = 73.25, p < 0.001, R^2 = 0.161). While this indicates greater atmospheric control over sap flow compared to *A. latifolia*, the low R^2 value (explaining ~16% of the variance) may indicate that other micro-meteorological factors, such as solar radiation, or internal stomatal regulation mechanisms at higher VPD thresholds (Liu *et al.,* 2017; Liu *et al.,* 2024), limit a strictly linear response. A stronger VPD coupling and substantially higher baseline sap velocity in *A. indica* (~5.6 cm hr^{-1} compared to ~0.5 cm hr^{-1} in *A. latifolia*) is likely driven by its persistent evergreen canopy and the higher baseline aridity of the Jodhpur site, though differences in tree size and inherent xylem architecture between the two populations may also contribute to this baseline divergence (Grossiord *et al.,* 2020). Higher VPD increases the atmospheric water vapor gradient, thereby enhancing transpiration flux when stomatal conductance allows (Oren *et al.,* 1999; Grossiord *et al.,* 2020). The observed ecohydrological divergence highlights how contrasting functional types navigate water limitations across dryland environments. The deciduous *A. latifolia* operates under a "pulse-responsive" strategy, where physiological activity rapidly increases following episodic rainfall but remains weakly coupled to atmospheric demand during dry periods (Schwinning and Ehleringer, 2001; Huxman *et al.,* 2004).

In contrast, the evergreen *A. indica* exhibits a more continuous, conservative sap flow regime; it maintains relatively stable water use across short-term rainfall variability and relies more heavily on stomatal regulation driven by atmospheric demand, specifically vapor pressure deficit (Oren *et al.,* 1999; Grossiord *et al.,* 2020). From a broader perspective, these contrasting responses emphasize the importance of differentiating between precipitation-driven and atmosphere-driven transpiration regimes in dry-land ecosystems. This divergence in hydraulic strategies directly influences ecosystem-scale water balances, determining whether a forest stand's transpiration responds primarily to erratic surface moisture inputs or to daily atmospheric conditions (Nelson *et al.,* 2020; Kang *et al.,* 2026). Understanding these functional differences is increasingly critical under projected climate scenarios that predict greater variability in rainfall timing, drought intensity and atmospheric demand in dryland ecosystems (Grossiord *et al.,* 2020; Fang *et al.,* 2023; Tang *et al.,* 2025). Because species traits and site conditions are inherently linked in this study design, these findings should be interpreted as illustrating general ecohydrological patterns rather than strictly isolating species effects. Also, the soil moisture was not directly measured during monitoring period. Consequently, the influence of rainfall events on subsurface water availability and tree water uptake could only be inferred indirectly through sap velocity responses. Ultimately, recognizing how canopy condition, phenology, and local environmental constraints dictate these short-term physiological responses will be essential for guiding species selection and predicting forest resilience in increasingly water-limited landscapes (Meinzer *et al.,* 2003; Zhang *et al.,* 2022).

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Authors' contribution: S. Kothari: Conceptualized the study, prepared original draft, created figures, and supervised the work; **A. Perwez:** Conceptualized the study, prepared original draft, and contributed to revision; **M. Sen, I. Bano and S. Bag:** Contributed to writing the original draft, revision and editing.

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