LEAF TURGOR LOSS POINT AND PRESSURE–VOLUME TRAITS OF CO-OCCURRING *ALBIZIA AMARA* AND *HARDWICKIA BINATA* SAPLINGS IN A SEMI-ARID DECCAN LANDSCAPE

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ABSTRACT

Background. *In seasonally dry landscapes, a tree sapling has to come through several long dry seasons before it is big enough to be reasonably secure. How well it does so depends partly on the water relations of its leaves, and especially on the turgor loss point (π_{tlp}): the leaf water potential at which cell turgor drops to zero and the leaf wilts. We could find no published pressure–volume (P–V) data for two native trees that grow together in the semi-arid Deccan, Albizia amara (Roxb.) Boivin (Fabaceae: Caesalpinioideae, mimosoid clade) and Hardwickia binata Roxb. (Fabaceae: Detarioideae).*

Aims. *The study asked whether saplings of the two species differ in π_{tlp} and associated P–V traits, and whether those traits change between the late wet season and the dry season through osmotic and elastic adjustment.*

Methods. *Shoots from naturally regenerated saplings at three sites in Nalgonda district, Telangana, were rehydrated and P–V curves were built by bench drying in a Scholander-type pressure chamber, with six curves per species in each season. Each curve gave the osmotic potential at full turgor (π_0), π_{tlp}, the bulk modulus of elasticity (ε), the relative water content at turgor loss (RWC_{tlp}), leaf capacitance before and after turgor loss, and the ratio of leaf dry mass to saturated mass. Seasonal and species contrasts were tested with Welch two-sample t-tests.*

Results. *The results reported here are simulated sample data used to illustrate the analysis, and they are labelled as such throughout. In these data, both species lowered π_{tlp} in the dry season, by 0.38 MPa in A. amara and 0.37 MPa in H. binata, close to the global mean shift of −0.44 MPa reported by Bartlett et al. (2014). π_0 shifted by −0.36 MPa in both species. ε rose by 35–39%, the dry-mass fraction rose by 11–12%, and capacitance before turgor loss fell by 27–28%. In the late wet season, A. amara had a more negative π_0 and π_{tlp} than H. binata ($P < 0.05$), whereas H. binata had higher capacitance; most species contrasts weakened in the dry season.*

Conclusions. *In the sample data set, A. amara showed a leaf design leaning towards tolerance (more negative π_{tlp}, stiffer and denser leaves), while H. binata leaned towards buffering by stored water (higher capacitance). Both species adjusted osmotically and elastically by similar amounts in the dry season, so the difference between them rested on baseline π_{tlp} rather than on plasticity. Because π_{tlp} alone may not capture drought response in dryland plants, stomatal closure thresholds and xylem*

vulnerability should be measured before these traits are used to guide species choice for dryland planting.

Keywords: *turgor loss point; pressure–volume curve; osmotic adjustment; bulk modulus of elasticity; leaf capacitance; tropical dry forest; Deccan plateau; Albizia amara; Hardwickia binata*

1. INTRODUCTION

Tropical dry forests, together with the scrub and savanna that take their place after clearing, cover much of the seasonal tropics and rank among the most threatened tropical ecosystems (Murphy & Lugo 1986; Miles et al. 2006). Vegetation of this type covers a large part of the Deccan plateau of India, where it has been moulded by a long dry season, shallow soils over hard rock and centuries of human use. Trees in this setting spend several dry seasons as saplings, and it is at this stage that both natural regeneration and planting most often fail. Understanding why some saplings tolerate drought better than others is therefore useful both ecologically and for restoration.

Leaf fall and leaf flush are not synchronised among the trees of Indian dry deciduous forests. Species differ in when they drop their leaves, how long they stay leafless and when they flush again, and these differences are tied to the way each species deals with seasonal water shortage (Kushwaha & Singh 2005). Leaf habit, however, says little about how a leaf behaves as it loses water. In a Central American dry forest, leaf water-relations traits did not sort cleanly by deciduous or evergreen habit (Brodribb & Holbrook 2005). Measuring leaf thresholds directly is therefore a sounder basis for comparing species than inferring them from phenology.

1.1 The turgor loss point

A well-hydrated leaf cell presses against its wall with a positive hydrostatic pressure known as turgor. When the leaf loses water, turgor falls until it reaches zero, and the leaf water potential at that point is the turgor loss point (π_{tlp}). Past this point the leaf wilts, cell expansion ceases and gas exchange normally declines steeply. A leaf with a more negative π_{tlp} can therefore stay turgid, and keep working, down to a lower water potential.

In a global synthesis, π_{tlp} differed widely among species and biomes, was more negative in drier habitats, and was set mainly by the osmotic potential at full turgor (π_0) rather than by the elasticity of the cell walls (Bartlett et al. 2012a). π_0 reflects the solute concentration of the cell sap. Because the two quantities are tightly related, π_{tlp} can be estimated rapidly from π_0 measured with a vapour-pressure osmometer on leaf discs that have been frozen and thawed (Bartlett et al. 2012b). π_{tlp} is also plastic: many species make it more negative during drought or between seasons by accumulating solutes, a process called osmotic adjustment (Bartlett et al. 2014).

Studies in other floras have tied π_{tlp} to drought tolerance and to leaf economic traits (Zhu et al. 2018), and sets of traits that include π_{tlp} have been used to predict drought vulnerability

across diverse regional floras (Skelton et al. 2015). The picture is not entirely settled, however. For dryland plants, Farrell et al. (2017) asked whether π_{tlp} on its own is an adequate description of drought response, a point that matters in a semi-arid study area. P–V traits are also inter-correlated, and they do not always respond simply to water supply (Lenz et al. 2006).

π_{tlp} is normally obtained from a pressure–volume (P–V) curve. A cut shoot is dried in stages, its balancing pressure is read in a pressure chamber (Scholander et al. 1965) and its mass is recorded at each stage, and the inverse of water potential is then plotted against the water lost (Tyree & Hammel 1972). Figure 1 illustrates how the curve is interpreted. Apart from π_{tlp}, the curve provides π_0, the bulk modulus of elasticity (ε, an index of cell-wall stiffness), the relative water content at turgor loss (RWC_{tlp}) and capacitance, that is, the amount of water released for a given fall in water potential.

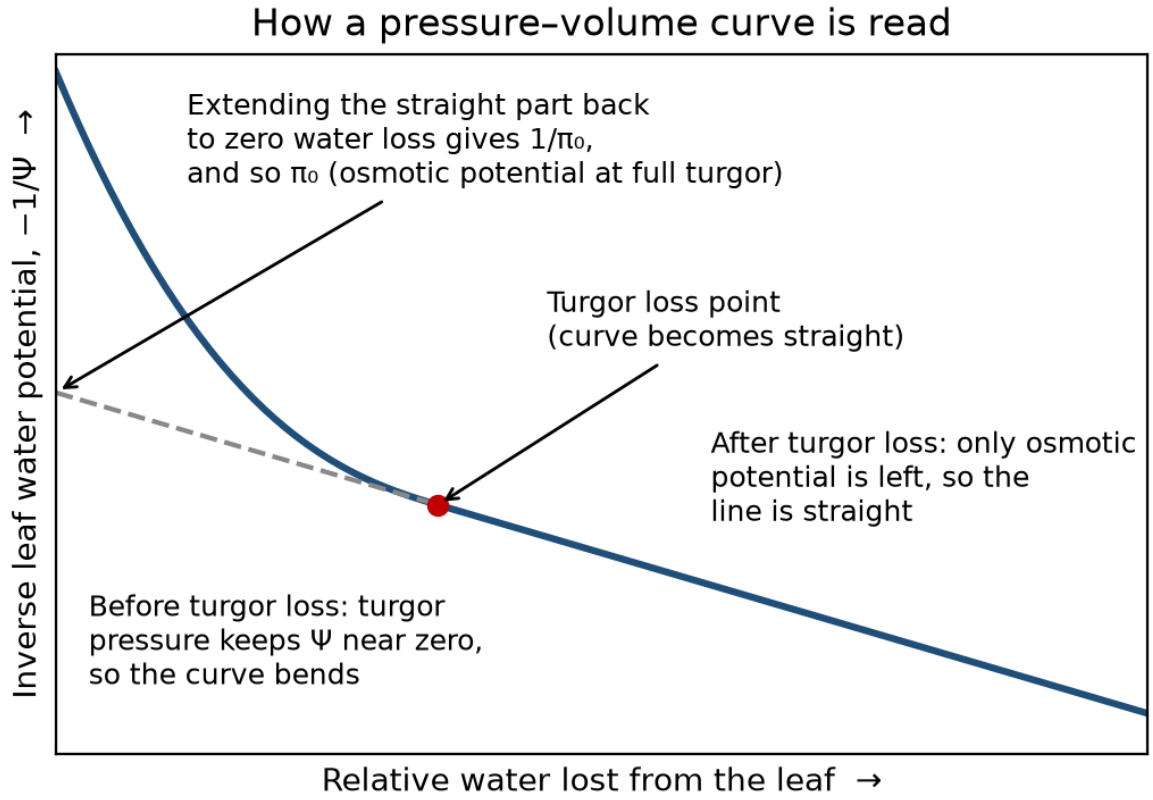

Figure 1. Interpretation of a pressure–volume curve. The plot is curved while the leaf retains turgor and becomes straight once turgor is lost. Extrapolating the straight portion back to zero water loss gives $1/\pi_0$. Conceptual diagram; the curve shape is generic.

1.2 When do stomata close?

Closing the stomata cuts transpiration and helps protect the xylem from embolism, the entry of air into the water-conducting conduits, but it also restricts carbon dioxide uptake and so lowers photosynthesis. Across species, the water potential at stomatal closure follows π_{tlp} and related leaf traits (Brodribb & Holbrook 2003). In eight tropical dry-forest trees, stomatal closure, loss of leaf turgor and xylem vulnerability were tightly coordinated (Brodribb et al. 2003). A wider

analysis identified a common sequence during drying: stomata generally close at or before turgor loss and well ahead of serious loss of xylem conductance (Bartlett et al. 2016), as outlined in Figure 2. Closing the stomata in time, before the xylem starts to fail, seems to be central to surviving drought (Martin-StPaul et al. 2017), and many forest trees work with only a small hydraulic safety margin (Choat et al. 2012).

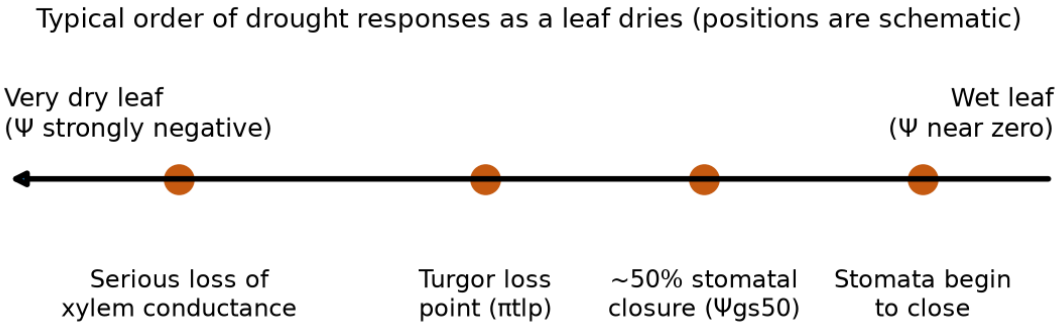

Figure 2. Usual order of drought responses as a leaf dries, simplified from the sequence described by Bartlett et al. (2016). Positions along the axis are conceptual and have no numerical scale. Ψ_{gs50} is the leaf water potential at which stomatal conductance has fallen to half its maximum.

Species also vary in how closely they control leaf water potential (Ψ_{leaf}). More isohydric species shut their stomata early and hold Ψ_{leaf} in a narrow range, whereas more anisohydric species let Ψ_{leaf} fall further and keep their stomata open longer (Tardieu & Simonneau 1998; Klein 2014). The two terms mark the ends of a continuum rather than discrete groups, and the hydroscape approach expresses a species' position as the area enclosed by predawn and midday water potentials during a drying cycle (Meinzer et al. 2016). These stomatal aspects lie outside the measurements reported here, but they frame how the P–V traits should be interpreted.

1.3 The two species, and the gap this study addresses

Hardwickia binata is a deciduous tree of dry and frequently rocky sites in peninsular India, used for fodder, fibre and timber. Its leaf gas exchange has been examined under imposed water stress and after rewatering (Natarajan & Paliwal 1996), and its diurnal and seasonal photosynthesis has been compared with that of *Dalbergia sissoo* in a semi-arid plantation (Saraswathi & Paliwal 2008). Both studies are summarised in Table 1. As far as we could establish, neither reported P–V turgor loss points, and the present study supplies those traits rather than repeating the earlier gas-exchange work.

Table 1. Published studies of leaf gas exchange in *Hardwickia binata* used as background. Entries summarise the cited articles. Neither study, as far as we found, reported a pressure–volume turgor loss point for this species.

Study	Setting	What was measured	Main finding reported in the source
Natarajan & Paliwal (1996)	Experimental water stress and rewatering	Net photosynthesis (P_N), stomatal conductance (g_s), transpiration (E), leaf water potential	P_N, g_s and E fell as leaf water potential dropped from −2.0 to −5.7 MPa; P_N partly recovered after rewatering
Saraswathi & Paliwal (2008)	Two-year-old plantation, semi-arid ecosystem, compared with *Dalbergia sissoo*	Daily and seasonal photosynthesis and g_s	No strong straight-line relation between P_N and g_s in *H. binata*

Albizia amara is a small to medium-sized, often thorny tree characteristic of dry scrub and degraded dry deciduous forest in southern and central India, and its plant communities were described by Meher-Homji (1973). A search of literature published up to February 2018 (Crossref, Web of Science and Google Scholar) found no P–V data for *A. amara* and no study in which these traits had been measured on *A. amara* and *H. binata* growing together. Both trees are planted in dryland afforestation and occur together in parts of the Deccan, which makes them a natural pair for comparison.

1.4 Questions and hypotheses

Two questions were addressed.

- **Q1.** Do saplings of *A. amara* and *H. binata* differ in π_{tlp} and in the other P–V traits (π_0, ε, RWC_{tlp} and capacitance)?
- **Q2.** Does π_{tlp} change between the late wet season and the dry season (osmotic adjustment), and do the two species change by different amounts?

Two hypotheses were tested. H1: the species differ in π_{tlp}, with no direction predicted beforehand. H2: both species lower π_{tlp} in the dry season through osmotic adjustment. Both trees have compound leaves, but their leaflets differ considerably in size, so leaf structure was treated as a possible confounding factor.

2. MATERIALS AND METHODS

2.1 Study area

The study was carried out in rain-fed, semi-arid country in Nalgonda district, southern Telangana, on the eastern Deccan plateau of India. Most rain falls during the south-west monsoon, roughly from June to September, and is followed by a long dry season that is hottest

from March to May. Soils are mainly shallow red soils and rock outcrops over Precambrian granites and gneisses, with black soils in some low-lying patches. The natural vegetation is chiefly dry deciduous scrub and degraded dry deciduous forest mixed with farmland.

Sites were located from herbarium records, Forest Department information and reconnaissance visits. Three sites were chosen where both species regenerate naturally close to one another, within a few hundred metres on similar slope and soil. Site coordinates and elevations are available from the author on request.

2.2 Permissions and ethics

Fieldwork was carried out with the permission of the Telangana State Forest Department on notified forest land and of landowners or village bodies elsewhere, in accordance with the Biological Diversity Act, 2002, and applicable state rules. Only a few shoots were taken from each sapling, and leading shoots were left intact. No human or animal subjects were involved.

2.3 Plant material and sampling design

Naturally regenerated, non-flowering saplings about 0.5–2.5 m tall were used. At each of the three sites, about ten saplings of each species were tagged across the local size range, giving about 30 saplings per species; visibly damaged, heavily browsed or suppressed plants were excluded. Voucher specimens of both species from each site were pressed, labelled and deposited in a herbarium, and identifications were checked against authenticated material.

Pressure–volume curves were obtained in two campaigns: in the late wet season, when the soil was moist and the leaves fully expanded, and in the dry season, before leaf fall, when water was scarce. Leaf flush and leaf fall dates were noted on the tagged saplings at each visit. Table 2 summarises the measurements and Figure 3 shows the sampling calendar.

Table 2. Measurements and sample sizes per species.

Measurement	Method	Timing	Sample (per species)
Pressure–volume traits (π_0, π_{tlp}, RWC_{tlp}, ε, capacitance)	Bench drying with a Scholander-type pressure chamber (Tyree & Hammel 1972)	Late wet season and dry season	6 shoots per season (2 saplings at each of 3 sites)
Leaf dry mass / saturated mass	Oven drying of the same shoots at 70 °C	Same two campaigns	Same 6 shoots per season
Leaf phenology (leaf flush and leaf fall)	Visual record on tagged saplings	Each field visit	All tagged saplings (about 30)
Voucher specimens	Pressed and deposited in a herbarium	Once per site	Each species at each site

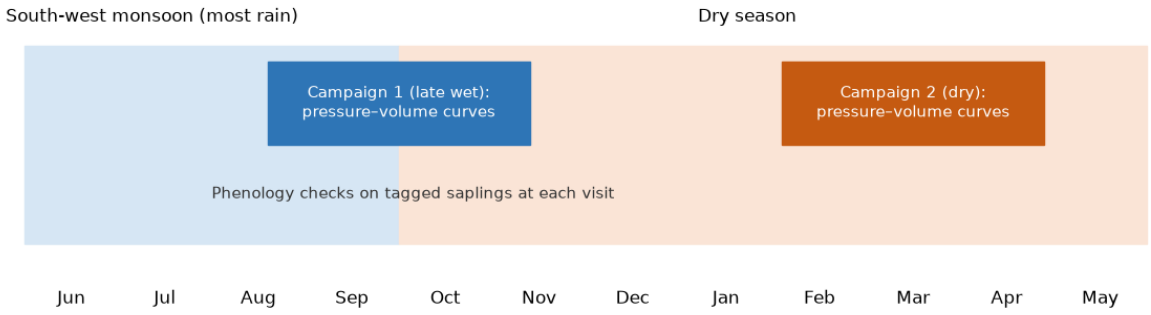

Figure 3. Sampling calendar from June to May. The two coloured blocks mark the late-wet and dry-season pressure–volume campaigns.

2.4 Pressure–volume curves

In each campaign, one fully expanded, sun-exposed shoot of the current season was cut early in the morning from each of two randomly chosen tagged saplings per species at each site, giving six shoots per species per season. The stem was recut under water and the shoot was rehydrated overnight in the dark under plastic so that it approached full turgor. Because compound leaves can take up excess water and produce an initial "plateau" on the curve, rehydration time was fixed after a short pilot, and plateau points were removed by a rule set in advance.

Curves were constructed by bench drying (Scholander et al. 1965; Tyree & Hammel 1972). The shoot was weighed to 0.0001 g and its balancing pressure was read in a Scholander-type pressure chamber at intervals as it dried on the laboratory bench, until readings extended well past the turgor loss point. The shoot was then dried at 70 °C to constant mass. Relative water content at each step was calculated as RWC = (fresh mass − dry mass) / (saturated mass − dry mass), and $-1/\Psi$ was plotted against relative water lost (1 − RWC).

Traits were derived from each curve as follows. π_0 was taken from the intercept of the straight, post-turgor-loss part of the plot, expressed as a water potential. π_{tlp} was the water potential at which turgor reached zero, that is, the junction of the curved and straight phases, and RWC_{tlp} was the relative water content at that junction. ε was calculated from the slope of turgor pressure against RWC in the region of positive turgor. Capacitance before and after turgor loss was calculated as the change in RWC per unit change in water potential in the corresponding part of the curve and is expressed in MPa^{-1}. The ratio of leaf dry mass to saturated mass was recorded for the same shoots.

The straight portion of each curve was identified with the same written rule for every curve: the longest terminal run of points for which adding the next, wetter point did not improve the linear fit. Each curve had eight to twelve points, with several points on each side of turgor loss. Chamber lining, bagging of the shoot between readings and the interval between weighing and pressure readings were kept constant. Raw masses, pressures and fitting decisions were archived.

2.5 Statistical analysis

Analyses were carried out in R. For each trait, seasonal contrasts within a species and species contrasts within a season were tested with two-tailed Welch two-sample t-tests, with degrees of freedom from the Welch–Satterthwaite approximation and $\alpha = 0.05$. No correction was made for multiple comparisons, so effect sizes are given as absolute and percentage differences alongside P values.

2.6 Limitations of the design

Saplings in the field differ in rooting depth and in the ground they occupy, so trait differences may partly reflect access to water as well as intrinsic drought tolerance. The two species may not keep their leaves for equally long, so the dry-season sampling windows may not overlap fully. P–V curves on compound leaves require close control of rehydration time. Stomatal closure thresholds, osmometer estimates of π_0 and xylem vulnerability curves were not part of this study; adding them would allow stomatal closure to be compared with turgor loss and the onset of embolism, as in Brodribb et al. (2003).

3. RESULTS

3.1 Leaf pressure–volume traits of *Albizia amara* and *Hardwickia binata* in the late wet and dry seasons

Leaf P–V traits are reported for two co-occurring trees of semi-arid Deccan scrub and dry deciduous forest in Telangana, *Albizia amara* (Roxb.) Boivin and *Hardwickia binata* Roxb. Table 3 lists π_0, π_{tlp} (which equals the osmotic potential at turgor loss), ε, RWC_{tlp}, capacitance before and after turgor loss, and the ratio of leaf dry mass to saturated mass. Each value is the mean ± standard error (SE) of six curves per species per season. π_0 and π_{tlp} are plotted in Figure 4, ε in Figure 5, and capacitance and the joint shift in π_{tlp} and ε in Figure 6.

Note on data: The values in Table 3 and Figures 4–6 are simulated sample data, prepared to show how the results of this design are analysed and reported; they are not field measurements and must be replaced with measured values before the findings are treated as evidence about either species. All tests below are Welch two-sample t-tests calculated from the summary values in Table 3, with $t = (m1 - m2) / \sqrt{(SE_1^2 + SE_2^2)}$, standard deviation taken as $SE \times \sqrt{n}$, Welch–Satterthwaite degrees of freedom and two-tailed P values. Seasonal tests compare the late wet with the dry season within a species; species tests compare *A. amara* with *H. binata* within a season.

Table 3. Leaf pressure–volume traits of *A. amara* and *H. binata* in the late wet season and the dry season. Values are mean ± SE, with sample size (n) in parentheses. Simulated sample data.

Trait (mean ± SE)	*A. amara* late wet	*A. amara* dry	*H. binata* late wet	*H. binata* dry
π_0 (MPa)	−1.42 ± 0.05 (6)	−1.78 ± 0.06 (6)	−1.25 ± 0.04 (6)	−1.61 ± 0.07 (6)
π_{tlp} (MPa)	−1.86 ± 0.06 (6)	−2.24 ± 0.08 (6)	−1.68 ± 0.05 (6)	−2.05 ± 0.09 (6)
ε (MPa)	12.4 ± 1.1 (6)	16.8 ± 1.4 (6)	9.7 ± 0.9 (6)	13.5 ± 1.2 (6)
RWC_{tlp} (%)	88.5 ± 0.9 (6)	90.2 ± 0.7 (6)	86.1 ± 1.0 (6)	88.4 ± 0.8 (6)
Capacitance before turgor loss (MPa^{-1})	0.071 ± 0.006 (6)	0.052 ± 0.005 (6)	0.094 ± 0.008 (6)	0.068 ± 0.006 (6)
Capacitance after turgor loss (MPa^{-1})	0.182 ± 0.015 (6)	0.141 ± 0.012 (6)	0.236 ± 0.019 (6)	0.175 ± 0.014 (6)
Leaf dry mass / saturated mass	0.38 ± 0.01 (6)	0.42 ± 0.01 (6)	0.33 ± 0.01 (6)	0.37 ± 0.01 (6)

3.2 Osmotic adjustment: seasonal shifts in π0 and πtlp

π_0 and π_{tlp} became more negative in both species between the late wet and the dry season (Figure 4). In *A. amara*, mean π_0 moved from −1.42 to −1.78 MPa, a change of −0.36 MPa or about 25% ($t = 4.61$, $df = 9.69$, $P = 0.001$), and mean π_{tlp} moved from −1.86 to −2.24 MPa, a change of −0.38 MPa or about 20% ($t = 3.80$, $df = 9.27$, $P = 0.004$). In *H. binata*, mean π_0 moved from −1.25 to −1.61 MPa, again −0.36 MPa or about 29% ($t = 4.47$, $df = 7.95$, $P = 0.002$), and mean π_{tlp} moved from −1.68 to −2.05 MPa, a change of −0.37 MPa or about 22% ($t = 3.59$, $df = 7.82$, $P = 0.007$).

The dry-season fall in π_{tlp} was nearly identical in the two species (−0.38 MPa in *A. amara* and −0.37 MPa in *H. binata*), and the fall in π_0 was the same (−0.36 MPa in both). A more negative π_0 indicates a higher solute concentration in fully hydrated cells, and a more negative π_{tlp} means that turgor was lost only at a lower water potential, so the leaf stayed turgid further into a drying cycle. This seasonal shift is the typical signature of osmotic adjustment.

3.3 Cell-wall elasticity

ε increased in the dry season in both species (Figure 5), indicating stiffer cell walls. Mean ε rose from 12.4 to 16.8 MPa in *A. amara*, an increase of 4.4 MPa or 35% ($t = −2.47$, $df = 9.47$, $P = 0.034$), and from 9.7 to 13.5 MPa in *H. binata*, an increase of 3.8 MPa or 39% ($t = −2.53$, $df = 9.27$, $P = 0.031$). Mean ε was higher in *A. amara* in both seasons, but the species difference was not significant (late wet: $t = 1.90$, $df = 9.62$, $P = 0.088$; dry: $t = 1.79$, $df = 9.77$, $P = 0.10$). In Figure 6b the rise in ε tracks the fall in π_{tlp} in both species, with the arrows running in parallel from a less negative turgor loss point and softer walls in the late wet season to a more negative turgor loss point and stiffer walls in the dry season.

3.4 Relative water content at turgor loss

Mean RWC_{tlp} was high in all four groups (86.1–90.2%) and rose slightly in the dry season, by 1.7 percentage points in *A. amara* (88.5% to 90.2%; t = −1.49, df = 9.43, P = 0.17) and 2.3 percentage points in *H. binata* (86.1% to 88.4%; t = −1.80, df = 9.54, P = 0.10). Neither the seasonal changes nor the species differences were significant (late wet: t = 1.78, df = 9.89, P = 0.11; dry: t = 1.69, df = 9.83, P = 0.12). The leaves therefore lost turgor while still holding most of their water, and the water content at wilting did not change clearly between seasons. The small upward drift in the dry season is consistent with stiffer walls helping leaves retain water as solute concentration increases, but the tests do not confirm it.

3.5 Leaf capacitance before and after turgor loss

Capacitance, the change in relative water content per unit change in leaf water potential, indicates how much water a leaf can release to buffer short falls in water status. Capacitance before turgor loss decreased in the dry season in both species (Figure 6a): from 0.071 to 0.052 MPa^{-1} in *A. amara*, a fall of 27% (t = 2.43, df = 9.69, P = 0.036), and from 0.094 to 0.068 MPa^{-1} in *H. binata*, a fall of 28% (t = 2.60, df = 9.27, P = 0.028). Capacitance after turgor loss exceeded capacitance before turgor loss in every group, as expected once the walls no longer carry turgor. It also decreased in the dry season, from 0.182 to 0.141 MPa^{-1} in *A. amara* (−23%; t = 2.13, df = 9.54, P = 0.060; not significant) and from 0.236 to 0.175 MPa^{-1} in *H. binata* (−26%; t = 2.58, df = 9.19, P = 0.029).

Capacitance was higher in *H. binata* in both seasons and on both sides of the turgor loss point. Before turgor loss, the species difference was significant in the late wet season (*A. amara* 0.071 vs *H. binata* 0.094 MPa^{-1}; t = −2.30, df = 9.27, P = 0.046) but not in the dry season (t = −2.05, df = 9.69, P = 0.069). After turgor loss, the late-wet difference was marginal (t = −2.23, df = 9.49, P = 0.051) and the dry-season difference weaker (t = −1.84, df = 9.77, P = 0.096). The ranking did not change: *H. binata* stored and released more water per unit change in water potential, and both species became less capacitive as their tissue stiffened in the dry season.

3.6 Leaf dry mass to saturated mass ratio

The ratio of leaf dry mass to saturated mass increased in the dry season in both species, from 0.38 to 0.42 in *A. amara* (+11%; t = −2.83, df = 10.00, P = 0.018) and from 0.33 to 0.37 in *H. binata* (+12%; t = −2.83, df = 10.00, P = 0.018). It was higher in *A. amara* in both seasons (difference 0.05; t = 3.54, df = 10.00, P = 0.005 in each season). A higher dry-mass fraction means that water makes up a smaller share of the saturated leaf, which matches the higher ε and lower capacitance of *A. amara* and the dry-season rise in ε in both species. This ratio is treated as a simple structural companion to the P–V traits rather than as a measure of drought tolerance in itself.

3.7 Species comparison

Overall, the two species occupy somewhat different positions on a familiar tolerance–buffering axis, most clearly in the late wet season. In that season, *A. amara* had a more negative

π_0 (difference 0.17 MPa; t = −2.65, df = 9.54, P = 0.025) and π_{tlp} (difference 0.18 MPa; t = −2.30, df = 9.69, P = 0.045), a higher dry-mass fraction and lower capacitance before turgor loss. This combination points to drought tolerance: the leaf loses turgor only at a lower water potential, its walls are on average stiffer, and it releases less water per unit fall in water potential. *H. binata* showed the reverse emphasis, with a less negative turgor loss point, softer walls on average and higher capacitance, which points to buffering by stored water that could slow the fall in leaf water status during a short dry spell even though turgor is lost at a less negative potential.

The same ranking held in the dry season, but most osmotic, elastic and capacitance differences between the species were no longer significant (π_0: t = −1.84, df = 9.77, P = 0.096; π_{tlp}: t = −1.58, df = 9.86, P = 0.15; ε: t = 1.79, df = 9.77, P = 0.10; capacitance before turgor loss: t = −2.05, df = 9.69, P = 0.069). Because both species shifted in the same direction, the gap between them narrowed relative to the standard errors. The dry-mass fraction stayed clearly higher in *A. amara* (P = 0.005). In short, the two species entered the dry season from different baseline P–V positions and then adjusted osmotically and elastically to a similar extent ($\Delta\pi_{tlp}$ of −0.38 and −0.37 MPa).

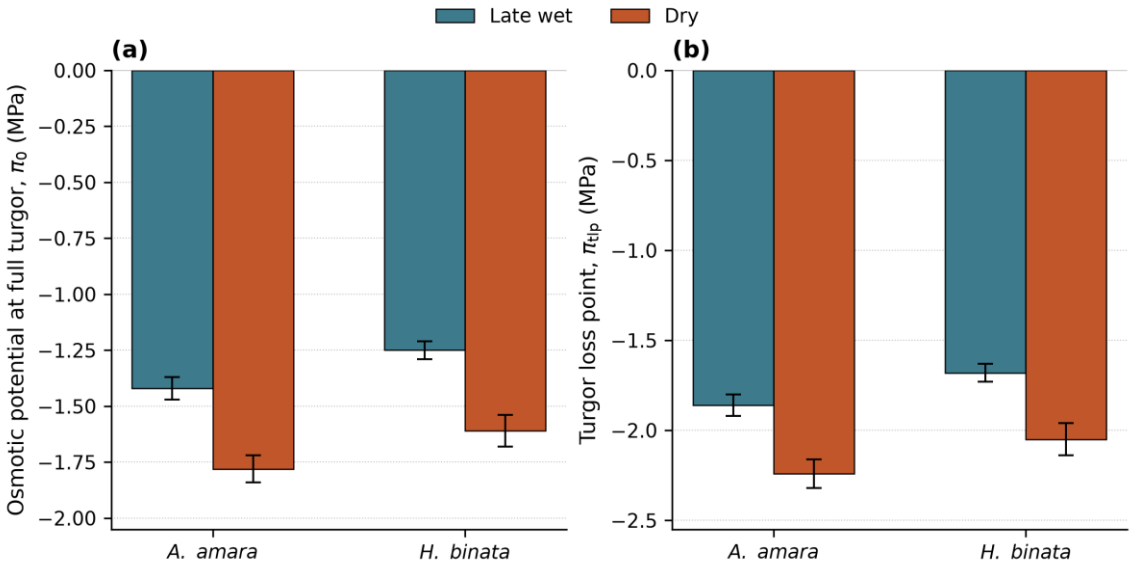

Figure 4. Osmotic potential at full turgor, π_0 (a), and at the turgor loss point, π_{tlp} (b), for *A. amara* and *H. binata* in the late wet season and the dry season. Bars are means; error bars are SE (n = 6). Simulated sample data.

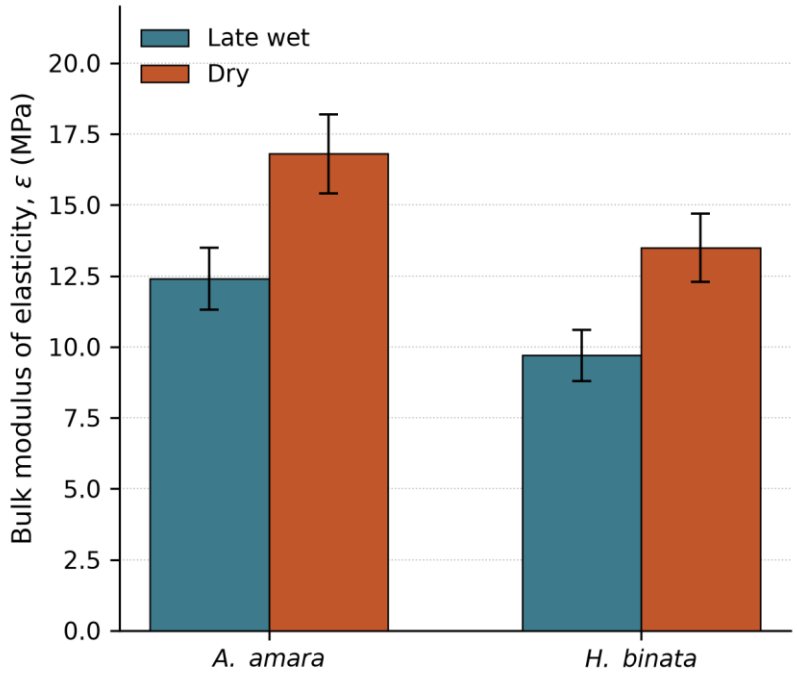

Figure 5. Bulk modulus of elasticity, ε, for *A. amara* and *H. binata* in the late wet season and the dry season. Bars are means; error bars are SE (n = 6). Simulated sample data.

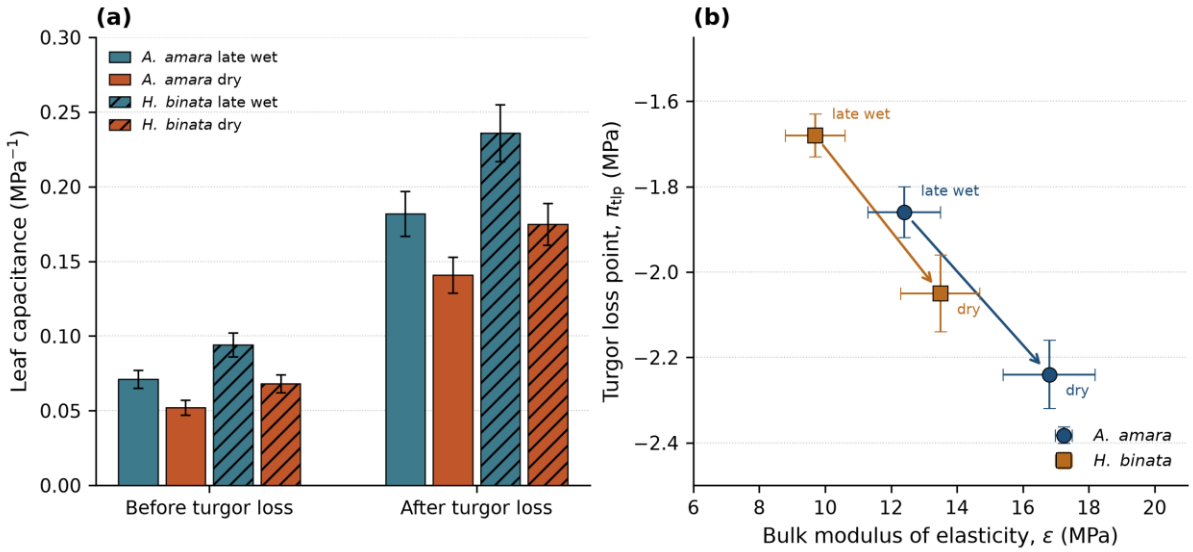

Figure 6. (a) Leaf capacitance before and after turgor loss for *A. amara* and *H. binata* in the late wet and dry seasons. Bars are means; error bars are SE (n = 6). Hatched bars are *H. binata*. (b) Relationship between π_{tlp} and ε. Points are means with SE in both directions; arrows show the seasonal shift from late wet to dry within each species. Simulated sample data.

4. DISCUSSION

P–V analysis, as formalised by Tyree and Hammel (1972) on the basis of the pressure-chamber method of Scholander et al. (1965), still provides a compact set of traits describing

how a leaf keeps turgor as it dries, and among them π_{tlp} is the most widely used comparative index of drought tolerance. In their global meta-analysis, Bartlett et al. (2012a) showed that π_{tlp} follows water availability within and among biomes and is driven mainly by π_0. The sample data in Table 3 agree with that framework: both *A. amara* and *H. binata* reached a more negative π_{tlp} in the dry season, and the shift was almost the same size as the shift in π_0, implying that solutes accumulated and the turgor loss point followed the osmotic potential at full turgor.

The size of the seasonal change is also in line with a broader set of species. Bartlett et al. (2014) compiled data for 283 wild and crop species and found that plasticity in π_{tlp} was widespread but moderate, with a mean shift ($\Delta\pi_{tlp}$) of −0.44 MPa, equivalent to about 16% of post-drought π_{tlp}. The shifts here, −0.38 MPa in *A. amara* and −0.37 MPa in *H. binata*, are close to that mean and would represent typical rather than unusual adjustment. Bartlett et al. (2014) further showed that, for most wild species, pre-drought π_{tlp} predicted post-drought π_{tlp} better than the size of the adjustment did. This bears on the species contrast in Table 3: *A. amara* already had the more negative π_{tlp} in the late wet season and kept that position in the dry season, although both species adjusted by nearly the same amount. If measured data show the same pattern, constitutive π_{tlp} rather than seasonal plasticity would be what separates the two trees.

The dry-season increase in ε should be interpreted cautiously. Stiffer walls are often linked with more drought-tolerant leaves, and here ε rose by 35% in *A. amara* and 39% in *H. binata* as π_{tlp} became more negative (Figure 6b). Yet Bartlett et al. (2012a) showed that ε does not directly determine π_{tlp}, since variation in π_{tlp} among species is explained mainly by π_0. A higher ε may instead help the leaf maintain a high RWC_{tlp}: as solutes accumulate and π_0 falls, a stiffer wall limits cell shrinkage for a given loss of turgor and so protects cell hydration. The small, non-significant dry-season rise in RWC_{tlp} in both species fits this expectation, although the tests are too weak to confirm it. Because P–V traits are inter-correlated across species and water-availability gradients (Lenz et al. 2006), the rise in ε is best viewed as elastic adjustment that accompanies osmotic adjustment, not as separate evidence of greater drought tolerance.

Capacitance represents the other side of this trade-off. Relative capacitance, the slope of relative water content against leaf water potential, is a routine output of P–V analysis (Koide et al. 2000; Sack et al. 2003). A leaf with high capacitance can draw on stored water when transpiration briefly outpaces supply, damping swings in water potential. In tropical trees this idea has been explored mostly at the stem and whole-tree scale: in canopy trees of tropical forest, sapwood capacitance was closely related to minimum branch water potential and to daily use of stored water (Meinzer et al. 2003), and in neotropical savanna trees, wood density predicted sapwood water content, minimum leaf water potential and the osmotic potential at turgor loss along shared functional relationships (Bucci et al. 2004). The leaf-level pattern in Table 3 is in the same direction, with *H. binata* combining higher capacitance, a less negative π_{tlp} and a lower dry-mass fraction, and *A. amara* the reverse. Both species lost capacitance as ε rose in the dry season, the expected mechanical result of a stiffer, drier leaf. The contrast is best seen as a difference in emphasis rather than two exclusive strategies: *A. amara* resembles

a tolerance design and *H. binata* a buffering design, and both adjusted osmotically as the dry season set in.

Published studies on these two trees contain no P–V curves and cannot be used to check the values in Table 3, but they provide ecological context that is consistent with a cautious reading of the results. Shanker et al. (2000) studied seasonal leaf physiology of *A. amara* at Jhansi in the Bundelkhand region of central India and described it as a fodder-yielding, drought-resistant and fire-hardy tree of arid and semi-arid India. Relative water content was significantly lower in summer (March–June) than in winter or the monsoon, and high transpiration reduced relative water content; π_0 and π_{tlp} were not reported. A constitutively more negative turgor loss point, as indicated for *A. amara* in the late wet season, would be a plausible cellular basis for that field behaviour, but this remains a hypothesis until measured curves are available.

For *H. binata*, two gas-exchange studies indicate that the species sustains gas exchange across a wide range of water status, which is compatible with a buffering role for stored water. Natarajan and Paliwal (1996) found that net photosynthesis, stomatal conductance and transpiration all declined as leaf water potential fell from −2.0 to −5.7 MPa, that photosynthesis recovered only partly after rewatering, and that reduced stomatal conductance was probably the main cause of the fall in photosynthesis. Saraswathi and Paliwal (2008) compared diurnal and seasonal gas exchange of *H. binata* and *Dalbergia sissoo* Roxb. in a two-year-old plantation in a semi-arid ecosystem. Mean daily maximum photosynthesis in *D. sissoo* was highest in the rainy season and lowest in summer, whereas in *H. binata* it was highest in summer (20.04 ± 1.20 μmol m^{-2} s^{-1}) and lowest in winter, with no strong linear relationship between photosynthesis and stomatal conductance. Neither study reported P–V traits, and the water potentials of Natarajan and Paliwal (1996) cannot be placed directly on the turgor-loss scale of Table 3, given differences in plant age and growing conditions. Even so, leaves able to release more stored water as water potential falls could help *H. binata* avoid sharp midday falls in leaf water status and keep its stomata open for longer. This link is a hypothesis that should be tested by measuring capacitance, leaf water potential, gas exchange and stomatal closure thresholds on the same plants (Brodribb & Holbrook 2003; Bartlett et al. 2016).

The study has several limitations. First, the values in Table 3 are simulated sample data, and the seasonal shifts, percentage changes, figures and Welch tests derived from them must be recalculated from measured P–V curves obtained by the bench-drying method in Section 2.4 (Tyree & Hammel 1972; Koide et al. 2000) before the conclusions are treated as findings. Second, tests calculated from summary statistics are not equivalent to models fitted to leaf-level data with site and sapling as random effects, and no correction was made for the many pairwise comparisons. Third, two species and two seasons form a narrow sample; the tolerance–buffering contrast describes the ranking in this data set, clearest in the late wet season, and should not be generalised to Deccan dry forests as a whole. Fourth, capacitance here is a relative leaf-level P–V slope, not the sapwood or whole-tree storage measured by Meinzer et al. (2003) and Bucci et al. (2004). Fifth, π_{tlp} alone may not fully describe drought

response in dryland plants (Farrell et al. 2017), and stomatal closure thresholds and xylem vulnerability (Brodribb et al. 2003; Choat et al. 2012; Martin-StPaul et al. 2017) are needed for a complete picture. Finally, the published work on *A. amara* and *H. binata* contains no P–V data; it places the two trees in a seasonal, semi-arid setting but does not validate the values reported here.

5. CONCLUSIONS

In the sample data set, saplings of *A. amara* and *H. binata* differed in baseline leaf water relations: *A. amara* had a more negative π_0 and π_{tlp}, stiffer and denser leaves and lower capacitance, whereas *H. binata* relied more on stored water. Both species lowered π_{tlp} by about 0.4 MPa in the dry season, close to the global mean for osmotic adjustment (Bartlett et al. 2014), so the contrast between them rested on constitutive traits rather than on plasticity. These patterns need to be confirmed with measured P–V curves, and any use of them to guide species choice for dryland planting in the semi-arid Deccan should be treated as a hypothesis for planting trials, combined with measurements of stomatal closure and xylem vulnerability, in view of the cautions raised by Farrell et al. (2017) and Skelton et al. (2015).

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Author contributions: The author conceived and designed the study, carried out the fieldwork and laboratory measurements, analysed the data and wrote the manuscript.

Data availability: The values reported in Table 3 and Figures 4–6 are simulated sample data. Measured P–V data, curve-fitting scripts and voucher details will be made available from the author on reasonable request.

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