

Faculté des bioingénieurs

How do transpiration, growth and stem water reserves vary within and between trees across two stands of contrasting successional stage?

Case study in a reforested area of the Atlantic forest in São Francisco Xavier, São Paulo, Brazil

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TABLE OF CONTRIBUTIONS

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Validation	Cohérence des résultats entre eux, gammes plausibles, comportement attendu, identification données erronées		Aide sur la recherche d'articles scientifiques pour valider les résultats
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Rédaction – révision et édition	Vocabulaire, logique, liens entre les différentes sections, approfondissement des explications, réécriture méthodes statistiques	Eric et Valérie Vermeulen	Traduction, vocabulaire, syntaxe, identification de répétitions et explications peu claires et non logiques
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TABLE OF CONTENTS

ACKNOWLEDGEMENTS	I
TABLE OF CONTRIBUTIONS	III
LIST OF ACRONYMS	IX
LIST OF FIGURES	XI
LIST OF TABLES	XVI
1. INTRODUCTION	1
2. CONTEXT	3
2.1. Climate	3
2.2. Geology and Soils	4
2.3. Vegetation and Land Cover	5
3. STATE OF THE ART	6
3.1. Carbon-water relations in trees: how transpiration demand shapes carbon assimilation and growth	6
3.1.1. The soil-plant-atmosphere continuum	6
3.1.2. Soil water availability and root water uptake	7
3.1.3. Stomatal regulation and vapour pressure deficit	7
3.1.4. Tree water-use strategies: from isohydric to anisohydric behaviour	8
3.1.5. Carbon allocation under water stress: why radial growth is the most sensitive sink	9
3.2. Transpiration of tropical trees and its environmental controls	10
3.2.1. Accessing transpiration at the individual-tree scale	10
3.2.2. Diurnal transpiration patterns in tropical forests	10
3.2.3. Atmospheric and edaphic controls	12
3.2.4. Demand-limited and supply-limited regimes, and interspecific variability	13
3.3. Water stress and radial growth: the role of turgor in controlling wood formation	13
3.3.1. Xylogenesis and the hydraulic control of cambial division	13
3.3.2. Growth phenology in the Atlantic Forest	15
3.3.3. The GPP-growth decoupling: an empirical signature	15
3.4. Linking transpiration, stem water status and radial growth: an integrative framework	16
4. OBJECTIVES	17

5. MATERIALS AND METHODS	18
5.1. Study site	18
5.2. Description of the two plots	19
5.3. Site Equipment	20
5.3.1. Weather station	20
5.3.2. Vapour pressure deficit	21
5.3.3. Reference and potential evapotranspiration	21
5.3.4. Soil Matric Potential	22
5.3.5. Tree probes	23
5.4. Tree characterization	24
5.4.1. Tree Inventory campaigns	24
5.4.2. Retrieval of DBH for 2020	25
5.4.3. Sapwood area determination	26
5.4.4. Height determination	28
5.4.5. Above-ground biomass increment	28
5.5. Signal pre-processing	29
5.5.1. Data Quality Control	29
5.5.2. Gap filling	33
5.6. Dendrometer signal processing	34
5.6.1. Zero-Growth decomposition	34
5.6.2. Drought stress indicators	35
5.6.3. Dry period detection	36
5.6.4. Growth phenology and growth drivers	37
5.6.5. Size normalisation	38
5.7. Sap flow data treatment	38
5.7.1. Granier conversion	38
5.7.2. Baseline ΔV_{max} determination	39
5.7.3. Whole-tree flow and daily water use	41
5.7.4. Stand transpiration	41
5.7.5. Reference transpiration	42
5.7.6. Stomatal sensitivity	43
5.7.7. Canopy conductance and atmospheric coupling	44
5.8. Cross-signal analyses	44
5.8.1. Using TWD as a proxy for stem water content	44
5.8.2. Stem storage contribution to transpiration ($f_{storage}$)	45
5.8.3. Nocturnal flux partition between transpiration and refilling	46
5.8.4. Water-use efficiency of stem biomass production	48
5.9. Uncertainty and sensitivity analysis	48
6. RESULTS AND DISCUSSIONS	50
6.1. Climatic and hydrological frame	50

6.2. Transpiration: regulation, drivers and scaling	51
6.2.1. Magnitude and scaling	51
6.2.2. Temporal Behaviour	52
6.2.3. Drivers	54
6.2.4. Regulation strategy	56
6.2.5. Upscaling and comparison RP R40	57
6.3. Radial growth: timing, magnitude and drivers	60
6.3.1. Growth phenology	60
6.3.2. Magnitude and scaling	62
6.3.3. Drivers	63
6.3.4. Synthesis: per-tree strategy and R40 vs RP positioning	65
6.4. Responding to water stress	66
6.4.1. Magnitude and frequency of dry periods	66
6.4.2. Drivers	67
6.4.3. The buffering: reservoir and capacitance	68
6.4.4. Functional consequence: suppression and recovery	70
6.4.5. Synthesis	72
6.5. Linking transpiration, stem reserve and growth	72
6.5.1. Using TWD as a proxy for stem water content	72
6.5.2. Contribution of the stem reserves to transpiration	74
6.5.3. Temporal dimensions of the buffer: diurnal lag and nocturnal flux	75
6.5.4. The water cost of wood production	77
6.6. Sensitivity analysis	78
7. LIMITS AND PERSPECTIVES	80
8. CONCLUSION	82
BIBLIOGRAPHY	84
APPENDIX	98
APPENDIX A – Climate and site	98
A.1 Daily meteo 2020	98
A.2 soil matric potential and root density along the two plots soil profiles	99
A.3 Root-density weights for Ψ_{soil}	99
APPENDIX B – Raw measurements of monitored trees (2018, 2023, 2026)	100
APPENDIX C – Quality control dendrometer	101
C.1 Dendrometer pipeline – full parameter reference	101
C.2 Per-tree data state	102
C.3 QC pipeline examples	103
APPENDIX D – QC SAP FLOW	104

D.1 Full parameter reference	104
D.2 Per-tree sap flow QC, annual coverage 2020	105
D.3 ANALYSIS WINDOWS	106
D.4 Complete QC pipeline example	107
D.5 Sap flow MDV gap-filling: full equations	107
D.6 Example gap filling: linear interpolation + MDV	108
APPENDIX E – Generalised Additive models (GAM)	108
APPENDIX F – Stratified test of pre-dawn sap flux density by stem reservoir state	110
APPENDIX G – Sensitivity analysis	112
G.1 OAT parameters perturbed	112
G.2 Baseline variants	113
G.3 Dendrometer pipeline sensitivity	113

LIST OF ACRONYMS

a.s.l.	Above sea level
ADC	Analog-to-digital converter
AGB	Above-ground biomass
ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
BAI	Basal area increment
C	Climax (successional strategy)
CI	Confidence interval
CORE	Reliable trees used for calibration
CRU TS	Climatic Research Unit Time-Series dataset
Cwa	Köppen-Geiger climate code (humid subtropical, dry winter, hot summer)
DBH	Diameter at breast height (1.30 m)
DOY	Day of year
DRG (or DRYING)	Drying transition (April–May)
DRY	Dry season (June–September)
ES	Early-secondary (successional strategy)
ESRI	Environmental Systems Research Institute (basemap provider)
ET	Evapotranspiration
ET ₀	Reference evapotranspiration
ETP (PET)	Potential evapotranspiration
ETR (AET)	Real (actual) evapotranspiration
FAO	Food and Agriculture Organization
FAO-56	FAO Irrigation and Drainage Paper No. 56 (Penman-Monteith)
FLUXNET	Global eddy-covariance database
f _{storage}	Stem-storage contribution to daily transpiration
GAM	Generalised additive model
GPP	Gross primary production
GRO	Irreversible radial growth
GUM	Guide to the expression of uncertainty in measurement
HDM	Heat dissipation method
HYDRUS-1D	Soil water and root uptake modelling software
IBGE	Instituto Brasileiro de Geografia e Estatística
INPE	Instituto Nacional de Pesquisas Espaciais (Brazilian National Institute for Space Research)
IQR	Interquartile range
JCGM	Joint Committee for Guides in Metrology
LAI	Leaf area index
‡	Low-confidence trees
LOCF	Last observation carried forward
LOESS	Locally estimated scatterplot smoothing
LS	Late-secondary (successional strategy)

MAD Median absolute deviation
 MDS Maximum daily shrinkage
 MDV Mean diurnal variation (gap-filling)
 OAT One-at-a-time (sensitivity analysis)
 OLS Ordinary least squares
 P Pioneer (successional strategy)
 PAR Photosynthetically active radiation
 † Reserve trees (intermediate reliability)
 R40 Secondary forest plot (~50 years old)
 Rc Recovery (Lloret et al. 2011)
 REW (or REWETTING) Rewetting transition (October–November)
 RGR Relative growth rate
 RH Relative humidity
 RMSE Root mean square error
 RP Reforested Pioneer plot (planted in 2009)
 Rs Resilience (Lloret et al. 2011)
 Rt Resistance (Lloret et al. 2011)
 SAI Sapwood area index
 Sapflower Integrated TDP pipeline
 SD Standard deviation
 SE Standard error
 Sen-ET Sentinel-2/3 evapotranspiration tool
 SFX São Francisco Xavier (study site)
 SiBCS Brazilian Soil Classification System
 SIRGAS Geocentric Reference System for the Americas
 SPAC Soil-Plant-Atmosphere Continuum
 TDP Thermal dissipation probe (Granier method)
 TLP Turgor loss point
 TWD Tree water deficit
 TWD_norm Normalised tree water deficit (Peters 2025)
 UTM Universal Transverse Mercator
 VPD Vapour pressure deficit
 WET Wet season (January–March)
 WGS World Geodetic System
 WRB World Reference Base for Soil Resources (FAO)
 WUE Water-use efficiency
 WUE_w Water-use efficiency on wood production

LIST OF FIGURES

Figure 1: Brazilian Atlantic Forest. (a) Original extent of the domain (black). (b) Main vegetation physiognomies. (c) Remaining forest cover in 2008 (Ribeiro et al., 2009). State abbreviations in (b) RN, Rio Grande do Norte; PB, Paraíba; PE, Pernambuco; AL, Alagoas; SE, Sergipe; BA, Bahia; GO, Goiás; RJ, Rio de Janeiro; SP, São Paulo; MS, Mato Grosso do Sul; PR, Paraná; SC, Santa Catarina; RS, Rio Grande do Sul. Source: Joly et al. (2014).....	1
Figure 2: Monthly climatograph for the State of São Paulo, climatological normals 1991-2020. Data: CRU TS climatological grids (Harris et al., 2020), aggregated at the state level via the World Bank Climate Change Knowledge Portal.....	4
Figure 3: Soil map of the State of São Paulo (IBGE Pedologia 1:5,000,000, SIRGAS 2000), with Brazilian SiBCS classes translated to their WRB equivalents (FAO 2014). Source: IBGE.....	4
Figure 4: Vegetation cover of São Paulo State (IBGE 2019), showing the study site (purple square).	5
Figure 5: Conceptual diagram of the soil-plant-atmosphere continuum (SPAC) showing the Ψ gradient from soil to atmosphere and the two main internal water storage pools (elastic storage and sapwood store) in the stem cross-section.	6
Figure 6: Theoretical 24-hour pattern of VPD (purple), solar radiation (orange) (top panel), and sap flux density (J_s , blue) (bottom panel), on a partially cloudy day. Grey shading marks night.	11
Figure 7: Location of the study site at São Francisco Xavier (Serra da Mantiqueira, southeastern Brazil). The right panel shows the two experimental plots, R40 (red outline) and RP (yellow outline), and the approximate on-site weather station (magenta dot), over an ESRI World Imagery base. Spatial reference: WGS 1984 UTM Zone 23S.	18
Figure 8: Photo of the R40 plot (left) and the RP plot (right) taken by Charlotte Vermeulen the 13/02/2026.	20
Figure 9: HOBO weather station (INPE) at the São Francisco Xavier study site. (a) Main tripod with cup anemometer, radiation-shielded T/RH probe, solar panel and datalogger (+ barometric sensor). (b) Tipping-bucket rain gauge. (c) Pyranometer. Taken by Lucas Jeangout, 13/02/2026.....	20
Figure 10: Left: sap flow (up) and dendrometer (down) sensors positioned on tree 14, Right: dendrometer sensor.	23
Figure 11: Principle of the heat dissipation method (Granier, 1985).	24
Figure 12: Diameter at breast height (DBH) distribution of the two stands, 2018 inventory (3 sub-plots of 100 m ² per stand, n = 347 stems for R40 and n = 228 stems for RP). Stem density is expressed in N ha ⁻¹ per 5-cm DBH class on a log scale. Tick marks on the x-axis identify the 27 monitored trees (15 in R40, 12 in RP).	25
Figure 13: Extraction of wood cores with an increment borer (right). Left up, visible colour differentiation between heartwood and sapwood, Left down, no colour differentiation visible.	27
Figure 14: Pooled A_s -DBH allometry fitted on the 25 cored trees of both forest plots. R40 (green circles, n = 10) and RP (orange triangles, n = 15). Solid line: fitted power-law $A_s = a \cdot DBH^b$, grey band (95 % confidence interval).....	27

Figure 15: DBH distribution of the 2018 inventory on R40 (left, $n = 347$ trees) and RP (right, $n = 228$ trees). Bars are 2-cm histograms (density on the y-axis), solid lines are kernel density estimates (Gaussian smoother, bandwidth $\times 1.2$).....	28
Figure 16: Zero-Growth decomposition (Zweifel et al. 2016) on tree T03, February 2020. Top: smoothed stem radius x_{smooth} (grey) and growth envelope GRO (blue), with $TWD = GRO - x_{smooth}$ shown as the blue ribbon. Bottom: TWD time series, dashed line at $TWD = 0$	35
Figure 17: Effect of the baseline method on Fd during a drying-season period (DG1, 10–16 April 2020, tree T10, R40). Top: cleaned ΔV with measured points (grey), interpolated points (orange), and the two baselines: DRY (green, ideal-night window 3/2) and WET (orange dashed, MAX per ideal night). Middle: Fd derived from each baseline. Bottom: VPD.....	39
Figure 18: Effect of the baseline method on Fd during a wet-season period (WE6, 10–21 March 2020, tree T10, R40). Grey shading: rainy days. Same conventions as Figure 17.	40
Figure 19: Kc, T sensitivity to the inventory pool (colours) and to the Fd -to-inventory rule (panels). Points: daily stand T against ET_0 on reference days. Lines: $Kc, T \cdot ET_0$. Dashed grey: 1:1. Retained production: $Kc, T = 0.349$ (all inventory $\times$ nearest-DBH).	43
Figure 20: Pre-dawn flux $Fd_{predawn}$ normalised by daytime maximum, plotted against pre-dawn VPD and stratified by stem reservoir state at 04–06 h. Left: reservoir refilled ($TWD_{pre} \leq 0.10$). Right: reservoir not refilled ($TWD_{pre} > 0.10$). Black line = hockey-stick breakpoint fit per stratum with breakpoint and R^2 annotated. Red dashed line at $VPD = 0.5$ kPa = baseline cut-off used in §5.7.2. Robustness of the threshold choice is shown in Fig. 52 (Appendix).	48
Figure 21: Climatic setting of 2020 by season (WET/DRG/DRY/REW). Top: mean diurnal cycles by season: global radiation ($W m^{-2}$), VPD (kPa), hourly ET_0 (Penman–Monteith FAO-56). Bottom left: root-weighted Ψ_{soil} (R40 green, RP orange). Bottom right: mean daily precipitation (bars) + air temperature (line); annotations = seasonal cumulative rainfall (mm) and duration (number of days).	50
Figure 22: Instantaneous flux metrics versus DBH (14 trees, 11 R40 + 3 RP, pooled over the year). (a) Fd, max , the 95th percentile of daily sap flux density ($g cm^{-2} h^{-1}$); (b) Js, max , the 95th percentile of daily whole-tree sap flow ($L h^{-1}$). Regression line $\pm 95\%$ CI, R^2 and p inset. labels = tree ID.	51
Figure 23: Mean diurnal cycle of sap flux density Fd per tree, by season (rain-free days, 5-min resolution; Fd in $g cm^{-2} h^{-1}$, free y-axes). Near-zero overnight, rise after sunrise (~ 06 h), midday peak, return to zero by 18 h. Headers: tree ID · forest plot · DBH.	52
Figure 24: Seasonal course of daily water use Q_{day} per tree (monthly mean $\pm$ SD; background shading = dominant season). Asterisks mark trees with fewer than 30 observation days (04, 06, 16), and the RP series rests on a single day in DRYING; these panels are indicative only. Headers: tree ID · forest plot · DBH.	53
Figure 25: Per-tree composite diurnal Fd –VPD hysteresis ($n = 14$; annual composite over rain-free days, 1-min resolution). Fd normalised 0–1 per tree; colour encodes the hour of day. Each panel reports the normalised loop area $ H $ (0 = closed loop, 1 = maximal), the loop direction (CW = clockwise), and the AM–PM offset (mean morning-minus-afternoon Fd across 10 VPD-quantile bins; positive = morning branch above afternoon). Headers: tree ID · forest plot · DBH.	54
Figure 26: Marginal response of Js to VPD (lower x-axis, blue) and to solar radiation (upper x-axis, orange), overlaid per tree ($n = 14$; 11 R40 + 3 RP). Curves are independent GAM smooths ($y \sim s(x)$) on rain-free daytime 1-min records. VPD and radiation covary strongly over the diurnal cycle (concurrency ~ 0.75), so the curves show	

response shape, not a driver ranking (settled separately by the multi-driver model, Appendix E). Headers: tree ID · forest plot · DBH. 55

Figure 27: m - g_{ref} coordination (Oren 1999) across the 14 monitored trees. Each point is one tree, summarised by the two parameters of $G_s = g_{ref} - m \cdot \ln(VPD)$ fitted on its boundary line (90th percentile per 0.2-kPa VPD bin, restricted to peak-sun hours 10–16 h, $Rad > 400 \text{ W m}^{-2}$, rain-free days). Dashed line = Oren (1999) prediction $m/g_{ref} = 0.6$; observed median = 0.66. Colour = DBH (viridis); shape = forest plot (R40 circle, RP triangle); labels = tree ID. 56

Figure 28: Stand transpiration of R40 (green) and RP (orange) across the 22 windows of 2020, x-axis ordered by season with seasonal background shading. (a) Absolute T (mm day^{-1}), with overlaid references: $ETP = Kc \cdot ET_0$ ($Kc = 1.16$, short-dashed grey) and T_{ref} ($Kc, T = 0.349$ calibrated on R40, long-dashed grey on 11 reference trees $\rightarrow$ 347 stems) (b) T/T_{ref} (R40 only, left axis) and T/ETP (both plots, right axis), line at 1 marking the non-limiting potential. 58

Figure 29: R40 versus RP comparison ($n = 14$; 11 R40 + 3 RP). (a) Canopy conductance G_c (Köstner 1992: G_c restricted to $Rad > 50 \text{ W m}^{-2}$, $VPD > 0.6 \text{ kPa}$, rain-free days); hourly median $\pm$ IQR per plot. (b) Decoupling coefficient Ω per tree (Jarvis–McNaughton 1986: Ω); point = median, bar = IQR, shaded background = canopy stratum. labels = tree ID. 59

Figure 30: Per-tree cumulative radial growth (absolute ΔGRO , mm), with trees split into small and large growers at 0.75 mm yr^{-1} . Lower panels give the climatic context: daily rainfall and forest-median root-weighted Ψ_{soil} . Dashed segments flag the post-shift correction of the dendrometer signal. † reserve, ‡ low confidence. 61

Figure 31: (a) Mean seasonal growth rate per tree ($\mu\text{m day}^{-1}$), trees sorted by zone (R40 first, then RP) and decreasing annual ΔGRO within each zone. (b) Basal area increment vs DBH per forest (dashed lm lines). (c) Relative growth rate $RGR = \Delta DBH / DBH$ vs DBH per forest. † reserve, ‡ low confidence. 62

Figure 32: Per-tree importance of the three climatic drivers of radial growth. Additive GAM per tree, $\Delta GRO \sim s(\text{daytime VPD}) + s(\Psi_{soil}) + s(\text{rain } 3d)$, on the daily series. Stacked bars = unique contribution of each driver (full-model deviance minus the term-dropped model); black diamond = total deviance of the full model. Rain (3 d) = PULSE, Ψ_{soil} = STOCK, daytime VPD = DEMAND. $n = 20$ trees. † reserve, ‡ low confidence. 63

Figure 33: Predicted daily stem growth as a function of atmospheric demand and soil water, per forest. Curves = ΔGRO ($\mu\text{m day}^{-1}$) predicted by the GAM with a $te(VPD, \Psi_{soil})$ interaction; bands = 95 % CI. Soil water at three levels: dry (low Ψ , orange), intermediate (purple), wet (high Ψ , blue). 64

Figure 34: Per-tree scatter of relative growth rate ($RGR = \Delta DBH / DBH, \text{yr}^{-1}$) against the relative weight of atmospheric demand in each tree's climate signal, $devVPD / devVPD + dev\Psi_{soil} + devrain$ from the per-tree GAMs (§3.3.3). † reserve, ‡ low confidence. 65

Figure 35: (a) Synchrony: percentage of trees exceeding, on each day, the notable-deficit threshold ($TWD_{norm} > 0.2$, light orange) and the drought-stress onset threshold ($TWD_{norm} > 1$, red; Peters et al., 2025). (b) Date $\times$ tree raster of the deficit level (three tiers), faceted by forest, trees ordered by their percentage of days in deficit. 66

Figure 36: (a) pre-dawn TWD_{norm} as a function of daytime VPD, stratified by root-zone Ψ_{soil} class (dry $< -200 \text{ kPa}$; drying -200 to -50 ; wet > -50); loess smoothing $\pm$ CI. Dashed line = stress-onset threshold ($TWD_{norm} = 1$; Peters et al., 2025). (b) Cumulative rain over the previous 3 days, on days with no recharge (TWD stays > 0) versus full recharge ($TWD \rightarrow 0$). 67

Figure 37: Stem water reservoir, relative and absolute size per tree. (a) $strainMDS = MDS_{max} / R_{ppm}$, the maximum daily shrinkage per unit radius, by forest (boxplot per-tree points labelled by tree id; med = forest

median). (b) Absolute maximum daily shrinkage MDS_{max} (μm) versus DBH, by forest. † reserve, ‡ low confidence. 68

Figure 38: Reservoir reactivity to atmospheric demand and its breakdown. (a) MDS versus daytime VPD, loess $\pm$ CI per forest. (b) Slope of MDS on VPD per tree ($\mu\text{m kPa}^{-1}$), with the Spearman ρ of each fit. (c) Buffer-break TWD_{norm} per tree; dashed lines = forest medians, dotted line = drought-stress onset ($TWD_{norm} = 1$, Peters et al., 2025). Panel (c) is restricted to the 15 trees with valid predawn coverage. † reserve, ‡ low confidence. 69

Figure 39: Probability of a growth event per day against the stem's pre-dawn water deficit. A growth event = $\Delta\text{GRO} > 1 \mu\text{m}$. Points = proportion of growth days per TWD_{norm} bin ($\pm 95\%$ CI, n labelled). Dashed line and shaded zone = drought-stress onset ($TWD_{norm} = 1$; Peters et al., 2025). 70

Figure 40: Growth recovery after deficit episodes. (a) Composite trajectory: the 7-day rolling growth rate relative to the pre-episode rate, aligned on rewetting (day 0 = episode end), median $\pm$ IQR per forest. Reference lines mark full recovery, the 75 % threshold, and the grey band shows the episode duration. (b) Per-tree strategy in the Lloret (2011) plane: resistance R_t (during/before) vs resilience R_s (after/before); point size = recovery time (days to regain 75 % of the pre-episode rate), $\times$ = trees never strongly suppressed. Suppressing episodes defined by $R_t < 0.5$. R40 in green, RP in orange. 72

Figure 41: TWD-proxy correction of the sap flow baseline (tree 12 R40, 22/08 to 19/09/2020). (a) Raw ΔV_{clean} (grey), production baseline (blue), and TWD-corrected baseline (red), built from the production baseline plus $\beta \cdot TWD_{norm,t} - TWD_{ref}$, capped at 15 % and floored at 0. (b) Regression $\Delta dV = env_{wide} - Max1$ vs $TWD_{predawn}$ over the n_{ideal} nights, with env_{wide} the rolling MAX width 7. OLS fit (line) and 95 % CI (grey band). (c) J_s (L h^{-1}) at 1-min resolution from each baseline. 73

Figure 42: Stem-storage contribution to daily transpiration per tree. Boxes = total storage from the morning-lag method (Phillips et al., 2003). Red diamonds = elastic-only estimate from the dendrometer. Shaded band and dashed lines = the 10 to 50 % range reported for tropical canopy trees (Goldstein et al., 1998). $n = 15$ (12 R40 + 3 RP). 74

Figure 43: Diurnal lag between transpiration and stem water deficit, per tree. (a) Hourly cross-correlation $F_d \leftrightarrow TWD$ for four representative trees (06, 07, 40, 36); dashed line = zero lag. (b) Peak lag per tree with 95 % bootstrap CI (24 h blocks, $B = 200$), ordered from most negative (top) to zero (bottom). Colour = lag reliability based on CI width (reliable ≤ 2 h, moderate ≤ 5 h, not interpretable > 5 h). 75

Figure 44: Nocturnal flux and overnight recovery of the stem reservoir. (a) Nocturnal share of daily water use $Q_{night}/Q_{day} + Q_{night}$, per plot and season (boxplots over tree-nights). (b) Overnight TWD recovery fraction vs nocturnal VPD, one point per tree-night, coloured by plot. Solid line = GAM fit with 95 % CI. 76

Figure 45: Synthesis of the dendrometer $\times$ sap-flow crossing. (a) Multi-trait space across the full dendrometer range: point size = DBH, colour = forest ($n = 19$, 13 R40 + 6 RP). (b) Wood-production water-use efficiency per tree, dashed lines = per-forest median; only sap-flow-instrumented trees appear (11 R40, 2 RP). † reserve, ‡ low confidence. 77

Figure 46: Uncertainty cascade along $F_d \rightarrow J_s \rightarrow T_{stand} \rightarrow Kc_T \rightarrow T/T_{ref} \rightarrow \Omega$ (rows = sources, columns = chain steps). The dV_{max} baseline and Granier coefficients dominate the per-tree fluxes. Shared rescalings cancel in T/T_{ref} , leaving only the baseline residual ($-4/+18\%$) and the Kc_T calibration ($\approx \pm 10\%$). Ω inherits T_{stand} uncertainty through G_c 78

Figure 47: Daily meteorological conditions at the São Francisco Xavier study site over 2020. From top to bottom: air temperature, relative humidity, vapour-pressure deficit (VPD), maximum solar radiation, wind speed, precipitation, and potential evapotranspiration (ETP). For temperature, relative humidity, VPD and wind speed, the coloured line shows the daily mean and the shaded envelope the daily minimum–maximum range. Solar

radiation is the daily maximum irradiance (filled area) and precipitation the daily total. Vertical shaded bands indicate the wet season (blue: January–March and December) and the dry season (orange: June–September). .. 98

Figure 48: Soil matric potential and fine-root density profiles. Each row pairs fine-root density (left, grey bars, % of total fine-root mass per layer, Delvoie 2023) with median soil matric potential h per sensor depth and season (right, coloured lines, 2020). R40 (top, ≈ 50 yr) shows steep root decline and sharp drying at depth, RP (bottom, ≈ 12 yr) a more spread root profile and weaker dry-season drying, consistent with the proximity of the groundwater table. 99

Figure 49: Dendrometer QC pipeline applied to tree 04 (R40, April 2020). (a) Cleaned signal (blue), GRO envelope (green dashed) and points flagged by the eight automated filters (Table 3.4.1). (b) Post-QC interpolated signal (blue points); orange ticks at the bottom mark minutes filled by linear interpolation (gaps ≤ 2 h). (c) Interpolated signal (grey) and the 31-min centred rolling median x_{smooth} (red line) used in the Zero-Growth decomposition. (d) Resulting tree water deficit $TWD = GRO - x_{\text{smooth}}$ 103

Figure 50: Sap flow QC pipeline applied to tree 10 (R40, March 2020). (a) Raw ΔV signal (blue) with points flagged by the 14 automated filters (Table 3.4.3). (b) Post-QC ΔV signal: measured points in blue, interpolated points in orange (linear interpolation for gaps ≤ 2 h, mean-diurnal-variation template for $2 \text{ h} < \delta \leq 18 \text{ h}$, see Annex D.5). (c) Post-QC signal (grey) and the 11-pt centred rolling median used for residual cleanup (red line). (d) Resulting sap flux density F_d ($\text{g cm}^{-2} \text{ h}^{-1}$) from the Granier conversion. 107

Figure 51: Sap flow gap-filling on a representative dry-period window (tree 03, 25 May – 4 June 2020). Black: measured ΔV signal (post-QC). Orange: linear interpolation applied to gaps ≤ 2 h. Magenta: mean-diurnal-variation (MDV) template applied to gaps $2 \text{ h} < \delta \leq 18 \text{ h}$, rescaled per gap by ordinary least squares and anchored at both edges (procedure detailed in Appendix D.5). Measured coverage rises from 54 % to 93 % after gap-filling. 108

Figure 52: Empirical breakpoint of the reservoir-state stratification. $\Delta(R^2) = R^2(\text{not refilled}) - R^2(\text{refilled})$ of $F_d^{\text{predawn}} \sim \text{VPD}$ across candidate thresholds for TWD_{pre} . Blue line = argmax (0.155, $\Delta(R^2) = 0.124$); grey dashed = production choice (0.10, $\Delta(R^2) = 0.117$). The plateau 0.05–0.22 supports 0.10 as a round value within the stable range. 111

Figure 53: Threshold sensitivity of the split. $F_d^{\text{predawn}} \sim \text{VPD}$ fitted per stratum at six thresholds (blue = refilled, red = not refilled, point size = n nights). At the production threshold (dashed, 0.10), $R^2 = 0.119$ in the not-refilled stratum vs ≈ 0.002 in the refilled stratum. The contrast persists across the plateau 0.05–0.20. 112

Figure 54: Impact of the dV_{max} baseline method, six variants relative to the per-night MAX (variant E, central). Bars: $J_{\text{s_max}}$ (daily peak, green), daytime flux Q_{day} (6–18 h, orange), night flux Q_{night} (18–6 h, blue). Q_{night} is the most baseline-sensitive ($\times 1.0$ – 5.7 across A–D, variant G excluded). 113

LIST OF TABLES

Table 1: Monitored trees and 2020 per-tree characteristics. DBH reconstructed on 1 January 2020; A_s from the pooled A_s –DBH allometry; H from the per-plot Michaelis–Menten H –DBH allometry; ρ by water displacement (* species-median substitution; — absence). Successional strategy (P / ES / LS / C) follows Swaine & Whitmore (1988) and Ribeiro et al. (2005). 26

Table 2: Dendrometer QC filters, parameters, median fraction removed (2020), and references. Percentages are non-exclusive. A minute flagged by k filters counts in each row. They refer to the 527 040 minutes of 2020 and exclude the four globally invalid sensors. Full parameter set in Appendix C.1 Table 8. 30

Table 3: Sap flow QC flags, parameters and contribution to the 2020 mask. Removed = % of all 1-min $\times$ tree records flagged. Unique = fraction of that flag exclusive to it. Full parameter set in Appendix Table 10. 32

Table 4: Daily sap flow integrals with production vs TWD-corrected baselines (tree 12 R40, 22/08 to 19/09/2020). Medians over the period. Q_{day} integrated 6:00 to 18:00. Difference = (corrected – production) / production $\times$ 100 %. 74

Table 5: Cross-signal sources of uncertainty on plot-median $WUE_w = \Delta AGB / Q_{year}$ (ΔAGB side). The Combined rows quadrature-sum these ΔAGB -side sources with the Q-chain envelope from the sap flow OAT (Appendix Table 13), giving the total uncertainty on plot-median WUE_w . Per-tree ranking is preserved across ρ alternatives (Spearman $\rho = 1.000$). 79

Table 6: Fine-root density weights used in the depth-averaged soil matric potential h . Weights are derived from the fine-root mass profiles (DR_{Finas} , $g\ dm^{-3}$) measured by Delvoie (2023) on the same two plots. Each tensiometer is assigned to the soil layer with nearest midpoint. The 0–5 cm surface layer is not weighted in (no tensiometer at that depth). Weights are normalised so that $\sum w_i = 1$ per plot. 99

Table 7: Inventory measurements 2018, 2023, 2026 — DBH and sapwood area A_s of the monitored trees. Rows labelled « X alt. » correspond to alternative individuals measured at the same position when the originally tagged tree could not be unambiguously identified in a later campaign. A_s is measured directly on cored individuals only ; empty A_s cells indicate that the tree was not cored that year. Empty DBH cells indicate that the tree was not measured that year. 100

Table 8: All parameters used in `R_dendro/01_qc_dendro.R` (run 14). Filters are listed in the order of application; reset detection runs after the automated filters and manual invalidation; interpolation and smoothing are applied to the reset-corrected signal. References are only repeated when the parameter follows a published convention or threshold; values calibrated from this dataset are tagged "this study". 101

Table 9: All percentages are computed relative to the total number of minutes in 2020 ($n = 527\ 040$ min). The detail of filter contributions is non-exclusive: a single minute flagged by k filters is counted in each filter row, so the sum of filter columns can exceed Flag total and may be larger than 100 % on heavily flagged trees. After QC is the valid fraction after all filters and manual invalidation; With interp is the valid fraction after gap filling (§X.X.3). The filters Range, Frozen and Diff didn't flag any values and are not shown in the table. 102

Table 10: All parameters used in `R_SF/01_qc_sapflow.R` (QC), `R_SF/02_convert_sapflow.R` (residual cleanup + smoothing), and `R_SF/gapfill_dV.R` (gap filling). Filters are listed in the order of application; the residual cleanup runs after the QC mask is established and before Granier conversion. References are repeated only when the parameter follows a published convention; values calibrated from this dataset are tagged "this study". 104

Table 11: All percentages are relative to the 527 040 minutes of 2020. Filter contributions are non-exclusive: a minute flagged by k filters is counted in each row, so column sums may exceed 100 %. PostPanne = re-

equilibration after a logger gap; Floor = stuck at ADC noise floor; Frozen = below-threshold rolling SD; FirstDiff = first-difference burst; LocalRange = inflated-variability window; Manual = visual invalidation. Excluded sensors (T01, T20, T31, T32, T33, T35, T39, T41) show partial profiles where the pipeline aborted early. After QC = valid fraction of dV_clean; With interp equals After QC at the year scale, since the diurnal template is applied within analysis windows only. 105

Table 12: Multi-day windows retained for sap flow analyses in 2020. Total 22 windows across the four seasons. 106

Table 13: Parameters perturbed in the OAT sensitivity analysis. Each parameter is varied within its plausible range while all others are held at their central best-estimate values. The perturbation is propagated along the full chain so that the effect is reported at every downstream stage. Production values are in bold..... 112

1. INTRODUCTION

Tropical forests cover less than 10 % of the land surface yet store roughly 60 % of the world's forest carbon and return nearly 40 % of incident precipitation to the atmosphere through transpiration (Pan et al., 2011; Schlesinger & Jasechko, 2014), regulating climate and hydrology at continental scales. They are also under mounting pressure: logging, fragmentation, fire and agricultural expansion combine with climate change to erode biodiversity and carbon storage, and tropical land-use change has become a major source of carbon emissions alongside fossil fuels (Wright, 2005; Laurance et al., 2012). With little of the biome strictly protected, human-modified landscapes now carry much of the burden of conservation and carbon sequestration (Gardner et al., 2009).

Brazil's Atlantic Forest (Mata Atlântica), a tropical rainforest that originally stretched along the eastern coast of Brazil and into small portions of Uruguay, Paraguay and Argentina, illustrates both this richness and this vulnerability. Once covering 1.45 million km² along the coast, less than 12 % of its original extent remains, fragmented into thousands of patches, most of them being smaller than 50 ha and lying within 100 m of an edge (Fig. 1; Ribeiro et al., 2009). It nonetheless ranks among the world's five biodiversity hotspots, with over 18,000 plant species and more than 65 % of its trees endemic, most of them threatened (de Lima et al., 2024). Two pressures combine on the remaining forest: fragmentation, which warms and dries the interior of each fragment through edge effects, and drought, which kills the largest trees through hydraulic failure. Both reduce biodiversity and carbon storage (Magnago et al., 2015; Rowland et al., 2015).

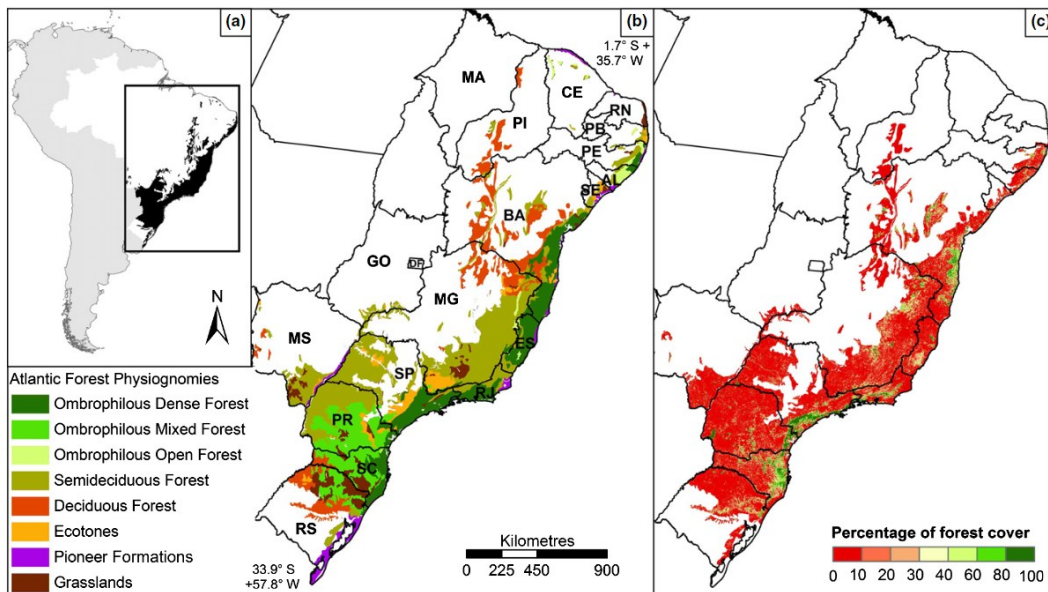


Figure 1: Brazilian Atlantic Forest. (a) Original extent of the domain (black). (b) Main vegetation physiognomies. (c) Remaining forest cover in 2008 (Ribeiro et al., 2009). State abbreviations in (b) RN, Rio Grande do Norte; PB, Paraíba; PE, Pernambuco; AL, Alagoas; SE, Sergipe; BA, Bahia; GO, Goiás; RJ, Rio de Janeiro; SP, São Paulo; MS, Mato Grosso do Sul; PR, Paraná; SC, Santa Catarina; RS, Rio Grande do Sul. Source: Joly et al. (2014).

The biome's water and carbon services are tightly linked. It sustains freshwater for some 125 million people and most of Brazil's hydropower production (World Bank, 2006), while its carbon sink depends on sustained wood formation across species and size classes (Stephenson et al., 2014). Reforestation is a central restoration strategy, and Brazil has pledged to restore 12 million hectares by 2030 (WRI, 2018). Yet afforestation can also reduce streamflow through higher evapotranspiration (Jackson et al., 2005), so managing restored forests for carbon cannot be dissociated from their water use. Successional stage sharpens the trade-off: young, fast-growing stands fix carbon rapidly through acquisitive, drought-sensitive traits, whereas older secondary stands store more biomass behind deeper, better-buffered hydraulic systems.

Stand-scale analysis provides integrated information on whole-forest behaviour, but it averages across species and size classes and cannot explain why structurally similar forests can show contrasting fluxes. Approaching forest-scale behaviour more closely therefore requires looking inside the forest, where the regulation takes place. Trees of different species and contrasting successional stages may regulate water use and growth differently, and these differences remain invisible to stand-level budgets: the individual tree must be observed. Transpiration draws water through the tree, and radial growth fixes carbon into wood; both depend on the tree's internal water status. Under high atmospheric demand, water is withdrawn from elastic stem tissues, producing a reversible stem shrinkage that tracks the turgor available for wood formation. Transpiration and growth do not necessarily decline together, because cambial expansion stops at a smaller water deficit than the one closing stomata.

Two complementary signals are therefore needed. Sap flow, measured with thermal dissipation probes (Granier 1985), quantifies whole-tree water use but remains sensitive to species, sapwood properties, baseline drift and non-negligible nocturnal flow (Peters et al. 2018). Point dendrometry resolves stem diameter variations into a reversible, water-driven shrinkage and an irreversible expansion, thereby quantifying both stem water status and radial growth (Zweifel et al. 2016), and provides an independent check on the sap-flow signal.

This thesis analyses paired sap-flow and dendrometer records from two reforested Atlantic Forest plots of contrasting age, located on the eastern slopes of the Serra da Mantiqueira near the village of São Francisco Xavier (São Paulo State, southeastern Brazil): a young pioneer/early-secondary plot planted in 2009, about eleven years old at the time of measurement (RP), and an older secondary plot of approximately fifty years (R40). The site is hosted by the *Instituto Nacional de Pesquisas Espaciais* (INPE), whose Impacts, Adaptations and Vulnerabilities Division co-supervised this work. Three questions follow: how atmospheric demand, modulated by soil water, controls individual-tree transpiration across seasons; how stem water status translates into radial growth, and when the two decouple; and whether the water-use and growth strategies of pioneer and older secondary trees genuinely diverge once both are read through the same coupled signal. Tying the three questions together is a more basic one: how much water a tree spends to build a unit of wood, a quantity that remains poorly resolved at the individual-tree scale in tropical secondary forests.

The remainder of the document is organised as follows. The State-of-the-Art reviews the conceptual framework linking plant water status, transpiration and radial growth, and situates Atlantic-Forest secondary stands within current restoration ecology. The Materials and Methods describe the study site, the two reforested plots, the instrumentation and the processing pipeline applied to sap-flow and dendrometer records. The Results are organised by signal rather than by plot, and each chapter follows the same reading principle: the individual tree is examined first, and the plot contrast is built only as a second step. Chapter 1 analyses whole-tree transpiration and its response to atmospheric demand and soil water across seasons. Chapter 2 turns to radial growth, its seasonal dynamics and its environmental drivers. Chapter 3 examines stem water status through the trunk water deficit and frames it within the trade-off between water supply and demand. Chapter 4 brings the three signals together to characterise the internal water reservoir, hydraulic regulation and the water cost of wood. Chapter 5 reports a sensitivity analysis of the main methodological choices. The Discussion synthesises these results across chapters, contrasts the two plots, and considers the broader implications for the water–carbon trade-off in restored tropical forests.

2. CONTEXT

2.1. Climate

The study area lies in the São Francisco Xavier district of São José dos Campos, on the slopes of the Serra da Mantiqueira in São Paulo State, southeastern Brazil, at an average altitude of about 720 m. The site falls within the Cwa Köppen–Geiger zone, a humid subtropical climate with a hot summer (warmest month above 22 °C) and a comparatively drier winter, although the cool season does not strictly qualify as dry under the Köppen criterion (mean rainfall of the driest month exceeds 10 % of the wettest; Peel et al. 2007). Summer rainfall is modulated by the South Atlantic Convergence Zone (SACZ; Escobar 2019), driving a marked contrast between austral summer (December–February: wet and warm) and austral winter (June–September: drier and cooler). Based on the gridded CRU TS dataset (Harris et al. 2020), accessed through the World Bank Climate Change Knowledge Portal, the 1991–2020 normals indicate a mean annual precipitation of ~1,658 mm, a reference evapotranspiration of ~1,450 mm and a mean annual temperature of 20.4 °C (Fig. 2). The year is organised around two main seasons: a wet season that concentrates most of the annual rainfall and recharges the rooting zone, and a dry season during which soil water reserves are progressively drawn down until water stress peaks in late August or early September.

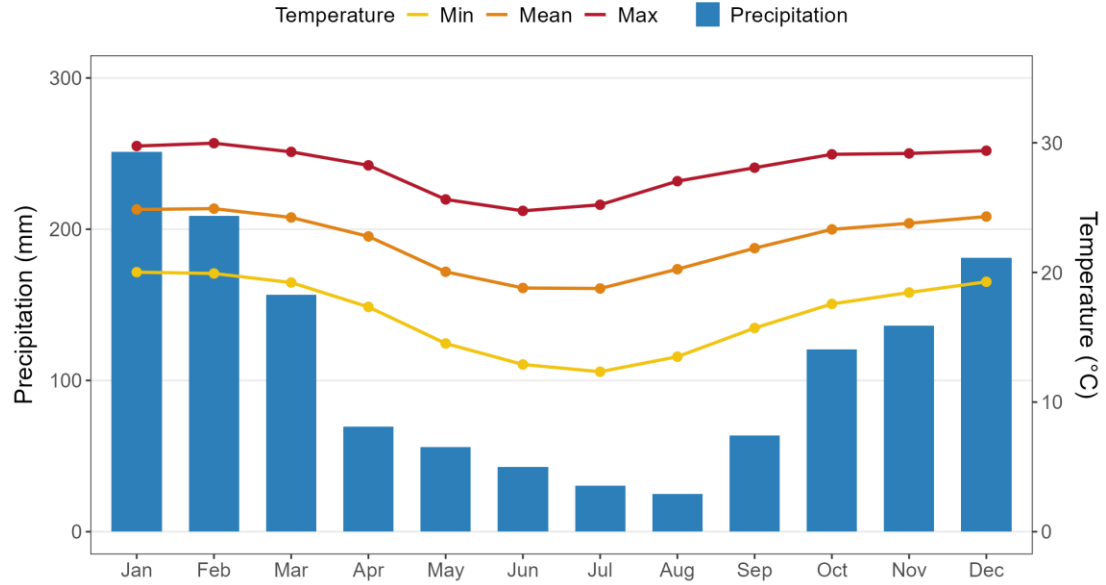


Figure 2: Monthly climatograph for the State of São Paulo, climatological normals 1991-2020. Data: CRU TS climatological grids (Harris et al., 2020), aggregated at the state level via the World Bank Climate Change Knowledge Portal.

2.2. Geology and Soils

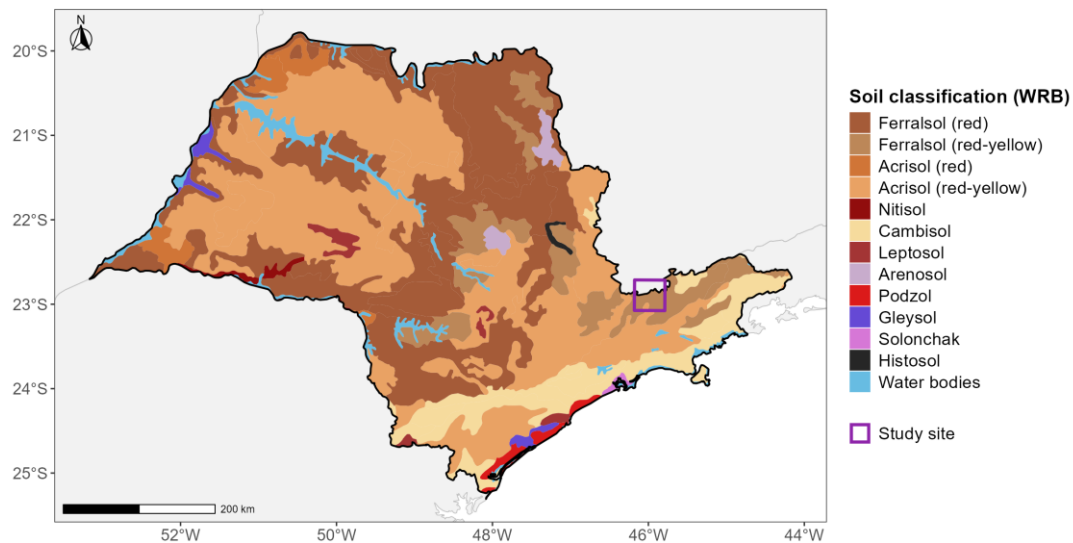


Figure 3: Soil map of the State of São Paulo (IBGE Pedologia 1:5,000,000, SIRGAS 2000), with Brazilian SiBCS classes translated to their WRB equivalents (FAO 2014). Source: IBGE.

Pedological maps show that red-yellow Ferralsols dominate the area on stable landscape positions (Fig. 3; Embrapa 1999; IUSS Working Group WRB 2015), with patches of Cambisol visible at finer resolution (ISRIC 2025; Poggio et al. 2021). These two products combine field surveys from the Brazilian RADAMBRASIL project (Embrapa, 1:5,000,000 polygons) and ISRIC SoilGrids (machine-learning predictions at 250 m trained on ~240,000 worldwide soil profiles). Ferralsols are deeply weathered and nutrient-poor, but their micro-aggregated structure holds water well when dry and drains well when wet (double porosity; Sanchez 2019). Cambisols are less developed, usually found on steeper slopes where erosion limits soil

development. They are richer in nutrients but hold less water. Combined with the steep slopes of the Mantiqueira range, these two soil types create strong variation in soil water availability. Downslope positions and Cambisol patches usually stay wetter through the dry season than upslope, Ferralsol-dominated areas.

2.3. Vegetation and Land Cover

The site sits within the Atlantic Forest biome, on the southeastern edge of São Paulo State, in the dense ombrophilous forest (Floresta Ombrófila Densa) that covers the seaward slopes of the Serra do Mar and Serra da Mantiqueira (Fig. 4, purple square; IBGE 2019). This evergreen, broadleaved formation is sustained by orographic rainfall and stable atmospheric humidity throughout the year (Veloso et al. 1991; SEMIL n.d.), and grades further inland into seasonal semideciduous forests on the plateau and savanna (cerrado) patches in drier interior basins. Locally, the dense ombrophilous forest forms a mosaic with secondary stands (*capoeiras* and *capoeirões*) and patches of high-altitude grasslands (*campos de altitude*), reflecting both environmental gradients and a long history of human disturbance (SEMIL 2024). At the regional scale, the Atlantic Forest is one of the most fragmented biomes in Brazil, and São Paulo holds the lowest proportion of remaining native vegetation among Brazilian states (MapBiomas 2023).

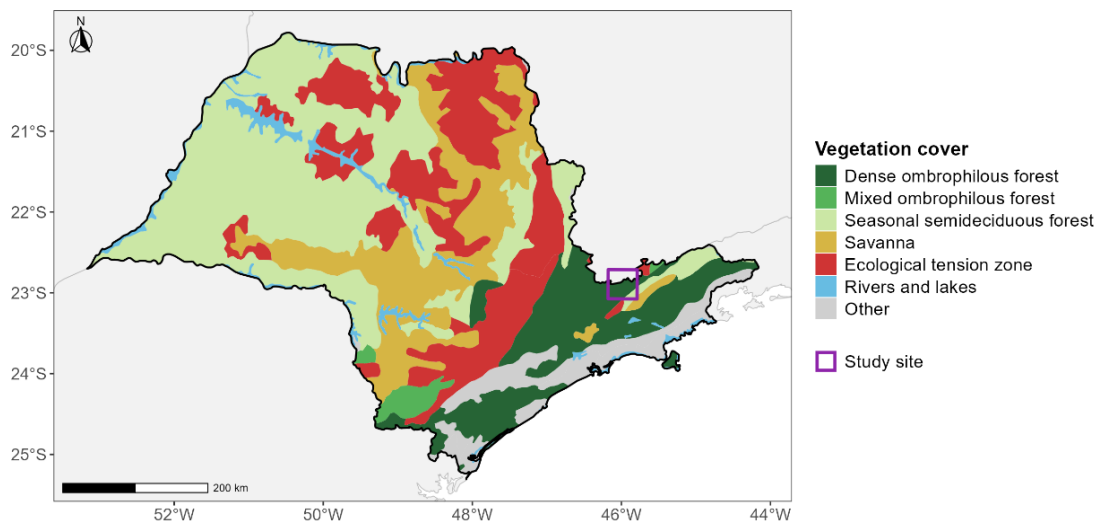


Figure 4: Vegetation cover of São Paulo State (IBGE 2019), showing the study site (purple square).

Dense ombrophilous Atlantic Forests rank among the most species-rich vegetation types in Brazil, with more than 200 tree species per hectare (Oliveira-Filho & Fontes 2000; Joly et al. 2012). The canopy and sub-canopy are typically dominated by Myrtaceae, Fabaceae, Lauraceae and Meliaceae, while Euphorbiaceae and Melastomataceae often prevail in early-successional and disturbed patches (Lorenzi 2002). The understorey is rich in Rubiaceae, palms and tree ferns, and abundant lianas and vascular epiphytes (Bromeliaceae, Orchidaceae, Araceae) reflect the year-round atmospheric humidity that sustains this vegetation type (Veloso et al. 1991).

3. STATE OF THE ART

3.1. Carbon-water relations in trees: how transpiration demand shapes carbon assimilation and growth

Trees face a constant trade-off: the stomata that capture CO_2 for photosynthesis also let water escape to the air. When evaporative demand rises, this balance becomes tighter, and the resulting water stress propagates through the whole transport pathway, from the soil through the roots, xylem and stomata to the cambium where wood is built. Because each step responds to that stress at its own sensitivity, transpiration and radial growth do not necessarily decline together. This section follows that pathway, from the physics of water transport to the ecological strategies trees use to manage the trade-off.

3.1.1. The soil-plant-atmosphere continuum

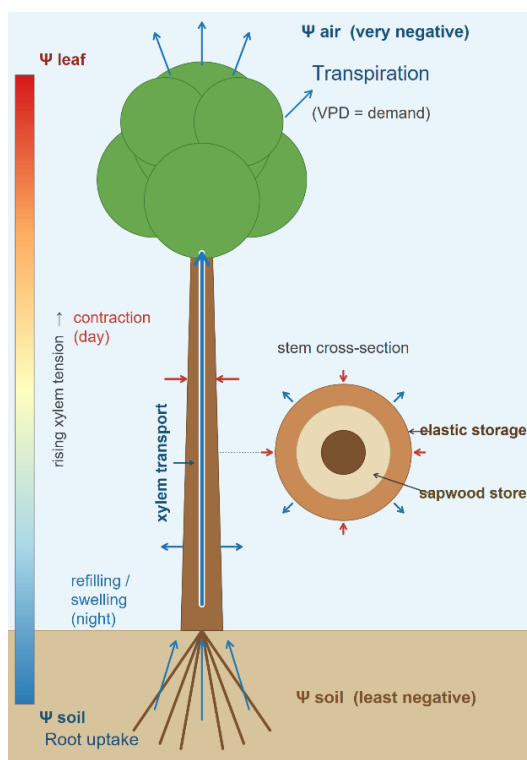


Figure 5: Conceptual diagram of the soil-plant-atmosphere continuum (SPAC) showing the Ψ gradient from soil to atmosphere and the two main internal water storage pools (elastic storage and sapwood store) in the stem cross-section.

Water moves through the tree along a gradient of decreasing water potential (Ψ), from the soil to the leaves (Figure 5), against a series of hydraulic resistances distributed along the soil-plant-atmosphere continuum (SPAC; Philip, 1966; Sperry & Love, 2015). The driving force is the vapour pressure difference between the leaf interior and the surrounding air. When evaporative demand rises, xylem tension increases, and beyond the cavitation threshold of the conduits, water transport breaks down.

A key buffer in this system is the hydraulic capacitance of woody tissues, their ability to store and release water. When canopy transpiration temporarily exceeds root water supply, the difference comes from water released from the elastic storage compartments of the stem (the living phloem, cambium and outer bark). This withdrawal is the direct cause of the stem contraction recorded by dendrometers and introduces a time lag between canopy transpiration and sap flow (Steppe et al., 2006; Meinzer et al., 2001). Across tropical species,

stored water contributes about 10 to 50 % of daily transpiration depending on tree size, wood density and hydraulic strategy (Meinzer et al., 2003), so internal storage is a meaningful component of the daily water balance and a central object of this thesis.

3.1.2. Soil water availability and root water uptake

The supply side of the SPAC has two components: the water held in the soil and the root system that extracts it. Soil water availability follows the retention curve, which links water content to soil water potential (Hillel, 2004). The plant-available reserve, between field capacity and the wilting point, limits how much transpiration a profile can sustain. Crucially, the unsaturated hydraulic conductivity of the soil falls by several orders of magnitude as it dries, so even when water remains in the profile, the rate at which it reaches the roots can become limiting (Sperry & Love, 2015). This soil-side limitation explains the supply-limited regime of §3.2.4: a tree can decouple from atmospheric demand not because soil water is absent, but because it cannot be delivered fast enough.

How much of the profile a tree exploits depends on its rooting depth, which varies by orders of magnitude across and within biomes (Canadell et al., 1996) and directly sets whether a tree stays demand-limited or becomes supply-limited during a dry period: deep-rooted individuals maintain transpiration when surface horizons dry, shallow-rooted ones are limited early. Two trees under the same atmospheric forcing, on the same plot, can therefore follow very different hydraulic trajectories if they tap soil horizons of different depth and water-holding capacity.

3.1.3. Stomatal regulation and vapour pressure deficit

Stomata sit at the core of the carbon-water coupling: their aperture simultaneously governs CO₂ uptake for photosynthesis and water vapour loss through transpiration. When stomata open to maximise carbon gain, water loss increases; when they close to limit water loss under high VPD or low soil water availability, carbon assimilation is reduced (Farquhar & Richards, 1984). Any atmospheric or soil water change that forces stomatal closure therefore constrains photosynthesis, and with it the carbon available for all downstream processes, including radial growth.

Vapour pressure deficit (VPD), the drying power of the air defined as the difference between the saturation and actual vapour pressures, is the main atmospheric driver of this regulation when water is not limiting. VPD acts in two ways at once: it strengthens the gradient pulling water vapour out of the leaf, and it triggers progressive stomatal closure to limit excessive xylem tension (Grossiord et al., 2020). The response of canopy-level stomatal conductance (g_s) to VPD follows a negative logarithmic relationship (Oren et al., 1999):

$$g_s = g_{s,ref} - m \times \ln(VPD) \quad (1)$$

where $g_{s,ref}$ is the reference conductance at $VPD = 1 \text{ kPa}$ and m is the sensitivity slope. The ratio $T_{s \tan d}/T_{ref}$, stomatal sensitivity to VPD, converges around 0.6 across a wide range of species, a value consistent with optimal stomatal theory, which predicts that trees regulate

stomatal aperture to maintain a constant marginal water-use efficiency (Oren et al., 1999). Hubbard et al. (2001) showed on mature *Pinus ponderosa* that this sensitivity is itself controlled by whole-plant hydraulic conductance. The tree's capacity to supply water to the canopy fixes the maximum stomatal conductance, and the VPD response then drives leaf water potential down to a species-specific minimum. The apparent VPD sensitivity of an individual tree therefore reflects both its stomatal regulation strategy and the hydraulic capacity of its conducting system. Deviations from this baseline value are systematic between functional groups, and rank among the key traits that distinguish the hydraulic strategies discussed in §3.1.4. In tropical forests, stomatal closure typically begins once VPD exceeds a threshold of the order of 1 kPa, though the exact threshold varies among species and with soil water availability (Motzer et al., 2005). Trees with access to deep soil water can maintain partial aperture through the dry season even when surface horizons are drying (Oliveira et al., 2021). When the canopy is strongly coupled to the atmosphere, variations in g_s translate directly into proportional variations in transpiration (Jarvis & McNaughton, 1986).

The resulting transpiration response to rising VPD is non-linear: transpiration first increases, then plateaus as stomata start to close, and eventually declines under extreme atmospheric demand combined with soil water limitation. The carbon-water trade-off therefore intensifies disproportionately under high-VPD conditions. Beyond this instantaneous effect, VPD also affects growth through the same hydraulic pathway: high midday VPD depletes internal stem reserves and can prevent full turgor recovery at night, which in turn can reduce growth on the following days even when photosynthesis was active (Peters et al., 2023).

3.1.4. Tree water-use strategies: from isohydric to anisohydric behaviour

Trees follow a continuum from isohydric to anisohydric behaviour in their regulation of leaf water potential under stress (Martínez-Vilalta & Garcia-Forner, 2017). Isohydric species maintain relatively constant Ψ_{leaf} by closing stomata early, which minimises cavitation risk but reduces carbon assimilation during drought. Anisohydric species let Ψ_{leaf} decline further by keeping stomata open longer, which sustains carbon gain but accepts higher hydraulic risk. Isohydric species typically exhibit higher stomatal sensitivity to VPD, while anisohydric species operate with lower sensitivity, consistent with their contrasting risk-benefit trade-offs. This continuum is not a fixed species property; it is modulated by soil water availability, hydraulic history, and stand structure (Martínez-Vilalta & Garcia-Forner, 2017).

The consequence for the carbon-water trade-off is direct: isohydric species sacrifice carbon gain to protect hydraulic integrity, while anisohydric species sacrifice hydraulic safety to maintain carbon gain. In tropical forests, this continuum broadly aligns with successional status: pioneer and early-secondary species tend to combine wide xylem vessels, low wood density, high sap flux densities and anisohydric-like regulation, while late-successional and climax species tend to combine denser wood, tighter stomatal control, deeper roots and isohydric-like behaviour (Oliveira et al., 2021; Kumar et al., 2023). This alignment, however, combines structural traits (wood density, vessel anatomy, rooting depth) with a regulatory

strategy, and the two can vary independently: a tree may pair an acquisitive architecture with near-optimal stomatal coordination. Distinguishing real isohydric from anisohydric regulation requires leaf water potential measurements rarely available in continuous-monitoring studies, and recent work argues the two behaviours are often hard to tell apart from differences in hydraulic architecture or sapwood area (Arend et al., 2026). The acquisitive–conservative contrast is therefore more robustly framed within the broader plant economics framework, which orders species from fast, cheaply built, resource-acquisitive tissues to slow, dense, conservative ones across leaves, wood and whole plants (Díaz et al., 2016).

In tropical montane forests specifically, low night-time temperatures slow root water uptake while daytime VPD can still be high, so a strictly anisohydric strategy carries a higher cost than at low elevation. Many montane evergreen species sit closer to the isohydric end, with conservative stomatal control and smaller daily variations in leaf water potential (Motzer et al., 2005). The hydraulic strategy of §3.1.3 and the iso/anisohydric continuum of §3.1.4 are two angles on the same system, so the same atmospheric driver can produce very different responses in two trees of contrasting hydraulic architecture.

A related trade-off ties this hydraulic architecture to cavitation risk: wide vessels carry more water per unit area but are more vulnerable to gas embolism under high xylem tension, so pioneer species combine high transport efficiency with a narrower safety margin against drought-induced hydraulic failure (Choat et al., 2018).

3.1.5. Carbon allocation under water stress: why radial growth is the most sensitive sink

Carbon fixed by photosynthesis is largely consumed by autotrophic respiration, which accounts for about half of GPP in mature tropical forests (Malhi, 2012). The remaining net primary production (NPP) is distributed among competing sinks (aboveground and belowground biomass, foliage, reproduction, defence, and non-structural carbohydrate (NSC) reserves), the fraction reaching stem wood being a minority that varies with stand age, species and environment (Malhi, 2012; Doughty et al., 2015). NSC reserves buffer the gap between photosynthetic supply and growth demand, allowing trees to sustain respiration through low-assimilation periods and to resume growth quickly afterwards. Under drought, allocation shifts toward roots and reserves at the expense of stem and leaf. Crucially, trees can stop growing even when reserves are abundant, so the limits to growth extend beyond carbon supply alone (Körner, 2015).

The key feature here is the asymmetry in sensitivity to water stress between photosynthesis and radial growth. Photosynthesis continues at reduced but appreciable rates well into moderate drought, because stomatal closure is gradual. Radial growth, by contrast, depends on cambial turgor exceeding a mechanical yield threshold. This threshold is reached at water potentials substantially less negative than those that suppress photosynthesis (Peters et al. 2021). As water stress intensifies, growth therefore stops before photosynthesis does. NSC

tend to accumulate rather than deplete, and the coupling between carbon assimilation and carbon allocation to wood weakens (Kannenberg et al., 2022).

Among all sinks competing for NPP, radial growth of the stem is the one whose water cost is most meaningful to track. Each new ring of xylem adds hydraulic conducting area, increasing the tree's capacity to sustain higher transpiration and supply a larger leaf area in following years (Tyree & Sperry, 1989). Most WUE studies in tropical forests report values per unit of GPP at the stand scale (Doughty et al. 2015), while the stem-specific WUE at the individual-tree scale remains poorly characterised, particularly in secondary forests.

3.2. Transpiration of tropical trees and its environmental controls

3.2.1. Accessing transpiration at the individual-tree scale

§3.1 introduced transpiration as the water cost of opening stomata to take up CO₂. Testing this framework empirically requires access to transpiration at the individual-tree scale, at a temporal resolution high enough to resolve both the diurnal cycle and the response to environmental events. Eddy covariance provides stand-integrated fluxes without separating individual contributions (Baldocchi, 2003), while leaf-level porometry captures instantaneous physiological control but not its integration at the tree scale (Percy et al., 1989). Thermal sap-flow methods fill this gap and have become the reference technique for continuous individual-tree monitoring over months (Poyatos et al., 2021).

The Thermal Dissipation Probe introduced by Granier (1985) is the most widely used implementation. Two needles are inserted radially into the sapwood, with the upper one heated at constant power. As sap flows past, convective cooling reduces the temperature difference ΔT between the heated and the reference needle. The dimensionless index $K = (\Delta T_{max} - \Delta T)/\Delta T$, where ΔT_{max} is the zero-flux reference reached at night, is then converted to sap flux density F_d through a species-pooled empirical calibration. Scaling F_d by the conducting sapwood area gives the whole-tree water use J_s .

3.2.2. Diurnal transpiration patterns in tropical forests

On a typical day in a tropical forest, sap flow follows a characteristic trajectory imposed by the coupling between radiation, VPD and tree hydraulics (Fig. 6). Before sunrise, flow is minimal and the stem has rehydrated overnight, if soil water is available and nocturnal transpiration is itself low. Under less favourable conditions (dry periods, high nocturnal

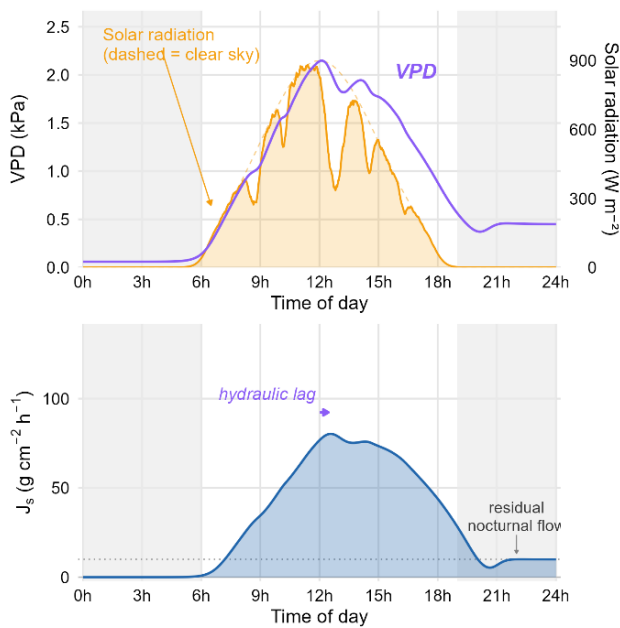


Figure 6: Theoretical 24-hour pattern of VPD (purple), solar radiation (orange) (top panel), and sap flux density (J_s , blue) (bottom panel), on a partially cloudy day. Grey shading marks night.

Absolute magnitudes vary widely with tree size, canopy position and species, and are generally lower in montane than in lowland forests, where reduced daytime temperatures and frequent morning fog limit VPD and evaporative demand (Motzer et al., 2005). A second source of inter-individual variability lies in the vertical structure of the forest itself. In closed tropical canopies, light, wind, leaf temperature and VPD vary by close to an order of magnitude between the emergent layer and the understorey, so two trees of similar diameter but at different canopy positions are not exposed to the same atmospheric forcing (Parker, 1995). In secondary forests this stratification builds up with stand age: the youngest stages are more open, with little vertical variation in microclimate, whereas older stages develop a multi-layered canopy and a steeper vertical microclimatic gradient. The contrast between successional plots therefore combines a contrast in species composition with a contrast in the atmospheric conditions experienced by the instrumented trees.

A pattern specific to tropical forests deserves attention: nocturnal flow is not negligible. Contrary to the classical assumption of zero flow at night, studies consistently report residual night fluxes of 5 to 25 % of daily flow depending on species and conditions (Alvarado-Barrientos et al., 2015). Two processes contribute: a residual nocturnal stomatal conductance that sustains actual transpiration under non-zero nocturnal VPD, and the recharge of internal stem reserves depleted during the day, the latter being a hydraulic flow without leaf-level water loss. Rosado et al. (2012) found that the relation between nocturnal transpiration and VPD, typically linear in lowland Atlantic Forest, becomes strongly non-linear at montane elevation, with no clear physiological explanation. This directly affects the determination of ΔT_{max} introduced above: a reliable nocturnal hydraulic zero is not guaranteed.

Two caveats frame how the method is best used. First, cumulative uncertainties on absolute fluxes are typically larger than the day-to-day or tree-to-tree contrasts within a single instrumented site, so the method is most informative for relative comparisons across trees, seasons and environmental drivers rather than for absolute magnitudes. Second, stand transpiration is the sum of individual fluxes, weighted by each tree's conducting sapwood area (Granier et al., 1996). A difference in water use between two forests can therefore come from two sources: how much water each tree moves per unit of sapwood (a physiological signal), or how much sapwood the forest carries (a structural signal). The two do not always change together.

3.2.3. Atmospheric and edaphic controls

Among the environmental variables that control transpiration, VPD stands out as the dominant driver at the global scale. Using the 1 858 sap flow series of SAPFLUXNET, Flo et al. (2022) showed that VPD explains more variance in canopy conductance than soil water content or incoming radiation, in nearly all forest biomes analysed. This dominance confirms at large scale the central role attributed to VPD by the optimal stomatal theory discussed in §3.1.

The role of PAR is more nuanced. PAR triggers stomatal opening in the morning and sets the maximum envelope of conductance but saturates at relatively low levels and ceases to be the limiting factor. Its role in daily flow is therefore concentrated on the first hours after sunrise, and its effect on cumulative flow remains modest once the day is well advanced (O'Brien et al., 2004; Motzer et al., 2005).

Temperature and relative humidity act primarily through their combined effect on VPD, although high temperatures can also force stomatal closure independently of hydraulic tension and modulate sap viscosity and xylem conductivity (McDowell et al., 2008). In montane tropical settings, frequent morning fog maintains high relative humidity and delays the rise of VPD, shifting the onset of morning transpiration relative to lowland forests (Motzer et al., 2005). On the windward slopes of the Serra da Mantiqueira this is expected to buffer canopy water status during the cool dry season.

A central point for interpreting data during the dry season concerns the interaction between VPD and soil water content (SWC). In the wet season, stomata respond primarily to VPD as described by Oren et al. (1999)'s logarithmic relation. When SWC declines below a critical threshold, stomata progressively decouple from VPD and respond primarily to leaf water potential, now dictated by soil water limitation (Grossiord et al., 2020). The same VPD value can then produce very different sap flows depending on the season, not because the atmospheric driver has changed, but because the edaphic context modulating the stomatal response is different.

3.2.4. Demand-limited and supply-limited regimes, and interspecific variability

The direct consequence of this $VPD \times SWC$ interaction is a seasonal switch between two regimes of transpiration control. In the demand-limited regime, soil water is not limiting, and transpiration follows the atmospheric envelope, approaching reference evapotranspiration (ET_0). In the supply-limited regime, the limitation comes from the soil or from internal hydraulic conductance, and transpiration decouples from ET_0 and falls below it. The ratio of actual transpiration to ET_0 is therefore a simple diagnostic of supply versus demand limitation (Souza et al., 2015; Silva et al. 2025).

In the seasonal Atlantic Forest of southeastern Brazil, evapotranspiration remains remarkably stable across seasons: actual ET stays close to or above its radiation-driven equilibrium value (ET_{eq}), with the ratio ET/ET_{eq} near or above unity even in the dry season. This stability is sustained by the deep-water reserve of the dystrophic latosol, so the trees remain energy-driven rather than supply-limited year-round (Guauque-Mellado et al., 2022). Whether a stand stays in this regime or switches to supply limitation depends critically on soil depth and root access to deep water: at wet equatorial Amazonian sites evapotranspiration is even higher in the dry season under radiation control, whereas in semi-arid Caatinga it becomes soil-limited in the dry season (Costa et al., 2010; Silva et al. 2025). Comparing measured transpiration to ET_0 from meteorological data therefore provides an empirical diagnostic of the control regime and can detect seasonal periods of decoupling indicative of a switch toward supply limitation in some individuals.

Interspecific variability adds a further dimension: pioneer species tend to display higher sap flux densities and stronger VPD sensitivity than late-successional species, in line with their more acquisitive architecture (Oliveira et al., 2021; Kumar et al., 2023), and stand structure and composition can modulate the baseline sensitivity of transpiration to VPD beyond local climate alone (Bachofen et al., 2023).

3.3. Water stress and radial growth: the role of turgor in controlling wood formation

§3.2 covered transpiration. This section turns to radial growth. §3.1 already introduced the key asymmetry (§3.1.5), that growth stops before photosynthesis, at water potentials well above those that close stomata.

3.3.1. Xylogenesis and the hydraulic control of cambial division

Wood formation proceeds through cell division, radial expansion, wall deposition and programmed cell death (Cuny et al., 2015). Because biomass accumulation lags radial growth

by more than a month (Cuny et al., 2015), the dendrometer signal and the wood eventually formed are not strictly simultaneous.

Of the four phases, cell expansion is the most directly controlled by tree water status. Lockhart (1965) formalised this as $dV/dt = \varphi \cdot (P - Y)$, where V is cell volume, φ the wall extensibility, P the turgor pressure and Y the yield threshold below which the wall does not expand. The equation imposes a strict limit: cambial cells cannot expand when turgor falls below Y , regardless of carbohydrate supply, and turgor follows the hydraulic state of the tree. Growth therefore “halts” at water potentials less negative than those that close stomata or threaten cavitation, the asymmetry developed in §3.1.5. Peters et al. (2025a) found stem-growth cessation across nine European species at a strikingly uniform pre-dawn leaf water potential near -1.2 MPa; no comparable threshold yet exists for tropical trees, where leaf turgor-loss points range from -1.3 to -3.2 MPa (Maréchaux et al., 2015; Kunert et al., 2021), suggesting a threshold that varies with habitat water availability.

Cambial expansion translates almost immediately into a micrometric change in stem radius, which makes continuous dendrometry the highest-resolution field access to growth available. Point dendrometers (the instrument used in this thesis) measure stem radius at the μm scale (Zweifel et al., 2021), but the raw signal is not pure growth: it sums an irreversible radial increment (GRO) and reversible bark-phloem shrinkage and swelling driven by the diurnal water balance (the tree water deficit, TWD; Steppe et al., 2006; Zweifel et al., 2016), and isolating GRO from TWD is the first step of any dendrometer-based growth analysis. Stem growth (GRO) is largely nocturnal, consistent with the need for overnight rehydration to restore turgor above the yield threshold Y . Point dendrometer records support robust relative comparisons across trees and seasons, but absolute quantitative interpretation requires careful processing of the raw signal.

Beyond its role in growth analysis, the tree water deficit (TWD) carries information on the tree's hydric stress state. Two summary signals coexist in the TWD trace: the daily amplitude, the maximum daily shrinkage (MDS), which reflects the elastic capacitance actively turned over each day, and the multi-day baseline that accumulates when overnight refilling becomes incomplete (Zweifel et al., 2014; Salomón et al., 2022). Both depend on tree-specific structural traits, so comparing two trees by their raw TWD or MDS magnitudes is confounded by size and species. Peters et al. (2025b) addressed this by normalising TWD by the tree-specific MDS_{max} , producing a TWD_{norm} index that is comparable across trees. Across temperate species, threshold values of TWD_{norm} around 0.5 and 0.8 were linked respectively to stomatal closure and turgor loss, suggesting a generic physiological signature behind the dendrometer signal. Unlike leaf water potential, this dendrometer-based stress index does not require destructive sampling and is available continuously, which makes it operationally useful for field monitoring.

3.3.2. Growth phenology in the Atlantic Forest

Growth seasonality in tropical trees follows cambial seasonality, set by soil water, temperature, photoperiod and leaf phenology, and within the Atlantic Forest two climatic regimes frame the biome. The ever-wet Serra do Mar coastal forests ($> 2\,000\text{ mm yr}^{-1}$, no true dry season) are evergreen and phenologically driven by photoperiod and temperature (Morellato et al., 2000), whereas the seasonal semi-deciduous forest of the interior plateau has a marked dry season, sheds leaves in the dry months and flushes new leaves at the dry-wet transition (Lisi et al., 2008). At the intermediate, montane altitude of the study site (Serra da Mantiqueira), both drivers contribute and a growth reduction rather than a complete cessation is expected in the cooler, drier months.

Growth seasonality is further modulated by functional strategy. Pioneer and early-secondary species (in the region, genera such as *Tibouchina*, *Cedrela* or *Sapium*) carry acquisitive traits, including low wood density, wide xylem vessels, high leaf-specific conductance and often shallow roots, that favour fast growth but narrow the hydraulic safety margin and increase dependence on surface-soil water (Poorter et al., 2010). Their growth is correspondingly sensitive to dry-season water supply: *Cedrela* ring chronologies track dry-season rainfall (Venegas-González 2018), and across tropical species fast-growing, low-density ones respond more strongly to VPD and radiation anomalies than slow-growing ones (Bauman et al., 2022). Late-successional species (evergreen Lauraceae such as *Ocotea*, hardwood *Aspidosperma*) combine denser wood, narrower vessels, higher hydraulic safety and deeper roots that buffer them against surface-soil drying (Kumar et al., 2023; Lima et al., 2020). Their growth is expected to be more evenly distributed through the year, its seasonal reductions driven by the $\text{VPD} \times \text{soil-water}$ interaction (§3.2.3) rather than by leaf loss.

Beyond traits, tropical secondary forests recover their structure (basal area, canopy height, leaf area index) within decades, but recovery of compositional and functional features is much slower. In the Atlantic Forest of southeastern Brazil, young regenerating stands (under 20 years) are dominated by short-lived pioneer species with acquisitive traits, while mid-successional stands (40 to 60 years) accumulate longer-lived secondary and emergent species with conservative traits (Poorter et al., 2021). The two stands compared in this thesis therefore represent two distinct stages of this recovery trajectory, with different expected hydraulic regulation strategies: faster and less buffered on the younger acquisitive side, slower and more buffered on the older conservative side.

3.3.3. The GPP-growth decoupling: an empirical signature

§3.1.4. framed the asymmetry between photosynthesis and radial growth as a structural feature of carbon allocation: growth stops before assimilation, so non-structural carbohydrates accumulate without being used for stem expansion. This subsection turns to its empirical signature.

The decoupling appears as a timing and magnitude mismatch between GPP (or its proxies) and radial growth. Across Central European forests, interannual radial growth correlates only weakly with ecosystem GPP, and post-drought growth reductions do not track GPP reductions (Kannenberget al., 2022). At the event scale, wood formation stays suppressed for weeks to months after a drought while canopy photosynthesis recovers within days, the so-called drought legacy effects (Martínez-Sancho et al., 2022). Beyond the magnitude of a response, its temporal structure is captured by the resistance–recovery–resilience framework of Lloret et al. (2011), which compares performance before, during and after a drought. Recovery tends to scale with tree size and with the depth of the deficit reached, so individuals of the same plot can differ markedly in how quickly they rebound (DeSoto et al., 2020).

For tropical forests the empirical basis is thinner. During the 2010 Amazon drought, total NPP remained constant while autotrophic respiration declined and stem growth was maintained, interpreted as carbon reallocation rather than supply limitation (Doughty et al., 2015), though the underlying turgor and water-status mechanisms cannot be resolved from flux-tower and census data alone. Using 49 years of data from 509 species, Bauman et al. (2022) confirmed that VPD and radiation anomalies reduce tropical tree growth and that fast-growing species are more sensitive than slow-growing ones.

3.4. Linking transpiration, stem water status and radial growth: an integrative framework

The physiological chain from atmospheric demand to wood increment is sequential and instrumentally accessible. Canopy transpiration drives a xylem potential gradient that sap flow at the stem base tracks under steady state, and a fraction of the demand is met from elastic storage, producing the stem-radius reduction recorded by dendrometers and integrated as the tree water deficit (TWD; Salomón et al. 2022). Stem water status in turn sets the turgor that drives cambial expansion through Lockhart (§3.3.1), so the dendrometer often carries the earliest signature of hydric stress, ahead of stomatal closure. Across tropical species, internal storage contributes about 10 to 50 % of daily transpiration depending on size, wood density and hydraulic strategy (Phillips et al. 2003; Meinzer et al. 2003), which produces the characteristic phase lag between sap flow and TWD and the overnight refilling visible on both signals. The chain has been formalised in process-based models that couple stem diameter to sap flow and turgor (Steppe et al. 2006; De Swaef & Steppe 2010), but their parameterisation requires species-specific calibrations rarely available outside controlled studies. The present thesis uses the chain conceptually rather than as a parameterised model, reading the combined record at complementary temporal resolutions, from the diurnal offset between demand and stem response to the cross-individual comparison of TWD normalised into a stress index whose thresholds coincide with stomatal closure and turgor loss (Peters et al. 2025b).

4. OBJECTIVES

The previous chapters established three points. First, the Atlantic Forest of southeastern Brazil is one of the most fragmented and threatened biomes of South America, and its hydrological functioning combines structural traits (sapwood area, canopy height, rooting depth) with regulation traits (stomatal control and internal water storage). Second, transpiration, radial growth and the tree water deficit form a closed physiological chain in which sap flow and dendrometer signals jointly carry information on atmospheric demand, soil supply and the buffering role of internal reserves. Third, most existing studies of forest water dynamics in the Atlantic Forest operate at the stand or catchment scale, where between-individual variability is averaged out and the water cost of wood production at the individual-tree scale remains poorly characterised, particularly in secondary forests.

This thesis addresses that gap with continuous sap flow and dendrometer records from two Atlantic Forest plots of contrasting successional age. Its overall question is:

How do transpiration, growth and trunk water reserves vary within and between two regenerating Atlantic Forest stands of contrasting successional age, and what do these signals reveal about the hydraulic strategies of individual trees?

To address this question, four specific sub-objectives are pursued.

- (1) Process and quality-check the raw signals. Chronic power interruptions on tropical sites and noisy raw records make a careful pipeline essential before any interpretation. This step identifies the usable subset of tree-period combinations and sets the support for every downstream analysis.
- (2) Characterise the per-tree dynamics of transpiration, radial growth and tree water deficit, and identify points of agreement and disagreement between trees of the same stand. This reveals whether individuals within a stand share a common environmental control or diverge into distinct hydraulic strategies.
- (3) Link the three signals through cross-signal analyses, testing the expected couplings between flow, growth and reserves, and positioning each tree on a comparative strategy space. The hypothesis is that growth and transpiration only partially track each other because the stem reservoir buffers the daily and seasonal mismatch between atmospheric demand and root supply.
- (4) Quantify the contrast between the two stands. Per-tree results are aggregated to the plot scale where data coverage allows, and the inter-stand contrast is interpreted in the light of the successional and structural differences anticipated for R40 (older, denser, conservative) and RP (younger, acquisitive).

5. MATERIALS AND METHODS

5.1. Study site

The study site is located in the Mantiqueira mountain range of southeastern Brazil (22°53'43" S, 45°58'53" W) and lies within the Atlantic Forest biome, locally classified as a montane ombrophilous dense forest (Floresta Ombrófila Densa Montana). It is established on a private property in the São Francisco Xavier district of São José dos Campos, State of São Paulo (Fig. 7), within the boundaries of the APA (*Área de Proteção Ambiental*), São Francisco Xavier environmental protection area. The site sits at approximately 1100 m above sea level on steep slopes draining into the Paraíba do Sul river basin (AGEVAP, 2014). It encompasses fragmented, regenerating and continuous forest patches and hosts an ecohydrological experimental station operated by the Laboratory of Isotopic Ecohydrology of the Brazilian National Institute for Space Research (INPE).

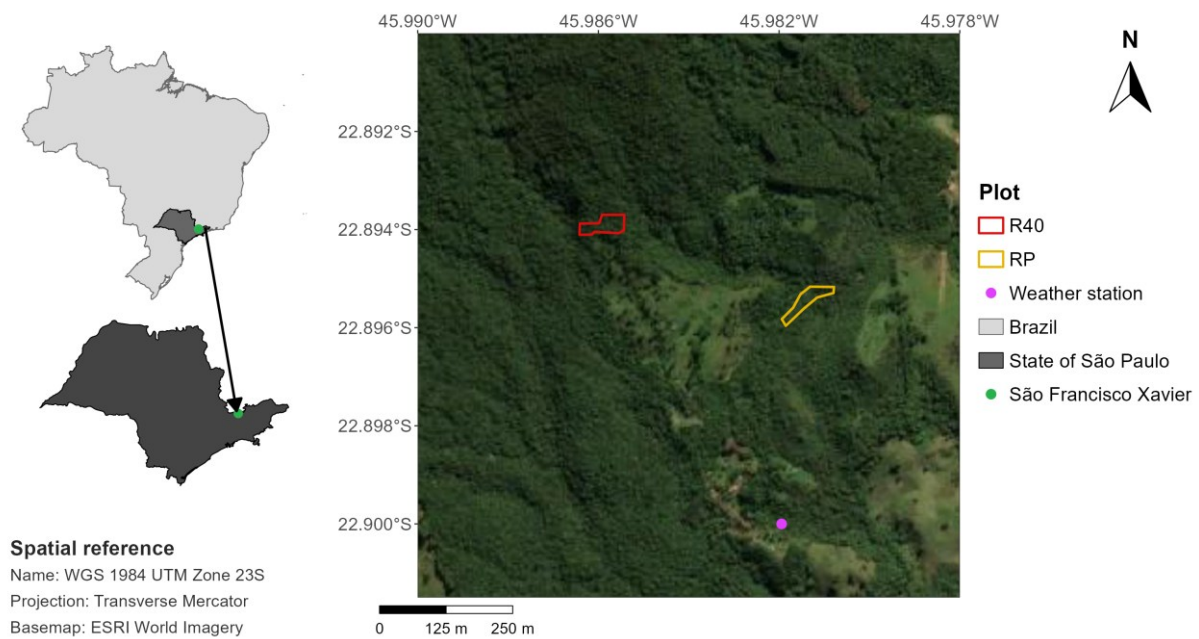


Figure 7: Location of the study site at São Francisco Xavier (Serra da Mantiqueira, southeastern Brazil). The right panel shows the two experimental plots, R40 (red outline) and RP (yellow outline), and the approximate on-site weather station (magenta dot), over an ESRI World Imagery base. Spatial reference: WGS 1984 UTM Zone 23S.

The area was originally covered by primary Atlantic Forest but underwent several land-use changes during the second half of the twentieth century. Until the 1970s the local economy was dominated by charcoal production from native wood. From the 1980s to the 1990s, large fractions of the property were converted to pine and eucalyptus monocultures, pasture and small-scale agriculture (MapBiomass, 2019). Active reforestation resumed in the 1990s and produced the present contrast of secondary stands of contrasting ages (Bandoria, 2020).

The hydrological year in this region typically begins with the first rains in October. To match the 2020 calendar year covered by the analysis, the year is divided into four seasons defined from the local rainfall regime: a wet season (January–March), a drying season (April–May), a dry season (June–September), and a rewetting season (October–November). The first rain of 20 to 22 September break the dry season and sets the start of the rewetting season. Compared with these normals, 2020 was a comparatively wet and cool year: annual precipitation reached 1946 mm, about 17 % above the 1991–2020 normal, and the mean annual temperature was 18.3 °C, roughly 2 °C below the normal. Over this period the on-site station recorded 1492 mm of rainfall against a potential evapotranspiration ($ETP = K_c \times ET_0$, with the crop coefficient $K_c = 1.16$) of 973 mm (§5.3.3.). Precipitation was strongly seasonal: the wet season accumulated 948 mm, the drying season 55 mm, the dry season 133 mm, and the rewetting season 356 mm. Despite this wet annual balance, the winter dry season was severe: daily rainfall remained below 1 mm for 82 consecutive days (30 June–19 September).

5.2. Description of the two plots

The present study focuses on two experimental plots representing contrasted stages of forest regeneration: R40 and RP (Fig. 7).

Plot R40 (Fig. 8, left) lies in the northern part of the site, on a red yellow Ferralsol (Fig. 3, WRB classification, FAO, 2014), on a slope of approximately 10 %. It covers approximately 370 m² and represents the oldest reforested area, with more than 50 years of regeneration, a tree density above 1 tree per m² (1.16) and a dense closed canopy. Species composition reflects an advanced successional stage, dominated by the long-lived early-secondary *Alchornea glandulosa* (Euphorbiaceae) with late-successional canopy species (Table 1).

Plot RP (Fig. 8, right) lies to the east of the site, on a mixture of Ferralsol and Cambisol (Fig. 3, WRB classification, FAO, 2014), on a gentle to nearly flat slope. It covers approximately 450 m² and was restored in 2009 by planting native tree species to rehabilitate a degraded pasture and protect a nearby water spring located approximately 50 m downslope. Tree density is lower (0.76 tree per m²) and the canopy is partially open. Because the plot lies downslope of R40, it is closer to the groundwater table, which can rise to within a few metres of the soil surface in the wet season. The canopy is dominated by the pioneer *Tibouchina pulchra* (Melastomataceae), with contributions from other pioneer to early secondary species (Table 1).

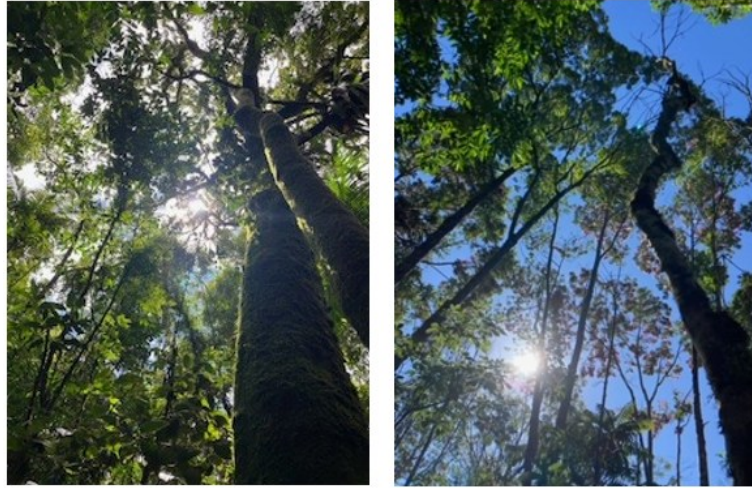


Figure 8: Photo of the R40 plot (left) and the RP plot (right) taken by Charlotte Vermeulen the 13/02/2026.

5.3. Site Equipment

5.3.1. Weather station

Meteorological conditions were monitored by a HOBO weather station (Fig. 9) belonging to INPE, installed approximately 400 m from the experimental plots (Fig. 7). The station recorded 5-min measurements over 23 January 2019 – 15 September 2021, fully covering the 2020 study year. Solar radiation was measured by a pyranometer (Fig. 9c), wind speed by a cup anemometer (Fig. 9a), precipitation by a tipping-bucket rain gauge (Fig. 9b), and atmospheric pressure by a barometric sensor housed in the datalogger enclosure (Fig. 9a). Air temperature and relative humidity were measured by a combined radiation-shielded T/RH probe (Fig. 9a), from which dew-point temperature was derived. Two limitations are acknowledged: the pyranometer lies approximately 15 m from three large trees that may shade incoming radiation, and the station sits within twice the surrounding canopy height, exposing the tipping-bucket gauge to random interception errors (Campbell Scientific, 2022).



Figure 9: HOBO weather station (INPE) at the São Francisco Xavier study site. (a) Main tripod with cup anemometer, radiation-shielded T/RH probe, solar panel and datalogger (+ barometric sensor). (b) Tipping-bucket rain gauge. (c) Pyranometer. Taken by Lucas Jeangout, 13/02/2026.

Each variable was screened against physical bounds (T 0–45 °C, RH 10–100 %, VPD 0–5 kPa, radiation 0–1300 W m⁻² and ≤ 10 W m⁻² at night, precipitation 0–50 mm per 5 min, wind 0–30 m s⁻¹) and against stuck-sensor artefacts (constant runs ≥ 30 –60 min during the day). Filtering was variable-specific. In 2020, no value fell outside its range. The 5-min series was 99.3 % complete, the missing 0.7 % concentrated in a ~51-h gap in mid-September, a ~14-h gap at year-end and 15 isolated radiation points.

For each gap, the gap duration $\delta = t_e^+ - t_s^-$ is computed, where t_s^- is the last valid point before the gap and t_e^+ the first valid point after. Short gaps ($\delta \leq 1$ h) were filled by linear interpolation: each missing value was reconstructed as a weighted average of the two bracketing valid values, with weights set by the time distance from each bracket. The 51-h September gap was reconstructed for the continuous variables (T, RH, radiation, pressure, wind speed) by a boundary-anchored mean-diurnal-variation (MDV) approach, composed of two steps. (i) Diurnal template: each missing value was estimated as the mean of the six surrounding same-time-of-day observations (three days before and three after the gap), which reproduces the shape of the daily course but not necessarily its exact level. (ii) Boundary anchoring: the residual between the template and the measurements was computed at each end of the gap, and a correction varying linearly from one end to the other was added to the template, ensuring continuity with the bracketing series. Precipitation was set to zero (the gap falls within the cumulative dry-season phase). The series is thus gap-free over the study period (January–November 2020). These meteorological variables can be found for the whole year in the Appendix A.1 Fig. 47.

5.3.2. Vapour pressure deficit

The vapour pressure deficit (VPD), the evaporative demand of the air, was recomputed at each 5-minute step from the gap-filled air temperature and relative humidity following the FAO-56 method (Allen et al. 1998). It can be defined as the difference between the saturative and the actual vapour pressure:

$$VPD [kPa] = e_s - e_a \quad (2)$$

The saturative vapour pressure e_s (kPa) was obtained from the Tetens-Magnus equation (Allen et al. 1998, Eq. 11) while the actual vapour pressure e_a (kPa) was then derived from e_s and RH (Allen et al. 1998, Eq. 19):

$$e_s[kPa] = 0.6108 \times \exp\left(\frac{17.27 T}{T + 237.3}\right) \quad (3); \quad e_a[kPa] = \frac{RH}{100} \times e_s \quad (4)$$

5.3.3. Reference and potential evapotranspiration

Reference evapotranspiration ET_0 , the standardised atmospheric evaporative demand over a hypothetical well-watered short grass surface, was computed at hourly time step from

the corrected meteorological series using the FAO-56 Penman-Monteith equation (Allen et al., 1998, Eq. 53):

$$ET_0 [mm h^{-1}] = \frac{0.408 \Delta (R_n - G) + \gamma \frac{37}{T + 273} u_2 (e_s - e_a)}{\Delta + \gamma (1 + 0.34 u_2)} \quad (5)$$

where R_n is net radiation (computed from FAO-56 Eq. 39 using site latitude -22.9° , longitude 45.98° W and Julian day), G is the soil heat flux ($0.1 \times R_n$ by day, $0.5 \times R_n$ by night; Eqs. 45–46), Δ is the slope of the saturation vapour-pressure curve, γ is the psychrometric constant, and u_2 is wind speed at 2 m. The numerator combines a radiation term (energy supply) and an aerodynamic term (wind-driven atmospheric demand). The denominator partitions the two under the FAO-56 short-grass stomatal resistance (70 s m^{-1}). The resulting series was validated against the independent on-site estimate of Delvoie (2023): the two annual totals agree to within 3 % (921 vs 942 mm yr^{-1}) and the daily values are highly correlated ($R^2 = 0.97$).

From ET_0 , a forest-evapotranspiration reference, ETP, was derived to represent whole-system water loss: canopy transpiration, soil evaporation and interception combined (Wilson et al., 2001) under non-limiting soil-water conditions:

$$ETP [mm h^{-1}] = K_c \cdot ET_0, \quad K_c = 1.16 \quad (6)$$

The crop coefficient K_c was taken from Ounifi (2025), who calibrated it on the Sen-ET dataset produced by Parmentier (2024). Both works are earlier master's theses at the same site. Sen-ET is a remote-sensing method that estimates actual evapotranspiration on the site by combining optical (Sentinel-2) and thermal (Sentinel-3) satellite data through a two-source surface energy balance model. The actual evapotranspiration of R40 was regressed on the actual evapotranspiration of the adjacent grassland, which was taken as a reference surface close to FAO conditions (Allen et al. 1998, $K_c \approx 1$). The intercept was fixed at zero and the slope of the regression ($R^2 = 0.99$) was taken as K_c . The same coefficient was applied to RP because the Hydrus-1D calibrations of Delvoie (2023) yield an optimum within 2 % of this value for both plots independently, another thesis at the same site.

5.3.4. Soil Matric Potential

Soil matric potential (h) was monitored with MPS-6 and TEROS 21 sensors (METER Group), which infer h from the water content of an internal porous ceramic disc via a factory retention curve. They cover -5 to $-100\,000$ kPa (± 10 %) and were not field-calibrated. Measurements become noisy below pF 4.2 and saturate above pF 2, so the wettest soil states are not captured. Seven sensors were installed per plot at 0.1, 0.2, 0.3, 0.5, 1.0, 1.5 and 2.0 m (the fourth at 0.6 m on RP), logged by Em50 or ZL6 dataloggers (METER Group). Daily averages at 12:00 (INPE) were used, with hourly resolution available only at 2 m.

Raw h data were quality-filtered by Delvoie (2023): hour-to-hour changes > 0.01 pF and values outside the 5th–95th percentile per depth were removed, and remaining gaps were partially filled by cross-depth interpolation. Less than 1 % of the daily root-zone values are missing on RP, against about 24 % on R40, concentrated in the drying (43 %) and dry (45 %) seasons and in the upper sensors (32 % at 0.1–0.3 m, 13 % at 0.5–1.0 m).

A daily root-zone h was computed per plot from the five shallowest sensors (0.1–1.0 m), the two deepest being below the active root zone. Each depth was weighted by the local fine-root density (DRFinas g dm^{-3} , Delvoie 2023, used as proxy for relative root length):

$$h_{rz} = \frac{\sum_i w_i h_i}{\sum_i w_i} \quad (7)$$

where w_i is the fine-root density at depth i . Each sensor is assigned to the nearest soil layer (0.1 m $\leftarrow$ 5–15 cm, 0.2 m $\leftarrow$ 15–25 cm, 0.3 m $\leftarrow$ 25–35 cm, 0.5 m [R40] / 0.6 m [RP] $\leftarrow$ 45–55 cm, 1.0 m $\leftarrow$ 95–105 cm). The 0–5 cm layer is excluded as no tensiometer was installed at that depth. Weights are reported in Appendix Table 6. The root-weighted h is used as the soil water-stress indicator. Seasonal h profiles and the fine-root density profile per plot are reported in Appendix Fig. 48.

5.3.5. Tree probes

Both plots are instrumented since 2018 with sap flow and dendrometer sensors (Fig. 10, left) on 28 trees in total, all connected to a single Plantem SF_DEN V1.0 datalogger (Eletrônica Medianeira / Plantem Tech, Brazil) powered by solar panels installed near the site. Because the panels are partially shaded by the surrounding canopy and occasionally covered by fallen leaves, power output is uneven and produces both short and prolonged interruptions in the recordings. Both signals are sampled at a nominal 66-s time step and stored on a microSD card retrieved periodically from the field.



Figure 10: Left: sap flow (up) and dendrometer (down) sensors positioned on tree 14, Right: dendrometer sensor.

The dendrometer is a ZN22-T-2IP point sensor (Fig.10 right ;Natkon, Switzerland), inserted in the monitored trees at the start of the campaign in 2018. The sensor consists of a sealed linear-motion potentiometer (IP54 protection) with a sensing rod pressed lightly against the bark. As the trunk expands or contracts, the rod displacement is converted into a voltage signal acquired by a 16-bit ADC over a fixed range. Each recorded value is the average of 30 readings sampled in a millisecond interval (hardware oversampling), which attenuates electromagnetic noise. The effective resolution of the acquisition chain is approximately 1 μm of stem radius, consistent with the empirical RMS noise floor measured on stable periods of the signal and within the range typically reported for high-resolution point dendrometers (Drew & Downes 2009).

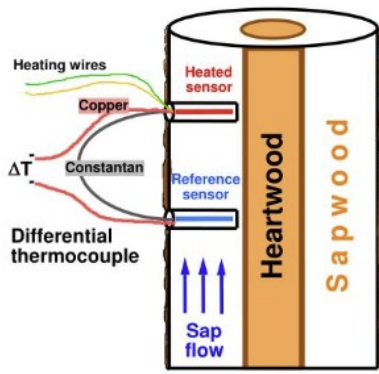


Figure 11: Principle of the heat dissipation method (Granier, 1985).

The sap flow uses the Heat Dissipation Method (HDM, Granier 1985). The probes were hand-built by INPE and consist of two cylindrical units inserted radially into the sapwood at breast height. The upper probe is continuously heated at constant power, the lower probe a few centimetres below serves as an unheated reference measuring the ambient wood temperature, and each probe contains a copper-constantan thermocouple at its centre (Fig. 11). The heated probe is sheathed in aluminium to ensure uniform heat distribution along its length. The thermal sensor is a differential type-T thermopile (copper-constantan-copper) that directly outputs the voltage difference ΔV (mV) between the two probes. ΔV is acquired by a 24-bit ADC on the same Plantem datalogger with the same hardware oversampling and used as a direct proxy for the temperature difference (Drebushchak 2015) in the Granier conversion of §5.7.1.

5.4. Tree characterization

5.4.1. Tree Inventory campaigns

Three campaigns covered the monitored trees over 2018–2026. The 2018 campaign sampled three 100 m^2 subplots per plot, identified all stems to species, and measured the diameter at breast height $DBH(\text{cm}) = CBH/\pi$ (8) and height H . The DBH distributions follow an inverse-J typical of regenerating tropical forests (Figure 12; Liebsch et al. 2008), with R40 extending to larger classes (max 30.7 cm) than RP (max 22.7 cm), and the 27 monitored trees (15 R40 + 12 RP) sit in the upper DBH classes. Each instrumented tree was further characterised for active sapwood area A_s , used to convert F_d to whole-tree flow J_s (§5.7.1), and wood density ρ , used in the WUE_w computation (§5.8.4). The 2023 campaign re-measured DBH and A_s on the R40 monitored trees and revealed inconsistencies, which were reassessed during a third 2026 campaign conducted as part of this thesis. The 2026 campaign also established a new 100 m^2 subplot in each plot for upscaling. In R40 the 2018 markers were still

in place, allowing tree-level matching with previous campaigns, while RP markers were lost and the 2026 RP inventory is therefore used as an independent stand-level reference.

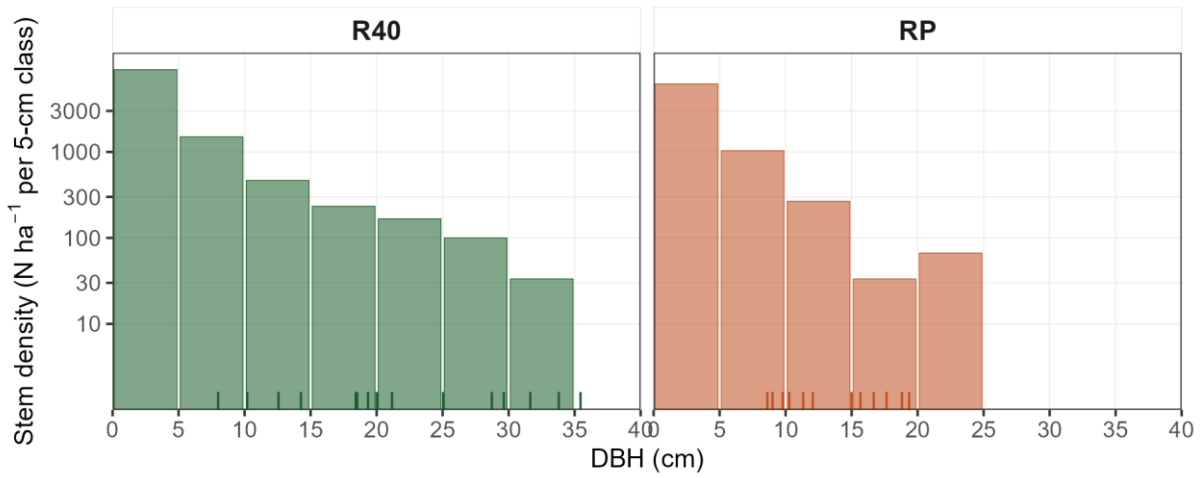


Figure 12: Diameter at breast height (DBH) distribution of the two stands, 2018 inventory (3 sub-plots of 100 m² per stand, $n = 347$ stems for R40 and $n = 228$ stems for RP). Stem density is expressed in $N\ ha^{-1}$ per 5-cm DBH class on a log scale. Tick marks on the x-axis identify the 27 monitored trees (15 in R40, 12 in RP).

5.4.2. Retrieval of DBH for 2020

No inventory was conducted in 2020. The 2020 DBH of each instrumented tree was reconstructed from the three campaigns combined with the 2020 dendrometer increment (Table 1, all in Appendix B Table 7). Inventory values showing negative growth, annual rates above species-group thresholds (1.5 cm yr⁻¹ pioneers / early-secondary, 0.8 cm yr⁻¹ late-successional ; Adame et al. 2014), or 2018–2023 versus 2023–2026 rates differing by more than a factor of three were discarded, the 2018 campaign being dropped first because it was the least consistent. A per-tree linear regression of DBH on calendar year was then fitted on the retained values and the 2020 DBH read on the fitted line, cross-checked against the 2020 dendrometer rate; when the two diverged, the nearest valid inventory served as anchor and the dendrometer rate carried the increment to 2020.

Table 1: Monitored trees and 2020 per-tree characteristics. DBH reconstructed on 1 January 2020; A_s from the pooled A_s –DBH allometry; H from the per-plot Michaelis–Menten H –DBH allometry; ρ by water displacement (* species-median substitution; — absence). Successional strategy (P / ES / LS / C) follows Swaine & Whitmore (1988) and Ribeiro et al. (2005).

Plot	No	Species	Family	DBH 2020 (cm)	A_s (cm ²)	H (m)	ρ g cm ⁻³	Strategy
R40	1	<i>Miconia cinerescens</i>	Melastomataceae	—	—	—	0.58	ES
	3	<i>Alchornea glandulosa</i>	Euphorbiaceae	14.3	125	13.1	0.46	ES
	4	<i>Tovomitopsis paniculata</i>	Clusiaceae	10.2	65	10.5	0.56	LS
	6	<i>Endlicheria paniculata</i>	Lauraceae	8.0	40	8.8	0.41	LS
	7	<i>Tovomitopsis paniculata</i>	Clusiaceae	12.6	98	12.1	0.34	LS
	8	<i>Alchornea glandulosa</i>	Euphorbiaceae	18.5	206	15.2	0.40	ES
	9	<i>Alchornea glandulosa</i>	Euphorbiaceae	21.2	269	16.3	0.36	ES
	10	<i>Alchornea glandulosa</i>	Euphorbiaceae	20.0	240	15.9	0.41*	ES
	11	<i>Alchornea glandulosa</i>	Euphorbiaceae	18.4	204	15.2	0.41*	ES
	12	<i>Casearia obliqua</i>	Salicaceae	19.3	224	15.6	—	LS
	14	<i>Miconia cinerescens</i>	Melastomataceae	25.0	370	17.7	0.34	ES
	16	<i>Alchornea glandulosa</i>	Euphorbiaceae	28.7	484	18.9	0.41*	ES
	17	<i>Aspidosperma olivaceum</i>	Apocynaceae	29.6	514	19.2	0.55	C
	18	<i>Schefflera</i> cf. <i>calva</i>	Araliaceae	35.4	728	20.6	—	LS
	19	<i>Aspidosperma olivaceum</i>	Apocynaceae	33.8	665	20.3	0.57	C
	20	<i>Alchornea glandulosa</i>	Euphorbiaceae	31.6	584	19.7	0.41	ES
RP	30	<i>Tibouchina estrellensis</i>	Melastomataceae	19.4	226	9.5	0.50	P
	31	<i>Tibouchina pulchra</i>	Melastomataceae	15.0	137	8.9	0.35	P
	32	<i>Senna multijuga</i>	Fabaceae	18.8	213	9.5	0.60	P
	33	<i>Baccharis lateralis</i>	Asteraceae	16.7	169	9.2	0.33	P
	34	<i>Tibouchina pulchra</i>	Melastomataceae	17.6	187	9.3	0.30	P
	35	<i>Tibouchina pulchra</i>	Melastomataceae	11.3	79	8.1	0.50	P
	36	<i>Cedrela fissilis</i>	Meliaceae	15.7	150	9.0	0.45	ES
	37	<i>Tibouchina pulchra</i>	Melastomataceae	10.3	66	7.8	0.30	P
	38	<i>Tibouchina pulchra</i>	Melastomataceae	12.1	90	8.3	0.43	P
	39	<i>Tibouchina pulchra</i>	Melastomataceae	9.0	51	7.4	0.50	P
	40	<i>Lafoensia pacari</i>	Lythraceae	8.6	47	7.2	0.50	ES
	41	<i>Tibouchina pulchra</i>	Melastomataceae	9.8	60	7.6	0.55	P

5.4.3. Sapwood area determination

The conductive sapwood area A_s , defined as the cross-sectional area of the active water-conducting xylem ring at breast height, was measured directly on cored trees and predicted from DBH for the remaining individuals through an allometry. Cores were extracted at breast height with an increment borer reaching the heartwood on 24 trees in R40 and 23 trees in RP, sampled across the local DBH range during the three campaigns (2018, 2023, 2026). Sapwood, bark and heartwood were differentiated on each core with a 1 % safranin stain (active xylem stains red, Figure 13). Sapwood depth d_s (cm) and bark thickness e (cm) were measured directly.



Figure 13: Extraction of wood cores with an increment borer (right). Left up, visible colour differentiation between heartwood and sapwood, Left down, no colour differentiation visible.

Assuming a circular stem, the sapwood area is the cross-sectional ring between the cambium (inner bark) and the sapwood–heartwood boundary (Granier 1987):

$$A_s[\text{cm}^2] = \pi(R - e)^2 - \pi(R - e - d_s)^2 \quad (9)$$

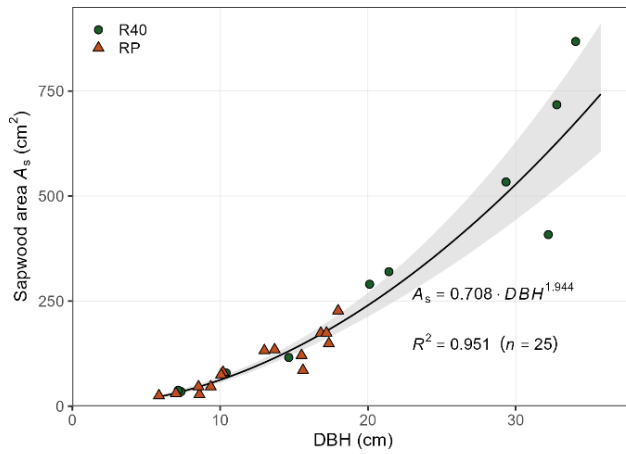


Figure 14: Pooled A_s –DBH allometry fitted on the 25 cored trees of both forest plots. R40 (green circles, $n = 10$) and RP (orange triangles, $n = 15$). Solid line: fitted power-law $A_s = a \cdot \text{DBH}^b$, grey band (95 % confidence interval).

solution (ordinary least squares). The fitted intercept is back transformed to recover $a = \exp(\log(a))$.

Cores without a clear safranin reaction or without clear heartwood identification were excluded. The retained 10 R40 (DBH 7.2–34.1 cm) and 15 RP (DBH 5.9–18.0 cm) trees were used for the fit. A single pooled relationship was fitted: $a = 0.708$, $b = 1.944$ ($R^2 = 0.951$, Figure 14). In the context of another study, a separate fit was done on the same species at the same plots and gives comparable exponents ($a = 0.91$, $b = 1.80$), supporting the pooled relationship retained here.

where $R = \text{DBH}/2$ is the stem radius (cm). On the cored trees, Equation (1) is applied with the directly measured e and d_s to obtain a reference A_s . The resulting (DBH, A_s) pairs form a calibration dataset on which an allometric power-law is fitted:

$$A_s[\text{cm}^2] = a \times \text{DBH}^b \quad (10)$$

The parameters a and b are obtained by minimising the sum of squared residuals between observed and predicted A_s on the calibration dataset. The log transformation makes the model linear in $\log(a)$ and b , so this minimisation has a closed-form

5.4.4. Height determination

Tree height (H) was measured during the first vegetation inventory (2018). Because individuals were not tagged at that time, these measurements could not be matched to the monitored trees. Height was therefore estimated for each monitored individual from a height–diameter allometry calibrated on the inventory, using DBH, the most reliably acquired variable as predictor. A Michaelis–Menten saturating model (Baia et al. 2025) was fitted, for both plots, to the inventory height–diameter data:

$$H [m] = \frac{a \times DBH}{b + DBH} \quad (11)$$

where a is the asymptotic height (m) and b the DBH at which half the asymptotic height is reached (cm). The parameters a and b are obtained by minimising the sum of squared residuals between observed and predicted heights, as in §5.4.3. (Sapwood area). The Michaelis–Menten model is non-linear in (a, b) so the minimum is reached iteratively by the Gauss–Newton algorithm (R function `nls`). Starting from $a_0 = \text{maximum observed height}$ and $b_0 = \text{median}$

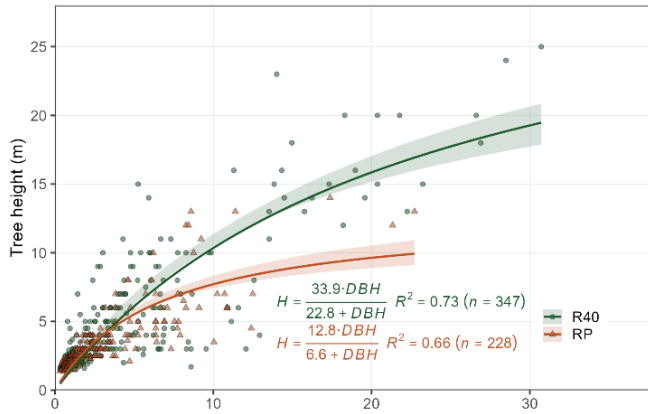


Figure 15: DBH distribution of the 2018 inventory on R40 (left, $n = 347$ trees) and RP (right, $n = 228$ trees). Bars are 2-cm histograms (density on the y-axis), solid lines are kernel density estimates (Gaussian smoother, bandwidth $\times 1.2$).

DBH, the algorithm linearises the model around the current estimate at each step, updates (a, b) on the residuals, and iterates until the change between two successive estimates falls below the convergence threshold. The fitted relationships (R40: $a = 33.9$, $b = 22.8$; RP: $a = 12.8$, $b = 6.6$) are applied to the reconstructed 2020 DBH. Predicted heights are 8.8–20.6 m on R40 and 7.2–9.3 m on RP (Fig. 15). They are used to compute the aerodynamic conductance g_a in §5.7.7.

5.4.5. Above-ground biomass increment

Per-tree above-ground biomass (AGB) is estimated from the pantropical model of Chave et al. (2014), which combines DBH, height and wood specific gravity ρ :

$$AGB[kg] = 0.0673 \times (\rho \times DBH^2 \times H)^{0.976} \quad (12)$$

The three inputs were obtained as follows. The equation is applied at the two endpoints of the 2020 hydrological year. AGB_{start} uses the DBH reconstructed for 1 January 2020. AGB_{end} uses $DBH + 2 \cdot \Delta R$, where ΔR is the annual radial increment derived from the dendrometer ΔGRO (§5.6.1). Height is recomputed at each endpoint from the H–DBH allometry (§5.4.4) to follow the change in stature.

Wood specific gravity was measured by water displacement (Chave et al. 2014) on the 25 cored trees: green volume from the displaced water, dry mass after oven-drying at 105 °C for 72 h, ρ being their ratio (Xavier et al. 2023). The species median was used for the four uncored R40 trees (T10, T12, T16, T18). Values fall within published ranges (Meinzer et al. 2001; Zanne et al. 2009); only *Tibouchina pulchra* (RP) varies strongly between individuals (0.30–0.55), the lowest values likely reflecting coring degradation, so its species median was used. Plot medians are nearly identical (R40 = 0.46, RP = 0.475), so wood density does not distinguish the two stands. The annual increment is the difference between endpoints:

$$\Delta\text{AGB} = \text{AGB}_{\text{end}} - \text{AGB}_{\text{start}} [\text{kg yr}^{-1}]. \quad (13)$$

The model carries about $\pm 10\%$ uncertainty at the species level (Chave et al. 2014), and ΔAGB covers stem biomass only, excluding leaves, branches and roots.

5.5. Signal pre-processing

Raw 66-s records were both resampled onto a regular 1-min grid. Each raw timestamp was rounded to the nearest minute, values falling in the same minute were averaged, and minutes with no raw observation were kept as NA. This preserves the position and duration of every gap in the original record. The signals then passed through a quality control (QC) pipeline, a window-selection step for sap flow only, and a signal-specific gap-filling step. Both pipelines were constantly checked visually on monthly diagnostic plots, which confirmed that filters remove artefacts while keeping the real biological signal.

5.5.1. Data Quality Control

Dendrometer

Eight automated filters are applied sequentially, followed by manual invalidation and a reset detection step (Table 2). Physical filters reject implausible values. *Range* flags values outside the physical bounds [0,10] mm. *First-difference* flags point-to-point jumps above the maximum physiological rate of stem-radius change. *Frozen* flags stuck signals, defined as runs in which $|\Delta x|$ stays below the sensor noise floor for at least 30 consecutive minutes.

Transient filters target mechanical and meteorological artefacts. *Post-gap* drops the first 45 valid points after any logger interruption $\geq 10\text{min}$, the time needed for the rod to re-stabilise. *Wind* drops minutes when the 15-min site-average wind speed exceeds 3.0 m s^{-1} , since gusts vibrate both the trunk and the sensor. *Orphan runs* removes short valid segments ($\leq 10\text{pts}$) isolated by long gaps ($\geq 10\text{pts}$), which lack the surrounding context needed for trend analysis.

Statistical filters target outliers and residual variability. *Hampel* is a robust outlier detector. For each point, the local median and median absolute deviation (MAD) are computed over a rolling ± 4 -h window, and the point is flagged when its deviation from the local median exceeds $3 \cdot \text{MAD}$ and an absolute floor of 10^{-3} mm (Peters et al. 2021). *Sub-diurnal noise* targets coherent variability that *Hampel* cannot detect. The signal is detrended by a 15-min rolling median, the residual standard deviation is computed over a sliding ± 30 -min window, and the zone is flagged when the SD exceeds an empirical threshold calibrated on a noisy reference month.

The three μm -scale thresholds (frozen, sub-diurnal noise, Hampel floor) follow the sensor noise floor of 3×10^{-4} mm in a coherent hierarchy. Manual invalidation flags instrumental failures (decoupling, drift) identified on the monthly diagnostic plots (Knüsel et al. 2021).

Table 2: Dendrometer QC filters, parameters, median fraction removed (2020), and references. Percentages are non-exclusive. A minute flagged by k filters counts in each row. They refer to the 527 040 minutes of 2020 and exclude the four globally invalid sensors. Full parameter set in Appendix C.1 Table 8.

Filter	Parameters	Removed (median)	Reference
Range	$[0, 10]$ mm	0 %	Zweifel et al. 2016
Frozen	$ \Delta x < 5 \times 10^{-4}$ mm over ≥ 30 pts	0 %	Vejmelka et al. 2012
Post-gap	First 45 valid pts after gap ≥ 10 min	2.0 % (R40) / 3.4 % (RP)	Drew & Downes 2009
Hampel	± 120 pts; $k = 3$; floor 10^{-3} mm; ceiling 0.3 mm	0.6 % (0.2–1.8 %)	Hampel 1974; Peters et al. 2021
Wind	mean wind $> 3.0 \text{ m s}^{-1}$ (15-min)	3.8 % (uniform)	Deslauriers et al. 2007
Sub-diurnal noise	residual SD $> 7 \times 10^{-4}$ mm vs 15-min runmed	0.5 % (0–10.8 %)	this study
First-difference	$ \Delta x > 0.01 \text{ mm step}^{-1}$	0 %	Zweifel et al. 2016
Orphan runs	valid run ≤ 10 pts flanked by gap ≥ 10 pts	0.7 %	analog. Vickers & Mahrt 1997
Manual	visual inspection	0 % (17 trees); up to 26 % (T35)	Knüsel et al. 2021

Wind, post-gap and sub-diurnal noise account for most of the rejection (Table 2). Range, frozen and first-difference never triggered in 2020. The remaining NA structure is concentrated overnight (≈ 80 % at 03–06 h, ≈ 30 % at midday), which leaves the daily aggregates (≥ 40 % coverage) robust.

Level shifts caused by mechanical readjustments are corrected after the automated filters. A candidate is any jump $|\Delta x| \geq 0.3 \text{ mm}$ or any first valid point after a gap $\geq 30 \text{ min}$. A reset is confirmed when the medians of the 20 preceding and 20 following valid points differ by $\geq 0.3 \text{ mm}$. The offset is subtracted from all subsequent values, with a 20-point buffer set to

NA. The procedure was applied to the eight trees with visually confirmed shifts (T04, T09, T11, T17, T18, T20, T33, T35), and T37 and T41 were corrected manually for the 16 June 2020 shock.

The 26 instrumented trees are stratified into four reliability classes. Six are excluded (T08, T31, T38, T39: sensor failures; T11: 270-day wiring duplicate with another retained tree; T40: no interpretable growth signal). For the 20 retained trees, post-QC coverage of the 1-min grid ranges from 22 % (T35) to 59 % (T14, T18, median 47 %) and rises to a median of 70 % after gap-filling. The classes LOW-CONFIDENCE (‡; T04, T10, T14, T20, T35), RESERVE (†; T07, T36) and RELIABLE (T01, T03, T06, T09, T12, T16, T17, T18, T19, T33, T34, T37, T41) are assigned by combining post-fill coverage with the fraction of valid data in the post-rewetting period (§5.5.2). ‡ and † trees still enter aggregated analyses.

Sap flow

Raw temperature-difference (ΔV) records were screened by a pipeline of fourteen flags organised in three families (instrumental, transient, statistical), followed by a residual cleanup stage (Table 3). The 14 flags are combined into a single rejection mask: a timestep is marked invalid as soon as at least one filter rejects it. The Granier conversion (§5.7.1) is then applied only to the timesteps that survive all flags.

Instrumental flags reject hardware dysfunctions and dead-sensor signatures. *Voltage*, *heating* and *temp* flag steps when the logger supply voltage, the heating-element voltage or the internal probe temperature falls outside the nominal operating range of the datalogger. *Post-outage* drops the 30 steps (~2.5 h) following any logger gap ≥ 30 min, the time needed for the heated probe to thermally re-equilibrate. *Negative* flags strictly negative ΔV , physically impossible under heat-dissipation theory (Granier 1985). *Range* flags ΔV above the maximum value plausible for Atlantic Forest hardwoods. *Floor* and *frozen* detect dead-sensor signatures on two complementary timescales: *floor* flags any window of ≥ 60 consecutive steps (~5 h) stuck within the ADC noise floor, and *frozen* extends the criterion to $\geq 1\,080$ steps (~18 h) of below-threshold rolling standard deviation, calibrated to discriminate failed sensors from legitimate nocturnal plateaus.

Transient flags target short-lived artefacts. *Hampel* applies the same logic as in the dendrometer pipeline (§5.5.1), adapted here with a ± 60 -pt window (~5 h), $k = 3$, an absolute floor of 0.010 mV, and 5 iterations to catch clusters of spikes around the same time. *First-difference* flags step-to-step jumps and short multi-point excursions (≤ 25 pts) that survive the Hampel cascade.

Statistical flags target coherent residual variability. *Local range* flags any sliding window whose max–min amplitude exceeds the maximum expected from a normal diurnal cycle. *t-coherence* cross-checks the thermal coherence between the heated and reference probes and flags any breakdown signalling probe drift or partial detachment.

Cleanup flags run after the QC mask is established. *Meteo-night* flags nocturnal steps with anomalously high ΔV inconsistent with the simultaneous low VPD and zero radiation. *Isolated* removes valid segments shorter than 30 consecutive points (~ 2.5 h) bounded by long NA gaps on both sides, on which the Granier baseline cannot be referenced.

Table 3: Sap flow QC flags, parameters and contribution to the 2020 mask. Removed = % of all 1-min $\times$ tree records flagged. Unique = fraction of that flag exclusive to it. Full parameter set in Appendix Table 10.

Family	Flag	Parameters	Removed	Reference
Instr.	voltage	supply V outside [10.5, 16.0] V	0.001 %	Plantem SF_DEN V1.0 spec.
	heating	heating V outside 5.70 ± 0.50 V	< 0.001 %	Plantem SF_DEN V1.0 spec.
	temp	probe T outside [5, 50] °C	< 0.001 %	Plantem SF_DEN V1.0 spec.
	post-panne	logger gap ≥ 30 min $\rightarrow$ flag next 30 steps (~ 30 min)	0.014 %	adapt. Drew & Downes 2009
	negative	$\Delta V < 0$ mV (strict)	1.5 %	Granier 1985
	range	$\Delta V > 2.20$ mV	0.11 %	empirical (Atlantic Forest hardwoods)
	floor	$\Delta V < 0.10$ mV in ≥ 60 -pt window	9.3 %	this study
Trans.	frozen	rolling SD < 0.012 mV over $\geq 1\,080$ pts (~ 18 h)	9.4 %	this study; cf. Vejmelka et al. 2012
	Hampel	± 60 pts (~ 5 h); $k = 3$; min dev 0.010 mV; 5 iterations, outlier replacement	14.7 %	Hampel 1974; Poyatos et al. 2021
	first-difference	$ \Delta \Delta V > 0.05$ mV step^{-1} , spike width ≤ 25 pts	0.004 %	this study
Stat.	local range	sliding window max-min > diurnal-cycle envelope	3.7 %	this study
	t-cohérence	inter-probe coherence drop (P5/P95 hour $\times$ month)	0.32 %	adapt. Poyatos et al. 2021
Cleanup	meteo-night	nocturnal ΔV inconsistent with low VPD + zero Rad	1.1 %	this study
	isolated	valid segment < 30 pts (~ 2.5 h) between NA gaps	5.7 %	analog. Vickers & Mahrt 1997

Hampel (14.7 % records, 90 % unique to it), frozen (9.4 %) and floor (9.3 %) account for most of the rejection (Table 3). The 22 % co-occurrence of frozen and floor reflects related signatures of the same dead-sensor pattern. Strictly instrumental flags total less than 0.2 % combined, which confirms a healthy raw acquisition chain.

The 27 sap flow trees are stratified into three classes by their participation in the analysis windows. Eleven are EXCLUDED (T01, T20, T31, T32, T33, T35, T39, T41 sensor failures; T11 wiring duplicate; T08, T37 with post-QC coverage too low for any window). Four LIMITED-PRESENCE trees (3–4 windows each: T04, T16, T19 (R40); T38 (RP)) support descriptive comparisons only. The CORE set of 12 trees is present in 7–21 windows (T03, T06, T07, T09, T10, T12, T14, T17, T18 (R40); T34, T36, T40 (RP)). Post-QC coverage of the 1-

min grid is higher on R40 (median 39 %, up to 70 % on T10 and T18) than on RP (median 8 %), which reflects chronic power interruptions on the RP plot.

5.5.2. Gap filling

For each gap in the post-QC 1-min series, the gap duration δ (defined in §5.3.1.) controls the choice of method. Dendrometer and sap flow records are filled separately because their gap-length distributions differ.

Dendrometer

Short gaps ($\delta \leq 2$ h) are filled by linear interpolation (§5.3.1). Two safeguards apply: any gap falling within a sub-diurnal noise zone (§5.5.1) is left as NA, and an interpolated segment is reverted to NA when its maximum point-to-point variation exceeds $5 \times 10^{-3} \text{ mm min}^{-1}$ (Zweifel et al. 2016). Long gaps ($\delta > 2$ h) are not filled. Linear interpolation over more than 4 h flattens the diurnal cycle (MDS underestimated by ≈ 10 % for a 12-h gap). Model-based alternatives (na_seadec, scaled diurnal template, nearest-neighbour) were tested but failed on noisy days. Days containing a long gap are therefore removed later by the coverage filter (§5.6.1).

This choice costs ≈ 5 % of tree-days (one tree-day = one tree monitored for one day) but removes all artificial flattening of the daily cycle. Across the 22 trees with non-zero post-QC signal, short-gap interpolation recovers a median of 41 % of the post-QC missing minutes (range 14–54 %), raising minute-level coverage from a median of 47 % to 70 % (Appendix Table 11). The full chain of events from QC to gap filling can be found in the Appendix in the Fig. 50.

Sap flow

Before the gap filling, analysis windows are selected for sap flow only, because the signal is highly fragmented. Periods of valid signal are often interrupted by days of poor quality remaining after the QC. Long valid periods are first identified, and suspicious days within them are manually discarded. This step is done here so that the donor days used in the MDV template are restricted to clean days, and so that the gap-filling procedure runs on a smaller, cleaner set of candidate days.

Windows are then selected per season to cover the four climatic regimes. A window is retained when a continuous stretch of at least 3 consecutive days satisfies the per-tree validity criterion (post-QC coverage ≥ 30 % of the minute grid). Window boundaries are refined iteratively against the per-tree QC mask to maximise the number of trees sharing common valid days. The procedure retains 22 windows covering 233 days in total: 7 windows totalling 88 days in the wet season, 5 windows totalling 42 days in the drying season, 6 windows totalling

72 days in the dry season, and 4 windows totalling 31 days in the rewetting season. Per-window tree composition is reported in Appendix Table 12.

Gap filling is restricted to the analysis windows. Three cases are distinguished.

(i) Short gaps ($\delta \leq 2h$) are filled by linear interpolation (§5.3.1.).

(ii) Intermediate gaps ($2h < \delta \leq 18h$) are filled by the boundary-anchored MDV approach (§5.3.1.), with sap-flow-specific extensions. The template is the average ΔV shape over the day, computed minute-by-minute from donor days. A donor day is a day with $\geq 80\%$ coverage in the transition and dry months. Wet months are excluded because their day-to-day variability is too high. Each donor day is centred on its own 24-h moving mean so that the template does not jump at midnight. The template is scaled to each gap by a least-squares fit on the measured points within ± 24 h, which gives a baseline level $\hat{a}$ and an amplitude $\hat{b}$. When fewer than 120 measured points are available within ± 24 h, the local fit is not reliable, and $\hat{b}$ is then taken as the median amplitude of the donor days.

(iii) Long gaps ($\delta > 18$ h) are not filled. The 18 h threshold was chosen from the distribution of gap lengths. An 18 h threshold recovers 9.6 % more of the minute grid than a 12 h threshold, while extending it to 24 h adds only 2.7 %. Gap-fills were also checked visually, and fills that changed the shape of the daily cycle were discarded.

Across the 152 trees $\times$ window pairs retained (16 trees), gap-filling brings the median per-window coverage from 73 % (raw) to 100 %. The > 18 h category is empty in practice: the window-selection step drops any tree $\times$ window pair containing such gaps. Of filled minutes, $\approx 32\%$ are linear interpolation and $\approx 68\%$ are template fill. On a few days, outliers that had passed the QC step were treated as valid data by the fit and produced false spikes in the filled signal. These days were rare and were removed by visual inspection. The template still recovers many days that would otherwise be lost. The full chain of events from QC to gap filling can be found in the Appendix in the Fig. 50.

5.6. Dendrometer signal processing

5.6.1. Zero-Growth decomposition

The interpolated signal $\tilde{x}(t)$ from §5.5.2 is decomposed into two components (Fig. 16) following the Zero-Growth method (Zweifel et al. 2016): irreversible radial growth (GRO) and tree water deficit (TWD). The method assumes that irreversible increases in trunk radius can only come from cambial cell division (Zweifel & Häslar 2000; Steppe et al. 2006), while contractions below the previous maximum reflect tissue dehydration.

The signal is first smoothed by a centred 31-min rolling median (zoo package, Zeileis & Grothendieck 2005): at each time t , the median of all valid values within ± 15 min of t is

computed and assigned to t . Windows with fewer than 7 valid points yield NA. The median is preferred over a rolling mean because it is robust to residual outliers that may have survived the QC step. The running maximum of x_{smooth} defines the growth envelope and TWD is the gap between the growth envelope and the smoothed signal (Fig. 16):

$$\text{GRO}(t) = \max_{s \leq t} x_{\text{smooth}}(s) ; \text{TWD}(t) = \text{GRO}(t) - x_{\text{smooth}}(t) \quad (14)$$

By construction, $\text{TWD} = 0$ when the envelope reaches a new maximum, and TWD is positive during contraction phases (Zweifel et al. 2014). Annual radial growth is then calculated as $\Delta \text{GRO} = \text{GRO}_{\text{end}} - \text{GRO}_{\text{start}}$ (15).

The GRO envelope is propagated across gaps ≤ 24 h by last-observation-carried-forward (LOCF) that holds the last valid value constant across the gap until the next valid observation. GRO is monotonic non-decreasing by construction: it can only stay the same or increase, and only a new observation can push it up. Over a gap of less than 24 h, the envelope is supposed to not have advanced, so it is held constant. Longer gaps are left as NA because extending GRO further would assume no growth across the missing period which could bias the downstream analyses.

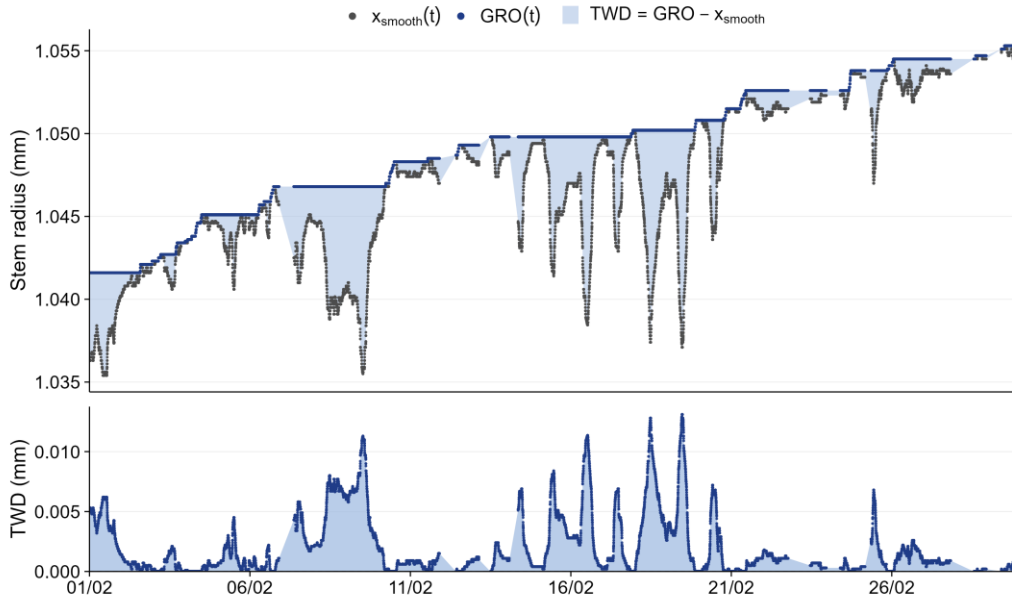


Figure 16: Zero-Growth decomposition (Zweifel et al. 2016) on tree T03, February 2020. Top: smoothed stem radius x_{smooth} (grey) and growth envelope GRO (blue), with $\text{TWD} = \text{GRO} - x_{\text{smooth}}$ shown as the blue ribbon. Bottom: TWD time series, dashed line at $\text{TWD} = 0$.

5.6.2. Drought stress indicators

Two complementary metrics characterise short-term water status: the maximum daily shrinkage (MDS) and the normalised tree water deficit (TWD_{norm}), following Peters et al. (2025) and Salomón et al. (2022). MDS is defined per tree-day:

$$\text{MDS}(j) = \max_{t \in \text{day } j} x_{\text{smooth}}(t) - \min_{t \in \text{day } j} x_{\text{smooth}}(t) \quad (16)$$

Large values indicate active cycling driven by strong daytime transpiration relative to overnight rehydration. A progressive decrease over a sustained drought reflects the collapse of this cycling capacity as the stem becomes too dehydrated to refill and contract normally (Peters et al. 2025).

Daily aggregates of MDS, $TWD_{\max}$ and $TWD_{\min}$ are retained only for tree-days with ≥ 40 % non-NA minutes, which captures both daytime contraction and overnight expansion. TWD and MDS are normalised per tree by the 99th percentile of the per-tree MDS distribution ($MDS_{\max}$, Peters et al. 2025):

$$TWD_{\text{norm}} = \frac{TWD_{\text{predawn}}}{MDS_{\max}} \quad (17); \quad MDS_{\text{norm}} = \frac{\text{MDS}}{MDS_{\max}} \quad (18)$$

TWD_{predawn} is the residual deficit at the pre-dawn stem-radius maximum, taken here as the daily TWD minimum. $MDS_{\max}$ reflects the overall capacity of the stem tissues to shrink (Peters et al. 2025). The threshold $TWD_{\text{norm}} = 1$ marks the onset of stomatal closure (Peters et al. 2025), with full turgor loss occurring at species-specific values well beyond unity.

5.6.3. Dry period detection

A dry period is defined following Zweifel et al. (2016) as a sequence of consecutive days during which the stem radius fails to reach a new maximum. The previous stem-radius maximum is denoted $SR_{\max}$ and is equal to the GRO envelope of §5.6.1. A day j enters a dry period when $TWD_{\min}(j) > 0$, meaning that x_{smooth} stays strictly below $SR_{\max}$ throughout the day. The period starts when this condition is first met and ends upon full rehydration ($TWD_{\min}(j) = 0$, when x_{smooth} reaches $SR_{\max}$ again).

For each tree, the daily series of $TWD_{\min}$ is scanned for runs satisfying $TWD_{\min} > \varepsilon$, with $\varepsilon = 5 \times 10^{-4} \text{mm}$ (below the sensor noise floor of $3 \times 10^{-4} \text{mm}$). Runs of duration ≥ 1 day are retained. A pre-dawn coverage criterion is added to the Zweifel definition. A day counts as dry only when its 00:00–06:00 window contains at least 30 valid minutes, and the pre-dawn TWD exceeds ε . Without this check, the rewetting season (which has near-zero overnight coverage) would have its afternoon contractions misclassified as residual deficit. This condition removes 4.4% of the candidate dry days, most of them on the RP plot where overnight coverage is more limited. Periods are flagged as censored and excluded from duration statistics when the daily series shows gaps longer than 3 consecutive days within the period, or when the period ends within the last two days of the year.

5.6.4. Growth phenology and growth drivers

Growth phenology

The Wood Growth Period (WGP, Zweifel et al. 2016) characterises when and over what duration growth was produced. Two trees with the same ΔGRO_{annual} can have very different WGP durations and rates, reflecting different phenological strategies.

WGP covers the main phase of annual growth. Its start is the first day on which the cumulative growth envelope GRO reaches the 5th percentile of its annual range. Its end is the first day on which GRO reaches the 95th percentile. The 5th and 95th percentile bounds discard the slow tails at the start and end of the year, where growth is dominated by noise on the lower side and by post-rewetting bark swelling on the upper side. The mean growth rate over this window is reported as $WGP_{rate} (\mu m day^{-1})$. For each tree, the fraction $frac_{dry}^{WGP}$ of WGP days that fall inside a dry period measures how often growth and stress co-occur.

Two scaling metrics complete the magnitude characterisation. The basal area increment $BAI = \pi \cdot R^2 - \pi \cdot (R - \Delta R)^2$ (19) is the cross-sectional area of new wood produced over the period. It is more robust than the radial increment ΔR alone, because BAI is derived from the circumference ($R = CBH / 2\pi$), which averages around the whole stem and is less sensitive to deviations from a perfectly circular cross-section (Biondi & Qeadan 2008). The relative growth rate $RGR = \Delta DBH / DBH$ (20) normalises growth by the tree's current size, allowing comparison between trees of different sizes.

Growth drivers

The atmospheric and edaphic drivers of growth are characterised at two levels. At the per-tree level, a generalised additive model (GAM) is fitted to the daily ΔGRO series with the mgcv R package (Wood 2017):

$$\Delta GRO \sim s(VPD_{diurnal}) + s(\psi_{soil}^{root-weighted}) + s(rain_{3d}) \quad (21)$$

A GAM expresses the response as a sum of flexible smooth functions $s(\cdot)$ estimated from the data, without assuming a fixed shape. This is appropriate here because growth responses to climatic drivers are typically non-linear. The unique contribution of each driver is quantified as the loss of explained deviance when its smooth is removed from the full model. The total deviance explained by the full model quantifies the fraction of daily ΔGRO variability that the three drivers jointly capture. A high value indicates that VPD, ψ_{soil} and $rain_{3d}$ together account for most of the day-to-day variation in growth, and that the chosen drivers form a sufficient set. The three drivers are interpreted as PULSE ($rain_{3d}$), STOCK (ψ_{soil}) and DEMAND (VPD). Full estimation details of GAM equations are reported in Appendix E.

At the forest level, the interaction between VPD and Ψ_{soil} is tested by a tensorial GAM following the supply $\times$ demand framework of Novick et al. 2016:

$$\Delta GRO \sim te(VPD, \Psi_{soil}) + s(rain_{3d}) + (1 | tree) \quad (22)$$

Two terms differ from the per-tree GAM. First, the additive smooths $s(VPD) + s(\Psi_{soil})$ is replaced by a single 2D smooth $te(VPD, \Psi_{soil})$, which fits a continuous surface over the joint (VPD, Ψ_{soil}) plane. The local slope along the VPD axis can take a different value at every position on the surface, so the response to VPD is allowed to change with Ψ_{soil} . This is what is required to test the supply $\times$ demand interaction of Novick et al. (2016), described in SoA §3.2.3 and §3.2.4. The additive form $s(VPD) + s(\Psi_{soil})$, by contrast, forces a single VPD response curve at every Ψ_{soil} (only vertically shifted), and cannot capture this interaction.

5.6.5. Size normalisation

To enable inter-tree comparisons of TWD and MDS amplitudes accounting for tree size, both metrics are also expressed as radial strain, the relative deformation of the stem normalised by its radius:

$$\text{strain} = \frac{\text{amplitude}}{R}, \quad \text{reported in ppm } (\times 10^6) \quad (23)$$

where R is the stem radius at start-2020. Strain (ppm) normalises the amplitude by the stem radius, so it is comparable between trees of different sizes. A 0.05 mm shrinkage represents a larger fractional deformation on a small stem than on a large one (Steppe et al. 2006).

5.7. Sap flow data treatment

5.7.1. Granier conversion

The dimensionless flow index K (Granier 1985, SoA §3.2.1) compares the current temperature differential $\Delta V(t)$ between the heated and reference probes to its zero-flow reference $\Delta V_{\max}(t)$, determined per tree in §5.7.2:

$$K(t) = \frac{\Delta V_{\max}(t) - \Delta V(t)}{\Delta V(t)} \quad (24)$$

K equals 0 when no flow is recorded ($\Delta V = \Delta V_{\max}$) and rises as the flow increases, because the moving sap carries heat away from the heated probe and reduces ΔV below $\Delta V_{\max}$. The ratio is dimensionless: both ΔV and $\Delta V_{\max}$ are voltages.

The sap flux density $F_d (gcm^{-2}h^{-1})$ is derived from K through the empirical power-law calibration of Granier (1987):

$$F_d(t) = 42.84 \cdot K(t)^{1.231} \quad (26)$$

F_d is normalised by the cross-sectional area of the active xylem, which makes it directly comparable between trees with different sapwood areas. It is computed at every 1-min step from the gap-filled ΔV . The original Granier (1987) coefficients were calibrated on temperate species and are retained as the conventional reference.

5.7.2. Baseline ΔV_{max} determination

The Granier conversion requires a per-tree zero-flow reference ΔV_{max} . Two mechanisms make a single-night estimate unreliable. First, ΔV_{max} depends on the water content of the wood surrounding the heated probe. Wetter wood carries away more heat and lowers ΔV , so when the wood dries the dissipation decreases and ΔV_{max} rises. This effect produces a seasonal drift of about 2 °C between dry and well-hydrated states (Vergeynst et al. 2014), and operates at the daily scale as well, tropical angiosperms showing diurnal stem water content changes of up to 18 % in dry periods (Scholz et al. 2007). Second, residual nocturnal transpiration and stem refilling maintain a non-zero flow on apparently zero-flow nights (Lu et al. 2004), so a reliable baseline must come from the upper envelope of multiple nights selected for low atmospheric demand (Oishi et al. 2008, 2016). The pipeline therefore uses a season-specific reference.

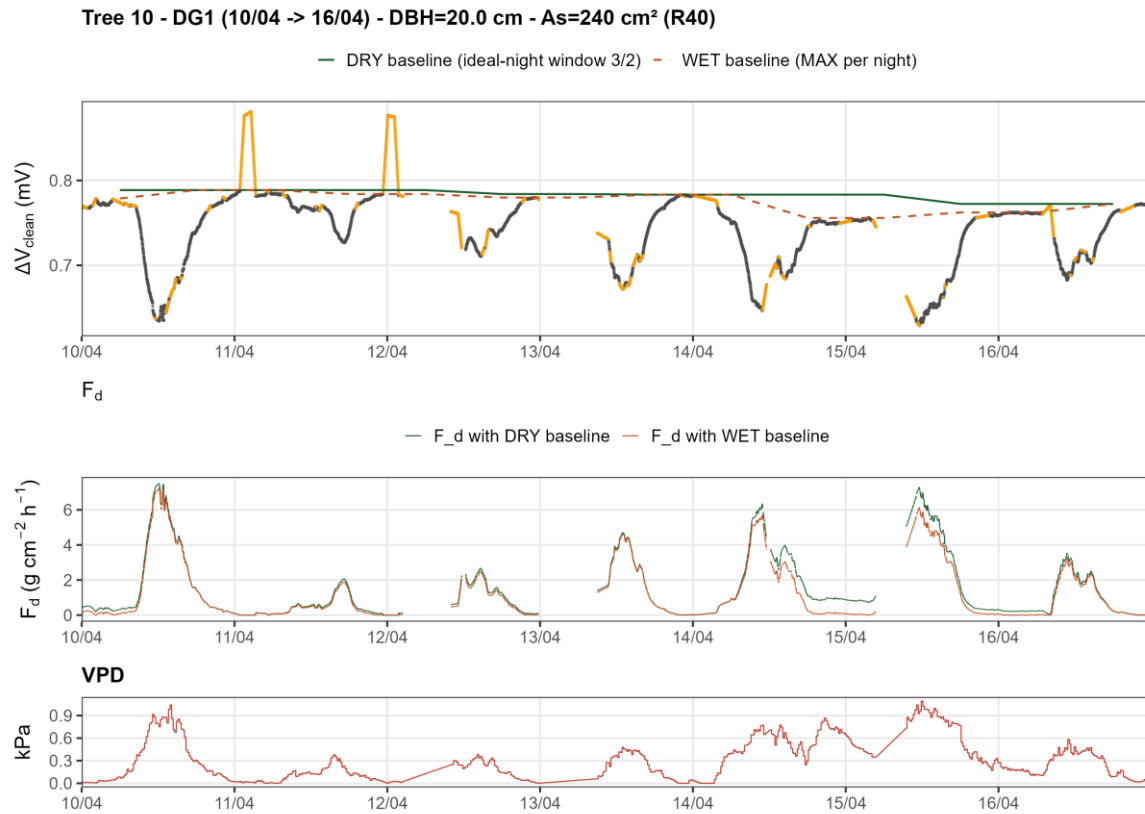


Figure 17: Effect of the baseline method on F_d during a drying-season period (DG1, 10–16 April 2020, tree T10, R40). Top: cleaned ΔV with measured points (grey), interpolated points (orange), and the two baselines: DRY (green, ideal-night window 3/2) and WET (orange dashed, MAX per ideal night). Middle: F_d derived from each baseline. Bottom: VPD.

In the dry regime (drying and dry seasons), ideal nights are defined as nights satisfying radiation $< 5 \text{ W m}^{-2}$, VPD $< 0.5 \text{ kPa}$ and no rain in the preceding 3 h. The per-night maximum of ΔV is computed on each ideal night, and a centred rolling maximum of width 3 ideal nights is applied across consecutive ideal nights. Non-ideal nights between two ideal nights inherit the maximum of their two nearest ideal-night values (Fig. 17).

In the wet regime (wet and rewetting seasons), frequent rainfall artefacts preclude smoothing across nights. The per-night maximum of ΔV is recorded for every night with at least one measured point, the maximum being preferred to a mean to limit the influence of brief rain-induced shifts. Nights fully flagged by QC are linearly interpolated from the surrounding plateau values, and occasional spikes from the interpolation are manually excluded (Fig. 18).

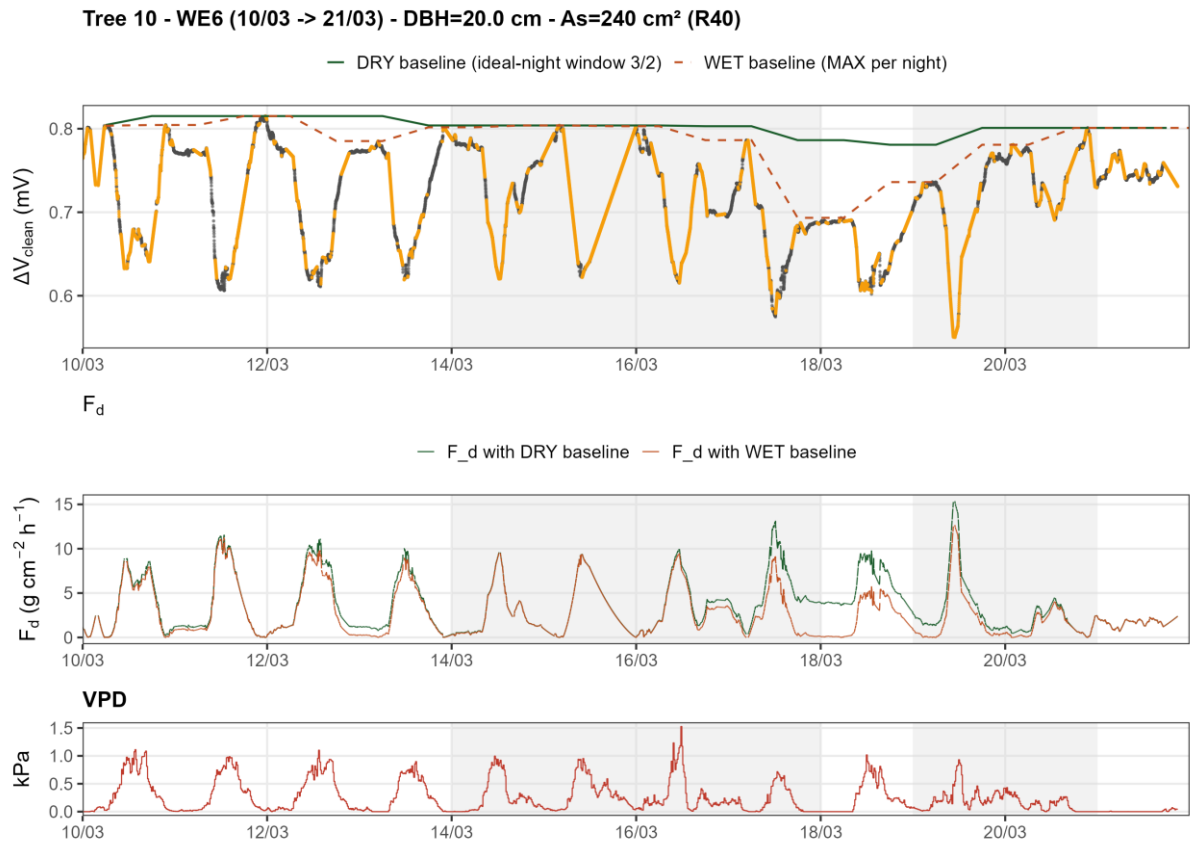


Figure 18: Effect of the baseline method on F_d during a wet-season period (WE6, 10–21 March 2020, tree T10, R40). Grey shading: rainy days. Same conventions as Figure 17.

Each per-night reference is then held as a constant plateau between 18:00 and 06:00 and linearly interpolated between consecutive plateaus to produce a continuous ΔV_{max} baseline. The choice between seven candidate variants of this procedure is the dominant source of uncertainty in the absolute flux and is quantified in §6.6.1.

5.7.3. Whole-tree flow and daily water use

The sap flux density F_d obtained from the Granier conversion is converted to whole-tree volumetric flow J_s by multiplying by the per-tree sapwood area A_s (§5.4.3.) and converting from g to L ($1 \text{ g} \approx 10^{-3} \text{ L}$):

$$J_s(t) [\text{L h}^{-1}] = \frac{F_d(t) \cdot A_s}{1000} \quad (27)$$

The daily integrated water use of an individual tree is computed as a Riemann sum (discrete approximation of an integral by a sum of rectangles) at the 1-min step on which the K and F_d series are evaluated:

$$Q_{\text{day}}(d) [\text{L day}^{-1}] = \sum_{t \in \text{day } d} J_s(t) \cdot \Delta t, \quad \Delta t = \frac{1}{60} \text{ h}. \quad (28)$$

Residual NAs surviving the gap-filling step are dropped before integration. Short gaps are bridged by extending the surrounding timestep width, while longer gaps are truncated at 1 min and downgrade the daily coverage metric. Days falling below the coverage threshold are excluded from downstream analyses, so residual underestimation does not propagate into the per-tree summaries. Day and night fractions are integrated separately using the on-site radiation record, with daytime defined as $\text{Rad} > 5 \text{ W m}^{-2}$ and night as $\text{Rad} \leq 5 \text{ W m}^{-2}$, which yields Q_{daytime} , Q_{night} and the nocturnal fraction $Q_{\text{night}}/(Q_{\text{daytime}} + Q_{\text{night}})$.

5.7.4. Stand transpiration

Two physical levels are reconstructed to read the stand against atmospheric demand. The stand-level transpiration T_{stand} aggregates the per-tree flows over the inventory into a single water flux per unit ground area. A reference transpiration T_{ref} is defined under non-limiting conditions. The ratio $T_{\text{stand}}/T_{\text{ref}}$ is then read as a measure of how far the stand operates from its theoretical non-limited potential.

The Sapwood Area Index (SAI) is the total sapwood area per unit ground area, summed over the inventory of trees in the plot:

$$\text{SAI} = \frac{1}{A_{\text{inv}}} \sum_{i \in \text{plot}} A_{s,i} \quad (29)$$

where the sum is taken over all inventory trees of a plot and A_{inv} is the inventory area (300 m^2). The two plots differ markedly: $\text{SAI} = 0.00273 \text{ m}^2 \text{ m}^{-2}$ in R40 and $0.00096 \text{ m}^2 \text{ m}^{-2}$ in RP, so the R40 stand carries $2.84\times$ more conductive xylem per unit ground area than RP.

Because sap flow is measured only on a subset of the trees in each plot, each non-instrumented tree is assigned the F_d of the instrumented tree of nearest DBH within the same plot and the same time window. Stand transpiration is then obtained by summing the resulting

whole-tree flows over the inventory and dividing by the inventory area where the factor 10 converts g cm^{-2} to mm of water column:

$$T_{\text{stand}}(t) = \frac{10}{A_{\text{inv}}} \sum_{i \in \text{plot}} F_{d,i}(t) \cdot A_{s,i} \quad (30)$$

The nearest-DBH rule preserves the size structure of the stand. Alternative extrapolations (linear $F_d - \text{DBH}$ regression with and without DBH-range extrapolation, restricted inventory subsets) are tested in the sensitivity analysis (3.8). A T_{stand} value enters the per-window aggregate only when the daily inventory coverage exceeds 50 %.

5.7.5. Reference transpiration

T_{ref} is the expected stand transpiration under non-limiting conditions, defined as the product of ET_0 and a plot-specific transpiration coefficient:

$$T_{\text{ref}}(t) = K_{c,T} \cdot ET_0(t) \quad (31)$$

$K_{c,T}$ is analogous to the FAO crop coefficient K_c but restricted to the transpiration component, excluding soil evaporation and interception. The ratio $T_{\text{stand}}/T_{\text{ref}}$ measures how close the stand operates to its non-limiting potential. Because $K_{c,T}$ is the mean ratio across reference days, daily values of $T_{\text{stand}}/T_{\text{ref}}$ naturally fluctuate around unity even within the calibration window.

$K_{c,T}$ is calibrated on the January–March wet season. A reference day satisfies $TWD_{\text{norm}} < 0.1$ on at least three CORE trees (§5.5.1), indicating that internal stem reserves are full and the canopy operates without storage withdrawal (Peters et al. 2025), with cumulative rainfall ≤ 0.5 mm on the day, ≤ 5 mm the day before and ≤ 10 mm two days before. Because trunk sap flow lags atmospheric demand within the day (§3.2.2), $K_{c,T}$ is taken as the daytime-integrated ratio $\sum T_{\text{day}} / \sum ET_{0,\text{day}}$ (32) averaged across reference days rather than as an instantaneous ratio. RP yields too few reference days for a plot-specific fit; stand-level results on RP are therefore reported as absolute T and as T/ET_p only.

$K_{c,T}$ depends on the inventory pool (all trees; $\text{DBH} \geq 5$ cm; instrumented only) and the F_d -to-inventory rule (nearest-DBH; F_d -DBH regression with or without extrapolation). The nine combinations span 0.216–0.349 (Fig. 19). The rule has little effect within a pool; the pool matters: $K_{c,T}$ falls from 0.32–0.35 on the full inventory to 0.22 on the instrumented sample because the eight instrumented trees omit the contribution of the many smaller stems that carry a large share of total sapwood area. The combination *all inventory* $\times$ *nearest-DBH* is retained as the production value, $K_{c,T} = 0.349$, which preserves the stand size structure without extrapolating F_d outside its calibrated DBH range.

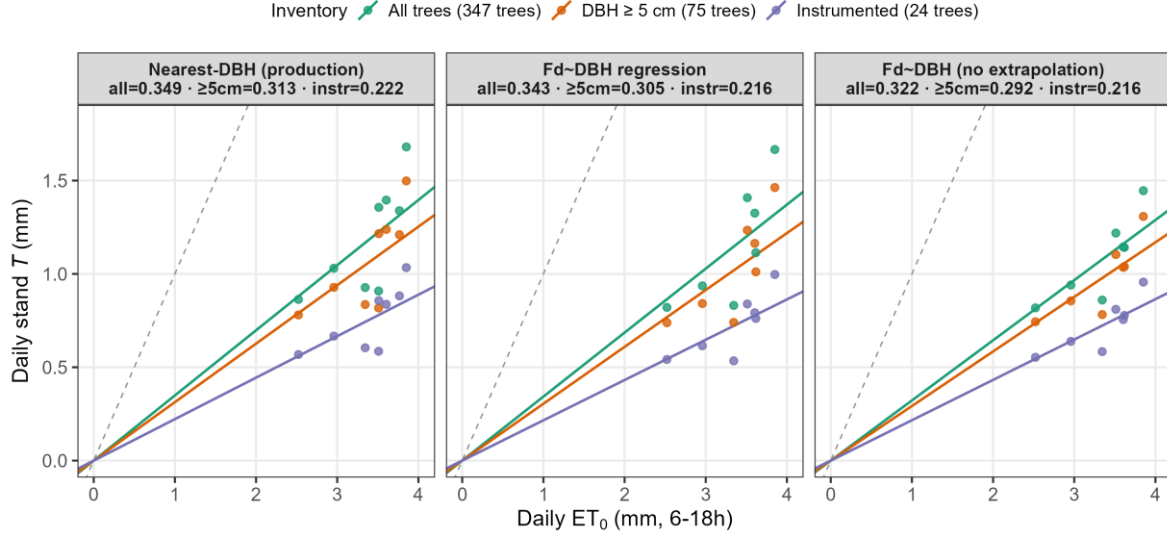


Figure 19: $K_{c,T}$ sensitivity to the inventory pool (colours) and to the Fd-to-inventory rule (panels). Points: daily stand T against ET_0 on reference days. Lines: $K_{c,T} \cdot ET_0$. Dashed grey: 1:1. Retained production: $K_{c,T} = 0.349$ (all inventory $\times$ nearest-DBH).

5.7.6. Stomatal sensitivity

Under well-coupled canopy conditions and steady state, canopy stomatal conductance scales with the ratio of transpiration flux to atmospheric vapour pressure deficit (Köstner et al. 1992, Ewers & Oren 2000). A sap-flow-based proxy of canopy stomatal conductance is therefore computed as:

$$G_s = \frac{F_d}{VPD} \quad (33)$$

in dimensionally arbitrary units. The analysis is restricted to 1-min steps satisfying radiation $> 400 \text{ W m}^{-2}$ (non-limiting light), local time within 10:00–16:00, VPD $> 0.6 \text{ kPa}$ (below which stomata are not yet limiting and the proxy carries little physiological signal; Oren et al. 1999) and daily rainfall $\leq 1 \text{ mm}$.

Each retained step yields one (VPD, G_s) pair. The resulting cloud mixes responses to all uncontrolled sources of variation (soil water, season, individual structure). The upper boundary line of the cloud is therefore extracted following Ewers & Oren (2000): VPD is binned in 0.2 kPa classes, the 90th percentile of G_s within each bin is taken as the envelope point, and bins containing fewer than 15 points are discarded for statistical reliability. The envelope points are interpreted as the conductance that can be reached when only VPD limits the response, and they are fitted by ordinary linear regression to the Oren et al. (1999) model:

$$G_s = g_{\text{ref}} - m \times \ln(VPD) \quad (1)$$

Parameters are estimated per tree at three temporal supports: annual, per season (wet, drying, dry, rewetting) and per plot (A_s -weighted).

5.7.7. Canopy conductance and atmospheric coupling

A stand canopy conductance G_c ($\text{mol m}^{-2} \text{s}^{-1}$) is computed from the stand transpiration T_{stand} by inverting the Penman-Monteith equation under the well-coupled canopy assumption $g_a \gg G_c$ (Granier et al. 1996):

$$G_c = \frac{\gamma \times \lambda E}{\rho \times c_p \times D} \quad (34)$$

where $\lambda E = \lambda \cdot T_{\text{stand}}$ (35) is the latent heat flux, λ the latent heat of vaporisation, $D = \text{VPD}$. G_c is then converted from m s^{-1} to $\text{mol m}^{-2} \text{s}^{-1}$ via the molar concentration of air at the measured temperature and pressure.

The well-coupled assumption is tested with the Jarvis & McNaughton (1986) decoupling coefficient $\Omega \in [0,1]$:

$$\Omega = \frac{\Delta/\gamma + 1}{\Delta/\gamma + 1 + g_a/G_c} \quad (36)$$

where Δ is the slope of the saturation vapour-pressure curve (§5.3.3) and g_a (m s^{-1}) is the aerodynamic conductance from the logarithmic wind profile, with displacement height $d = 0.67 \cdot h$ (37) and roughness length $z_0 = 0.123 \cdot h$ (38), h being the canopy height from the H-DBH allometry (§5.4.4). $\Omega \rightarrow 0$ marks a fully coupled canopy where stomata govern λE and G_c can be read directly as stomatal conductance, while $\Omega \rightarrow 1$ marks a fully decoupled canopy where λE tracks the equilibrium evaporation set by radiation. G_c and Ω are computed per 1-min step from the gap-filled meteorological series and summarised per tree and per plot by their diurnal median over rain-free daytime windows.

5.8. Cross-signal analyses

The dendrometer and sap flow records capture complementary aspects of the tree water economy. Pairing them allows the tree to be analysed as a single integrated system, where the dynamics of internal reserves can be related to those of atmospheric exchange. A direct test of the instantaneous coupling between TWD and F_d was carried out during the analysis pipeline but put aside. The result duplicates the per-tree reactivity already captured by the MDS-on-VPD slope of §6.4.3, since F_d tracks VPD closely on the diurnal scale.

5.8.1. Using TWD as a proxy for stem water content

The Granier conversion assumes ΔV_{max} constant within each night. Vergéyest et al. (2014) showed that ΔV_{max} in fact rises during the day as the trunk loses free water and its thermal conductivity drops. Vandegehuchte & Steppe (2012) report that TDP is the most water-content-sensitive thermal method. TWD_{norm} is used as a co-located proxy for the trunk water state; the dendrometer and the sap flow probe sit on the same trunk segment, so no lag is applied between them. The correction reuses the dry baseline from the main pipeline (§ 5.7.2), applied to one tree (12) and one dry period in September.

The dry baseline $\text{Max1}(n)$ carries two overlapping signals: a slow multi-day drift of the dry baseline, and a per-night depression caused by residual nocturnal flow that pulls ΔV below the true zero-flux reference. § 6.5.4 attributes this nocturnal flow mostly to trunk refilling, with tree 17 the single case where a true transpiration component is also detected. Both grow on drier nights, so the depression of $\text{Max1}(n)$ is expected to scale with $\text{TWD}_{\text{predawn}}(n)$ if nighttime flux is happening. The drift is captured by a wide-window maximum ($\text{env}_{\text{wide}}(n)$) which tracks the local upper bound of Max1 , anchored on the cleanest nights where residual flow is weakest. The per-night depression between the envelope and each daily maximum is then isolated by subtraction:

$$\Delta dV(n) = \text{env}_{\text{wide}}(n) - \text{Max1}(n) \quad (39)$$

with the drift already absorbed by env_{wide} . The slope of this residual signal is fitted as:

$$\Delta dV(n) = \beta \cdot \text{TWD}_{\text{predawn}}(n) + \alpha + \varepsilon \quad (40)$$

over the ideal nights of the period, with $\text{TWD}_{\text{predawn}}$ the mean of TWD_{norm} between 00:00 and 06:00. β is retained only when $R^2 \geq 0.30$ and $\beta > 0$, in line with Vergeynst's predicted direction (drier trunk, higher ΔV_{max}). Otherwise $\beta = 0$ and the production baseline is left unchanged. TWD_{ref} is set to the 10th percentile of TWD_{norm} over the period, representing the most-rehydrated state at which the production baseline is assumed to capture the true ΔV_{max} already.

The correction is then applied at the 1-min step as:

$$\Delta V_{\text{max,corr}}(t) = \Delta V_{\text{max,prod}}(t) + \min(\beta \times (\text{TWD}_{\text{norm}}(t) - \text{TWD}_{\text{ref}}), 0.1 \times \Delta V_{\text{max,prod}}(t)) \quad (41)$$

floored at 0. Two safeguards bound the correction. An upper limit caps it at 15 % of the production baseline, preventing over-correction at extreme TWD values where the linear approximation no longer holds. A zero floor blocks negative corrections, so that the baseline can only be raised. Gaps of $\leq 2\text{h}$ in TWD_{norm} are linearly interpolated; longer gaps leave the corrected baseline as NA and propagate to F_d and J_s . Both versions of F_d and J_s are recomputed, and daily medians of Q_{day} , $J_{s,\text{max}}$ and $F_{d,\text{max}}$ are compared.

The correction is applied on one tree and one period as an illustration and is not propagated to the 22-tree production pipeline.

5.8.2. Stem storage contribution to transpiration (f_{storage})

The stem-reservoir contribution to daily transpiration is quantified following Goldstein et al. (1998) and Phillips et al. (2003), from the morning lag between atmospheric demand and basal sap flow. The radiation-driven evaporative demand at the canopy is captured by the

equilibrium evapotranspiration $E_{eq}(t)$. It corresponds to the radiation-only term of the Penman-Monteith equation used for ET_0 (§5.3.3), without the aerodynamic VPD- and wind-driven term. At sunrise, $E_{eq}(t)$ rises rapidly while basal sap flow $J_s(t)$ initially lags behind, because the canopy first draws water from the internal stem reservoir before pulling water from the roots. The volume drawn from the reservoir over the morning is the integral of the gap between demand and supply between the morning onset of demand t_0 and the time t^* at which J_s catches up with E_{eq} :

$$V_{storage} = \int_{t_0}^{t^*} [E_{eq}(t) - J_s(t)] dt \quad (42)$$

Expressed as a fraction of the daily sap flow integral Q_{day} (§5.7.3.):

$$f_{storage}^{lag} = \frac{V_{storage}}{Q_{day}} \quad (43)$$

The analysis is restricted to rain-free days within the analysis windows and summarised per tree by the median across retained days.

The same quantity is also computed from the daily dendrometer contraction. The maximum daily shrinkage MDS is converted into a stem-water volume by combining the geometry of the contraction layer with the elasticity coefficient ε of bark and phloem:

$$V_{MDS} = \pi \cdot DBH \cdot h \cdot MDS \cdot \varepsilon \quad (44)$$

where h is the stem height over which the radial change applies and $\varepsilon \approx 0.20$ (Zweifel et al. 2014) is the fraction of the geometric volume change that corresponds to water released from the elastic tissue. The corresponding fraction:

$$f_{storage}^{MDS} = \frac{V_{MDS}}{Q_{day}} \quad (45)$$

is reported as a complementary lower bound that captures only the elastic compartment (bark and phloem). The gap $f_{storage}^{lag} - f_{storage}^{MDS}$ (46) thus reflects the contribution of the xylem-stored water, which the dendrometer does not detect.

5.8.3. Nocturnal flux partition between transpiration and refilling

Nocturnal sap flow on tropical hardwoods reflects either residual transpiration or refilling of the stem reservoir (Lu et al. 2004). The two are separated by pairing F_d with TWD, using two complementary tests.

Overnight recovery fraction

The dendrometer water balance $dW/dt = U - E$ (47) links root uptake U and canopy transpiration E . Since $dW/dt = -dTWD/dt$ (48), a stem that rehydrates overnight ($dTWD/dt < 0$) has $U > E$. A stem that keeps shrinking has $E > U$. For each tree and each night, the fraction of the daytime deficit resorbed by dawn is

$$recovery(d) = \frac{TWD_{dusk} - TWD_{predawn}}{TWD_{dusk}} \quad (49)$$

with TWD_{dusk} at 17:00–18:00 and $TWD_{predawn}$ at 04:00–06:00. The recovery equals 1 when the reservoir is fully refilled and 0 when there is no recharge. The dependence of the recovery on nocturnal VPD is described by a GAM (§5.6.4) with a thin-plate spline basis (Wood 2017):

$$recovery(d) = s(VPD_{night}) + \varepsilon \quad (50)$$

A recovery that decreases as nocturnal VPD increases identifies trees where residual transpiration competes with refilling.

Stratified pre-dawn flux test

A second test reads the dependence of pre-dawn sap flux on pre-dawn VPD, stratified by the stem reservoir state at the same moment, characterised by TWD_{pre} (the pre-dawn TWD_{norm} value; Fig. 20). The interpretation differs by stratum:

- Refilled stratum ($TWD_{pre} \leq 0.10$): any residual VPD-dependence signals genuine nocturnal transpiration.
- Non-refilled stratum ($TWD_{pre} > 0.10$): a VPD-dependence may instead reflect refilling driven by the root-to-stem gradient strengthening under high VPD.

The pre-dawn flux is normalised by the daytime maximum, and only nights with at least 6 valid pre-dawn measurements (02–05 h) are retained.

The threshold $TWD_{pre} = 0.10$ is set by sweeping a discrete grid $\{0.01, 0.025, 0.05, 0.10, 0.20, 0.30\}$ and reading the R^2 of $F_d^{predawn} \sim VPD$ per stratum (Appendix Fig. 53): the non-refilled stratum plateaus at $R^2 \sim 0.11$ from 0.05 upward, while the refilled stratum stays at $R^2 \sim 0$ regardless. A continuous sweep of the threshold confirms a stable plateau $\Delta(R^2) \approx 0.11 - 0.12$ between 0.05 and 0.22 (Appendix Fig. 52, argmax at 0.155). The 0.10 value sits on this plateau and yields balanced sample sizes (132 refilled vs. 204 non-refilled nights).

A caveat applies to the refilled stratum, which is mostly confined to $VPD < 1\text{ kPa}$ because full overnight recharge under high VPD is physically rare. The hockey-stick fit on this stratum is therefore dominated by the flat low-VPD baseline: the breakpoint position (0.38 kPa) and the apparent descent above it are model artefacts. The absence of VPD-dependence in this stratum rests instead on the overall $R^2 = 0.01$ of the linear fit and on the threshold sensitivity analysis (Appendix Fig. 53). The absence of refilled nights at high VPD is itself part of the result and confirms that refilling requires low atmospheric demand.

Both analyses cover rain-free nights within the analysis windows for the 12 sap flow CORE trees (§5.5.1) with simultaneous TWD signal.

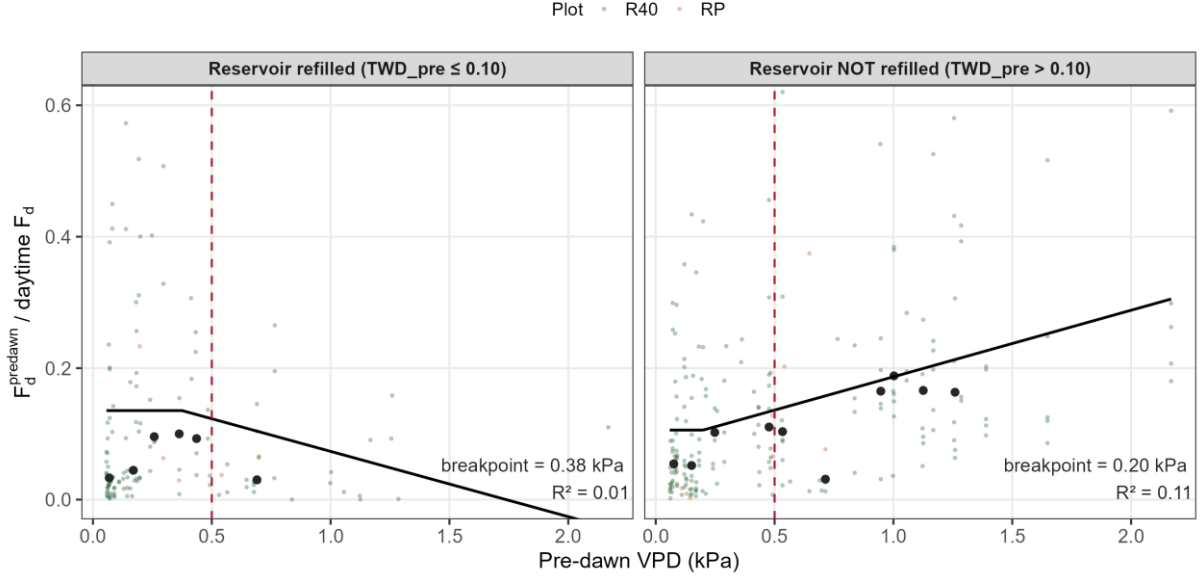


Figure 20: Pre-dawn flux F_d^{predawn} normalised by daytime maximum, plotted against pre-dawn VPD and stratified by stem reservoir state at 04–06 h. Left: reservoir refilled ($\text{TWD}_{\text{pre}} \leq 0.10$). Right: reservoir not refilled ($\text{TWD}_{\text{pre}} > 0.10$). Black line = hockey-stick breakpoint fit per stratum with breakpoint and R^2 annotated. Red dashed line at $\text{VPD} = 0.5 \text{ kPa}$ = baseline cut-off used in §5.7.2. Robustness of the threshold choice is shown in Fig. 52 (Appendix).

5.8.4. Water-use efficiency of stem biomass production

The combination of the per-tree biomass increment ΔAGB derived from the dendrometer-based application of the Chave allometry (§5.4.5) and the cumulative transpiration measured by the sap flow allows an estimate of the water cost of stem biomass production. The water-use efficiency of stem biomass production is computed per tree as

$$\text{WUE}_w = \frac{1000 \cdot \Delta\text{AGB}}{Q_{\text{cum}}} [\text{g L}^{-1}], \quad (51)$$

where Q_{cum} is the annual sum of Q_{day} over 2020 and the factor 1000 ensures consistency of units. The metric depends strongly on wood density: a tree with a high radial increment but light wood may yield a similar ΔAGB to a slower-growing tree with dense wood, so apparent WUE_w differences between forests must be interpreted considering the wood density distribution (§5.4.5).

5.9. Uncertainty and sensitivity analysis

Parameter sensitivity is quantified by the one-at-a-time (OAT) approach (Saltelli et al. 2008). Each parameter X_i is perturbed within its literature uncertainty range while the others are held at central values, and the local sensitivity is approximated by finite difference:

$$S_i = \frac{\Delta Y / Y}{\Delta X_i / X_i} \quad (52)$$

which reads as follows: $|S_i| = 1$: 10 % on X_i gives 10 % on Y ; $|S_i| < 1$: attenuation along the chain. OAT does not capture parameter interactions, a simplification accepted given the multiplicative power-law structure of the Granier chain (Hernandez-Santana et al. 2008).

The sap flow chain is perturbed on eight parameters: the ΔV_{max} baseline (six alternative strategies, Appendix G2 Fig. 54), the Granier coefficients (Bush et al. 2010, Steppe et al. 2010), DBH 2020 (± 15 %), the A_s -DBH allometry (95 % CI on the pooled $n = 25$ dataset), the H-DBH Michaelis-Menten allometry (± 10 % on predicted H), the inventory pool (full, DBH ≥ 5 , DBH ≥ 10 cm), the A_s assignment rule (nearest-DBH vs linear regression), and the KcT calibration (leave-one-out and bootstrap on reference days). Because the baseline is itself a nightly maximum, a baseline shift propagates near-binarily at night ($\Delta V_{clean} \approx \Delta V_{max} \Rightarrow K \approx 0$) but only weakly during daytime; baseline sensitivities are therefore reported separately for Q_{day} (6–18 h), $J_{s,max}$ (daily peak) and Q_{night} (18–6 h). The output is the annual R40 stand transpiration T_{stand} (mm yr⁻¹), with Kc_T for calibration and pool rows, and stand-level ΔAGB (kg, propagated through Chave et al. 2014) for the H-DBH row.

The uncertainty budget on $WUE_w = \Delta AGB / Q_{year}$ (53) combines the sap flow chain with the wood-density choice specific to the ΔAGB side. Three options for ρ are tested: per-tree direct (production), species-median and plot-median substitution. The output is the per-tree WUE_w (g L⁻¹), summarised by plot median and compared to the production by Spearman rank correlation. The seven Q -affecting sap flow rows are combined into a single sap flow chain effect by quadrature on T_{stand} (independent multiplicative sources) and propagated to WUE_w via the $1/Q$ scaling. The budget reports four sources: the sap flow chain effect, the H-DBH allometry (± 10 %), and the two plot-specific ρ -choice ranges.

The dendrometer pipeline is deterministic by construction ($GRO = \text{cumulative maximum of the smoothed signal, } TWD = GRO - x$), so it is less prone to absolute-value uncertainty than the sap flow chain. A four-parameter test confirms that the per-tree ranking is preserved: the normaliser is varied between MDS_{max} (Peters et al. 2025b, production) and TWD_{max} (Zweifel et al. 2021); DBH 2020 by ± 15 % (affecting only the size-normalised strain MDS_{max}/radius , the stress and growth metrics being DBH-free); the TWD_{norm} onset threshold at 0.8 / 1.0 (production) / 1.2; the Lloret (2011) R_t threshold at 0.3 / 0.5 (production) / 0.7. Spearman $\rho \approx 1$ across alternatives, so the results are documented in the sensitivity report (Appendix Figure 55) rather than in the main chapter.

6. RESULTS AND DISCUSSIONS

6.1. Climatic and hydrological frame

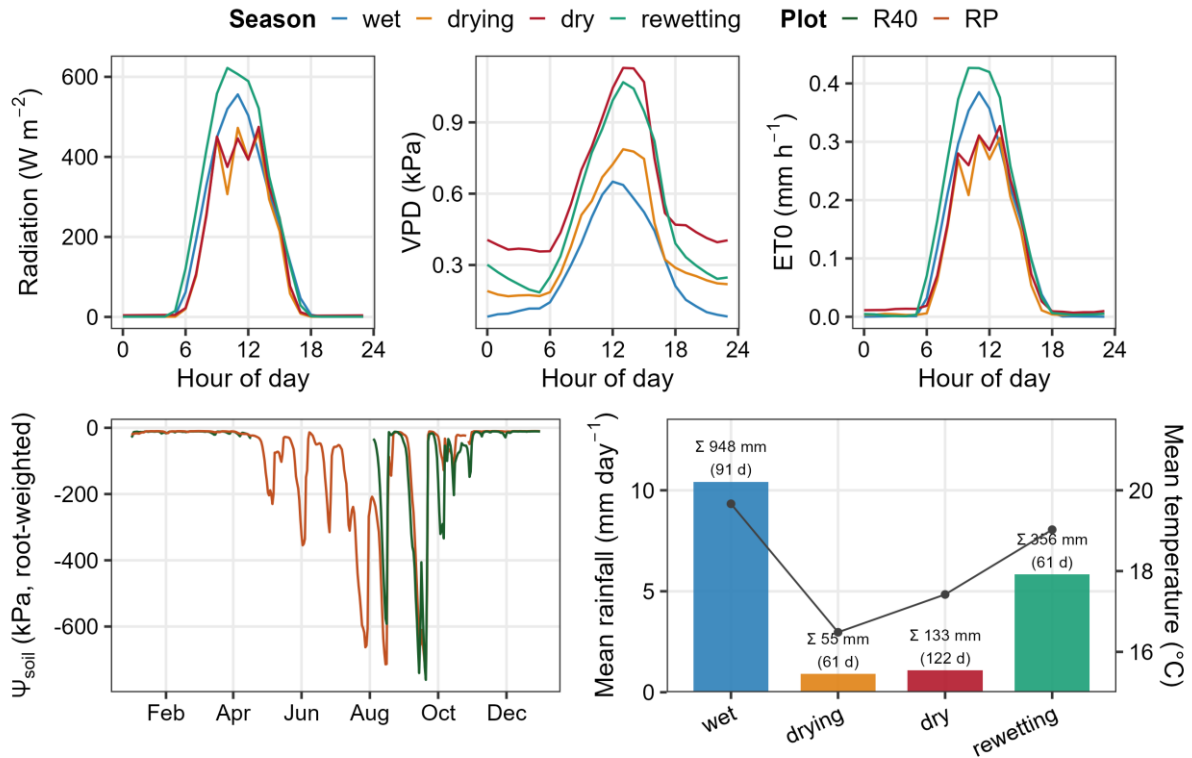


Figure 21: Climatic setting of 2020 by season (WET/DRG/DRY/REW). Top: mean diurnal cycles by season: global radiation ($W m^{-2}$), VPD (kPa), hourly ET_0 (Penman–Monteith FAO-56). Bottom left: root-weighted Ψ_{soil} (R40 green, RP orange). Bottom right: mean daily precipitation (bars) + air temperature (line); annotations = seasonal cumulative rainfall (mm) and duration (number of days).

Although all trees share the same climate and soil, they respond to these conditions in distinct ways. Characterising this shared environmental context from the meteorological data first is therefore essential before interpreting individual responses.

Energy and temperature follow a classical seasonal cycle (Fig. 21): solar radiation and reference evapotranspiration (ET_0) reach their peaks during REWETTING and WET, then decline to lower, comparable levels through DRYING and DRY. Maximum air temperatures occur in WET, with the minimum reached at the DRYING transition. Atmospheric demand, by contrast, does not track energy. Diurnal VPD shows a much stronger seasonal contrast than radiation or temperature. This decoupling reveals that demand is governed not by energy input but by the water available to humidify the air (recent rainfall, soil moisture). Four distinct regimes follow from this dynamic.

WET (January–March) receives more than ten times the rainfall of DRY leading to a saturated soil and a humid atmosphere. The diurnal VPD is therefore at its lowest and nocturnal demand drops to near zero, despite the season's high temperatures. DRYING (April–May)

inherits a still-recharged soil that sustains evaporation, producing only moderate atmospheric demand. DRY (June–September) brings rare rainfall and marked soil stress (median $\Psi_{\text{soil}} \approx -159$ kPa in RP, -79 kPa in R40). Although this is the coolest and least radiative season, it carries the highest diurnal VPD and a sustained nocturnal demand. REWETTING (October–November) finally combines the first returning rains over a recharging soil with still-elevated radiation and temperature, producing a high diurnal VPD alongside a limited nocturnal demand.

6.2. Transpiration: regulation, drivers and scaling

6.2.1. Magnitude and scaling

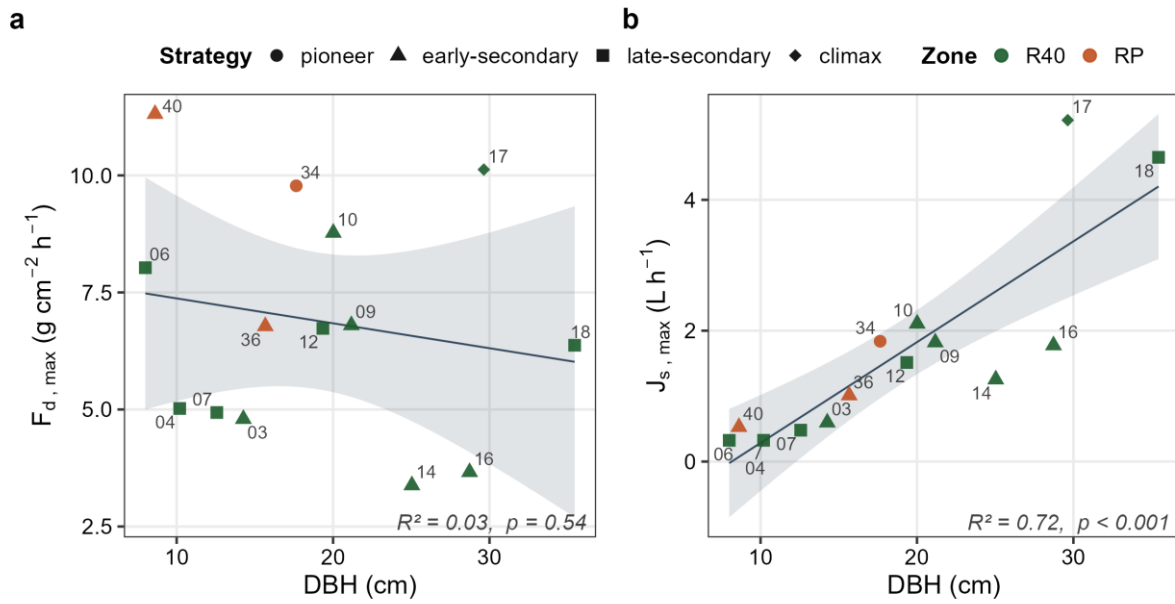


Figure 22: Instantaneous flux metrics versus DBH (14 trees, 11 R40 + 3 RP, pooled over the year). (a) $F_{d,max}$, the 95th percentile of daily sap flux density (g cm⁻² h⁻¹); (b) $J_{s,max}$, the 95th percentile of daily whole-tree sap flow (L h⁻¹). Regression line $\pm$ 95 % CI, R^2 and p inset. labels = tree ID.

The velocity of water transport through the xylem, $F_{d,max}$ (panel a) ranges from 3.5 to 11.6 g cm⁻² h⁻¹, placing the trees in the upper range of values reported for humid tropical forests (Meinzer 2001: 2–8 for 10–20 cm trees, 5–15 above 25 cm; Horna et al. 2011: 1.4–4.7 in perhumid stands). F_d shows no dependence on DBH ($R^2 = 0.03$, $p = 0.54$), the trend even slightly decreasing: two trees of similar diameter (16 and 17, both around 30 cm) differ by a factor of three.

Integrating this velocity over the conducting sapwood area, $J_{s,max}$ (panel b) ranges from 0.3 to 4.1 L h⁻¹ and increases strongly with DBH ($R^2=0.72$, $p<0.001$), because A_s itself follows an allometric function of DBH. The residual scatter reflects the underlying variability in F_d : a high J_s can be reached either through a high flux density (tree 17) or through a large sapwood area combined with a moderate F_d (tree 18). Together, these two metrics establish that xylem velocity is an individual trait whereas total water use is dictated by tree size through the sapwood.

6.2.2. Temporal Behaviour

Diurnal cycle

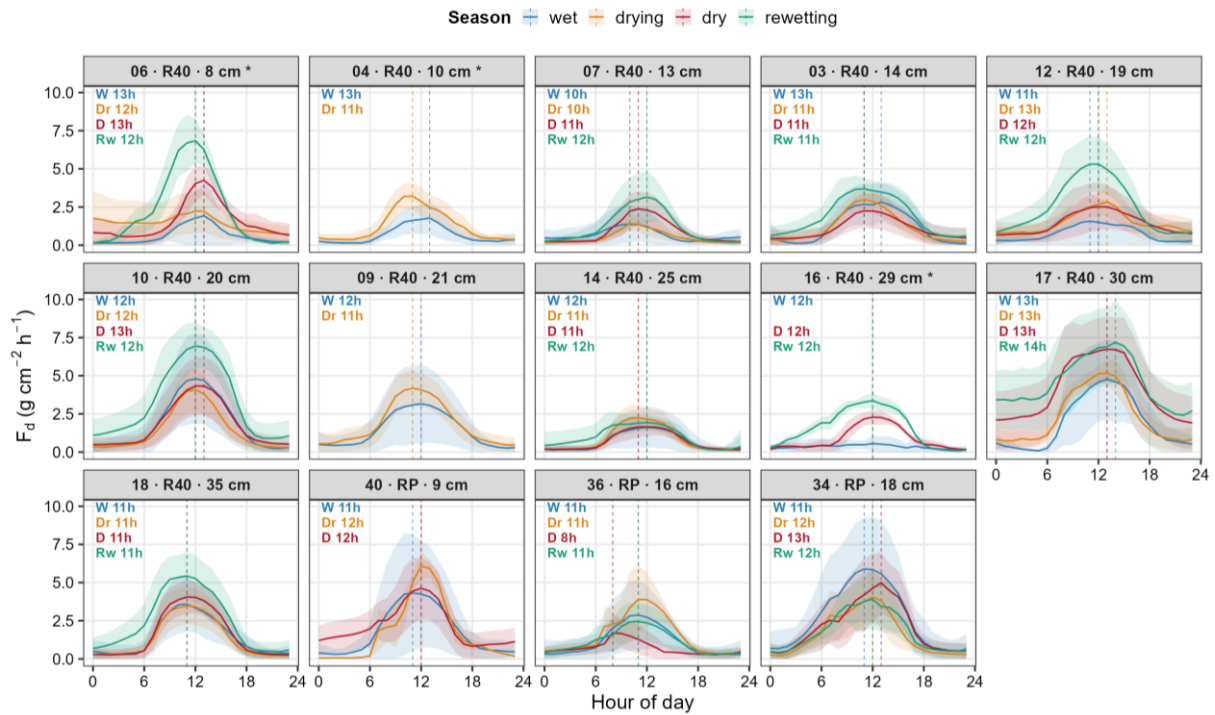


Figure 23: Mean diurnal cycle of sap flux density F_d per tree, by season (rain-free days, 5-min resolution; F_d in $\text{g cm}^{-2} \text{h}^{-1}$, free y-axes). Near-zero overnight, rise after sunrise (~ 06 h), midday peak, return to zero by 18 h. Headers: tree ID · forest plot · DBH.

All trees follow the same diurnal pattern, the one expected for tropical trees (O'Brien et al. 2004): F_d is near zero overnight, rises shortly after sunrise (~ 06 h), peaks around midday, and returns to zero by 18 h (Fig. 23). The systematic return to zero confirms the quality of the baseline correction. For most trees the peak hour stays stable across seasons. Tree 17 is the clear exception, with its DRY peak shifted to ~ 14 h. Solar radiation peaks around 11 h and VPD around 13 h (§6.1). Within this shared envelope, the timing of the daytime peak already separates two behaviours: early peaks (07, 18, 36, 40 at ~ 11 –12 h, close to the radiation maximum) and later peaks (12, 34 at ~ 12 –13 h, 17 up to ~ 14 h in DRY, closer to the VPD maximum). Whether this reflects light or demand control is tested in §6.2.3.

Some trees show flat, broad peaks (14, 12, 16, 03, 07), others sharp ones. A curve that plateaus at midday points to an early stomatal closure as VPD and radiation rise, while a peaked curve follows demand without strong limitation. This within-day form is largely conserved across seasons, tree 17 aside, what changes most between seasons being the peak amplitude, whose annual course is treated as the integrated daily water use in §6.2.2. The regulation hypothesis is tested directly through the VPD sensitivity (Oren) and canopy conductance analyses (§6.3.3, §6.3.5).

Integrating F_d over the night window gives a small but noticeable nocturnal share: ~ 6 –12 % of daytime flow in R40 and ~ 4 –8 % in RP, at the lower end of the 5–25 % reported for

tropical trees (Alvarado-Barrientos et al. 2015), including the Atlantic Forest (Rosado et al. 2012). This share rises in the dry and drying seasons, when the overnight signal stays slightly elevated, consistent with incomplete overnight rehydration after deeper daytime deficits. Tree 17 is the only individual whose nocturnal F_d clearly grows with night-time VPD, a pattern consistent with genuine night transpiration on drier nights.

Seasonal cycle

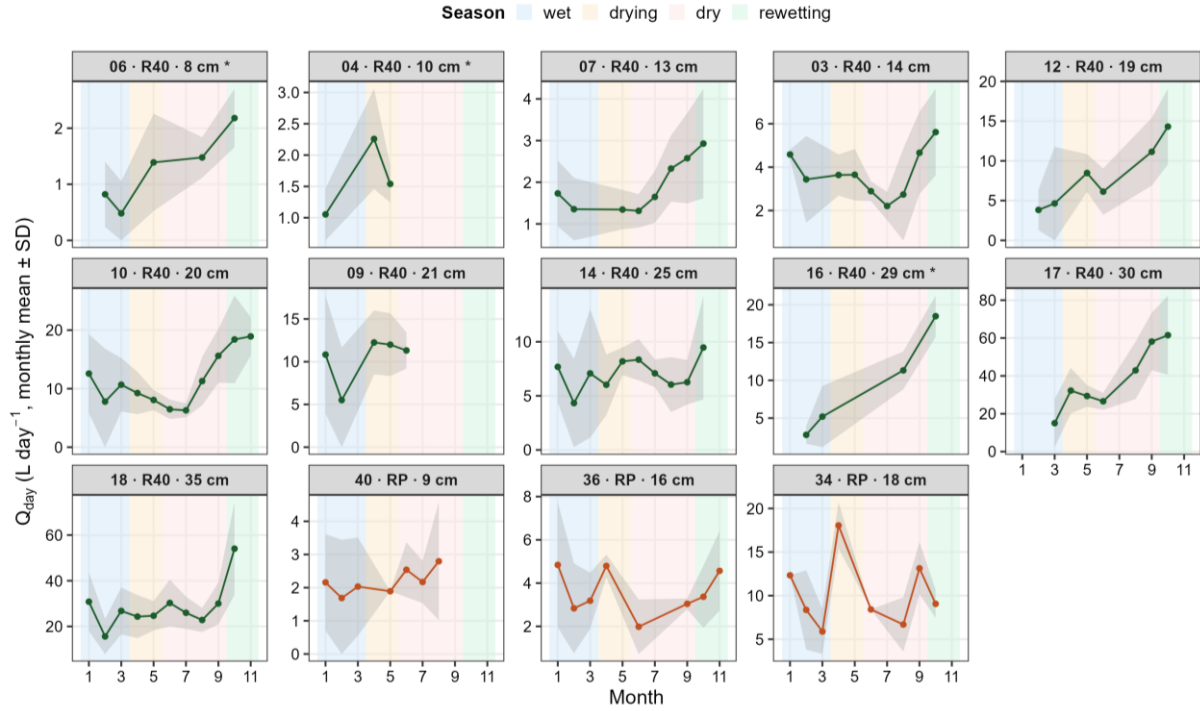


Figure 24: Seasonal course of daily water use Q_{day} per tree (monthly mean $\pm$ SD; background shading = dominant season). Asterisks mark trees with fewer than 30 observation days (04, 06, 16), and the RP series rests on a single day in DRYING; these panels are indicative only. Headers: tree ID · forest plot · DBH.

Each panel shows the monthly mean Q_{day} (L Day⁻¹) for one tree across 2020 (Fig.24). Some trees (04, 09, 40) lack data to analyse the full year. Tree 34 shows a spike in drying, probably an artefact from the QC pipeline. Three broad patterns emerge.

A U-shaped trajectory is the main pattern in R40, with relatively high values in WET, a dip through DRYING and the middle of DRY, and a strong rebound in REWETTING (03, 09, 10, 14, 18) with the first rains. This shape tracks the seasonal balance between soil supply and atmospheric demand: WET combines a wet soil with high radiation and temperature, the dry-season trough reflects the mid-year drop in radiation and temperature, and REWETTING brings back high demand on a recharging soil. A subset of trees breaks away from the U with a continuous rise across the year. Tree 17 R40 is the clearest case, climbing from ~ 20 Lday⁻¹ in WET to ~ 65 Lday⁻¹ in REWETTING, with its Q_{day} intensifying steadily through DRY in line with its elevated diurnal F_d (§6.2.1). Trees 07, 12 and 16 R40 follow a similar steady ramp, all peaking in REWETTING. The RP trees (40, 36, 34) stay at the low end of the y-axes throughout the year. Their individual F_d values are high, but their stand-level flow is lower. Within the RP

set, 34 stands out with a sharp DRYING peak ($\sim 17 \text{ L day}^{-1}$) followed by a drop, while 40 and 36 stay relatively flat all year.

6.2.3. Drivers

Hysteresis

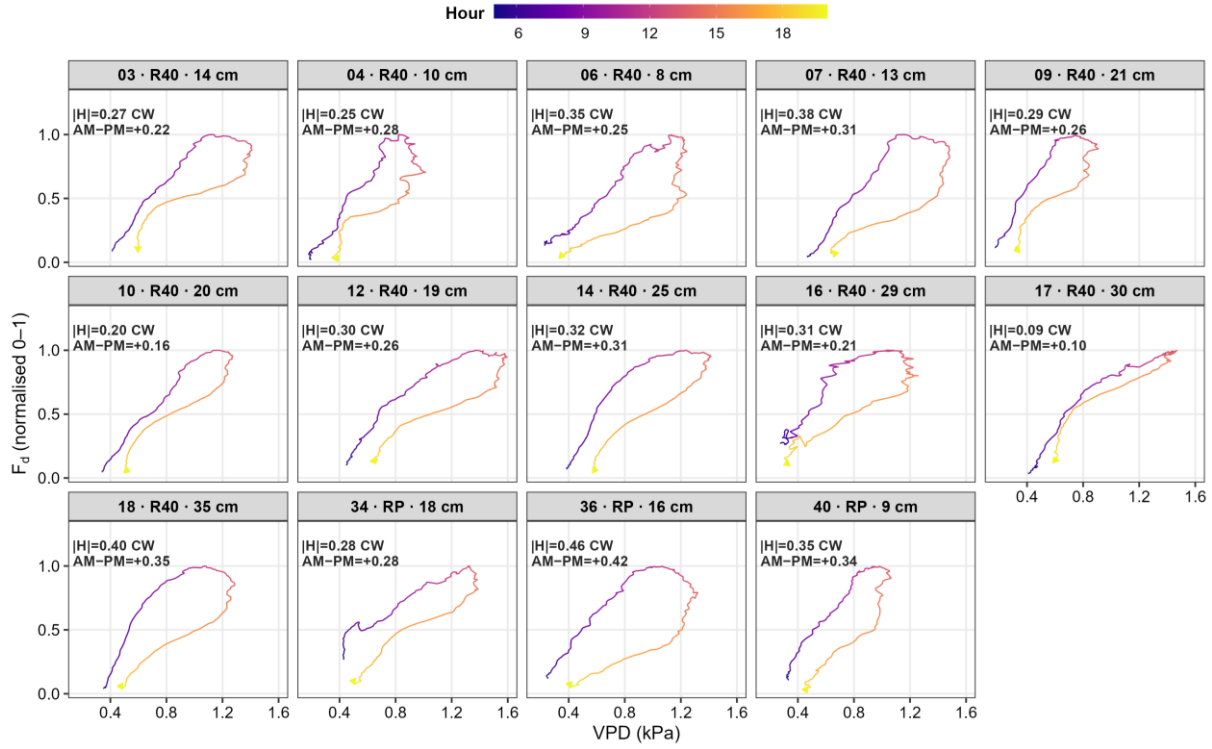


Figure 25: Per-tree composite diurnal F_d –VPD hysteresis ($n = 14$; annual composite over rain-free days, 1-min resolution). F_d normalised 0–1 per tree; colour encodes the hour of day. Each panel reports the normalised loop area $|H|$ (0 = closed loop, 1 = maximal), the loop direction (CW = clockwise), and the AM–PM offset (mean morning-minus-afternoon F_d across 10 VPD-quantile bins; positive = morning branch above afternoon).

Headers: tree ID · forest plot · DBH.

Having described how the flux varies in time, the question is what regulates it. The F_d –VPD hysteresis loop (Fig. 25) is a good starting point: across the average day, at a given VPD the flux differs between morning and afternoon, so the loop captures both the response to VPD, and an internal lag linked to stem capacitance.

All fourteen trees trace the loop clockwise: at equal VPD, F_d is higher in the morning than in the afternoon. This direction reflects the combined effect of stomata closing gradually as the day advances and of a stem water store that is drawn down during the day and refilled overnight. Two independent measures quantify the loop: its area $|H|$, normalised between 0 (a fully closed loop, no hysteresis) and 1 (maximal), which measures how far the morning and afternoon paths differ; and the offset AM–PM, the morning-minus-afternoon difference in F_d at comparable VPD. Both span a wide range, from a nearly closed loop in tree 17 ($|H| = 0.09$, $AM - PM \approx +0.10$), so closely coupled to the air that its F_d follows VPD almost without lag, to the widest loops in trees 36, 18 and 07 ($|H|$ up to 0.46, AM–PM up to +0.42). The median $|H|$ is about 0.30, and F_d leads the VPD peak by roughly 42 min.

Like F_d , this hysteresis does not depend on tree size: the largest tree (18) and one of the smallest (06, low-confidence) both show wide loops, while the 30-cm tree 17 has the narrowest loop of all. Capacitance is therefore present in every tree, since the flux is systematically higher in the morning than in the afternoon. How strong this effect seems to follow each tree's stomatal behaviour more than the size of its stem reservoir, because loop width does not increase with diameter.

Light vs demand limitation

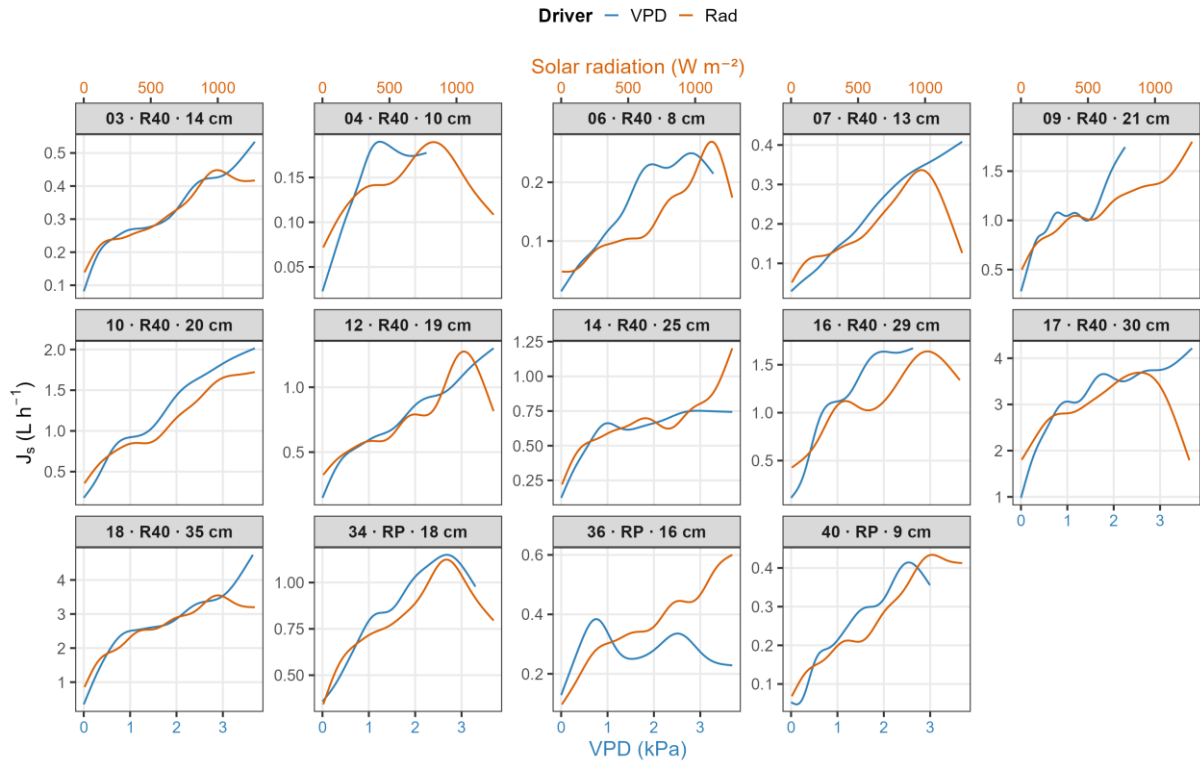


Figure 26: Marginal response of J_s to VPD (lower x-axis, blue) and to solar radiation (upper x-axis, orange), overlaid per tree ($n = 14$; 11 R40 + 3 RP). Curves are independent GAM smooths ($y \sim s(x)$) on rain-free daytime 1-min records. VPD and radiation covary strongly over the diurnal cycle (concurrency ~ 0.75), so the curves show response shape, not a driver ranking (settled separately by the multi-driver model, Appendix E). Headers: tree ID · forest plot · DBH.

Plotting J_s against both radiation and VPD on the same axis (Fig. 26) answers two questions the loop cannot: at what VPD regulation begins, and whether light or atmospheric demand finally limits the flux. Radiation saturates early. In most trees J_s rises steeply at low light, then levels off near 350 W m^{-2} (median 357 , IQR $324\text{--}418$), where it stops responding to light. This early light saturation matches reports for tropical canopy trees (O'Brien et al. 2004; Motzer et al. 2005). Beyond the shoulder, J_s often keeps rising. The continued rise is no longer a light effect: through the morning, radiation and VPD climb together, so once light saturation is reached any further increase in flux is sustained by the still-climbing VPD that accompanies it. Conversely, where the curve bends downward at the highest radiation values, this descent reflects the afternoon hours, when VPD has started to fall while radiation is still high and the falling VPD drags the flux down. This downward limb is the afternoon branch of the $F_d - \text{VPD}$ hysteresis loop (§6.3.1) read on the radiation axis. The radiation-only curve therefore

mixes a genuine early light saturation with the VPD signal beyond it, the two becoming separable only in a multi-driver framework (Appendix E).

The VPD response, by contrast, separates the trees into two groups. Demand followers (03, 10, 12, 17, 18; 07, weak fit) raise J_s steadily up to 3–3.5 kPa without levelling off, so the flux stays tied to demand over the whole range. Tree 17 is the clearest case, in line with its near-closed loop. Early regulators (04, 09, 14, 16, 34, 36) instead level off or decline from 0.8–1.5 kPa. In the RP trees 34 and 36, this bell-shaped fall is the stomatal closure that produces their wide hysteresis. The two remaining trees, 06 and 40, fall between the groups. Light therefore saturates everywhere near 350 W m^{-2} , a common ceiling. It is the VPD threshold that truly separates the trees: absent or late in the followers, early in the regulators.

6.2.4. Regulation strategy

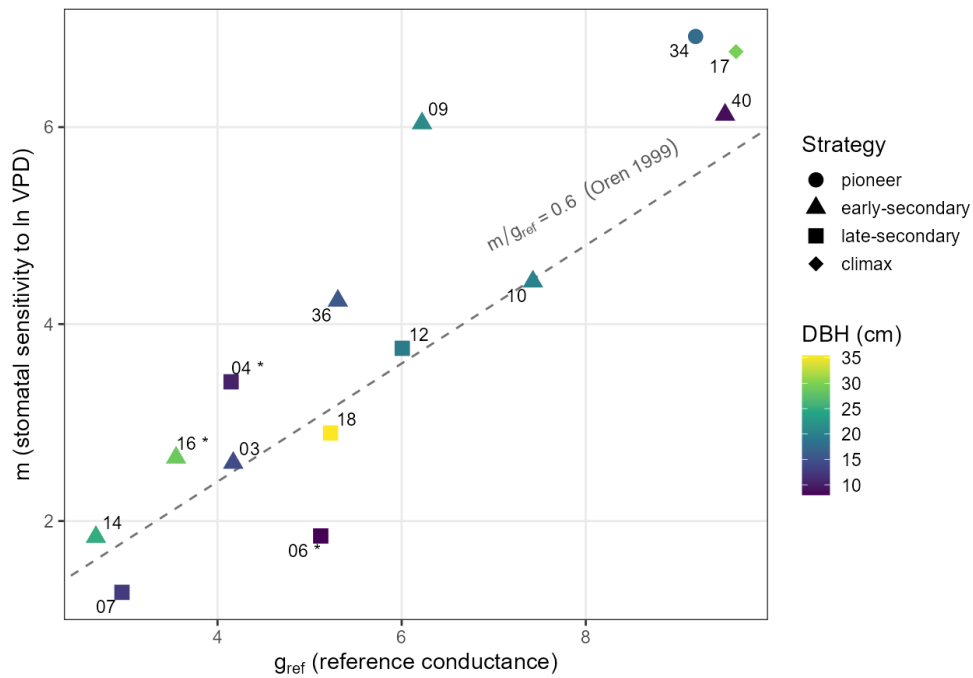


Figure 27: m – g_{ref} coordination (Oren 1999) across the 14 monitored trees. Each point is one tree, summarised by the two parameters of $G_s = g_{ref} - m \cdot \ln(VPD)$ fitted on its boundary line (90th percentile per 0.2-kPa VPD bin, restricted to peak-sun hours 10–16 h, $Rad > 400 \text{ W m}^{-2}$, rain-free days). Dashed line = Oren (1999) prediction $m/g_{ref} = 0.6$; observed median = 0.66. Colour = DBH (viridis); shape = forest plot (R40 circle, RP triangle); labels = tree ID.

Fitting the Oren (1999) boundary-line model per tree (all fits significant, R^2 0.82–0.96; Appendix E) reveals a coordination shared by every tree (Fig. 27): g_{ref} and m rise together almost proportionally. This coupling reflects the hydraulic constraint behind the Oren framework: a tree that opens wider at low VPD (high g_{ref}) draws water faster through its xylem and must therefore close more steeply as VPD climbs (high m) to keep its minimum leaf water potential from dropping into damaging values (Hubbard et al. 2001). The ratio m/g_{ref} therefore stays near 0.6 (median 0.66, IQR 0.56–0.82) even though g_{ref} varies by a factor of

3.6 across the population (2.7 in tree 14 to 9.6 in tree 17). Trees differ mostly in how widely they open, not in the shape of their regulation: the ratio sets how steeply stomata respond to a given VPD increment, and this response shape is conserved across the sample regardless of the absolute opening.

The smaller variation that remains in m/g_{ref} shows the light vs demand split of §6.2.3. The six early regulators average 0.80, above the Oren isohydric reference, which indicates a closure steeper than what the trade-off would require for a given level of opening. The eight demand followers average 0.59, right at the reference, consistent with a regulation that keeps the minimum leaf water potential constant under rising demand. Three low-confidence cases (09, and the small trees 06 and 07) sit outside the trend.

The three RP trees stand apart with high g_{ref} and m (about $1.8\times$ the R40 medians) and a slightly higher m/g_{ref} (0.75 versus 0.62). RP individuals therefore open more per unit of sapwood at low VPD and close more steeply per unit of opening, a combination consistent with an acquisitive pioneer habit: aggressive exploitation of the wet-air window backed by tighter closure once the air dries.

6.2.5. Upscaling and comparison RP R40

Stand transpiration

At the stand scale (Fig. 28), R40 transpires $0.28\text{--}1.36\text{ mm day}^{-1}$ (median ≈ 0.7 , peaking in mid-November and lowest in the heart of the dry season), about 257 mm yr^{-1} , while RP transpires only $0.14\text{--}0.51\text{ mm day}^{-1}$ (median ≈ 0.25), some 2.5 to 3 times less. This is not a flux-per-tree effect but an area effect: the sapwood area index is $0.00273\text{ m}^2\text{ m}^{-2}$ in R40 against 0.00096 in RP, a 2.84 ratio that almost exactly matches the transpiration ratio. The contrast therefore reflects from canopy structure rather than from individual behaviour, a point the conductance analysis (§6.5.2) makes explicit.

These values can be checked against a fully independent estimate on the same site and plots, the HYDRUS-1D soil water balance of Delvoie (2023). The two estimates agree on the climatic forcing (reference evapotranspiration of 921 mm yr^{-1} here against $\sim 875\text{--}940$ in the HYDRUS model) and on the direction of the contrast. For transpiration itself, the soil model gives $\sim 900\text{ mm yr}^{-1}$ against ~ 257 here, a threefold gap that frames the true value from both sides: the thermal-dissipation method underestimates the real flux (by about $1.6\text{--}2.3\times$, Chapter Sensitivity Analysis) and the present upscaling captures only the instrumented trees, whereas an inverse soil model assigns all non-drained, non-evaporated water to root uptake and so tends toward an upper bound. The actual stand transpiration most plausibly lies between the two.

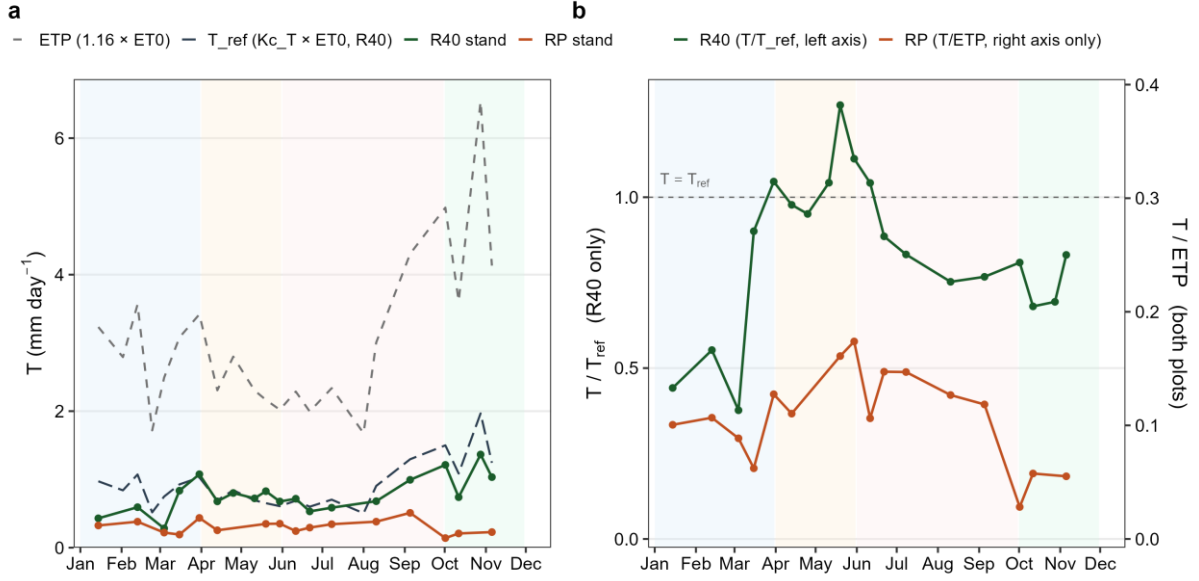


Figure 28: Stand transpiration of R40 (green) and RP (orange) across the 22 windows of 2020, x-axis ordered by season with seasonal background shading. (a) Absolute T (mm day^{-1}), with overlaid references: $ETP = K_c \cdot ET0$ ($K_c = 1.16$, short-dashed grey) and T_{ref} ($K_c, T = 0.349$ calibrated on R40, long-dashed grey on 11 reference trees $\rightarrow$ 347 stems) (b) T/T_{ref} (R40 only, left axis) and T/ETP (both plots, right axis), line at 1 marking the non-limiting potential.

Turning to the seasonal behaviour, T/T_{ref} follows a clear gradient: it stays around 0.5 in WET, climbs to about 1 in DRYING (occasionally up to ~ 1.3), and settles at 0.73–0.79 in DRY and 0.74–0.83 in REWETTING. Its deviation from 1 does not by itself signal water stress. $K_{c,T}$ is calibrated on a narrow March window with $VPD \geq 0.5$ kPa, so $T/ET0$ can deviate outside that window for purely atmospheric reasons. The WET versus DRY distinction is the key one: both fall below 1 but for opposite reasons: in WET the saturated air limits transpiration despite a wet soil, in DRY the depleted soil limits it despite a high VPD. The same numerical deviation carries opposite physiological meanings, so T/T_{ref} must be read together with the seasonal Rad/VPD context rather than as a stand-alone stress index.

For RP, where no plot-specific $K_{c,T}$ is available, only T/ETP is interpretable: R40 represents 11–38 % of ETP (median 26 %) and RP 3–17 % (median 10 %). The lower RP share reflects again its smaller sapwood area rather than stress.

Canopy conductance and coupling

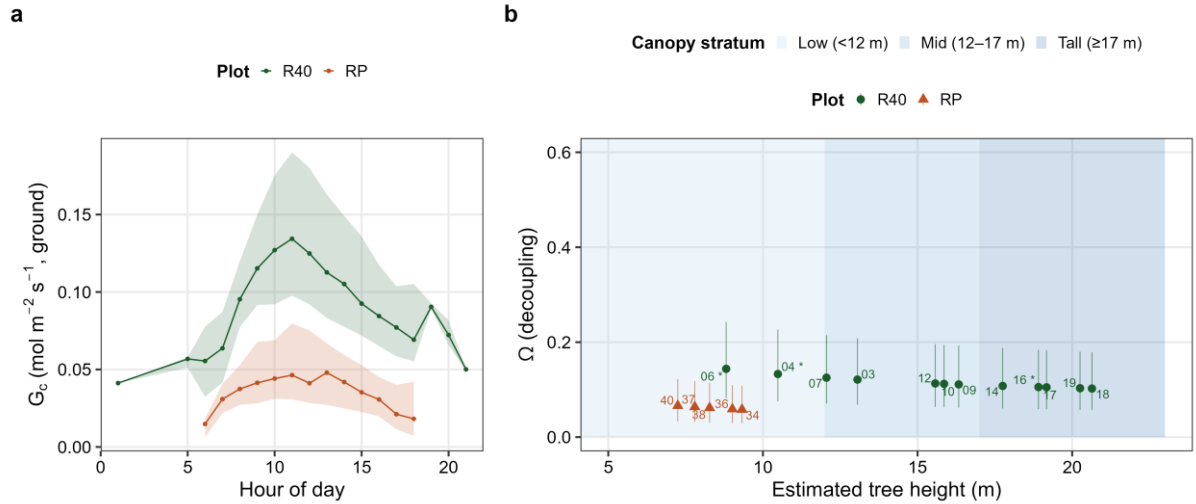


Figure 29: R40 versus RP comparison ($n = 14$; 11 R40 + 3 RP). (a) Canopy conductance G_c (Köstner 1992: G_c restricted to $R_{ad} > 50 \text{ W m}^{-2}$, $VPD > 0.6 \text{ kPa}$, rain-free days); hourly median $\pm$ IQR per plot. (b) Decoupling coefficient Ω per tree (Jarvis–McNaughton 1986: Ω); point = median, bar = IQR, shaded background = canopy stratum. labels = tree ID.

Having quantified the stand transpiration contrast, the regulation behind it is examined at the plot scale (Fig. 29) through the canopy conductance G_c (Penman–Monteith inversion, Köstner 1992) and the decoupling coefficient Ω (Jarvis–McNaughton 1986). Ω uses an aerodynamic conductance derived from the H–DBH allometry of each plot, whose asymptotic canopy heights differ greatly (33.9 m in mature R40 against 12.8 m in still-young RP), so the RP canopy is lower, smoother and less coupled to the air.

The canopy conductance (Fig.29, panel a) follows the same daily course in both plots, rising in the morning, peaking at 10–11 h and declining in the afternoon as stomata close, but its magnitude differs sharply: peak G_c is about $135 \text{ mmol m}^{-2} \text{ s}^{-1}$ in R40 against 49 in RP. This 2.8 gap is not a separate result, since G_c is derived from the same transpiration and scaled up through sapwood area. Sapwood area index, stand transpiration and canopy conductance are therefore one structural signal read at successive stages, not three independent measures. Both peaks are in the lower range of tropical values and below the montane canopy mean of about $165 \text{ mmol m}^{-2} \text{ s}^{-1}$ reported for the southern Ecuadorian Andes (Motzer et al. 2005), consistent with the modest size of the instrumented trees and, for RP, a young canopy close to understory values. Applied to G_c , the Oren framework gives $m/g_{ref} \approx 0.65$ in R40 and 0.75 in RP, matching at the stand scale the per-tree ratios of §6.2.4: the g_{ref} – m coordination carries through to the stand scale, both plots sharing one regulation rule at very different levels of opening.

The decoupling coefficient (Fig.29, panel b) marks a strongly coupled canopy typical of montane forests. Ω stays between 0.05 and 0.20 everywhere (median ≈ 0.11), with no difference between plots and no trend with tree height. Lowland tropical forests are strongly decoupled (Ω 0.7–0.9 across four moist-forest species, Meinzer et al. 1997), whereas montane forests are far better coupled (Ω 0.25–0.43 in the Ecuadorian Andes, Motzer et al. 2005). The site median of

0.11 lies at or just below that montane range, a gap that disappears once the ± 25 to $+90$ % methodological uncertainty on the absolute value is considered.

These results reconcile the two scales. §6.2.4. found RP individuals more open per unit of sapwood ($g_{ref} \sim 1.8 \times R40$), yet the RP canopy conductance is 2.8 times lower. The decomposition $F_d \times SAI$ resolves the apparent paradox: RP combines open individuals with little sapwood per m^2 , R40 moderate individuals with abundant sapwood, so individual opening cannot compensate for the smaller sapwood area. The R40/RP contrast is therefore structural rather than physiological, the same regulation rule holding on two contrasting stand architectures: RP as acquisitive trees forming a discontinuous canopy, R40 as moderate trees forming a dense one.

6.3. Radial growth: timing, magnitude and drivers

6.3.1. Growth phenology

The cumulative trajectories split into two regimes that the figure separates into two panels at 0.75 mm yr^{-1} (Fig. 30): a small-growers panel grouping the 14 trees below this threshold (mostly R40), and a large-growers panel grouping the 6 RP pioneers plus the single R40 exception tree 18. Solid lines show the raw dendrometer trajectory and dashed segments mark a post-shift correction applied where a discontinuity in the raw signal required the trajectory to be reconnected. The rainfall and root-weighted Ψ_{soil} time series below provide the climatic context against which both regimes can be read.

In R40, growth is concentrated in the first months of the year: a fast rise from January to April that tracks the rainfall, a clear plateau from June to September aligned with the rainfall gap, then a moderate rebound at rewetting once the rains return (a median 68 % of ΔGRO falls in the wet season and 8 % in the dry). The stair-step shape of the small-growers curves reflects growth events tightly clustered between rainfall episodes, with each rise typically following a rain peak by one to two days. The high-performing RP pioneers (41, 33, 37, 35†) instead accumulate steadily and almost linearly across all four seasons, their trajectories still climbing even as RP Ψ_{soil} collapses for long periods in the bottom panel (dry-season median $\approx -159 \text{ kPa}$, minimum -728).

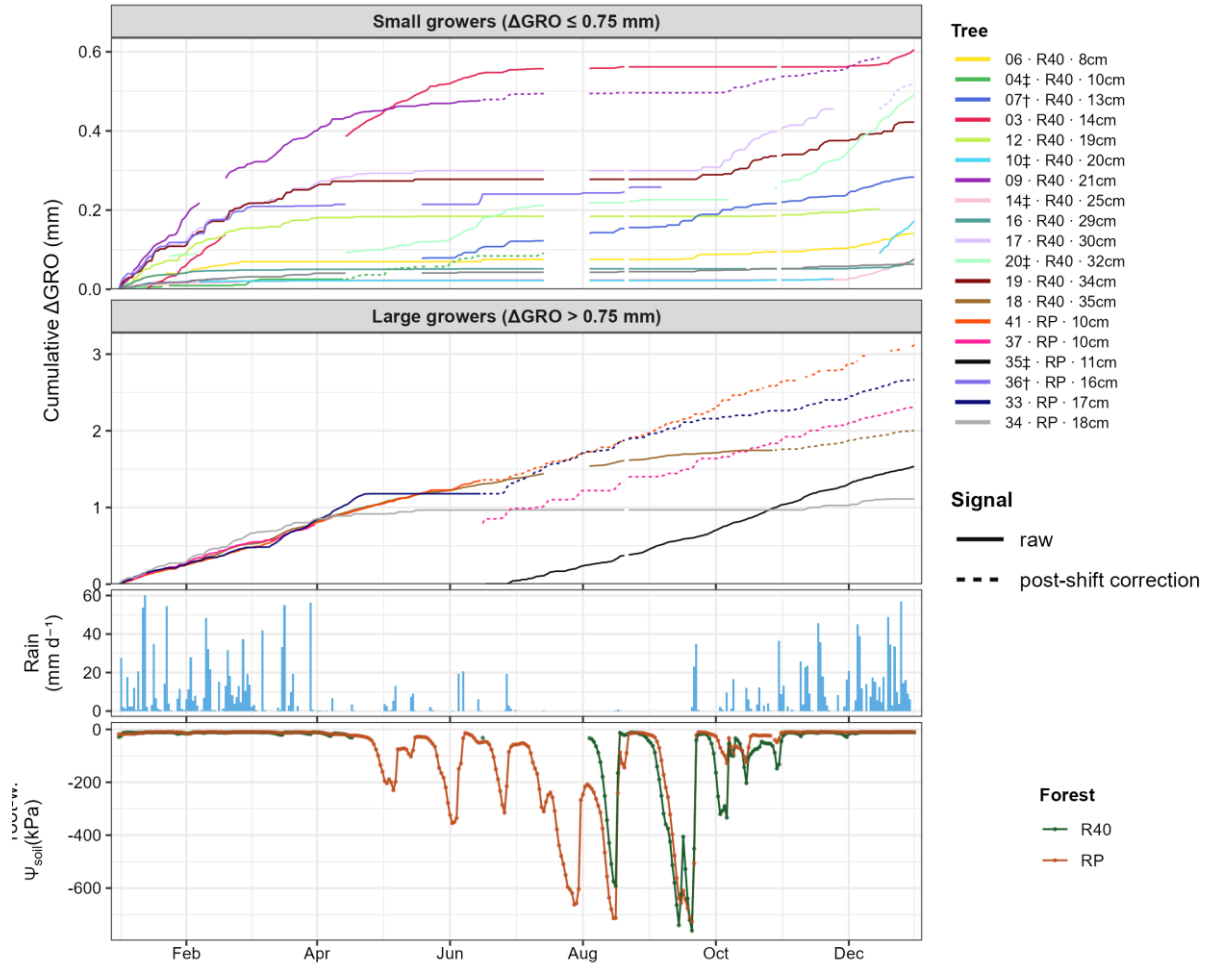


Figure 30: Per-tree cumulative radial growth (absolute ΔGRO , mm), with trees split into small and large growers at 0.75 mm yr^{-1} . Lower panels give the climatic context: daily rainfall and forest-median root-weighted Ψ_{soil} . Dashed segments flag the post-shift correction of the dendrometer signal. † reserve, ‡ low confidence.

Across the full sample, annual increments differ by two orders of magnitude, from below 0.1 mm yr^{-1} in the slowest R40 trees (06, 09, 14, 16), corresponding to the trees with lowest confidence, to nearly 3 mm yr^{-1} in the fastest RP pioneers (41, 33). These values sit in the lower half of the 0.45 to 4.35 mm yr^{-1} range reported by Valverde et al. (2024) for a Costa Rican wet forest, with most R40 trees falling below 0.45 mm yr^{-1} and the RP pioneers in the middle. The 68 % wet-season concentration in R40 falls at the upper end of the 40 to 70 % wet-season fraction reported in the same study, consistent with the strongly seasonal regime of the montane Mantiqueira site. The RP pioneers depart from this seasonal pattern, their year-round growth showing no wet-season concentration of the kind seen in the Costa Rican lowland reference. The single R40 exception is the large tree 18 (35.4 cm), whose continuous rise matches the RP pioneers, attributed to its size and possibly deeper rooting.

6.3.2. Magnitude and scaling

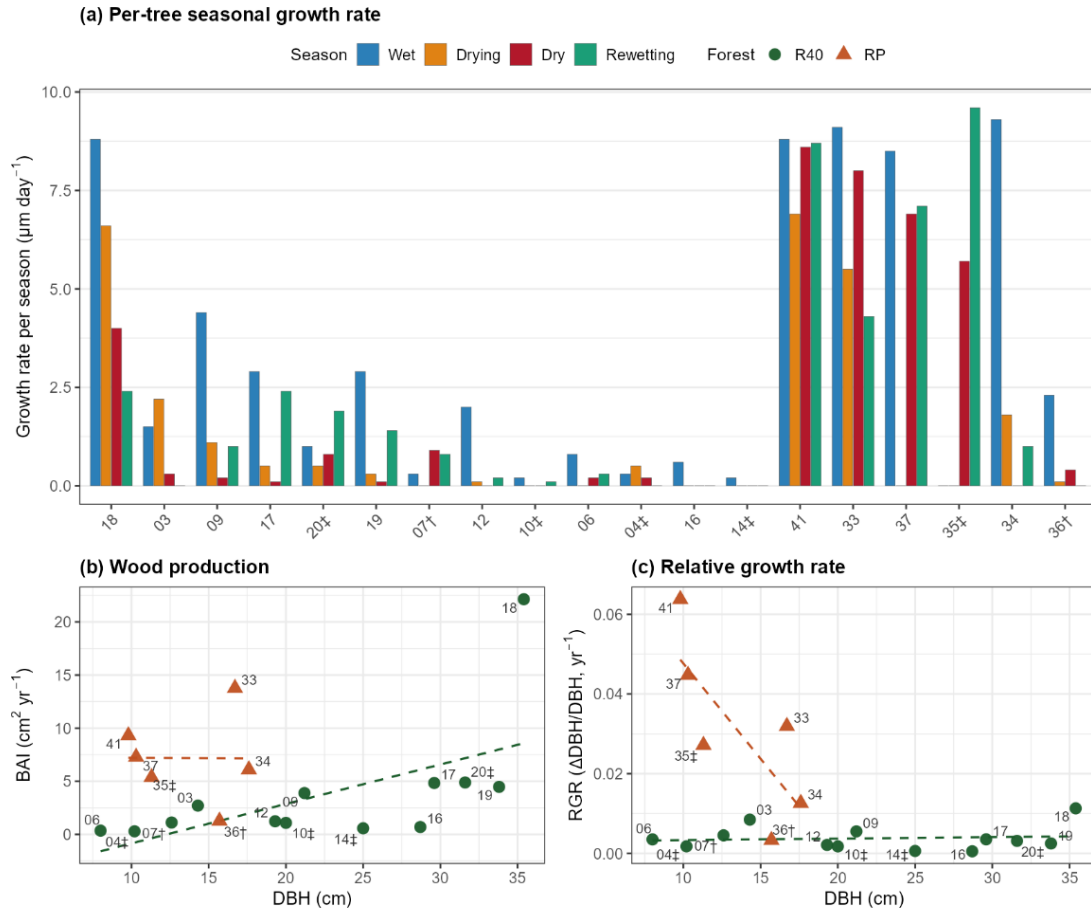


Figure 31: (a) Mean seasonal growth rate per tree ($\mu\text{m day}^{-1}$), trees sorted by zone (R40 first, then RP) and decreasing annual ΔGRO within each zone. (b) Basal area increment vs DBH per forest (dashed lm lines). (c) Relative growth rate $\text{RGR} = \Delta\text{DBH}/\text{DBH}$ vs DBH per forest. † reserve, ‡ low confidence.

Panel (a) of Figure 31 shows the per-tree seasonal growth rate. In R40 the wet season carries most of the growth in 12 of the 13 trees, the other seasons near zero, and the dry-season rate stays around $0.1 \mu\text{m day}^{-1}$. The high-performing RP pioneers (41, 33, 37, and the low-confidence 35‡) instead keep rates of about 5 to $9 \mu\text{m day}^{-1}$ in every season, so their dry-season rate ($\sim 6 \mu\text{m day}^{-1}$) is roughly 60× the R40 median, matching the year-round accumulation seen in the cumulative curves. Some trees depart from these patterns. In R40, 03 spreads its growth across wet and drying ($1.5 / 2.2 \mu\text{m day}^{-1}$), 07† is dry-dominant (0.9 against $0.3 \mu\text{m day}^{-1}$ in the wet), and 17 and 19 peak at rewetting ($\sim 2.4 \mu\text{m day}^{-1}$). Tree 18, the exception noted above, shows $8.8 / 6.6 / 4.0 / 2.4 \mu\text{m day}^{-1}$ across the seasons. In RP, the largest tree 34 (17.6 cm) switches to a wet-dominant rate ($9.3 \mu\text{m day}^{-1}$ in the wet, near zero elsewhere) and 36† stays flat ($2.3 \mu\text{m day}^{-1}$ in the wet season only, 0.26 mm yr^{-1} in total).

BAI (Fig. 31b) rises steeply with DBH in R40 ($\rho = 0.75$, $p = 0.005$, the only significant size effect in the analysis): the large tree 18 produces $\sim 22 \text{ cm}^2 \text{yr}^{-1}$, well ahead of all the others, and the bigger R40 trees (17, 19, 20‡) produce more than the smaller ones. In RP the relationship is flat ($\rho = -0.14$, NS): the small pioneers ($41 \approx 9.4 \text{ cm}^2$) produce as much basal

area as the largest RP trees ($34 \approx 6.2$), their high radial rate making up for a small radius. In this sample it is the large trees, R40 18 above all, that build the most wood, despite a modest radial rate.

The ranking flips when looking at relative growth (Fig. 31c). In R40 the RGR is low and nearly constant ($\sim 0.005 \text{ yr}^{-1}$, $\rho = 0.05$), a relative rate independent of size, a conservative pattern. In RP it falls steeply ($41 = 0.064$ to $34 = 0.012 \text{ yr}^{-1}$, $\rho = -0.71$): the smallest pioneers grow fast relative to their size, and the relative rate drops as size increases. This drop in RGR with size matches the pattern expected for fast, acquisitive pioneers (Poorter et al. 2010), though it comes from comparing different-sized trees rather than tracking individuals over time. The largest RP trees approach the slower R40 range.

6.3.3. Drivers

Importance per-tree drivers

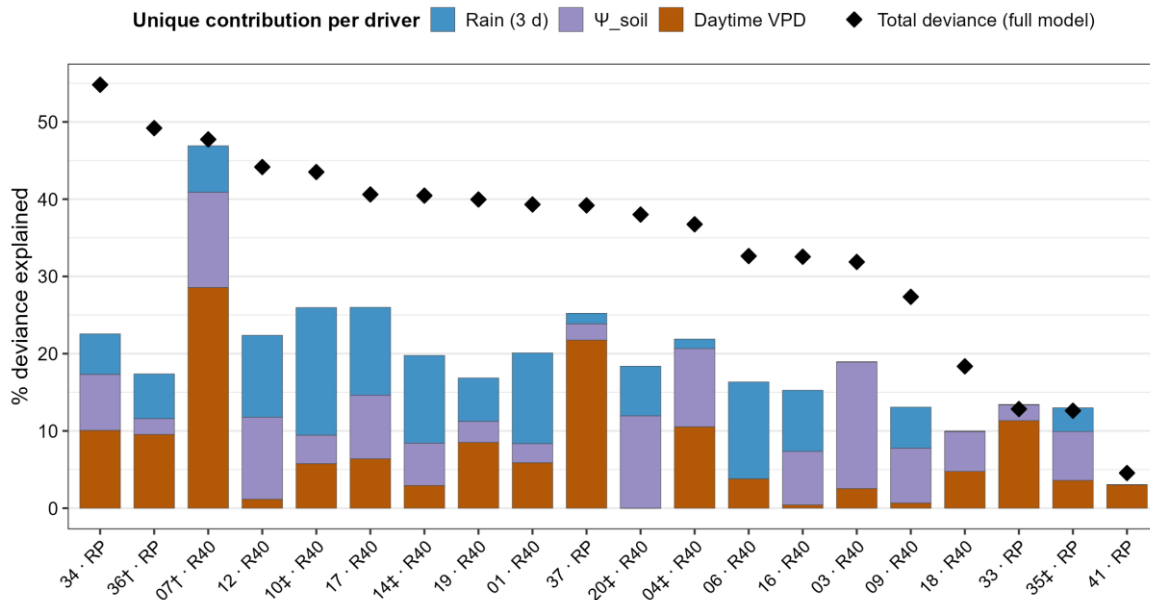


Figure 32: Per-tree importance of the three climatic drivers of radial growth. Additive GAM per tree, $\Delta \text{GRO} \sim s(\text{daytime VPD}) + s(\Psi_{\text{soil}}) + s(\text{rain } 3d)$, on the daily series. Stacked bars = unique contribution of each driver (full-model deviance minus the term-dropped model); black diamond = total deviance of the full model. Rain (3 d) = PULSE, Ψ_{soil} = STOCK, daytime VPD = DEMAND. $n = 20$ trees. † reserve, ‡ low confidence.

The three drivers tested cover three aspects of water control (Fig. 32). PULSE is the rainfall summed over a 3-day rolling window, a short-term trigger. STOCK is the root-zone soil water potential, the longer-lasting reserve. DEMAND is the daytime VPD, the air's evaporative demand. These three drivers test, tree by tree, whether growth responds more to the rain event, to the soil reservoir, or to atmospheric demand. Three findings stand out.

Total deviance varies widely between trees (5 to 55 %). The trees best explained by climate alone are 34 RP (55 %), 36 RP† (49 %) and 07 R40† (48 %). At the other end, 41 RP (5 %) and 18 R40 (18 %), the two trees that grow continuously through the year, are the least

predictable from climate alone: their steady, opportunistic growth points to internal factors (reservoir mobilisation, allocation, ontogeny) that the atmospheric drivers do not capture.

Of the 20 trees, six are rain-dominant (10‡, 14‡, 16, 17, 01 and 06, all R40), six are Ψ_{soil} -dominant (12, 20‡, 03, 09 and 18 R40, plus 35‡ RP), and eight are VPD-dominant (07‡, 19 and 04‡ R40, plus 34, 36‡, 37, 33 and 41 RP). The main pattern is that every reliable RP pioneer is VPD-dominant, whereas R40 is split across all three. This points to a more demand-driven, acquisitive habit in RP, growth responding to VPD rather than to rain events or the soil reservoir. The rain-dominant R40 are largely the small growers (§6.3.1): growth limited by rain episodes, a direct dependence on the PULSE.

Plot synthesis – interaction $VPD \times \Psi_{soil}$

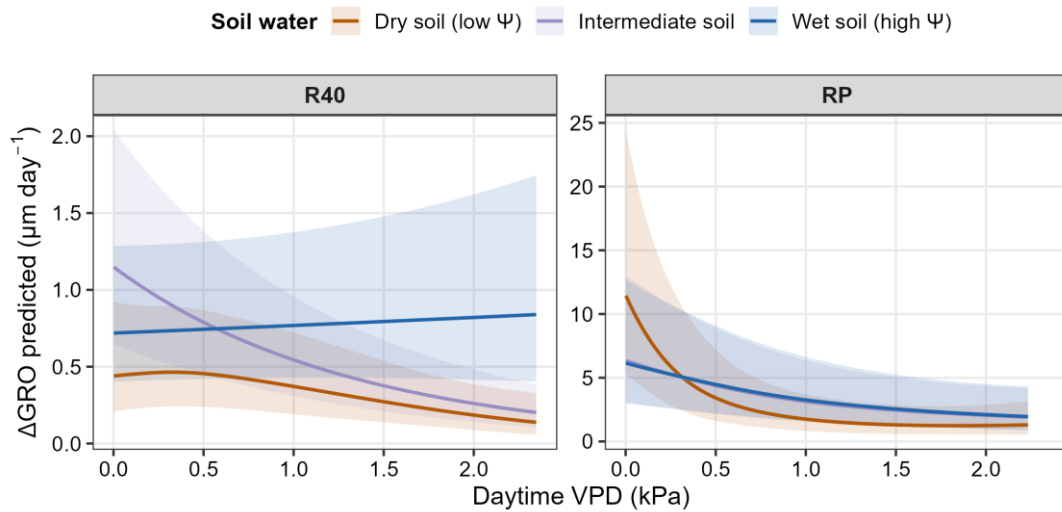


Figure 33: Predicted daily stem growth as a function of atmospheric demand and soil water, per forest. Curves = ΔGRO ($\mu m day^{-1}$) predicted by the GAM with a $te(VPD, \Psi_{soil})$ interaction; bands = 95 % CI. Soil water at three levels: dry (low Ψ , orange), intermediate (purple), wet (high Ψ , blue).

At the scale of the two stands (Fig. 33), a tensor-product GAM $te(VPD, \Psi_{soil})$ with rainfall held constant confirms a highly significant interaction (R40 dev = 44 %, $p < 10^{-10}$, RP dev = 27 %, $p < 10^{-10}$). In R40, growth is flat against VPD when the soil is wet but collapses once the soil reaches intermediate or dry states, so growth is gated by the soil reservoir (STOCK). In RP, growth is highest under dry soil combined with low VPD (10 to 11 $\mu m day^{-1}$) and erodes as VPD rises. When the soil is wet, RP growth is moderate and insensitive to VPD. This dry-soil, low-VPD corner is sparsely sampled, however (wide confidence band), so the apparent low-demand window should be read with caution. This stand-level interaction is consistent with the per-tree drivers above and adds their shape: R40 growth is released or paused by soil water, RP growth by demand.

6.3.4. Synthesis: per-tree strategy and R40 vs RP positioning

The per-tree analyses converge on a forest-level contrast. R40 grows in tight coupling with water supply: production concentrated in the wet season and tied to rainfall (§6.3.1), built mostly by a few large individuals (§6.3.2), with a climatic signal shared between rain pulse and soil reservoir (§6.3.3). The RP pioneers grow steadily through the year, modest in absolute basal area but high in relative growth (§6.3.2), even as their soil dries more deeply and for longer (§6.3.1), their climatic signal pointing to atmospheric demand rather than water (§6.3.3).

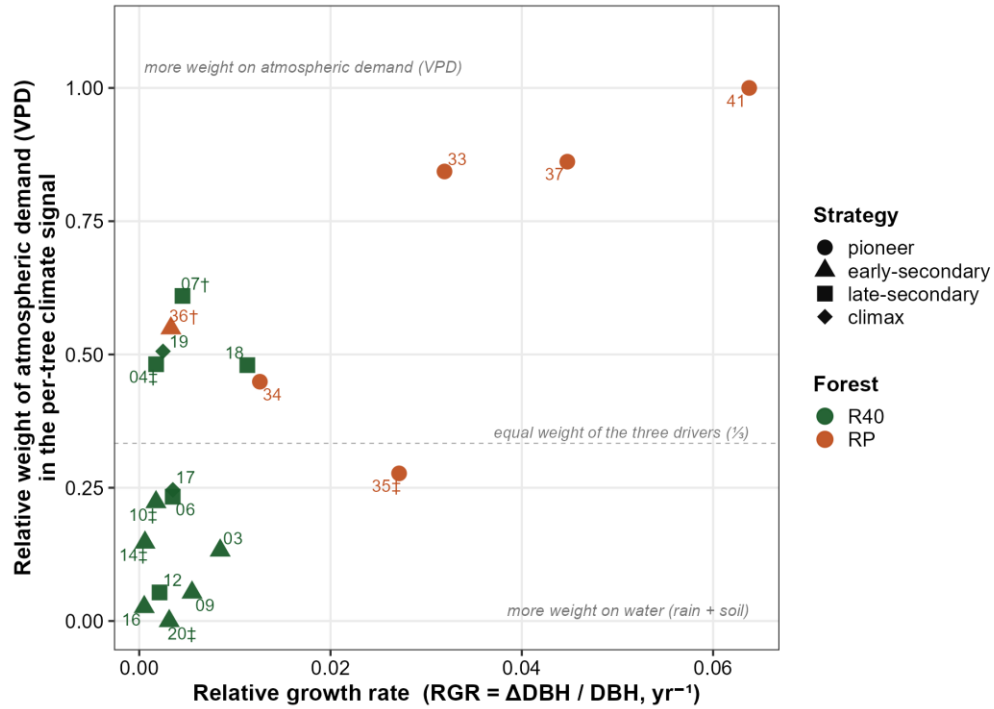


Figure 34: Per-tree scatter of relative growth rate ($\text{RGR} = \Delta\text{DBH} / \text{DBH}$, yr^{-1}) against the relative weight of atmospheric demand in each tree's climate signal, $\text{dev}_{\text{VPD}} / (\text{dev}_{\text{VPD}} + \text{dev}_{\psi_{\text{soil}}} + \text{dev}_{\text{rain}})$ from the per-tree GAMs (§3.3.3). † reserve, ‡ low confidence.

Placed in this space, the two forests separate but overlap at the edges (Fig. 34). The reliable RP pioneers (41, 37, 33) sit in the upper right: they grow fast relative to their size, and their climatic signal leans toward demand. The R40 trees cluster in the lower left: slower relative growth and a signal weighted toward water. The separation is relative rather than absolute, since in a montane setting all trees remain water-limited (Motzer et al. 2005). The axis only shows which trees tilt more toward demand than the others in this sample.

The two largest trees, 18 (R40) and 34 (RP), fall near the centre and connect the clusters. Position is therefore shaped by size as much as by plot: the large R40 individual drifts toward the steadier, less water-tracking regime, while the largest RP pioneer drifts back toward the water-weighted side. The trees flagged for reliability (07 (†), 36 (†), 35 (‡)) lie off the main trend and are read with caution.

What this analysis cannot resolve is the mechanism: why the RP pioneers keep expanding through the dry season once the soil is drying?

6.4. Responding to water stress

6.4.1. Magnitude and frequency of dry periods

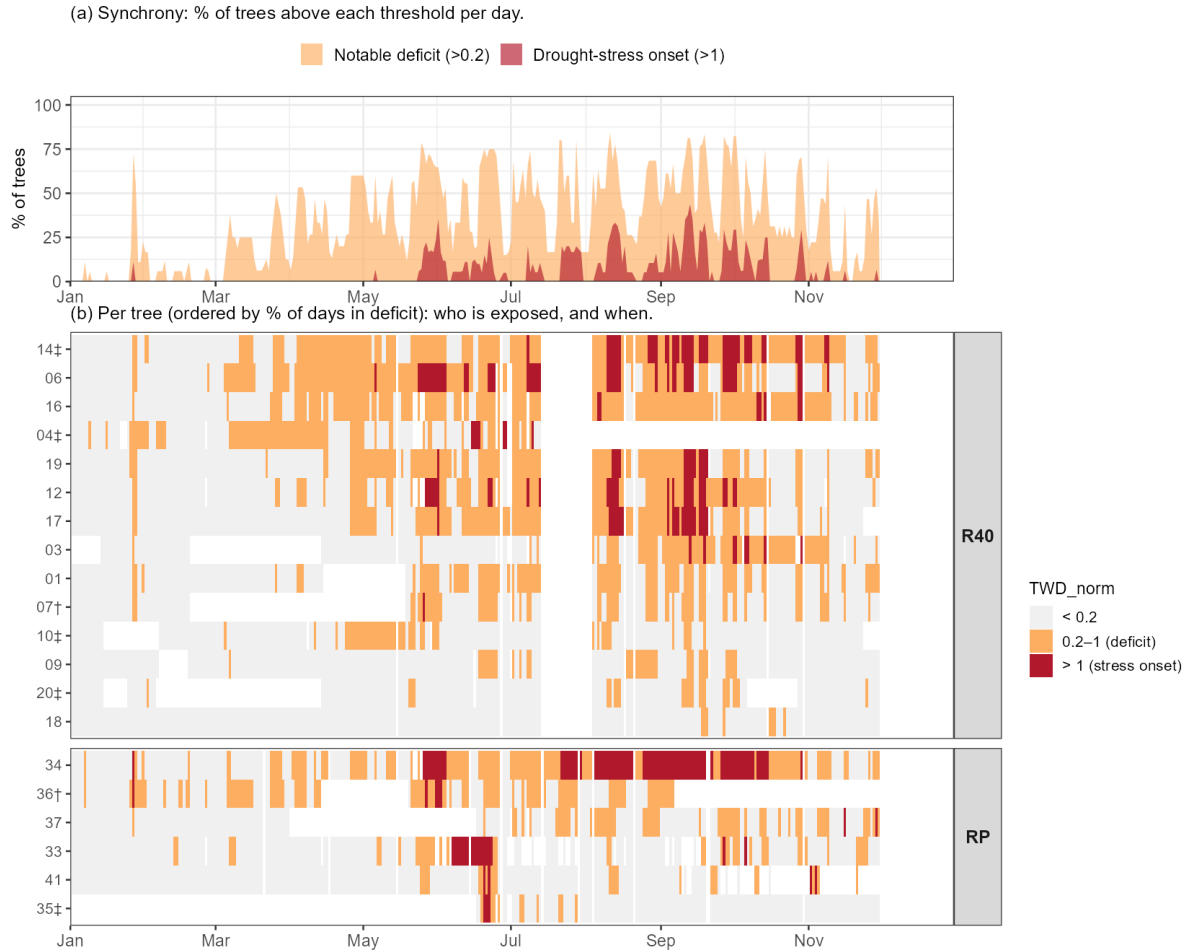


Figure 35: (a) Synchrony: percentage of trees exceeding, on each day, the notable-deficit threshold ($TWD_{norm} > 0.2$, light orange) and the drought-stress onset threshold ($TWD_{norm} > 1$, red; Peters et al., 2025). (b) Date $\times$ tree raster of the deficit level (three tiers), faceted by forest, trees ordered by their percentage of days in deficit.

This Figure 35 shows when and for how long trees experience stress. Detecting these episodes requires choosing the right marker. Of the two normalised signals of Peters et al. (2025), TWD_{norm} , the sustained deficit not recovered overnight, is the stress marker of choice: it crosses the stress-onset threshold ($TWD_{norm} > 1$) and separates trees clearly. MDS_{norm} , by contrast, measures the amplitude of the reversible daily contraction (water exchange, transpiration demand). It would wrongly label well-supplied trees under high VPD as stressed and is therefore not used here as a stress index. TWD_{norm} is read at two levels: > 0.2 , a descriptive onset of notable deficit, and > 1 .

The deficit is not continuous but occurs in short bursts from May to October, during which the notable deficit reaches up to 75 to 80 % of trees at once. Crossing the stress onset reaches at most about 25 to 30 % of trees, in two distinct sub-episodes (June, then the main August to September cluster). In other words, the deficit is widespread in the dry season, but the water buffer keeps most trees below the onset. Synchrony never reaches 100 %: it is partial, driven by the dry-season climate.

The exposure gradient follows the buffer, not the plot. The most exposed to notable deficit are 14 (65 %), 06 (60 %) and 16 (60 %) in R40, and 34 (60 %) in RP. Tree 34 (RP) is the only one to exceed the onset for a long period (26 % of days, dense red from August to October). At the other end, the least exposed (onset crossing ≈ 0 %) are the large buffered R40 trees (18, 20, 09, 10) and the small RP pioneers (35, 41). Because TWD_{norm} is normalised by each tree's own maximum shrinkage (MDS_{max}), it measures deficit relative to each tree's reservoir. This is why the large-reservoir pioneers rarely cross the threshold despite high demand.

6.4.2. Drivers

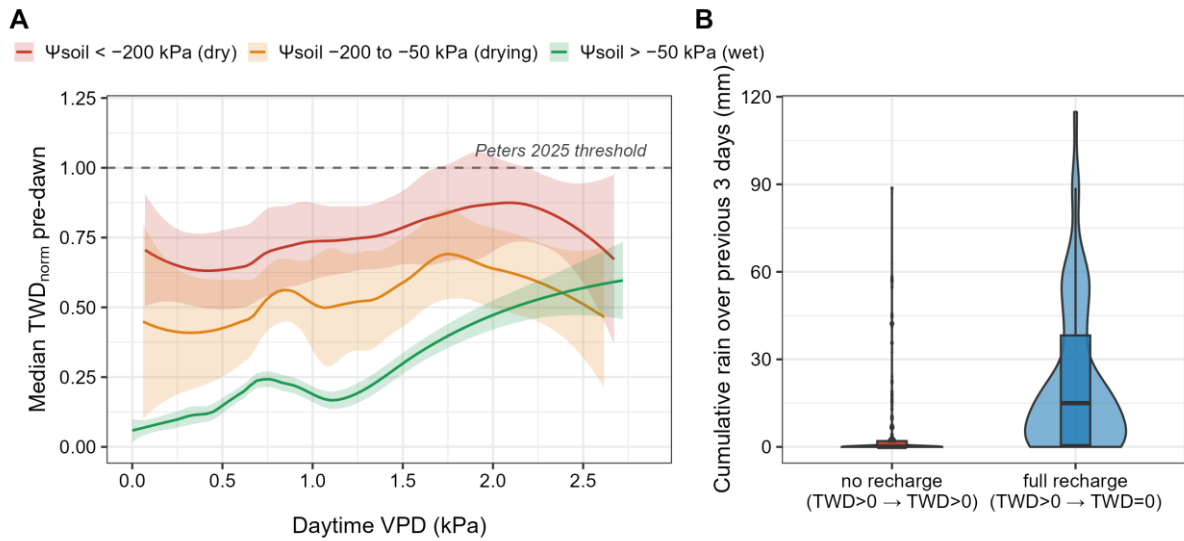


Figure 36: (a) pre-dawn TWD_{norm} as a function of daytime VPD, stratified by root-zone Ψ_{soil} class (dry < -200 kPa; drying -200 to -50 ; wet > -50); loess smoothing $\pm$ CI. Dashed line = stress-onset threshold ($TWD_{norm} = 1$; Peters et al., 2025). (b) Cumulative rain over the previous 3 days, on days with no recharge (TWD stays > 0) versus full recharge ($TWD \rightarrow 0$).

The deficit builds up under a supply-and-demand regime (Fig. 36A). Its structure follows the framework of Novick et al. (2016). When the soil is wet (green), the pre-dawn deficit is low (~ 0.05 to 0.25) and rises with VPD (up to ~ 0.6 at 2.5 kPa): a demand-limited regime, where VPD deepens the deficit if water is available. When the soil is dry (red, $\Psi_{soil} < -200$ kPa), the deficit is already high at low VPD (~ 0.7) and almost insensitive to VPD (0.7 to 0.85 plateau): a soil-water-limited regime, where soil supply, not demand, now sets the deficit. The drying class is intermediate, and the three curves converge at high VPD (~ 0.5 to 0.6 near

2.5 kPa), the expected transition from VPD-limitation to soil-limitation. The medians stay below the stress-onset threshold, consistent with §6.4.2.

The deficit is relieved by rain (Fig. 37B). Days of full recharge (TWD brought back to 0) have a much higher 3-day cumulative rainfall (median ~18 mm, up to 100 mm) than days without recharge (~0 mm). The deficit is therefore not relieved gradually but by rain pulses, matching the rainfall control of growth (§6.4.3). The dry-season stress corresponds to the soil-limited regime of this diagram, and its relief depends on rain episodes.

6.4.3. The buffering: reservoir and capacitance

Reservoir size: relative strain and absolute amplitude

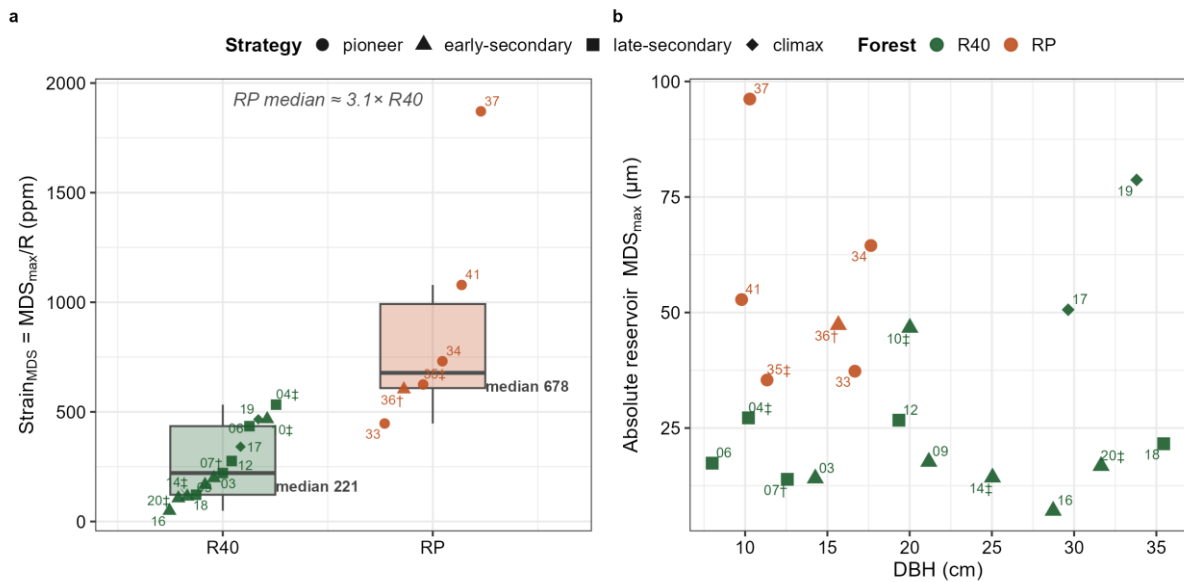


Figure 37: Stem water reservoir, relative and absolute size per tree. (a) $strain_{MDS} = MDS_{max}/R$ (ppm), the maximum daily shrinkage per unit radius, by forest (boxplot per-tree points labelled by tree id; med = forest median). (b) Absolute maximum daily shrinkage MDS_{max} (μm) versus DBH, by forest. † reserve, ‡ low confidence.

The deficit is damped by the stem water reservoir, the elastic tissues that release and reabsorb water over the day. Its relative size, measured as $strain_{MDS}$ (Peters et al., 2025), separates the forests cleanly (Fig. 37a): the R40 median is about 221 ppm against 678 ppm in RP, a factor of roughly 3.

Because strain carries a $1/R$ term, this contrast could come from the RP pioneers being smaller. The absolute shrinkage rules that out (Fig. 37b): even in μm , the small RP pioneers draw far more stem water per day than most R40 trees. Tree 37 RP (10 cm) reaches 94 μm , against 21 μm for the largest R40 (18, 35 cm) and 7 μm for 16. The reservoir contrast is therefore real, not a size artefact. The pattern is not a strict split, since two large and reactive R40 trees (19 and 17) also have sizeable absolute reservoirs (79 and 51 μm).

In §6.4.2., two groups of trees rarely crossed the stress onset: the large buffered R40 (18, 20, 09, 10) and the small RP pioneers (35, 41). This may explain how each group avoids stress through different mechanisms. R40 seems to rely mainly on an external buffer, a relatively high soil-water reserve (Ψ_{soil} , possibly via deeper rooting) backing a small stem reservoir, whereas the RP pioneers seem to rely on an internal one, a large stem reservoir (capacitive storage as defined by Meinzer et al. 2003, Scholz et al. 2007). The most exposed trees have a weaker version of both. This internal reservoir likely supports the continuous growth of the RP pioneers between rains, which growth data alone could not show. The next section examines how strongly the reservoir responds to atmospheric demand and at what point it stops working.

How the stem reservoir responds to atmospheric demand

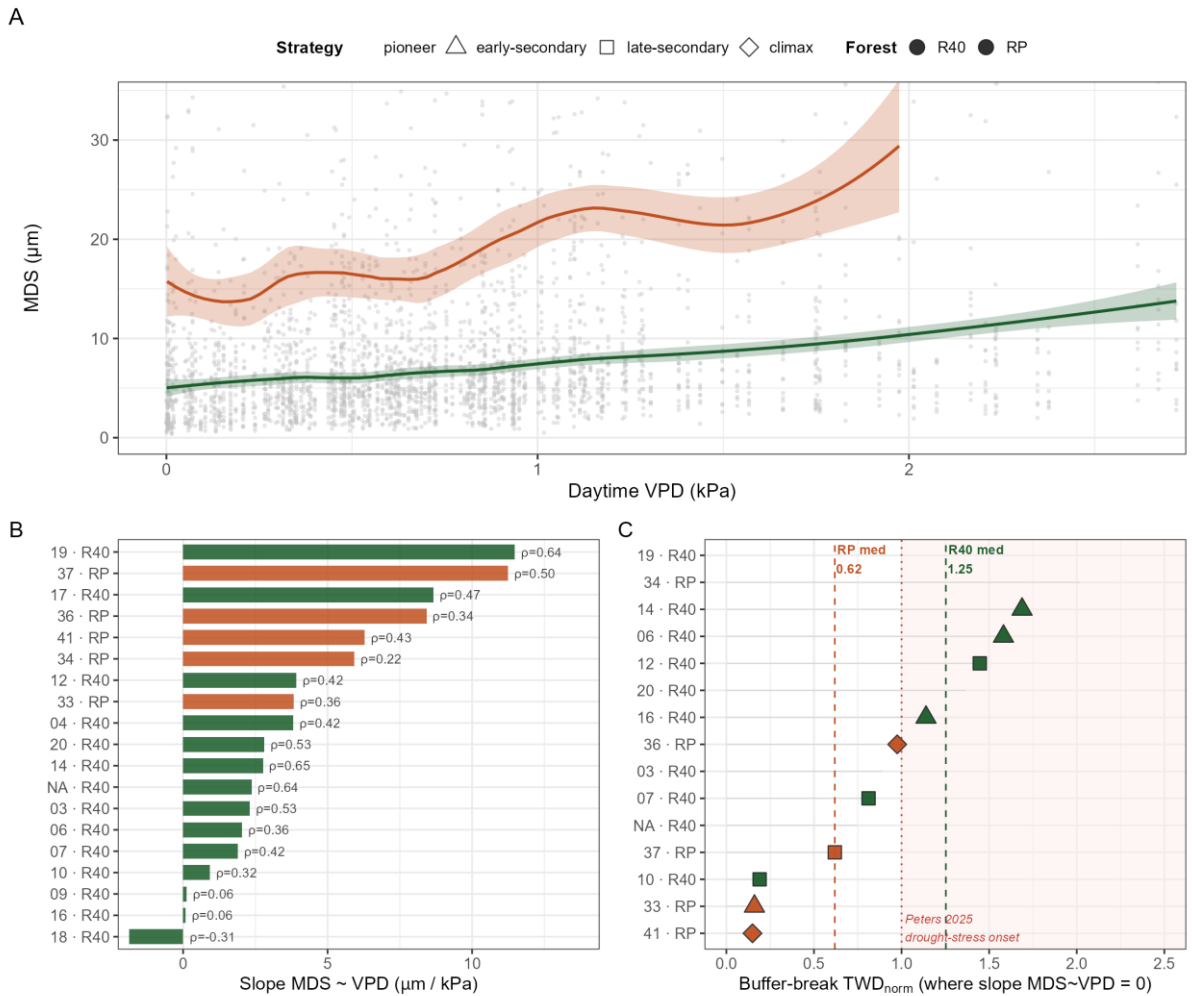


Figure 38: Reservoir reactivity to atmospheric demand and its breakdown. (a) MDS versus daytime VPD, loess $\pm$ CI per forest. (b) Slope of MDS on VPD per tree ($\mu\text{m kPa}^{-1}$), with the Spearman ρ of each fit. (c) Buffer-break TWD_{norm} per tree; dashed lines = forest medians, dotted line = drought-stress onset ($TWD_{norm} = 1$, Peters et al., 2025). Panel (c) is restricted to the 15 trees with valid predawn coverage. † reserve, ‡ low confidence.

The reservoir differs not only in size but in how strongly it responds to atmospheric demand. At the forest scale, the daily shrinkage rises with VPD far more steeply in RP, reaching a plateau around 20 μm at high VPD, whereas in R40 it stays low and almost linear (Fig. 38a).

The RP reservoir is heavily drained as demand rises and then reaches its limit. The R40 reservoir is barely touched.

Per tree, the slope of MDS on VPD confirms a continuum rather than a clean split (Fig. 38b): the most reactive tree is 19 R40, ahead of the RP pioneers 37, 34 and 41, while several R40 (18, 16, 09) stay nearly flat. Reactivity is an individual trait that the forest contrast captures but does not impose.

This reactivity has a limit. Beyond a deficit threshold the daily shrinkage stops tracking VPD, the point where the reservoir can no longer follow demand (Fig. 38c). The RP pioneers reach this buffer-break well before the drought-stress onset (median TWD_{norm} 0.62), whereas R40 reaches it around or past the onset (median 1.25). The strongly reactive reservoirs of the pioneers therefore also reach their limit earliest, consistent with their year-round depletion. This panel rests on the 15 trees with valid predawn coverage.

6.4.4. Functional consequence: suppression and recovery

Growth, the first function to give way

§6.4.3. showed that the stem reservoir buffers atmospheric demand up to a limit. Once it can no longer hold turgor, growth is the first process to stop.

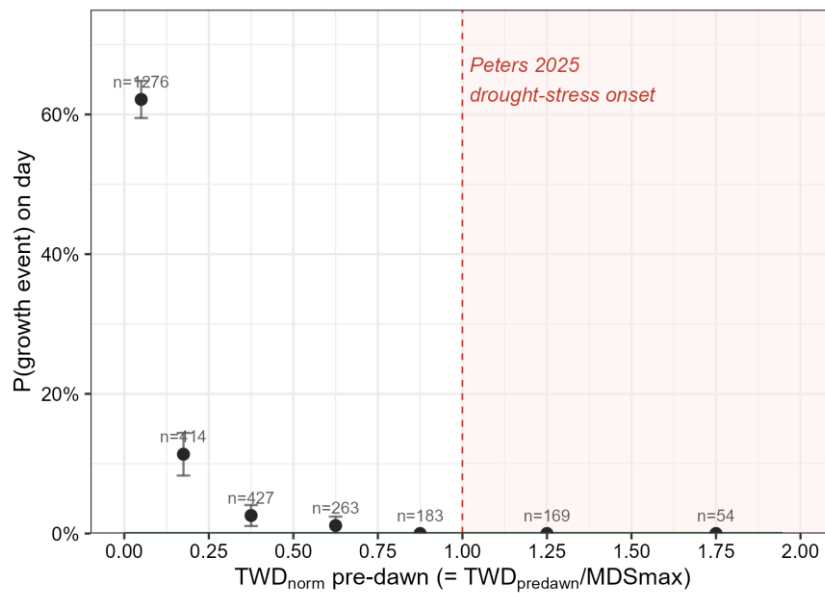


Figure 39: Probability of a growth event per day against the stem's pre-dawn water deficit. A growth event = $\Delta GRO > 1 \mu m$. Points = proportion of growth days per TWD_{norm} bin ($\pm 95\%$ CI, n labelled). Dashed line and shaded zone = drought-stress onset ($TWD_{norm} = 1$; Peters et al., 2025).

Each tree-day is treated as a binary question: was there an irreversible increment, $\Delta GRO > 1 \mu m$? The probability of growth falls sharply and almost predictably with the stem's pre-dawn water deficit (Fig. 39). When the stem is nearly rehydrated at dawn ($TWD_{norm} \leq 0.1$), 62 % of days show growth ($n = 1276$). The proportion drops to 12 % between 0.1 and

0.25, to 3 % between 0.25 and 0.5, to about 1 % between 0.5 and 0.75, and is effectively zero beyond 0.75. Growth therefore stops at a deficit well below the threshold where stomatal regulation begins ($TWD_{norm} = 1$; Peters et al., 2025), itself far below leaf turgor loss ($TWD_{norm} \gg 1$, species-specific).

The thresholds form a clear hierarchy. Cambial expansion stops at a low deficit (the turgor threshold of Lockhart, 1965). Stomatal closure begins later ($TWD_{norm} = 1$), and turgor loss later still ($\gg 1$). Growth is thus suppressed early, before the tree enters real hydraulic stress. Atmospheric demand acts as a forcing, not as the direct control. VPD also suppresses growth (§6.3.3; Zweifel et al., 2021), but it does so by increasing the stem deficit. What governs expansion directly is the integrated water state of the stem, its turgor, read here through TWD_{norm} .

Almost no tree lives in sustained stress across the year. No median regime crosses the onset, and turgor loss stays episodic. The exposed trees are those already identified in §6.4.2, and the episodes are mostly brief, a few days, relieved by the next rain (§6.4.3). Only the most exposed trees (04 R40, 34 RP) have long ones. The RP pioneers reach the highest absolute deficit peaks (mean peak TWD 0.027 to 0.038 mm against 0.003 to 0.023 mm in R40). This reflects strong reservoir use (§6.4.4), not unrelieved stress. The system is resilient at the episode scale: the buffer absorbs the deficit, growth pauses, and the tree resumes once the next rain recharges it.

Recovery dynamics

Does growth resume as fast as it stops? The Lloret et al. (2011) framework is applied to per-tree deficit episodes. For each episode that suppressed growth (resistance $R_t < 0.5$, with $n = 27, 19$ in R40 and 8 in RP), the resilience R_s (rate after / before) and the time to regain 75 % of the pre-episode rate are measured against the local rate of the 14 preceding days (Fig. 40).

The recovery composite (Fig. 40a) shows that growth falls to 30 to 45 % of its pre-episode rate but returns within 1 to 5 days (median 3, recovery time encoded as point size in Fig. 40b), with most trees matching or exceeding their earlier rate ($R_s \geq 1$). The per-tree Lloret plane (Fig. 40b) shows that this recovery is set by the individual rather than the forest: R40 splits into two groups, with both the best recoverers (07, 06, 04: $R_s \geq 1.5$ to 1.8) and the most vulnerable (17, 14, 16, 01: $R_s < 0.4$), while the RP pioneers recover more consistently ($R_s \geq 1$ for 37, 33, 41), though on few trees and with low confidence.

This reading rests on a low n per tree, with several single-episode trees and therefore fragile R_t and R_s . The thresholds ($R_t < 0.5$, 75 %) are descriptive, and the Lloret framework is adapted from an annual to an episodic grain. The slight late drop of R40 in the composite (Fig. R40a) may reflect a residual seasonal effect, the post-window reaching into the dry season.

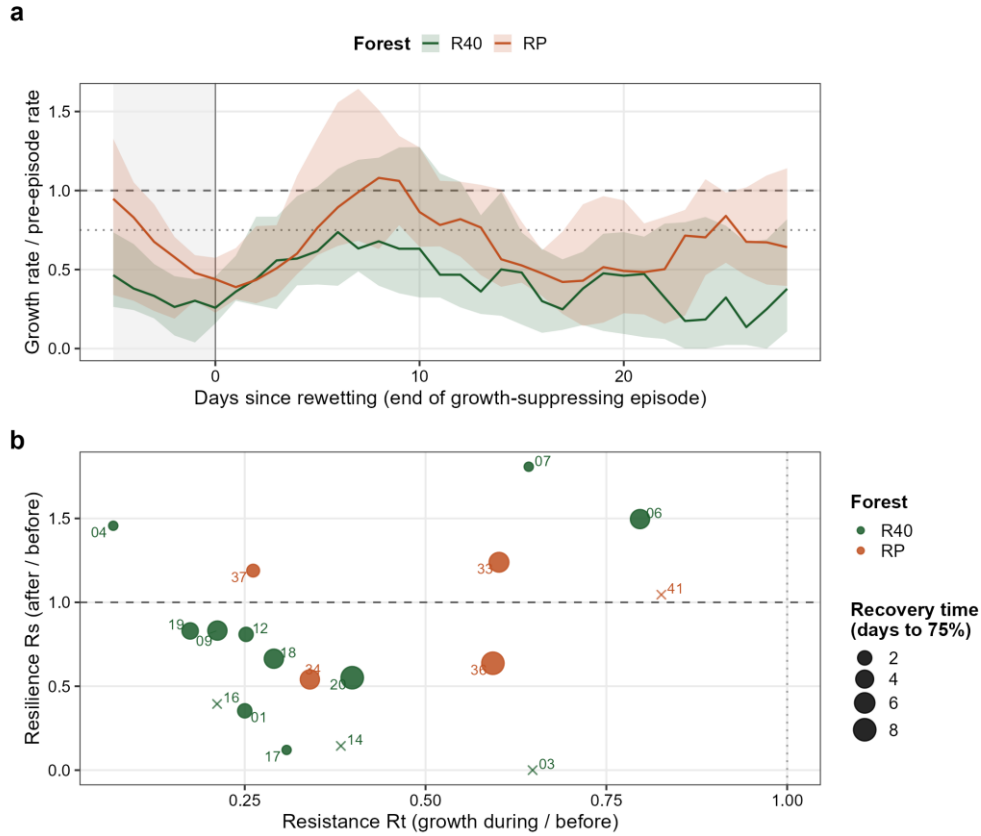


Figure 40: Growth recovery after deficit episodes. (a) Composite trajectory: the 7-day rolling growth rate relative to the pre-episode rate, aligned on rewetting (day 0 = episode end), median $\pm$ IQR per forest. Reference lines mark full recovery, the 75 % threshold, and the grey band shows the episode duration. (b) Per-tree strategy in the Lloret (2011) plane: resistance R_t (during/before) vs resilience R_s (after/before); point size = recovery time (days to regain 75 % of the pre-episode rate), $\times$ = trees never strongly suppressed. Suppressing episodes defined by $R_t < 0.5$. R40 in green, RP in orange.

6.4.5. Synthesis

The deficit cycle is now complete. It builds in dry-season events, is set by the $\Psi_{soil} \times$ VPD supply-and-demand regime and is buffered by stem capacitance. When the buffer is depleted, growth is the first process suppressed, well before stomatal regulation and turgor loss, and the deficit clears at the next rain. By forest, consistent patterns appear. The RP pioneers show a larger and more reactive stem reservoir (§6.4.4), exhaust it earlier under demand (§6.4.4), reach the highest absolute deficits, and recover growth more fully after episodes (§6.4.5). Their high deficits mark strong reservoir use, not unrelieved stress. The R40 trees rely on a smaller stem reservoir backed by deep soil water and split into well- and poorly buffered trees.

6.5. Linking transpiration, stem reserve and growth

6.5.1. Using TWD as a proxy for stem water content

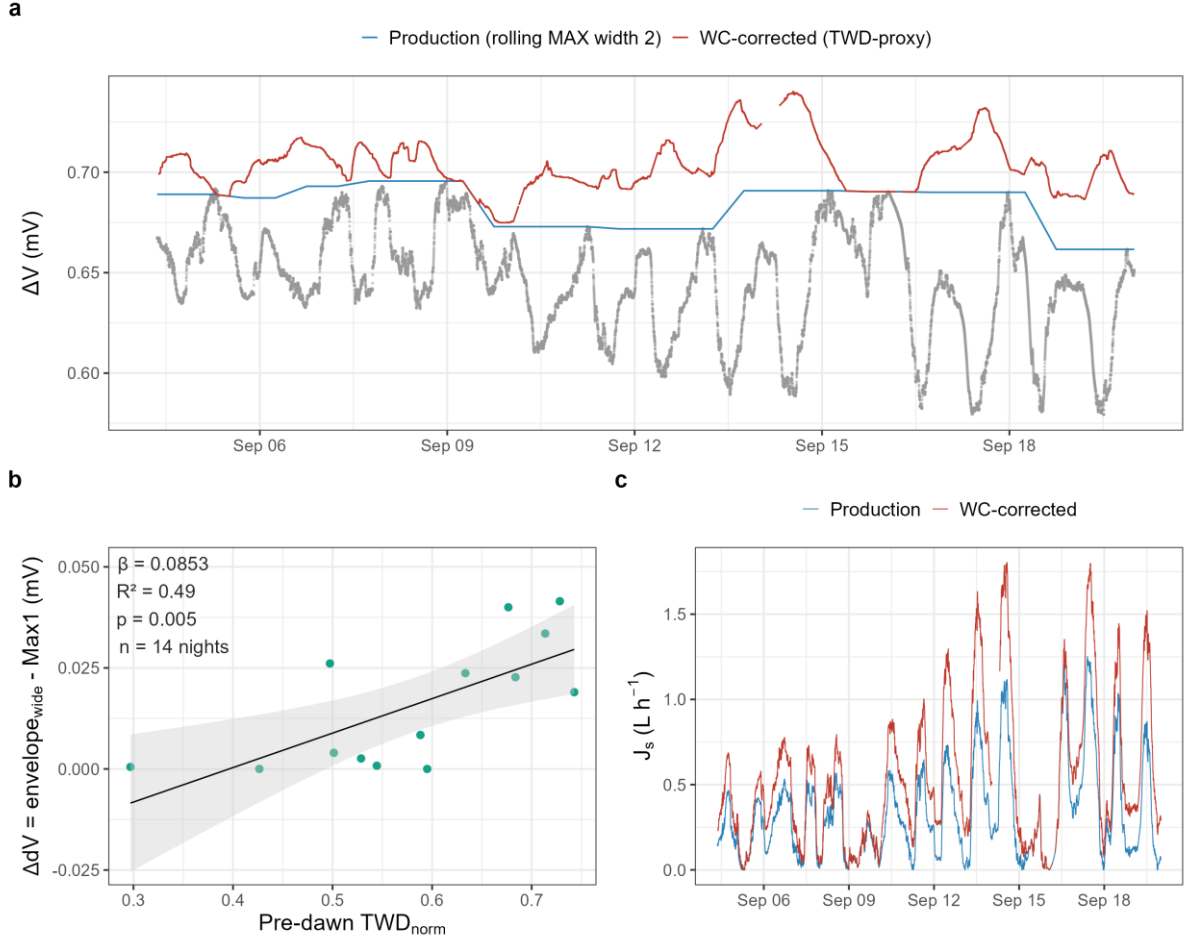


Figure 41: TWD-proxy correction of the sap flow baseline (tree 12 R40, 22/08 to 19/09/2020). (a) Raw ΔV_{clean} (grey), production baseline (blue), and TWD-corrected baseline (red), built from the production baseline plus $\beta \cdot (TWD_{norm}(t) - TWD_{ref})$, capped at 15 % and floored at 0. (b) Regression $\Delta dV = envwide - Max1$ vs $TWD_{predawn}$ over the n_{ideal} nights, with $envwide$ the rolling MAX width 7. OLS fit (line) and 95 % CI (grey band). (c) J_s ($L h^{-1}$) at 1-min resolution from each baseline.

The Granier baseline calibrated on ideal nights (M&M §5.7.2) cannot follow the within-day drop in wood water content that raises the true ΔV_{max} (Vergeynst et al. 2014). The TWD signal can serve as a continuous proxy of this drop and lift the baseline accordingly. The correction was tested on tree 12 (R40, DBH 26.4 cm) over the 22/08–19/09 dry window, chosen for its near-complete TWD coverage (88 %) and its position in the middle of the dry season. The regression $\Delta dV TWD_{predawn}$ yields $\beta = 0.0853$ mV per unit TWD_{norm} ($R^2 = 0.49$, $p = 0.005$, $n = 14$ nights; Fig. 41b), matching Vergeynst's predicted direction drier trunk raises the zero-flux reference.

Applied across the period, the correction lifts the production baseline by up to 6 %, with a sharper rise on the driest days (15–18 September ; Fig. 41a), and raises median Q_{day} by +63 % ($5.06 \rightarrow 8.24 L day^{-1}$) and $J_{s,max}$ by +53 % ($0.62 \rightarrow 0.94 L h^{-1}$; Table 4, Fig. 41c). The larger effect on Q_{day} reflects accumulation of the bias through the afternoon, when trunk water loss is steepest. The 53 % shift on the daily maxima sits in the upper part of the 15–43 % range reported by Vergeynst et al. (2014) on potted apple, consistent with tree 12 reaching deeper TWD_{norm} values. The correction is presented here as a proof-of-concept on one tree; its

application to the full sample requires validation across configurations and TWD coverage levels (§7).

Table 4: Daily sap flow integrals with production vs TWD-corrected baselines (tree 12 R40, 22/08 to 19/09/2020). Medians over the period. Q_{day} integrated 6:00 to 18:00. Difference = (corrected – production) / production $\times 100$ %.

Variable	Production baseline	TWD-corrected	Difference
Median Q_{day} (L Day ⁻¹)	5.06	8.24	+62.8 %
Median $J_{s,max}$ (L h ⁻¹)	0.62	0.94	+53.4 %
Median $F_{d,max}$ (g cm ⁻² h ⁻¹)	2.74	4.19	+53.4 %

6.5.2. Contribution of the stem reserves to transpiration

On the daily timescale, the stem reservoir contributes to transpiration. The median stem-storage contribution, estimated by the morning-lag method (Phillips et al., 2003; M&M §X), is about 6 % (p75 10 to 22 %, Fig. R4.1). This sits below the 10 to 50 % range reported across tropical trees (Goldstein et al., 1998), and even below the 9 to 15 % Goldstein measured on Panama canopy trees, consistent with a montane forest of modest-sized trees. The dendrometer-only estimate ($MDS \times \varepsilon$) captures the elastic bark and phloem alone and reaches only ~ 0.2 %, roughly 30-fold less (red diamonds, Fig. R4.1). This 30-fold gap suggests that most of the stem-drawn water comes from the sapwood, which the dendrometer cannot see. The conclusion is sensitive to ε but anatomically consistent with the few-millimetre bark observed on site. Crossing the dendrometer with sap flow is therefore needed to capture the sapwood store.

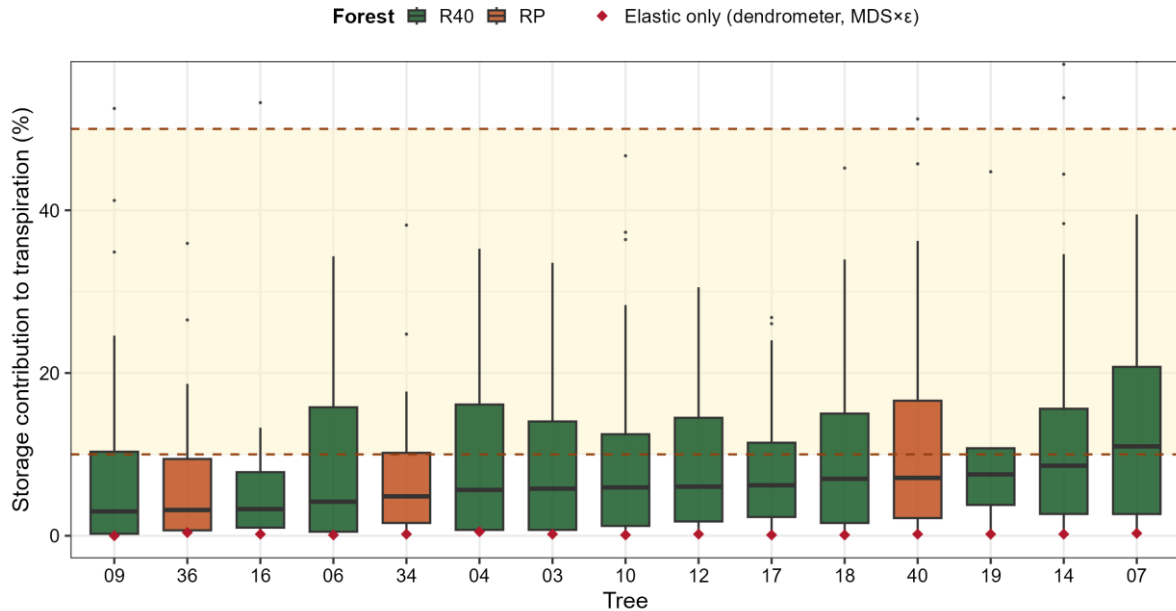


Figure 42: Stem-storage contribution to daily transpiration per tree. Boxes = total storage from the morning-lag method (Phillips et al., 2003). Red diamonds = elastic-only estimate from the dendrometer. Shaded band and dashed lines = the 10 to 50 % range reported for tropical canopy trees (Goldstein et al., 1998). $n = 15$ (12 R40 + 3 RP).

6.5.3. Temporal dimensions of the buffer: diurnal lag and nocturnal flux

Diurnal $F_d \leftrightarrow TWD$ lag

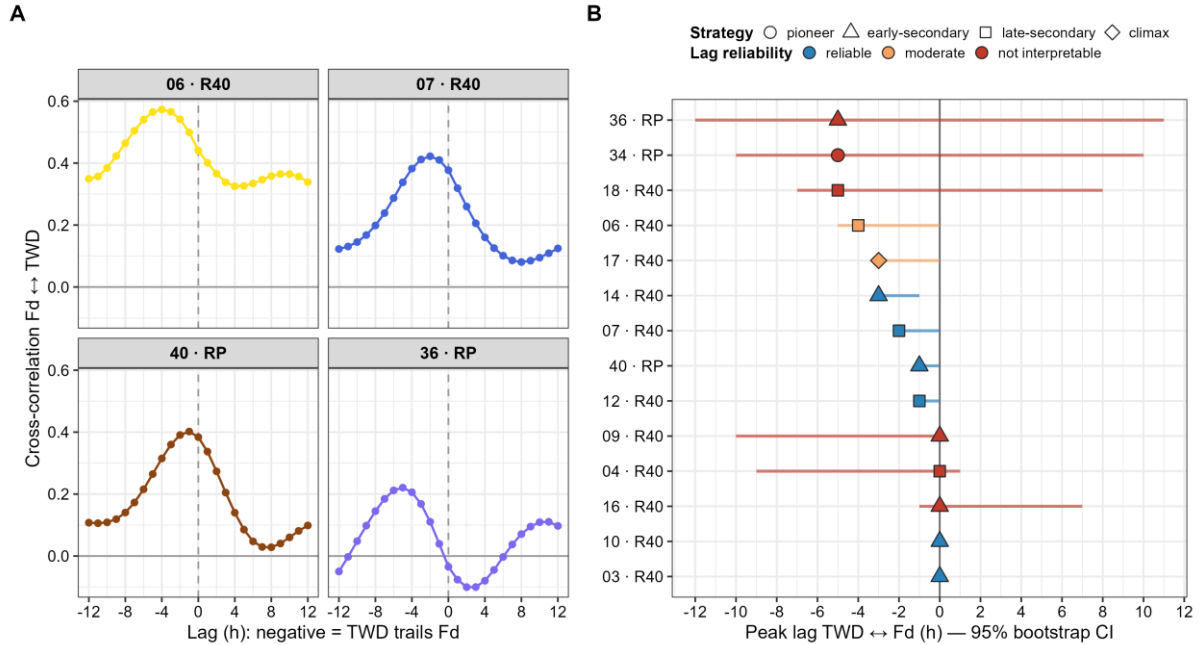


Figure 43: Diurnal lag between transpiration and stem water deficit, per tree. (a) Hourly cross-correlation $F_d \leftrightarrow TWD$ for four representative trees (06, 07, 40, 36); dashed line = zero lag. (b) Peak lag per tree with 95 % bootstrap CI (24 h blocks, $B = 200$), ordered from most negative (top) to zero (bottom). Colour = lag reliability based on CI width (reliable ≤ 2 h, moderate ≤ 5 h, not interpretable > 5 h).

The $F_d - TWD$ cross-correlation per tree (Fig. 43) provides the diurnal lag between transpiration and deficit. A negative lag, where TWD follows F_d , marks capacitive buffering of the reservoir. A usable estimate is obtained for only a minority of trees.

Three R40 trees show clear buffering, the deficit following transpiration by 3 to 4 h (06 at -4 h $[-5, 0]$; 14 at -3 h $[-3, -1]$, the only tight CI; 17 at -3 h $[-3, 0]$). Their cross-correlation peaks are sharp and high (06 at ~ 0.57 , 14 at ~ 0.45), meaning that F_d and TWD vary closely together at the optimal lag with little noise. The 3 to 4 h delay matches the 2 to 4 h reported by Köcher et al. 2013 on unmanaged beech and signals an elastic reservoir large enough that the radial contraction arrives only well after the flow peak.

Two further R40 trees (07, 12) and the single reliable RP tree (40, -1 h) are near-synchronous. Their peaks are still well defined (height ~ 0.4 , tight CI) but sit close to zero lag, meaning that TWD tracks F_d almost in real time. Either the elastic compartment is too small to introduce a detectable delay or the hydraulic resistance between sapwood and bark is too low to slow the radial contraction.

For three trees (18 R40, 34 and 36 RP) the CI spans zero by more than 14 h, so the apparent -5 h peak reflects noise rather than buffering. The peak is low (~ 0.2) and broad,

meaning that F_d and TWD do not co-vary in a stable way, and the lag cannot be read, regardless of its central value.

Diurnal buffering is therefore measurable only in a minority of R40 trees and is absent or undetectable elsewhere. This individual variability is consistent with the per-tree reservoir reactivity established in §6.4.4 (Fig. 43b).

Partition of nocturnal flux: refilling or genuine transpiration?

The nocturnal flux ($Q_{night} = 4$ to 12 % of daily flux, §6.2.2) is ambiguous, since it may arise either from stem recharge after the daytime deficit or from genuine night-time transpiration with stomata held partly open under high nocturnal VPD. The $F_d \times$ TWD crossing separates the two: for each tree-night, pre-dawn flux (02 to 05 h, $Rad < 5 \text{ W m}^{-2}$) is compared with pre-dawn VPD, given the state of the reservoir at the same moment (TWD_{pre} , expressed as TWD_{norm} , the fraction of MDS_{max}). Two signatures converge on refilling.

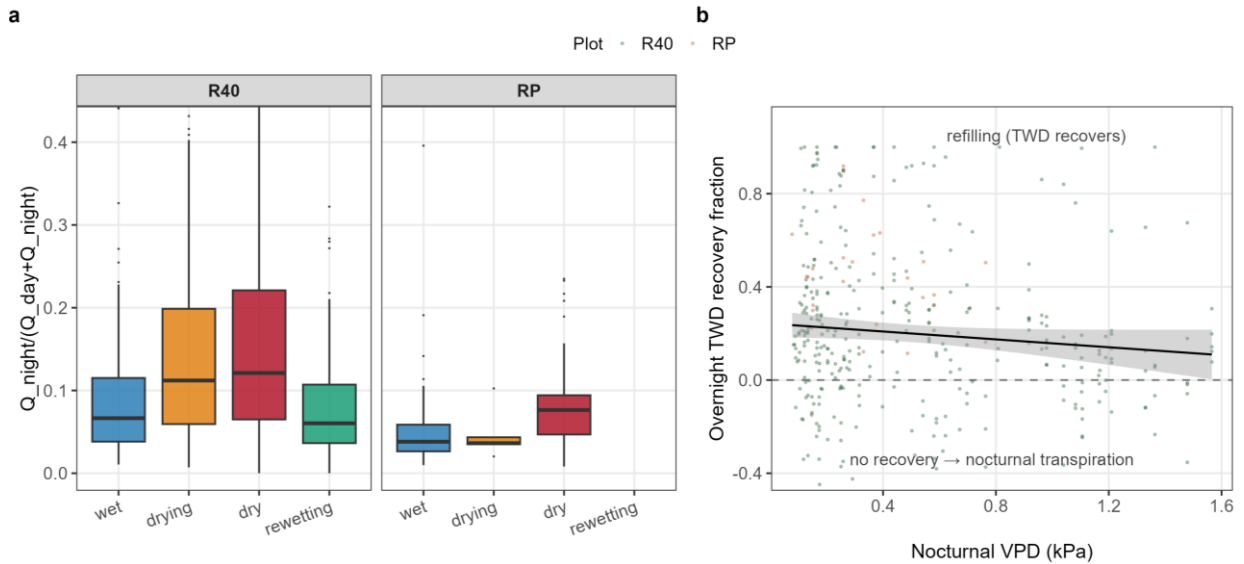


Figure 44: Nocturnal flux and overnight recovery of the stem reservoir. (a) Nocturnal share of daily water use $Q_{night} / (Q_{day} + Q_{night})$, per plot and season (boxplots over tree-nights). (b) Overnight TWD recovery fraction vs nocturnal VPD, one point per tree-night, coloured by plot. Solid line = GAM fit with 95 % CI.

First, overnight recovery of the deficit (Fig. 44b) stays high and largely independent of nocturnal VPD: 72 % of nights recover at least partly, and the downward trend with VPD is too weak to be conclusive ($r = -0.09$, NS). Refilling is therefore not disrupted by night-time demand, which already points to recharge rather than VPD-driven transpiration.

Second, the stratified test (Appendix F) confirms this reading. When the reservoir is refilled ($TWD_{pre} \leq 0.10$), pre-dawn flux stays flat at about 0.10 regardless of VPD ($R^2 = 0.01$, slope NS), with no night-time transpiration signal at the population scale. When it is not refilled, flux rises with VPD ($R^2 = 0.11$, slope = +0.10, $p < 0.001$). This dependence is still

consistent with refilling rather than transpiration proper, if the root-to-stem gradient strengthens under high VPD, an interpretation the present data cannot formally test.

Overall, in both stands the nocturnal flux is dominated by refilling. The rise in Q_{night} through the dry season (up to 12 % in R40, Fig. 44a) reflects deeper pre-dawn deficits left to refill, not increased night-time transpiration. This independent check justifies the per-night MAX baseline that consider less nocturnal transpiration.

6.5.4. The water cost of wood production

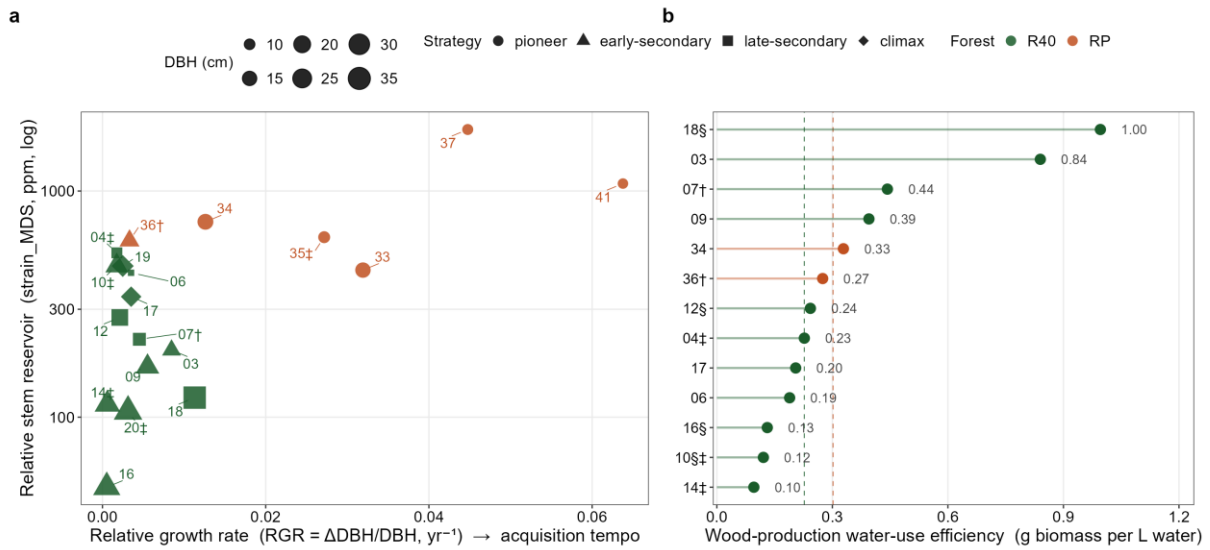


Figure 45: Synthesis of the dendrometer $\times$ sap-flow crossing. (a) Multi-trait space across the full dendrometer range: point size = DBH, colour = forest ($n = 19$, 13 R40 + 6 RP). (b) Wood-production water-use efficiency per tree, dashed lines = per-forest median; only sap-flow-instrumented trees appear (11 R40, 2 RP). † reserve, ‡ low confidence.

Bringing the three signals into one space sets the per-tree results of §6.5.2 to §6.5.4 against growth (§6.3) and reservoir size (§6.4). In this space (Fig. 45a) the two forests occupy distinct regions: the RP pioneers cluster at high RGR and large relative reservoir, at small DBH, while the R40 trees spread at low RGR across the full range of reservoir sizes. The separation is robust where it rests on the whole collection (acquisition tempo and relative reservoir, $n_{RP} = 6$); it is weak for wood density and absent for the regulation traits, which either follow a shared law (the Oren coordination, §6.2.4) or appear in only a handful of R40 (the diurnal buffering of §6.5.1). The forests therefore part on how fast they build and how large a relative reserve they carry, not on how they regulate water.

In absolute terms, the biomass increment ΔAGB (Chave et al. 2014) is dominated at R40 by a single individual: 18 (DBH 35.4 cm) alone produces 9.85 kg yr^{-1} , more than half of the eleven-tree total (18.5 kg yr^{-1} , per-tree median 0.49 kg yr^{-1}). The two RP pioneers instrumented for sap flow (34, 36†, DBH 15.7–17.6 cm) yield 1.21 and 0.37 kg yr^{-1} respectively, a per-tree median of 0.79 kg yr^{-1} . At comparable DBH the RP stems therefore convert their volume into biomass faster than their R40 equivalents, in line with the RGR contrast of Fig. 45a.

One question then closes the crossing: once regulation and the reservoir are accounted for, how much water does each tree spend to build wood? Wood-production water-use efficiency (Fig. 45b) spans a tenfold range within the R40 stand-alone (from 0.10 in 14 $\ddagger$ to 1.00 in 18), and the two measured pioneers (34, 36 $\dagger$) fall mid-ranking, their per-forest medians being nearly coincident ($R40 \approx 0.23$; $RP \approx 0.30$). These per-tree medians are in the order of magnitude expected from stand-level biomass increment in tropical secondary forests ($\approx 2\text{--}8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ depending on stand age; Poorter et al. 2016, Rozendaal et al. 2019) divided by typical Atlantic forest transpiration ($800\text{--}1200 \text{ mm yr}^{-1}$; Cabral et al. 2010), giving a stand-level WUE_w of $\approx 0.2\text{--}1.0 \text{ g L}^{-1}$. Among the measured trees, the efficiency of converting water into wood does not separate the two forests: a faster build does not come at a measurably different water price.

This efficiency reading stays exploratory and descriptive, at the tree level. The biomass increment compounds several assumptions (wood density, predicted height), the top of the ranking (18) rests on a reference density, and the metric is not scaled to the stand, since RP stand transpiration rests on only one to two trees per period and the most productive pioneers are not instrumented for sap flow. The multi-trait space itself is read relatively, both of its axes carrying a $1/\text{DBH}$ term.

6.6. Sensitivity analysis

Transpiration chain

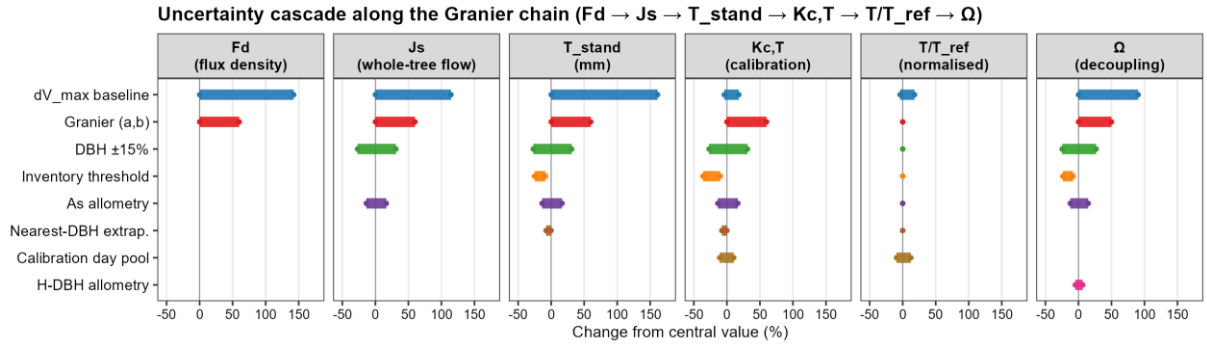


Figure 46: Uncertainty cascade along $F_d \rightarrow J_s \rightarrow T_{\text{stand}} \rightarrow K_{c,T} \rightarrow T/T_{\text{ref}} \rightarrow \Omega$ (rows = sources, columns = chain steps). The dV_{max} baseline and Granier coefficients dominate the per-tree fluxes. Shared rescalings cancel in T/T_{ref} , leaving only the baseline residual ($-4/+18\%$) and the $K_{c,T}$ calibration ($\approx \pm 10\%$). Ω inherits T_{stand} uncertainty through G_c .

First, F_d carries the smallest number of perturbation sources during daytime (Fig. 46), depending only on the Granier coefficients ($\times 1.00$ to 1.60 , Bush 2010 $\rightarrow$ Steppe 2010); J_s adds the per-tree DBH and A_s allometry (DBH $\pm 15\% \rightarrow \pm 31\%$, $A_s \pm 17\%$). The dV_{max} baseline reaches the largest single amplitude across the cascade (F_d up to $\times 2.4$) but its effect is almost entirely nocturnal, so the daytime dynamics underlying 6.2 and 6.5 stay robust.

Second, scaling to the stand adds the extrapolation uncertainty (T_{stand}). $DBH \pm 15\%$ propagates to $\times 0.73 / \times 1.31$ on T_{stand} through $A_s \propto DBH^{1.94}$, and the inventory threshold ($B_{all} \rightarrow B_{dbh10}$) lowers T_{stand} by -25% . Per-tree dynamics (F_d, J_s) stay unchanged.

Third, the ratio T/T_{ref} is robust by construction: Granier, DBH , A_s , the inventory threshold and the nearest- DBH extrapolation cancel exactly, because KcT is calibrated from the same F_d , allometry and inventory as the production output. Only two residuals remain: a baseline term ($-4/+18\%$, the wet-season calibration only partly tracks it) and the calibration day pool ($\approx \pm 10\%$; $KcT = 0.349$, bootstrap 95 % CI [0.31, 0.39]). By contrast T/ETP uses an external Kc , $ETP = 1.16$ (Delvoie 2023), which does not cancel: that ratio inherits the full absolute uncertainty (Granier $\times 1.0$ to 1.6 , $DBH \pm 30\%$, $A_s \pm 17\%$) and is to be read as an order of magnitude. The decoupling coefficient Ω closes the chain through G_c and inherits the T_{stand} uncertainty profile.

The most influential choice is the dV_{max} baseline. Seven variants cover an annual T_{stand} range of $\times 1.00$ to 2.61 (Fig. 46). The spread is almost entirely nocturnal ($Q_{night} \times 1.0$ to 5.7 vs $Q_{day} \times 1.0$ to 2.2). The pipeline uses a season-specific baseline (per-night MAX in the wet season, rolling MAX $w = 2$ over ideal-nights windows in the dry season, M&M §2.4), which matches the most restrictive variants; on T/T_{ref} the effect is reduced to $\times 0.96$ to 1.18 .

Uncertainty budget

Table 5: Cross-signal sources of uncertainty on plot-median $WUE_w = \Delta AGB / Q_{year}$ (ΔAGB side). The Combined rows quadrature-sum these ΔAGB -side sources with the Q -chain envelope from the sap flow OAT (Appendix Table 13), giving the total uncertainty on plot-median WUE_w . Per-tree ranking is preserved across p alternatives (Spearman $\rho = 1.000$).

Component	Source	Central value (perturbed)	Absolute interval	Low / High (%)
Numerator (ΔAGB)	ρ choice [R40]	$\rho_A median = 0.41 \text{ g cm}^{-3}$	[0.41, 0.41] g cm^{-3} *	-45.4 / 0
	ρ choice [RP]	$\rho_A median = 0.38 \text{ g cm}^{-3}$	[0.38, 0.48] g cm^{-3}	0 / +33.1
	H-DBH	$\Delta AGB_{stand} = 5120.7 \text{ kg}$	[4620, 5620] kg	-9.8 / +9.7
	allometry ($\pm 10\%$)			
Denominator (Q)	Sap flow chain	$Q_{year} median \approx 2.79 \text{ m}^3 \text{ tree}^{-1} \text{ yr}^{-1}$	[1.65, 7.70] $\text{m}^3 \text{ tree}^{-1} \text{ yr}^{-1}$	-40.9 / +175.9
WUE_w bilan	Combined R40	$WUE_w, R40 = 0.227 \text{ g L}^{-1}$	[0.048, 0.386] g L^{-1}	-78.9 / +69.9
	Combined RP	$WUE_w, RP = 0.302 \text{ g L}^{-1}$	[0.107, 0.536] g L^{-1}	-64.5 / +77.4

* Per-tree shifts between A/B/C drive the WUE_w effect, plot-median ρ unchanged.

The uncertainty on plot-median $WUE_w = \Delta AGB / Q_{year}$ is decomposed by side of the ratio (Table 5). On the numerator side, the wood-density choice dominates at R40, where the species-median (B) and plot-median (C) substitutions shift ΔAGB by -45 , and -26 , relative to the per-tree direct measurement (A). At RP the effect is opposite (B = $+23$, C = $+33$,) because

the plot-median ρ (0.475 g cm^{-3}) exceeds the two per-tree direct values (0.30 and 0.45 g cm^{-3} , $n = 2$). The H-DBH allometry contributes a smaller ± 10 , perturbation propagated through Chave et al. (2014). Per-tree WUE_w ranking is preserved across the three ρ options (Spearman $\rho = 1.000$). On the denominator side, the full sap flow chain covers $-41 / +176$, on the per-tree annual flux Q_{year} , which propagates inversely to WUE_w via the $1/Q$ scaling and dominates the budget at both plots.

Combining numerator and denominator by quadrature, the total uncertainty on plot-median WUE_w covers $[0.048, 0.386] \text{ g L}^{-1}$ at R40 and $[0.107, 0.536] \text{ g L}^{-1}$ at RP. The central values $\text{WUE}_{w,R40} = 0.227$ and $\text{WUE}_{w,RP} = 0.302 \text{ g L}^{-1}$ should be read as order-of-magnitude estimates, while the $R40 < RP$ contrast remains robust because no single source reverses its sign within the plausible bounds.

7. LIMITS AND PERSPECTIVES

The sensitivity analysis (§6.6.1) confirms that relative signals and between-tree rankings stay within about $\pm 10 \%$, while absolute magnitudes, starting with stand transpiration, should be read as orders of magnitude. Two confounds also weigh on every chapter. F_d mixes sun and shade leaves (Zhang et al. 2014). The shade fraction is larger under the closed R40 canopy than under the open RP plantation, which can bias the g_{ref}/Ω comparison in chapter 6.2. The root-weighted Ψ_{soil} profile also treats each plot as uniform, when soil moisture varies on a metre scale in tropical forest (Bréda et al. 1995). Part of the between-tree variability in chapters 6.4 and 6.5 may therefore reflect different soil microsites rather than physiological differences.

Stand upscaling and cross-method validation. Stand transpiration was scaled up from only eight trees, all in the upper diameter range (smallest DBH 20 cm), while much of the inventory sapwood is carried by thinner stems. No clear F_d -DBH relationship was found on the instrumented set, so attributing each inventory tree to its nearest-DBH instrumented neighbour transfers a behaviour from large trees to thinner ones. This unbalanced sample probably contributes to the threefold gap with the inverse water balance on the same plot (Delvoie 2023, ≈ 257 vs $\approx 900 \text{ mm yr}^{-1}$). No single method closes the tropical ET budget to better than 20% (Wilson et al. 2001). Combining sap flow with HYDRUS-1D would let each method check the other. A richer inventory, with DBH, height, species and successional strategy (P / ES / LS / C), combined with a mixed-effects $F_d \sim \text{size}$ model (Berdanier et al. 2016), would allow a size-resolved upscaling with explicit uncertainty bounds.

Probe assumptions and imported thresholds. The TDP probe measures a single radial depth, while F_d decreases toward the inner sapwood in tropical diffuse-porous species (Berdanier et al. 2016, Meinzer et al. 2003). Wounding around the heated needle can cause a $10\text{--}30 \%$ drift over a year (Wiedemann et al. 2016), which looks like a real seasonal decline. Several downstream thresholds also come from temperate work. The stress threshold $TWD_{\text{norm}} > 1$ (Peters et al. 2025) is an order of magnitude above the plateau found here (0.05--

0.22), which suggests a lower threshold for tropical diffuse-porous species. The SOTA storage range (10–50 %, Goldstein et al. 1998) was established on large old trees. The $f_{storage} \approx 6\%$ measured on the young RP pioneers (DBH 10–20 cm) is more likely a size effect (Meinzer et al. 2003) than a physiological anomaly. A mid-season re-installation of the probes, a radial profile on a few trees, and a local recalibration of these thresholds would help the next campaign.

$K_{c,T}$ calibration and ΔV_{max} baseline. The flux signal is noisier in the wet season, when frequent rain causes diurnal jumps and baseline shifts that degrade F_d . This adds uncertainty at the very first step of the pipeline. No calibration window is fully clean. The strict wet window is conservative but noisy, and the wider window tested as an alternative includes mild limitations under the TWD threshold. The envelope of $K_{c,T}$ across inventory choices remains wide (0.24–0.35). ΔV_{max} also) and depends on stem water content, which drops during the day (Vergeynst et al. 2014), and adjusting it by season trades correction for coverage. In the OAT cascade (§6.6.1), 84 % of the upper flux envelope comes from this baseline choice alone among seven methodological variants. This is more a choice between methods than a true statistical uncertainty. Removing it cuts the envelope in half. The $R40 < RP$ contrast, the between-tree ranking (Spearman $\rho = 1$) and the relative comparisons remain robust, nonetheless. A continuous baseline correction driven by a proxy of stem water content, combined with a species-specific gravimetric calibration of the Granier coefficients (Pasqualotto et al. 2019), are the most direct ways to narrow the absolute magnitudes.

Data acquisition, quality control and future monitoring. Solar power does not always cover late night and early morning, especially on RP, which weakens pre-dawn diagnostics (Köcher et al. 2013). The mean-diurnal gap-filling (§5.5.2) restores coverage but adds an internal correlation in the analyses that use it. Three automated QC tools were tested on the raw signal and dropped in favour of tree-by-tree manual QC: Baseline for the flux (Oishi et al. 2016), dendrometeR for the dendrometer (van der Maaten et al. 2016) and Sapflower for the full TDP pipeline. Each signal has its own noise pattern, and the automation flagged almost all points on several trees. A reasonable next step is a semi-automated mode in which each tree is validated by eye. The lack of leaf water potential also rules out a strict iso/anisohydric reading (Martínez-Vilalta et al. 2014), and the water-use efficiency here only covers wood production. A larger pioneer sample, leaf water potential measurements, and a multi-year follow-up including a marked drought would strengthen the conclusions, which are now bounded to a single year without extreme stress. Such a follow-up would also allow testing of legacy effects on growth (Salomón et al. 2022). In the global sap flow context, however, $n = 8$ trees per plot is still at the median of the SAPFLUXNET database (Poyatos et al. 2021), which makes this limit a structural constraint of the field rather than a specific weakness of this study.

8. CONCLUSION

Tropical forests hold a large share of the world's terrestrial carbon and return a substantial fraction of the rain they receive to the atmosphere through transpiration, so the way each stand combines water use and wood production matters far beyond its own boundaries. In the Brazilian Atlantic Forest, where less than a tenth of the original cover remains and most of the standing forest is now at an early successional stage, this balance carries both ecological and management weight. The carbon stored by a regrowing stand depends on how its trees use water and how that water is converted into wood, yet measurements that couple the two at the individual-tree scale remain scarce in tropical secondary forests. At São Francisco Xavier, on the eastern slopes of the Serra da Mantiqueira, a young pioneer plot planted in 2008 (RP, about twelve years old at the time of measurement) and an older secondary plot of about fifty years (R40) sit side by side on the same slope, the same soil and the same climate, which makes it possible to read this trade-off through a controlled successional contrast.

The overall question of this work is how transpiration, growth and stem water reserves vary within and between these two stands, and what these coupled signals reveal about the hydraulic strategies of individual trees. Four sub-objectives organise the answer. A careful processing of the raw sap flow and dendrometer records first identifies the usable tree-period support. A per-tree reading of transpiration, radial growth and tree water deficit then characterises the agreement or disagreement between trees of the same stand. A cross-signal analysis positions each tree on a comparative strategy space. Finally, a stand-scale aggregation quantifies the contrast between R40 and RP, relative to the structural and successional differences expected between them.

This work was carried out in collaboration with the research team of Laura Borma at the Brazilian National Institute for Space Research (INPE), which has been monitoring the two plots for several years. The analyses focus on the 2020 hydrological year, for which an instrumented set-up was available on both plots. Granier thermal-dissipation probes recorded sap flux density on twenty-two trees from four successional strategies, point dendrometers tracked stem-radius variation on the same trees in parallel, and an on-site weather station provided rainfall, air temperature, humidity and radiation, from which reference evapotranspiration was computed (FAO-56 Penman-Monteith). A full inventory of the two plots provides the support for stand-scale upscaling. Both signals pass through a quality-control pipeline that combines automated filters with tree-by-tree manual checking. This step was one of the most decisive of the work: the raw records were noisy and broken by frequent power gaps and recovering them tree by tree is what made them reliable enough for every later analysis.

Sapwood area was estimated from species-specific allometries, soil water potential in the root zone was rebuilt from a depth profile weighted by fine-root density, and a site-level transpiration coefficient was calibrated against flux conservation on non-limiting wet-season nights, so the sap flow signal can be read as a normalised transpiration ratio. The dendrometer

signal was broken down following Zweifel into a growth term (GRO), a tree water deficit (TWD) and a maximum daily shrinkage (MDS), each normalised tree-by-tree against its own maximum to remove the size effect. The two signals were then crossed at four-time scales: the diurnal lag between sap flow and stem refilling, daily growth thresholds against atmospheric and stem-water indices, seasonal stomatal sensitivity and recovery after dry windows, and yearly stand transpiration and water-use efficiency of wood production. The methodological choices were checked by a one-at-a-time sensitivity cascade that ran from the raw flux to the stand-level ratio.

The second objective was to follow each tree on its own, analysing its transpiration, radial growth and stem water reserves as separate signals. At the individual scale, the two forests shared a single stomatal regulation rule, close to the theoretical Oren optimum. The pioneers opened their stomata somewhat more per unit of sapwood, but this difference is one of degree, not of regulation type. Across every signal, the variation between trees exceeded the contrast between forests. Which tree was most exposed, which emptied its reservoir first and which recovered best was decided at the tree level. Once a deficit set in, recovery was fast and was set mainly by the tree itself, along a slow-fast continuum.

The third objective was to link these three signals. Bringing flux and growth together showed that transpiring is not growing. Transpiration follows atmospheric demand, while wood is built only when demand and soil water meet inside a window where turgor stays high enough. Growth thus stops at a milder deficit than the one that closes the stomata, which explains why transpiration continued in the dry season while growth had already stopped. The tree water deficit emerged as the variable linking the water transpired, the water stored and released, and the wood that is not built. It also clarifies how the normalised transpiration index should be read: a value below its reference does not signal stress on its own, since a low value reflected low atmospheric demand as much as a real soil limit.

The final step scaled these individual signals to the plot and contrasted the two successional stages. The lower stand transpiration of the pioneer plot does not come from a different regulation. It is mainly structural, the pioneer plot carrying almost three times less conductive sapwood per unit of ground. The weak canopy-to-air decoupling, similar in both plots, confirmed that these montane forests are tightly coupled to the air. The stem reservoir contributed comparably to daily water use in both forests, but its amplitude diverged: the pioneers drew on a relatively larger internal reserve, while the secondary trees appeared more buffered by a deeper soil store. The water cost of a unit of wood did not set the two stands apart, the faster growth of the pioneers owing more to lighter wood than to a better conversion of water into biomass.

These conclusions rest on relative and intrinsic signals that held up against the methodological choices, while the absolute magnitudes, including stand transpiration, remain affected by the uncertainty of the thermal-dissipation method and should be read as orders of magnitude. The study was further bounded by a single year without extreme drought, by the absence of leaf water potential, and by a small pioneer sample.

Coming back to the question that opened this work, pioneer and secondary stages do diverge, but not where a textbook reading would place the divergence. They do not differ in how each tree controls its stomata, nor in how efficiently water is turned into wood. They differ in how much conductive sapwood the stand carries, in how much each tree leans on its own stem reservoir rather than on the soil, and in the density of the wood it builds. Successional stage therefore sets the structural frame and the share of the water budget that runs through the internal reserve, while the regulation itself and the fate of the trees inside that frame are set by the tree, along a continuum rather than across a clean pioneer-versus-secondary boundary.

Overall, the objectives were largely met, though some uncertainty remains and the central question is only partly answered. At the tree level, several analyses were robust enough to identify both differences and similarities between individuals. At the plot level, the comparison yielded some points of contrast, but these were not always robust, mainly because of the limited data in the pioneer plot. These findings nonetheless provide a good basis and a direction for further analysis.

Under these reservations, this work shows the value of pairing sap flow and dendrometry to track, at the individual-tree scale, the trade-off between water use and wood building in reforested secondary forests. Extended over several years and combined with leaf water potential measurements and a species-specific calibration, such an approach would help predict how the regrowing slopes of the Mantiqueira respond to rising atmospheric dryness and better reconcile their roles in carbon storage and water regulation.

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APPENDIX

APPENDIX A – Climate and site

A.1 Daily meteo 2020

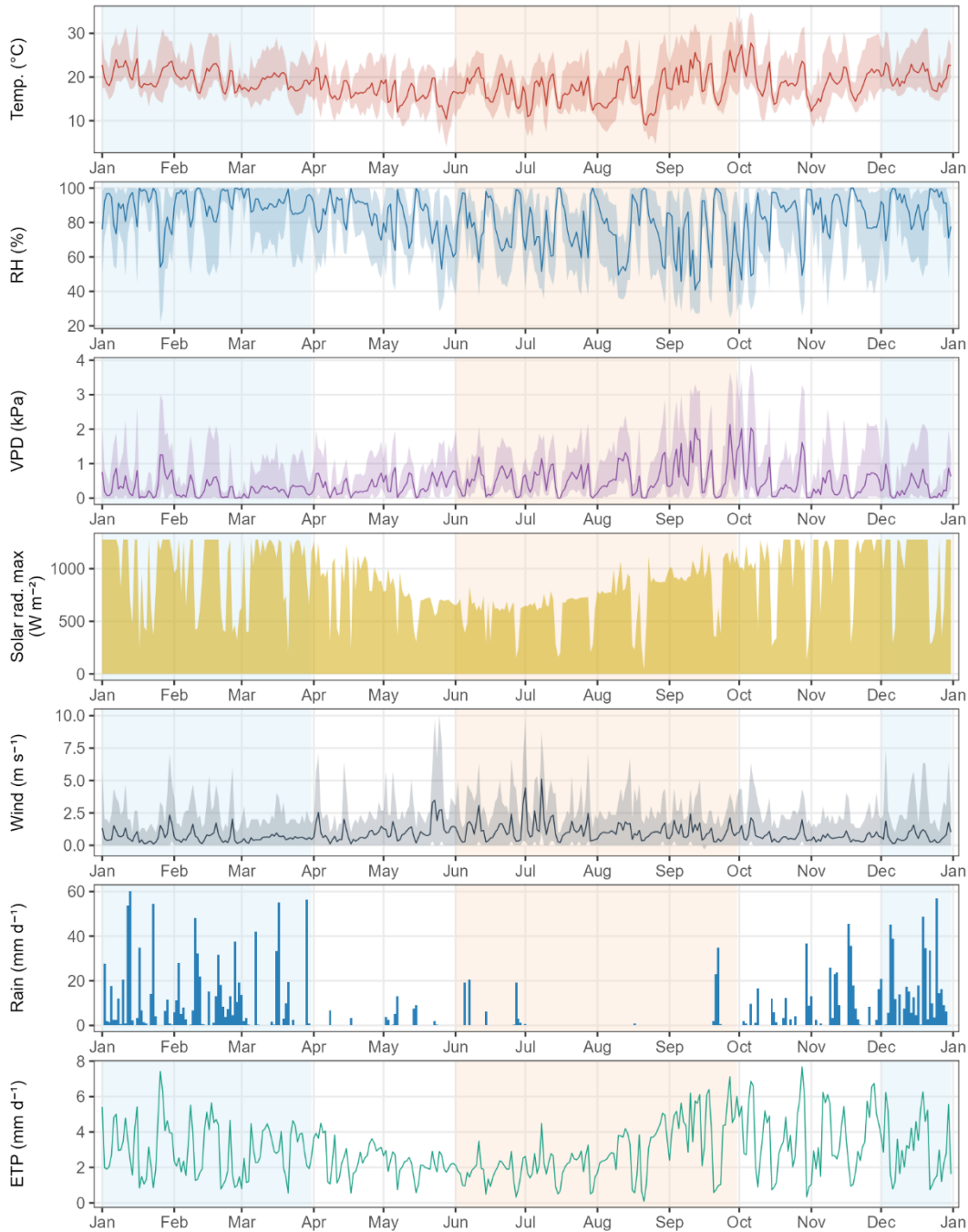


Figure 47: Daily meteorological conditions at the São Francisco Xavier study site over 2020. From top to bottom: air temperature, relative humidity, vapour-pressure deficit (VPD), maximum solar radiation, wind speed, precipitation, and potential evapotranspiration (ETP). For temperature, relative humidity, VPD and wind speed, the coloured line shows the daily mean and the shaded envelope the daily minimum–maximum range. Solar radiation is the daily maximum irradiance (filled area) and precipitation the daily total. Vertical shaded bands indicate the wet season (blue: January–March and December) and the dry season (orange: June–September).

A.2 soil matric potential and root density along the two plots soil profiles

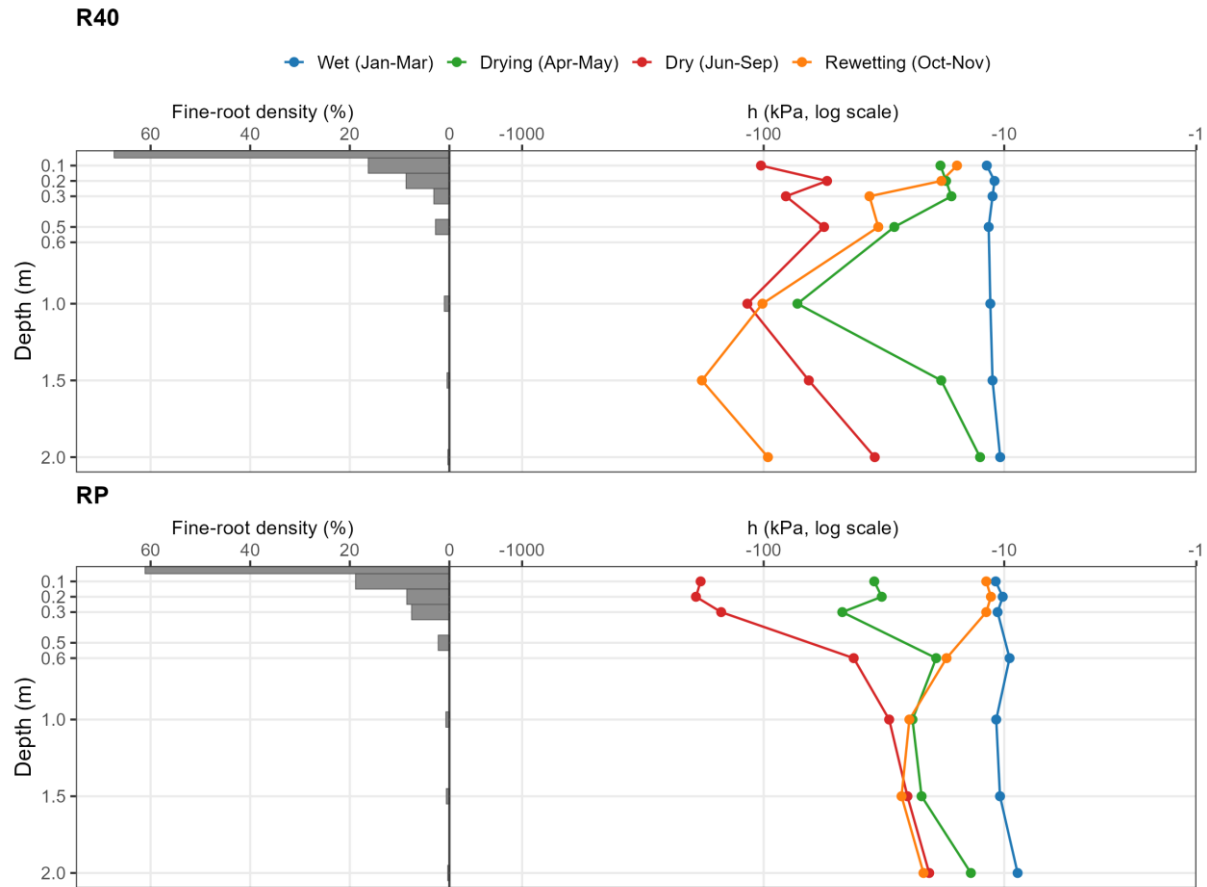


Figure 48: Soil matric potential and fine-root density profiles. Each row pairs fine-root density (left, grey bars, % of total fine-root mass per layer, Delvoie 2023) with median soil matric potential h per sensor depth and season (right, coloured lines, 2020). R40 (top, ≈ 50 yr) shows steep root decline and sharp drying at depth, RP (bottom, ≈ 12 yr) a more spread root profile and weaker dry-season drying, consistent with the proximity of the groundwater table.

A.3 Root-density weights for Ψ_{soil}

Table 6: Fine-root density weights used in the depth-averaged soil matric potential h . Weights are derived from the fine-root mass profiles (DRFinas , g dm^{-3}) measured by Delvoie (2023) on the same two plots. Each tensiometer is assigned to the soil layer with nearest midpoint. The 0–5 cm surface layer is not weighted in (no tensiometer at that depth). Weights are normalised so that $\sum w_i = 1$ per plot.

Sensor depth (m)	Soil layer (cm)	w_R40	w_RP
0.1	5–15	0.50	0.50
0.2	15–25	0.27	0.23
0.3	25–35	0.10	0.20
0.5 (R40) / 0.6 (RP)	45–55	0.09	0.06
1.0	95–105	0.03	0.02

APPENDIX B – Raw measurements of monitored trees (2018, 2023, 2026)

Table 7: Inventory measurements 2018, 2023, 2026 — DBH and sapwood area A_s of the monitored trees. Rows labelled « X_{alt} » correspond to alternative individuals measured at the same position when the originally tagged tree could not be unambiguously identified in a later campaign. A_s is measured directly on cored individuals only ; empty A_s cells indicate that the tree was not cored that year. Empty DBH cells indicate that the tree was not measured that year.

Tree	Plot	Specie	Family	DBH 2018 (cm)	DBH 2023 (cm)	DBH 2026 (cm)	As 2018 (cm ²)	As 2023 (cm ²)	As 2026 (cm ²)
1	R40	<i>Miconia cinerescens</i> Miq.	Melastomataceae	29.92			27.44		
3	R40	<i>Alchornea glandulosa</i> Poepp.	Euphorbiaceae	31.21	14.64	15.41	56.61	115.7	
4	R40	<i>Tovomitopsis paniculata</i> (Spreng.) Planch. & Triana	Clusiaceae	7.64		10.41	69.28		79.0
6	R40	<i>Endlicheria paniculata</i> (Spreng.) J.F. Macbr.	Lauraceae	23.89	8.09	7.89	32.57	43.8	
7	R40	<i>Tovomitopsis paniculata</i> (Spreng.) Planch. & Triana	Clusiaceae	12.42	12.83	12.83	117.58	113.3	
8	R40	<i>Alchornea glandulosa</i> Poepp.	Euphorbiaceae	7.64	18.91	19.29	143.99	262.7	
9	R40	<i>Alchornea glandulosa</i> Poepp.	Euphorbiaceae	17.52	21.68	22.19	227.75	341.8	
10	R40	<i>Alchornea glandulosa</i> Poepp.	Euphorbiaceae	15.29	20.12	21.42	158.92	290.1	307.9
11	R40	<i>Alchornea glandulosa</i> Poepp.	Euphorbiaceae	18.31			207.52		
12	R40	<i>Casearia obliqua</i> Spreng.	Salicaceae	26.43		19.61	202.68		277.8
14	R40	<i>Miconia cinerescens</i> Miq. Ou <i>Vernonanthura discolor</i> (verificar)	Melastomataceae	23.57	25.08	25.27	17.04	462.3	
16	R40	<i>Alchornea glandulosa</i> Poepp.	Euphorbiaceae	13.69	28.78	29.35	445.79	169.3	232.4
17	R40	<i>Aspidosperma olivaceum</i> Müll. Arg.	Apocynaceae	23.57	29.95	31.45	393.83	684.9	
18	R40	<i>Schefflera cf. calva</i> (Cham.) Frodin & Fiaschi	Araliaceae	18.15	37.24	39.04	510.14	1053.2	
19	R40	<i>Aspidosperma olivaceum</i> Müll. Arg.	Apocynaceae	10.51	34.06	35.71	327.04	867.8	
20	R40	<i>Alchornea glandulosa</i> Poepp.	Euphorbiaceae	26.43	32.21	32.79	488.77	408.3	717.3
30	RP	<i>Tibouchina estrellensis</i> (Raddi) Cogn.	Melastomataceae	17.36			148.98		
31	RP	<i>Tibouchina pulchra</i> (Cham.) Cogn.	Melastomataceae	12.99			132.32		
32	RP	<i>Senna multijuga</i> (Rich.) H.S. Irwin & Barneby	Fabaceae	16.82			173.98		
33	RP	<i>Baccharis lateralis</i> Baker	Asteraceae	15.61			85.43		
34	RP	<i>Tibouchina pulchra</i> (Cham.) Cogn.	Melastomataceae	17.20			174.02		
35	RP	<i>Tibouchina pulchra</i> (Cham.) Cogn.	Melastomataceae	10.19			81.00		

36	RP	<i>Cedrela fissilis</i> Vell.	Meliaceae	15.51	120.78
37	RP	<i>Tibouchina pulchra</i> (Cham.) Cogn.	Melastomataceae	9.36	46.23
38	RP	<i>Tibouchina pulchra</i> (Cham.) Cogn.	Melastomataceae	10.06	74.72
39	RP	<i>Tibouchina pulchra</i> (Cham.) Cogn.	Melastomataceae	7.01	30.46
40	RP	<i>Lafoensia pacari</i> A. St.-Hil.	Lythraceae	8.60	27.88
41	RP	<i>Tibouchina pulchra</i> (Cham.) Cogn.	Melastomataceae	8.54	46.22

APPENDIX C – Quality control dendrometer

C.1 Dendrometer pipeline – full parameter reference

Table 8: All parameters used in *R_dendro/01_qc_dendro.R* (run 14). Filters are listed in the order of application; reset detection runs after the automated filters and manual invalidation; interpolation and smoothing are applied to the reset-corrected signal. References are only repeated when the parameter follows a published convention or threshold; values calibrated from this dataset are tagged "this study".

Parameter	Value	Justification / Reference
Resampling grid	1 min	Regularises the native 66-s acquisition for filter applicability and downstream alignment
Filters		
Physical range	[0, 10] mm	2× maximum annual amplitude observed on Atlantic Forest stands — Zweifel et al. 2016
Post-gap — minimum gap duration	10 min	Empirical threshold above which the re-stabilisation profile becomes identical (<i>diag_postgap_empirical.R</i>)
Post-gap — invalidated points	45 pts (≈ 45 min)	p95 of re-stabilisation duration on T01 (median 7 min, p95 42 min, $n = 264$ gaps)
Frozen — minimum run length	30 pts (≈ 30 min)	Shortest plausible duration of a mechanically failed sensor
Frozen — Ax threshold	5×10^{-4} mm	$\approx 1.5 \times$ sensor noise floor (RMS of successive differences on stable periods $\approx 3 \times 10^{-4}$ mm)
Hampel — half-window	120 pts (± 4 h, total 4 h)	Wider than the 60-pt default of SAPFLUXNET to bracket thermal arcs (1–3 h)
Hampel — robustness multiplier k	3.0	Standard robust threshold (Pearson 2002); $k = 2.5$ tested but too aggressive on legitimate fluctuations
Hampel — absolute floor	10^{-3} mm	Above the sensor noise floor — Peters et al. 2021
Hampel — absolute ceiling	0.3 mm	Aligned with the reset minimum jump; defers larger steps to reset detection
Sub-diurnal noise — residual SD threshold	7×10^{-4} mm	95th-pct of residual SD on a deliberately noisy reference month (T03, August 2020) — this study
Sub-diurnal noise — detrending window	15-min running median (31 pts)	Removes diurnal trend while preserving noise structure
Sub-diurnal noise — evaluation window	± 30 min (61 pts)	Stable local SD estimate at the diurnal scale
Sub-diurnal noise — boundary dilation	± 2 pts	Bracket the noisy zone fully
First-difference threshold	$0.01 \text{ mm step}^{-1}$	Maximum instantaneous physiological rate of stem-radius change — Zweifel et al. 2016
Wind threshold	3.0 m s^{-1} (15-min site average)	Site-specific calibration; uniform across trees
Orphan — minimum run length	10 pts (≈ 10 min)	Preserves the fragmented signals of the RP plot

Orphan — minimum flanking gap	10 pts	Relaxed from 1 pt to avoid over-flagging
Reset detection		
Minimum jump	0.3 mm	Aligned with Hampel ceiling; smallest real reset observed = 0.58 mm
Minimum gap for boundary	30 min	Captures short dropouts followed by a persistent level shift
Persistence window	20 pts before / 20 pts after	Median comparison for level-shift confirmation
Transition buffer	20 pts set to NA	Prevents the corrected-point spike from capping GRO via the cumulative maximum
Gap filling		
Maximum interpolation gap	2 h	Less than half a diurnal cycle (treenetproc default: 30 min, stricter)
Maximum interpolation rate	$5 \times 10^{-3} \text{ mm min}^{-1}$	Physiological limit on stem-radius rate of change — Zweifel et al. 2016
GRO envelope LOCF horizon	24 h	Preserves cumulative-maximum continuity across short gaps
Coverage filters		
Daily coverage threshold (MDS aggregation)	40 % of 1 440 min	Sufficient to capture both daytime contraction and overnight expansion phases
Window coverage threshold (analysis stage)	to confirm	The 15 % value used in earlier runs needs to be aligned with the 40 % MDS threshold
Smoothing		
Centred rolling median for ZG decomposition	31 min (≥ 7 valid pts)	Separates time scales from Hampel (240 min) and the diurnal cycle (24 h)
GRO computation	cumulative maximum of <code>x_smooth</code>	Standard Zero-Growth approach — Zweifel et al. 2016; treenetproc; dendRoAnalyst

C.2 Per-tree data state

Table 9: All percentages are computed relative to the total number of minutes in 2020 ($n = 527\,040$ min). The detail of filter contributions is non-exclusive: a single minute flagged by k filters is counted in each filter row, so the sum of filter columns can exceed Flag total and may be larger than 100 % on heavily flagged trees. After QC is the valid fraction after all filters and manual invalidation; With interp is the valid fraction after gap filling (§X.X.3). The filters Range, Frozen and Diff didn't flag any values and are not shown in the table.

Tree	Plot	Gap raw	Flag Tot	Post-Gap	Hampel	Wind	Residual SD	Orphan	Manual	After QC	With interp
T01	R40	43.2	7.3	2.0	0.7	3.8	0.1	0.7	0.0	51.2	71.7
T03	R40	51.6	9.8	2.0	0.7	3.8	2.5	0.7	0.0	41.2	57.7
T04	R40	36.1	33.1	2.1	1.5	3.8	2.8	0.5	22.3	33.3	43.8
T06	R40	36.1	7.3	2.1	0.4	3.8	0.3	0.7	0.0	58.3	80.0
T07	R40	55.5	6.9	1.8	0.5	3.8	0.2	0.6	0.0	39.5	57.4
T08	R40	62.8	40.4	1.4	0.1	3.8	0.0	0.0	35.0	0.0	0.0
T09	R40	40.8	7.1	2.0	0.6	3.7	0.2	0.7	0.0	53.7	73.9
T10	R40	44.0	8.1	1.9	0.7	3.8	0.9	0.8	0.0	49.9	69.1
T11	R40	36.0	56.0	2.1	0.8	3.8	1.1	0.1	48.0	9.8	12.4
T12	R40	38.4	9.7	2.0	1.1	3.7	2.2	0.8	0.0	54.1	73.1
T14	R40	36.1	7.1	2.1	0.4	3.8	0.0	0.7	0.0	58.3	80.7
T16	R40	36.2	10.3	2.1	0.9	3.8	2.7	0.7	0.0	56.0	75.5
T17	R40	38.9	6.7	1.9	0.2	3.8	0.1	0.6	0.0	56.1	75.4
T18	R40	36.0	6.9	2.1	0.2	3.8	0.0	0.7	0.0	58.7	80.5
T19	R40	36.2	8.3	2.2	1.1	3.8	0.4	0.8	0.0	57.3	79.4

T20	R40	56.5	6.6	1.7	0.4	3.8	0.1	0.6	0.0	38.8	55.5
T31	RP	44.8	57.7	3.4	1.1	3.8	0.9	0.0	48.4	0.0	0.0
T33	RP	45.2	15.7	3.4	1.8	3.8	5.3	1.3	0.0	42.5	64.1
T34	RP	44.8	10.8	3.4	1.5	3.8	1.2	0.8	0.0	47.0	70.4
T35	RP	44.8	35.4	3.4	0.9	3.8	0.5	0.5	26.2	22.1	32.9
T36	RP	49.9	22.5	3.1	1.2	3.8	7.1	0.5	6.7	31.2	48.4
T37	RP	44.9	19.4	3.4	1.6	3.8	0.3	0.7	9.4	38.1	56.4
T38	RP	44.9	57.2	3.4	0.5	3.8	0.0	0.0	49.4	0.0	0.0
T39	RP	48.3	53.9	3.4	0.2	3.8	0.1	0.0	46.3	0.0	0.0
T40	RP	44.9	10.5	3.4	1.4	3.8	0.8	1.0	0.0	47.0	70.7
T41	RP	44.7	20.9	3.4	1.7	3.8	10.8	1.1	0.0	38.7	58.9

C.3 QC pipeline examples

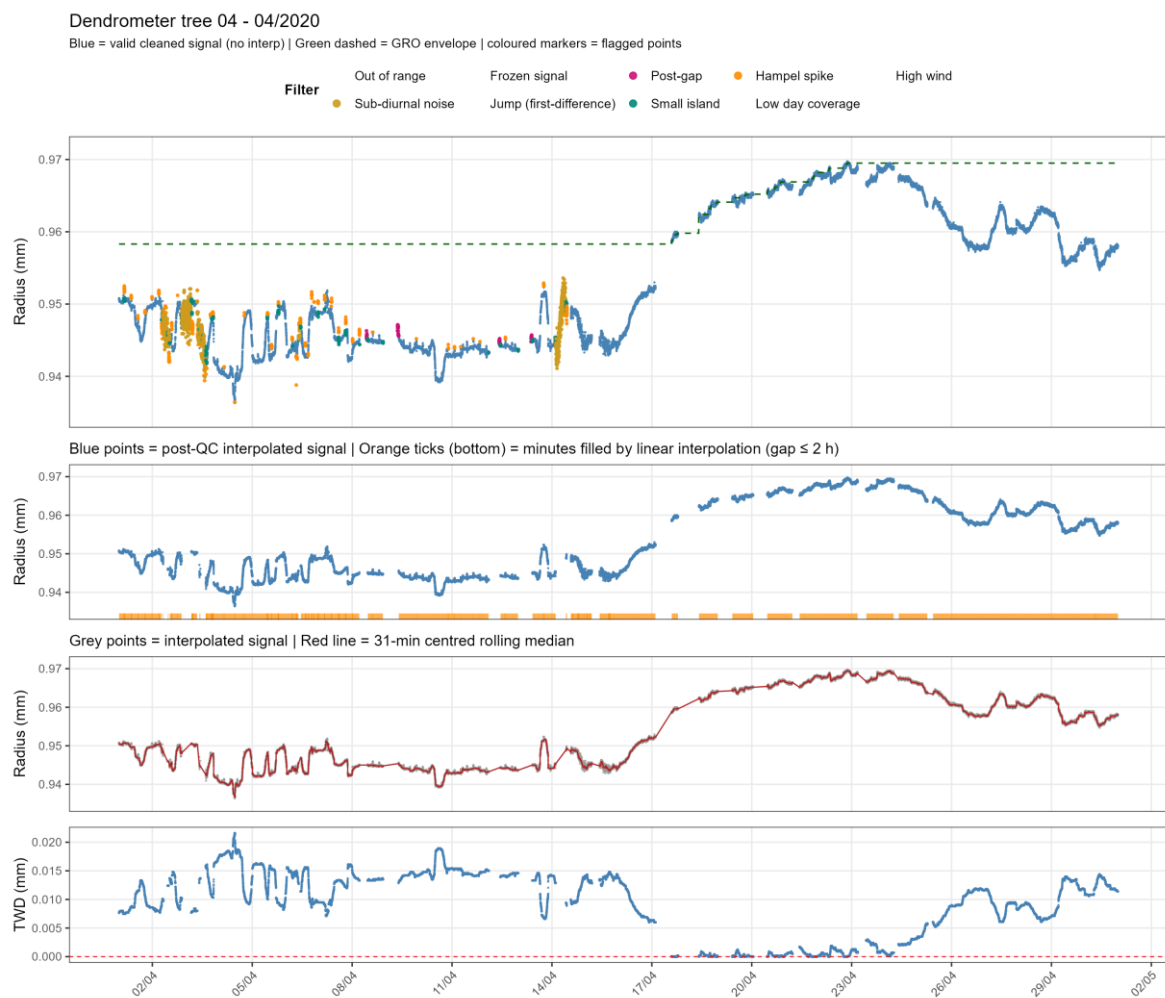


Figure 49: Dendrometer QC pipeline applied to tree 04 (R40, April 2020). (a) Cleaned signal (blue), GRO envelope (green dashed) and points flagged by the eight automated filters (Table 3.4.1). (b) Post-QC interpolated signal (blue points); orange ticks at the bottom mark minutes filled by linear interpolation (gaps ≤ 2 h). (c) Interpolated signal (grey) and the 31-min centred rolling median x_{smooth} (red line) used in the Zero-Growth decomposition. (d) Resulting tree water deficit $TWD = GRO - x_{smooth}$.

APPENDIX D – QC SAP FLOW

D.1 Full parameter reference

Table 10: All parameters used in *R_SF/01_qc_sapflow.R* (QC), *R_SF/02_convert_sapflow.R* (residual cleanup + smoothing), and *R_SF/gapfill_dV.R* (gap filling). Filters are listed in the order of application; the residual cleanup runs after the QC mask is established and before Granier conversion. References are repeated only when the parameter follows a published convention; values calibrated from this dataset are tagged "this study".

Parameter	Value	Justification / Reference
Resampling grid	1 min (5-min for analysis)	Regularises the native 66-s acquisition; 5-min step used downstream
<i>Family A — Instrumental flags</i>		
Voltage — operating range	[10.5, 16.0] V	Nominal range of the Plantem SF_DEN V1.0 supply
Heating — nominal voltage	5.70 V	Plantem SF_DEN V1.0 specification
Heating — tolerance	± 0.50 V	Tolerance below which heating remains stable
Probe T — operating range	[5, 50] °C	Plausible probe internal temperature
Post-panne — minimum gap	30 min	Captures complete logger outages (battery dropouts)
Post-panne — invalidated points	30 steps (~30 min after recovery)	Thermal re-equilibration of the heated probe
Negative ΔV	strict (< 0 mV)	Physically impossible under heat-dissipation theory
Range — upper bound	2.20 mV	Above maximum ΔV physiologically plausible for Atlantic Forest hardwoods
Floor — threshold	0.10 mV	Below the gap in the empirical bimodal distribution (artefacts < 0.05 vs real data > 0.43 mV across 26 trees) — this study
Floor — minimum run	60 pts (~1 h, sliding window)	Captures sustained collapse without flagging short transpiration dips
Frozen — minimum run	1 080 pts (~18 h)	Above the longest plausible nocturnal plateau — this study
Frozen — relaxed SD threshold	0.012 mV	Below the normal nocturnal noise (0.03–0.10 mV) of a functional probe — this study
<i>Family B — Transient flags</i>		
Hampel — half-window	60 pts (~5 h total)	Wide enough to bracket spike clusters; short enough to stay quasi-stationary
Hampel — robustness multiplier k	3.0	Standard robust threshold (Pearson 2002)
Hampel — absolute floor	0.010 mV	Above the nocturnal MAD (≈ 0.002 – 0.003 mV) to prevent flagging legitimate sub-noise oscillations — Peters et al. 2021
Hampel — max iterations	5	Captures spike shoulders that become outliers once the centre is removed
Hampel — outlier replacement	enabled	Outliers replaced by the local median so downstream filters see a smoothed signal — Poyatos et al. 2021
First-difference threshold	$0.05 \text{ mV step}^{-1}$	Above maximum physiological 5-min rate (TDP thermal time constant $\gg 5$ min)
First-difference — max spike width	25 pts	Captures multi-point excursions up to ~2 h
<i>Family C — Statistical flag</i>		
Local range — window	sliding (sub-diurnal scale)	Bracket-window evaluation of max–min amplitude — this study
Local range — max amplitude	exceeds normal diurnal cycle	Calibrated as upper percentile of within-window amplitude on healthy trees
T-coherence — inter-probe coherence	enabled diagnostic	Cross-check between heated and reference thermocouple; probe drift / partial detachment

Flag dilation	± 3 pts	Bracket each flagged event fully to prevent residual contamination of adjacent points
<i>Residual cleanup (02_convert_sapflow.R)</i>		
Residual Hampel — half-window	30 pts (~2.5 h total)	Second-pass outlier removal on the already-cleaned signal
Residual Hampel — k, min deviation, iter	$k = 3$; 0.005 mV; 5 iterations	Stricter floor than primary Hampel to catch residual outlier clusters
Decoupled-baseline filter	60-min running median (baseline) vs 180-min running MAD (variability)	Catches slow U-shaped drifts of ΔV
Absolute upper bound	2 % of max observed ΔV	Flags bursts beyond the maximum physiological signal
Absolute lower bound	20 % of annual max	Flags signal collapse (sensor decoupling)
Centred smoothing	11-pt running median (~55 min)	Attenuates residual high-frequency oscillations while preserving diurnal dynamics
<i>Family D — Cleanup</i>		
Meteo-night — anomaly threshold	nocturnal ΔV inconsistent with low VPD + zero radiation	Catches residual nocturnal artefacts
Isolated — minimum segment length	30 pts (~2.5 h)	Below this, the Granier baseline cannot be referenced
<i>Gap filling (gapfill_dV.R)</i>		
Short-gap threshold τ_1	2 h	Below this, linear interpolation is appropriate (ΔV approximately linear)
Long-gap threshold τ_2	18 h	Above 12–18 h the gap exceeds the bulk of a diurnal cycle; +9.6 pp coverage gained on 12–18 h, only +2.7 pp by extending to 24 h
Donor day — minimum coverage	≥ 80 % temporal coverage (15-min bins)	Robust template anchoring
Donor day — selection	transition + dry months, outside fill window	Avoid contamination by the window being filled
Baseline rolling window 2H+1	24 h ($H = 720$ min)	Continuous baseline that preserves anomaly continuity across midnight
Template circular smoothing	31 min	Removes high-frequency noise in the diurnal shape without losing dynamics
Template normalisation	unit standard deviation	Dimensionless template, rescaled per gap by OLS
Per-gap fit — minimum measured pts	120 in W_G	Below this, fallback to median donor-day amplitude and median local baseline
Boundary anchoring	linear interpolation of edge residuals	Guarantees seamless join with bracketing measurements

D.2 Per-tree sap flow QC, annual coverage 2020

Table 11: All percentages are relative to the 527 040 minutes of 2020. Filter contributions are non-exclusive: a minute flagged by k filters is counted in each row, so column sums may exceed 100 %. PostPanne = re-equilibration after a logger gap; Floor = stuck at ADC noise floor; Frozen = below-threshold rolling SD; FirstDiff = first-difference burst; LocalRange = inflated-variability window; Manual = visual invalidation. Excluded sensors (T01, T20, T31, T32, T33, T35, T39, T41) show partial profiles where the pipeline aborted early. After QC = valid fraction of dV_clean ; With interp equals After QC at the year scale, since the diurnal template is applied within analysis windows only.

Tre e	Plot	Gap raw	Flag tot	PostPanne	Negative	Floor	Frozen	Hampel	FirstDiff	LocalRange	Manual	After QC
01	R40	38.5	62.1	—	0	—	0	—	—	0.27	61.5	0
03	R40	51.6	20.7	1.4	0	0.3	0	14.2	0.83	1.4	0	27.8
04	R40	36.1	72.7	1.5	50.3	1.1	17.3	2.1	0.11	0.2	0	8.8
06	R40	36.1	59.1	1.5	0	22.5	4.7	22.1	2.23	3.2	0	12.9
07	R40	55.5	16.4	1.2	0	0.1	0.9	10.9	0.85	0.5	0	28.1

08	R40	62.8	37.4	1.0	19.2	4.5	1.6	9.0	0.43	0.8	0	3.7
09	R40	40.8	48.7	1.3	0.2	18.3	9.7	16.1	0.76	0.7	0	20.6
10	R40	44.0	20.8	1.2	0	0.4	0.2	15.5	0.62	0.8	0	35.0
11	R40	36.0	25.3	1.5	0	1.4	0.2	18.3	0.46	0.9	0	38.9
12	R40	38.4	45.9	1.3	0.1	16.1	6.5	16.4	2.04	2.0	0	22.6
14	R40	36.1	20.0	1.5	0	0	0	15.3	0.44	1.2	0	43.8
16	R40	36.2	68.0	1.4	23.2	16.0	4.4	16.6	1.83	2.9	0	6.7
17	R40	38.9	43.1	1.3	1.3	7.4	2.0	23.4	1.90	2.0	0	21.8
18	R40	36.0	26.0	1.5	0.1	1.0	0	17.8	1.31	1.0	0	38.0
19	R40	36.2	71.7	1.5	20.2	18.1	9.4	17.5	1.84	2.1	0	3.9
20	R40	56.5	70.7	—	12.4	—	1.6	—	—	0.12	43.5	0
31	RP	44.8	132.	—	31.3	0	0	—	1.0	0.13	100	0
			5									
32	RP	98.6	1.4	—	1.1	—	0	—	—	0	0	0
33	RP	45.2	120.	—	18.5	—	0	—	—	0.06	100	0
			7									
34	RP	44.8	33.6	2.3	0	5.1	6.0	16.6	0.84	0.8	0	26.6
35	RP	44.8	140.	—	21.7	—	0	—	—	0.30	100	0
			8									
36	RP	49.9	23.4	2.1	0	0	1.2	15.9	0.41	0.6	0	26.1
37	RP	44.9	87.4	2.3	23.0	12.0	33.4	12.6	1.32	1.3	0	2.4
38	RP	44.9	63.0	2.3	3.2	17.8	18.2	17.1	1.15	0.7	0	14.5
39	RP	48.3	101.	—	0	—	0	—	—	0.15	100	0
			3									
40	RP	44.9	37.9	2.3	0	7.2	1.3	19.4	2.69	2.0	0	17.6
41	RP	44.7	144.	—	40.4	—	0	—	—	0.08	100	0
			1									

Filters omitted (always < 0.5 % across all retained trees, contributing < 0.1 % combined to the global mask): Voltage, Heating, Temp, Range, T-coherence, Meteo-night, Isolated.

D.3 ANALYSIS WINDOWS

Table 12: Multi-day windows retained for sap flow analyses in 2020. Total 22 windows across the four seasons.

ID	Season	Start	End	Duration (days)	ID	Season	Start	End	Duration (days)
W1	wet	1 Jan	28 Jan	28	D1	dry	25 May	4 Jun	11
W2	wet	29 Jan	6 Feb	9	D2	dry	9 Jun	13 Jun	5
W3	wet	8 Feb	18 Feb	11	D3	dry	17 Jun	26 Jun	10
W3b	wet	21 Feb	27 Feb	7	D4	dry	3 Jul	13 Jul	11
W4	wet	2 Mar	6 Mar	5	D5a	dry	30 Jul	3 Aug	5
W4b	wet	10 Mar	21 Mar	12	D5b	dry	5 Aug	16 Aug	12
W4c	wet	23 Mar	7 Apr	16	D6	dry	22 Aug	19 Sep	29
Dr1	drying	10 Apr	16 Apr	7	Rw1	rewetting	25 Sep	8 Oct	14
Dr2	drying	19 Apr	1 May	13	Rw2	rewetting	9 Oct	14 Oct	6
Dr3	drying	9 May	13 May	5	Rw3	rewetting	27 Oct	29 Oct	3
Dr4	drying	17 May	22 May	6	Rw4	rewetting	2 Nov	9 Nov	8

D.4 Complete QC pipeline example

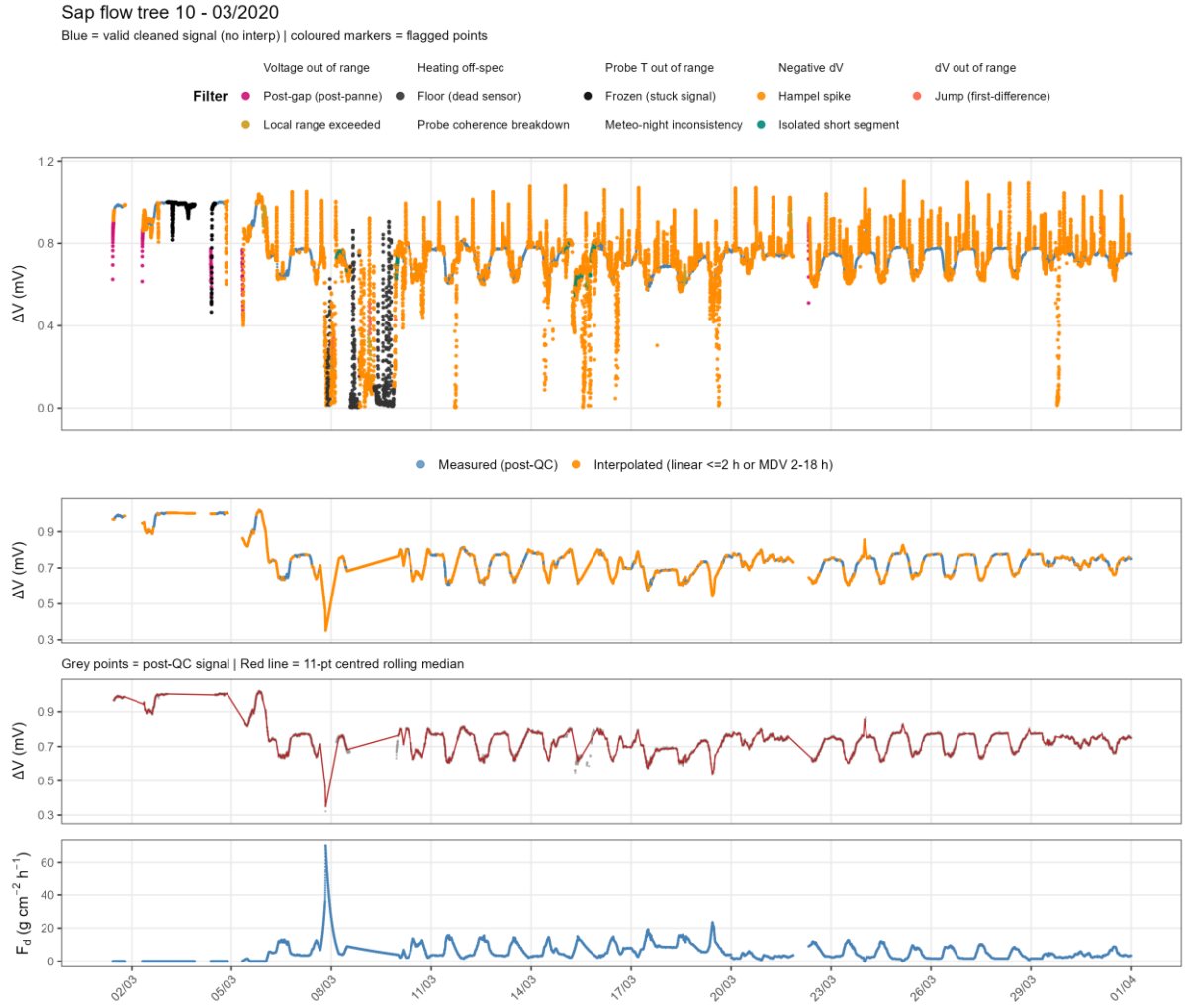


Figure 50: Sap flow QC pipeline applied to tree 10 (R40, March 2020). (a) Raw ΔV signal (blue) with points flagged by the 14 automated filters (Table 3.4.3). (b) Post-QC ΔV signal: measured points in blue, interpolated points in orange (linear interpolation for gaps ≤ 2 h, mean-diurnal-variation template for $2 \text{ h} < \delta \leq 18 \text{ h}$, see Annex D.5). (c) Post-QC signal (grey) and the 11-pt centred rolling median used for residual cleanup (red line). (d) Resulting sap flux density F_d ($\text{g cm}^{-2} \text{h}^{-1}$) from the Granier conversion.

D.5 Sap flow MDV gap-filling: full equations

This section details the per-tree boundary-anchored mean-diurnal-variation template used to fill intermediate sap flow gaps ($2 \text{ h} < \delta \leq 18 \text{ h}$). The full parameter set is reported in Tab. D1. A donor day d is retained when its temporal coverage exceeds 80 % over the transition and dry months, excluding the analysis window being filled. For each donor day, the diurnal anomaly per minute-of-day $\varphi \in [0, 1440)$ is computed relative to a 24-h centred moving average:

$$a_d(\varphi) = \Delta V_d(\varphi) - \Delta \bar{V}_d^{24h}(\varphi) \quad (54)$$

The mean anomaly across donor days is circularly smoothed (31-min running mean) and rescaled to unit standard deviation, yielding a dimensionless template $T(\varphi)$. Per-gap rescaling. For each gap with local fitting window W (± 24 h, ≥ 120 measured points), the template is rescaled by ordinary least squares:

$$\Delta V(t) = \hat{a} + \hat{b} \cdot T(\varphi(t)) + \varepsilon \quad (55)$$

The fitted prediction is anchored at both edges of the gap by linearly interpolating the two edge residuals $r_s = \Delta V(t_s) - [\hat{a} + \hat{b} \cdot T(\varphi(t_s))]$ (56) and $r_e = \Delta V(t_e) - [\hat{a} + \hat{b} \cdot T(\varphi(t_e))]$ (57) across the gap:

$$r(t) = r_s + \frac{t - t_s}{t_e - t_s} \cdot (r_e - r_s) \quad (58)$$

$$\Delta V_{\text{filled}}(t) = \hat{a} + \hat{b} \cdot T(\varphi(t)) + r(t) \quad (59)$$

Fallback. When fewer than 120 measured points are available in W , $\hat{b}$ defaults to the median donor-day amplitude.

D.6 Example gap filling: linear interpolation + MDV

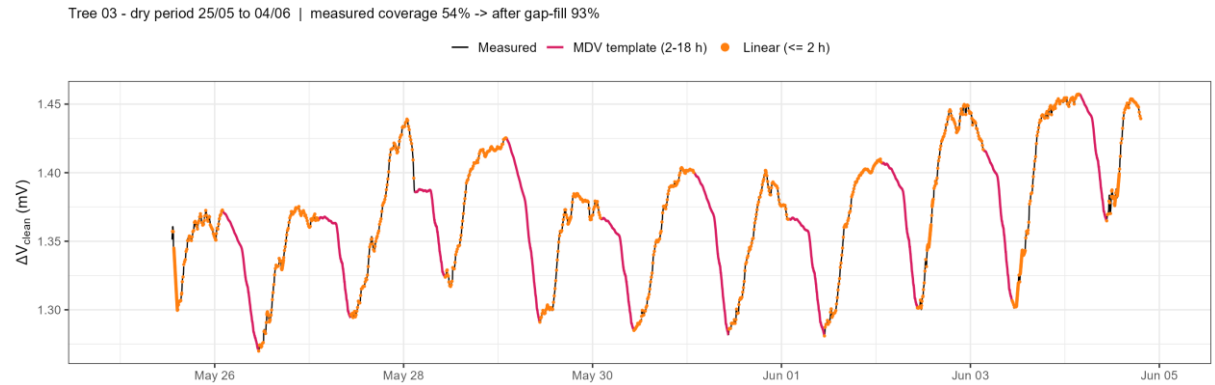


Figure 51: Sap flow gap-filling on a representative dry-period window (tree 03, 25 May – 4 June 2020). Black: measured ΔV signal (post-QC). Orange: linear interpolation applied to gaps ≤ 2 h. Magenta: mean-diurnal-variation (MDV) template applied to gaps $2 \text{ h} < \delta \leq 18 \text{ h}$, rescaled per gap by ordinary least squares and anchored at both edges (procedure detailed in Appendix D.5). Measured coverage rises from 54 % to 93 % after gap-filling.

APPENDIX E – Generalised Additive models (GAM)

A generalised additive model (GAM, Wood 2017) is

$$y_i = \beta_0 + \sum_{j=1}^p s_j(x_{ij}) + \varepsilon_i \quad (60)$$

with smooth functions s_j on each predictor x_j , intercept β_0 and residuals ε_i . The smooths replace the fixed linear coefficients of ordinary regression and are estimated from the data without a prescribed parametric shape. Each s_j is expanded on a cubic-spline basis:

$$s_j(x) = \sum_{k=1}^K \beta_{jk} B_k(x) \quad (61)$$

where B_k are piecewise cubic polynomials joined at fixed knots with continuous value and first two derivatives. The basis dimension K sets the maximum flexibility of the smooth. Default $K = 10$ is used, reduced to 5–7 when fewer than 60 valid days are available per tree.

The coefficients β_{jk} are obtained by minimising

$$\sum_{i=1}^n (y_i - \hat{y}_i)^2 + \sum_{j=1}^p \lambda_j \int (s_j''(x))^2 dx \quad (62)$$

The second term penalises the integrated squared second derivative of each smooth, controlled by the smoothing parameter λ_j . Larger λ_j enforces straighter smooths, smaller λ_j allows more curvature. The λ_j are estimated by restricted maximum likelihood (REML), which treats the spline coefficients as Gaussian random effects with variances $\sigma_j^2 \propto 1/\lambda_j$ and maximises the marginal likelihood (Wood 2017). The unique contribution of driver j to the model is quantified by

$$\Delta D_j = D_{\text{full}} - D_{\text{full} \setminus s_j} \quad (63)$$

where D is the residual deviance. The reduced model is refitted from scratch with s_j removed and all λ re-estimated, so that ΔD_j measures the explanatory power of s_j over and above what the remaining smooths can recover. Additive smooths $s(x) + s(y)$ assume that the effect of x on the response is independent of y . When interaction is tested, the additive form is replaced by a tensor product smooth

$$\text{te}(x, y) = \sum_{k=1}^{K_x} \sum_{l=1}^{K_y} \beta_{kl} B_k(x) B_l(y) \quad (65)$$

whose basis is the Kronecker product of the two marginal cubic-spline bases. Penalisation is anisotropic, with one smoothing parameter per direction, so that the surface can be smoother along one axis than the other. Hierarchical data are handled by adding a random intercept per group to the formula, here $(1 \mid \text{tree})$. Each tree gets an intercept $b_i \sim \mathcal{N}(0, \sigma_{\text{tree}}^2)$, fitted jointly with the smooths and the fixed intercept by REML. The smooths then describe within-tree responses to the predictors and the between-tree variability is absorbed in b_i .

All GAMs are fitted with the `mgcv` R package (Wood 2017). The `te()` constructor builds the tensor product smooth and `s(tree, bs = "re")` adds the random intercept. Per-tree GAMs are fitted independently for each tree, with K reduced when the number of valid days is small. Forest-level GAMs pool all trees and include the random intercept.

APPENDIX F – Stratified test of pre-dawn sap flux density by stem reservoir state

This APPENDIX reports the complementary test of nocturnal flux partition introduced in §3.7.4. The test compares the pre-dawn sap flux density between two groups of nights defined by the residual stem deficit at pre-dawn. It is reported here rather than in the main body because the recovery test of §3.7.4 already provides the primary diagnostic, while the stratified test serves as an independent cross-check on the per-tree classification.

The pre-dawn sap flux density $F_d^{predawn}$ is the mean F_d between 02:00 and 05:00, the window in which the overnight recharge is largely complete on most nights. The residual deficit at pre-dawn is denoted TWD_pre and is expressed in TWD_norm units, so that TWD_pre indicates how much of the stem reservoir has not yet been refilled by dawn. The nights are sorted into a refilled group ($TWD_pre \leq \text{threshold}$) and a not-refilled group ($TWD_pre > \text{threshold}$), and the regression $F_d^{predawn} = a + b \cdot VPD$ (66) is fitted within each group.

The logic of the partition is the following. If a tree shows a positive $F_d^{predawn}$ that rises with VPD on nights in the refilled group, this flow cannot be refilling, because the reservoir has no remaining deficit to fill. It can only correspond to true nocturnal transpiration. If a tree shows a positive $F_d^{predawn}$ that rises with VPD on nights in the not-refilled group, the flow is consistent with VPD-driven refilling, because a stronger nocturnal demand draws more strongly from the soil into the stem. The diagnostic for nocturnal transpiration is therefore the slope of $F_d^{predawn}$ against VPD in the refilled group.

The threshold of TWD_pre that defines the two groups was selected from the data rather than taken from the literature, because the published frameworks of Forster (2014) and Caird et al. (2007) do not provide a reference value for tropical diffuse-porous species. For each candidate threshold between 0.005 and 0.30, the nights are split, the two regressions are fitted, and the discrimination index

$$\Delta(R^2) = R_{\text{not refilled}}^2 - R_{\text{refilled}}^2 \quad (67)$$

is recorded. $\Delta(R^2)$ is large when the partition separates the data into a not-refilled group where $F_d^{predawn}$ rises strongly with VPD (refilling is active) and a refilled group where $F_d^{predawn}$ does not depend on VPD (recharge is complete).

The shape of the $\Delta(R^2)$ curve is interpretable in three regimes. At very low candidate thresholds, almost all nights are classified as not refilled and the refilled group is too small to fit a reliable regression, so $\Delta(R^2)$ is essentially zero. At very high candidate thresholds, the not-refilled group becomes too small and $\Delta(R^2)$ falls back to zero. In between, both groups are populated and the regressions are stable, and $\Delta(R^2)$ reaches a stable range where the partition gives the same separation regardless of the exact threshold value.

The stable range observed here lies between 0.05 and 0.22 in TWD_{norm} units, on which $\Delta(R^2)$ stays at approximately 0.11 to 0.12. The production threshold of 0.10 is taken as a round value within the stable range, yielding populated groups on both sides (132 refilled nights and 204 not refilled nights).

A tree is identified as a candidate for true nocturnal transpiration when its slope $F_d^{predawn}$ against VPD is positive and significant in the refilled group. The classifications from the stratified test are compared to those from the recovery test of §3.7.4. Trees classified consistently by both tests are reported as robust candidates. Trees with discrepant classifications are reported as inconclusive.

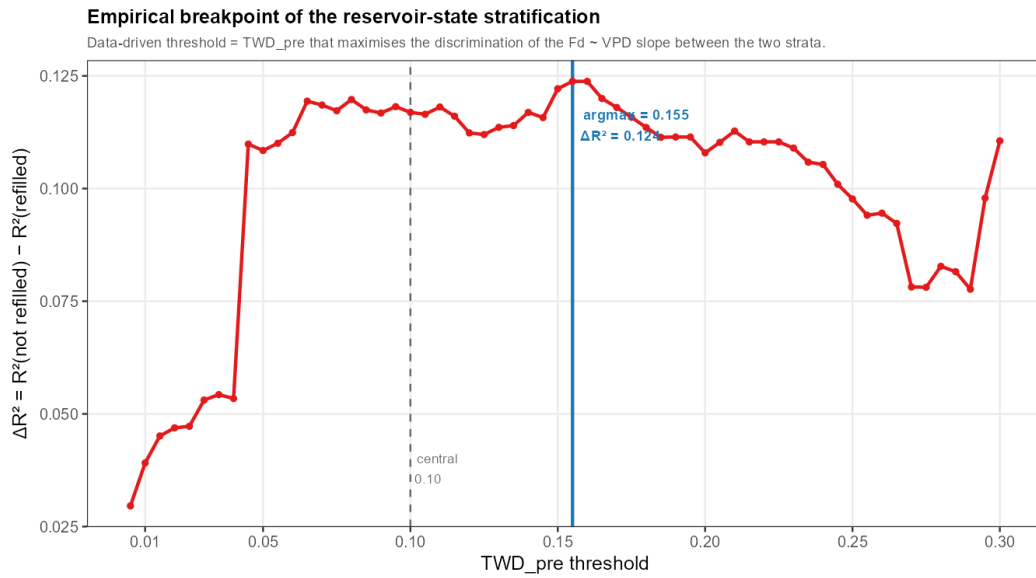


Figure 52: Empirical breakpoint of the reservoir-state stratification. $\Delta(R^2) = R^2(\text{not refilled}) - R^2(\text{refilled})$ of $F_d^{predawn} \sim VPD$ across candidate thresholds for TWD_pre . Blue line = argmax (0.155, $\Delta(R^2) = 0.124$); grey dashed = production choice (0.10, $\Delta(R^2) = 0.117$). The plateau 0.05–0.22 supports 0.10 as a round value within the stable range.

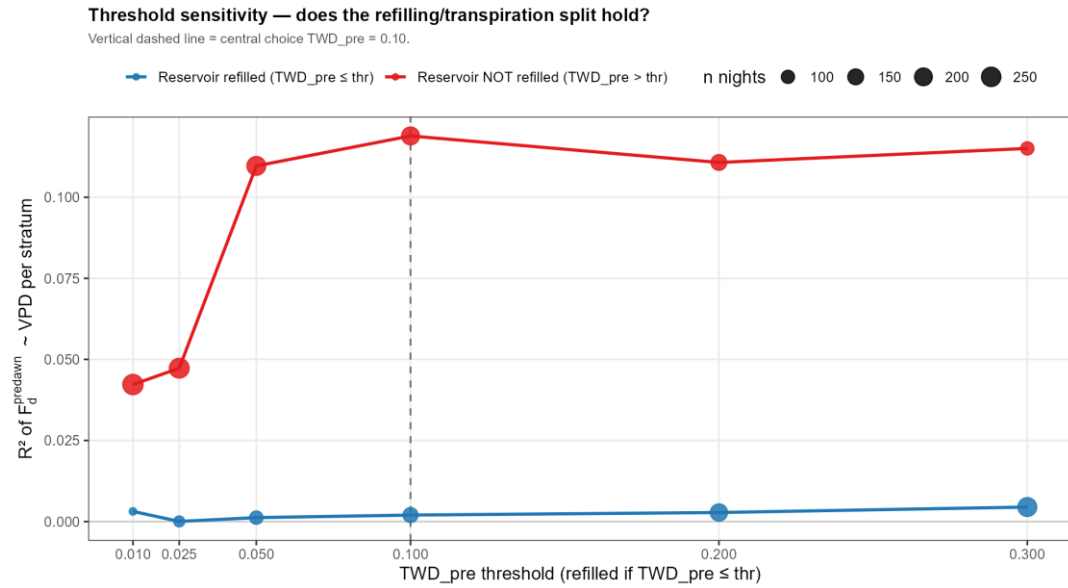


Figure 53: Threshold sensitivity of the split. $F_d^{\text{predawn}} \sim \text{VPD}$ fitted per stratum at six thresholds (blue = refilled, red = not refilled, point size = n nights). At the production threshold (dashed, 0.10), $R^2 = 0.119$ in the not-refilled stratum vs ≈ 0.002 in the refilled stratum. The contrast persists across the plateau 0.05–0.20.

APPENDIX G – Sensitivity analysis

G.1 OAT parameters perturbed

Table 13: Parameters perturbed in the OAT sensitivity analysis. Each parameter is varied within its plausible range while all others are held at their central best-estimate values. The perturbation is propagated along the full chain so that the effect is reported at every downstream stage. Production values are in bold.

Pipeline	Parameter group	Perturbation range or variants
Sap flow cascade	ΔV_{max} baseline	7 variants: per-night MAX (central), rolling MAX ($w = 2, 3, 5$), rolling mean ($w = 3$), ideal-night MAX, annual MAX
Sap flow cascade	Granier coefficients (a, b)	diffuse-porous angiosperm range, from Bush et al. 2010 ($\times 1.00$) to Steppe et al. 2010 ($\times 1.60$)
Sap flow cascade	DBH 2020 reconstruction	$\pm 15\%$ (all DBH; A_s and nearest-DBH matching recomputed)
Sap flow cascade	A_s –DBH allometry	95 % CI on the pooled log-log fit (stand ΣA_s)
Sap flow cascade	$K_{c,T}$ calibration day pool	leave-one-out and bootstrap resampling
Sap flow cascade	Inventory pool (inclusion threshold)	full (B_{all}) / $\text{DBH} \geq 5 \text{ cm}$ / $\text{DBH} \geq 10 \text{ cm}$
Sap flow cascade	H–DBH allometry ($\rightarrow \Delta \text{AGB}$)	$\pm 10\%$ on predicted H, propagated to stand ΔAGB (Chave et al. 2014)
Sap flow cross-signal	WUE_w wood density	per-tree direct measurement, species median, plot median
Dendrometer	Normaliser	MDS_{max} (Peters et al. 2025b) vs TWD_{max} (Zweifel et al. 2021)
Dendrometer	DBH 2020 reconstruction (strain only)	$\pm 15\%$
Dendrometer	TWD_norm onset threshold	0.8, 1.0 (central, Peters et al. 2025b), 1.2
Dendrometer	Lloret R_t threshold for suppressing episodes	0.3, 0.5 (central), 0.7

G.2 Baseline variants

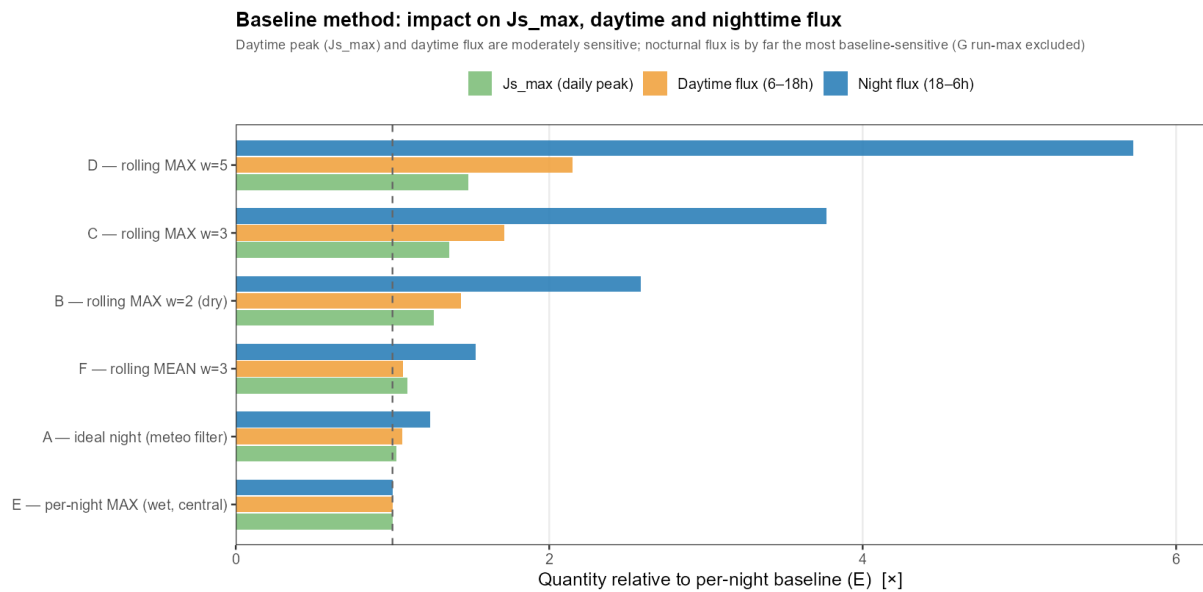
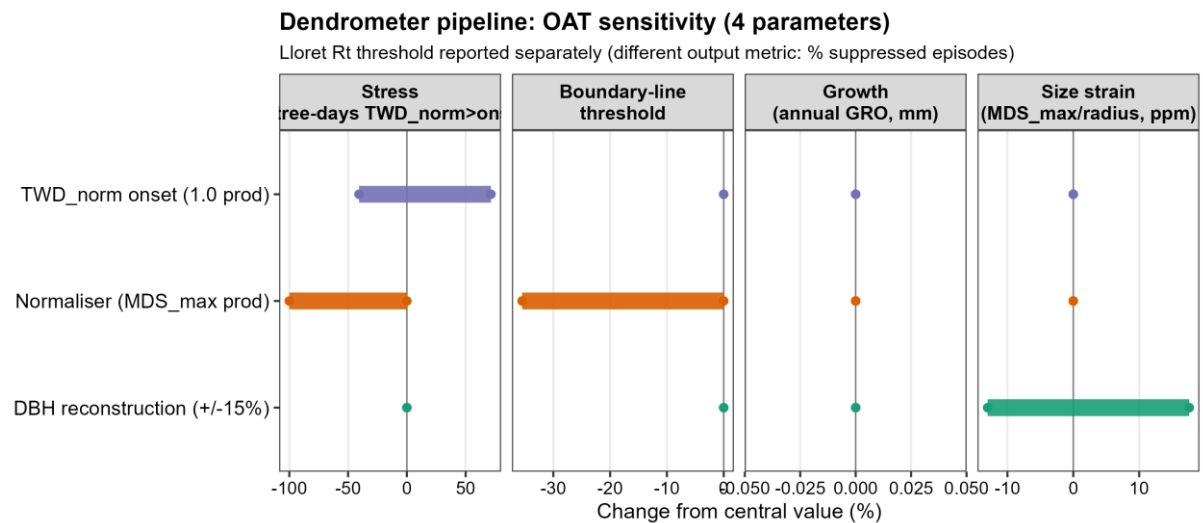


Figure 54: Impact of the dV_max baseline method, six variants relative to the per-night MAX (variant E, central). Bars: J_s_max (daily peak, green), daytime flux Q_day (6–18 h, orange), night flux Q_night (18–6 h, blue). Q_night is the most baseline-sensitive ($\times 1.0$ – 5.7 across A–D, variant G excluded).

G.3 Dendrometer pipeline sensitivity



Tropical secondary forests store a large share of regrowing carbon and return much of the rain they receive to the atmosphere, yet how individual trees combine water use and wood production remains poorly resolved. Over the 2020 hydrological year, Granier sap flow probes and point dendrometers were combined on 22 trees of two Brazilian Atlantic Forest plots of contrasting successional stage, a young pioneer and an older secondary stand, at São Francisco Xavier. Transpiration, radial growth and stem water reserves, the latter captured through the tree water deficit, were analysed tree by tree, linked from daily to annual time scales, and scaled to the stand alongside evapotranspiration.

At the individual scale, the two stands shared a single stomatal regulation rule, close to the theoretical Oren optimum, with pioneers opening their stomata slightly more per unit of sapwood. Radial growth stopped at a milder water deficit than the one that closed the stomata, and the tree water deficit emerged as the variable linking the water transpired, stored and built into wood. The stem reservoir contributed comparably to daily water use in both stands, but pioneers relied more on their internal reserve while secondary trees appeared more buffered by the soil. Variation between trees exceeded the contrast between stands. The lower stand-level transpiration of the pioneer plot was structural, reflecting almost three times less conductive sapwood per unit of ground rather than a different regulation, and its faster growth reflected lighter wood rather than a more efficient conversion of water into biomass.

These conclusions rest on relative, intrinsic signals that proved robust to the methodological choices, whereas absolute magnitudes, including stand transpiration, remain constrained by the uncertainty of the thermal-dissipation method, a single year without extreme drought, the absence of leaf water potential, and a small pioneer sample. Within these limits, successional stage set the structural frame, while regulation and the fate of individual trees were set at the tree level, along a continuum rather than across a sharp pioneer-versus-secondary boundary.